Variation in diatom and bryophyte communities along a temperature gradient in sub-Arctic streams: model surrogates for trends in larger ecosystems?

Rakel Gudmundsdottir1*, Snaebjorn Palsson1, Gisli Mar Gislason1, Jon S. Olafsson2, and Brian Moss3

1 Institute of Biology, University of Iceland, Sturlugata 7, IS-101 Reykjavik, Iceland
2 Institute of Freshwater Fisheries, Keldnaholt, IS-112 Reykjavik, Iceland
3 School of Environmental Sciences, Nicholson Building, University of Liverpool, Liverpool L69 3GS, UK

* Corresponding author email: rakelgud@hi.is

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Abstract

Streams within geothermal areas in Iceland that vary in a syndrome of temperature-linked variables, including discharge and potential grazing pressure (snails vs. chironomid larvae), provided a test of how microvegetation structure might change systematically with such drivers. We examined if such streams could form a parallel with biome sequences, for example with similar change in overall structure and organism traits found from tundra to Boreal forest. The warmer streams had an over-story of bryophytes with more open patches of epilithic algae and Cyanobacteria, and a grazer community of snails and blackfly larvae; the vegetation of the colder streams consisted mainly of epilithic algae and Cyanobacteria, dominated by grazing chironomid larvae. Diatom species comprising the epilithic assemblages were generally smaller in the warmer streams compared with the colder streams. Temperature and discharge did not significantly influence the diversity of diatoms (Shannon Index, Sørensen Index, Evenness, Species richness), although more species were observed in the colder streams compared with the warmer streams. Trait diversity was greatest in the coldest streams, but despite high grazing pressure only one growth form (attachment by a mucilage stalk) was predominant in the warmer regimes. Grazers may have influenced diatom species traits but did not significantly suppress the diatom biomass. Analogy with the sequence from tundra, through taiga to boreal forest, over a comparable temperature gradient, showed some parallel features but important differences. Microorganism systems may thus not always be the useful surrogates for larger systems that some ecologists have suggested.

Key words: bottom up, grazing, Iceland, top down, traits, warming

Introduction

Streams harbour primary producers from small unicellular Cyanobacteria, green algae, and diatoms to more obvious bryophytes, liverworts, and macrophytes. Diatoms are often the most diverse and abundant algae in streams (Allan 2006, Gudmundsdottir et al. 2011a), with biofilms made up of various growth forms that may reflect differing niches (Ros et al. 2009). The growth forms are characterised by mode of attachment (mucilage stalks, mucilage pads, or the entire length of the raphe), filamentous modes, and free-living motility (Yallop and Kelly 2006). Size is also a trait, with some diatoms 2 or more orders of magnitude greater in volume than others. The trait structure of biofilms has been ignored, perhaps because when biofilm is scraped from stones for the purpose of examination, its physiognomy is destroyed.

Currently, microorganism-based laboratory systems are becoming popular as inexpensive surrogates for investigating possible changes, due to warming and other factors, in larger systems where field experimentation is more expensive and for examining theoretical concepts (Harte and Shaw 1995, Lawton 1995, Petchey et al. 1999, Benton et al. 2007). Terrestrial ecosystems vary greatly in
structure and traits, driven by geology, soils, and grazing, but particularly by climate, reflected in temperature and precipitation (Zimov et al. 1995, Krebs 2001). Streams with various temperature regimes might be seen as parallels to temperature influenced-terrestrial habitats for predicting the effects of current warming trends. They are more easily examined and, although more complex and with fewer controls than laboratory systems, may offer greater reality, especially if groups of streams are available that vary strongly in temperature over a small area.

Thus, the diatom microvegetation of cold streams could form an analogue to tundra with its short growth season, low temperatures, low biomass (Bonan et al. 1992), low biodiversity, and frequent disturbance through ice formation and melting (Chapin and Shaver 1981). Warmer streams might be seen as analogues of the tree line vegetation, or taiga, with higher temperature than tundra and scattered trees paralleled by sparse bryophytes in the streams. The warmest streams might be compared with boreal forests, with their evergreen coniferous trees paralleling evergreen bryophytes observed in warm streams (Gudmundsdottir et al. 2011a).

Temperature, however, is not the only factor influencing vegetation structure; grazing may also be important. All land systems have many small grazers, from arthropods to small vertebrates, but some have a substantial part of their grazer biomass in macroherbivores comparable in size to or much bigger than the plants they eat. These macroherbivores have a great potential impact on vegetation structure.

Native macroherbivores on tundra include reindeer and musk oxen. In high densities, reindeer can change the vegetation communities from moss and dwarf shrubs to grass (Oksanen et al. 1995). Boreal forests have higher plant biomass per unit area than tundra and taiga (Bonan et al. 1992) but a lower biomass density of macroherbivores such as moose, wood buffalo, deer, and beaver, yet imposed grazing can have major effects. Introduction of domestic animals in Iceland with the settlement of humans in the 9th century resulted in an almost complete deforestation of Icelandic birch forest (Betula pubescens Ehrh.) within a few hundred years (Hallsdottir 1987).

Therefore, in the tundra to boreal forest sequence, temperature tends to increase (Krebs 2001) while there is a reverse trend in macro-herbivore importance. In parallel, streams have the equivalents of macroherbivores, including some insect larvae and snails, which are much bigger than the algae and bacteria on which they feed.

We applied this analogy with terrestrial systems to a set of streams where the relative influences of climate, measured by temperature, and macroherbivore grazing by insects and snails could be assessed. Some of the streambeds were extensively covered by bryophytes, the analogues of trees; others were covered only by algal films, the equivalents of grasslands and sedge meadows in tundra. Other streams were covered with scattered bryophytes (Gudmundsdottir et al. 2011a), the equivalents of scattered trees in the taiga. Thus, a passable set of parallels exists between the macrovegetation sequence from tundra to boreal forest and the smaller-scale vegetation of the streams. This might be a tempting, inexpensive system to employ to predict effects of temperature increase on key characteristics of ecosystems, with the advantage of increased reality over laboratory systems, which use simple structures and single drivers.

We used 8 adjacent streams in southwest Iceland that varied in temperature and to some extent in conductivity, but other physical and chemical parameters were similar (Gudmundsdottir et al. 2011a, 2011b) and thus avoided the confounding factors of biogeography that are usually problematic in temperature studies. Our overall hypothesis was that changes in vegetation structure, particularly diversity of species and growth forms, would parallel those linked with temperature familiar in the sequence from tundra through taiga to boreal forest. We tested 4 related subhypotheses:

1. Species richness, evenness, and diversity of diatom growth forms would increase with temperature, which is the usual successional pattern of terrestrial vegetation (Odum 1969).

2. High grazing pressure would restrict the growth forms of diatoms and reduce species richness and evenness; heavy grazing by macroherbivores tends to produce a more uniform sward (Davidson 1993, Yang et al. 2011).

3. Bryophytes would be least abundant where the grazing pressure is highest; macroherbivores are very effective in preventing development of tree seedlings and succession to forest (Belsky and Blumenthal 1997), as illustrated by the widespread conversion of forest to grassland by grazing stock in Europe (Arnalds 1987, Hallsdottir 1987).

4. With increased temperature, species with small-sized individuals would be more abundant than those with larger individuals (Daufresne et al. 2009). This is a well-established phenomenon for homeotherms that may benefit from greater surface to volume ratios in warm habitats and the reverse in colder ones (Freckleton et al. 2003, Hurd and van Anders 2007), but reasons for a similar phenomenon in microorganisms are less clear. Daufresne et al. (2009) consider this feature of size variation in individual species to be important, a third universal ecological response to global warming in aquatic systems in addition to the shift of species ranges toward higher altitudes and latitudes, and seasonal shifts in life cycle events.
Study site

The study was conducted in the Hengill geothermal area in southwest Iceland (64°05′N, 21°30′W; 360–380 m a.s.l.). The area is an active volcanic area covering 173 km², with a mean air temperature of 8–10 °C in July (Bjornsson 2003) and a mean annual precipitation of 1870–3080 mm (Crochet et al. 2007).

Within the study area, many small streams emerge from the hillsides and run into the same river (Hengladalsá). The bedrock is mainly hyaloclastite and the vegetation is mostly monocotyledonous (Gudjonsson and Egilsson 2006). Sedges, grasses, and cotton grass (Carex bigelowii Torr. Ex Schwein, Carex nigra [L.] Reichard, Agrostis capillaris [L.], and Eriophorum angustifolium Honckeny) dominate, with a few low shrub species (Empetrum nigrum L. and Vaccinium uliginosum L.) occasionally observed (Elmarsdottir et al. 2005, Gudjonsson et al. 2006, Kristinsson et al. 2007). Trees are absent, so leaf litter and woody debris input to the streams is minimal (Friberg et al. 2009, Woodward et al. 2010).

About 20 small streams are found in the study area; we used 8 small, largely first-order streams for our study (Gudmundsdottir et al. 2011a, 2011b). Their summer mean temperatures vary from 6 to 22 °C, with the warmer streams not fed directly by hot springs, but rather absorbing heat from the warm rocks below (Arnason et al. 1967). The temperature of the colder streams was typical of high latitude and high altitude streams (Olafsson et al. 1967). The temperature of the warmer ones was comparable with lower altitudes (Allan 2006). The stream slopes ranged from 0.5 to 19.7 cm m⁻¹, the depth ranged from 0.05 to 0.17 m, and the width from 0.63 to 1.75 m. Structural and some major biological features (algal biomass and vascular macrophyte biomass) did not correlate with temperature (Friberg et al. 2009).

We identified 35 invertebrate taxa, most to the species level. Chironomids (mainly Eukiefferiella minor Edw.) were dominant and negatively correlated with temperature. Other common invertebrates were Simulium vittatum (Zetterstedt) and Radix peregra (Müller), which were both positively linked to temperature. Density ranged from 3000 to 16 000 individuals per m², and the greatest density was in streams ranging in temperatures from 13 to 16 °C. Collectors and gatherers were the dominant functional feeding groups of the 4 colder streams, while scrapers and filter feeders dominated the 4 warmer streams. The greatest species diversity (Shannon Index) was at 10 °C but declined rapidly as the temperature rose above 15 °C (Friberg et al. 2009, Woodward et al. 2010, Gudmundsdottir et al. 2011b). Woodward et al. (2010) concluded that temperature was the key variable structuring these invertebrate communities.

Methods

Sampling

Most physical and chemical variables were assessed monthly between May and August 2007. The discharge was measured with a SonTek Flow Tracker Handled Velocity Meter 5 times in total from May to August 2006 and May to August 2007. A Multiprobe Sonde YSI 600 XLM (Yellow Springs Instruments, Yellow Springs, Ohio, USA) was used to measure conductivity, pH, and temperature. The temperature varied little from upstream to downstream (OP Olafsson, pers. comm.). Seasonal variation was low, especially in the warmest streams.

Each month water samples for chemical analysis were collected in 1 L polyethylene bottles from each stream. Samples were brought to the laboratory, filtered through GF/C filters, and then frozen (−18 °C) before analysis in Denmark at the National Environmental Research Institute. Samples for ammonium (N-NH₄) were obtained 4 times during the summer 2007 and analysed using the salicylate method (Antweiler et al. 1996) on the day of sampling. Ammonium was used as the main variable explaining nitrogen content in our study because it is the main source of inorganic nitrogen for primary producers in the absence of significant amounts of nitrate (Friberg et al. 2009). Total phosphorus was colourimetrically measured 4 times during summer 2007 using method DS 292/DS/EN 6878 (Danish Standard 292 1985), which involves predigestion using persulphate.

Dry weight of vascular macrophytes, bryophytes, macro algae, and macrophytes was assessed on 13 July 2007. At 5 randomly determined points in a grid covering the entire area of each stream, a 14 × 14 cm frame (Surber sampler) was placed on the stream bed and the cover was harvested. The macrophytes were brought to the laboratory, separated into groups, and identified. The macrophytes and mosses were then dried at 60 °C for 24 h before weighing. Mosses were identified using keys for Icelandic mosses by Johannsson (1996, 2001). Stream bed structure (i.e., sand and pebbles) was assessed using the same random points used for the benthic samples. The stream bed was classified according to diameter of stone particles: sand <0.02 cm, gravel 0.02–1.59 cm, pebbles 1.6–6.39 cm, cobbles 6.4–24.9 cm, and boulders >25 cm (Giller and Malmquist 2006).

During the first week of August 2004 (Christensen 2006), 5–10 macroinvertebrate samples were obtained from each stream using a Surber sampler with mesh size 200 µm. The samples were stored in 70% ethanol before identification. To validate whether the data from 2004 could be used to explain diatom communities in August 2007, we correlated relative abundances of different inver-
tebrate groups with data for 6 of the 8 streams from August 2007; correlations between the 2004 and 2007 data for density and community composition ranged from 0.77 to 0.99, all significant at p < 0.05. Climate variations (temperature and precipitation) were small and therefore not likely to have influenced invertebrate densities between different years. Stream temperatures were also similar (Gudmundsdottir et al. 2011b). These data collectively support our use of the more complete invertebrate dataset from 2004 as drivers in multivariate analysis (RCCA) for diatom data from summer 2007 (Gudmundsdottir et al. 2011a).

Diatom samples were obtained by randomly collecting 3 stones (5–35 cm in diameter) from the grids laid out in each stream each month from May to August 2007 (96 samples). This sampling provided the data on community composition and morphological traits, but to estimate the relationship between temperature and diatom size we used monthly data from summers 2006 and 2007, totalling 9 sampling occasions, yielding 216 diatom samples. The stones were wrapped in aluminium foil in the field to prevent light damage, transported to the laboratory, and kept cool until processing began.

**Laboratory analysis**

Algae were collected by using a toothbrush to brush a delineated area of each stone into a tray. The brushed area was measured by outlining it on an overlain squared tracing paper and was brushed until the surface had a grainy, nonmucilaginous texture. The brushings from each stone were suspended in Lugol’s iodine solution. For diatom species identification, subsamples of about 10 mL were heated in nitric acid (65%) for up to 24 h to remove all organic material and then were repeatedly centrifuged and resuspended in distilled water until the acid was removed. A subsample of 0.5 mL of resuspended material was air-dried onto a round microscope cover glass (15 mm wide) and mounted in Naphrax®. Diatoms were identified to species level using standard keys, and up to 2000 frustules were counted within defined transects on each slide.

To determine size category we did not digest the samples with acid. Aliquots of about 50–500 μL (depending on the density of algae) were pipetted into a counting chamber, which was filled with distilled water and left for 20–24 h before identifying, counting, and measuring. Biovolume and the size categories were estimated according to Hauer and Lamberti (2007) and expressed as μL cm⁻³. Diatoms <5 μm in width were classified as small; diatoms ≥5 μm and up to 12 μm in width were classified as medium; and diatoms >12 μm in width and/or >25 μm in length were classified as large (Hauer and Lamberti 2007).

Macroinvertebrates were identified to species level when possible. Hoyer’s medium (Anderson 1954) was used to mount the chironomids on glass slides before identification at 400–1000× magnification with a Leica DM 3000 microscope with Leica DFC 290 camera. Identification keys used were Gislason (1979), Cranston (1982), Wiederholm (1983), Dall and Lindegaard (1995), Merritt and Cummings (1996), Nilsson (1996, 1997), and Thorp and Covich (2001).

**Statistical analysis**

The R statistical software (version 2.9.2; R Development Core Team 2011) was used for all statistical analyses. All nonlinear data except bryophyte data were log transformed before analysis. Spearman’s rank correlation was used to determine the relationship between bryophytes and temperature. We used Regularized Canonical Correlation Analysis (RCCA) to ordinate most of the relevant variables with the diatom assemblages (species and traits). RCCA with its regularizing step is appropriate when there are few samples but many variables (in this case many diatom species) in the dataset (Gonzalez et al. 2008). A correlation value R = 0.707 is the critical value for 6 df (p ≤ 0.05) and 0.834 for p < 0.01. The RCCA was based on the 8 means from the different streams.

To summarize the association of different diatom species across streams we conducted hierarchical cluster analysis on pairwise distances derived from correlations of the frequencies in different streams (1−r). The package pvclust (Shimodaira 2004) in R (R Development Core Team 2011) was used for the analysis. Clustering confidence was evaluated with 1000 bootstrap samples.

We used one-way ANOVA to test if the various environmental factors were significantly different among streams. A linear mixed effect model, taking the replicate measurements within streams into account as a random effect, was used to determine if there was a relationship between temperature and diatom size categories (Crawley 2002). Correlation was used to estimate if there was a relationship between various growth forms of diatoms and invertebrates and if there was a relationship between evenness and species richness (Magurran 2004) with invertebrates or abiotic factors.

**Results**

**Physiochemical features**

The streams differed significantly in temperature (ANOVA, F = 3786, p < 0.001), ranging between 6.6 and 22.2 °C (Table 1). Conductivity was also significantly different among streams (ANOVA; F = 17.27, p < 0.001)
within the range of 96 and 497 µS cm\(^{-2}\). Most values fell in the range 194–280 µS cm\(^{-2}\), but one was unusually low and one somewhat higher. Ammonium (NH\(_4\) -N), total P, and pH were not significantly different among streams. Temperature and pH were, however, significantly negatively correlated (r = -0.75, p = 0.03). The values of pH were negatively correlated with dimension 1 (Fig. 1). Ammonium and total P were not significantly related to temperature. The highest discharge was observed in the 4 warmest streams (Table 1) and was positively correlated with dimension 1 (Fig. 1). Discharge was correlated with temperature (r = 0.74, p = 0.05), cobbles (%), and the depth of the streams; conductivity was negatively linked with dimension 2; and temperature was positively linked with dimension 1 (Fig. 1).

Macrophytes and bryophytes

Vascular macrophytes were rare, their density negligible, and they were most commonly observed in the colder streams (Fig. 1). The vascular macrophyte densities were positively linked with dimension 2 (Table 2) and positively correlated with low conductivity (Fig. 1). Fontinalis antipyretica (Hedw.), the only observed moss, was abundant in warmer streams but also found in sparse patches in cooler streams. Its cover correlated positively with temperature (S = 2884, p < 0.001, r = 0.73; Fig. 2) and was positively linked to dimension 1 (Table 2; Fig 1). The liverwort Jungermannia exsertifolia (Steph.) was very sparse and present only in the coldest streams. Its cover was negatively correlated with temperature (S = 14466, p = 0.02, r = -0.36) but positively linked with dimension 2 (Fig. 1 and 2).

Invertebrates

We identified 30 invertebrate taxa; 16 were larval Chironomidae with Eukiefferiella minor (Edw.), the most abundant, and were found in highest densities in the colder streams (Fig. 3). Numbers of chironomids declined significantly with temperature and were positively linked to dimension 2 of an RCCA analysis relating communities to driving variables (Fig. 1). The gastropod species Radix peregra dominated the macrobenthos in the warmer streams and was positively correlated with temperature and positively linked to dimension 1 (Fig. 1 and 3). The black-fly species Simulium vittatum was also abundant in the warmer streams and was positively correlated with dimension 1 and temperature (Fig. 1 and 3). Other dipterans were sparse, and numbers did not correlate with temperature (Fig. 1 and 3). The only larval caddis observed in the streams was Potamophylax cingulatus (Steph.). Its density was low (Fig. 3) and not correlated with any environmental factors, but it was negatively linked to dimension 1 and thus linked to high conductivity and low water temperature. The 4 warmest streams had higher total invertebrate densities than the 4 coldest streams (Fig. 3), but the total density was not correlated with temperature (p > 0.05; Fig. 1).

Diatom community structure

Diatom population density varied between streams (Table 1), and 64 diatom taxa were identified overall; the majority were identified to species level (44 species of 64 taxa). After removal of rare species (<0.5% density and species observed in no more than one stream), 34 diatom species were left for RCCA analysis and cluster analysis (Fig. 1).

Table 1. Mean and standard errors for key physical and chemical variables of the Hengill streams along with the mean and standard deviations for diatom frustule counts in the streams. Streams are listed in order of increasing temperature.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Temperature (°C) (n = 3)</th>
<th>Conductivity (µS cm(^{-1}) at 25 °C) (n = 3)</th>
<th>pH (at 25 °C) (n = 3)</th>
<th>NH(_4)-N (mg L(^{-1})) (n = 3)</th>
<th>Total P (mg L(^{-1})) (n = 5)</th>
<th>Discharge (m(^{3}) s(^{-1})) (n = 3)</th>
<th>Number of diatom frustules (mean cm(^{-2}) ± standard deviation) (n = 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>6.63 ± 0.02</td>
<td>96 ± 1.2</td>
<td>8.3 ± 0.17</td>
<td>0.035 ± 0.003</td>
<td>0.030 ± 0.004</td>
<td>1.3 ± 0.40</td>
<td>5.0 × 10(^{6}) ± 4.8 × 10(^{6})</td>
</tr>
<tr>
<td>14</td>
<td>8.56 ± 0.04</td>
<td>204 ± 36.4</td>
<td>8.6 ± 0.27</td>
<td>0.033 ± 0.011</td>
<td>0.014 ± 0.008</td>
<td>1.9 ± 0.40</td>
<td>1.7 × 10(^{3}) ± 2.3 × 10(^{3})</td>
</tr>
<tr>
<td>11</td>
<td>10.03 ± 0.03</td>
<td>497 ± 71.4</td>
<td>8.0 ± 0.17</td>
<td>0.028 ± 0.005</td>
<td>0.020 ± 0.004</td>
<td>1.1 ± 0.58</td>
<td>5.8 × 10(^{4}) ± 2.2 × 10(^{4})</td>
</tr>
<tr>
<td>10</td>
<td>13.15 ± 0.04</td>
<td>194 ± 1.6</td>
<td>8.5 ± 0.17</td>
<td>0.021</td>
<td>0.030 ± 0.002</td>
<td>0.3 ± 0.04</td>
<td>2.1 × 10(^{6}) ± 1.2 × 10(^{6})</td>
</tr>
<tr>
<td>6</td>
<td>16.66 ± 0.02</td>
<td>231 ± 11.7</td>
<td>8.0 ± 0.20</td>
<td>0.034 ± 0.004</td>
<td>0.029 ± 0.002</td>
<td>4.1 ± 1.39</td>
<td>3.9 × 10(^{5}) ± 5.2 × 10(^{5})</td>
</tr>
<tr>
<td>5</td>
<td>17.61 ± 0.02</td>
<td>234 ± 8.19</td>
<td>7.8 ± 0.25</td>
<td>0.033 ± 0.002</td>
<td>0.029 ± 0.003</td>
<td>5.6 ± 1.43</td>
<td>3.1 × 10(^{4}) ± 4.7 × 10(^{4})</td>
</tr>
<tr>
<td>1</td>
<td>17.76 ± 0.03</td>
<td>229 ± 17.4</td>
<td>7.8 ± 0.16</td>
<td>0.030 ± 0.001</td>
<td>0.027 ± 0.003</td>
<td>2.9 ± 0.49</td>
<td>2.5 × 10(^{4}) ± 1.9 × 10(^{4})</td>
</tr>
<tr>
<td>8</td>
<td>22.21 ± 0.004</td>
<td>280 ± 19.4</td>
<td>7.9 ± 0.13</td>
<td>0.028 ± 0.005</td>
<td>0.030 ± 0.001</td>
<td>5.0 ± 1.34</td>
<td>9.2 × 10(^{5}) ± 1.6 × 10(^{6})</td>
</tr>
</tbody>
</table>
Fig. 1. Results of a Regularized Canonical Correlation Analysis (RCCA) showing the similarities of diatom species (regular type) and their relationship with environmental factors (bold type) and dominant macroinvertebrates (large, gray, and bold type). Only species that had >0.5% abundance in some of the 8 streams were included, and species that were only found in only one stream were not included. A full list of diatom species is given in Appendix 1. Abbreviations for environmental features are: jung = Jungermannia exsertifolia, macrophy = macrophytes, sand = sand, Cobl = cobbles, depth = depth, width = width, ph = pH, grav = gravel, pebl = pebbles, cond = conductivity, bryo = Fontinalis antipyretica, tp = total phosphorus, amm = ammonium, temp = temperature, disch = discharge. Abbreviations for invertebrates are: invdens = invertebrate density, tricopt = Potamophylax cingulatus (caddisfly), otherdip = other dipteral groups, chiro = chironomids, simvit = Simulium vittatum, and rper = Radix peregra.

Fig. 2. Observed moss (F. antipyretica, white boxes) and liverwort (J. exsertifolia, gray boxes) cover (dry weight in g) in the 8 streams. Circles represent outlier values.
There were 3 main diatom clusters according to RCCA analysis (Fig. 1). The first dimension represented temperature and the second represented conductivity (Table 2). The first diatom community contained *Diatomella balfourina*, *Nitzschia inconspicua*, and diatoms not fully identified and given a code number (66). They were very small *Achnanthes* or *Navicula* spp. and were positively related to dimension 1 (Table 3), and therefore low conductivity, and negatively linked to dimension 2 and temperature (Fig. 1; Table 3). These diatom species were also linked to *J. exsertifolia*, macrophytes, and Chironomids (Fig. 1).

A second diatom community was negatively related to both dimensions (Table 3) and thus related to high conductivity and low water temperature (Fig. 1). These diatom species were *Meridion circulare*, *Nitzschia aequorea*, *N. dissipata*, and *N. amphibia*. The caddis larva *P. cingulatus* and dipterans other than simuliids and chironomids were correlated with this community (Fig. 1).
The third community was positively correlated with dimension 1 and therefore with high temperature and high discharge (Fig. 1; Table 3) but not linked to dimension 2. Bryophytes (*F. antipyretica*), depth, high temperature, discharge, ammonium, cobbles (%), *S. vittatum*, and *R. peregra* were the most important correlates for these diatoms, dominated by *Rhoicosphenia curvata*, *Gomphonema parvulum*, and *Cocconeis* spp. (Fig. 1). Most of the diatom species had little or no correlation with either dimension and therefore straddled the 3 distinct communities (Fig. 1; Table 3).

We used cluster analysis to establish alternatively how diatom communities were related to environmental factors. The dendrogram showed 2 major distinctions,
based on temperature. One of the major clusters (Fig. 4, left) contained 10 species or taxa that were commonly observed in warmer streams. Among those species were Cocconeis spp., Gomphonema parvulum, and Rhoicosphenia curvata, the same species that were clustered around temperature, discharge, bryophytes, S. vittatum, and R. peregra on the RCCA graph (Fig. 1 and 4). The other major group was linked to lower water temperature and contained 24 species. Diatomella balfourina, code 66, Nitzschia inconspicua, N. dissipata, N. aequorea, and Meridion circulare were among those 24 species. The cold water species were divided into 2 clusters on the dendrogram. The ones to the right were closely linked to cold water environmental features on the RCCA graph and those species to left (middle branch on the dendrogram) were species scattered between streams on the RCCA graph (Fig. 1 and 4). Invertebrate density had no influence on the diatoms or other environmental factors (Fig. 1).

Diatom taxonomic diversity

Diatom evenness was unaffected by temperature or other important environmental features (conductivity, pH, ammonium, TP, F. antipyretica, J. exsertifolia, and discharge; P > 0.05). Species richness and the Shannon Index showed the same pattern as evenness (P > 0.05). Sorensen Index was also unaffected by these environmental features (P > 0.05).

Diatom traits and biomass

Diatom traits for individual species and genera (Appendix 1) indicate that motile diatoms (MO) were closely linked to low temperature (Fig. 5), low conductivity, presence of J. exsertifolia, and macrophytes. These diatoms were mainly Nitzschia inconspicua and other rarer Nitzschia spp. (Fig. 1). Mucilage pad (MP) diatoms were also linked to lower temperature but not strongly. Most of the MP diatoms (e.g., Achnanthes spp., a common genus

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**Fig 5.** A biplot based on Regularized Canonical Correlation Analysis (RCCA) showing the relationship between various environmental features and growth form traits of diatoms. The growth form traits were MS = mucilage stalk, AR = attached on raphe, MO = motile, CF = chain forming, MP = mucilage pads, MT = mucilage tubes. See Fig. 3 for abbreviations for other environmental features.
in the streams) were found in many streams and therefore not likely to be closely linked to either low or high temperature (Table 4).

Mucilage stalk (MS) diatoms were found in all streams and were mainly Gomphonema spp. and Rhoicopsis curvata. Because Gomphonema spp. were more often observed in colder streams (except for Gomphonema parvulum, which was linked to the warmer streams) than warmer and were more common than R. curvata, the RCCA plot showed a closer link between MS diatoms with colder water compared with warmer water. Chain-forming diatoms (CF) and diatoms attached by their raphe (AR) were positively linked to high conductivity and low water temperature. Meridion circulare and 3 Nitzschia spp. were found where the conductivity was high along with chain-forming Fragilaria spp., although they were scattered on the RCCA plot due to rather high occurrence in most streams.

Total diatom biovolume was not significantly related to temperature or invertebrates (p > 0.05).

In 2006, temperature had negative influences on population density of large diatoms (b = –2.02, t = –2.15, p = 0.035), and in 2007 population densities of smaller diatoms were close to being significantly favoured by temperature (b = 4.23, t = 2.89, p = 0.06).

Discussion

The RCCA analysis was particularly useful because it showed a syndrome of linked environmental factors consistently affecting the streams. Temperature, depth, flow, bryophyte cover, and features of the invertebrate community were all strongly linked. We argue that the master variable is temperature. The flows were all comparatively low and increased only modestly with temperature, perhaps as a function of lesser permanent ice formation in the soils from which the water percolated. Flow and depth are obviously related, and we cannot argue that shear stress was greatly different among flows as low as these. We assume that opportunities for colonization of bryophytes and invertebrates were equal because the streams were in a confined area with no obvious biogeographical barriers between them. There is thus a picture of temperature strongly influencing these variables, and an argument for treating them together, as a temperature driven syndrome, in examining the hypotheses posed. Water chemistry was comparatively uniform with only 2 anomalies in conductivity; conductivity formed a separate variable that was separately accounted for in the analyses.

We posed 4 hypotheses, 3 based on parallels with a macrovegetation changing along a temperature gradient, and the fourth relating to recent metaanalyses of organism

<table>
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<th>Trait</th>
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<th>8.6</th>
<th>10.0</th>
<th>13.6</th>
<th>16.7</th>
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<td>20.4</td>
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<td></td>
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<td>2.8</td>
<td>9.2</td>
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<tr>
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</table>

size in relation to temperature. The first hypothesis, that temperature would have significant positive influences on diversity of diatoms, growth form diversity, evenness, and community composition, was rejected. Temperature had no influences on diatom evenness, species richness, or Shannon Index. Species richness was generally slightly higher in colder streams compared with warmer streams. Studies on effects of temperature increase within tundra communities have shown loss of plant biodiversity (Walker et al. 2006), although diversity and species richness of many groups of organisms generally increase with decreasing latitude, and therefore average temperature, at comparable altitudes. The discharge was higher in the warmest streams compared with the colder streams but did not have significant influence on the diatom diversity indices and did not affect the density of invertebrates.

Growth form diversity was also greater in the coldest streams because species diversity was slightly higher, although the effect was statistically insignificant. MO diatoms were very common in the coldest streams, and thus we conclude that the motile growth form is highly linked to low temperature and associated environmental factors in our stream system. Although MO diatoms were found in all streams, they dominated where water temperature was lowest, with both low conductivity and high conductivity. Based on the dendrogram, we found these Nitzschia species to be linked together in the last cluster (cluster branch to right) where cold water species were clustered together. Gudmundsdottir et al. (unpublished) found motile diatoms to benefit from low nutrient status, and they retreated when nutrient was added to the streams. According to these findings Nitzschia spp. and some Navicula spp. seem to benefit from low water temperature and low nutrient pollution, in contrast to other studies (Kelly et al. 2001, Kelly 2003, Yallop and Kelly 2006, Yallop et al. 2009). The growth form of MP diatoms was also linked with both dimensions and was mainly found in cold streams with and without high conductivity. These species were also
linked together on the dendrogram, indicating that they were commonly found together in colder streams. *Achnanthes lanceolata*, *A. minutissima*, and code 66 were among those species on both the RCCA graph (Fig. 1) and the dendrogram (Fig. 5). Perhaps MP diatoms are at some disadvantage compared with mucilage stalk diatoms when competition for light in biofilms exists. Because we observed rather few diatom species in the warm streams, the growth form diversity was also low compared with that in the cold streams. Overall, our analogy with the diversity of terrestrial habitats did not hold.

We partly accepted the second hypothesis regarding the negative influences of grazers on growth form diversity. The warmer streams contained fewer growth forms than the colder streams, and no growth form was linked with high temperature on the RCCA graph (Fig. 5). These streams had the highest abundance of the scraper, *R. peregra*, an effective herbivore (Steinman 1996). The grazing from *R. peregra* may be responsible for low growth form diversity in the warmest streams, analogous with reindeer in tundras, which are responsible for lowering biodiversity where they are found (Väre et al. 1995, Austrheim and Eriksson 2001). *R. peregra* was absent from the coldest streams, but Chironomidae were dense. Chironomidae are a diverse group, and many species are collectors and gatherers and feed on the loosely attached and loose periphyton (Allan 2006). The most abundant species was a collector–gatherer rather than an efficient grazer–scraper. Studies on the effects of chironomids on epilithic algae are fewer than those focused on gastropods and show both positive and negative effects on epilithic biomass (Steinman 1996). We found no association between environmental features, diatom assemblages, and density of invertebrates and therefore conclude that grazing did not influence the abundance of diatoms, although it may influence the community composition.

Terrestrial habitats contain macroherbivores that could be regarded as an analogue to *R. peregra* because they are much larger than their prey. In tundra, reindeer and musk oxen are known to strongly impact some areas by grazing if their density is high enough. These animals often occur in large herds on small tundra areas. Reindeer can alter the vegetation by transforming it from dwarf shrubs and moss to grasslands (Olofsson 2006). Macroherbivore grazers in the boreal forest are much sparser and therefore may have less influence on the vegetation. Paradoxically, the warm streams mimicked tundra while the cold streams resembled boreal forest in the effects of large grazers. Warm streams that contain abundant bryophytes had high densities of *R. peregra* and *S. viitatum* in contrast to the forests that contain few large herbivores.

Diatoms attached on their raphe, such as *Cocconeis* spp., and are thus flattened to the substratum, were one of the most common growth forms where grazing was most intense (Steinman 1996, Yallop and Kelly 2006). *Cocconeis placentula* was weakly favoured by higher temperature while *Cocconeis pediculus* was more linked to lower temperature. These diatoms (*Cocconeis* spp., *Rhopalodia* spp., and *Epithemia* spp.) had similar abundances in most streams and were thus not related to grazing pressure or other factors. Diatoms were abundant in all the streams, suggesting that grazing did not significantly limit the production.

The third hypothesis, that in streams with low grazing pressure we would find high abundance of bryophytes, was not accepted. The warmest streams contained the greatest abundance of bryophytes (*F. antipyretica*) but the greatest density of the most efficient grazer, *R. peregra*. Bryophytes are the “trees” of these streams and form dense biomass, potentially shading the underlying vegetation (small algae and Cyanobacteria). *F. antipyretica* overwinters in the streams, as conifers do in boreal forests. Tall trees are usually immune to grazing while the vegetation on the forest floor is easily grazed; thus, grazing does not limit the tall trees of the forests or the bryophytes of the streams, but it affects the vegetation on the forest floor and epilithic algae in streams.

We accepted the fourth hypothesis that higher temperature would favour small diatom taxa while large diatom taxa would be more common in cold streams. With climate change, one of the most prominent effects has been shifts of species toward the poles and higher altitudes. But other effects of climate change have been detected, such as smaller body size and decreased size at maturity (Daufresne et al. 2009). Body size influences fecundity, population growth rate, and competition interaction. Few studies have been conducted on ectotherm species, although they are the majority of all species on earth. Daufresne et al. (2009) conducted a metaanalysis of the effects of increased temperature on ectotherm species and found significant influences from increased temperature on the body size of various organisms (fish, phytoplankton, and copepods). The diatoms in our streams showed a pattern of smaller diatoms in warmer streams and larger diatoms in colder streams. The likely reasons for this are not clear. Smaller organisms have greater surface to volume ratios, and among microorganisms they may have advantages in nutrient uptake; however, the availability of nutrients is likely to be greater with increased temperature owing to higher recycling rates, although denitrification rates may possibly increase. These streams are nitrogen limited (Friberg et al. 2009). Some diatoms with nitrogen-fixing endosymbionts were present (e.g., *Epithemia* sp.), but no
clear relationship between their abundance and nitrogen concentrations was found, largely because the latter were relatively uniform.

Thus, 2 of our hypotheses were rejected and 2, those concerning the lesser growth-form diversity with grazing and the higher incidence of smaller sized diatoms in warmer streams, were accepted. The cold streams paradoxically mimicked the boreal forest rather than the tundra regarding diversity and growth form diversity, and the warm streams mimicked the tundra. Grazing by snails seems to have reduced diatom diversity and growth form diversity, again in contrast to the tundra–Boreal forest analogy where macroherbivore grazing is more significant in the cooler habitat. Grazing did not suppress the abundance of diatoms, however, and thus the streams are considered to be bottom-up controlled rather than top-down controlled. Temperature and grazing pressure are important drivers on the diatom communities because they are on higher plants in terrestrial habitats; however, the effects are not parallel, and our results suggest that using microorganism communities as surrogates for larger systems should not be uncritically accepted.

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**References**


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