Environmental Science and Management
Faculty Publications and Presentations

Environmental Science and Management

7-1-2004

Effects of Experimental Greenhouse Warming on Phytoplankton and Zooplankton Communities in Fishless Alpine Ponds

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Citation Details

Effects of experimental greenhouse warming on phytoplankton and zooplankton communities in fishless alpine ponds

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Abstract

The impacts of global warming on aquatic ecosystems are expected to be most pronounced at higher trophic levels in cold-water environments. Therefore, we hypothesized that warming of fishless alpine ponds would suppress large-bodied consumers (e.g., cladocerans, copepods) and stimulate fast-growing microorganisms (e.g., phytoflagellates, rotifers), thereby altering the community composition and total abundance of zooplankton and phytoplankton. This hypothesis was tested using three blocks of four experimental mesocosms (1000-liter capacity) that were located next to alpine ponds in Banff National Park, Canada. Each block received unfiltered pond water and sediment from a pond following ice out in June 2000. A warming treatment (control vs. 3.6°C warmed) was achieved by controlling the ventilation of greenhouse canopies that were suspended over each of the mesocosms. By the end of our 50-d experiment, warming significantly suppressed total zooplankton biomass because large cladocerans (*Daphnia pulex*) declined while rotifer (*Keratella cochlearis, Conochilus unicornis*) abundance increased during the second half of the experiment. In contrast, warming did not affect total phytoplankton biomass but significantly altered community composition by favoring phytoflagellates (*Mallomonas, Synura, Trachelomonas*) over larger filamentous green algae (*Mougeotia, Phymatodocis*). Warming did not significantly increase dissolved nitrogen and phosphorus concentrations. Therefore, warmer growing conditions and reduced grazer biomass best explained the increased abundance of more edible, fast-growing phytoflagellates in the warmed mesocosms. Our findings support the hypothesis that moderate warming can destabilize plankton dynamics, thereby potentially reducing the reliability of water quality and food resources for higher trophic levels (e.g., planktivorous fish) in shallow cold-water ecosystems.

Global circulation models predict an increase of 1.5°C to >5°C in average air temperature in North America by the year 2100, based on a doubling of carbon dioxide (CO_2) and concomitant increases in other atmospheric greenhouse gases (Intergovernmental Panel on Climate Change 2001). Consequently, climate warming is expected to increase the surface temperatures of northern lakes by 1–7°C (Magnuson et al. 1997). Warmer air temperatures resulted in higher average annual water temperatures (~2°C) in boreal lakes of the Experimental Lakes Area (ELA) in northwestern Ontario over a 20-yr period (Schindler et al. 1990; Findlay et al. 2001).

Alpine and polar aquatic ecosystems are considered to be especially sensitive to climate warming (Hauer et al. 1997). Warmer temperatures decrease the amount of snow cover,

which results in reduced albedo and increased heat absorption by vegetation and soils (Fyfe and Flato 1999). As a result, small alpine lakes can become warmer and more chemically concentrated because of increased mineralization rates (e.g., Sommaruga-Wögrath et al. 1997).

To date, little is known about the effects of climate warming on zooplankton in cold-water ecosystems. However, evidence suggests zooplankton are more sensitive to changes in temperature than phytoplankton in other environments. For example, moderate warming enhances the growth and feeding rates of many filter-feeding zooplankton species, such as *Daphnia magna* (e.g., McKee and Ebert 1996). Beisner et al. (1997) showed that a 50-d period of constantly warmer conditions (25°C vs. 18°C) accelerated the growth of *Daphnia* populations in mesocosms, which resulted in overexploitation of their algal food supply and ultimately their extinction. Thereafter, total phytoplankton biomass increased and was comprised mainly of grazer-resistant taxa. Also, Benndorf et al. (2001) related midsummer declines in cladoceran abundance to overexploitation of their food resources during warmer winter and early-spring conditions. Similarly, Petchey et al. (1999) showed that warming (2°C per week) suppressed herbivorous protozoans and increased primary production during a 7-week microcosm experiment.

Several lines of evidence suggest that the size-structure of zooplankton assemblages shifts toward smaller species and individuals under warmer environmental conditions (*see* review Moore et al. 1996). Warmer temperatures can favor smaller zooplankton because warming disproportionately increases developmental (i.e., molting) and respiratory costs more than ingestion. In addition, large cladocerans and copepods may show reduced fecundity at elevated temperatures. For example, Taylor and Mahoney (1988) showed that

total zooplankton abundance declined because lethal increases in water temperatures above 45°C resulted in crustacean species being replaced by smaller rotifers. Patalas and Salki (1984) reported that larger cold-water specialists significantly increased in a northern lake following a diversion project that lowered water temperatures by only ~3°C. Warming is therefore predicted to induce a shift to smaller zooplankton sizes, which in turn should substantially alter grazing dynamics (Moore et al. 1996).

Phytoplankton responses to warmer temperatures also have not been demonstrated empirically in cold-water ecosystems. However, annual algal abundance in mountain lakes and ponds can be positively correlated with climate-driven events, such as warmer and longer ice-free growing seasons (Byron and Goldman 1990; Sommaruga-Wögrath et al. 1997). Culturing experiments show that warming can enhance gross primary production as an increase of 10°C doubles enzymatic rates (Davison 1991). However, algal growth rates increase only over a certain temperature range because respiratory costs may exceed enzymatic benefits at higher temperatures. Other temperature-dependent ecological trade offs (e.g., increased photosynthesis vs. increased grazing pressure) also confound predictions of whether warming will enhance aquatic primary production. For example, an experimental increase of 3°C did not affect phytoplankton biomass in temperate, macrophyte-dominated mesocosms despite a warming-induced increase in phosphorus concentration and the presence of zooplanktivorous fish (McKee et al. 2003).

Algal community composition may be altered in cold-water environments as a consequence of warming because of differential species responses to changes in temperature (Reynolds 1984). Collectively, diatoms exhibit the greatest tolerance of temperature, ranging from 0°C to 30°C (Patrick 1969). In contrast, chrysophytes are generally considered cold-water species that prefer temperatures <20°C (Sandgren 1988), while most dinoflagellates are more abundant during warmer summer months (Pollingher 1988). Chlorophytes and cyanobacteria can dominate phytoplankton communities at 15–30°C and >30°C, respectively (Patrick 1969). Phytoflagellates often replace diatoms under warmer and drier climatic conditions (Reynolds and Reynolds 1985; Findlay et al. 2001).

Differences in temperature-dependent competitive abilities affect differential responses by phytoplankton taxa to warming. Culture experiments have shown that chlorophytes and cyanobacteria are better competitors at higher temperatures (>20°C) than are diatoms (Tilman et al. 1986). Smaller algal taxa are also favored competitively under warmer conditions because a higher surface area : volume ratio enables them to realize faster nutrient-uptake and growth rates. A wide range of temperature optima for maximal growth rates has been reported for several phytoplankton species (Reynolds 1984). Therefore, total phytoplankton biomass may not be affected by warming because there exists a strong potential for compensatory species dynamics within this diverse community (e.g., Vinebrooke et al. 2003).

We conducted a mesocosm experiment using three alpine ponds to determine the effects of warming on the abundance and community composition of zooplankton and phytoplank-
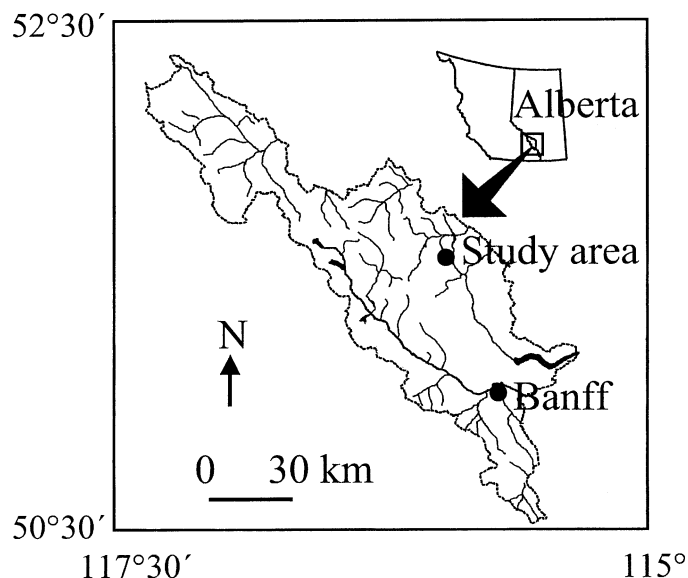

Fig. 1. Location of study area (51°36′N, 115°49′W) consisting of three alpine ponds in Banff National Park, Alberta, Canada.

ton. We hypothesized that warming would have a stronger effect on zooplankton than on phytoplankton because higher trophic levels are often more sensitive to environmental change (e.g., Beisner et al. 1997; Petchey et al. 1999). Furthermore, the earliest responses of freshwater communities to environmental change typically involve variables at the species level, rather than at the community level (Schindler 1995; Vinebrooke et al. 2003). If tolerant species are present that can compensate for sensitive competitors, then aggregate properties (e.g., total community abundance) are buffered against the impacts of environmental change (e.g., Vinebrooke et al. 2003). Therefore, we also expected that warming would have a greater effect on community composition than on total biomass.

Methods

Experimental design—The 50-d experiment was conducted following ice out in June 2000 at an altitude of 2300 m above sea level along the eastern Front Range of the Canadian Rocky Mountains in Banff National Park, Alberta (Fig. 1). All materials were flown in via a helicopter to Snowflake Pond 1 (SF1; 51°36′N, 115°49′W), Snowflake Pond 2 (SF2; 51°35′N, 115°49′W), and Grouse Pond (51°34′N, 115°48′W). These remote ponds were selected on the basis of their relative permanency, similar surface area (<1 ha), and close proximity to each other. All ponds were shallow (<1 m maximum depth) with low nitrogen : phosphorus ratios. Each pond was fishless and devoid of macrophytes despite an abundance of peaty sediment.

We used a single-factor, randomized-block design with repeated measures to test our hypotheses. The experiment consisted of two temperature treatment levels that were replicated twice within each block for a total of four black, round (2-m diameter, 0.5-m deep) polyethylene mesocosms (1000-liter capacity) beside each pond. The pond served as an in-
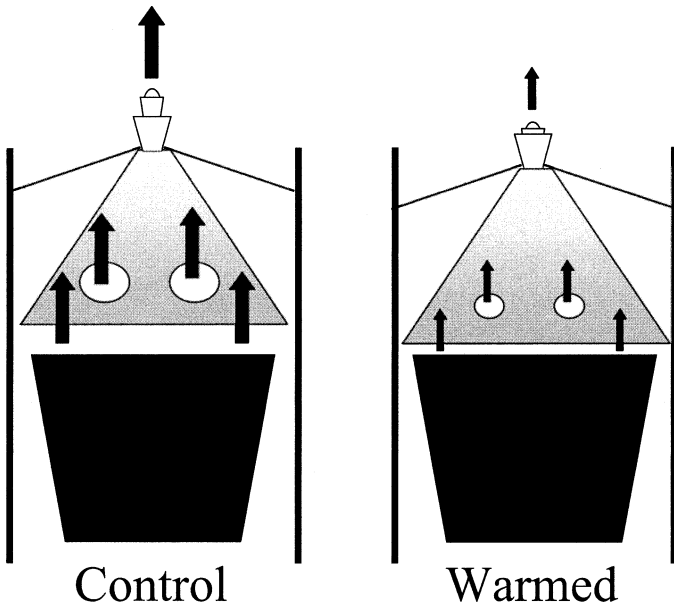
Control   Warmed

Fig. 2. Schematic diagram showing greenhouse canopies suspended over pond mesocosms. Warmed mesocosms were passively heated and convective heat loss controlled using canopy vents to increase average water temperature by 3.6°C during the experiment. Arrows are representative of the degree of convective heat loss from beneath the sides of the canopies and through the ventilation ducts in each canopy.

oculum for a single block as 900 liters of water and 40 liters of sediment were transferred into each mesocosm and allowed to settle for 5 d prior to the experiment. Solar-powered electric fencing was placed around the mesocosms to exclude elk, grizzly bears, and bighorn sheep.

The temperature factor consisted of two treatment levels that involved suspending individual greenhouse canopies over each mesocosm (Fig. 2). Canopies were constructed of Armin Tufflite® greenhouse sheeting material and were tightly affixed to a conical polyvinyl chloride frame to prevent the buildup of water or snow. Each canopy was secured in place using four steel corner posts that were driven ~50 cm into the soil. Canopies were suspended 1 cm above the warmed mesocosms and 4 cm above the controls to allow greater convective heat loss. Each canopy was suspended above the mesocosm using a pulley and ropes attached to a centrally located air vent. Three additional vents along the outer rim of each canopy were also used to control heat loss. Vents remained completely open in the control mesocosms and partially open in warmed mesocosms. Temperature was measured at the midpoint of the water column in each mesocosm and pond at 1-h intervals using StowAway® TidbiT® temperature monitors. Temperature readings were also conducted regularly with a handheld thermometer to determine whether a 3–5°C difference was being maintained between the control and warmed mesocosms and whether control mesocosms were tracking the ambient thermal regime of the pond. A Hewlett Packard photodiode array spectrophotometer was used to confirm that the greenhouse sheeting had a spectral transmittance (400–700 nm wavelength band) profile that transmitted ~70% ambient irradiance. Use of green-

house canopies provided a simple and inexpensive means of passively warming without the need for electrical power or heating fuels. Although greenhouse-warming field studies involve limited temperature control and altered light and precipitation regimes, natural temperature fluctuations are tracked well, while other environmental conditions are held constant, across all experimental units. A more sophisticated approach to experimental warming of aquatic mesocosms (e.g., Baulch et al. 2003; McKee et al. 2003) was not possible because of the lack of electricity at our remote field site.

Sampling protocol and analyses—Mesocosms and ponds were sampled during midday for water chemistry, phytoplankton, and zooplankton at 10-d intervals from 1 July (day 0) to 19 August 2000 (day 50). Water samples were integrated by pooling five 2-liter Van Dorn samples collected from one central and four equally spaced peripheral locations from a 0.3-m depth in each mesocosm and pond. A precise volume of water was filtered through Whatman GF/F (0.7-μm pore size) filters, and the filtrate (500 ml) was collected for nutrient analysis. Filtered water samples were kept cold in an alpine creek until transportation to the laboratory for nutrient analysis. Total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN) were measured using standard colorimetric techniques (Wetzel and Likens 1991). Unfiltered samples (125 ml) were taken and fixed with 2% glutaraldehyde for taxonomic enumeration of phytoplankton. The remaining water was poured back into each mesocosm after it had been passed through a 64-μm stainless steel sieve to collect and concentrate zooplankton in neutralized formalin. Entire zooplankton samples were later taxonomically enumerated using a Leica MZ7.5 stereomicroscope. Biomass of crustacean zooplankton was estimated directly from 30 unpreserved individuals that had been oven dried (60°C) to constant mass (Vinebrooke and Leavitt 1999), and rotifer biomass was calculated using genus-specific geometrical formulae (McCauley 1984).

Phytoplankton were settled in Utermöhl chambers and counted using a Leica DM-IRB inverted microscope at 400× and 1000× magnification. A minimum of 300 cells was counted in each sample. Biovolumes were calculated by measuring cell dimensions using Openlab™ version 2.2.0 and approximating cell shape with geometric solids of known volumes. Biovolumes were converted to biomass by assuming a specific gravity of one. Taxa were identified to genus using Prescott (1982) and Starmach (1985).

Statistical analyses—A randomized-block analysis of variance with repeated measures (RB-RM-ANOVA) was performed using Systat version 9.0 to test for time-dependent effects of warming on total phytoplankton and zooplankton biomass over a 50-d period. Univariate repeated-measures analyses were conducted, and if the assumption of sphericity was rejected using Mauchly's criterion, then agreement between Huynh–Feldt and Greenhouse–Geisser corrected alpha values was used to establish the statistical significance of warming and time effects (von Ende 2001). Repeated-measures multivariate analysis of variance (RM-MANOVA) was used to test for the time-dependent effect of warming on
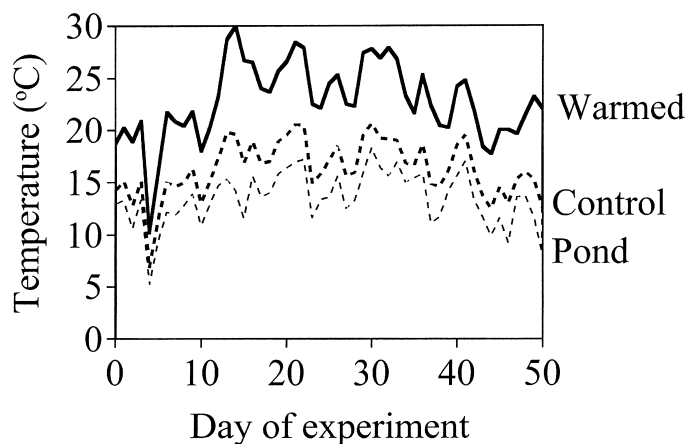
Fig. 3. Representative temperature readings from a control, warmed mesocosm, and an adjacent alpine pond (Snowflake Pond 1) from 1 July to 20 August 2000. Readings were obtained hourly using data loggers suspended at a depth of 0.3 m from the midpoint of each mesocosm and the pond.
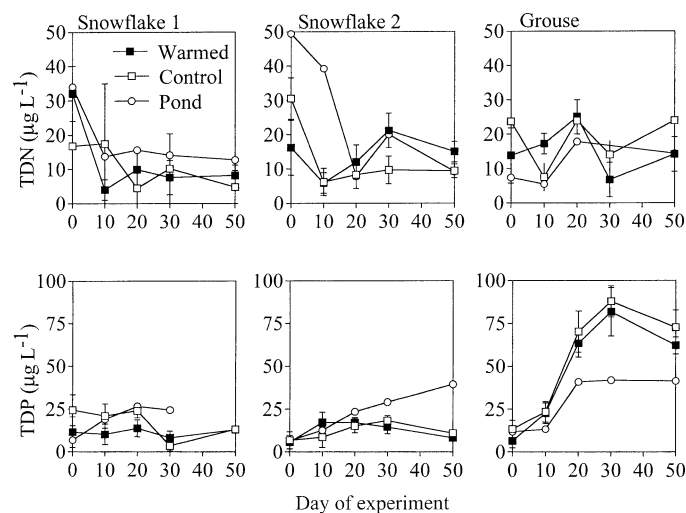

Fig. 4. Total dissolved nitrogen and phosphorus concentrations in warmed and control mesocosms located next to Snowflake Pond 1, Snowflake Pond 2, and Grouse Pond over a 50-d period. Bars indicate ± 1 SE ($n = 2$).

zooplankton community composition. Within-block replication enabled us to test for interactions between blocking and warming effects. Data were $\log_{10}$ transformed prior to analysis to improve homogeneity of variances.

Canonical correspondence analysis (CCA) was conducted using CANOCO version 4.0 (ter Braak 1998) to examine the effects of warming, time, grazer biomass, and nutrients on phytoplankton community composition during the experiment. Genus-level biomass data were $\log_{10}$ transformed prior to analysis to reduce the influence of the few large genera (e.g., filamentous green algae) that otherwise dominate ordinations. Preliminary ordination analyses showed that the pond-blocking effect strongly influenced the ordination of genera and experimental mesocosms, and, therefore, a separate CCA was performed for each block. CCAs were conducted using both categorical environmental variables that represented the two warming treatment levels on the final three sampling dates and continuous variables (nutrient concentrations, grazer biomass, and time). Forward selection was conducted to determine the significance of each measured environmental variable and the amount of variance it captured within the taxonomic data set. Monte Carlo unrestricted permutation testing (199 permutations) was used to test for the statistical significance of the ordination of taxa and experimental mesocosms in each block. The proximity of genera to environmental scores in each CCA plot represented how closely they were associated with the different warming treatment levels on different sampling dates, while environmental vectors showed the magnitude and direction of the effects of warming and time on taxonomic composition.

Results

Abiotic conditions—Our experimental manipulation increased water temperatures in the warmed mesocosms by an average of 3.6°C (Fig. 3). Warmed mesocosms averaged 19.4°C and ranged between 5.5°C and 30.1°C, while the con-

trols averaged 15.8°C and ranged between 4.2°C and 26.6°C. Natural ponds averaged 13.9°C and ranged between 2.7°C and 25.5°C during the experiment. N : P ratios remained low (<10) and did not differ consistently between the controls and the warmed mesocosms during the experiment (Fig. 4).

Zooplankton—Warming had significant time- and block-dependent negative effects on total zooplankton biomass (Table 1; Fig. 5). A significant warming–time interaction occurred because warmed mesocosms contained less zooplankton than did controls during the second half of the experiment. A significant warming–block interaction was detected because warming suppressed total zooplankton biomass in only cladoceran-dominated mesocosms (Snowflake 2 and Grouse) and not in copepod-dominated mesocosms (Snowflake 1). A significant time–block interaction occurred because zooplankton biomass increased only in the Grouse block during the experiment. Controls and natural ponds

Table 1. Randomized-block repeated-measures ANOVA comparing the effects of warming, blocking, and time on log-transformed total zooplankton biomass in experimental mesocosms. Greenhouse-Geisser adjusted probabilities were used for the F statistics.

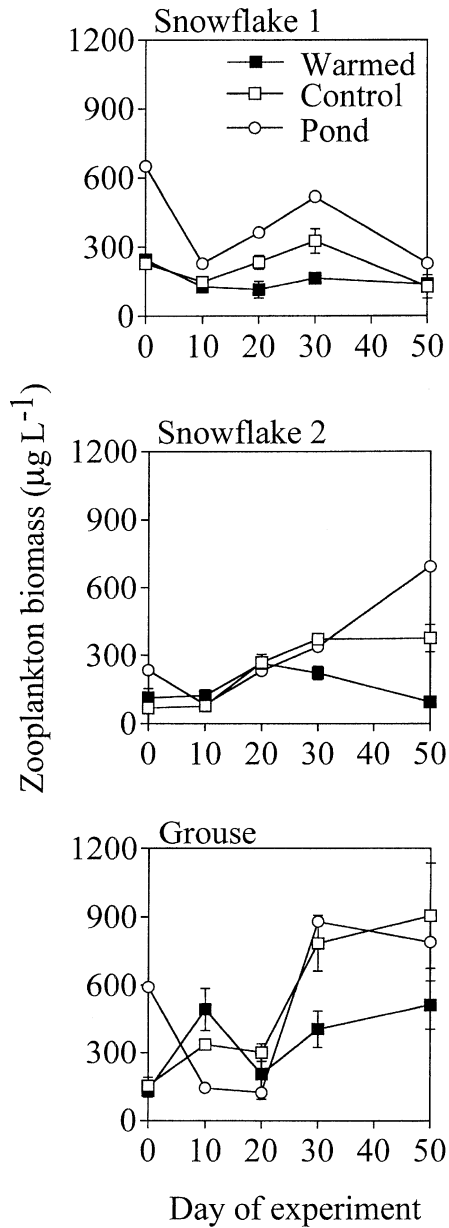| Source	df	MS	F	P
Between subjects				
Warming	1	1.03	5.92	0.061
Block	2	3.43	19.73	0.002
Warming × block	2	0.02	0.08	0.92
Within subjects				
Time	4	1.34	17.08	<0.001
Time × warming	4	0.49	6.26	0.009
Time × block	8	1.01	12.96	<0.001
Time × warming × block	8	0.24	3.03	0.048
Error	24	0.07		

Fig. 5. Total zooplankton dry weight in warmed and control mesocosms located next to Snowflake Pond 1, Snowflake Pond 2, and Grouse Pond over a 50-d period. Bars indicate ± 1 SE ($n = 2$).
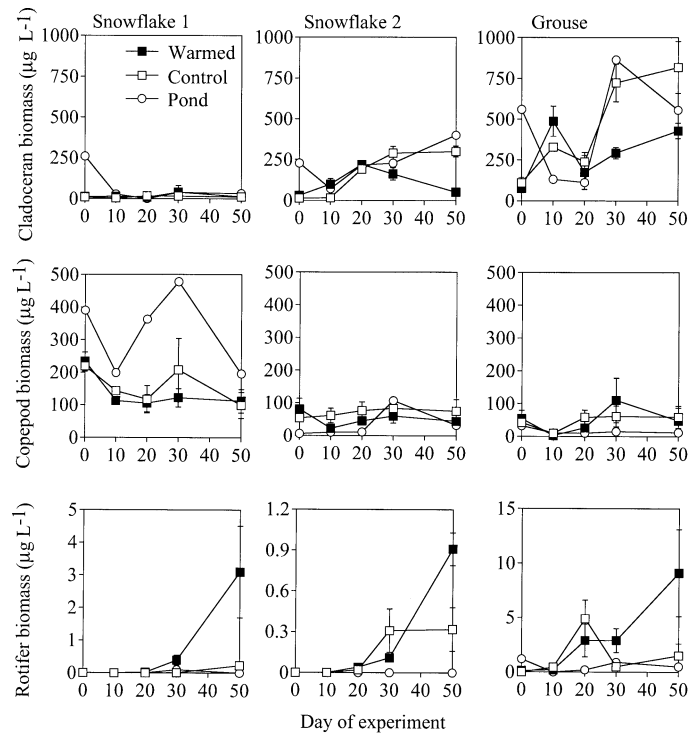

Fig. 6. Cladoceran, copepod, and rotifer biomass in warmed and control mesocosms located next to Snowflake Pond 1, Snowflake Pond 2, and Grouse Pond over a 50-d period. Bars indicate ± 1 SE ($n = 2$).

contained similar amounts of zooplankton, except in Snowflake 1 where total biomass was consistently lower than in the controls.

Zooplankton community composition (Fig. 6) was also affected significantly by warming as determined using RM-MANOVA (warming–time interaction; $F_{11,66} = 3.78$, $p = 0.0003$). Cladoceran abundance, consisting mainly of *Daphnia pulex* and few *Ceriodaphnia,* was suppressed significantly by warming during the second half of the experiment in the Snowflake 2 and Grouse blocks (RM-ANOVA, warming–time–block interaction; $F_{6,18} = 4.31$, $p = 0.046$). Copepod (*Diacyclops thomasi, Diaptomus nudus*) biomass was not affected significantly by warming (RM-ANOVA, warm-

ing–time interaction; $F_{3,18} = 1.49$, $p = 0.34$). Rotifer (*Keratella cochlearis, Conochilus unicornis*) abundance increased significantly in all of the warmed mesocosms (RM-ANOVA, warming–time interaction; $F_{3,18} = 31.19$, $p = 0.003$).

Phytoplankton—Warming did not significantly affect total phytoplankton biomass (Table 2, Fig. 7). A significant blocking effect was attributable to the Grouse mesocosms containing greater phytoplankton abundance. A significant time effect involved an overall increase in total biomass. Controls

Table 2. Randomized-block repeated-measures ANOVA comparing the effect of warming, blocking, and time on log-transformed phytoplankton biomass in experimental mesocosms. Greenhouse-Geisser adjusted probabilities were used for the F statistics.

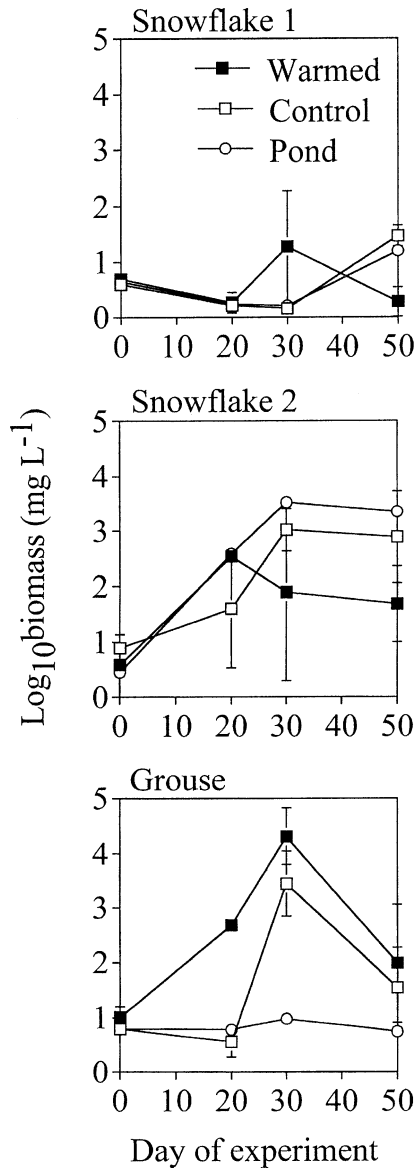| Source	df	MS	F	p
Between subjects				
Warming	1	0.31	0.60	0.583
Block	2	9.87	19.15	0.002
Warming $\times$ block	2	1.86	3.61	0.111
Within subjects				
Time	3	5.29	6.70	0.003
Time $\times$ warming	3	1.52	1.92	0.162
Time $\times$ block	6	2.00	2.53	0.059
Time $\times$ warming $\times$ block	6	0.58	0.74	0.624
Error	18	0.79		

Fig. 7. Total phytoplankton biomass in warmed and control mesocosms located next to Snowflake Pond 1, Snowflake Pond 2, and Grouse Pond over a 50-d period. Bars indicate ±1 SE (*n* = 2).

and ponds contained similar amounts of phytoplankton, except at Grouse Pond where total biomass was substantially less in the mesocosms than in the pond on days 30 and 50.

CCA showed that warming had a significant time-dependent effect on phytoplankton community composition in each block (Fig. 8). Monte Carlo permutation testing showed that each CCA was significant (SF1, $F_{3,8}$ = 1.46, p < 0.05; SF2, $F_{3,8}$ = 1.40, p < 0.01; Grouse: $F_{3,8}$ = 1.33, p < 0.05). The first two CCA axes for SF1, SF2, and Grouse Pond ordinations accounted for 24.5%, 23.8%, and 22.8%, of the total taxonomic variance, respectively. In each case, the primary CCA axis (x-axes) of the SF1 (λ_1 = 0.32), SF2 (λ_1 = 0.30), and Grouse (λ_1 = 0.31) plots represented a temporal gradient along which samples and genera were ordered according to sampling date. Secondary CCA axes (y-axes) in
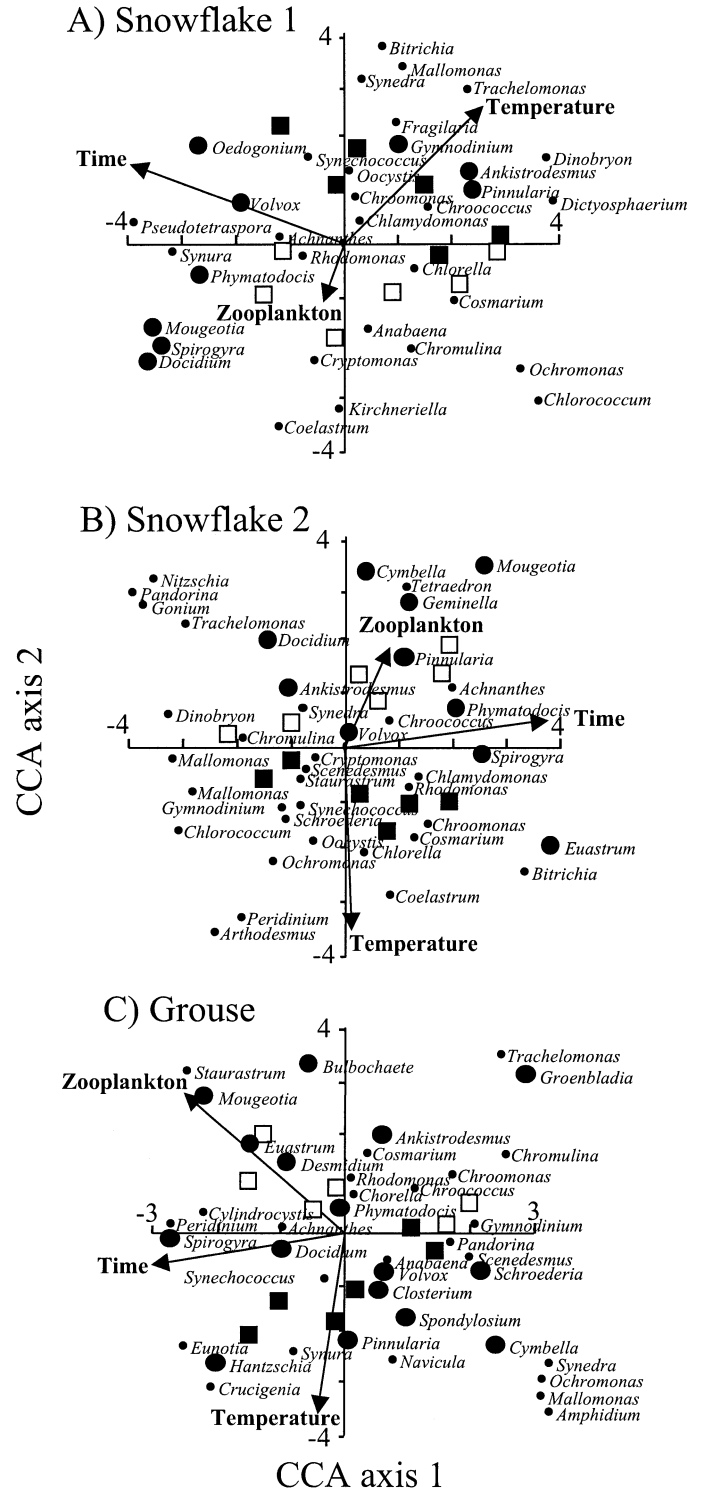
Fig. 8. Associations of phytoplankton genera, experimental warming, and time based on a CCA of algae and experimental mesocosms located next to Snowflake Pond 1, Snowflake Pond 2, and Grouse Pond. CCA scores for replicated (*n* = 2) controls (open squares) and warmed (filled squares) mesocosms are shown for day 20, day 30, and day 50. Environmental vectors were increased 10× to better illustrate their associations with experimental treatment levels and taxa. The maximum cell diameter of each taxon is depicted using a point that represents a size category (small circle = <35 μm; large circle = >35 μm).

the SF1 ($\lambda_2 = 0.10$), SF2 ($\lambda_2 = 0.14$), and Grouse ($\lambda_2 = 0.20$) plots separated controls and warmed mesocosms, demonstrating the effect of experimental warming on phytoplankton community composition (Fig. 6). CCAs were performed using all 68 identified genera.

In the SF1 plot (Fig. 8), CCA axis 1 separated early successional genera, such as small chrysophytes (*Chromulina, Dinobryon, Ochromonas*), from larger, late-successional taxa (*Mougeotia, Oedogonium, Phymatodocis, Volvox*). CCA axis 2 contrasted warmed phytoplankton consisting mainly of small flagellates and diatoms (*Bitrichia, Mallomonas, Fragilaria, Gymnodinium, Trachelomonas*) from controls that contained higher abundances of large chlorophytes (*Docidium, Mougeotia, Phymatodocis, Spirogyra, Coelastrum*) by day 50. *Mougeotia, Spirogyra,* and *Volvox* accounted for ~90% of the final total biomass in the controls, while large unicellular chlorophytes (*Cosmarium, Oocystis*) were more abundant in SF1 pond.

In the SF2 plot (Fig. 8), CCA axis 1 discriminated smaller chrysophytes (*Chromulina, Dinobryon, Mallomonas*) from larger filamentous green algae (*Phymatodocis, Spirogyra*), which were more abundant during the latter half of the experiment. Warmed and control phytoplankton communities were separated along CCA axis 2 because large filamentous green algae (*Geminella, Mougeotia*) were more abundant in the control mesocosms during the second half of the experiment. *Volvox, Spirogyra,* and *Phymatodocis* accounted for 95% of the total final phytoplankton biomass within the controls and SF2 pond.

In the Grouse Pond plot (Fig. 8), CCA axis 1 captured a shift from small algae (*Chromulina, Mallomonas, Scenedesmus*) to larger, late-successional genera (*Peridinium, Spirogyra*). CCA axis 2 contrasted control mesocosms that contained higher abundances of large filamentous green algae (*Bulbochaete, Desmidium, Mougeotia*) from warmed mesocosms in which flagellates and several diatoms (*Synura, Eunotia, Hantzchia, Pinnularia, Crucigenia*) were more common by day 50. *Spirogyra* and *Docidium* comprised ~95% of the total final biomass in the controls, while *Cosmarium, Chroococcus,* and *Rhodomonas* were the dominant taxa in the pond.

Discussion

Alpine zooplankton and phytoplankton showed striking differences in their responses to an average temperature increase of 3.6°C over a 50-d period. Our findings supported the hypothesis that warming has a more pronounced impact on the total biomass of consumers than primary producers (Petchey et al. 1999) because zooplankton biomass was suppressed while phytoplankton biomass remained unaffected in the warmed mesocosms. However, both communities showed significant taxonomic responses to environmental warming, likely in part because of the emergence of resting stages from the pond sediments (e.g., Hansson 1996). Warmer temperatures resulted in a size shift toward rotifers that did not compensate for the decline of larger cladocerans, while phytoflagellates succeeded larger filamentous green algae. Therefore, species-level responses were more prevalent

than functional responses during the experiment. Below, we consider potential explanations for differences between species- and community-level responses by zooplankton and phytoplankton to environmental warming.

Warming and zooplankton—Warmer temperatures are often hypothesized to negatively affect zooplankton, especially in unproductive ecosystems, because of strong synergistic interactions between thermal stress and food limitation on growth and reproduction (Moore et al. 1996). In our experiment, warming did negatively affect total zooplankton abundance when it consisted primarily of daphnids, and not copepods. Similarly, Beisner et al. (1997) showed that zooplankton biomass, consisting of *D. pulex*, declined significantly in more productive mesocosms that were heated from 18°C to 25°C. Overexploitation of food resources, increased metabolic costs, and a shift toward inedible filamentous cyanobacteria were considered to be the primary causes of the decline and of the extinction of daphnids in the warmed mesocosms (Beisner et al. 1997). In comparison, the amplitude and periodicity of population growth by the daphnids (*D. pulex, Ceriodaphnia*) in our warmed mesocosms were less pronounced, likely because the cyclical dynamics were slowed and dampened by the colder average temperature of 19.4°C. However, we suspect that the taxonomic shift toward inedible filamentous green algae also precluded daphnids from balancing higher metabolic costs with increased food consumption. The decline of daphnids in the warmed mesocosms would likely have persisted past day 50, and possibly to ice on in September, because gravid individuals were rarely detected. In contrast, total cladoceran abundance in plant-dominated temperate mesocosms was not affected by an experimental warming of 3°C, possibly because greater genetic and species diversity stabilized the community (McKee et al. 2003).

Copepod abundance was not affected by the 50-d period of experimental warming. Large copepods, such as *D. nudus,* likely have relatively slow growth rates and can diapause in response to environmental change (Williamson and Reid 2001), which could preclude a population response to warming. Most studies of temperature effects on zooplankton have focused on cladocerans rather than copepods, and therefore it is difficult to assess our results. However, development rates of many copepods generally increase, while fecundity declines, at temperatures between 10°C and 15°C (Moore et al. 1996). Although warming may have suppressed adult copepods if the experiment had been conducted over an entire alpine ice-free season (60–90 d), warmer temperatures could also have stimulated resting eggs to hatch in fall, which would have not provided sufficient time for them to mature before freezing (e.g., Chen and Folt 1996).

A potential explanation for increased rotifer abundance in the warmed mesocosms involves the combined effect of warmer growing conditions and release from competition. In particular, direct effects of warming on rotifer population growth are expected to account for their increased abundance at Snowflake 1 because warmer temperatures did not significantly suppress predatory copepods (Paul and Schindler 1994). However, the decline of *D. pulex* in the warmed mesocosms also likely stimulated *K. cochlearis* populations be-

cause this small rotifer is highly susceptible to mechanical interference from this daphnid (Gilbert 1988). Interestingly, rotifers also appeared to experience competitive release from larger zooplankton in an oligotrophic lake during a mesocosm experiment when the average temperature was 11.5°C, but not during the previous summer when water temperature was warmer by 4.5°C (Neill 1988).

Warming and phytoplankton—Warming altered phytoplankton community composition as shown by the divergence of warmed and control mesocosms in ordination space between days 20 and 50. This result was expected because algae collectively show a diversity of growth responses to changes in temperature (e.g., Reynolds 1984). The greater relative abundance of phytoflagellates (*Chroomonas, Volvox*) in the warmed mesocosms was consistent with positive associations between cryptophytes, green flagellates, and warm water temperatures (Reynolds and Reynolds 1985; Findlay et al. 2001). The positive response of phytoflagellates to warming likely reflected their ability to optimize their position in the water column relative to temperature, light, and nutrient gradients. Lower relative abundance of filamentous greens (*Docidium, Mougeotia, Phymatodocis*) in the warmed mesocosms also agreed with net photosynthetic rates of related taxa (*Spirogyra*) being negatively affected by warming in excess of 25°C (Adrian Berry and Lembi 2000). Lack of a strong cyanobacterial response during the experiment may have been due to the absence of pronounced heating events. Water temperature reached 30°C only once in the warmed mesocosms, yet cyanobacteria often require warmer temperatures to realize their maximum growth potential (Coles and Jones 2000). In addition, a decline of large-bodied herbivorous zooplankton also likely allowed for phytoplankton succession to proceed toward smaller, more edible taxa in the warmed mesocosms.

A possible explanation for the lack of a temperature effect on phytoplankton biomass is because warming did not increase dissolved nutrient concentrations. This finding runs contrary to a study of 57 alpine catchments in the eastern Alps in which warmer air temperatures (~1°C) over a 10-yr period resulted in higher mineralization rates and more concentrated water chemistries in lakes (Sommaruga-Wögrath et al. 1997). In comparison, experimental warming may not have increased nutrient levels in our mesocosms because of their isolation from potential allochthonous nutrient inputs. Nevertheless, our mesocosms contained pond sediments, which functioned as sources of nutrients. For example, McKee et al. (2003) showed that experimental warming significantly increased the release of phosphorus from sediments but did not affect phytoplankton biomass. However, increased release of phosphorus would likely have not promoted phytoplankton growth in our mesocosms because low $N:P$ values suggested that these algae were limited by nitrogen and not phosphorus. Another possible reason why warming did not stimulate phytoplankton biomass is that greater respiratory costs offset increases in photosynthesis.

An alternative explanation for the lack of a significant effect of warming on phytoplankton biomass is that our experiment lacked statistical power. Unfortunately, methodological constraints typically preclude better replication of experimental designs that are conducted at remote alpine study sites (e.g., Vinebrooke and Leavitt 1999). Nevertheless, power analysis (Quinn and Keough 2002) revealed that our level of replication generated a probability of 72% for statistically detecting a warming-induced increase in total algal biomass of 40%. Therefore, we are relatively confident that our nonsignificant result for phytoplankton biomass represented an effect of less than 40%, which was expected based on the predicted response of algal growth rates to an average temperature increase of 4°C (Davison 1991; Finlay et al. 2001).

Our demonstrated effect of environmental warming on phytoplankton community composition in ponds is likely scale dependent. By the end of the experiment, filamentous taxa were more abundant in the mesocosms than in the ponds likely since the former provided a more sheltered habitat for larger algae. A deeper water column and wind-driven mixing would favor smaller, nonfilamentous phytoplankton and ameliorate warming events.

Although little is known about the potential impacts of climate warming on cold-water ecosystems, our findings suggest that higher trophic groups and processes are most at risk. It is not surprising that the warming-induced shift toward smaller zooplankton resulted in a decline in total biomass because species-poor cold-water communities often lack the functional redundancy that is required to withstand environmental change (Schindler 1995; Vinebrooke et al. 2003). Consequently, higher trophic levels (e.g., planktivorous fish) may also be adversely affected by warming in other cold-water ecosystems as a result of reduced food availability. The diverse phytoplankton community was relatively more resistant, and taxonomic responses appeared to be the result of the impact of warming on the zooplankton. Clearly, future empirical research must address how environmental conditions (e.g., availability of cold deep water refugia, disturbance, trophic status) and interactions with other human stressors associated with global change determine the direct and indirect effects of climate-related events (e.g., summer heating spells) on aquatic biodiversity and ecosystem functioning.

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