Impacts of Climate Warming and Nitrogen Deposition on Alpine Plankton in Lake and Pond Habitats: an In Vitro Experiment

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Impacts of Climate Warming and Nitrogen Deposition on Alpine Plankton in Lake and Pond Habitats: an *In Vitro* Experiment

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Abstract

The combined effects of multiple ecological stressors determine the net impact of global change on environmentally sensitive alpine and polar environments. For example, climate warming and nitrogen deposition both increasingly affect ecosystems at high elevations. We hypothesized that the net impact of warming and nitrogen on alpine plankton differs between consumers and producers because of the greater environmental sensitivity of higher trophic levels. Also, we expected that habitat conditions would mediate the responses of plankton to these two stressors as sediments function as ecological buffers against environmental change. These hypotheses were tested in a growth chamber by applying temperature (8 vs. 15°C) and nitrogen (200 vs. 1000 μg N L^{-1}) treatments to a planktonic alpine community in the presence and absence of sediments obtained from Pipit Lake, Banff National Park, Alberta. A significant nitrogen-temperature interaction affected phytoplankton abundance because the positive effect of fertilization depended on warming. Warming also amplified the effect of nitrogen on herbivores while suppressing the fecundity of omnivores. The presence of sediments suppressed the positive effect of warming on herbivores, but stimulated omnivores. The observed prevalence of non-additive effects highlights the strong potential for global change causing future ecological surprises in alpine environments.

Introduction

Mountain lakes and ponds are increasingly viewed as sentinels of the impacts of global change (Battarbee et al., 2002; Vinebrooke and Leavitt, 2005). For example, climate warming is expectedly most pronounced in alpine environments where increased melting of snowpack and ice cover amplifies the absorbance of solar irradiance (Bradley et al., 2004). Concurrently, increased use of agricultural fertilizers and combustion engines since 1850 has more than doubled atmospheric nitrogen deposition over certain eastern ranges of the North American Rocky Mountains (Baron et al., 2000). Further, alpine lakes are especially susceptible to increased nitrogen deposition because pollutant-laden cloud droplets are intercepted as they pass over mountains (Grennfelt and Hultberg, 1986). Consequently, nitrate concentrations have increased in many alpine lakes in both North America and Europe (Kopácek et al., 1995; Baron et al., 2000).

Few studies have examined the ecological impacts of either temperature or nitrogen deposition on aquatic alpine communities. Holzapfel and Vinebrooke (2005) showed that the impact of an increase of 7°C on alpine plankton differed across trophic groups. Specifically, warming suppressed alpine zooplankton, thereby stimulating phytoplankton abundance via a hypothesized release from grazing pressure. Similarly, Strecker et al. (2004) demonstrated experimentally that summer heating events in excess of 25°C reduced the abundance of herbivorous zooplankton while only altering the taxonomic composition of phytoplankton communities in alpine ponds. Experimental evidence suggests that increased nitrogen deposition over lakes can also suppress zooplankton because the phytoplankton community shifts to less edible species, such as cyanophytes (Lafrancois et al., 2004; Nydick et al., 2004).

Elevated nitrogen levels can stimulate primary production and change phytoplankton community structure in many mountain lakes that are nitrogen-limited (Morris and Lewis, 1988; Interlandi and Kilham, 1998; Nydick et al., 2004). However, the joint impact of warming and nitrogen deposition on alpine plankton remains untested. The cumulative impact of these two stressors will be difficult to predict based on these earlier findings if these environmental factors interact to generate non-additive ecological surprises (Christensen et al., 2006).

The impacts of stressors of environmental change on freshwater communities are often habitat-specific (e.g., Vinebrooke and Leavitt, 1999a). Planktonic habitats in alpine freshwaters range from the open waters of deep lakes to shallow ponds (Vinebrooke and Leavitt, 1999b; McMaster and Schindler, 2005). In particular, the mediating influence of sediments against environmental change is more pronounced in shallow habitats because of the higher sediment surface:water volume ratio and increased resuspension due to wind events (Hobbie, 1980). For example, extremely low nitrogen:phosphorus ratios in alpine pond ecosystems highlight how phosphorus release from sediments may result in nitrogen-limitation and a greater sensitivity to increased nitrogen deposition than exists in lakes (McMaster and Schindler, 2005). Further, wind-driven resuspension of sediments in ponds can facilitate the release of nutrients, which potentially increases primary production and food availability for consumers (Schallenberg and Burns, 2004). Conversely, suspended sediments may impair feeding efficiencies by mechanically interfering with filtering mechanisms and diluting the caloric content of ingested material (Kirk, 1991; Levine et al., 2005).

The main goal of our study was to compare the potential impacts of warming and nitrogen deposition on plankton

communities across shallow and deep alpine environments. We hypothesized that warming would synergistically amplify the positive effect of nitrogen deposition on phytoplankton abundance by (1) stimulating growth rates released from nitrogen limitation, and (2) suppressing sensitive coldwater grazers. Also, we expected a non-additive negative impact of these stressors on alpine zooplankton because warming can (1) exert a substantial metabolic cost on large-bodied consumers, and (2) accelerate grazing rates, which are however then not supported by a nitrogen-induced shift toward less edible phytoplankton. Finally, we predicted that sediment would mediate both the positive effect of nitrogen deposition on primary producers by functioning as a source of phosphorus, and the negative effects of warming on consumers by providing a supplementary source of food and seed bank for colonists (Hairston, 1996).

Methods

EXPERIMENTAL DESIGN

Plankton, water, and sediment were collected from a remote fishless alpine lake (Pipit Lake, 2217 m a.s.l.) located on the eastern front range of the Canadian Rocky Mountains in Banff National Park, Alberta ($51°37'$N, $115°51'$W). This lake was chosen because of its regular use as an unperturbed reference lake for other studies in the region (Vinebrooke and Leavitt, 1999a; Holzapfel and Vinebrooke, 2005; Parker and Schindler, 2006). Zooplankton were collected on 11 August 2005 using vertical tows of a 64 μm mesh-sized net, and consisted solely of herbivorous *Daphnia middendorffiana* and omnivorous *Hesperodiaptomus arcticus*. Zooplankton were transported in a 20-L plastic carboy containing surface water. Sediment was collected on the same date using a scoop to collect the top 5-cm layer in the littoral zone at a 20-cm depth, and was transported in a 30-L cooler. Surface water was collected in 20-L plastic carboys on 12 July and 11 August 2005. Two collection dates were used to obtain an adequate volume of water because of space and weight limitations in the helicopter. All samples were collected from a rowboat at the mid-lake marker and transported by helicopter and truck back to the University of Alberta within 12 hours. Samples were then stored in a growth chamber at $8°C$ until the experiment was set up.

A randomized three-factor experimental design was replicated four times for a total of thirty-two 8-L glass aquaria in a growth chamber at the University of Alberta. Ambient conditions were set at a temperature of $8°C$ and a 12-h light/dark cycle. Half of the aquaria received 500 mL of lake sediment prior to lake water addition, an amount based on the methods of Holzapfel and Vinebrooke (2005). Aquaria with sediments simulated pond habitat while the sediment-free aquaria mimicked lake habitat. Water from Pipit Lake was filtered through a 63-μm sieve, and 3 L of July water combined with 3 L of August water was added to each of the 20 aquaria to standardize the water chemistry among all microcosms. An initial water sample was taken from each aquarium and filtered through a GF/F glass-fiber filter (0.45 μm pore size) and was frozen for future analysis. Due to high sediment resuspension, the aquaria were left untouched for three days to allow for the sediment to settle.

To simulate atmospheric nitrogen deposition, 1000 μg of NO_3-N as KNO_3 dissolved in 50 mL of double deionized water was added to the nitrogen-amended aquaria. The 1000 μg increase in NO_3-N concentration was chosen to be consistent methodologically with other atmospheric nitrogen addition experiments performed in the Rocky Mountains (Nydick et al., 2004). The
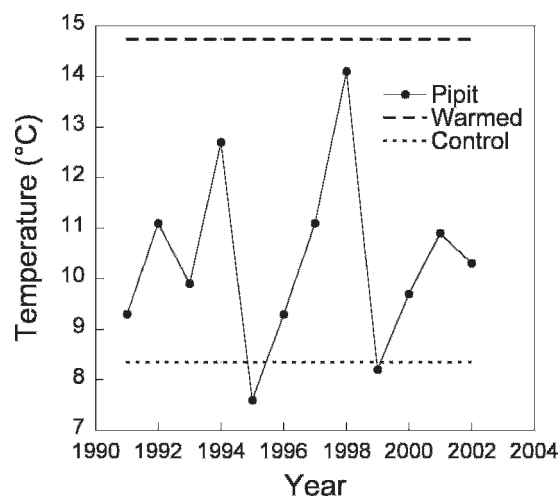

FIGURE 1. Yearly maximum surface water temperatures of Pipit Lake (Brian Parker and David Schindler, University of Alberta. unpublished data) compared with the mean temperatures of the control and warmed aquaria.

nitrogen amendment resulted in a final concentration of about 1200 μg L^{-1}, estimated from the measured total dissolved nitrogen (TDN) in the initial water plus the added 1000 μg L^{-1}. The non-amended aquaria received 50 mL of double deionized water to standardize water levels. Ambient TDN concentrations fluctuate between 25 and 560 μg L^{-1} in Pipit Lake during the ice-free season (Vinebrooke and Leavitt, 1999a; unpublished data).

Twenty adults of *D. middendorffiana* and *H. arcticus* were added to each aquarium. Zooplankton were allowed to acclimate overnight before the warming treatment of $6°C$ was applied. Ambient ($8°C$) and warmed ($14°C$) temperatures simulated the coldest and warmest maximum surface water temperatures recorded in Pipit Lake between 1991 and 2002 (Fig. 1). Warming was achieved using 50-W thermostat-controlled aquaria heaters (Big Al's, Woodbridge, Ontario, Canada). Water temperature was measured using a handheld alcohol thermometer (Fisher Brand, Nepean, Ontario, Canada). In addition, temperature was measured at 1 hour intervals using StowAway® TidbiT® thermal probes (Onset Computer, Pocasset, Massachusetts, U.S.A.) in two of the controls, and all of the warmed aquaria. The experiment ran for 34 days to provide adequate time for the *D. middendorffiana* to produce at least one cohort, enabling measurement of reproductive response (Holzapfel and Vinebrooke, 2005). Aquaria temperatures were monitored daily, and heaters were adjusted as needed. To account for evaporation losses, double deionized water was added, when necessary, to maintain a 6-L volume in each aquarium.

Adult *D. middendorffiana* and total *H. arcticus* individuals were used as a measure of survival since these individuals were added at the beginning of the experiment. Juvenile *D. middendorffiana* were used as a measure of *Daphnia* reproduction since these individuals were a product of reproduction over the course of the experiment. Copepod fecundity was calculated as the average number of eggs per female *H. arcticus*.

SAMPLING PROTOCOL

On day 34, 1 L of water from each aquarium was filtered using a GF/F glass-fiber filter (0.45 μm pore size) to concentrate phytoplankton. The filtrate as well as the initial water sample were tested for TDN and total dissolved phosphorous (TDP) according
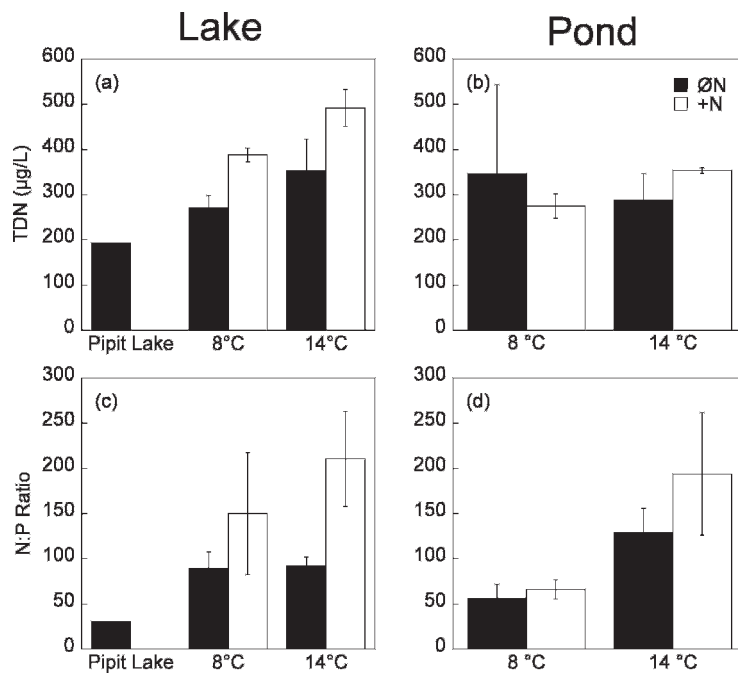
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FIGURE 2. Average concentrations of total dissolved nitrogen (TDN) (a, b) and N:P ratios (c, d) calculated from TDN and total dissolved phosphorous (TDP) in each treatment at the end of the experiment in simulated lake (no sediments) and pond (sediments) habitats. ØN refers to the treatments with no added nitrogen. +N refers to the treatments with 1000 µg N-NO$_3$ L^{-1} added. The bar for Pipit Lake represents the concentration of the combined water from July and August sampling dates that was used in the experiment. Error bars show 1 standard error ($n = 4$ except for 8°C with nitrogen in the lake habitat where $n = 2$, and 12°C with nitrogen in the pond habitat where $n = 3$).

to the University of Alberta, Biogeochemical Analytical Laboratory procedures. The filter papers were then frozen before being analyzed for pigments using standard HPLC procedure (Vinebrooke and Leavitt, 1999a, 1999b). Five mL of water was collected and preserved with Lugol's solution to be analyzed qualitatively for algal species under an inverted Leica DM-IRM microscope (Leica Mikroskopie und Systeme GmbH, Heerburg, Switzerland) to confirm the results of the HPLC analysis. The remaining water was then filtered through a 63-µm stainless steel sieve to collect all live zooplankton, which were preserved in 95% ethanol.

Enumeration of *H. arcticus* including maximum body length, sex, and egg number was performed using a Leica MZ9.5 dissecting scope (Leica Mikroskopie und Systeme GmbH, Heerburg, Switzerland) and a connected Micropublisher 3.3 digital camera (Qimaging™, Burnaby, British Columbia, Canada). Images were analyzed using Openlab™ version 3.1.5. software (Improvision® Inc., Lexington, Massachusetts, U.S.A.). *D. middendorffiana* were measured for maximum body length and separated into adult and juvenile classes using a boundary of 1500 µm in length, which seemed to be a natural division between adults and juveniles. A similar division was used by Beisner et al. (1997) when classifying *Daphnia pulex*. Copepod fecundity was calculated from the average number of eggs per female in each aquarium. Due to measurement problems encountered, absolute number of zooplankton rather than biomass was used; many *D. middendorffiana* ruptured when preserved in the ethanol, so any biomass calculations made from these measurements would be flawed. However, we feel that these measurements were sufficiently accurate to maintain the size distinction between juvenile and adult *D. middendorffiana*. Two of the warmed, nitrogen amended aquaria with no sediment were removed from the final analysis because of contamination.

STATISTICAL ANALYSIS

All zooplankton, pigment, and nutrient data were log$_{10}$-transformed to improve homogeneity of variance and normality

before being analyzed using three-factor analysis of variance tests (ANOVA) to test for between-treatment and interactive differences. Subsequent two-factor analyses of variance were conducted to examine the effects of two environmental factors in isolation from the third factor. A multivariate ANOVA (MANOVA) was conducted to determine between-treatment and interactive differences in the taxonomic species composition. Correlation analyses related zooplankton biomass and chlorophyll-inferred phytoplankton abundance. Statistics were analyzed using SPSS v.11.0.4 (SPSS Inc., 2005).

Results

TREATMENTS

The warming treatment averaged 14.74°C (SE = 0.0098, $n = 32,560$), while the ambient temperature averaged 8.35°C (SE = 0.0093, $n = 3307$), a difference of 6.39°C (Fig. 1). The initial TDN concentration in water from Pipit Lake was 194 µg L^{-1} with a TDN:TDP ratio of 31 (Fig. 2). Although nitrogen amendments increased TDN and TDN:TDP values (Fig. 2), the direct effects of fertilization were not significant (TDN, $F_{1,21} = 2.92$, $P = 0.11$; TDN:TDP, ($F_{2,10} = 3.52$, $P = 0.075$). However, nitrogen addition in the absence of sediments increased significantly the TDN concentration at the end of the experiment to an average of 458 µg L^{-1} ($F_{1,10} = 5.91$, $P = 0.035$) with an average TDN:TDP ratio of 180, while the ambient nitrogen treatment averaged 312 µg L^{-1} with an average TDN:TDP ratio of 90.78. The TDN:TDP ratios were based on weight and are a conservative estimate of nitrogen limitation compared to the suggested measure using DIN:TDP (Morris and Lewis, 1988); therefore, limitation and co-limitation would occur at higher values than those suggested by the Redfield ratio (Redfield, 1958). Warming significantly increased the TDN:TDP ratios ($F_{1,21} = 7.69$, $P = 0.011$), a result driven by the pond aquaria containing sediment. Visual observation showed that the pond aquaria remained turbid relative to the lake aquaria during the experiment.
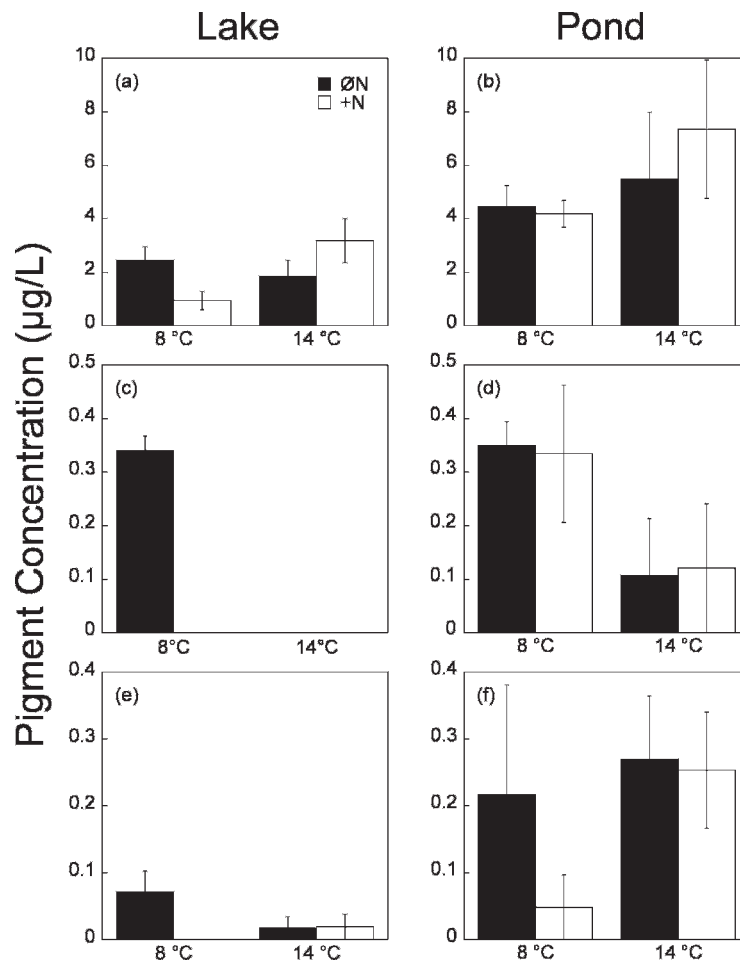
FIGURE 3. Average concentration of chlorophyll *a* (a, b), chlorophyll *b* (c, d), and chlorophyll *c* (d, e) at the end of the experiment in simulated lake (no sediments) and pond (sediments) habitats. ØN refers to the treatments with no added nitrogen. +N refers to the treatments with 1000 μg N-NO$_3$ L^{-1} added. Error bars show 1 standard error ($n = 4$ except for 8°C with nitrogen in the lake habitat where $n = 2$, 12°C with no nitrogen amendment in the pond habitat where $n = 3$, and 12°C with nitrogen in the pond habitat where $n = 3$).

PHYTOPLANKTON

The expected positive effect of nitrogen on chlorophyll *a*-inferred total phytoplankton abundance occurred only under warmed conditions (temperature-nitrogen interaction; $F_{1,20} = 4.75$, $P = 0.042$; Fig. 3). In addition, sediments significantly doubled chlorophyll *a* levels in the pond aquaria (sediment effect, $F_{1,20} = 22.14$, $P<0.001$; Fig. 3). Also, the pigment-inferred community composition of phytoplankton was significantly altered by the experimental treatments (MANOVA, temperature-nitrogen-sediment interaction, $F_{7,14} = 6.64$, $P<0.001$). Warming significantly suppressed only the chlorophyll *b*-inferred biomass of green algae (Fig. 3; temperature effect; $F_{1,20} = 14.47$, $P<0.001$), which were more abundant in the pond aquaria (sediment effect; $F_{1,20} = 7.31$, $P = 0.14$). Sediments also increased significantly the chlorophyll *c*- and fucoxanthin-inferred abundance of golden-green algae (Fig. 3; sediment effect; $F_{1,20} = 9.51$, $P = 0.006$). Use of light microscopy confirmed qualitatively the pronounced abundance of large colonial golden-green algae (*Dinobryon* spp.) in the pond aquaria.

ZOOPLANKTON

Warming also generated a significantly positive effect of nitrogen on *D. middendorffiana*, including both adults (warming-nitrogen interaction; $F_{1,22} = 11.39$, $P = 0.003$) and juveniles ($F_{1,22} = 6.74$, $P = 0.016$) (Fig. 4). However, warming suppressed the abundance of adult and juvenile daphnid in the pond aquaria (warming-sediment interaction; $F_{1,22} = 77.54$, $P<0.001$; Fig. 4).

In contrast, the presence of sediment caused a significant increase in the abundance of *H. arcticus* ($F_{1,22} = 8.11$, $P = 0.009$) and its fecundity ($F_{1,22} = 9.74$, $P = 0.005$) (Fig. 5). Although warming reduced fecundity ($F_{1,22} = 15.89$, $P<0.001$), it did not affect the abundance of adult copepods (Fig. 5). None of the measured variables of *D. middendorffiana* were significantly correlated with algal pigments, while the abundance of adult copepods was positively correlated with chlorophyll *a* ($P = 0.005$), *b* ($P = 0.010$), and *c* ($P = 0.008$).

Discussion

Our findings demonstrated that the effects of warming and nitrogen differ both between trophic levels and aquatic alpine habitats. The results supported our first hypothesis concerning the synergistic positive effect of warming and nitrogen on phytoplankton abundance, which was best attributed to a direct physiological response. Our second hypothesis was partially supported as warming and nitrogen suppressed the herbivorous *D. middendorffiana,* but only under pond conditions. Therefore, these results did not support our third hypothesis because sediments did not mediate against the effects of either warming or nitrogen amendments. Instead, the presence of sediments in pond aquaria increased the abundance of phytoplankton and the planktonic omnivore *H. arcticus*, while suppressing herbivores. Further, these stressors did not reduce the abundance of omnivores; however, warming did reduce their fecundity. Below, we offer potential explanations for these findings.
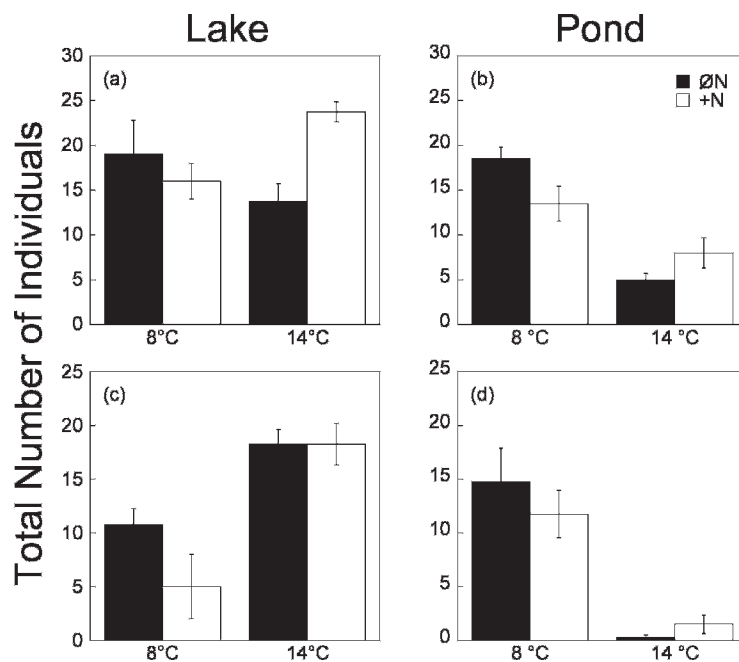
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Lake

Pond

FIGURE 4. Total number of adult (>1500 μm in length) (a, b) and juvenile (<1500 μm in length) (c, d) *Daphnia middendorffiana* in each treatment in simulated lake (no sediments) and pond (sediments) habitats at the end of the experiment. ØN refers to the treatments with no added nitrogen. +N refers to the treatments with 1000 μg $N\text{-}NO_3$ L^{-1} added. Error bars show 1 standard error ($n = 4$ except for 8°C with nitrogen in the lake habitat where $n = 2$).

ABIOTIC EFFECTS OF WARMING AND FERTILIZATION

Our temperature treatment reflected the inter-annual variability of surface water temperatures in Pipit Lake. Therefore, plankton can experience these cold and warm temperatures in alpine lakes, but over a longer time scale than captured by our experiment. Nevertheless, more extreme summer heating and freezing events typically occur diurnally in smaller alpine ponds because they closely track ambient air temperatures during the ice-free season (e.g., Strecker et al., 2004; McMaster and Schindler, 2005). Thus, our temperature treatment represented an intermediate level of thermal stress relative to that found in more thermally stable alpine lakes and highly variable, warmer ponds.

Nitrogen concentrations remained elevated only in the amended aquaria that lacked sediments. A potential explanation for the lack of a significant fertilization of the pond aquaria is that the sediments absorbed the added nitrogen (Reddy et al., 1996). Therefore, atmospheric nitrogen deposition is expected to have a greater impact on planktonic communities in lakes because of increased bioavailability of the nutrient in the water column. Furthermore, lower TDN:TDP ratios in the warmed pond aquaria likely resulted from increased microbial release of phosphorus from the sediments (Schallenberg and Burns, 2004).

PHYTOPLANKTON RESPONSES

Warming stimulated the fertilizing effect of nitrogen on alpine phytoplankton abundance. This response reflects how assimilation of nutrients by phytoplankton differs as a function of temperature (e.g., Tilman et al., 1986). Phytoplankton assimilate nitrates via nitrate reductase, and fixes dissolved gaseous nitrogen using nitrogenase, which are both enzymes that are stimulated by
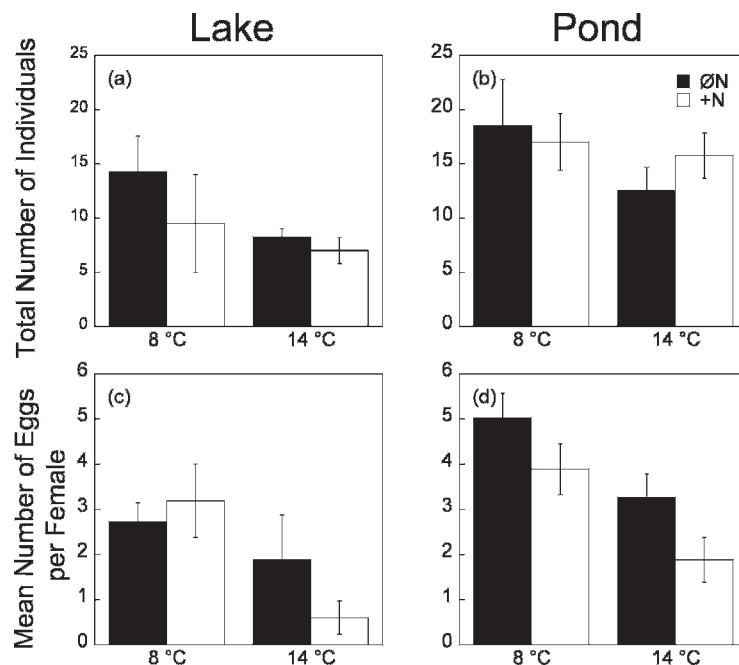
Lake

Pond

FIGURE 5. *Hesperodiaptomus arcticus* abundance (a, b) and average number of eggs per female (c, d) in each treatment in simulated lake (no sediments) and pond (sediments) habitats at the end of the experiment. ØN refers to the treatments with no added nitrogen. +N refers to the treatments with 1000 μg $N\text{-}NO_3$ L^{-1} added. Error bars show 1 standard error ($n = 4$ except for 8°C with nitrogen in the lake habitat where $n = 2$).

warming (Davison, 1991; Seefeldt et al., 2004). Therefore, cold alpine conditions may impair the ability of phytoplankton to assimilate these inorganic forms of nitrogen. Our alternate hypothesis that warming enhanced phytoplankton abundance by suppressing grazing pressure was not supported owing to the lack of a significant negative correlation between the abundance of the primary herbivore *D. middendorffiana* and chlorophyll *a*. In addition, the positive correlation between *H. arcticus* abundance and chlorophyll *a* suggested that this consumer had a positive effect on phytoplankton biomass, possibly by enhancing nutrient recycling via feeding activity.

The positive direct effect of sediments on chlorophyll-inferred phytoplankton abundance was primarily attributable to release from phosphorus limitation. This explanation is supported by final N:P ratios, which were lower in the presence of sediments. Rapid biological uptake of phosphorus in natural waters (Hudson et al., 1999) further suggests that these final values represent only a small fraction of the phosphorus that was released from the sediments during the experiment. Immigration of sediment-dwelling algae into the water column (Hansson, 1996) could also have contributed to phytoplankton abundance.

Our experimental manipulations also collectively exerted a highly significant net impact on phytoplankton community composition. This finding involved the differential responses of three major algal groups, namely cyanobacteria, green, and golden-green algae. Warming suppressed the chlorophyll *b*-inferred abundance of chlorophytes, especially in the absence of sediments. This finding agreed with a previously reported negative effect of warming on large filamentous green algae in alpine ponds (Strecker et al. 2004). However, we did not detect a significant positive effect of nitrogen on green algae as reported elsewhere by Lafrancois et al. (2004), possibly owing to species composition differing between the two study sites.

ZOOPLANKTON RESPONSES

Positive interactive effects of warming and nitrogen on the abundance of both phytoplankton and daphnids suggested that these herbivores had benefited from increased food availability. However, this increase in herbivore abundance did not generate an overall negative consumptive impact of phytoplankton biomass (i.e., weak grazing pressure). Thus, our hypothesis that warming would result in overexploitation of the food source was not supported, possibly owing to the low density of herbivorous zooplankton. Therefore, we did not observe a warming- or nitrogen-induced shift towards inedible algal species as reported by Lafrancois et al. (2004) and Nydick et al. (2004).

In addition, the positive temperature-nitrogen impact on daphnid juveniles can be attributed to the direct stimulatory effect of warming on reproduction. In general, zooplankton growth rates increase with temperature even though fecundity often declines (Moore et al., 1996); the overall result is an increase in reproduction because of acceleration of generation times and developmental rates (Gillooly, 2000). Supporting this theory, we noticed multiple reproductive events in many of the warmed aquaria during the experiment.

In contrast, warming suppressed the fecundity of adult copepods while not increasing their mortality. Copepods are known to reproduce slowly especially under low temperatures and they often respond to environmental changes by going into diapause (Williamson and Reid, 2001). Consequently, copepod population responses to environmental change are relatively difficult to detect in the short term. For instance, Strecker et al.

(2004) also did not detect a significant difference in adult copepod abundance between ambient and 3.6°C-warmed alpine ponds over a 50-d period. However, a more pronounced warming of 7°C did suppress adult *H. arcticus* during a 28-d experiment (Holzapfel and Vinebrooke, 2005), demonstrating the potential lethality of extreme summer heating events. Further, our finding of decreased copepod fecundity under warmed conditions highlights the potential long-term detrimental impacts of warming on copepod abundance in alpine systems.

The presence of sediments exerted contrasting effects on daphnids and copepods. A possible explanation for the negative effect of sediments on daphnids in the warmed aquaria involved suspended sediments interfering with the filter-feeding apparatus of this generalist herbivore (Levine et al., 2005). Conversely, the positive effect of sediments on copepod survival and fecundity was likely attributable to these raptorial feeders experiencing increased food availability in the form of sediment-dwelling algae and other microbes.

Conclusion

Although many studies have interpreted that recent climate change and atmospheric nitrogen deposition have directly altered alpine (Saros et al., 2003) and arctic (Wolfe et al., 2006) phytoplankton communities, our results highlight that environmental change could also affect higher trophic levels, thereby generating potential indirect effects on primary producers via altered trophic interactions. The spatial and temporal scales of our experimental findings best demonstrate the potential short-term impacts of warming and nitrogen on planktonic processes rather than net annual production in fishless alpine ecosystems. The observed differential responses of daphnids and copepods to environmental change indicate that global change could fundamentally alter the dynamics of grazing in alpine lakes and ponds. The warming- and nitrogen-induced taxonomic shift from raptorial-feeding copepods to more effective filter-feeding daphnids could alter both energy transfer to higher trophic levels (e.g., planktivorous fish), and various aspects of water quality in alpine lakes.

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