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Effects of warming on benthic communities in a boreal lake: Implications of climate change

H. M. Baulch[1] *and D. W. Schindler*
Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

M. A. Turner, D. L. Findlay, and M. J. Paterson
Department of Fisheries and Oceans, 501 University Cres., Winnipeg, Manitoba R3T 2N6, Canada

R. D. Vinebrooke[2]
Department of Biology, University of Regina, Regina, Saskatchewan S4S 0A2, Canada

Abstract

We experimentally warmed a series of shallow enclosures by 4.5°C and measured responses of the epilithon (biofilm on rocky surfaces) and invertebrates. Maximum rates of net photosynthesis increased by 28–115% and rates of dark respiration increased by 29–103% as a result of warming. Long-term analyses using data from unmanipulated Lake 239 corroborated these findings, showing that rates of light-saturated photosynthesis and dark respiration were positively correlated with water temperature. Warming effects differed between communities (on natural and tile substrates, as well as well-developed and early successional communities). Warming consistently led to increased bacterial cell densities, but increases in total algal biovolume and diatom biovolume were seen only in an early successional tile community. Effects on the composition of the invertebrate community (studied only on well-developed tile biofilms) were small. We observed warming-related increases in carbon accrual within one community, and late in the experiment observed a change in carbon : phosphorus ratios of another community, possibly indicative of a degradation of food quality. Our study suggests that climate warming effects on epilithic community composition are likely to be heterogeneous and difficult to predict; however, the agreement between long-term and experimental results suggests that increased temperatures will increase metabolic rates of the epilithon.

Humans have altered the thermal regime of rivers, ponds, and lakes by diverting water, creating impoundments, harvesting forests, and releasing heated effluents. Although these alterations are local in scale, the threat of global warming is ubiquitous. Current climate models predict that global surface temperatures will increase by 1.4°C to 5.8°C between 1990 and 2100 (Intergovernmental Panel on Climate Change 2001). Corresponding to this change, surface water temperatures of stratified lakes in the Precambrian Shield and Laurentian Great Lakes regions are expected to rise by 1–7°C (Magnuson et al. 1997). Relatively little is known about thermal responses of littoral communities, despite their importance as an energy source to higher trophic levels in most lakes (Hecky and Hesslein 1995; Vander Zanden and Vadeboncoeur 2002).

Studies of phytoplankton cultures have shown that temperature sets an upper limit for photosynthetic rates (Davison 1991). Effects of temperature on benthic metabolism have received less attention. Optimum temperatures for photosynthesis also vary among algal species, which suggests that taxonomic shifts induced by increased temperatures could lead to increased photosynthetic rates (DeNicola 1996). If algal biovolume increased as a result of warming, this too could contribute to increased photosynthetic rates. Respiration rates of the epilithon (biofilm on rocky surfaces) depend upon the cumulative respiration rates of four major community constituents: algae, bacteria, fungi, and invertebrates. Each of these groups has shown increased respiration with increased temperature (e.g., Graham et al. 1996; Höckelmann and Pusch 2000; Pomeroy and Wiebe 2001). As a result, increased benthic respiration is expected because of warming.

The taxonomic composition of epilithic algal communities may be affected by many factors including temperature,

[1] Present address: Department of Environmental and Resource Studies, Trent University, 1600 West Bank Drive, Peterborough, Ontario K9J 7B8, Canada.

[2] Present address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

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light, nutrient availability, pH, competition, grazing, and wave action. In general, temperatures below 20°C are expected to favor diatoms. Chlorophytes generally dominate at temperatures between 15°C and 30°C and cyanobacteria are favored at high temperatures (reviewed by DeNicola 1996). In addition, warmer waters (within an optimal range) are expected to lead to increased algal growth rates (Finlay et al. 2001) and higher algal biomass (Gruendling 1971). Increases in spring water temperatures of 3–4°C have been predicted to lead to stimulation of algal growth rates by approximately 40% (Finlay et al. 2001). However, higher grazing rates may moderate these responses (e.g., Beisner et al. 1997; Petchey et al. 1999).

Increased temperatures are expected to directly stimulate bacterial growth rates (Edwards and Meyer 1986) and lead to higher bacterial abundance (Lamberti and Resh 1983). Warming may also indirectly affect bacterial abundance. For example, higher algal biomass may increase the amount of substrate available to bacteria, allowing increased growth. In contrast, stimulation of grazing rates by increased water temperatures (Dumont and Schorreels 1990) could directly reduce bacterial abundance. Increased grazing, however, could increase the availability of dissolved organic matter to bacteria and thus indirectly lead to greater bacterial abundance (del Giorgio and Scarborough 1995; Møller and Nielsen 2001).

Studies of thermal pollution and controlled experimental studies have shown that warming leads to a decline in the abundance of many consumers (Petchey et al. 1999) including species of benthic macroinvertebrates in streams (Ferguson and Fox 1978; Lamberti and Resh 1983; Hogg and Williams 1996) and meiofauna in a reservoir (Oden 1979). Declines in the abundance of Ephemeroptera, Hemiptera, Odonata, and Trichoptera have been observed in warmed areas of lakes (Ferguson and Fox 1978). In contrast, the abundance of ostracods and gastropods has been shown to increase in warmed ponds (McKee et al. 2003), whereas responses of dipterans to warming have been variable (Ferguson and Fox 1978; Hogg and Williams 1996). Zooplankton responses are also varied. Strecker et al. (2004) found that warming of shallow alpine ponds by 3.6°C led to a reduction in zooplankton biomass due to a decline in large cladocerans. However, in more biologically diverse temperate experimental ponds, McKee et al. (2003) found no effect of a 3°C warming on large cladocerans.

Warming-induced changes in food quality may contribute to the effects of increased temperatures on invertebrates. Changes in algal nutrient quotas (Goldman 1979; Rhee and Gotham 1981), nutrient uptake rates (Rhee and Gotham 1981), rates of carbon (C) fixation, or growth rates (Chalup and Laws 1990) have resulted from changes in water temperature. The temperature dependence of algal nitrogen (N) to phosphorus (P) (Goldman 1979) and C : N ratios (Thompson et al. 1992) has been illustrated in culture studies of single species, but has not been studied in benthic communities. In addition to algae, other components of the epilithon could contribute to a change in stoichiometry via changes in their abundance or nutrient content.

In this study we investigated how increased water temperatures, within the range of climate change predictions, affected epilithon. Specifically, we studied effects on epilithic metabolism and community composition, including effects on bacteria, algae, invertebrates, carbon accrual, and stoichiometry. An in situ heating experiment was used to study the effects of warming on the composition and metabolism of the epilithon. Complementary long-term data collected in the same lake over a 24-yr period were used to determine whether metabolic rates were correlated with temperature. The experiment used both the natural bedrock community and two communities on artificial substrates (well-developed and early successional), although in some cases response variables were measured for only one or two of the communities. The long-term study used only the natural bedrock community.

We hypothesized that: (1) experimental warming would stimulate respiration and light-saturated photosynthetic rates and result in metabolic rates being positively related to temperature in the long-term data. We performed experiments to determine whether changes in rates of photosynthesis and respiration were attributable to temperature effects, changes in composition of the epilithon, or both; (2) warming would lead to increases in bacterial cell densities (Lamberti and Resh 1983); (3) total algal biovolume would increase as a result of warming. An increase in chlorophyte biovolume and a decline in diatom biovolume were predicted. We expected this increase in algal biovolume to lead to an increase in the proportion of epilithic C contained within algal cells; (4) warming would suppress total invertebrate abundance (Oden 1979; Lamberti and Resh 1983) and alter community composition (Ferguson and Fox 1978; Oden 1979); (5) warming would alter epilithic stoichiometry as a result of altered algal nutrient composition (Goldman 1979; Rhee and Gotham 1981). In conjunction with stoichiometry, we anticipated that areal C accrual would increase as a result of increased algal photosynthesis; (6) warming would have more pronounced effects during the early stages of biofilm development when cells within a thinner biofilm have greater access to light and nutrients.

Materials and methods

Long-term data analyses—The long-term study was performed in reference lake 239 (L239) at the Experimental Lakes Area in northwestern Ontario (49°40′N, 93°44′W). L239 is a clear, oligotrophic lake with a narrow littoral zone dominated by bedrock, boulders, and sand. The average length of the L239 ice-free season (1981–2002) was 203 d, and average water temperature at 1 m from May to October (1981–2004) was 16.1°C. Epilithic metabolism data were collected from 1981 to 2004 during the open-water season, although sampling from 1996–1998 and 2000–2004 was restricted to the months of July and August. No sampling was performed in 1999. Metabolic incubations were performed in the middle littoral zone, at depths of approximately 0.5–2.5 m (average = 1.5 m). Concurrent measurements of surface irradiance were made during the incubations (Li190SA Li-Cor quantum cosine sensor).

Measurements of net photosynthesis were made in clear acrylic chambers that sealed to the bedrock substrate. De-

cline in dissolved inorganic carbon (DIC) within the chambers (on the basis of initial and final measurements) was normalized to the surface area of the bedrock and the duration of the incubation to obtain measurements of photosynthetic rates (Turner et al. 1987, 1991). In 1981 and 1982, incubations were performed in 0.85-liter acrylic chambers that sealed to the substratum and enclosed 200 cm^2 of bedrock. Subsequent incubations were performed in smaller chambers (0.43 liter) that enclosed 100 cm^2 of bedrock. Incubations were approximately 1.5 h long. Rates of dark respiration were measured in the same manner, but by measuring release of DIC by communities within black acrylic chambers. Concentrations of DIC were measured in acidified samples using an infrared gas analyzer (Li-Cor model LI-6252).

We used measurements of the attenuation coefficient and surface irradiance to calculate irradiance at depth, and restricted our analyses to data that reflected rates of light-saturated photosynthesis. Turner et al. (1991) estimated 200 μmol quanta m^{-2} s^{-1} to be the threshold for light-saturated photosynthesis for natural epilithic communities in L239 at these study depths. We recognize that this threshold may vary with environmental conditions and community change; however, it excludes measurements that were most likely to reflect light limitation. In approximately 5% of respiration incubations, low rates of C uptake were measured. These measurements were assumed to reflect experimental error at low respiration rates and set to zero for subsequent calculations. The alternative approach of excluding these data from our analyses had a minimal effect on the r^2 values.

Typically, three replicate incubations were performed for both photosynthesis and respiration. The respective means were used in the analyses, with the considerations noted earlier. The Pearson coefficient of determination (r^2) was used to measure the correlation between temperature and metabolic variables on 128 dates. All analyses were performed in SYSTAT 8.0.

Experimental study

Heat treatment—The effects of a 4.5°C temperature increase on the epilithon were studied using eight 700-liter enclosures constructed along the western shore of L239. Four enclosures were heated for 8 weeks (3 August 2000–27 September 2000) using a closed circulation heat-exchange system (Baulch et al. 2003), and four were maintained as controls at near-ambient lake temperatures. The experiment was set up using a randomized-block design, with adjacent enclosures designated as blocks to minimize the effects of spatial heterogeneity along the lakeshore.

The enclosures were made of woven polyethylene (Canfab Products) with an external wooden frame. All enclosures were 1.4 m × 1.4 m, with sloping bottoms that approximately paralleled the bedrock slope. Enclosures were 0.5 to 0.6 m tall on the shallow side and 0.7 m tall on the deeper side. They were uncovered, but the benthic communities were subject to shading from the walls for part of the day. The mean depth at the middle of the enclosures was 0.5 m. To minimize heat loss, enclosure walls were insulated with

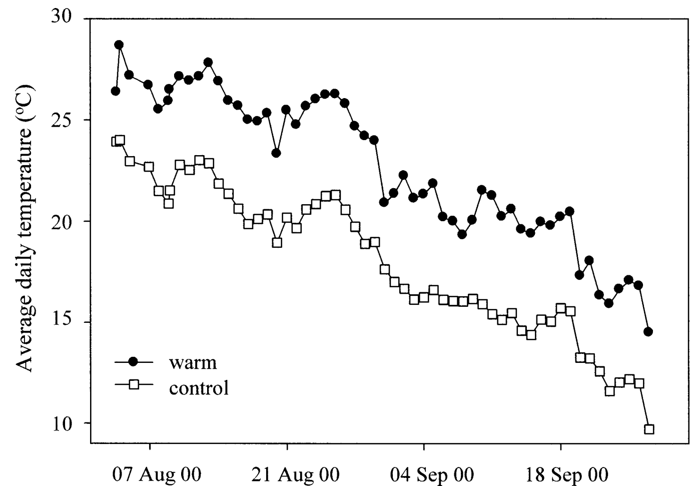

Fig. 1. Average daily temperatures in warmed and control enclosures during the experiment.

closed-cell foam (Shippers Supply). Enclosures were open to the bottom to allow colonization of artificial substrata by natural communities, and the enclosures were secured by placing sandbags on a 0.7-m-wide skirt. Some water exchange between the lake and the enclosures occurred because of an incomplete seal at the bottom. The water renewal time of the enclosures at the end of the experiment was estimated as 5.6 d (Baulch 2002).

The heat treatment was established by pumping hot water through a 10-m coil of 1.3-cm internal diameter heat exchange pipe (Kitex Al-pex, Ipex) installed in the bottom of each warmed enclosure. There was no water exchange between the heating system and the enclosures. Heat exchange pipes were also placed in control enclosures, but were not connected to the heating system. Temperature was controlled electronically, with the exception of a period from 30 August 2000 to 7 September 2000 when the system was incapacitated by lightning. Temperature was controlled manually during this period until repairs could be completed. Water temperatures were monitored every 15 min in each enclosure and in the lake using continuously recording thermocouples (HoboTemp, Onset). Maximum average temperatures were observed shortly after the initiation of the experiment and declined thereafter, reaching minimum temperatures of 9.3°C in control enclosures and 14.3°C in warmed enclosures on the final date of the experiment (Fig. 1; Baulch et al. 2003). Temperatures within control enclosures were slightly cooler than in adjacent areas of the lake because of shading from the enclosure walls (Baulch et al. 2003). Diurnal temperature variation was considerable; however, patterns of temperature variation within warmed enclosures paralleled the patterns observed within control enclosures. Average temperatures in warmed enclosures over the course of the experiment were 22.5°C, and were 18°C in control enclosures. Average deviation of individual control enclosures from the mean (measured at 15-min intervals) was 0.3°C. In warmed enclosures, this was 0.6°C, owing to a large degree to the lightning strike. A more detailed description of the heating system and its performance is included in Baulch et al. (2003).

Water chemistry within enclosures was monitored approx-

Table 1. Sampling dates for community and metabolic variables. Bolded dates indicate the dates on which exchange experiments were performed concurrently with regular sampling. The year, unless otherwise indicated, is 2000.

	Early successional tiles (experimental)	Precolonized tiles (experimental)	Natural bedrock substratum (experimental)	Natural bedrock substratum (long-term data)
Photosynthesis		13, 16 Aug		1981–2004
		22, 23 Aug		
		13 Sep		
		21 Sep		
Photosynthesis–irradiance experiment		30 Aug		
Respiration		14, 17 Aug		1981–2004
		25, 26 Aug		
		11, 12 Sep		
		22 Sep		
Stoichiometry, C accrual	16 Sep	05 Aug	25 Sep	
		14, 17 Aug		
		25, 26 Aug		
		13 Sep		
		22 Sep		
Algae	16 Sep	05 Aug		
		25, 26 Aug		
		22, 24 Sep		
Bacteria	16 Sep	05 Aug	25 Sep	
		25, 26 Aug		
		22, 24 Sep		
Invertebrates		19 Sep		

imately every second week (dip samples). Water samples (integrated epilimnetic samples, or samples from a depth of 1 m) overlying the deepest part of the lake were also obtained biweekly, and water chemistry was analyzed according to Stainton et al. (1977).

Experimental study communities—Epilithon was studied on both unglazed ceramic tiles and the natural bedrock substrata. Before placement, the tiles (23 cm^2—approximately 200 per enclosure) were combusted at 600°C for a minimum of 1 h, scrubbed, soaked in dilute hydrochloric acid overnight, thoroughly rinsed with deionized water, and dried. To minimize differences between the tile community and the natural epilithon, tiles were precolonized in L239 for 8 weeks before the start of the experiment, when they were transferred to the enclosures. Tiles were placed a minimum of 10 cm away from the heat exchange pipes to minimize the influence of the thermal gradient and of the thermophilic pipe community on our study communities (Baulch et al. 2003).

Additional colonization experiments were performed to determine whether warming effects on early successional tile communities differed from effects on more mature (precolonized) tile communities. We placed bare tiles in the enclosures on 19 August 2000. After 4 weeks of colonization, tiles were harvested and processed.

The natural bedrock substratum within enclosures was sampled near the end of the experiment (25 September 2000) to assess warming effects on this community. Samples of epilithon were obtained from areas that were not visibly disturbed and were located a minimum of 10 cm from the heating pipes. Samples of epilithon were obtained from bedrock using a scraping brush sampler (Turner et al. 1991) and three or four scrapings (5 cm^2 per scraping) from each sampling site were combined.

Epilithic metabolism—experimental—Rates of net photosynthesis and community dark respiration were measured on the precolonized tiles. Eight randomly selected tiles were gently placed in acrylic trays and transferred into 0.41-liter (23 × 11.5 × 2.5 cm with 23 × 11.5 × 0.6-cm inserts) chambers containing lake water. Photosynthetic chambers were constructed of OP4 acrylic and chambers for measurement of dark respiration were made with black acrylic. Incubations were performed within the enclosures in the morning and lasted approximately 90 min. Two incubations for each parameter (two chambers of eight tiles each) were performed in each enclosure, and the mean of the two measurements was used in subsequent analyses, for a total of four replicates (one per enclosure) per treatment. Metabolic rates were measured by monitoring changes in DIC as in the long-term data (Turner et al. 1987, 1991). Photosynthetic incubations were performed only on high-light days, and were intended to reflect rates of light-saturated photosynthesis. Irradiance in the chambers was 310–850 μmol quanta m^{-2} s^{-1} during the photosynthetic incubations.

Photosynthesis and respiration incubations were made during four periods of the experiment (Table 1). Photosynthesis and respiration incubations were always performed on different days, but the same tiles were used, and later processed for particulate analyses. Generally, incubations for photosynthesis were split between 2 d, as were incubations for respiration. However, we minimized resulting temporal variability by ensuring that entire blocks were always sampled on the same day. The plotted date (e.g., Fig. 2) corresponds to the first date (Table 1).

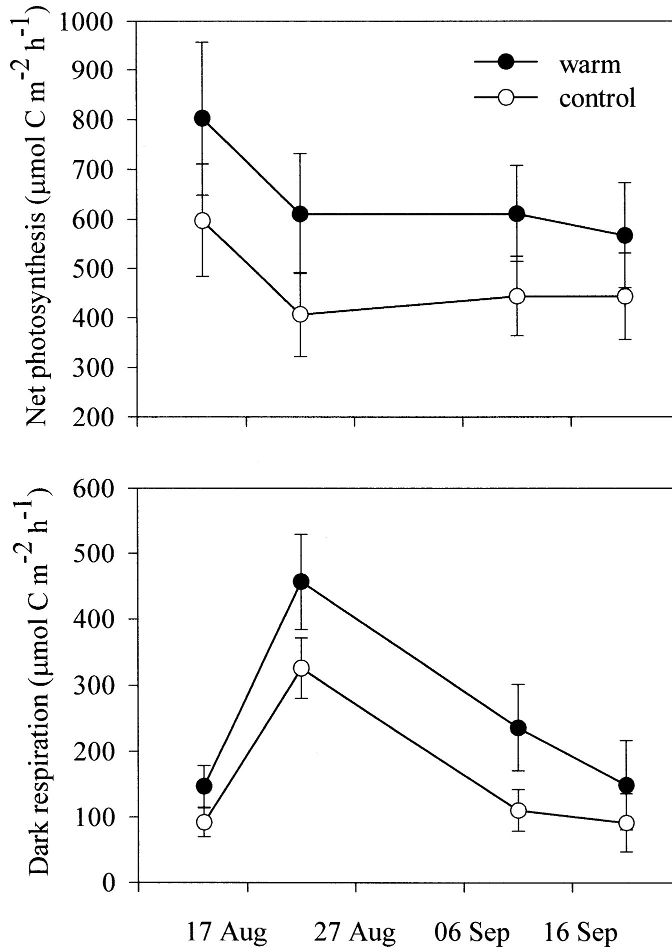

Fig. 2. Rates of net photosynthesis and dark respiration in warm and control enclosures (on precolonized tiles). Error bars show ±1 standard error.

To determine whether the heat treatment affected the maximum photosynthetic rate or the initial slope of the photosynthesis–irradiance curve, we measured metabolic rates at several light intensities on 30 August 2000 using the methods described earlier. Intermediate light treatments were established by covering the clear acrylic chambers with neutral-density black screens. Rates of dark respiration were measured concurrently. Light levels within the chambers averaged approximately 584, 193, 72, and 0 μmol quanta m^{-2} s^{-1} (Li190SA Li-Cor quantum cosine sensor). Two replicates for each combination of heat and light treatment were studied using composite samples. The eight tiles used in each replicate consisted of four tiles from two separate enclosures of the same treatment. Composite samples were incubated in two warm and two control enclosures. The maximum photosynthetic rate and the initial slope of the photosynthesis–irradiance curve were estimated using the Fee model (1998). Results were analyzed using one-way fixed-effects analyses of variance (ANOVAs).

Several exchange experiments were performed to assess whether changes in metabolic rates were a direct metabolic effect resulting from increased temperature, or whether changes resulted from a shift in community composition. Tiles were selected and sealed in incubation chambers before being exchanged between paired warm and control enclosures. Chambers were opened and tiles were allowed to acclimate for approximately 1 h before metabolic rates were measured. If the metabolic rates of tiles transferred from warm to control enclosures did not differ from tiles maintained within control enclosures, we concluded that direct metabolic effects were driving the temperature response. However, if metabolic rates of the tiles from warmed enclosures exceeded the rates of those from control enclosures when both sets of tiles were incubated at the same temperature, we concluded that community change was a contributor to the temperature response. Two sets of exchange experiments were performed for both photosynthesis and respiration (Table 1).

Particulate sampling—Particulate sampling on the precolonized tiles was performed during five periods of the experiment (Table 1). Tiles were collected as described for the metabolic experiments and were then stored at approximately 4°C for up to 1 d until processing. The epilithon (from 16 tiles within each enclosure) was scraped into 1 liter of lake water using plastic scrapers and then blended for 10 s at low speed to homogenize the samples, transferred to stirred beakers, and subsampled using a wide-bore syringe. Two duplicate suspensions from each enclosure were sampled for chemical analyses, and the mean of these two values was used in statistical analyses. Bacterial samples were preserved in 2% formaldehyde and stored at 4°C. Algal samples were fixed with acid Lugol's (4% final concentration). Algal and bacterial counts were performed on the precolonized tiles only on three dates (Table 1) and the early successional tile community was sampled only once (Table 1). Samples collected from the bedrock were also processed as above.

Algal community—Algae were enumerated using the modified Utermöhl technique (Nauwerck 1963). Samples were sonicated at 20 kHz (Sonifer Cell Disruptor, model W140, Heat Systems, Ultrasonic) for two 15-s intervals. Subsamples were stained with fast green FCF (Fisher Scientific) and allowed to settle overnight. Cells were identified to the lowest taxonomic unit using a phase-contrast inverted microscope at ×125 and ×400 magnification until a minimum of 100 cells of the dominant taxon was counted. Only viable cells that showed the presence of cellular structures were enumerated (Owen et al. 1978). Preserved subsamples of the natural bedrock community within enclosures were examined to allow qualitative comparison to the tile community.

In each sample, 50 cells of each of the most common taxa were measured and estimates of algal cell or colony biovolume were obtained using regressions for different taxa (Vollenweider 1974). For less common taxa, cells were measured as they were encountered, and estimates of cell size were based on less than 50 measurements. Biovolume measurements were obtained by applying the geometric formula best fitted to the cell shape (Rott 1981).

Bacteria—Samples were homogenized by sonicating for 15 1-s intervals (Vibra cell, 15 W) following the addition of

sodium pyrophosphate (final concentration 0.175 g L^{-1}). Subsamples were taken using a wide-bore pipette, and the diluted sample was stained with 0.49 μg ml^{-1} 4′,6-diamidino-2-phenylindole for 20 min and filtered onto 0.22-μm black polycarbonate filters (Osmonics). Filters were mounted and enumerated using epifluorescence microscopy. A minimum of 300 cells and 10 randomly selected fields of view were enumerated.

Benthic invertebrates—On 19 September 2000 we removed 40 precolonized tiles (921 cm^2 in total) from each enclosure for invertebrate sampling. Tiles were obtained as described previously, scraped with plastic rulers, and samples were preserved in 6% formaldehyde. Although the sampling method may have allowed escape of some highly motile species, it was consistent between treatments. Samples were sieved through a 77-μm sieve, stained with rose bengal and counts continued until approximately 200 microcrustaceans were identified in each sample. The sample was then sieved through a 500-μm sieve and counted entirely for amphipods, annelids, snails, and large insects.

Elemental analyses—Subsamples of the epilithic slurry were filtered onto preashed glass fiber filters (GF/C, 1.2 μm particle retention) for elemental analyses. Samples for C analyses were dried, frozen, and analyzed using a CHN control equipment 440 elemental analyzer. Phosphorus subsamples were frozen, ashed at 500°C for 1 h, digested in 1 N hydrochloric acid at 104°C for 2 h, and analyzed using the ascorbic acid–molybdate reaction (modified from Stainton et al. 1977). We also estimated the proportion of total C contributed by algae by assuming 10% of algal wet weight is C and that the density of algae is equal to that of water.

Statistical analyses—A significance level of $\alpha = 0.05$ was selected for all analyses (performed using SYSTAT 8.0 or 10.0). We used Huynh–Feldt corrected repeated-measures (RM) randomized-block (RB) ANOVAs to assess treatment effects on all variables that were measured more than once during the experiment. When a parameter was measured only once (e.g., all bedrock and early successional tile-related parameters, invertebrates on the precolonized tiles), RB-ANOVAs were used. The only exception to this approach was in our analysis of the effects of warming on the photosynthesis–irradiance curve. Data were tested for adherence to the assumptions of the analyses. Data were log transformed if necessary to correct for nonnormality. If the heterogeneity of variances assumption was violated, we used Taylor's (1961) power law to transform the data. Assumptions of the analyses were met in all cases, using either transformed or nontransformed data.

If multiple analyses were performed on related parameters (e.g., metabolic parameters), we first performed a multivariate ANOVA (MANOVA) that included the related variables (e.g., photosynthesis and respiration). These are the variables listed below the MANOVA results in statistical tables. If the MANOVA was not significant for treatment or for time × treatment effects, these effects within RM-ANOVAs were compared to a more conservative Dunn–Šidák-adjusted α' (reported in the table header). If the MANOVA was significant for either treatment or time × treatment effects, we used the unadjusted significance level of $\alpha = 0.05$. However, the Dunn–Šidák-adjusted α' was used in tests for effects on individual invertebrate taxa and on C accrual and C : P ratios of early successional and bedrock communities because the assumptions of the MANOVA could not be met, even using transformed data.

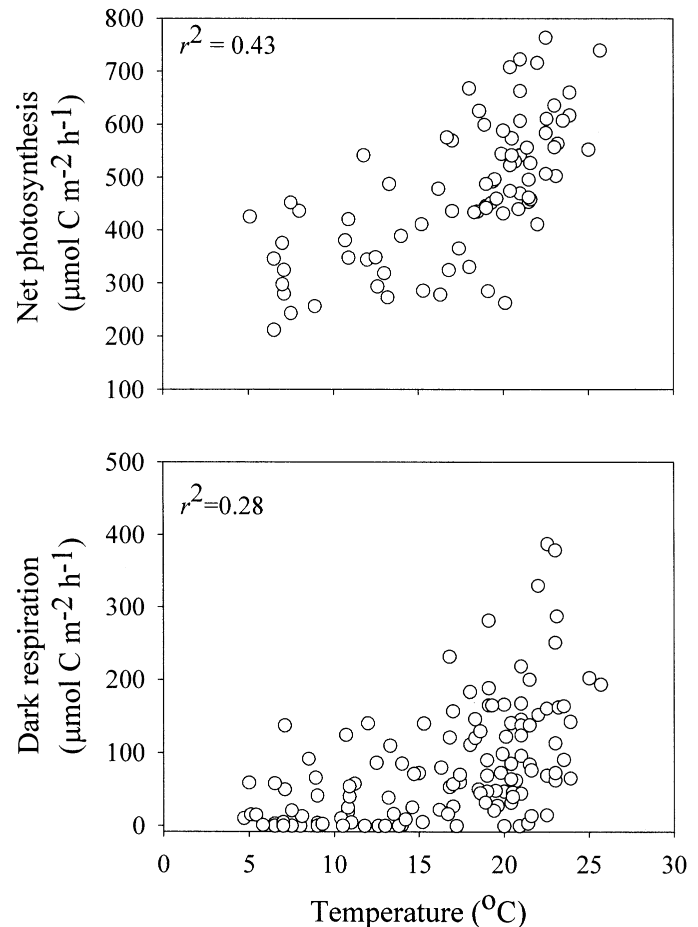

Fig. 3. Relationship between temperature and metabolic variables during the open-water season, 1981–2004 (natural bedrock substratum).

Results

Long-term data analysis—Light-saturated photosynthesis and dark respiration were positively correlated with water temperature. Temperature explained 43% of the variance in rates of photosynthesis and 28% of the variance in rates of dark respiration (Fig. 3).

Experimental results

Water chemistry—Water chemistry was similar in the warmed enclosures, controls, and the lake (Table 2), with the exception of total N, which was higher in enclosures than in the lake.

Table 2. Average water chemistry during the experiment. Enclosures were sampled four times. The lake was also sampled four times, although sampling dates differed from those for the experiment.

	Lake	Control enclosures	Warmed enclosures
pH	7.0	7.2	7.2
DIC (μmol L^{-1})	140	150	140
Dissolved organic carbon (μmol L^{-1})	700	720	710
TP* (μmol L^{-1})	0.23	0.17	0.17
TN* (μmol L^{-1})	11	23	23

* TP, total phosphorus; TN, total nitrogen.

Metabolism—In the photosynthesis–irradiance experiment, rates of light-saturated photosynthesis (P_{max}) in warmed enclosures were more than double those within controls (one-way fixed-effects ANOVA; $F_{1,2} = 58.8$; $p < 0.02$). P_{max} in control enclosures was 265 ± 16 (SD) and 571 ± 95 (SD) μmol C m^{-2} h^{-1} in warmed enclosures. These experiments also demonstrated that light levels within the chambers during photosynthetic incubations were at or near levels of light saturation (Fig. 4). No statistically significant effect of temperature on light-limited photosynthesis was observed (one-way fixed-effects ANOVA; $F_{1,2} = 0.08$; $p = 0.80$).

Rates of light-saturated net photosynthesis increased by 28–115% as a result of the heat treatment, and varied significantly over time (Figs. 2, 4, 5; Table 3). Dark respiration rates in warmed enclosures were 29–103% higher than controls (Figs. 2, 5) and also differed over time (Table 3).

The exchange experiments showed that the source of the tiles had no significant effect on photosynthetic rates when all tiles were incubated within control enclosures (Fig. 5). When tiles were incubated in warm enclosures, the warm-enclosure communities had higher rates of net photosynthesis than the control-tile community (Fig. 5; Table 4). This suggests that changes within the algal community explain some of the differences in metabolic responses between warmed and control enclosures. There was no statistically significant difference between rates of dark respiration on tiles colonized within warm enclosures and tiles transferred to warmed enclosures (Fig. 5; Table 4). There was a time × treatment interaction effect on respiration rates of tiles transferred from warm enclosures to controls, and those maintained within control enclosures (Fig. 5; Table 4). The change in the magnitude of the difference between tiles of different sources on these two dates drove this interaction effect.

Algae—There was no significant warming effect on total algal biovolume on the precolonized tiles, aside from a time

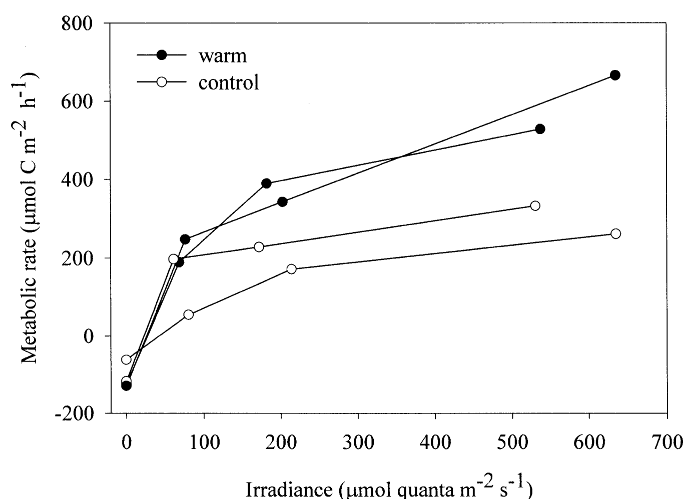

Fig. 4. Net photosynthesis–irradiance relationships on precolonized tiles in warm and control enclosures on 30 August 2000. Negative metabolic rates show rates of dark respiration.

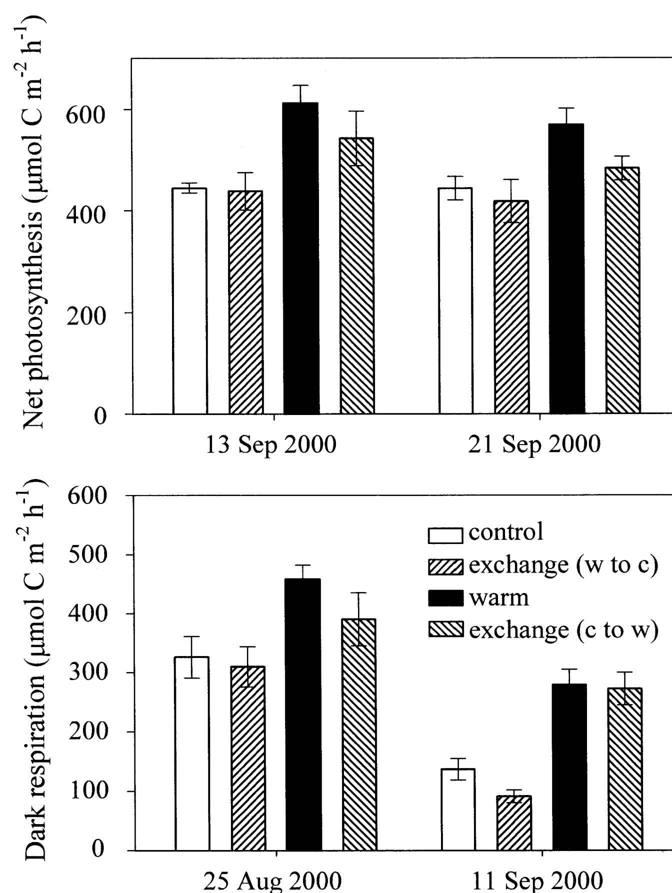

Fig. 5. Rates of net photosynthesis and dark respiration on precolonized tiles in control and warm enclosures on tiles maintained within and transferred between treatments. The direction of exchange is indicated in brackets, with the tile source listed first (w indicates warm, c indicates control) and the tile destination listed second. Error bars show ±1 standard error.

Table 3. Results of RM-RB-MANOVA and univariate tests on the effect of the heat treatment on rates of net photosynthesis and community dark respiration on precolonized tiles during the experiment. Statistically significant values are indicated by an asterisk.

Source of variation	df	F	p
MANOVA			
Heat treatment	1, 3	8.82	0.06
Time	3, 9	9.08×10^2	<0.001*
Time × treatment	3, 9	31.5	<0.001*
Net photosynthesis			
Heat treatment	1, 3	28.7	0.01*
Time	3, 9	22.0	<0.001*
Time × treatment	3, 9	2.4	0.13
Dark respiration			
Heat treatment	1, 3	65.5	0.004*
Time	3, 9	41.8	<0.001*
Time × treatment	3, 9	0.74	0.56

× treatment effect driven by a minor difference shortly after the start of the experiment (Table 5). Diatoms dominated the algal community on precolonized tiles in both warm and control enclosures, contributing 51–85% of total algal biovolume during the experiment. Chlorophytes and cyanobacteria comprised the balance of algal biovolume (Fig. 6). Tests for effects of the heat treatment on the biovolume of algal groups (on precolonized tiles) showed no effects of the heat treatment or of a time × treatment interaction (Fig. 6; Table 5).

Algal taxonomic composition and biovolume on the early successional tiles were significantly affected by the heat treatment. Algal biovolume was more than four times higher in warmed enclosures than in control enclosures. There was a sevenfold increase in diatom biovolume in warmed enclosures, accompanied by a near doubling in biovolume of cyanobacteria and an almost fourfold increase in the biovolume of chlorophytes (Fig. 6; Table 6). However, the magnitude of the increase in diatoms meant that the chlorophyte contribution to total algal biovolume was unchanged and the percentage contribution of cyanobacteria to algal biovolume actually declined. The increase in diatom biovolume was driven by a more than 20-fold greater biovolume of *Rhopalodia* in warmed enclosures than in control enclosures (Table 6). If the response of *Rhopalodia* is removed, warming effects on diatom biovolume were not statistically significant (RB-ANOVA, $F_{1,3} = 2.5$, $p = 0.21$). Similarly, the increase in *Lyngbya* biovolume also drove the increase in cyanobacteria biovolume (Table 6). There was no significant effect of the heat treatment on the biovolume of the group once this taxa was removed (RB-ANOVA, $F_{1,3} = 0.54$, $p = 0.52$).

Bacteria—Bacterial density increased significantly in warmed enclosures on precolonized tiles, early successional tiles, and on bedrock (Fig. 7; Table 7). Bacterial density was similar among the three study communities (Fig. 7).

Benthic invertebrates—Cladocerans, cyclopoid copepods, and dipterans were numerically dominant in the enclosures. The cladoceran community was dominated by *Alona* spp., *Alonella* spp., and *Acroperus* cf. *harpae* (Table 8). The invertebrate community showed little change as a result of warming, with no effect on total invertebrate abundance. *Chydorus* cf. *brevilabris* was the only species to show a

Table 4. Effect of tile source (warm or control enclosures) on rates of net photosynthesis and dark respiration during exchange experiments using precolonized tiles. RM-RB-MANOVAs and RM-RB-ANOVAs were used to test the hypothesis that rates of net photosynthesis or dark respiration differed between tiles that were maintained within an enclosure, and those transferred to an enclosure from the differing heat treatment. The direction of exchange is indicated in brackets, with the tile source listed first, and the tile destination listed second. Statistically significant values are indicated by an asterisk.

Date	Source of variation	$F_{1,3}$	p
Net photosynthesis			
MANOVA	Heat treatment	20.9	0.02*
	Time	29.0	0.01*
	Time × treatment	2.04	0.25
Control vs. exchange (warm to control)	Heat treatment	0.37	0.59
	Time	0.75	0.45
	Time × treatment	0.63	0.49
Warm vs. exchange (control to warm)	Heat treatment	13.6	0.03*
	Time	1.84	0.27
	Time × treatment	0.04	0.85
Dark respiration			
MANOVA	Heat treatment	102	0.002*
	Time	7.21	0.07
	Time × treatment	0.05	0.84
Control vs. exchange (warm to control)	Heat treatment	9.12	0.06
	Time	719	<0.001*
	Time × treatment	20.4	0.02*
Warm vs. exchange (control to warm)	Heat treatment	3.88	0.14
	Time	33.1	0.01*
	Time × treatment	1.34	0.33

Table 5. Results of RM-RB-ANOVAs assessing the effect of the heat treatment on epilithic algal biovolume and community composition on the precolonized tiles. The lack of significance of the RM-RB-MANOVA for treatment and time × treatment effects indicates that these effects should be compared to a more conservative Dunn-Šidák-adjusted α′ of 0.013 (α = 0.05, number of groups = 4). Statistically signficant values are indicated by an asterisk.

Parameter	Source of variation	df	*F*	*p*
MANOVA	Heat treatment	1, 3	0.09	0.79
	Time	2, 6	83.4	<0.001*
	Time × treatment	2, 6	0.11	0.89
Total algal biovolume	Heat treatment	1, 3	0.96	0.40
	Time	2, 6	2.18	0.19
	Time × treatment	2, 6	11.1	0.01*
Diatom biovolume	Heat treatment	1, 3	0.26	0.64
	Time	2, 6	2.77	0.14
	Time × treatment	2, 6	0.15	0.86
Chlorophyte biovolume	Heat treatment	1, 3	0.33	0.61
	Time	2, 6	0.45	0.66
	Time × treatment	2, 6	0.53	0.62
Cyanobacteria biovolume	Heat treatment	1, 3	0.14	0.73
	Time	2, 6	23.1	0.002*
	Time × treatment	2, 6	3.26	0.11

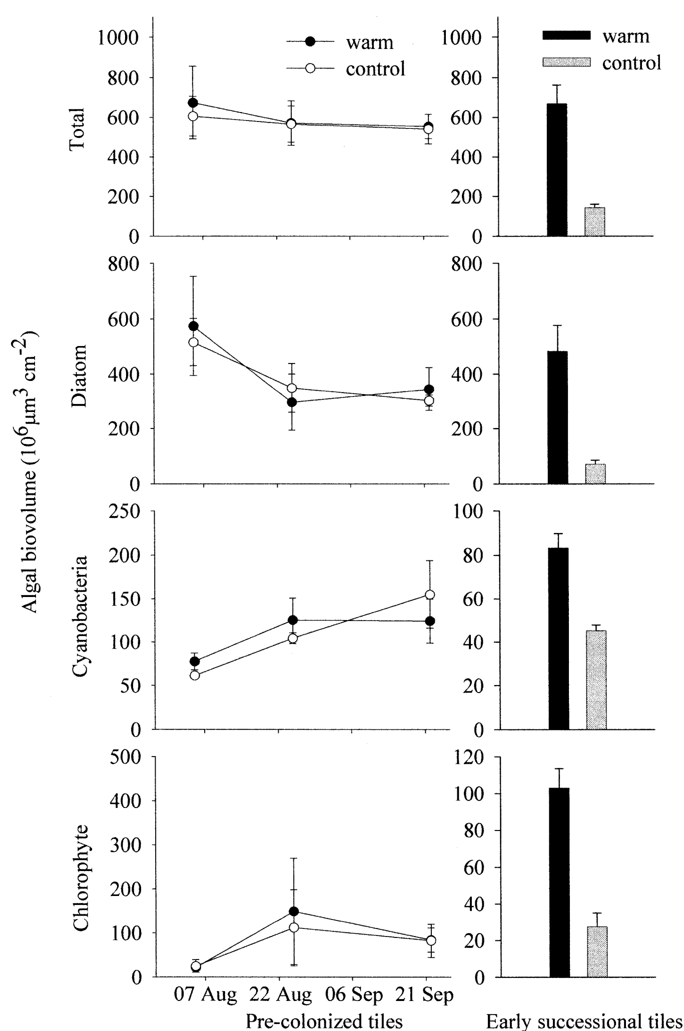

Fig. 6. Mean total algal biovolume and biovolume of individual groups on precolonized tiles and early successional tiles in control and warm enclosures. Error bars show 1 standard error.

statistically significant response, doubling in abundance as a result of the heat treatment (Table 8).

Carbon—Carbon accrual was 40% greater on bedrock within warmed enclosures than within controls (Fig. 8; Table 9). However, C accrual on the early successional tiles and precolonized tiles did not differ significantly between experimental treatments (Fig. 8; Table 9). Accrual of C was much greater on the bedrock than within either tile community (Fig. 8). Outside of the enclosures at depths of 0.5–0.6 m, C accrual on bedrock was 2,680 ± 320 (SE) μg cm^{-2}, higher than measurements within control enclosures (Fig. 8).

There was no change in the proportion of total C contributed by algae on the precolonized tiles as a result of the heat treatment (RM-RB-ANOVA: time × treatment $F_{2,6} = 0.37$, $p = 0.71$; treatment $F_{1,3} = 0.11$, $p = 0.77$), although this proportion did decrease over time ($F_{2,6} = 7.83$, $p = 0.02$). A change in this proportion resulted from warming the early successional tiles, with algae contributing significantly more of the C in the warmed enclosures (24.3% ± 13.5%) than within the controls (8.3% ± 3.3%; RB-ANOVA: $F_{1,3} = 22.0$, $p = 0.02$).

Stoichiometry—Molar C : P ratios on the precolonized tiles showed a significant interaction between time and treatment effects (Fig. 8; Table 9) as a result of increased C accrual in warmed enclosures in the final sampling period. Phosphorus accumulation was unaffected during this period (data not shown). The heat treatment did not significantly affect nutrient ratios on the natural bedrock substratum or on the early successional tiles (Fig. 8; Table 9). Ratios of C : P were greatest on bedrock, with lower values on precolonized and early successional tiles (Fig. 8). Molar C : P ratios on bedrock were higher outside the enclosures (2,320 ± 55 SE) than within the enclosures (Fig. 8).

Discussion

Epilithic metabolism—The effects of temperature on respiration and light-saturated photosynthesis in both the long-

Table 6. Biovolume of three dominant species of each algal group in warmed and control enclosures on the early successional tiles after the 4-week incubation period. Mean epilithic algal biovolume (10^6 μm^3 cm^{-2}) in four enclosures is shown with the standard error indicated in brackets (n.d. indicates that the taxon was not detected). Results of RB-ANOVAs assessing the effect of the heat treatment on biovolume of dominant taxa present on early successional tiles after the 4-week colonization period are shown. *Gloeotrichia* sp., *Surirella ovata*, and *Aulocoseira binderana* were excluded from analyses because they were present in only one enclosure. Multivariate tests are reported for the three groups, and for the six species that were analyzed (RB-MANOVA). Statistically significant values are indicated by an asterisk.

	Control	Warm	$F_{1,3}$	p
RB-MANOVA (species)			92.6	0.002*
RB-MANOVA (groups)			43.7	0.007*
Total algal biovolume			43.6	0.007*
Diatoms			26.1	0.01*
Rhopalodia sp.	14.0 (14.0)	317.8 (27.2)	100.7	0.002*
Surirella ovata Kützing	n.d.	55.1 (55.1)		
Aulocoseira binderana Kützing	n.d.	39.6 (39.6)		
Chlorophytes			59.1	0.005*
Mougeotia sp.	8.0 (8.0)	35.4 (17.2)	1.1	0.37
Oedogonium sp.	1.3 (0.8)	36.4 (12.8)	6.9	0.08
Bulbochaete sp.	15.2 (8.3)	14.5 (8.1)	0.05	0.84
Cyanobacteria			22.2	0.02*
Lyngbya sp.	36.4 (3.1)	77.4 (8.3)	36.4	0.009*
Gloeotrichia sp.	n.d.	3.8 (3.8)		
Chroococcus limneticus Lemmermann	1.8 (1.3)	1.7 (1.2)	0.0006	0.98

term data and experimental data (on the precolonized tiles) indicate that increased water temperatures associated with climate change are likely to affect the metabolism of the epilithon and C flow in the littoral zone.

The stimulation of light-saturated photosynthesis by moderate warming is consistent with numerous studies of marine and freshwater phytoplankton (e.g., Iriarte and Purdie 1993; Rae and Vincent 1998) and benthic species (e.g., Blanchard and Guarini 1997; Tang and Vincent 1999). At the community level, several studies also support these findings in streams (Phinney and McIntire 1965; DeNicola 1996), lake epipelon (Gruendling 1971), and lake epiphyton (Hickman and Klarer 1975). There are numerous mechanisms that may stimulate light-saturated photosynthesis at increased temperatures including increased enzymatic activity and accelerated transport processes (Davison 1991). Algae may also acclimate to increased temperatures by increasing their pigment content (e.g., Kübler and Davison 1995; Coles and Jones 2000), a trend shown in preliminary analyses of our study communities (Baulch 2002).

Our exchange experiments provided insight into whether the increase in rates of light-saturated net photosynthesis associated with warming was a direct metabolic response or whether the increase was driven by community change. Although we did not observe changes in algal community composition or biovolume on the precolonized tiles, warm-acclimated tiles had higher light-saturated photosynthetic rates than controls when incubated in warmed enclosures. This suggests that acclimation to increased temperatures, possibly by increasing pigment content, conferred greater photosyn-

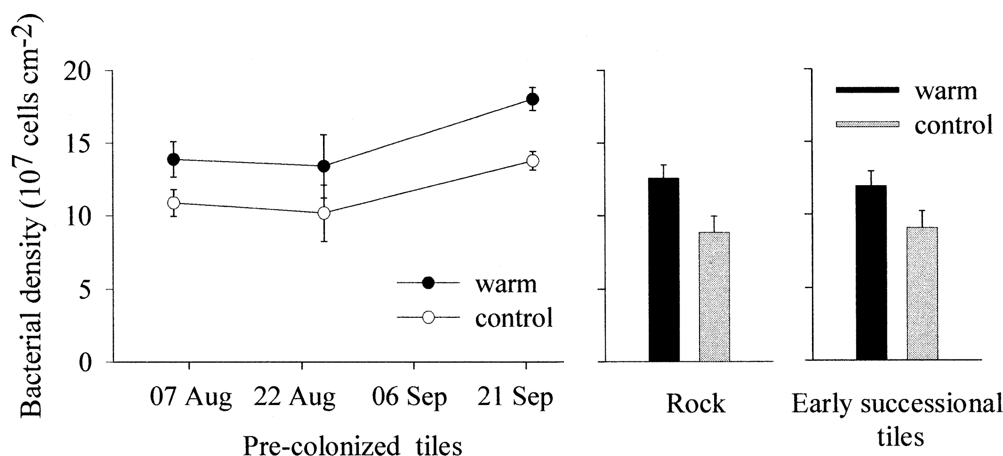

Fig. 7. Mean density of bacteria in control and warm enclosures. Error bars show 1 standard error.

Table 7. Results of statistical analyses assessing effects of warming on bacterial density on the precolonized tiles, early successional tiles, and natural bedrock substratum. Statistically significant values are indicated by an asterisk.

Community	Statistical test	Source of variation	df	*F*	*p*
Precolonized tiles	RM-RB-ANOVA	Heat treatment	1, 3	26.8	0.01*
		Time	2, 6	30.8	0.001*
		Time × treatment	2, 6	0.71	0.53
Early successional tiles	RB-ANOVA	Heat treatment	1, 3	18.9	0.02*
Bedrock	RB-ANOVA	Heat treatment	1, 3	70.2	0.004*

thetic capacity on the warm-acclimated tile communities. On the basis of this, we speculate that effects would be observable at increased temperatures only when electron transport and other temperature-sensitive processes were stimulated. This hypothesis is consistent with our finding that when tiles from warm and control enclosures were incubated within control enclosures, photosynthetic rates did not differ significantly.

Similar to our results, several studies have not observed a temperature effect on the initial slope of the photosynthesis–irradiance curve when examining phytoplankton (e.g., Iriarte and Purdie 1993; Rae and Vincent 1998) or epilithon in a laboratory stream (Phinney and McIntire 1965). Light-limited photosynthesis is often considered a temperature-independent process limited by the rates of photochemical reactions (Steemann-Nielsen and Jørgensen 1968). Davison (1991), however, contends that the temperature dependence of enzymes active in photosynthesis could lead to temperature dependence of light-limited photosynthesis, a result also supported by a number of studies (e.g., Tang and Vincent 1999; Coles and Jones 2000). This question deserves further attention at the community level and has important implications in littoral communities, as shoreside shading is natural in forested catchments and may limit effects of warming. As well, thick epilithic biofilms are likely to exhibit some degree of self-shading. In this experiment, the enclosures also contributed to shading (although not during photosynthetic incubations), which may have buffered the effects of increased photosynthesis on community change.

The observed positive correlation between temperature and respiration rates and the warming-related stimulation of respiration was expected, given that respiration rates of algae, bacteria, and invertebrates are known to increase with temperature. Respiration rates of stream periphyton (Kevern and Ball 1965; Phinney and McIntire 1965) have also been shown to increase with temperature. The exchange experiments suggested that respiration rates were more dependent on incubation temperature than on the source of the tiles (warmed or control enclosures). We cannot discount the possibility of community change contributing to the stimulation of respiration rates but we speculate that metabolic responses were the primary factor responsible for change. We also note that the bacterial counts include cells that may show a wide range of levels of metabolic activity (Smith and del Giorgio 2003). As a result, increased bacterial abundance may not necessarily equate to increased respiratory activity.

Community composition—Our analyses of community composition suggest that biotic responses to climate change are also not easily understood or predicted. We found that responses oftentimes differed among different types of communities, suggesting that disturbance history may be an important determinant of the rapidity or occurrence of community changes.

Algal taxonomy and biovolume: The effects of warming on algal biovolume and composition depended on the maturity of the community. The lack of warming effect on algal communities on the precolonized tiles is contrary to the expectation that communities of benthic algae should shift from diatom dominance at temperatures less than 20°C to chlorophytes as temperatures increase from 15°C to 30°C and to cyanobacteria at temperatures above 30°C (reviewed by DeNicola 1996). Average weekly temperatures ranged from 12°C to 22°C within control enclosures and 17°C to 27°C in warmed enclosures, suggesting that a decline in diatoms and increase in chlorophytes would be expected in warmed enclosures.

The responses of the early successional tile communities again differed from our predictions, with the increase in biovolume in warmed enclosures driven by a greater than 20-fold increase in *Rhopalodia*, a large diatom that contains N-fixing endosymbionts. The symbiont found within *Rhopalodia gibba* is closely related to the cyanobacteria *Cyanothece* sp. (Prechtl et al. 2004), which raises interesting questions about whether increases in *Rhopalodia* reflected a benefit to the cyanobacterial symbiont at higher temperatures.

The early successional tile community with its lower C accrual probably had greater access to nutrients through a thinner biofilm and boundary layer. As well, light limitation was less likely in the understory of the early successional tile community. We suggest that with greater access to resources and light, algae within the early-successional tile community were more able to show an increase in growth rate with increased temperature. However, other explanations are possible. For example, the 8-week duration of the experiment may have been insufficient to induce change in an already well-developed community, although the time-related effects on algal biovolume and taxonomy of the precolonized tiles suggest that this is not the case. Environmental conditions during the 4-week incubation of the early-successional tiles were similar to those during the rest of the experiment, suggesting that differences in temperature regime or water chemistry are unlikely to explain the different responses.

Bacteria: Bacterial density in each of the study communities increased in warmed enclosures, even during late sum-

Table 8. Effect of the heat treatment on invertebrate abundance on precolonized tiles. The mean abundance (number per m^2) in four enclosures is shown with the standard error indicated in brackets. Copepodite stages 1-2 are indicated by c1-2, and c3-5 indicates copepodite stages 3-5. (n.d. indicates the taxon was not detected.) Statistical analyses (RB-ANOVA) were restricted to the taxa that were present in three or more enclosures. Results of ANOVAs should be compared to the more conservative Dunn–Šidák-adjusted α'-value of 0.0017 (α = 0.05, number of groups = 30). Statistically significant differences are indicated by an asterisk.

Taxa	Control	Warm	$F_{1,3}$	p
Total invertebrates	29,400 (3,500)	27,800 (5,000)	0.06	0.81
Arthropoda				
Arachnida				
Acari	11 (11)	n.d.		
Crustacea				
Total microcrustacea	14,300 (2,600)	15,900 (3,100)	0.07	0.80
Malacostraca				
Amphipoda	164 (62)	73 (12)	2.80	0.19
Brachiopoda				
Cladocera				
Chydoridae				
Acroperus cf. harpae	1,210 (340)	1,520 (1,140)	0.16	0.72
Alona guttata	103 (72)	23 (23)	2.43	0.22
Alona quadrangularis/affinis	981 (378)	1,960 (486)	6.02	0.09
Alona rustica	1,900 (420)	1,530 (530)	0.15	0.72
Alona setulosa	253 (79)	1,230 (840)	0.02	0.89
Alonella cf. excisa	886 (650)	473 (171)	0.02	0.91
Alonella nana	2,066 (963)	792 (303)	2.74	0.20
Chydorus cf. brevilabris	89 (40)	195 (34)	187	0.001*
Chydorus gibbus	15 (15)	n.d.		
Chydorus piger	n.d.	47 (47)		
Disparalona acutirostris	87 (29)	218 (94)	2.22	0.23
Rhynchotalona falcata	n.d.	23 (23)		
Bosminidae				
Bosmina longirostris	26 (26)	320 (235)	102	0.002
Macrothricidae				
Ophryoxus gracilis	n.d.	27 (27)		
Streblocerus serricaudatus	n.d.	70 (70)		
Ilyocryptus sp.	213 (45)	1,420 (510)	61.8	0.004
Polyphemidae				
Polyphemus pediculus	15 (15)	95 (95)		
Daphniidae				
Scapholeberis sp.	n.d.	32 (32)		
Sididae				
Diaphanosoma birgei	15 (15)	n.d.		
Latona setifera	177 (139)	87 (47)	0.01	0.93
Sida crystallina	84 (40)	445 (238)	2.75	0.20
Ostracoda	195 (45)	220 (138)	1.22	0.35
Copepoda				
Nauplii	550 (133)	732 (266)	0.06	0.82
Harpacticoida	1,240 (110)	1,300 (520)	0.35	0.60
Calanoida	37 (25)	33 (20)	0.01	0.98
Cyclopoida				
unidentified cyclopoids	22 (22)	13 (13)		
Small cyclopoids (includes all c1-2 and *Microcyclops* c3-5)	3250 (620)	2370 (320)	0.91	0.41
Cyclopidae Sars				
Acanthocyclops cf. vernalis	628 (222)	886 (141)	0.71	0.46
Diacyclops bicuspidatus thomasi	15 (15)	n.d.		
Mesocyclops edax	18 (18)	n.d.		
Microcyclops varicans	30 (30)	n.d.		

Table 8. Continued.

Taxa	Control	Warm	$F_{1,3}$	p
Cyclopidae Sars				
Eucyclops agilis	348 (129)	259 (97)	0.20	0.69
Macrocyclops albidus	550 (205)	482 (135)	0.078	0.79
Paracyclops poppei	15 (15)	n.d.		
Insecta				
Trichoptera	13 (8)	13 (5)	0.24	0.66
Diptera	9,920 (2,340)	6,620 (1,370)	1.32	0.33
Ephemeroptera	73 (20)	91 (13)	0.38	0.58
Annelida				
unidentified annelids	78 (20)	148 (38)	1.70	0.28
Oligochaeta	4,120 (330)	3,950 (1,030)	0.019	0.90
Cnidaria				
Hydra sp.	15 (15)	13 (13)		
Mollusca				
Gastropods	16 (3)	40 (15)	3.88	0.14

mer when water temperatures were naturally high. This is consistent with studies in streams that have shown that increased temperatures can lead to increased bacterial density (e.g., Lamberti and Resh 1983). Increased substrate availability may also have contributed to higher bacterial cell densities; however, given the large pool of C available in the benthos, and the community-dependent effects of warming on C accrual and algal biovolume, it seems likely that temperature was the main factor leading to increases in bacterial abundance.

Benthic invertebrates: We did not detect statistically significant changes in the total density of macroinvertebrates or microcrustaceans. This is in contrast to Oden's (1979) findings of a decline in meiofaunal abundance in a heated reservoir and stream studies showing warming-related declines in macroinvertebrate density (Lamberti and Resh 1983).

The taxonomic composition of the invertebrate community also showed little impact of the heat treatment. A longer experiment would likely be required to show effects on longer-lived taxa, although even meiofaunal species, which typically have short life spans, showed very limited effects. High variability may have obscured warming effects on some species, and potential effects on *Bosmina longirostris* and *Ilyocryptus* sp. deserve further study. However, on the basis of these results, short-term periods of warming, even when water temperatures are naturally high, are not expected to lead to marked changes in the composition of the inver-

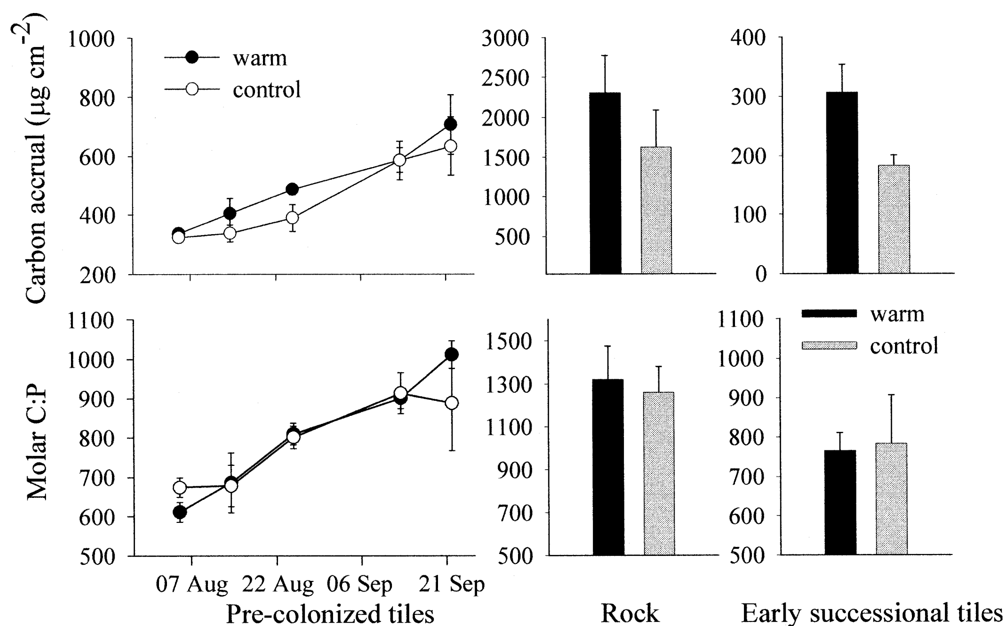

Fig. 8. C accrual and C : P ratios of the epilithon on the three types of experimental substrata in control and warm enclosures. Error bars show 1 standard error.

Table 9. Results of statistical analyses assessing effects of warming on C : P ratios and C accrual. The lack of significance of the RM-RB-MANOVA for treatment and time × treatment effects indicates that these effects should be compared to a more consevative Dunn–Šidák-adjusted α' of 0.025. MANOVAs could not be run on the early successional tile data or the bedrock data, and as a result, p values should be compared to a Dunn–Ŝidák-adjusted α' of 0.025. Statistically significant differences in all analyses are indicated by an asterisk.

Community	Parameter	Source of variation	df	*F*	*p*
Precolonized tiles	MANOVA	Heat treatment	1, 3	0.49	0.53
		Time	4, 12	112	<0.001*
		Time × treatment	4, 12	2.36	0.11
	C	Heat treatment	1, 3	2.97	0.18
		Time	4, 12	67.0	<0.001*
		Time × treatment	4, 12	1.36	0.31
	C : P	Heat treatment	1, 3	0.79	0.44
		Time	4, 12	1.3×10^5	<0.001*
		Time × treatment	4, 12	4.46	0.02*
Early successional tiles	C	Heat treatment	1, 3	7.49	0.07
	C : P	Heat treatment	1, 3	0.16	0.72
Bedrock	C	Heat treatment	1, 3	18.9	0.02*
	C : P	Heat treatment	1, 3	0.05	0.84

tebrate community. Invertebrates within the littoral zone are adapted to considerable natural diurnal and annual fluctuations in water temperature.

Carbon accrual and stoichiometry: Increased C accrual may reflect increases in the biovolume or C content of algae, bacteria, or invertebrates; increases in the detrital contribution to total epilithic C; or a combination of these factors. Carbon accrual was generally higher in warmed enclosures on the early successional tiles, precolonized tiles, and on the natural bedrock substratum; however, differences were only statistically significant on bedrock. The increase in C accrual on bedrock suggests that warming will potentially lead to increased food availability for grazers, although the ecological effects of an increase in C availability for grazers may be minimal because epilithon in L239 is naturally C rich (Turner unpubl. data).

Molar C : P ratios showed a significant interaction between time and treatment on the precolonized tiles that was driven by higher ratios in warmed enclosures on the final sampling date. Because littoral benthic invertebrates within L239 are P limited (Frost and Elser 2002), this suggests that bulk food quality may have been degraded in warmed enclosures.

Enclosure effects and effects of artificial substrata—Although taxonomic composition of algal communities frequently differs between natural and artificial substrata (Tuchman and Stevenson 1980; Barbiero 2000), our communities were qualitatively similar. The only major taxonomic difference was that *Lyngbya* abundance was greater on tiles than on the natural substrata. Also, metabolic rates of the well-developed tile communities were slightly greater than those of the epilithon on the natural bedrock substratum (Baulch 2002).

Scaling effects from the enclosures and the possibility of divergence from the natural ecosystem should also be considered. For example, the small size of the enclosures may have affected natural grazing rates by fish (darters) present in the enclosures. In addition, communities within the enclosures were exposed to lower-than-natural light levels due to shading from the enclosure walls and associated insulation, suggesting that taxa with higher light requirements (e.g., some chlorophytes, Richardson et al. 1983) could have experienced light limitation for part of the day. However, because shading from shoreside vegetation is a natural phenomenon in many littoral sites, we do not expect this to affect the applicability of our results. Water chemistry was similar in the enclosures and the lake, although minor differences were apparent. Water exchange may have allowed invertebrate migration, which could dampen effects on invertebrate populations (Cooper et al. 1990), although on the basis of the design of the enclosures we believe that the migration rate (through or between multiple rows of sandbags) was low.

Potential implications of climate change—Increases in rates of light-saturated photosynthesis and respiration, in conjunction with increases in C accrual (on bedrock), suggest that epilithic C cycling, at least within some lakes, will be affected as a result of increased temperature associated with climate change. Given that littoral C can be an important C source to higher trophic levels (Hecky and Hesslein 1995), further larger-scale impacts of warming may result. However, the relatively narrow littoral zone of our study lake may limit these effects. Warming responses of macrophyte-dominated systems are likely to differ. Work of McKee et al. (2003) showed that these systems may be fairly resilient to increased temperatures, although warming was associated with increased P concentrations and decreased oxygen saturation, suggesting that eutrophication may be accelerated.

Within the epilithon, we believe that community-level responses to increased water temperatures are likely, at least within some communities. The differences in responses among our study communities suggest that simple predictions for epilithic responses cannot be made without considering differences in substrate characteristics and disturbance regimes. Under a climate-warming scenario, the composition and biovolume of recently disturbed benthic algal commu-

nities within L239 are likely to change as a result of increased temperatures. We speculate that more established communities may also show changes if climate change leads to concurrent effects upon nutrient availability or light—or with prolonged warming.

Baseline nutrient and light conditions as well as climate change-induced changes in light and nutrients are likely to affect temperature-related changes in the algal community. For example, if diatoms are superior competitors for P in the epilithon as proposed by Tilman et al. (1986) for planktonic communities, potential warming responses of chlorophytes and cyanobacteria may have been minimized by low P concentrations in our study lake. Temperature changes can also induce shifts in nutrient ratios at which different taxa become dominant (Tilman et al. 1986), suggesting that warming effects should be studied along a resource gradient or in multifactor experiments to more fully understand the potential effects of climate change on the composition of benthic algal communities. It seems likely that under different conditions of light and nutrients, warming effects on competitive outcomes of the algae may vary.

Interestingly, we detected very little response within the invertebrate community. This indicates that temperatures in warmed enclosures did not exceed lethal limits for survival of the benthic invertebrates. However, over the longer term, climate change may increase the probability of extreme events that exceed the thermal tolerances of some taxa. Effects upon epilithic stoichiometry could lead to further effects on invertebrate and fish communities.

More work needs to be done to examine how nutrient availability and other factors such as dissolved organic C interact with temperature to affect benthic communities and lake ecosystems. In particular, long-term experiments with a broader spatial scale would be advantageous in understanding the effects of warming on the littoral zone, and encompassing the range of natural variability within epilithon, macrophytes, and other littoral assemblages. A better understanding of the seasonality of warming effects is also important, as climate change predictions vary in terms of both the timing and extent of warming. Warming in this study may have had less effect than warming in the early spring, when nutrients may be more abundant, epilithic communities are at an earlier successional stage, and temperatures are lower. However, the rate of warming should also be considered—the heat treatment was established quickly in this study—and although this summer heating event does not appear to have led to die-off of any species, responses to more gradual warming may differ. Finally, more work needs to be done in different types of lakes to identify the potential range of warming responses.

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