

## **Regulation of algal structure and function by nutrients and grazing in a boreal wetland**

Author(s): Allison R. Rober, Kevin H. Wyatt, and R. Jan Stevenson

Source: JNABS Journal, 30(3):787-796. 2011.

Published By: North American Benthological Society

URL: <http://www.bioone.org/doi/full/10.1899/10-166R.1>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is an electronic aggregator of bioscience research content, and the online home to over 160 journals and books published by not-for-profit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

## Regulation of algal structure and function by nutrients and grazing in a boreal wetland

Allison R. Rober<sup>1</sup>, Kevin H. Wyatt<sup>2</sup>, AND R. Jan Stevenson<sup>3</sup>

*Department of Zoology, Michigan State University, East Lansing, Michigan 48824 USA*

**Abstract.** We evaluated the potential for grazers to regulate benthic algal biomass and taxonomic composition in an Alaskan marsh after enrichment with nutrients that are expected to increase in the region with ongoing climate change. We nested caged and uncaged substrates together inside mesocosm enclosures with natural abundances of snails or no snails and with or without nutrient enrichment (NO<sub>3</sub> + PO<sub>4</sub> + Si). Algal biomass was greater in all nutrient-enriched enclosures than in controls. Algal biomass was greater in enclosures where grazers were present but excluded by a cage than in enclosures where grazers were allowed to graze or where grazers were absent. In the presence of nutrients, grazed communities were dominated by small coccoid green algae and cyanobacteria, which were overgrown by filamentous green algae when grazers were excluded. In the absence of nutrients, grazers had little effect on algal biomass or taxonomic composition. However, grazers recycled a small but potentially important amount of nutrients in their waste, suggesting that consumer-driven nutrient recycling may have played a role in maintaining algal biomass when grazers were present. Our data show that grazers regulate algal responses to nutrients by suppressing algal accumulation but increasing productivity through nutrient recycling in a northern boreal wetland.

**Key words:** algae, wetland, grazer, nutrient, Alaska, climate change, nutrient recycling.

Algae can be abundant in wetlands and are significant contributors to many of the physical, chemical, and biological processes that characterize wetland ecosystems (Goldsborough and Robinson 1996, Wetzel 2006). In shallow wetlands where sufficient light reaches the bottom, benthic algae can exert considerable control over dissolved O<sub>2</sub> concentrations (Browder et al. 1994, Richardson 2008), sediment formation (Gleason and Spackman 1974, McCormick et al. 1998), and nutrient uptake and retention (Wetzel 1996, Gaiser et al. 2004), and can account for a significant fraction of total primary production (Robinson et al. 2000, Richardson 2010, Wyatt et al. 2010). Nevertheless, relatively little is known about the factors that regulate algal communities in wetlands, particularly in boreal regions, where wetlands are abundant and processes related to ongoing climate change are expected to have widespread effects on aquatic ecosystems (Rouse et al. 1997, Schindler 1998).

Benthic algae are sensitive to changes in water quality, and nutrients are among the most important factors regulating algal assemblages in aquatic ecosystems (Borchardt 1996). Addition of nutrients can result in significant increases in biomass (Francoeur 2001) and shifts in species composition (Fairchild et al. 1985, Gaiser et al. 2006), both of which can alter important ecosystem processes related to energy flow and nutrient cycling in aquatic ecosystems. Research examining the effects of nutrient enrichment on wetland ecosystems has stemmed largely from studies conducted in subtropical (McCormick and O'Dell 1996, McCormick et al. 2001, Gaiser et al. 2005) and temperate regions (Gabor et al. 1994, Murkin et al. 1994, McDougal et al. 1997), which are subject to nutrient contamination from increasing urban and agricultural land use (i.e., Sklar et al. 2005). The effects of nutrient enrichment on wetland algal communities at northern latitudes have been less studied, perhaps because these latitudes have been less directly affected by human development. However, boreal regions are undergoing rapid climate changes, which have led to longer growing seasons with higher temperatures (Chapin et al. 2006). Changes in thermal regime are expected to increase the extent of seasonal

<sup>1</sup> E-mail addresses: roberall@msu.edu

<sup>2</sup> wyattkev@msu.edu

<sup>3</sup> rjstev@msu.edu

ice thaw and could promote N and P mineralization in the expanded active soil layer (Bridgman et al. 1995). Regional variability in nutrient inputs may be significant, but these changes are expected to have widespread effects on nutrient concentrations in aquatic systems throughout the boreal forest (Rouse et al. 1997).

Nutrient enrichment is expected to increase algal productivity (Rouse et al. 1997), but some evidence indicates that northern aquatic ecosystems may not show the same positive relationship between increasing nutrient concentrations and algal biomass as those occurring at lower latitudes (Flanagan et al. 2003). In a meta-analysis of lakes across a wide latitudinal gradient, Flanagan et al. (2003) found that above 60°N, algal biomass decreases with increasing latitude independently of nutrient concentration. This trend indicates strong environmental controls on the algal response to nutrients at high latitudes. This control could occur via physiological constraints associated with extremes in temperature and day length or via top-down regulation of algal primary production, in which grazers are free to consume any increase in algal biomass that may be stimulated by nutrient enrichment (Hansson 1992).

In the absence of nutrient limitation, grazing strongly influences the quantity and quality of algal biomass as well as the taxonomic composition and growth form of the algal assemblage (McCormick and Stevenson 1991, Feminella and Hawkins 1995, Steinman 1996). Grazing generally causes a reduction in algal biomass and can maintain low biomass accumulation even in conditions of increased resource availability (e.g., nutrients and light) (Feminella and Hawkins 1995, Hill et al. 1995, Rosemond et al. 2000). Despite reductions in biomass, grazing also can lead to increased productivity of the algal assemblage through the use of excreted nutrients (McCormick and Stevenson 1991, Hillebrand 2002). The extent to which these regulatory processes operate in wetlands is largely unknown because evidence of grazing in wetland ecosystems has been largely circumstantial (Robinson et al. 2000).

We investigated the independent and interactive effects of grazing by the snail *Lymnaea* and nutrient enrichment on a benthic algal community in an Alaskan marsh to evaluate the potential for grazers to regulate benthic algal biomass and community composition given projected future increases in nutrient concentrations. Wyatt et al. (2010) reported the effects of nutrient enrichment alone in a concurrent study. We report the effect of grazers on algal community structure and biomass following enrichment with limiting nutrients. We also examined the

role of grazers in wetland biogeochemical cycling by evaluating the potential of consumer-driven nutrient recycling to influence algal accumulation. We tested the hypotheses that nutrient enrichment stimulates algal accumulation and grazers regulate algal responses to nutrients by suppressing algal accumulation but increasing productivity via nutrient recycling.

## Methods

### *Study site*

We conducted this study in a freshwater marsh in the floodplain of the Tanana River near the Bonanza Creek Experimental Forest, ~35 km southwest of Fairbanks, Alaska, USA (lat 64°42'N, long 148°18'W). This region has a relatively short growing season ( $\leq 135$  d) with  $>21$  h of light/d in June. The floodplain lies within an intermontane plateau characterized by wide alluvium-covered lowlands with poorly drained, shallow soils over discontinuous permafrost (Begét et al. 2006). Oxbows and thaw ponds dominate the floodplain landscape, and fluvial deposition and erosion are annual disturbances (Begét et al. 2006). The study site is characteristic of other marsh habitats that occur in the floodplain and has dense stands of beaked sedge (*Carex utriculata*) and swamp horsetail (*Equisetum fluviatile*) surrounding open-water pools with sparse emergent vegetation. The wetland supports grazer fauna including wood frog tadpoles (*Rana sylvatica*) in early spring and the common pond snail *Lymnaea* spp., which is the most abundant grazer in the marsh ( $\sim 30/m^2$ ) throughout the summer growing season. Background concentrations of inorganic nutrients were generally low during the study and were within the range of other wetlands and lakes in the region (reviewed in Wyatt et al. 2010). A detailed description of background physical and chemical conditions for our study site was given by Wyatt and Stevenson (2010).

### *Experimental design*

We manipulated nutrient supply and grazers in situ from 29 June to 22 July 2007 in mesocosms modified from the design described by Greenwood and Lowe (2006). We constructed a raised boardwalk prior to the beginning of the study to prevent the disturbance of wetland sediments during experimental set-up and regular sampling. We constructed 16 mesocosm enclosures by rolling welded wire mesh into a cylinder (40 cm in diameter) and wrapping each cylinder with a layer of 0.1-mm-thick clear window vinyl. Enclosures were evenly spaced throughout an open-water area of the wetland with  $\sim 10\%$  vegetation cover and a water

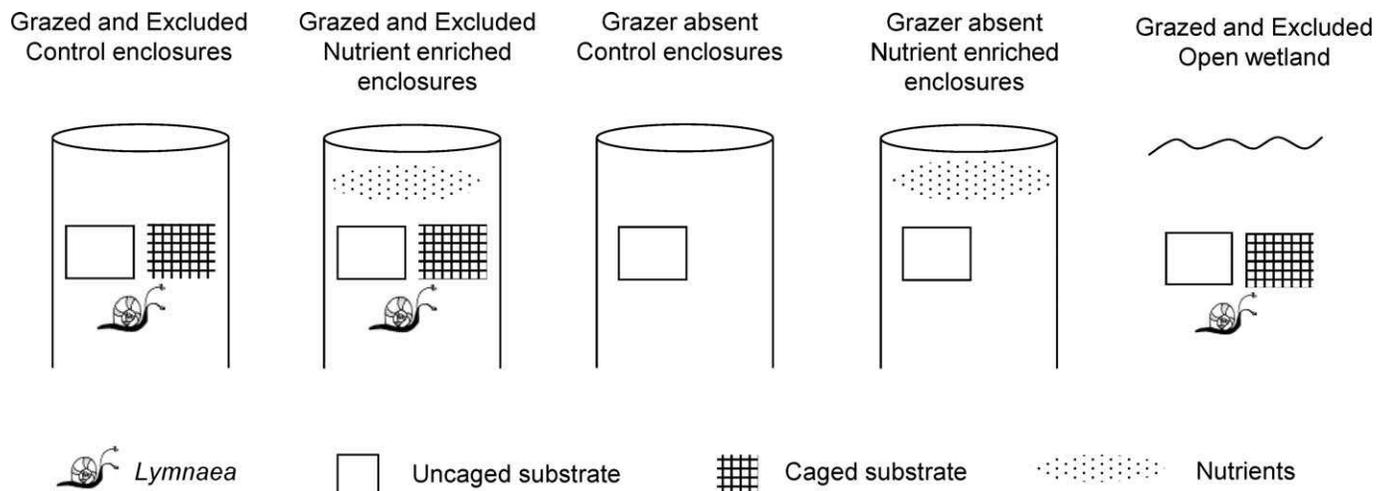


FIG. 1. Schematic diagram of enclosure design. Enclosures were constructed of welded wire mesh (40 cm in diameter  $\times$  85 cm tall) and held  $\sim$ 60 L of water. The top 75 cm of each cylinder was wrapped with 0.1-mm clear window vinyl and embedded 10 cm into sediments with an open top extending 15 cm above the water column. We suspended all substrates attached to frames to maintain a consistent depth of 5 cm below the water surface. We nested caged and uncaged substrates together inside enclosures (grazer-exclusion and grazed treatments) and added natural abundances of snails. All snails were removed from grazer-absent treatment enclosures.

depth of 44–49 cm. Enclosures were pushed into the sediments so that  $\sim$ 15 cm extended above the water surface, which allowed water inside enclosures to be in contact with sediments and kept vegetation intact to simulate natural wetland conditions. We placed 4 ceramic tiles (25 cm<sup>2</sup>) into each enclosure as artificial substrates for algal colonization. We suspended all substrates horizontally by attaching them to a wire frame that could be repositioned to maintain a consistent depth of 5 cm below the water surface.

We used a factorial combination of nutrient enrichment (enriched or control) and grazing (grazed, grazer exclusion, or grazer absent) with 4 replicates of each treatment combination (Fig. 1). We added nutrients from a stock solution every 4 d to achieve water-level concentrations for N = 1000  $\mu$ g/L NaNO<sub>3</sub>, P = 100  $\mu$ g/L NaPO<sub>4</sub>, and Si = 10 mg/L Na<sub>2</sub>O<sub>3</sub>Si after each addition. We assumed these nutrient levels would saturate algal growth rates because they exceeded concentrations reported to be limiting for benthic algae in studies reviewed by Borhardt (1996). We began enrichment after the late-spring thaw to simulate nutrient inputs from groundwater or surface-water runoff (McDougal et al. 1997). We manipulated grazer access inside nutrient enriched and control enclosures by removing grazers completely (grazer absent treatment) or by nesting caged (grazer-exclusion treatment) and uncaged (grazed treatment) substrates together inside enclosures with natural abundances of the snail *Lymnaea* (Fig. 1). Cages around substrata within mesocosm enclosures prohibited

grazing but allowed exchange of water between the grazed and grazer-exclusion treatments to give algae access to nutrients excreted by grazers. Algae in grazer-absent treatments received nutrients only from amendments. Cages were made of 1-mm clear polyethylene Nitex screen (Dynamic Aqua-Supply Ltd., Surrey, British Columbia). We evaluated mesocosm enclosure effects by monitoring conditions at 4 designated sites within the wetland using caged and uncaged substrates without enclosures or nutrient manipulation (open wetland treatment).

#### Sampling methods

We collected and filtered water for dissolved nutrient analysis immediately after each nutrient addition (every 4 d) using a 0.45- $\mu$ m Millex<sup>®</sup>-HA syringe-driven filter unit (Millipore Corporation, Bedford, Massachusetts). We determined concentrations of dissolved inorganic N (DIN) as NO<sub>3</sub> + NO<sub>2</sub>-N (Cd reduction method; APHA 1998) and of silicate (SiO<sub>2</sub>) (molybdate method; APHA 1998) with a Skalar<sup>®</sup> auto-analyzer (Skalar Analytical, Breda, The Netherlands), and of soluble reactive P (SRP) (ascorbic acid method; APHA 1998) with a Genesys<sup>™</sup> 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, UK). We measured water depth, temperature, pH, and conductivity inside and outside each enclosure every 4 d with a meter stick and a calibrated model 556 YSI<sup>®</sup> Multi-Probe (Yellow Springs Instruments, Yellow Springs, Ohio).

In each enclosure, we removed algae from tiles with a toothbrush after 24 d and split the resulting homogenous algal slurry volumetrically for analysis of ash-free dry mass (AFDM) and benthic algal abundance. We were unable to measure chlorophyll *a* because we could not preserve samples in this remote field location. Thus, algal biomass was measured as AFDM, cell density, and total biovolume. We determined AFDM ( $\text{mg}/\text{cm}^2$ ) by drying samples for 24 h at  $105^\circ\text{C}$  and combusting them for 1 h at  $500^\circ\text{C}$  in preweighed aluminum pans to determine the difference between dry mass and ashed mass, respectively (APHA 1998). We preserved a whole water sample in a 2% formalin solution for algal community analysis. We used standard protocols to characterize algal biomass and dominant taxonomic composition. We counted  $\geq 300$  algal cells or colonies/sample in a Palmer–Maloney nanoplankton counting chamber and identified the algae to genus at  $400\times$  magnification (Charles et al. 2002). We quantified benthic algal abundance (cells/ $\text{cm}^2$  of substrate) with the formula provided by Lowe and Laliberte (2006). We calculated biovolume ( $\mu\text{m}^3/\text{cm}^2$  of substrate) by multiplying algal cell density by the estimated cell volume using geometric formulae from Hillebrand et al. (1999).

We evaluated the potential for grazers to recycle N and P by estimating the daily rate of nutrient excretion by the snails. We collected 24 snails from the open wetland and placed each snail in a centrifuge tube filled with 40 mL of filtered water. After a 24 h incubation period, we measured DIN and SRP concentrations with the methods described previously.

#### Statistical analyses

We  $\log(x + 1)$ -transformed all data for statistical analyses if necessary to correct for nonnormal distribution and unequal variances among treatments prior to analysis. We used an unbalanced partly nested analysis of variance (ANOVA) (Quinn and Keough 2002) to determine the effects of nutrient enrichment and grazers on benthic algal biomass as AFDM, cell density, and total biovolume. We examined differences in biovolume of common genera (occurring at  $\geq 5\%$  relative abundance) among treatments with 1-way ANOVA. We used Bonferroni corrections for the algal assemblage analyses to preserve the experiment-wise Type I error rate of  $\alpha = 0.05$ . We used repeated-measures ANOVAs to determine effects of treatments on dissolved nutrients, water depth, water temperature, pH, and conductivity measured throughout the experiment.

In instances when ANOVA indicated significant differences among treatments, we used Tukey post hoc comparison of means tests to discriminate between different factor levels. We performed all statistical analyses with SYSTAT (version 11; SYSTAT Software Inc., Point Richmond, California).

## Results

### Water chemistry

Background levels of inorganic nutrients were low (mean  $\pm$  SE: DIN =  $8.02 \pm 1.28$   $\mu\text{g}/\text{L}$ , SRP =  $8.69 \pm 1.28$   $\mu\text{g}/\text{L}$ ,  $\text{SiO}_2$  =  $12.09 \pm 0.49$   $\text{mg}/\text{L}$ ) and remained nearly constant over the 24-d experiment (Fig. 2A–C). Nutrient levels in the open wetland and control enclosures with and without snails did not differ significantly from each other ( $p > 0.05$ ). Nutrient enrichment increased water-column concentrations of DIN ( $1124.3 \pm 705.6$   $\mu\text{g}/\text{L}$ ), SRP ( $49.6 \pm 47.6$   $\mu\text{g}/\text{L}$ ), and Si ( $35.7 \pm 14.2$   $\text{mg}/\text{L}$ ) to levels significantly greater than in the open wetland and control enclosures ( $p < 0.05$ ; Fig. 2A–C). Water-column dissolved nutrient concentrations inside nutrient-enriched enclosures did not differ between treatments with or without snails ( $p > 0.05$ ). Water depth ( $45.1 \pm 0.5$  cm), temperature ( $16 \pm 0.05^\circ\text{C}$ ), pH ( $7.5 \pm 0.3$ ), and conductivity ( $0.37 \pm 0.006$   $\mu\text{S}/\text{cm}$ ) varied during the experiment but did not differ significantly among treatments ( $p > 0.05$ ; data not shown).

### Algal biomass

Significant effects of grazing were observed only after enrichment. Benthic algal biomass was similar between the open wetland and control enclosures across all grazing treatments ( $p > 0.05$ ; Figs 3A, B, 4A, B). AFDM ( $F_{2,13} = 81.91$ ,  $p < 0.0001$ ; Fig. 3A), cell density ( $F_{2,13} = 122.6$ ,  $p < 0.0001$ ; Fig. 3B), and total biovolume ( $F_{2,13} = 14.86$ ,  $p = 0.004$ ; Fig. 4C) were significantly greater in nutrient-enriched than in control enclosures. In nutrient-enriched enclosures, AFDM ( $F_{2,11} = 7.88$ ,  $p = 0.01$ ; Fig. 3A), cell density ( $F_{2,11} = 7.26$ ,  $p = 0.01$ ; Fig. 3B), and total biovolume ( $F_{2,11} = 7.92$ ,  $p = 0.01$ ; Fig. 4C) were significantly lower in grazed than in grazer-exclusion treatments. In nutrient-enriched enclosures, algal AFDM, cell density, and total biovolume was significantly greater in the grazer-exclusion treatment than in grazed and grazer-absent treatments ( $p < 0.05$ ) but did not differ significantly between the grazed and grazer-absent treatments ( $p > 0.05$ ). The nutrient  $\times$  grazer interaction term was significant for AFDM ( $F_{3,11} = 5.37$ ,  $p = 0.02$ ) and total biovolume ( $F_{3,11} = 4.64$ ,  $p = 0.02$ ).

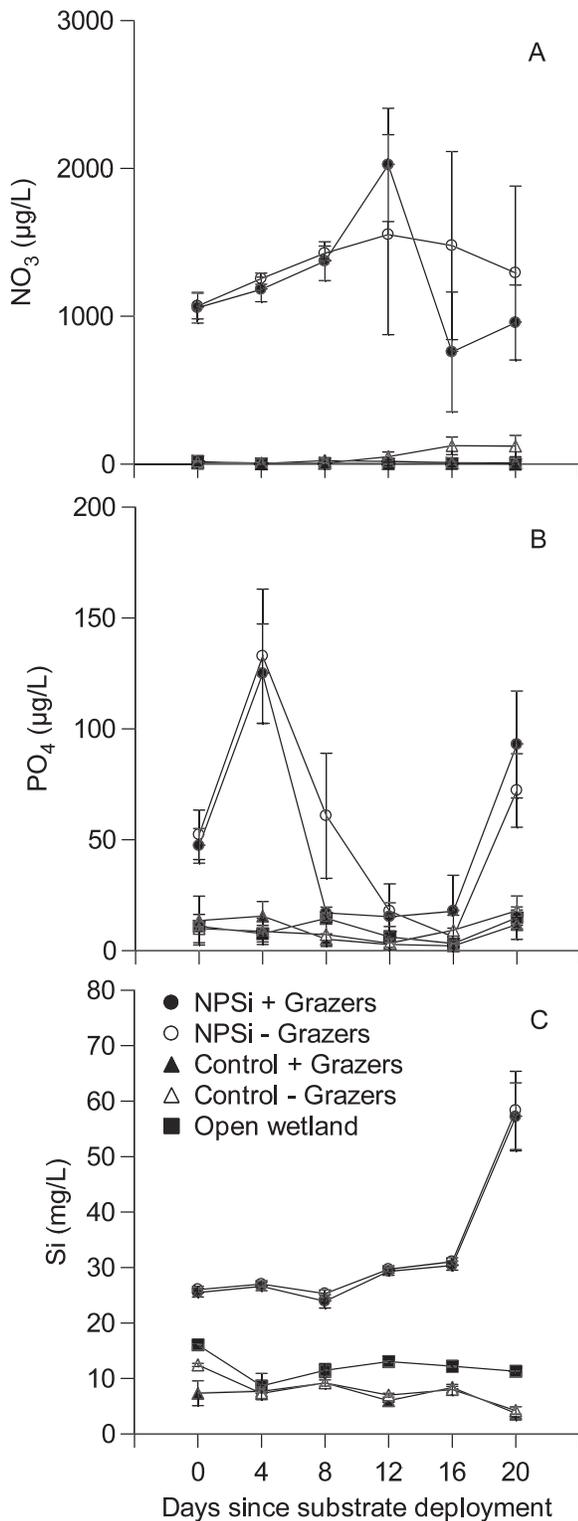


FIG. 2. Dissolved nutrient concentrations of  $\text{NO}_3$  (A),  $\text{PO}_4$  (B), and Si (C) in nutrient enriched, control, and open wetland enclosures with (+) and without (-) grazers.

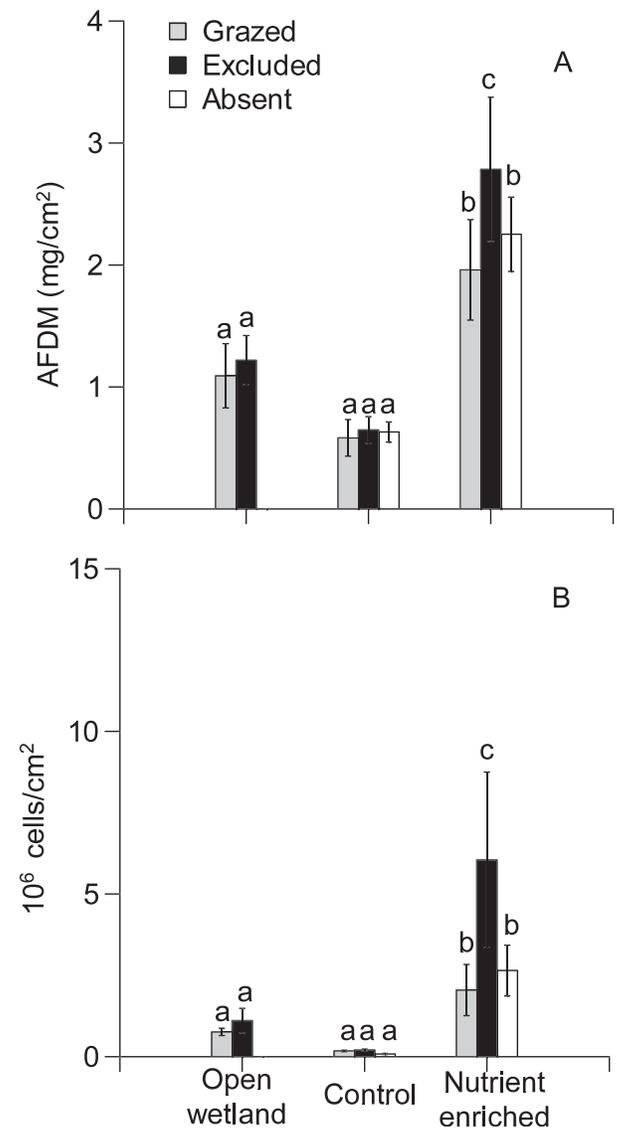


FIG. 3. Mean ( $\pm 1$  SE;  $n = 4$ ) ash-free dry mass (AFDM) (A) and cell density (B) in the open wetland, control, and nutrient-enriched enclosures with and without grazers. Bars with the same letter are not significantly different among treatments.

#### Taxonomic composition

The algal community in the open wetland consisted of primarily *Mougeotia* and *Gloeocystis* (Chlorophyta), *Trachelomonas* and *Euglena* (Euglenophyta), and *Chroococcus* (Cyanobacteria), which made up  $\sim 90\%$  of the total biovolume (Fig. 4A). All taxa represented a similar proportion of total biovolume in the control treatment compared to in the open wetland except the proportion of *Euglena* ( $F_{7,29} = 17.2$ ,  $p < 0.001$ ) was significantly greater in the control treatment than the open wetland (Fig. 4B). Nutrient enrichment

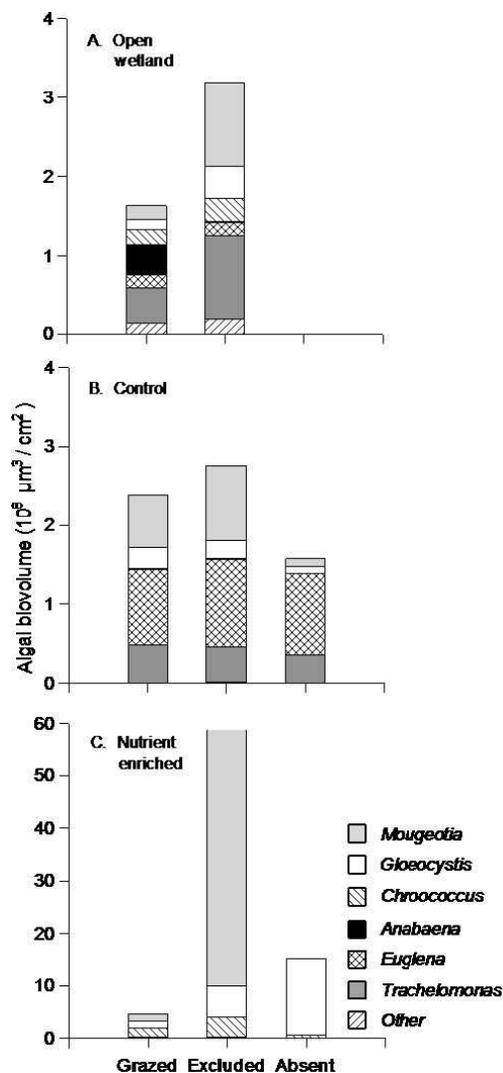


FIG. 4. Taxonomic composition and total biovolume of algae with >5% relative abundance in the open wetland (A), control (B), and nutrient-enriched (C) enclosures with and without grazers.

increased the proportion of *Mougeotia*, *Gloeocystis* ( $F_{7,29} = 14.8$ ,  $p < 0.001$ ), and *Chroococcus* ( $F_{7,29} = 44.7$ ,  $p < 0.001$ ) compared to the control (Fig. 4C). Grazing had little effect on the algal community under low-nutrient conditions. However, in nutrient-enriched enclosures, the proportion of *Mougeotia* was significantly lower ( $F_{7,24} = 2.5$ ,  $p = 0.04$ ; Fig. 4C) and the proportions of *Chroococcus* ( $F_{7,24} = 29.6$ ,  $p < 0.001$ ) and *Gloeocystis* ( $F_{7,24} = 12.3$ ,  $p < 0.001$ ) were significantly higher in grazed than in grazer-exclusion treatments. Grazer-absent treatments in nutrient-enriched enclosures were dominated by *Gloeocystis* and *Chroococcus* and lacked *Mougeotia*. A combination of *Limnothrix*, *Aphanocapsa*, *Ophiocytium*, *Ulothrix*, and *Nitzschia* made up <10% of the total biovolume in any 1 treatment.

#### Nutrient recycling by grazers

Excretion rates of DIN and SRP were  $0.0004 \text{ mg snail}^{-1} \text{ d}^{-1}$  and  $0.045 \text{ mg snail}^{-1} \text{ d}^{-1}$ , respectively. We multiplied the excretion rates of DIN and SRP by the estimated number of snails in the wetland ( $30 \text{ snails/m}^2$ ), and calculated that snails could regenerate N at a rate of  $7.5 \text{ mg/d}$  and P at  $844.8 \text{ mg/d}$ . When we estimated concentration changes by accounting for the approximate volume of water in the wetland, we calculated that snails could regenerate N at a rate of  $0.0002 \text{ mg L}^{-1} \text{ d}^{-1}$  and P at  $0.019 \text{ mg L}^{-1} \text{ d}^{-1}$ .

#### Discussion

As predicted, addition of nutrients resulted in a significant increase in benthic algal biomass and a shift in taxonomic composition in this northern boreal wetland. An increase in N and P availability with increased soil weathering and organic matter mineralization is expected for the region because of climate-change processes (Bridgman et al. 1995, Rouse et al. 1997). Our results suggest that this increase probably will increase benthic algal biomass in northern boreal wetlands. The increase in algal biomass in response to a combination of N and P in our study was similar to increases reported in other wetland studies conducted within the Tanana River Floodplain (Wyatt et al. 2010) and to those in temperate regions (Wu and Mitsch 1998, Robinson et al. 2000, Scott et al. 2005). Our findings differ from results from the subtropical Everglades where nutrient enrichment, especially P, causes an overall decrease in algal biomass because of the loss of the native cyanobacterial mat (reviewed by McCormick and Stevenson 1998, Gaiser et al. 2006, Richardson 2010).

The shift in algal taxonomic composition from a diverse assemblage in ambient conditions to one dominated by green algae and cyanobacteria after nutrient enrichment also has been documented in temperate and subtropical wetlands receiving nutrient enrichment from urban or agricultural runoff (Murkin et al. 1991, McCormick et al. 2001). The ability of some filamentous green algae to exploit high nutrient concentrations and to outcompete other taxa for light and space (i.e., Graham et al. 1996) may explain the increase in *Mougeotia* following nutrient enrichment in this shallow boreal wetland. Our findings are consistent with those reported from the Florida Everglades (McCormick and O'Dell 1996) and Delta Marsh, Manitoba (Robinson et al. 1997), where direct nutrient amendments and nutrient-release from reflooded sediments, respectively, resulted in an overall increase in taxa from the family Zygnemataceae (*Mougeotia*, *Spirogyra*, *Zygnema*).

Grazing decreased algal biomass with and without nutrient enrichment, but results varied in magnitude between treatments. In the absence of nutrient limitation, grazing strongly influenced the quantity of algal biomass as well as the taxonomic composition and growth form of the algal assemblage. This effect is consistent with trophic theory ( Hairston et al. 1960, Persson et al. 1988) where, in the absence of a higher predator, grazers are free to consume any increase in algal biomass that may be stimulated by nutrient enrichment. This finding indicates that, much like in lake and stream ecosystems (Hansson 1992, Feminella and Hawkins 1995, Steinman 1996, Hillebrand 2002), benthic grazers can maintain low algal biomass accumulation in northern boreal wetlands even in conditions of increased resource availability.

The decrease in *Mougeotia* on grazed substrates is consistent with results of other studies, in which taxa that extended above the substratum were removed at a higher rate than those with a more-prostrate or low-profile growth form (Cuker 1983, Steinman 1996, Hillebrand et al. 2002). The lower abundance of *Mougeotia* in the grazer-absent treatment may have been the result of different proportions of nutrients made available by snails within the periphyton matrix (see discussion below). The removal of a large overstory species like *Mougeotia* promotes the growth of smaller, faster-growing understory species and leads to an increase in overall algal productivity because of increased resource availability (McCormick and Stevenson 1991). This process may explain the increased proportion of *Chroococcus* and *Gloeocystis* in grazed and grazer-absent treatments and suggests that these taxa were able to take advantage of nutrient inputs but were unable to compete for other resources, such as light, in treatments where filamentous taxa dominated the algal community.

The significant interaction between nutrients and grazers suggests that the algal community is under dual control from the bottom-up (nutrient limitation) and from the top-down (consumption by herbivores). These interacting and opposing influences of nutrients and grazing are consistent with results reported in the literature from lakes and streams (Rosemond et al. 1993, Hillebrand 2002), reflecting a similar importance of their regulatory effects on benthic algal biomass and taxonomic composition in boreal wetlands. However, our results suggest that the relative strengths of top-down vs bottom-up control were not equivalent. Our experimental design allowed us to examine both independent and interactive effects of nutrients and grazing, so we were able to see that nutrients had a consistently greater effect on algal biomass and taxonomic composition than did grazing, a result

indicating that nutrient limitation was the stronger regulatory factor at our study site. This finding differs from results reported by Hillebrand (2002), who determined through meta-analysis that grazers are the stronger regulatory factor influencing algal assemblages more often than nutrients in lakes, streams, and coastal environments.

Despite the small direct effects of grazers under low-nutrient conditions, our results suggest that they may influence algal biomass indirectly by recycling the low concentrations of nutrients that are present. We expected that algal biomass would be similar between the grazer-exclusion and grazer-absent treatments because neither treatment was grazed and that algal biomass in both would be greater than in grazed treatments. Instead, algal biomass was similar in grazer-absent and grazed treatments. Moreover, algal biomass increased 2× in grazer-exclusion treatments. Snails are large and highly mobile consumers that are capable of recycling nutrients at large spatial scales, which facilitates the resuspension and movement of nutrients for algal uptake and use (Frost et al. 2002, Vanni 2002, Abbott and Bergey 2007). Snails in our study site excreted a small but potentially important amount of nutrients, especially P, in their waste. Algae in the grazed treatment may have been able to use recycled nutrients to regenerate biomass after consumptive losses. The absence of consumer-driven nutrient recycling in grazer-absent enclosures may have limited biomass accumulation to the point that it was more similar to biomass in the grazed treatment than in the grazer-exclusion treatment. Algal biomass excluded with a cage was inaccessible to grazers and exposed to excreted nutrients, which may explain the greater biomass in grazer-exclusion than in grazed and grazer-absent treatments in enriched enclosures.

Evidence exists for the positive effects of consumer-driven nutrient recycling on algal growth rates in lakes (Elser et al. 2000, Vanni et al. 2002, Liess and Haglund 2007) and streams (McCormick and Stevenson 1991, Evans-White and Lamberti 2006), but our results suggest that consumer-driven nutrient recycling may strongly affect algal growth in shallow boreal wetlands. In many wetland habitats, primary production depends on the rate of nutrient mineralization. Therefore, the slower nutrients are released by decomposition, the less available nutrients are to the ecosystem (de Mazancourt et al. 1998). Consumer-driven nutrient recycling may be an important source of N and P to autotrophs in the water column and benthos in boreal wetlands, where large quantities of nutrients are locked away in permanently frozen soils (Carpenter et al. 1992, Duff et al. 1999, Hinzman et al.

2005), than in regions with faster rates of nutrient remineralization (Frost et al. 2002).

The available literature on benthic algal assemblages and the factors that regulate their structure and function is much less for freshwater wetlands than for lakes and streams (Robinson et al. 2000). This lack of information is particularly acute for northern boreal regions where wetlands are abundant and extremely vulnerable to disturbances associated with climate change. Our data provide evidence that nutrients and grazing are important factors regulating benthic algal biomass and community composition in a northern boreal wetland. They suggest that nutrients were the stronger regulatory factor, but grazing quickly became important after nutrient addition. Therefore, grazing may play an increasingly important role in the future if nutrient inputs increase as expected with climate change (i.e., increased permafrost collapse and soil weathering). Our results support our hypothesis that nutrient enrichment stimulates algal accumulation and demonstrate that the strong positive relationship observed between nutrient addition and algal biomass at lower latitudes persists in high-latitude aquatic ecosystems. The ability of grazers to suppress algal accumulation following enrichment supports our hypothesis and may provide insight to the dampened response of algae to nutrients previously observed in high-latitude regions (i.e., Flanagan et al. 2003). Furthermore, our results suggest the potential importance of consumer-driven nutrient recycling to algal productivity and wetland biogeochemistry, which may be particularly significant for northern boreal regions where large quantities of nutrients are rendered inaccessible by the slowly decomposing organic matter.

### Acknowledgements

This research was supported by the Grant-in-Aid of Research from the Phycological Society of America, a North American Benthological Society President's award to ARR, and a Center for Water Sciences Venture Grant at Michigan State University awarded to RJS. This research also was supported by the Bonanza Creek Long-Term Ecological Research (LTER) program (US Forest Service grant number PNW01-JV11261952-231 and National Science Foundation grant number DEB-0080609). We thank Merritt Turetsky for logistical support while working in Alaska and the members of the J. B. Jones laboratory in the Bonanza Creek LTER and D. Masiak in the School of Natural Resources and Agricultural Sciences at the University of Alaska Fairbanks for their assistance in analyses. We thank 2 anonymous referees and

Michelle Baker for helpful comments on earlier versions of this manuscript.

### Literature Cited

- ABBOTT, L. L., AND E. A. BERGEY. 2007. Why are there so few algae on snail shells? The effects of grazing, nutrients and shell chemistry on the algae on shells of *Helisoma trivolvis*. *Freshwater Biology* 52:2112–2120.
- APHA (AMERICAN PUBLIC HEALTH ASSOCIATION). 1998. Standard methods for the examination of water and wastewater. 20<sup>th</sup> edition. American Public Health Association, American Water Works Association, and Water Environment Federation, Washington, DC.
- BEGÉT, J. E., D. STONE, AND D. L. VERBYLA. 2006. Regional overview of interior Alaska. Pages 12–20 in F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (editors). *Alaska's changing boreal forest*. Oxford University Press, New York.
- BORCHARDT, M. A. 1996. Nutrients. Pages 183–227 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York.
- BRIDGHAM, S. D., C. A. JOHNSTON, J. PASTOR, AND K. UPDEGRAFF. 1995. Potential feedbacks of northern wetlands on climate change. *BioScience* 45:262–274.
- BROWDER, J. A., P. J. GLEASON, AND D. R. SWIFT. 1994. Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. Pages 379–418 in S. M. Davis and J. C. Ogden (editors). *Everglades: the ecosystem and its restoration*. St Lucie Press, Delray Beach, Florida.
- CARPENTER, S. R., S. G. FISHER, N. B. GRIMM, AND J. G. KITCHELL. 1992. Global change and freshwater ecosystems. *Annual Review of Ecological Systems* 23:119–139.
- CHAPIN, F. S., M. W. OSWOOD, K. VAN CLEVE, L. A. VIERECK, AND D. L. VERBYLA (EDITORS). 2006. *Alaska's changing boreal forest*. Oxford University Press, New York.
- CHARLES, D. F., C. KNOWLES, AND R. S. DAVIS. 2002. Protocols for the analysis of algal samples collected as part of the U.S. Geological Survey National Water-Quality Assessment program. Report No. 02–06. Academy of Natural Sciences, Philadelphia, Pennsylvania.
- CUKER, B. E. 1983. Grazing and nutrient interactions in controlling the activity and composition of the epilithic algal community of an Arctic lake. *Limnology and Oceanography* 28:133–141.
- DE MAZANCOURT, C., M. LOREAU, AND L. ABBADIE. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* 79:2242–2252.
- DUFF, K., T. E. LAING, J. P. SMOL, AND D. R. LEAN. 1999. Limnological characteristics of lakes located across Arctic treeline in northern Russia. *Hydrobiologia* 391: 205–222.
- ELSER, J. J., W. J. O'BRIEN, D. R. DOBBERFUHL, AND T. E. DOWLING. 2000. The evolution of ecosystem processes: growth rate and elemental stoichiometry of a key herbivore in temperate and arctic habitats. *Journal of Evolutionary Biology* 13:845–853.

- EVANS-WHITE, M. A., AND G. A. LAMBERTI. 2006. Stoichiometry of consumer-driven nutrient recycling across nutrient regimes in streams. *Ecology Letters* 9:1186–1197.
- FAIRCHILD, G. W., R. L. LOWE, AND W. B. RICHARDSON. 1985. Algal periphyton growth on nutrient-diffusing substrates: an in situ bioassay. *Ecology* 66:465–472.
- FEMINELLA, J. W., AND C. P. HAWKINS. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *Journal of the North American Benthological Society* 14:465–509.
- FLANAGAN, K. M., E. MCCAULEY, F. WRONA, AND T. PROWSE. 2003. Climate change: the potential for latitudinal effects on algal biomass in aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 60:635–639.
- FRANCOEUR, S. N. 2001. Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. *Journal of the North American Benthological Society* 20:358–368.
- FROST, P. C., R. S. STELZER, G. A. LAMBERTI, AND J. J. ELSER. 2002. Ecological stoichiometry of trophic interactions in the benthos: understanding the role of C:N:P ratios in lentic and lotic habitats. *Journal of the North American Benthological Society* 21:515–528.
- GABOR, T. S., H. R. MURKIN, M. P. STANTON, J. A. BOUGHEN, AND R. D. TITMAN. 1994. Nutrient additions to wetlands in the Interlake region of Manitoba, Canada: effects of a single pulse addition in spring. *Hydrobiologia* 280: 497–510.
- GAISER, E. E., D. L. CHILDERS, R. D. JONES, J. H. RICHARDS, L. J. SCINTO, AND J. C. TREXLER. 2006. Periphyton responses to eutrophication in the Florida Everglades: cross-system patterns of structural and compositional change. *Limnology and Oceanography* 51:617–630.
- GAISER, E. E., L. J. SCINTO, J. H. RICHARDS, K. JAYACHANDRAN, D. L. CHILDERS, J. D. TREXLER, AND R. D. JONES. 2004. Phosphorus in periphyton mats provides best metric for detecting low level P enrichment in an oligotrophic wetland. *Water Research* 38:507–516.
- GAISER, E. E., J. C. TREXLER, J. H. RICHARDS, D. L. CHILDERS, D. LEE, A. L. EDWARDS, L. J. SCINTO, K. JAYACHANDRAN, G. B. NOE, AND R. D. JONES. 2005. Cascading ecological effects of low level phosphorus enrichment in the Florida Everglades. *Journal of Environmental Quality* 34:717–723.
- GLEASON, P. J., AND W. SPACKMAN. 1974. Calcareous periphyton and water chemistry in the Everglades. Pages 146–181 in P. J. Gleason (editor). *Environments of south Florida: present and past, memoir 2*. Miami Geological Society, Miami, Florida.
- GOLDSBOROUGH, L. G., AND G. G. C. ROBINSON. 1996. Patterns in wetlands. Pages 77–117 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York.
- GRAHAM, J. M., P. ARANCIBIA-AVILA, AND L. E. GRAHAM. 1996. Effects of pH and selected metals on growth of the filamentous green alga *Mougeotia* under acidic conditions. *Limnology and Oceanography* 41:263–270.
- GREENWOOD, J. L., AND R. L. LOWE. 2006. The effects of pH on a periphyton community in an acidic wetland, USA. *Hydrobiologia* 561:71–82.
- HAIRSTON, N., F. SMITH, AND L. SLOBODKIN. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- HANSSON, L. A. 1992. The role of food chain composition and nutrient availability in shaping algal biomass development. *Ecology* 73:241–247.
- HILL, W. R., M. G. RYON, AND E. M. SCHILLING. 1995. Light limitation in a stream ecosystem: Responses by primary producers and consumers. *Ecology* 76:1297–1309.
- HILLEBRAND, H. 2002. Top-down versus bottom-up control of autotrophic biomass: a meta-analysis on experiments with periphyton. *Journal of the North American Benthological Society* 21:349–369.
- HILLEBRAND, H., C. D. DÜRSELEN, D. B. KIRSCHTEL, U. POLLINGER, AND T. ZOHARY. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35:403–424.
- HILLEBRAND, H., M. KAHLERT, A. L. HAGLUND, U. G. BERNINGER, S. NAGEL, AND S. WICKHAM. 2002. Controls of microbenthic communities by grazing and nutrient supply. *Ecology* 83:2205–2219.
- HINZMAN, L. D., N. D. BETTEZ, W. R. BOLTON, F. S. CHAPIN, M. B. DYURGEROV, C. L. FASTIE, B. GRIFFITH, R. D. HOLLISTER, A. HOPE, H. P. HUNTINGTON, A. M. JENSEN, G. J. JIA, T. J. GENSON, D. L. KANE, D. R. KLEIN, G. KOFINAS, A. H. LYNCH, A. H. LLOYD, A. D. MCGUIRE, F. E. NELSON, W. C. OECHEL, T. E. OSTERKAMP, C. H. RACINE, V. E. ROMANOVSKY, R. S. STONE, D. A. STOW, M. STURM, C. E. TWEEDIE, G. L. VOURLITIS, M. WALKER, D. A. WALKER, P. J. WEBBER, J. M. WELKER, K. S. WINKER, AND K. YOSHIKAWA. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* 72:251–298.
- LISS, A., AND A. L. HAGLUND. 2007. Periphyton responds differentially to nutrients recycled in dissolved or faecal pellet form by the snail grazer *Theodoxus fluviatilis*. *Freshwater Biology* 52:1997–2008.
- LOWE, R. L., AND G. D. LALIBERTE. 2006. Benthic stream algae: distribution and structure. Pages 327–356 in F. R. Hauer and G. A. Lamberti (editors). *Methods in stream ecology*. 2<sup>nd</sup> edition. Academic Press, San Diego, California.
- MCCORMICK, P. V., AND M. B. O'DELL. 1996. Quantifying periphyton responses to phosphorus in the Florida Everglades: a synoptic-experimental approach. *Journal of the North American Benthological Society* 14: 450–468.
- MCCORMICK, P. V., M. B. O'DELL, R. B. E. SHUFORD, J. G. BACKUS, AND W. C. KENNEDY. 2001. Periphyton responses to experimental phosphorus enrichment in a subtropical wetland. *Aquatic Botany* 71:119–139.
- MCCORMICK, P. V., R. B. E. SHUFORD, J. G. BACKUS, AND W. C. KENNEDY. 1998. Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, U.S.A. *Hydrobiologia* 362:185–208.

- McCORMICK, P. V., AND R. J. STEVENSON. 1991. Grazer control of nutrient availability in the periphyton. *Oecologia* (Berlin) 86:287–291.
- McCORMICK, P. V., AND R. J. STEVENSON. 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. *Journal of Phycology* 34:726–733.
- McDOUGAL, R. L., L. G. GOLDSBOROUGH, AND B. J. HANN. 1997. Responses of a prairie wetland to press and pulse additions of inorganic nitrogen and phosphorus: production by planktonic and benthic algae. *Archiv für Hydrobiologie* 140:145–167.
- MURKIN, H. R., J. B. POLLARD, M. P. STANTON, J. A. BOUGHEN, AND R. D. TITMAN. 1994. Nutrient additions to wetlands in the Interlake region of Manitoba, Canada: effects of periodic additions throughout the growing season. *Hydrobiologia* 280:483–495.
- MURKIN, H. R., M. P. STANTON, J. A. BOUGHEN, J. B. POLLARD, AND R. D. TITMAN. 1991. Nutrient status of wetlands in the interlake region of Manitoba, Canada. *Wetlands* 11: 105–122.
- PERSSON, L., G. ANDERSSON, S. HAMRIN, AND L. JOHANSSON. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. Pages 46–65 in S. Carpenter (editor). *Complex interactions in lake communities*. Springer, New York.
- QUINN, G. P., AND M. J. KEOUGH. 2002. Split-plot and repeated measures designs: partly nested analyses of variance. Pages 301–338 in G. P. Quinn and M. J. Keough (editors). *Experimental design and data analysis for biologists*. Cambridge University Press, New York.
- RICHARDSON, C. J. 2008. *The Everglades experiments: lessons for ecosystem restoration*. Springer, New York.
- RICHARDSON, C. J. 2010. The Everglades: North America's subtropical wetland. *Wetlands Ecology and Management* 18:517–542.
- ROBINSON, G. G. C., S. E. GURNEY, AND L. G. GOLDSBOROUGH. 1997. Response of benthic and planktonic algal biomass to experimental water-level manipulation in a prairie lakeshore wetland. *Wetlands* 17:167–181.
- ROBINSON, G. G. C., S. E. GURNEY, AND L. G. GOLDSBOROUGH. 2000. Algae in prairie wetlands. Pages 163–198 in H. R. Murkin, A. G. van der Valk, and W. R. Clark (editors). *Prairie wetland ecology: the contribution of the Marsh Ecology Research Program*. Iowa State University Press, Ames, Iowa.
- ROSEMOND, A. D., P. J. MULHOLLAND, AND S. H. BRAWLEY. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. *Canadian Journal of Fisheries and Aquatic Sciences* 57:66–75.
- ROSEMOND, A. D., P. J. MULHOLLAND, AND J. W. ELWOOD. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74:1264–1280.
- ROUSE, W. R., M. S. V. DOUGLAS, R. E. HECKY, A. E. HERSHEY, G. W. KLING, L. LESACK, P. MARSH, M. McDONALD, B. J. NICHOLSON, N. T. ROULET, AND J. P. SMOL. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes* 11:873–902.
- SCHINDLER, D. W. 1998. A dim future for boreal waters and landscapes. *BioScience* 48:157–164.
- SCOTT, J. T., R. D. DOYLE, AND C. T. FILSTRUP. 2005. Periphyton nutrient limitation and nitrogen fixation potential along a wetland nutrient-depletion gradient. *Wetlands* 25: 439–448.
- SKLAR, F. H., M. J. CHIMNEY, S. NEWMAN, P. V. McCORMICK, D. GAWLIK, S. MIAO, C. McVOY, W. SAID, J. NEWMAN, C. CORONADO, G. CROZIER, M. KORVELA, AND K. RUTCHEY. 2005. The ecological-societal underpinnings of Everglades restoration. *Frontiers in Ecology and the Environment* 3:161–169.
- STEINMAN, A. D. 1996. Effects of grazers on freshwater benthic algae. Pages 341–373 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York.
- VANNI, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecological Systems* 33: 341–370.
- VANNI, M. J., A. S. FLECKER, J. M. HOOD, AND J. L. HEADWORTH. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecology Letters* 5:285–293.
- WETZEL, R. G. 1996. Benthic algae and nutrient cycling in lentic freshwater ecosystems. Pages 641–667 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York.
- WETZEL, R. G. 2006. Wetland ecosystem processes. Pages 285–312 in D. P. Batzer and R. A. Sharitz (editors). *Ecology of freshwater and estuarine wetlands*. University of California Press, Los Angeles, California.
- WU, X., AND W. J. MITSCH. 1998. Spatial and temporal patterns of algae in newly constructed freshwater wetlands. *Wetlands* 18:9–20.
- WYATT, K. H., AND R. J. STEVENSON. 2010. Effects of acidification and alkalization on a periphytic algal community in an Alaskan wetland. *Wetlands* 30: 1193–1202.
- WYATT, K. H., R. J. STEVENSON, AND M. R. TURETSKY. 2010. The importance of nutrient co-limitation in regulating algal community composition, productivity, and algal-derived DOC in an oligotrophic marsh in interior Alaska. *Freshwater Biology* 55:1845–1860.

Received: 14 December 2010

Accepted: 9 May 2011