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THE ROLE OF LIGHT AVAILABILITY AND HERBIVORY ON ALGAL RESPONSES TO NUTRIENT ENRICHMENT IN A RIPARIAN WETLAND, ALASKA[1]

Allison R. Rober,[2,3] *R. Jan Stevenson, and Kevin H. Wyatt*[2]

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

We investigated how the relative availability of solar radiation in the presence or absence of grazing alters the ability of benthic algae to respond to nutrient enrichment in an Alaskan marsh. We used a factorial mesocosm experiment that included nutrient enrichment (enriched or control), grazing (grazed or ungrazed), and light (unshaded or shaded) to simulate shading by macrophytes early and late in the growing season, respectively. We found stronger effects of grazers and nutrients compared to light on benthic algal biomass and taxonomic composition. Algal biomass increased in nutrient-enriched treatments and was reduced by grazing. Shading did not have an effect on algal biomass or taxonomic composition, but the concentration of chl *a* per algal biovolume increased with shading, demonstrating the ability of algae to compensate for changes in light availability. Algal taxonomic composition was more affected by grazer presence than nutrients or light. Grazer-resistant taxa (basal filaments of *Stigeoclonium*) were replaced by diatoms (*Nitzschia*) and filamentous green algae (*Ulothrix*) when herbivores were removed. The interacting and opposing influences of nutrients and grazing indicate that the algal community is under dual control from the bottom-up (nutrient limitation) and from the top-down (consumption by herbivores), although grazers had a stronger influence on algal biomass and taxonomic composition than nutrient enrichment. Our results suggest that low light availability will not inhibit the algal response to elevated nutrient concentrations expected with ongoing climate change, but grazers rapidly consume algae following enrichment, masking the effects of elevated nutrients on algal production.

Key index words: **Alaska; algae; boreal; climate change; grazing; light; nutrients; wetland**

Wetlands are ecosystems defined by their hydrology, soil characteristics, and vegetation structure. Algal communities can be abundant in wetlands and contribute to many of the chemical and biological processes that characterize wetland ecosystems (Goldsborough and Robinson 1996). Although algal communities typically have less standing biomass in wetlands compared to plants, net energy production (i.e., basal resources) from algae can surpass that of macrophytes due to the rapid turnover and labile nature of algal cells (Robinson et al. 2000, Richardson 2010). During growth, algae transform and regulate the fate of nutrients in wetlands directly through the release and uptake of nutrients within the water column (Wetzel 2006, Wyatt et al. 2012), and indirectly by oxygenating the sediment–water interface during photosynthesis, which can inhibit the release of nutrients from sediments (Carlton and Wetzel 1988). Despite their role in these, as well as other wetland functions, we know relatively little about the factors that regulate algal communities in wetlands, especially in northern boreal regions, where wetlands are abundant and likely to be altered by ongoing climate change (Chapin et al. 2006).

Across aquatic ecosystems, algal primary production is generally controlled by factors regulating from the bottom-up (resources) and from the top-down (herbivory). Although these structuring forces are widely accepted to be interactive in aquatic ecosystems (Hillebrand 2002, Liess and Kahlert 2007), the degree to which each process influences producer biomass varies among ecosystems (Hillebrand et al. 2007). In northern wetlands, algal production tends to be constrained by low nutrient levels (Rober et al. 2014), which limits energy transfer to consumers. Increasing nutrient availability releases constraints on algal productivity (Wyatt et al. 2010), which increases energy transfer to higher trophic levels (Rober et al. 2011). Increased herbivory can, in turn, reduce algal biomass and alter the size and composition of algal communities available for ecosystem functions (Feminella and Hawkins 1995, Bell 2002).

Processes associated with ongoing climate change are expected to alter nutrient cycling in northern ecosystems with potential implications for the regulation of algal communities in wetlands. In particular, altered thermal regimes in northern ecosystems are expected to increase the extent of seasonal ice thaw (Schuur et al. 2013) and stimulate microbial decomposition, which will likely promote nutrient

[1]Received 11 December 2014. Accepted 27 January 2015.
[2]Present address: Department of Biology, Ball State University, Muncie, Indiana 47306, USA.
[3]Author for correspondence: e-mail arrober@bsu.edu.
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mineralization in the expanded active soil layer across northern ecosystems (Bridgham et al. 1995, Mack et al. 2004). Elevated nutrient levels are expected to increase primary production in aquatic ecosystems, including wetlands (Rouse et al. 1997, Wyatt et al. 2010). Although increased algal production in conditions of elevated nutrient availability is anticipated to promote energy transfer to higher trophic levels (Schindler et al. 1997, Estes et al. 2011), it is unknown how other factors unique to wetlands, including light availability, will interact with nutrients to regulate the role of algal communities in the wetland food web.

Light availability is among the most important factors regulating benthic algal communities in aquatic ecosystems (Hill 1996). Light conditions in wetlands are dynamic and include seasonal changes in incident radiation and light attenuation associated with shading by macrophytes (Robinson et al. 2000), which serve as a primary substrate for algal colonization (Vis et al. 2006). Shading by macrophytes is especially important in shallow northern wetlands where biomass accumulates rapidly in response to long days (over 20 h of daylight) during the summer growing season (Chapin et al. 2006). Light penetration to benthic habitats in wetlands is also reduced by colored humic substances (Ask et al. 2009), which are derived from the decomposition of organic matter and absorb incident light (Carpenter et al. 1998). Consequently, potential light constraints make it difficult to evaluate the ability for algae to acquire and use essential nutrients (Grimshaw et al. 1997, Karlsson et al. 2009, Liess et al. 2009) that are expected to be made available with accelerated nutrient cycling associated with ongoing climate change.

The aim of this study was to investigate how the relative amount of solar radiation in the presence and absence of grazing influences the ability of benthic algae to respond to nutrient enrichment in a northern boreal wetland. We tested the following hypotheses: (i) Nutrient enrichment stimulates algal accumulation, (ii) grazers regulate algal responses to nutrients by suppressing algal accumulation, and (iii) shading by macrophytes reduces the ability of algae to respond to nutrient enrichment. The results of this study add insight into the balance between resource availability and consumption, which ultimately determines the biomass and taxonomic composition of primary producers.

MATERIALS AND METHODS

Study site. We conducted this study in a freshwater marsh located on the floodplain of the Tanana River near the Bonanza Creek Experimental Forest, situated ~35 km southwest of Fairbanks, Alaska, USA (latitude 64.42° N, longitude 148.18° W). The area within interior Alaska has large seasonal fluctuations in daylight with more than 21 h in June and less than 3 h in December. The low sun angle in both summer and winter limits the solar radiation that reaches the surface in interior Alaska. In Fairbanks (65° N), the maximum solar angle is 48.5° at the summer solstice, resulting in daily solar radiation of 22,375 kJ $\cdot$ m^{-2} $\cdot$ d^{-1} in June (Hinzman et al. 2006). The study site is characteristic of other marsh habitats that occur in oxbows along the flood plain (Rober et al. 2014), which are shallow with 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. that is the most abundant grazer in the marsh (~30 m^{-2}) throughout the summer growing season. Background concentrations of inorganic nutrients were generally low (3.57 $\pm$ 0.11 μg $\cdot$ L^{-1} dissolved inorganic nitrogen [DIN]; 3.31 $\pm$ 2.74 μg $\cdot$ L^{-1} soluble reactive phosphorous [SRP]; Table 1) during the study and within the range of other wetlands and lakes in the region (see review in Wyatt et al. 2010). Mean dissolved organic carbon concentration (May to July) was 13.95 $\pm$ 2.4 mg $\cdot$ L^{-1} and blocked ~20% of photosynthetically active radiation (PAR).

Experimental design. We manipulated light, grazing, and nutrient concentrations inside in situ mesocosm enclosures using a factorial combination of nutrient enrichment (enriched or control), grazing (grazed or ungrazed), and light (shaded or unshaded) with four replicates of each treatment combination. Prior to the initiation of the study, a boardwalk was constructed to prevent the disturbance of sediments during experimental setup and regular sampling. We constructed open-ended cylinder enclosures by rolling welded wire mesh into a cylinder (40 cm in diameter and 85 cm tall) and wrapping each cylinder with a layer of 0.1 mm clear (transmitted 90% of PAR and 80%–90% UV) polyvinylidene film (Rober et al. 2011). We placed enclosures in an area of the wetland with similar water depth (17–21 cm; Table 1) and open canopy and embedded each enclosure ~10 cm into the sediment. We placed four ceramic tiles (25 cm^2) into each enclosure and grazer exclusion cage (see below) as artificial substrates for algal colonization. We suspended all substrates attached to a wire frame that could be repositioned to maintain a consistent depth of 5 cm below the water surface. Care was taken not to disrupt the algal biofilm when repositioning substrates.

Experimental light manipulation was based on the range of light levels that occur in wetlands within the floodplain (Rober et al. 2014). The low light treatment (shaded) simulated light levels measured at peak macrophyte biomass (206.6 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}), and the light transparent treatment (unshaded) simulated light levels (920.3 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) measured during early growing season when macrophyte biomass was low. Unshaded treatments received full sunlight. Shading was achieved using solar screening (New York Wire, Mt. Wolf, PA, USA) that blocked 75% of light. There was no additional shading by macrophytes in shaded or unshaded treatments during the experiment. We attached shade screen to 40 cm diameter rings made of pipe insulation, which allowed the screen to float on the water surface and move freely up and down with water-level fluctuation without disturbing the substrates. Shade screen was wrapped around the outside of enclosures to reduce scattered light penetration from the water column.

In a previous study, both nitrogen (N) and phosphorous (P) were determined to be colimiting to algal growth (Wyatt et al. 2010). Therefore, we added a combination of N and P from a stock solution every 4 d for 16 d beginning on June 23, 2008, to achieve water-level concentrations of N = 1000 μg $\cdot$ L^{-1} $NaNO_3$ and P = 100 μg $\cdot$ L^{-1} $NaPO_4$ 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

TABLE 1. Mean (± SE) of PAR, DIN, SRP, conductivity, water temperature, DO, water depth, and pH among treatments and the open wetland.

Variable	Units	Unshaded		Shaded		Open wetland
		Control	NP	Control	NP	
PAR	μmol photons · m^{-2} · s^{-1}	703.9 (66.5)	665.8 (20.7)	79.8 (8.52)	79.6 (9.36)	763.9 (85.8)
DIN	μg · L^{-1}	3.44 (0.55)	2,091.9 (321.6)	5.35 (0.86)	2,515.0 (258.3)	3.57 (0.11)
SRP	μg · L^{-1}	2.82 (0.98)	184.2 (44.1)	2.69 (0.15)	284.9 (69.6)	3.31 (2.74)
Conductivity	μS	0.25 (0.02)	0.31 (0.005)	0.28 (0.003)	0.30 (0.01)	0.29 (0.02)
Water temperature	°C	15.4 (1.38)	15.6 (1.42)	14.9 (1.17)	14.97 (1.19)	14.7 (1.08)
DO	mg · L^{-1}	5.61 (0.57)	6.51 (0.43)	4.25 (0.45)	5.60 (0.49)	3.69 (0.77)
Water depth	cm	17.3 (1.86)	17.3 (1.30)	18.7 (1.09)	16.3 (0.55)	21.2 (0.93)
pH		7.2 (0.08)	7.2 (0.12)	7.1 (0.07)	7.1 (0.04)	7.3 (0.17)

PAR, photosynthetic active radiation; DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus; DO, dissolved oxygen.

by Borchardt (1996). We began enrichment after the late-spring thaw to simulate nutrient inputs from groundwater or surface water runoff (McDougal et al. 1997). Our goal with enrichments was to ensure alleviation of nutrient limitation in order to evaluate the influence of grazing and light on the algal response to nutrient enrichment.

We manipulated grazer access inside nutrient-enriched and control enclosures at the start of the experiment by nesting both caged (ungrazed treatment) and uncaged (grazed treatment) substrates together inside enclosures with natural abundances of the snail *Lymnaea* (16 snails per enclosure). Cages enclosing substrata within mesocosms prohibited grazing but allowed algae access to nutrients (Rober et al. 2011). Cages were 30 cm^2 and made of 1 mm clear polyethylene Nitex screen (Dynamic Aqua-Supply Ltd., Surrey, BC, Canada). We evaluated enclosure effects by monitoring conditions at four designated sites within the wetland using caged and uncaged substrates without enclosures, nutrient enrichment, or light manipulation (open wetland treatment).

Sampling procedure. We measured PAR (μmol photons · m^{-2} · s^{-1}) 5 cm below the water surface every four d in each enclosure and open wetland using a LI-COR submersible quantum sensor and LI-250 light meter (Li-Cor, Lincoln, NB, USA) at peak sunlight. We collected and filtered water for dissolved nutrient analysis every 4 d using a 0.45 μm Millex®-HA syringe-driven filter unit (Millipore Corporation, Bedford, MA, USA). We determined concentrations of DIN as nitrate + nitrite-N (cadmium reduction method, American Public Health Association (APHA) 1998) using a Skalar® auto-analyzer (Skalar Analytical, Breda, the Netherlands), and of SRP (ascorbic acid method, American Public Health Association (APHA) 1998) using a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, UK). We measured water depth with a meter stick and conductivity, water temperature, dissolved oxygen (DO), and pH in each enclosure every 4 d using a calibrated 650 YSI meter (YSI Incorporated, Yellow Springs, OH, USA).

Following the completion of the study, we removed algae from substrates with a toothbrush and split the resulting homogenous algal slurry volumetrically for analysis of chl *a*, ash-free dry mass (AFDM), and cell counts. We measured chl *a* concentrations (mg · m^{-2}) from a subsample collected on a Whatman glass fiber filter (GF/F; Whatman, Maidstone, UK) following 24 h extraction with 90% ethanol in the dark and analyzed with a Turner model 700 fluorometer (Turner Designs, Sunnyvale, CA, USA) (American Public Health Association (APHA) 1998). We determined AFDM (mg · cm^{-2}) after drying samples for 24 h at 105°C and ashing for 1 h at 500°C in preweighed aluminum pans to determine the difference between dry mass and ashed mass, respectively (American Public Health Association (APHA) 1998). We preserved the remaining aliquot with a 2% formalin solution for algal community analysis. We used standard protocols to characterize algal cell density and taxonomic composition by counting and identifying at least 300 natural units per sample using a Palmer–Maloney nanoplankton counting chamber and identified algae to genus at 400× magnification (Charles et al. 2002). We quantified benthic algal abundance (cells · cm^{-2} of substrate) by dividing cell abundances for each genus by the product of the area sampled and the proportion of the sample counted (Lowe and Laliberte 2006). We calculated biovolume (μm^3 · cm^{-2} of substrate) by multiplying algal cell density by the estimated cell volume for each genus using geometric formulae from Hillebrand et al. (1999).

Statistical analyses. All data for statistical analyses were log + 1-transformed if necessary to correct for nonnormal distribution and unequal variances among treatments prior to analysis. We used a three-way ANOVA to determine the effects of light manipulation, nutrient enrichment, and grazing on benthic algal chl *a*, AFDM, cell density, and total biovolume. We examined differences in taxonomic composition (genera occurring at ≥5% relative abundance) among treatments with a MANOVA. We used repeated-measures ANOVAs to determine the effects of treatments on PAR, dissolved nutrients, water depth, water temperature, DO, pH, and conductivity measured throughout the experiment. We used Tukey's 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, CA, USA).

RESULTS

Environmental parameters. Light was significantly lower in shaded treatments (80 μmol photons · m^{-2} · s^{-1}) compared to unshaded treatments and the open wetland (665–764 μmol photons · m^{-2} · s^{-1}; $F_{1,22} = 24.7$, $P < 0.05$; Table 1). Mean DIN and SRP concentrations in the control enclosures were low and remained relatively constant over the 16 d experiment (Table 1). Nutrient concentrations in enriched enclosures were significantly greater than the control enclosures (DIN: $F_{1,22} = 16.9$, $P < 0.0001$; SRP: $F_{1,22} = 6.1$, $P = 0.001$; Table 1). Nutrient concentrations were slightly elevated in shaded treatments compared to unshaded treatments; however, differences were not significant (Table 1). Nutrient concentrations in the open wetland were not significantly different from control enclosures (Table 1). Mean water depth, conductivity, water temperature, DO, and pH varied during the experi-

ment but did not differ among treatments or the open wetland (Table 1).

Algal biomass. Light did not have a significant effect on algal biomass independently or in its interaction with nutrients or grazers (Table 2). The positive effect of nutrients on algal biomass was reduced by grazing, resulting in a significant nutrient × grazer interaction (chl *a*: $F_{1,22} = 4.09$, $P = 0.05$; AFDM: $F_{1,22} = 4.77$, $P = 0.05$; cell density: $F_{1,22} = 11.04$, $P = 0.007$; biovolume: $F_{1,22} = 4.07$, $P = 0.06$; Table 2). Grazing significantly decreased chl *a* ($F_{1,22} = 66.6$, $P < 0.0001$; Fig. 1A), AFDM ($F_{1,22} = 40.5$, $P < 0.0001$; Fig. 1B), cell density ($F_{1,22} = 39.4$, $P < 0.0001$; Fig. 1C), and algal commu-

TABLE 2. Analysis of variance table showing the responses of benthic algal biomass measured as chl *a*, ash-free dry mass (AFDM), algal cell density, algal biovolume, and ratio of chl *a* to biovolume to light, nutrient, and grazer manipulation. *P*-values for significant treatment effects are indicated by bold font.

Effect	df	SS	*F*	*P*
Chl *a*				
Light	1	2.82	0.19	0.67
Nutrient	1	22.7	15.2	**0.001**
Grazer	1	99.9	66.6	**<0.0001**
Light × Nutrient	1	0.28	0.02	0.89
Light × Grazer	1	6.18	0.41	0.53
Nutrient × Grazer	1	61.4	4.09	**0.05**
Light × Nutrient × Grazer	1	0.01	0.001	0.98
Error	22	32.9		
AFDM				
Light	1	0.01	3.25	0.09
Nutrient	1	0.003	1.82	0.20
Grazer	1	0.18	40.5	**<0.0001**
Light × Nutrient	1	0.002	0.90	0.36
Light × Grazer	1	0.003	0.01	0.93
Nutrient × Grazer	1	0.02	4.77	**0.05**
Light × Nutrient × Grazer	1	0.002	0.39	0.55
Error	22	0.07		
Cell density				
Light	1	0.001	0.08	0.79
Nutrient	1	0.02	1.31	0.28
Grazer	1	1.13	39.4	**<0.0001**
Light × Nutrient	1	0.03	1.49	0.25
Light × Grazer	1	0.03	1.01	0.34
Nutrient × Grazer	1	0.32	11.0	**0.007**
Light × Nutrient × Grazer	1	0.02	0.85	0.34
Error	22	0.51		
Biovolume				
Light	1	0.12	1.34	0.27
Nutrient	1	0.01	0.15	0.71
Grazer	1	0.78	18.6	**0.001**
Light × Nutrient	1	0.10	1.14	0.31
Light × Grazer	1	0.04	1.04	0.33
Nutrient × Grazer	1	0.17	4.07	**0.06**
Light × Nutrient × Grazer	1	0.07	1.74	0.21
Error	22	1.41		
Ratio Chl *a*: Biovoume				
Light	1	146.1	8.17	**0.01**
Nutrient	1	208.9	11.7	**0.002**
Grazer	1	182.7	10.2	**0.004**
Light × Nutrient	1	142.7	7.98	**0.01**
Light × Grazer	1	29.4	1.64	0.21
Nutrient × Grazer	1	0.81	0.05	0.83
Light × Nutrient × Grazer	1	6.20	0.35	0.56
Error	22	393.7		

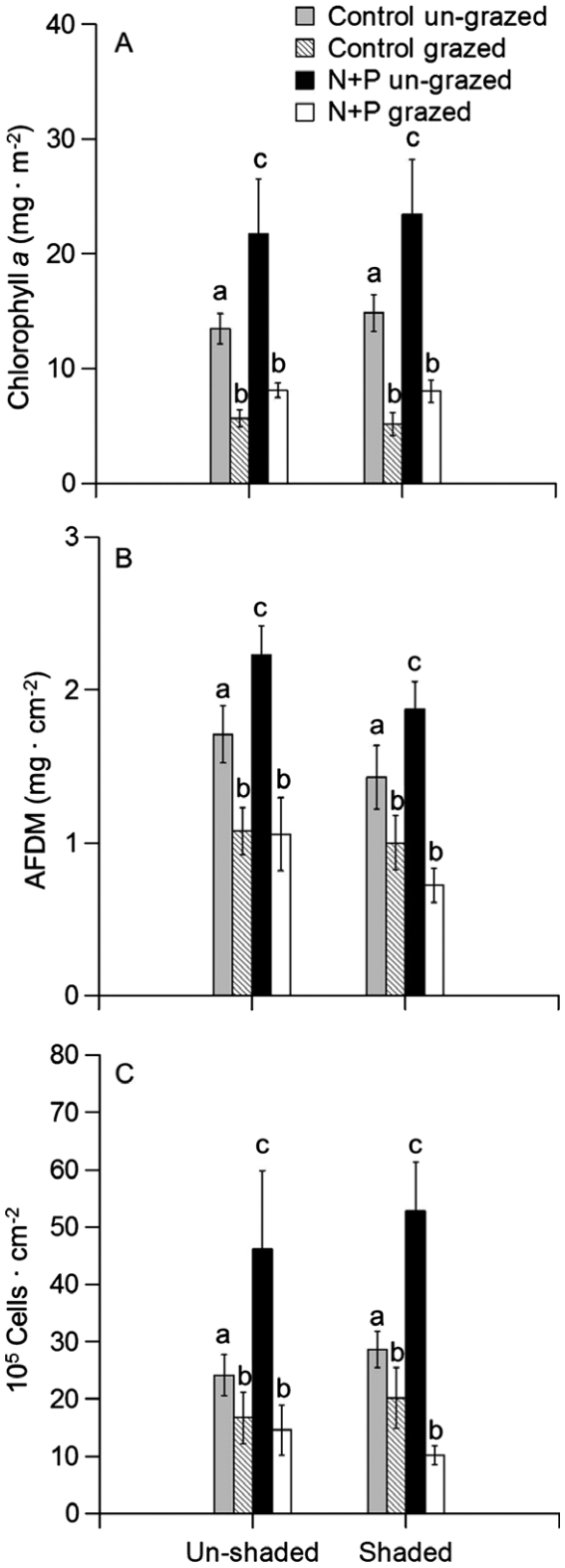

FIG. 1. Benthic algal biomass measured as chl *a* (A), ash-free dry mass (AFDM) (B), and cell density (C) in control and nutrient-enriched enclosures with and without grazers in shaded and unshaded treatments. Bars represent the mean of four replicates ± SE, and bars with the same letter are not significantly different among treatments.

nity biovolume ($F_{1,22}$ = 18.6, P = 0.001; Fig. 2) compared to ungrazed treatments independent of nutrient and light manipulation (Table 2). Algal biomass was similar between the open wetland and control enclosures among treatments (data not shown).

Nutrients regulated the algal response to light by influencing the chl *a* to biovolume ratio (Table 2). Shading significantly increased the chl *a* to biovolume ratio compared to unshaded treatments with nutrient enrichment ($F_{1,22}$ = 7.98, P = 0.01; Table 2), indicating higher chl *a* content in low light conditions (Fig. 3). Shading did not affect the chl *a* to biovolume ratio in unenriched treatments (Fig. 3). Grazing had a negative effect on the chl *a* to biovolume ratio ($F_{1,22}$ = 10.2, P = 0.004; Fig. 3) by probably altering the size structure of the algal community, but was not significant in its interaction with nutrients or light (Table 2).

Taxonomic composition. Shading did not affect algal community composition. Of the ten genera that were present in greater than 5% relative abundance, none responded to changes in light (Fig. 2). Green algae, especially *Gloeocystis*, comprised 54%–68% of the total cell density in all treatments. Diatoms, especially *Nitzschia*, were more abundant in nutrient-enriched enclosures compared to the control ($F_{7,22}$ = 2.20, P = 0.07; Fig. 2). Grazing decreased *Nitzschia* compared to ungrazed treatments in both nutrient-enriched and control enclosures ($F_{7,22}$ = 5.48, P = 0.03; Fig. 2). The filamentous green algae *Ulothrix* was more abundant in nutrient-enriched enclosures compared to the control, but was significantly reduced by grazing ($F_{7,22}$ = 2.46, P = 0.05; Fig. 2). The basal cells of *Stigeoclonium* were more abundant in grazed than ungrazed treatments with nutrient enrichment ($F_{7,22}$ = 7.92, P =0.01; Fig. 2). Nutrient-enriched enclosures had a significantly lower abundance of *Gloeocapsa* (cyanobacteria; $F_{7,22}$ = 5.58, P = 0.001) and *Stigeoclonium* (Chlorophyta; $F_{7,22}$ = 4.12, P = 0.005) independent of grazing. Taxa from euglenoid (*Trachelomonas*), Xanthophyceae (*Ophiocytium*), and Cyanophyta (*Aphanocapsa* and *Chroococcus*) were unaffected by light, nutrient, or grazer manipulation (Fig. 2).

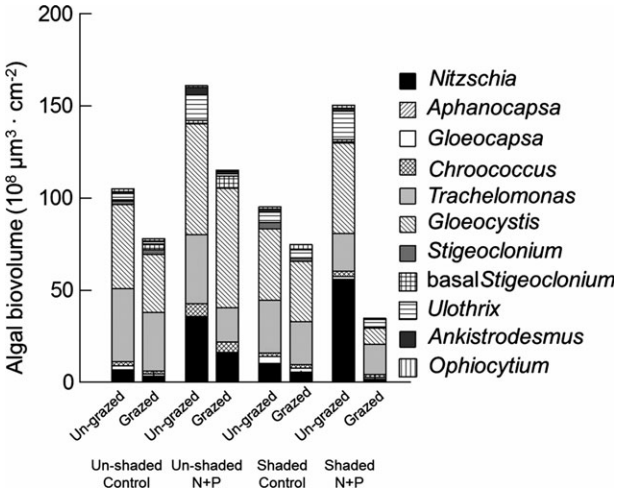

FIG. 2. Grazed and ungrazed algal taxonomic composition and total algal biovolume in shaded and unshaded nutrient-enriched and control enclosures. Figure includes only taxa comprising ≥5% relative abundance.

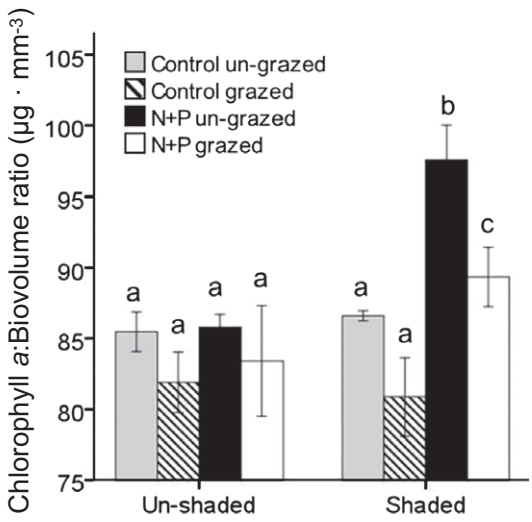

FIG. 3. Chl *a* to biovolume ratios in unshaded and shaded treatments with and without nutrient enrichment and grazers. Bars represent the mean of four replicates ± SE, and bars with the same letter are not significantly different among treatments.

DISCUSSION

Grazing and nutrients, but not light, determined algal biomass and taxonomic composition within this riparian wetland in interior Alaska. The addition of nutrients increased benthic algal biomass and grazers suppressed algal accumulation, supporting our first two hypotheses. The interacting and opposing influences of nutrients and grazing suggest that the algal community is under dual control from the bottom-up (nutrient limitation) and from the top-down (consumption by herbivores), which is consistent with the results from previous research conducted in wetlands within this area of interior Alaska (Rober et al. 2011). However, our results indicate that the relative strengths of top-down versus bottom-up control were not equivalent and suggest a shift in the primary regulatory factor (from nutrients to grazers) between subsequent growing seasons. Our experimental design allowed us to examine both the independent and interactive effects of grazing and nutrients; therefore, we were able to determine that grazers had a greater effect on algal biomass and taxonomic composition. The stronger influence of grazing in the current study was indicated by a reduction in algal biomass by grazers with and without nutrient enrichment, whereas in a previous study we found that grazing

only had an influence on algal biomass in nutrient-enriched conditions (Rober et al. 2011). Together, these results suggest that the degree to which either factor regulates algal parameters may be influenced by interannual variability in environmental conditions (Rosemond et al. 2000, Hillebrand et al. 2002).

Recent research has demonstrated that algal production in high-latitude aquatic ecosystems may not respond as strongly to nutrient inputs as would be expected in low-latitude ecosystems due to physiological constraints on algal photosynthesis (i.e., short growing season with low average annual temperature and incident radiation; Flanagan et al. 2003, Ask et al. 2009, Karlsson et al. 2009). However, our findings suggest that strong top-down regulation of algal primary production may be driving the algal response to nutrient inputs previously observed in high-latitude regions. Support for this hypothesis was particularly evident in nutrient-enriched treatments where grazers reduced algal biomass to levels similar to unenriched treatments, masking the increase in algal biomass stimulated by nutrient enrichment. Although the ability of grazers to maintain low levels of algal biomass with greater nutrient availability has been widely demonstrated in lakes, streams, and coastal environments (Feminella and Hawkins 1995, Hillebrand 2002), few studies have evaluated the role of grazers in regulating algal production in wetlands, particularly at high latitudes (Rober et al. 2011). Thus, our findings provide valuable insight into food web processes in boreal wetlands and suggest that in the absence of higher predators (i.e., fishes), grazers may be driving observed patterns in algal abundance in high-latitude ecosystems rather than light availability.

Experimentally manipulating light availability did not affect algal biomass or taxonomic composition. This finding was unexpected and differs from studies demonstrating that light limitation due to increases in macrophyte abundance (Grimshaw et al. 1997, McCormick et al. 1998, Hillebrand 2005) or high concentrations of light-absorbing humic substances (Ask et al. 2009, Karlsson et al. 2009) reduces benthic algal biomass. Our results suggest that light is not limiting to algal primary production in this marsh. Similar findings have been reported in the Florida Everglades where experimentally reducing light by up to 98% (40–56 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) had no effect on algal primary production or community composition and was attributed to the ability of algal community to maintain photosynthetic rates within their acclimated irradiance regime (Thomas et al. 2006). Subsurface light availability measured in shaded treatments was below the range (200–400 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) reported to saturate algal growth (Hill 1996, Baulch et al. 2005), but above low light conditions (10 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) at which active net photosynthesis has been shown to occur (Carlton and Wetzel 1987, 1988), despite self-shading (Rier et al. 2006). Yet, light levels similar to our study (100 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) have been shown to limit algal biomass in other ecosystems with saturating nutrient concentrations (Steinman and McIntire 1987, Lamberti et al. 1989, DeNicola and McIntire 1991, McIntire et al. 1996).

The observed increase in chl *a* content per algal biovolume in shaded treatments (with nutrients) indicates an increase in pigment density within algal cells grown in low light conditions (Falkowski and LaRoche 1991). Since algal taxonomic composition was similar among shaded and unshaded treatments (without grazers), differences in the chl *a* to biovolume ratio were likely not the result of altered species composition, but instead an increase in the pigment density within the same taxa exposed to varying light levels. This finding is consistent with previous studies with similarly reduced light levels (40–80 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}; Hillebrand et al. 2004, Thomas et al. 2006) and suggests that in the absence of nutrient limitation, the algal community may be capable of making physiological adjustments to compensate for changes in light availability by increasing photosynthetic efficiency (Hill et al. 1995, Baulch et al. 2009).

Algal taxonomic composition was similar among nutrient and light treatments, suggesting that the algal community was controlled more by the presence or absence of grazers than by changes in resources. The observed changes in algal taxonomic composition among treatments suggest that there are trade-offs between herbivore-resistant and resource competitive species. Basal filaments of *Stigeoclonium*, which are considered resistant to grazing (Marks and Lowe 1989, McCormick and Stevenson 1991, Steinman 1996), were more abundant in grazed treatments. Algal taxa with high growth potential (e.g., *Nitzschia*) responded to increases in resources only after grazers were excluded. The replacement of grazer-resistant species by resource competitive species when herbivores are removed has been demonstrated in lakes (Marks and Lowe 1989), streams (Steinman and McIntire 1987, McCormick and Stevenson 1991, Rosemond et al. 1993, 2000), and coastal environments (Lubchenco 1978).

Algal taxonomic composition was more diverse than has been previously observed at this site (Rober et al. 2011) and may reflect the ability of taxa within the community to compensate for low light conditions. The abundance of *Nitzschia* differs from earlier investigations where silica concentrations were considered to be below minimum requirements for diatom colonization (Wyatt et al. 2010, Rober et al. 2011). We observed a significant increase in diatom relative abundance with nutrient enrichment, and the increase was most pronounced in shaded treatments. Although the increase in diatoms was quickly masked by grazing, greater abundances of diatoms

in light-limited conditions are consistent with expectations from the literature, indicating that diatoms tend to thrive in low light environments (e.g., Steinman et al. 1989, Mosisch et al. 2001, Rier et al. 2006). Additionally, *Nitzschia* can migrate vertically within the algal mat, enabling them to thrive in environments with variable light conditions (Stevenson et al. 1991, Hill 1996). Euglenoids are also motile taxa and therefore able to compensate for low light conditions in environments with high levels of light-absorbing dissolved organic matter (Rosowski 2003), which may explain the abundance of *Trachelomonas* among light treatments regardless of nutrients or grazers. The abundance of *Trachelomonas* in this study is a shift in the dominant euglenoid taxa from previous measures of *Euglena* (Wyatt and Stevenson 2010, Rober et al. 2011).

We found stronger effects of grazers and nutrients compared to light on benthic algae in this northern boreal wetland. The positive relationship observed between nutrient enrichment and algal biomass in the absence of grazers suggests that the relationship between increasing nutrient concentrations and algal biomass occurring at lower latitudes (i.e., Flanagan et al. 2003) also occurs in high-latitude wetlands. Therefore, greater nutrient availability with increased permafrost thaw (Schuur et al. 2013) and decomposition of organic matter (Bridgham et al. 1995, Rouse et al. 1997) associated with ongoing climate change will probably increase benthic algal biomass in northern boreal wetlands. Our results demonstrate that low light availability is unlikely to inhibit the algal response to elevated nutrient concentrations, but grazers rapidly consume algae following enrichment, masking the effects of elevated nutrients on algal production and promoting energy transfer through the food web.

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