REGULATION OF BENTHIC ALGAL STRUCTURE AND FUNCTION IN NORTHERN BOREAL WETLANDS

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ABSTRACT

REGULATION OF BENTHIC ALGAL STRUCTURE AND FUNCTION IN NORTHERN BOREAL WETLANDS

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Algae are important to many of the processes that characterize wetland ecosystems. Despite their importance, we know relatively little about the factors that regulate algal communities in wetlands. This is particularly true for northern boreal regions where wetlands are abundant and are considered to be extremely vulnerable to disturbances associated with climate change. My dissertation research investigates how nutrients, grazing, light, and hydrology regulate algal primary production and taxonomic structure in high latitude wetlands.

I documented spatial and temporal variability in algal structure and function in six northern boreal wetlands in interior Alaska to determine the contribution of algal primary production to wetland primary production and evaluate the relationships between environmental parameters characteristic of different wetland types and algal productivity, abundance, and taxonomic composition. There were significant spatial and seasonal differences in algal biomass and taxonomic composition both within and between wetlands. Measures of algal productivity were equivalent, and sometimes higher, than macrophyte production, contributing up to 50% of wetland primary production. Water depth and nutrients were significant predictors of algal taxonomic composition.

In Chapter 3 I evaluated the potential for grazers to regulate benthic algal communities in boreal wetlands with future increases in nutrient concentrations using an *in situ* mesocosm experiment in an Alaskan marsh. I tested the hypothesis that nutrient enrichment stimulates algal accumulation and grazers regulate algal responses to nutrients by suppressing algal accumulation

but increasing productivity through nutrient recycling. My results support my hypothesis and provide some of the first evidence that nutrients and grazing are important factors regulating benthic algal biomass and community composition in a northern boreal wetland. My data also suggest the potential importance of consumer-driven nutrient recycling to algal productivity and wetland biogeochemistry.

In Chapter 4 I investigated how changes in light availability, in the presence and absence of grazing, limit the ability for algae to respond to nutrient inputs using an *in situ* mesocosm experiment. I hypothesized that light limitation and herbivory are both responsible for regulating the algal response to nutrient enrichment. My analyses indicate that grazers are responsible for maintaining low algal biomass even with increased nutrient availability, not light.

In the final chapter, I evaluated how changes in hydrology predicted with climate change might influence algal community structure in boreal peatlands. I monitored shifts in algal taxonomic composition in response to an ecosystem-scale water table manipulation, including both drought and flooding conditions in a rich fen in interior Alaska. The observed changes in algal taxonomic composition in response to fluctuations in water table suggests that increased frequency of drought and flooding events expected with climate change may significantly alter algal structure and function in boreal wetlands. Furthermore, my results suggest the potential importance of nitrogen-fixation by cyanobacteria to wetland biogeochemistry.

The results of this dissertation improve our understanding of the abiotic and biotic factors that regulate benthic algal productivity and taxonomic composition in northern boreal wetlands. My results indicate that algae are an ecologically important component of wetland ecosystems. These results have important implications for energy flow in boreal wetlands and indicate that the current wetland structure and function may be altered by climate change.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Benthic algal ecology in freshwater wetlands

Algae are important to many of the processes that characterize wetland ecosystems. They can exert considerable control over dissolved oxygen concentrations (Browder et al. 1994, McCormick et al. 1997, Richardson 2010), sediment formation (Gleason and Spackman 1974, McCormick et al. 1998), nutrient uptake and retention (Wetzel 1996, Gaiser et al. 2004, Wyatt et al. 2012), and can account for a significant amount of total primary production (Robinson et al. 2000, Richardson 2010, Wyatt et al. 2010). Despite their importance, we know relatively little about the factors that regulate algal communities in wetlands. This is particularly true for northern boreal regions where wetlands are abundant and are considered to be extremely vulnerable to disturbances associated with climate change. Understanding the regulation of algal dynamics in wetlands is essential to predicting and understanding the implications of environmental variation, anthropogenic effects, and changes in climate, all of which can alter the current wetland ecosystem infrastructure.

1.2 Environmental regulation of benthic algae in wetlands

The factors that influence benthic algal structure and function in wetlands are not clearly understood. Conceptual models attribute environmental factors such as climate, geology,

hydrology, flood disturbance frequency, substrata type and size, water chemistry, canopy cover and light availability, and grazer density as strong influences on benthic algal productivity and community structure (Figure 1.1) (Goldsborough and Robinson 1996). Much of our current understanding about these regulatory processes has been adapted from hypotheses generated in other aquatic ecosystems (Batzer et al. 2006). However, given the unique physical, chemical, and biological properties of wetland environments, there is a need to investigate these processes to evaluate the magnitude and characteristics of effects in wetlands and how they vary among different types of wetlands.

Water-level fluctuations are common and frequent in wetlands, and are one of the dominant controls on wetland plant and animal communities as well as on primary productivity and decomposition (Gottlieb et al. 2005, Jackson 2006). Changing hydrological processes are responsible for the movement and delivery of limiting nutrients into and out of wetland ecosystems (Jonasson and Shaver 1999), and are therefore extremely important in regulating algal distribution and abundance (Browder et al. 1994, Robinson et al. 2000). Even small changes in depth of only a few millimeters can expose algal communities to variations in nutrient concentrations and dissolved gases which can induce significant changes in community metabolism (Kahn and Wetzel 1999). Flooding reduces macrophyte abundance and releases nutrients from dead vegetation, litter, and sediments that may subsequently stimulate algal production (Murkin 1989, Robinson et al. 2000). Drought and exposure of sediments re-oxygenate anaerobic soils, facilitating the release of nutrients upon re-inundation (Schoenberg and Oliver 1988, Goldsborough and Robinson 1996, Thomas et al. 2006).

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). The

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 within 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 it has been less directly impacted by human development. However, boreal regions are experiencing rapid changes in climate, which have led to a longer growing season with higher temperatures (Chapin et al. 2006). Changes in thermal regime are expected to increase the extent of seasonal ice thaw, which will potentially promote nitrogen and phosphorus mineralization in the expanded active soil layer (Bridgham et al. 1995). While regional variability of nutrient inputs may be significant, these changes are expected to have widespread impacts on nutrient concentrations of aquatic systems throughout the boreal forest (Rouse et al. 1997).

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 can also lead to increased productivity of the algal assemblage through the utilization of excreted

nutrients (McCormick and Stevenson 1991, Hillebrand 2002). The extent to which these regulatory processes operate in wetlands is largely unknown, as evidence of grazing in wetland ecosystems has been largely circumstantial (Robinson et al. 2000).

Since light is required to carry out photosynthesis, it is commonly considered the most important resource regulating algal communities (Hill 1996). Light conditions in wetlands are extremely dynamic. Not only are wetlands exposed to seasonal changes in incident radiation but light attenuation also varies with the degree of shading by overlying macrophytes (Robinson et al. 2000). As opposed to stream ecosystems, where light limitation can be avoided by colonizing a variety of substrates, macrophytes are the primary substrate available for benthic algal colonization in wetlands. This poses an interesting problem for light limited algal primary production, especially in northern boreal wetlands that receive over 20 hours of daylight during the summer growing season, resulting in rapid macrophyte growth (Chapin et al. 2006). This is further complicated by climate change processes which have led to a longer growing season (Magnuson et al. 2000, Chapin et al. 2006), with a subsequent increase and duration of macrophyte production.

1.3 Investigating environmental controls on wetland algal structure and function

In this dissertation, I examine the role of hydrology, grazing, nutrients, and light in regulating algal productivity, abundance, and taxonomic composition in northern boreal wetlands, along with the spatial and temporal trends in these biotic and abiotic factors. I chose these factors in order to gain a better understanding of how algae will respond to environmental factors that are predicted to be altered by climate change processes. Chapter 2 describes the

spatial and temporal variation in physical and chemical factors in six wetlands (4 marshes and 2 peatlands) in interior Alaska and examines the relationships between these environmental parameters and algal productivity, abundance, and taxonomic composition. These data are useful for understanding the natural distribution and abundance of algae in boreal wetlands, which is necessary to predict how processes related to anthropogenic activity and climate change will influence wetland primary production, biogeochemistry, and food-web structure. Chapter 3 describes the independent and interactive effects of grazing and nutrients on benthic algal biomass and taxonomic composition in an *in situ* mesocosm experiment. Additionally, since grazers can recycle significant amounts of nutrients into the water column, I evaluated the influence of consumer-driven nutrient recycling on algal biomass. Chapter 4 describes the independent and interactive effects of grazing, nutrients, and light on benthic algal biomass and taxonomic composition in an *in situ* mesocosm experiment. Specifically, I investigated how changes in light availability, in the presence and absence of grazing, limit the ability for algae to respond to nutrient inputs. Chapter 5 describes algal community response to experimental and interannual variation in hydrology in an Alaskan boreal fen. I monitored shifts in algal taxonomic composition at sites exposed to a long-term water table manipulation, including drought and flooding conditions in an Alaskan fen. While continuous algal colonization would typically only occur in flooded conditions in previous years, a spring flood provided a unique opportunity to examine algal community response to rewetting after long-term drought as well. This allowed me to investigate how much ecosystem memory of the antecedent water table manipulations regulated the ability of taxa to recolonize sites following prolonged drought compared to sites that had been continuously flooded.

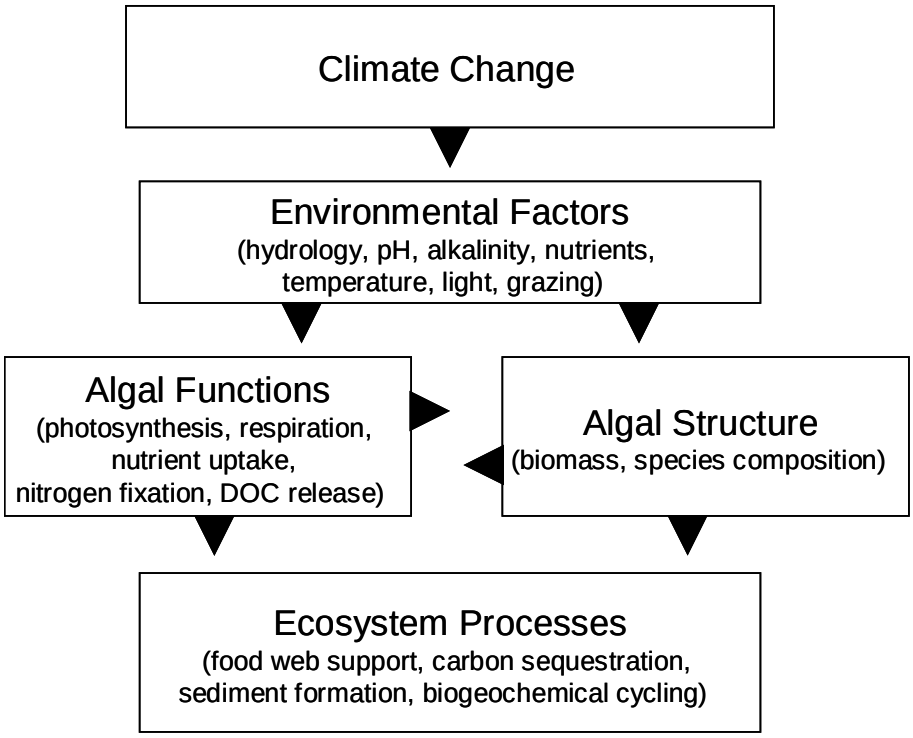

Figure 1.1 Conceptual model describing the potential influences of climate change on wetland ecosystem processes due to the relationship between environmental factors and algal structure and function.

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LITERURE CITED

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CHAPTER 2

SPATIAL AND TEMPORAL VARIABILITY OF ALGAL COMMUNITY DYNAMICS AND PRODUCTIVITY IN LATERAL FLOODPLAIN WETLANDS ALONG THE TANANA RIVER, ALASKA

2.1 Introduction

Few studies have examined the structure and function of benthic algae in wetlands or their relationships with the physical and chemical conditions characteristic of different wetland types. Determining the spatial and temporal patterns of benthic algal communities is important for understanding wetland ecosystem function because algae play a critical role in many ecosystem processes. In shallow wetlands where sufficient light reaches the bottom, benthic algae contribute significantly to wetland primary production (Robinson et al. 2000, Richardson 2010, Wyatt et al. 2010), biogeochemical cycling (Wetzel 1996, Gaiser et al. 2004, Wyatt et al. 2012), sediment formation (Gleason and Spackman 1974, McCormick et al. 1998), and oxygen production (Browder et al. 1994, McCormick et al. 1997, Richardson 2010).

The factors that influence benthic algal structure and function in wetlands are not clearly understood. Conceptual models attribute regional environmental factors such as climate, geology, and hydrology, and local factors such as flood disturbance frequency, substrata type and size, water chemistry, canopy cover and light availability, and grazer density as strong influences on benthic algal productivity and community structure (Goldsborough and Robinson 1996). Much of our current understanding about these regulatory processes has been adapted from hypotheses generated in other aquatic ecosystems (Batzer et al. 2006). However, given the unique physical, chemical, and biological properties of wetland environments, there is a need to

investigate these processes to evaluate the magnitude and characteristics of effects in wetlands and how they vary among different types of wetlands.

Most direct measurements of algal structure and function in wetlands have come from studies conducted in subtropical (Browder et al. 1994, Richardson 2008) and temperate regions (Goldsborough and Robinson 1996, Robinson et al. 2000). The abundance and distribution of algal communities have been less studied at northern latitudes where wetlands are the dominant land cover type. In Alaska alone, wetlands cover over 43 percent of the total surface area (Hall et al. 1994). Given the importance of boreal wetlands as major stores of carbon, considerable effort has been made to quantify primary productivity in these ecosystems (cf. Thormann and Bayley 1997, Weltzin et al. 2000, Bayley and Mewhort 2004, Chivers et al. 2009). However, the majority of these studies have focused on macrophyte production (McCormick et al. 1998, Wieder 2006) and has mostly ignored the potential role of algae contributing to wetland primary production and ecosystem function.

Wetlands occurring in boreal regions can be classified as either peatlands or marshes. Peatlands are defined as ecosystems that have accumulated at least 40 cm of peat (National Wetlands Working Group 1997). They are the dominant wetland type in boreal regions (Vitt et al. 2006), mainly because cold temperatures and slow rates of decomposition facilitate accumulation of organic matter. Peatlands in boreal regions tend to have little standing water since water level is highly dependent on changes in rates of precipitation and evapotranspiration. Marshes often occur within floodplains of large river systems and are characterized by shallow water with submerged, floating, and emergent macrophytes. Marshes vary considerably in physical and chemical nature (Mitsch and Gosselink 2006), which likely influences algal structure and function.

Understanding the natural distribution and abundance of algae in boreal wetlands is necessary to predict how processes related to climate change will influence wetland primary production, biogeochemistry, and food-web structure. Climate change processes are already having significant effects on northern boreal regions. Increased evapotranspiration with longer, drier growing seasons (Serreze et al. 2000, Euskirchen et al. 2006), drainage after permafrost thaw (Hinzman et al. 2005, Riordan et al. 2006), and/or encroachment of wetland vegetation (Roach et al. 2011) have reduced the surface area of extensive portions of open water bodies in wetland-rich landscapes of interior Alaska. However, some wetland areas in Alaska are expanding due to hydrologic upwelling and increased flooding from melt-water runoff from surrounding uplands (Osterkamp et al. 2000). Increased frequency of drought and flooding events associated with climate change will likely alter the physical and chemical conditions of aquatic ecosystems in the boreal region, including the movement of limiting nutrients into and out of wetlands (Rouse et al. 1997). Furthermore, changes in thermal regime are expected to increase the extent of seasonal ice thaw, and could promote N and P mineralization in the expanded active soil layer (Bridgham et al. 1995). These changes are expected to have widespread effects on aquatic ecosystems throughout the boreal forest (Rouse et al. 1997).

In this study I documented the spatial and temporal variation in physical and chemical factors in six wetlands (4 marshes and 2 peatlands) in interior Alaska. I then examined the relationships between these environmental parameters and benthic algal productivity, abundance, and taxonomic composition. I was specifically interested in determining the contribution of algal primary production to wetland primary production, documenting algal community composition in both peatlands and marshes, and determining which environmental variable(s) best predict the distribution and abundance of the algal communities. These data have important implications for

wetlands in the boreal region, but also more broadly, for carbon cycling in the boreal forest. Furthermore, these data allow us to expand our knowledge from lakes and streams to boreal wetlands, where benthic habitats have rarely been explored.

2.2 Methods

Study Site

For twelve weeks during the summer of 2009, I conducted the field work to characterize the spatial and temporal changes in water depth, surface water chemistry, macrophyte biomass, light attenuation, and algal productivity and taxonomic composition in six wetlands within the Tanana River Floodplain just outside the Bonanza Creek Experimental Forest (35 km southeast of Fairbanks, Alaska) (Figures 2.1 and 2.2). My study sites were located in two peatlands and four marshes. I chose these sites to capture a range of physical and chemical conditions present in a diversity of peatland and marsh types. Three of the wetlands used in this study (F1, M1, M2) were characterized by Kashichke et al. (2009).

The Tanana River valley is about 150 to 250 km south of the Arctic Circle, and is part of the circumpolar band of boreal forest. The area is underlain by discontinuous permafrost and is a mosaic of forest, grassland, shrubs, and wetlands. The area has large fluctuations in daylight and experiences more than 21 h of light per day in June and less than 3 h per day in December. The growing season is short (approximately 135 days), lasting from May to August. This region within interior Alaska has large fluctuations in temperature, with a mean annual temperature of -2.9°C, and low levels of precipitation (269 mm/y), of which approximately 30 percent falls as snow (Hinzman et al. 2006).

The first site (F1) is a moderately rich fen and is dominated by brown moss species, *Sphagnum*, and emergent vascular plants, beaked sedge (*Carex utriculata*), common horsetail (*Equisetum sp.*), and *Potentilla palustris*. F1 is minerotrophic receiving water from surface water runoff and precipitation, and to some extent, groundwater. Peat thickness exceeds 1 m at this site. This site is currently being used for the Alaska Peatland Experiment (APEX) and is described in more detail in Turetsky et al. (2008).

The second site (F2) is a poor fen located approximately 50 m from the APEX site and is dominated by emergent marsh vegetation including *Equisetum, Carex,* and *Potentilla palustris* with the moss community composed of *Sphagnum* species.

The third site (M1) is approximately 50 m from sites F1 and F2, but did not have ≥ 40 cm of peat, and is thus classified as a marsh. The dominant vegetation is short tussock grasses, where inter-tussock spaces tend to be saturated with water. M1, F1, and F2 are surrounded by lowland black spruce (*Picea mariana*) forest.

The forth site (M2) is a marsh and is dominated by emergent vegetation including *Carex* and *Equisetum* species as well as the floating macrophyte *Menyanthes trifoliate* (Buck Bean). This site has a very thin layer of organic soil on top of the mineral soil layer, and is characterized by extreme annual hydrologic changes likely linked to river flow conditions. Several small open water pools are present within the marsh complex.

The fifth site (M3) is a shallow riverine marsh and is a near monoculture of emergent *Equisetum fluviatile* surrounded by alder (*Alnus*), aspen (*Populus balsamifera*), and white spruce (*Picea glauca*) forest. This site, although in close proximity (~200m) to M4, has very low concentrations of dissolved organic matter in the water column and high dissolved oxygen.

The sixth site (M4) is a shallow riverine marsh and is dominated by emergent vegetation including swamp horsetail (*Equisetum fluviatile*), beaked sedge (*Carex utriculata*), and water parsnip (*Sium suave*) and submerged vegetation including flat leaved bladderwort (*Utricularia intermedia*) and yellow water-crowfoot (*Ranunculus gmelinii*). This site has been the location of several *in situ* mesocosm experiments looking at the effects of nutrient enrichment (Wyatt et al. 2010), pH (Wyatt and Stevenson 2010), and grazing (Rober et al. 2011) on benthic algal structure and function.

Sampling procedure

Starting in May 2009, I sampled surface water chemistry and algal parameters weekly, and then every two weeks beginning in July until August, or until the water table fell below the soil surface, to evaluate algal responses to changes in environmental parameters. On each sampling date I measured water depth using a meter stick, and water temperature, dissolved oxygen (DO), and pH using a calibrated model 556 YSI® Multi-Probe (YSI Incorporated, Yellow Springs, OH, U.S.A.). I filtered water for dissolved nutrient analysis using a 0.45 μm Millex®-HA syringe-driven filter unit (Millipore Corporation, Bedford, MA, U.S.A.) into 120 mL acid-rinsed polyethylene bottles. Samples were stored on ice until returning to the lab, where a portion of each filtered sample was analyzed for dissolved organic carbon (DOC) using a Shimadzu TOC-V carbon analyzer (Shimadzu Scientific Instruments, Columbia, MD, U.S.A.). The remaining portion of each sample was frozen and stored until analysis. I analyzed water samples for dissolved inorganic nitrogen (DIN) as $NO_3 + NO_2$ following the cadmium reduction method using a Skalar® auto-analyzer (Skalar Analytical, Breda, Netherlands). Soluble reactive phosphorus (SRP) was measured following the ascorbic acid colorimetric method using a

Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, U.K.) (APHA 1998). I determined total nitrogen (TN) and total phosphorus (TP) concentrations following oxidation with persulfate digestion and second derivative UV spectroscopy and ascorbic acid methods respectively (APHA 1998).

I quantified macrophyte height and density in replicate m^2 plots as percent cover and stem density of each plant type. I harvested above ground plant biomass biweekly in randomly selected m^2 plots for estimates of plant biomass. Plants were dried, weighed, and converted to g C/m^2 assuming 40 percent of dry mass is carbon (Robinson et al. 2000). Since the APEX site is part of a long-term experimental study, I did not harvest plants at the F1 site. However I compared algal productivity at the F1 site to estimates of macrophyte gross primary production (GPP) reported by Chivers et al. (2009). I measured photosynthetically active radiation (PAR) at the wetland surface and at subsequent intervals below the waters surface until the bottom was reached using a LI-COR submersible quantum sensor and LI-250 light meter (LI-COR, Lincoln, NE, U.S.A.). I made measurements without disturbing the canopy by attaching the underwater sensor to the end of a pole that was lowered into the macrophyte stand.

I collected algae from six randomly selected locations in each wetland for estimates of benthic algal biomass, productivity, and taxonomic composition. Each sample consisted of four 25 cm^2 subsamples collected from peat surface (if present) and the submersed portions of four stems of the dominant emergent macrophyte. I used a plastic syringe to remove algae from each 25 cm^2 quadrat until there were no loosely attached algae or biofilms present. In cases where algae were attached to erect plant stems, I scraped the submersed portion of four stems clean with a plastic spoon, and adjusted the surface area in calculations. Each algal sample was

homogenized in 120 mL of water for analysis of chlorophyll *a*, ash-free dry mass (AFDM), and benthic algal abundance (algal cells/cm^2). Chlorophyll *a* (mg/m^2) was measured from a subsample collected on a Whatman GF/F glass fiber filter. Filters were frozen and chlorophyll *a* was measured using a Turner model 700 fluorometer (Turner Designs, Sunnyvale, CA, U.S.A.) after extraction with 90% ethanol and correction for phaeophytin (APHA 1998). I determined AFDM (g/m^2) by drying samples at 105 °C for 48-72 h and combusting them for 1 h at 500 °C in preweighed aluminum pans to determine the difference between dry mass and ashed mass respectively (APHA 1998). I preserved a subsample in a 2% formalin solution for algal compositional analysis. I used standard protocols to characterize algal 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 400X magnification (Charles et al. 2002). I quantified benthic algal abundance (cells/cm^2 of substrate) using the formula provided in Lowe and Laliberte (2006).

I split a final portion of each homogenized sample into two separate biological oxygen demand (BOD) bottles to measure benthic algal productivity (mg $C/m^2/h$) following McCormick et al. (1998). I filled each BOD bottle with filtered water from the wetland and recorded initial DO using a Hach HQ 40d luminescent DO probe (Hach Company, Loveland, CO, U.S.A.). I wrapped one bottle from each set with aluminum foil for incubation in the dark and determined production by measuring oxygen changes produced by algal samples incubated *in situ* in light and dark bottles. Light and dark bottles were used to measure net primary productivity (NPP) and respiration, respectively. I calculated GPP following Wetzel and Likens (2000) and

converted GPP values into units carbon based on a C:O molar ratio of 0.375 and a photosynthetic quotient of 1.2 (Wetzel and Likens 2000).

Data Analysis

The distributions of variables were log (x + 1) transformed if necessary to correct for non-normal distribution and unequal variances among sites prior to analysis. I used repeated measures analysis of variance models with an adjusted Bonferroni significance level ($p < 0.016$) and Tukey's test for post hoc comparison of means to determine if algal productivity and biomass were different between sites. I used a bivariate Pearson Correlation test to determine if any of the environmental variables were correlated. Several of the environmental variables were correlated and therefore could not be included in any model together. Therefore, I include water depth, TN, TP, PAR, and wetland site in a linear mixed model to predict changes in algal productivity and biomass, with the assumption that correlated variables (pH, water temperature, DO, DIN, SRP, and DOC) would respond similarly (Zar 2010). All statistical analyses were performed using general linear models in SPSS 18 (SPSS inc., Chicago, IL, U.S.A.).

I plotted the relationship between environmental variables and algal taxonomic composition among sites with Non-metric Multidimensional Scaling (NMS) using PC-ORD (version 5, MjM Software, Gleneden Beach, OR, U.S.A). I analyzed similarities in algal taxonomic composition among wetland sites and sampling dates with a 2-way analysis of similarities (ANOSIM) test using PRIMER (version 5, PRIMER-E Ltd, Plymouth, UK). I calculated all algal community data as a proportion of the total before analysis and only included taxa present at > 5% relative abundance. I square root transformed data prior to ordination and ANOSIM.

2.3 Results

Surface water chemistry and water level characteristics

Mean TP concentration was lower in M2 compared to all other wetlands ($p < 0.05$; Table 2.1). Mean TP was not different between peatlands F1 and F2 ($p > 0.05$). Mean TP was similar among marshes M2, M3, and M4 ($p > 0.05$), which had higher concentrations compared to the other wetlands (Table 2.1). Mean TN concentration was higher in M2 compared to all other wetlands ($p < 0.05$). Mean TN concentrations in F2 and M1 were similar ($p > 0.05$) but were greater than TN concentrations in F1, M3 and M4, which were similar to one another (Table 2.1). Mean SRP concentration was below 4 µg/L in all wetlands, and was slightly higher at M3 compared to the other wetlands (Table 2.1). Mean DIN was significantly greater at M1 compared to all other wetlands ($p < 0.05$). Mean DIN was lowest at M4 and was similar among all other wetlands (Table 2.1).

Water depth was greatest immediately following the spring thaw in all wetlands and decreased throughout the growing season (Table 2.1). Mean water depth was greater in the marshes compared to the peatlands and was greatest in M4 ($p < 0.05$; Table 2.1). Mean pH was similar between the peatlands (F1 and F2) ($p > 0.05$) and was more acidic than in the marshes (Table 2.1). Mean pH was slightly alkaline at M3 and was greater than all other wetlands ($p < 0.05$). Mean pH in M1 and M2 was similar and just below neutral (Table 2.1). The pH in M4 was near neutral (Table 2.1). Mean water temperature was similar among all six wetlands throughout the growing season. Mean DO concentration was highest in M3 but was similar to F1, F2, and M4 ($p > 0.05$). DO was similar between marshes M1 and M2 ($p > 0.05$), which were lower than all other sites ($p < 0.05$; Table 2.1). Mean DOC concentration was lowest in wetlands

located closest to the Tanana River (M3 and M4) (Table 2.1). Mean DOC concentration was similar in F2 and M2 ($p > 0.05$), which were greater than all other wetlands (Table 2.1). F1 and M1 had similar mean DOC concentrations that were slightly lower than F2 and M2 (Table 2.1). Although a repeated measures multivariate analysis of variance and Tukey's post-hoc comparisons of means test indicated that environmental variables were significantly different among wetlands, they were not significant predictors of algal biomass or productivity within wetlands.

Algal biomass and primary production

Mean chlorophyll *a* concentration was significantly greater in M2 compared to all other wetlands ($p \leq 0.028$; Figure 2.3A), which were not significantly different from each other ($p > 0.05$). Mean AFDM was greater in F2 compared to F1, M1, M3, and M4 ($p \leq 0.009$; Figure 2.3B). AFDM in M2 was similar to F2 ($p = 0.983$) and was greater than F1, M1, and M3, but was not significantly different than M4 ($p > 0.05$; Figure 2.3B). Mean AFDM in wetlands F1, M1, M3, and M4 were not significantly different from one another ($p > 0.05$). Mean algal productivity was greater at F2 compared to F1, M1, M3, and M4 ($p \leq 0.014$; Figure 2.3C). Mean productivity at M2 was similar to F2 ($p = 0.8$) and was greater than F1, M1, and M4 ($p \leq 0.005$) but was not significantly different than M3 ($p > 0.05$; Figure 2.3C). Algal productivity in F1, M1, M3, and M4 were not significantly different from one another ($p > 0.05$). Algal cell density was significantly greater at M2 ($p \leq 0.0001$; Figure 2.3D) compared to all other wetlands which were not significantly different from one another ($p > 0.05$).

Mean algal productivity in the peatland F1 represented about 7% of the total ecosystem GPP during the early part of the summer growing season (Figure 2.4). Mean algal productivity

in the peatland F2 represented nearly 50% of wetland primary production during the early part of the summer growing season, and decreased to about 23% during late growing season (Figure 2.4). Mean algal productivity in the marsh M1 represented approximately 19% of wetland primary production during the early part of the summer growing season, and decreased to about 3% during late growing season (Figure 2.4). Mean algal productivity in the marsh M2 represented approximately 64% of wetland primary production during the early part of the summer growing season, and decreased to about 18% during late growing season (Figure 2.4). Mean algal productivity in the marsh M3 represented about 22% of wetland primary production during the early part of the summer growing season, and decreased to < 1% during late growing season (Figure 2.4). Mean algal productivity in the marsh M4 represented about 16% of wetland primary production during the early part of the summer growing season, and decreased to approximately 9% during late growing season (Figure 2.4).

Algal taxonomic composition

Algal taxonomic composition was strongly influenced by both hydrology and time (NMS final stress = 7.36 for 2-dimensional solution and 55 iterations; Figure 2.5). Algal community composition was equally influenced in direction and magnitude by TN and TP (Figure 2.5). The effect of environmental variables that co-varied with water depth (water temperature, DO, pH) could not be separated from the influence of water depth, but likely influence that algal community in similar direction and much lower magnitude. Similarly, DIN and SRP co-varied with TN and TP, and would therefore likely have influence in similar direction and magnitude. PAR co-varied with DOC, but since PAR did not strongly contribute to the ordination it is likely that DOC may not be very important in influencing algal community composition. Axis 1 and 2

in NMS accounted for 77% and 16% of the variability in the ordination respectively, for a cumulative 93% or variance explained by the ordination (Figure 2.5). Monte Carlo test indicates that the axes selected are significantly different than could be selected by chance ($p = 0.02$). Algal taxonomic composition was more similar within wetland sites than between wetland sites, yielding an ANOSIM with significant differences between wetland sites (Global R = 0.155; $p = 0.015$). ANOSIM also suggests that time was an important factor determining algal taxonomic composition within wetlands (Global R = 0.291; $p = 0.001$).

Averaged across all sampling dates, there were 22 algal genera that were present at >5% relative abundance in any one wetland (Table 2.2). *Dinobryon* was the dominant Chrysophyte and was present in greater abundances in both peatlands (F1 and F2), particularly the rich fen (F1), compared to the marshes (Table 2.2). Filamentous green algae (Chlorophyta) such as *Microspora*, *Oedogonium*, *Spirogyra*, and *Ulothrix* were abundant in both peatlands and marshes (Table 2.2). Chain forming desmids, such as *Bambusina* and *Desmidium* were particularly abundant in peatlands (Table 2.2). Cyanobacteria, particularly nitrogen-fixing taxa (i.e., *Nostoc*, *Anabeana*, *Haplosiphon*), were present in large quantities in both peatlands and marshes (Table 2.2). These taxa become more abundant over the course of the growing season as nutrients concentrations and water table declined in all wetlands (Figure 2.5). Diatoms did not contribute greatly to algal abundance, however *Tabellaria* was the dominant diatom in peatlands, particularly the rich fen (F1), while *Nitszchia* was more abundant in marsh sites M3 and M4 (Table 2.2).

2.4 Discussion

The six wetlands used in this study capture a range of physical and chemical conditions that were important in regulating algal productivity, abundance, and taxonomic composition. There were significant spatial differences in algal biomass and taxonomic composition between wetlands and seasonal differences within wetlands. Algal biomass and productivity were greatest in a poor fen (F2) and a large riverine marsh (M2), suggesting that algae are important contributors to primary production and therefore ecosystem function in both peatlands and marshes. Algal taxonomic composition was more similar within wetland sites than between wetland sites, suggesting that the physical and chemical environment indicative of different wetland types is important for structuring algal taxonomic composition.

Mean productivity values among all wetland sites are within the range (0-500 g $C/m^2/y$) of values reported from in the literature of temperate freshwater marshes (see review in Goldsborough and Robinson 1996). During peak productivity, estimates of algal productivity fall within the lower range of productivity values reported for the subtropical Florida Everglades (300-600 g $C/m^2/y$; McCormick et al. 1998, Ewe et al. 2006). Assuming that peak macrophyte productivity among wetland sites (70-170 g $C/m^2/y$) is equivalent to annual net productivity (g $C/m^2/y$), measured values of 30-230 g $C/m^2/y$ for benthic algae (based on 135 day ice-free period) are equivalent, and in some cases higher, than macrophyte production. The measures of algal productivity in a poor fen (F2) are higher than many of the values reported for marshes and show that algae can contribute up to 50% of wetland primary production in peatland ecosystems.

Hydrology was the most important environmental factor influencing algal taxonomic composition during this study. Water level is extremely dynamic within these sites and frequent water level fluctuations have been shown to influence many of the physical and chemical factors

characteristic of wetland habitats (e.g., nutrients, light, temperature, substrate availability), and therefore algal communities (Goldsborough and Robinson 1996). Research examining how algae respond to changes in hydrology has come mainly from the work conducted in the Florida Everglades (i.e., McCormick et al. 1998, Gottlieb et al. 2005, 2006, Iwaniec et al. 2006), where wetland hydrology has been significantly altered by human development (Sklar et al. 2005). Changes in wetland hydrology in boreal regions are occurring, in part because temperature regimes that have constrained water at or near the surface of permanently frozen soils in the region are increasing rapidly and will continue to increase during this century (Serreze et al. 2000, Hinzman et al. 2005, McGuire et al. 2007). Peatlands may be particularly sensitive to changes in hydrology because water level is highly dependent on changes in rates of precipitation and evapotranspiration (Hinzman et al. 2006). Therefore, my results indicating that algal communities are most affected by changes in water depth suggest that altered hydrology associated with climate change will have significant impacts on algal community composition.

As water depth decreased throughout the growing season, macrophyte density increased. The increase in macrophyte biomass, and subsequently lower PAR reaching the waters surface, was predicted to have limited algal biomass and productivity at some of the sites, particularly the sedge dominated marsh (M1). However, following ordination analysis, the significance of water depth in determining algal taxonomic composition suggests that water depth was a more important determinant of algal parameters than light availability. This pattern is consistent with an *in situ* mesocosm experiment conducted within the shallow riverine marsh (M4), where light was found not to have a significant effect on algal biomass or taxonomic composition (unpublished data; Chapter 4). Given that high latitude ecosystems receive nearly 20 h per day of saturating light for the duration of the growing season, algal communities in northern latitude

ecosystems may receive sufficient light despite large seasonal changes in macrophyte cover. Even in the sedge dominated marsh (M1), which had the highest density of macrophyte cover, PAR ranged from 1111 μmol quanta/m^2/s early in the growing season to 64.4 μmol quanta/m^2/s during peak macrophyte production, which is a sufficient amount of light to saturate photosynthesis (Hill 1996). The results of this study are consistent with findings from the Florida Everglades where experimentally reducing light availability had no effect of on periphyton primary production or community composition (Thomas et al. 2006). These results suggest that although the summer growing season is lengthening due to climate change processes (Magnuson et al. 2000, Chapin et al. 2006), the subsequent decrease in light attenuation due to an increase in the duration of macrophyte production may have little influence on algal biomass or taxonomic composition.

Nutrients were an important environmental factor influencing algal productivity and taxonomic composition. Both N and P influenced algal taxonomic composition in the same direction and magnitude indicating that both nutrients are co-limiting within these ecosystems. Similar co-limitation was reported in previous studies conducted within the Tanana River floodplain, where the addition of a combination of N and P produced the greatest increase in algal productivity and altered taxonomic composition compared to the addition of either nutrient alone (Wyatt et al. 2010). Furthermore, nutrients released from previously dried peatland soils have been shown to facilitate a spike in algal productivity (Schoenberg and Oliver 1988, Wyatt et al. 2012) and favor the growth of filamentous green algae (Rober et al. accepted). Increased nutrient availability may explain the higher than expected algal biomass and productivity observed in the poor fen (F2) where wetland soils were rewetted from a flood that occurred during 2008-2009. These results suggest that an increase in N and P availability with increased

soil weathering and organic matter mineralization because of climate change processes (Bridgham et al. 1995, Rouse et al. 1997) will probably increase benthic algal biomass in northern boreal wetlands. Furthermore, my results suggest that although algal productivity is typically low in peatlands, spikes in algal productivity could become more prevalent with increased frequency of flooding and drying, especially when it influences nutrient mineralization and availability in surface soils (Wyatt et al. 2012).

Individual genera within the major algal groups exhibited interesting patterns of abundance and distribution that were related to variation in environmental parameters. Both water depth and nutrient concentrations declined over time in all wetland sites. A previous study conducted at the F1 site (rich fen) reported that when nutrient concentrations and water table position were low, nitrogen (N)-fixing cyanobacteria increased in abundance (Rober et al. accepted). The results from this study are similar where cyanobacteria (*Nostoc*, *Anaebena*, *Haplosiphon*) increased in abundance as the growing season progressed and nutrient concentrations and water table position decreased, which was particularly prevalent in the rich fen (F1), large riverine marsh (M2), and *Equisetum* dominated marsh (M3). The ability for these taxa to fix atmospheric N enables them to survive in low nutrient environments and has been described as the most important source of N to many arctic and boreal regions, contributing as much as 80% of total annual ecosystem N (Solheim et al. 2006). The abundance of N-fixing cyanobacteria in these sites suggests that they are likely contributing to N inputs in both peatlands and marshes within the Tanana River floodplain. This is consistent with previous findings from a Swedish mire where N-fixing cyanobacteria (*Nostoc*, *Anaebena*, *Haplosiphon*) were found in association with several moss species and accounted for a significant amount of N input (Granhall and Selander 1973) and also in feather mosses within the boreal forest (Deluca et

al. 2002). This study is among the few to suggest the potential importance of N-fixing cyanobacteria to wetland N inputs, which may particularly important in northern boreal regions where large quantities of nutrients are currently rendered inaccessible by the slowly decomposing organic matter. Furthermore, potential increases in moss and vascular plant production facilitated by nutrients made available by N-fixing cyanobacteria could increase the carbon storage potential within boreal wetlands.

Filamentous green algae have been described as the most important contributors to algal biomass in North American bogs due to their ability to tolerate periods of desiccation, fluctuations in temperatures and light, and high acidity (Yung et al. 1986, Graham et al. 1996). Filamentous green algae, such as *Microspora*, *Oedogonium*, *Spirogyra*, and *Ulothrix* were abundant in both peatlands and marshes and were often found tangled among plant stems and mosses. Chain forming desmids, such as *Bambusina* and *Desmidium* were particularly abundant in peatlands. The large surface to volume ratio of these taxa has been hypothesized to increase their ability to photosynthesize under nutrient limited conditions (Yung et al. 1986). Large growths of filamentous green algae commonly appeared as grayish white clouds likely due to infestation by fungi which are important for the degradation of algal tissue (Yung et al. 1986). In addition to supporting fungi, labile dissolved organic carbon released from these taxa is also important for supporting bacterial production (Wyatt et al. 2012, Rober et al. accepted). Increases in bacterial density in the presence of algal exudates could increase the ability of the bacterial community to decompose more recalcitrant carbon substrates (i.e., Hamer and Marschner 2005), and thus influence wetland carbon cycling (Wyatt et al. 2012).

This is the first study to quantify spatial and temporal differences in algal biomass, productivity, and algal taxonomic composition in relation to environmental factors in peatlands

and marshes in Alaska. While this study is limited in scope, having only covered one summer growing season within a single floodplain, these data are useful for understanding the natural distribution and abundance of algae in boreal wetlands, which is necessary to predict how processes related to anthropogenic activity and climate change will influence wetland primary production, biogeochemistry, and food-web structure. This is particularly important in Alaska given the dominance of wetlands in the Alaskan landscape and the ecosystem services they provide (e.g., carbon storage). Furthermore, my relatively high estimates of the algal contribution to wetland primary production in both peatlands and marshes provide further support for the inclusion of algal primary production in estimates of total wetland primary production.

Table 2.1 Mean (ranges) of surface water parameters in six wetlands (2 peatlands, 4 marshes) over 12 weeks during the 2009 summer growing season.

Characteristic	F1	F2	M1	M2	M3	M4
TP (µg/L)	21.8	22.7	29.4	20.5	29.5	25.2
	(6.4-33.3)	(19.8-25.9)	(21.1-41.7)	(8.81-1464.7)	(13.3-43.7)	(13.3-49.5)
TN (µg/L)	989.4	1155.4	1199.6	1403.8	682.4	744.5
	(876.9-1098.1)	(967.9-1229.8)	(1029.9-1560.3)	(1221.1-1679.7)	(342.0-924.9)	(657.3-862.8)
SRP (µg/L)	1.38	2.45	3.10	1.85	3.28	1.93
	(0-4.12)	(0-5.24)	(0-6.4)	(0.7-4.0)	(2.5-4.3)	(0.12-3.13)
DIN (µg/L)	11.6	7.77	33.0	18.6	12.9	4.99
	(0.96-39.1)	(0-23.6)	(1.17-114.8)	(4.9-48.1)	(0-40.6)	(0-13.4)
Water depth (cm)	7.2	11.8	15.9	17.8	12.3	20.0
	(10-0)	(39-0)	(42-0)	(29-4)	(25-0)	(45-0)
pH	5.53	5.69	6.57	6.31	8.39	7.60
	(6.5- 4.61)	(5.84-5.48)	(6.5-6.6)	(6.18-6.72)	(8.28-8.61)	(7.4-7.8)
Water temperature (°C)	20.9	19.1	19.5	20.2	18.9	16.4
	(15.4-25)	(15-25.1)	(18.5-20.1)	(18.2-20.9)	(18.0-19.25)	(14.7-18.2)
DO (mg/L)	12.1	9.80	6.70	6.79	12.5	9.23
	(10.3-16.7)	(11.6-7.6)	(5.7-9.8)	(6.3-8.4)	-	(8.7-9.2)
DOC (mg/L)	28.7	47.9	35.3	40.7	10.8	13.95
	(25.3-33.7)	(37.7-67.6)	(31.7-40)	(38.2-50.1)	(8.6-15.2)	(11.6-17.5)
PAR (µmol/cm^2/s)	713.5	862.4	357.8	758.3	556.7	698.8
	(1154-424)	(1297-337)	(1114-66.4)	(1208-326.7)	(1433-117.7)	(1395-206.6)

Note: TP = total phosphorus, TN = total nitrogen, SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen, DO = dissolved oxygen, DOC = dissolved organic carbon, PAR = photosynthetically active radiation.

Table 2.2 Mean relative abundance of algal taxa in six wetlands (2 peatlands, 4 marshes) over 12 weeks during the 2009 summer growing season. Table includes only taxa with >5% relative abundance in at least one of the wetland sites.

Algal genera	F1	F2	M1	M2	M3	M4
Chyrosophytes						
Dinobryon	21.3	9.22	4.92	5.91	4.03	1.45
Sum	**21.3**	**9.22**	**4.92**	**5.91**	**4.03**	**1.45**
Greens						
Bambusina	6.34	9.52	4.81	1.37	0.10	1.05
Desmidium	6.17	1.28	1.68	3.03	–	0.33
Gloeocystis	7.51	9.19	8.73	5.95	9.10	5.28
Microspora	3.31	15.9	2.76	0.39	1.99	0.86
Oedogonium	5.73	5.42	4.21	2.31	3.85	4.66
Palmella	–	0.22	3.28	–	6.87	9.05
Radiofilium	8.77	0.41	3.02	–	1.69	1.18
Sphaerocystis	5.34	2.59	2.92	1.41	1.07	1.96
Spirogyra	2.11	5.09	0.60	0.39	1.03	5.88
Ulothrix	3.34	2.51	5.37	3.73	4.33	28.6
Sum	**48.6**	**52.1**	**37.4**	**18.6**	**30.0**	**58.9**
Cyanobacteria						
Anabeana	3.64	7.28	2.86	36.1	–	6.72
Aphanocapsa	17.5	5.15	14.9	4.67	2.66	–
Calothrix	–	6.47	6.28	6.99	15.4	–
Chroococcus	6.51	3.94	6.17	2.90	3.02	5.24
Gloeocapsa	6.91	6.32	9.11	3.93	9.96	4.80
Haplosiphon	6.34	7.71	0.50	17.2	–	–
Merismopedia	6.09	2.78	12.0	5.23	–	–
Nostoc	12.9	13.0	21.8	6.96	22.2	12.5
Phormidium	1.33	–	–	10.2	–	–
Sum	**61.2**	**52.7**	**73.6**	**94.2**	**53.2**	**29.3**
Diatoms						
Nitszchia	0.82	0.22	0.83	2.02	7.00	5.68
Tabellaria	7.83	2.46	2.84	2.00	–	–
Sum	**8.65**	**2.68**	**3.67**	**4.02**	**7.00**	**5.68**

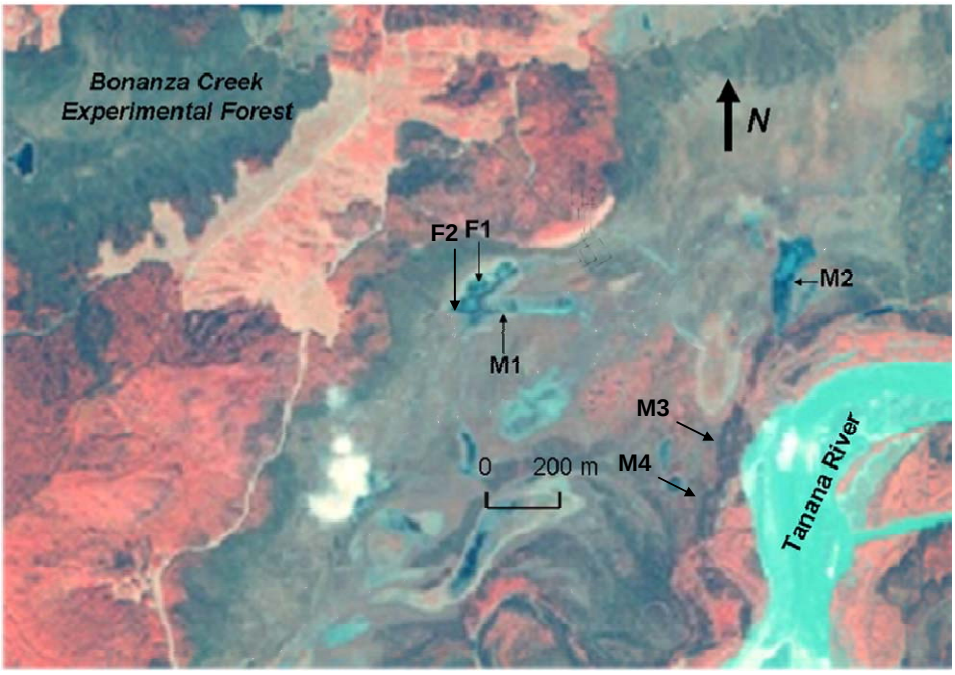

Figure 2.1 Aerial photograph outlining the location of the six wetland study sites.

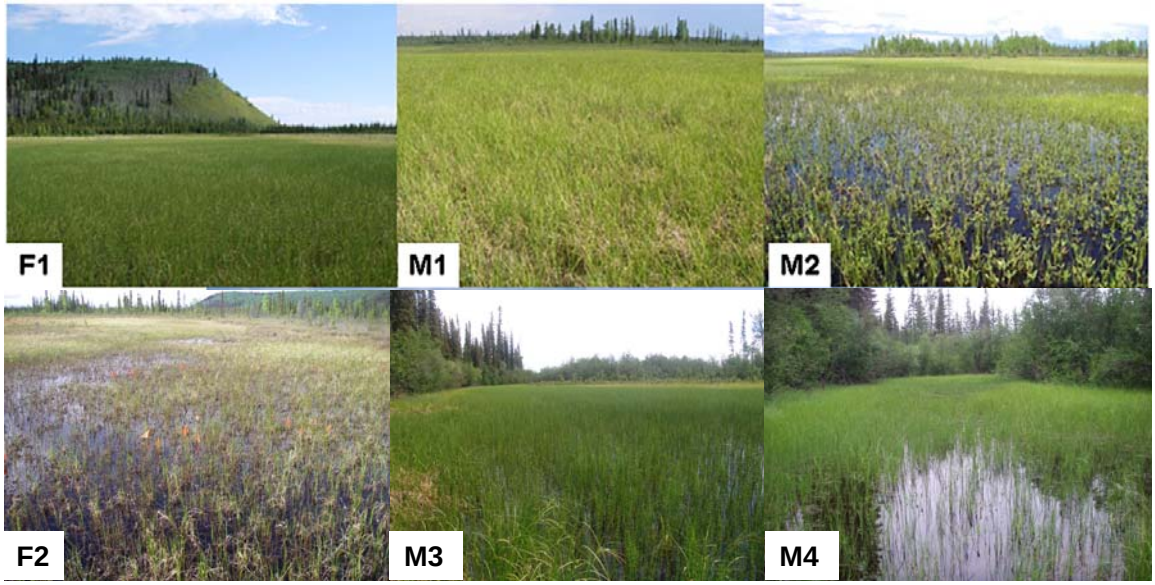

Figure 2.2 Images of the six wetland sites used in this study. F1 is a rich fen. F2 is a poor fen. M1 is a densely vegetated marsh with tussock grasses creating saturated hallows. M2 is a large marsh complex with large open water areas covered with floating macrophytes. M3 is a shallow riverine marsh dominated by *Equisetum fluviatile*. M4 is a shallow riverine marsh with a diversity of floating and emergent macrophytes.

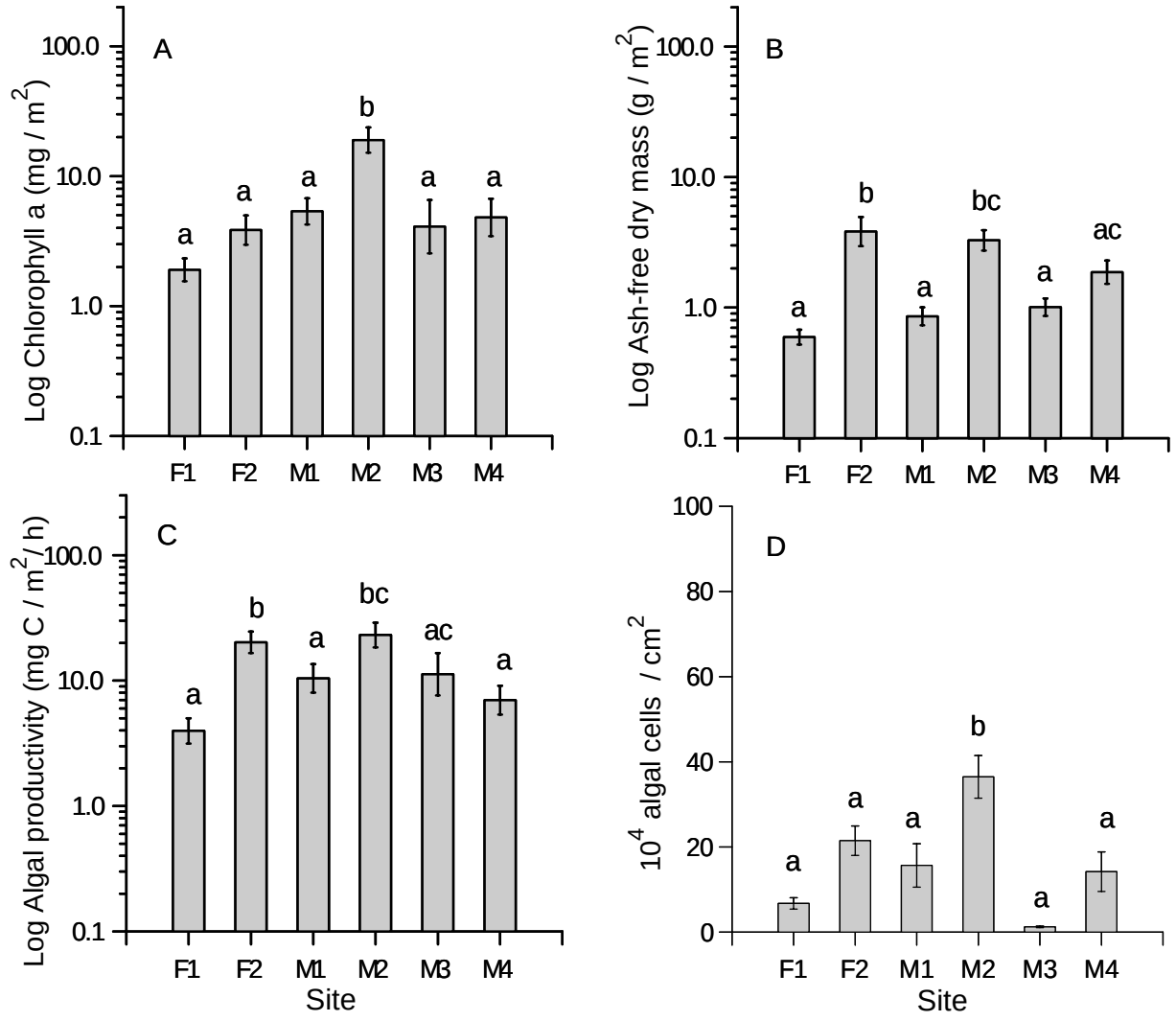

Figure 2.3 Mean ± SE algal chlorophyll a concentration (A), ash-free dry mass (B), productivity (C), and cell density (D) in six Alaskan boreal wetlands during the 2009 summer growing season. Bars with the same letter are not significantly different among sites.

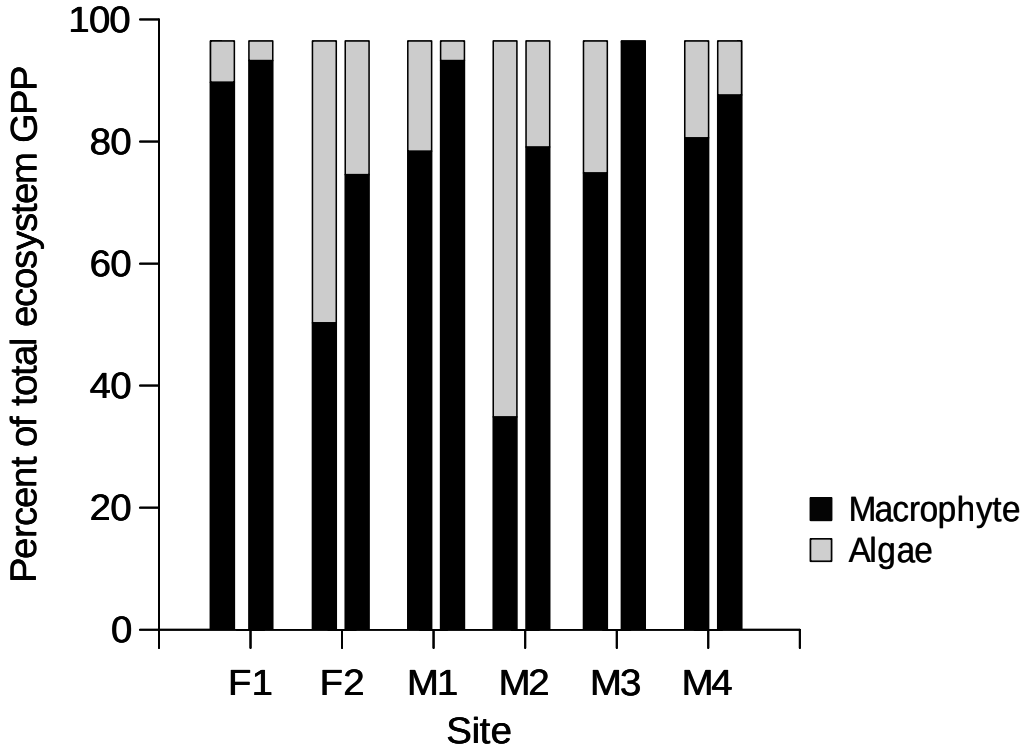

Figure 2.4 Aboveground macrophyte and algal contribution to wetland primary production in six wetlands during early (first bar in each pair) and late (second bar in each pair) growing season 2009.

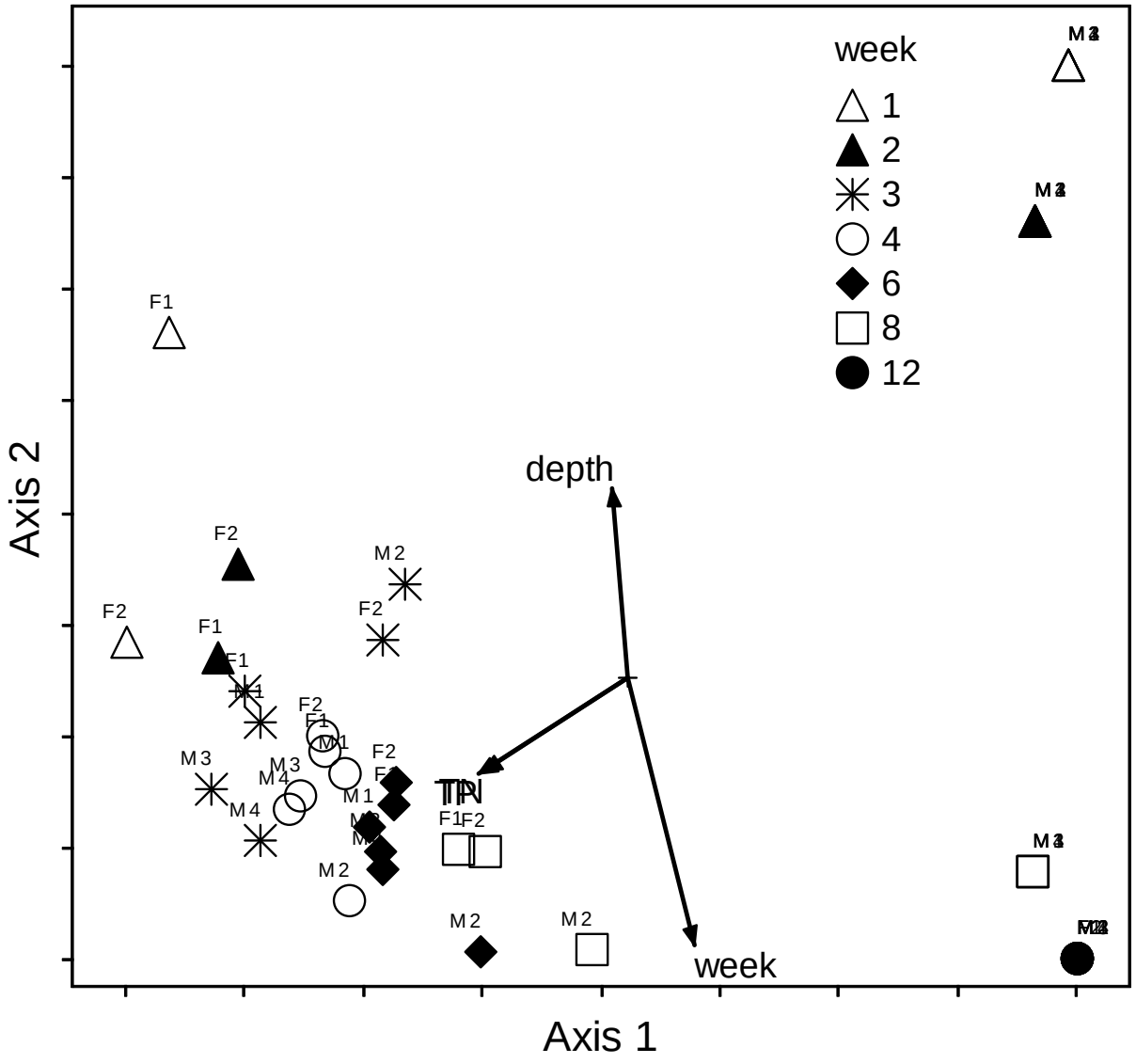

Figure 2.5 NMS between relative algal abundances and surface-water chemical variables and time from six wetlands in the Tanana River floodplain, Alaska (final stress = 7.36 for 2-dimensional solution and 55 iterations). All symbols are labeled with the wetland site. Different symbols indicate week sampled during the growing season. Axis 1 and 2 accounted for 77% and 16% of the variability in the ordination respectively, for a cumulative 93% or variance explained by the ordination.

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CHAPTER 3

REGULATION OF ALGAL STRUCTURE AND FUNCTION BY NUTRIENTS AND GRAZING IN A BOREAL WETLAND

3.1 Introduction

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 oxygen 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 ice thaw, and could promote N and P mineralization in the expanded active soil layer (Bridgham 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).

I 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. I report the effect of grazers on algal community structure and biomass following enrichment with limiting nutrients. I also examined the role of grazers in wetland biogeochemical cycling by evaluating the potential of consumer-driven nutrient recycling to influence algal accumulation. I 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.

3.2 Methods

Study site

I 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 (≤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 (~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 my study site was given by Wyatt and Stevenson (2010).

Experimental design

I 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). I 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. I 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 ~10% vegetation cover and a water depth of 44–49 cm. Enclosures were pushed into the sediments so that ~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. I placed 4 ceramic tiles (25 cm^2) into each enclosure as artificial substrates for algal colonization. I 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.

I 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 (Figure 3.1). I added nutrients from a stock solution every 4 d to achieve water-level concentrations for N = 1000 µg/L $NaNO_3$, P = 100 µg/L $NaPO_4$, and Si = 10 mg/L Na_2O_3Si after each addition. I assumed these nutrient levels would saturate algal growth rates because they exceeded concentrations reported to be limiting for benthic algae in studies reviewed by Borchardt (1996). I began enrichment after the late-spring thaw to simulate nutrient inputs from groundwater or surface-water runoff (McDougal et al. 1997). I 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* (Figure 3.1). 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). I 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

I collected and filtered water for dissolved nutrient analysis immediately after each nutrient addition (every 4 d) using a 0.45-µm Millex®-HA syringe-driven filter unit (Millipore Corporation, Bedford, Massachusetts). I determined concentrations of dissolved inorganic N (DIN) as NO_3 + NO_2-N (Cd reduction method; APHA 1998), and of silicate (SiO_2) (molybdate method; APHA 1998) with a Skalar® auto-analyzer (Skalar Analytical, Breda, The Netherlands), and of soluble reactive P (SRP) (ascorbic acid method; APHA 1998) with a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, UK). I 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® Multi-Probe (Yellow Springs Instruments, Yellow Springs, Ohio).

In each enclosure, I 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. I was unable to measure chlorophyll *a* because I could not preserve samples in this remote field location. Thus, algal biomass was measured as AFDM, cell density, and total biovolume. I determined AFDM (mg/cm^2) by drying samples for 24 h at 105°C and combusting them for 1 h at 500°C in preweighed aluminum pans to determine the difference between dry mass and ashed mass, respectively (APHA 1998). I preserved a whole water sample in a 2% formalin solution for algal community analysis. I used standard protocols to characterize

algal biomass and dominant taxonomic composition. I counted ≥300 algal cells or colonies/sample in a Palmer–Maloney nanoplankton counting chamber and identified the algae to genus at 400× magnification (Charles et al. 2002). I quantified benthic algal abundance (cells/cm^2 of substrate) with the formula provided by Lowe and Laliberte (2006). I calculated biovolume ($\mu m^3/cm^2$ of substrate) by multiplying algal cell density by the estimated cell volume using geometric formulae from Hillebrand et al. (1999).

I evaluated the potential for grazers to recycle N and P by estimating the daily rate of nutrients excretion by the snails. I 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, I measured DIN and SRP concentrations with the methods described previously.

Statistical analyses

I $\log(x + 1)$-transformed all data for statistical analyses if necessary to correct for nonnormal distribution and unequal variances among treatments prior to analysis. I 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. I examined differences in biovolume of common genera (occurring at ≥5% relative abundance) among treatments with 1-way ANOVA. I used Bonferroni corrections for the algal assemblage analyses to preserve the experiment-wise Type I error rate of $p = 0.05$. I 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, I used Tukey post hoc comparison of means tests to discriminate between different factor levels. I performed all

statistical analyses with SYSTAT (version 11; SYSTAT Software Inc., Point Richmond, California).

3.3 Results

Water chemistry

Background levels of inorganic nutrients were low (mean ± SE: DIN = 8.02 ± 1.28 µg/L, SRP = 8.69 ± 1.28 µg/L, SiO_2 = 12.09 ± 0.49 mg/L) and remained nearly constant over the 24-d experiment (Figure 3.2A–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 ± 705.6 µg/L), SRP (49.6 ± 47.6 µg/L) and Si (35.7 ± 14.2 mg/L) to levels significantly greater than in the open wetland and control enclosures ($p < 0.05$; Figure 3.2A–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 ± 0.5 cm), temperature (16 ± 0.05°C), pH (7.5 ± 0.3), and conductivity (0.37 ± 0.006 µS/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 3.3A, B, 3.4A, B). AFDM ($F_{2,13} = 81.91$, $p < 0.0001$; Figure 3.3A), cell density ($F_{2,13} = 122.6$, $p < 0.0001$; Figure 3.3B), and total biovolume ($F_{2,13} = 14.86$, $p = 0.004$; Figure

3.4C) were significantly greater in nutrient-enriched than in control enclosures. In nutrient-enriched enclosures, AFDM ($F_{2,11} = 7.88$, $p = 0.01$; Figure 3.3A), cell density ($F_{2,11} = 7.26$, $p = 0.01$; Figure 3.3B), and total biovolume ($F_{2,11} = 7.92$, $p = 0.01$; Figure 3.4C) 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 × grazer interaction term was significant for AFDM ($F_{3,11} = 5.37$, $p = 0.02$) and total biovolume ($F_{3,11} = 4.64$, $p = 0.02$).

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 ~90% of the total biovolume (Figure 3.4A). 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 (Figure 3.4B). Nutrient enrichment 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 (Figure 3.4C). Grazing had little effect on the algal community under low-nutrient conditions. However, in nutrient-enriched enclosures, the proportion of *Mougeotia* was significantly lower ($F_{7,24} = 2.5$, $p = 0.04$; Figure 3.4C) 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 mg snail^{-1} d^{-1} and 0.045 mg snail^{-1} d^{-1}, respectively. I multiplied the excretion rates of DIN and SRP by the estimated number of snails in the wetland (30 snails/m^2), and calculated that snails could regenerate N at a rate of 7.5 mg/d and P at 844.8 mg/d. When I estimated concentration changes by accounting for the approximate volume of water in the wetland, I calculated that snails could regenerate N at a rate of 0.0002 mg L^{-1} d^{-1} and P at 0.019 mg L^{-1} d^{-1}.

3.4 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 (Bridgham et al. 1995, Rouse et al. 1997). My 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 this

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). My 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. My findings are consistent with those reported from the Florida Everglades where direct nutrient amendments (McCormick and O'Dell 1996) and from Delta Marsh, Manitoba, where nutrient-release from reflooded sediments (Robinson et al. 1997) resulted in an overall increase in taxa from the family Zygemataceae (*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, my results suggest that the relative strengths of top-down vs bottom-up control were not equivalent. My experimental design allowed me to examine both independent and interactive effects of nutrients and grazing,

so I was 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 in my 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, my results suggest that they may influence algal biomass indirectly by recycling the low concentrations of nutrients that are present. I 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 my 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 my 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. My 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 are 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). My results support the 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 latitudes aquatic ecosystems. The

ability of grazers to suppress algal accumulation following enrichment supports my 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, my 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.

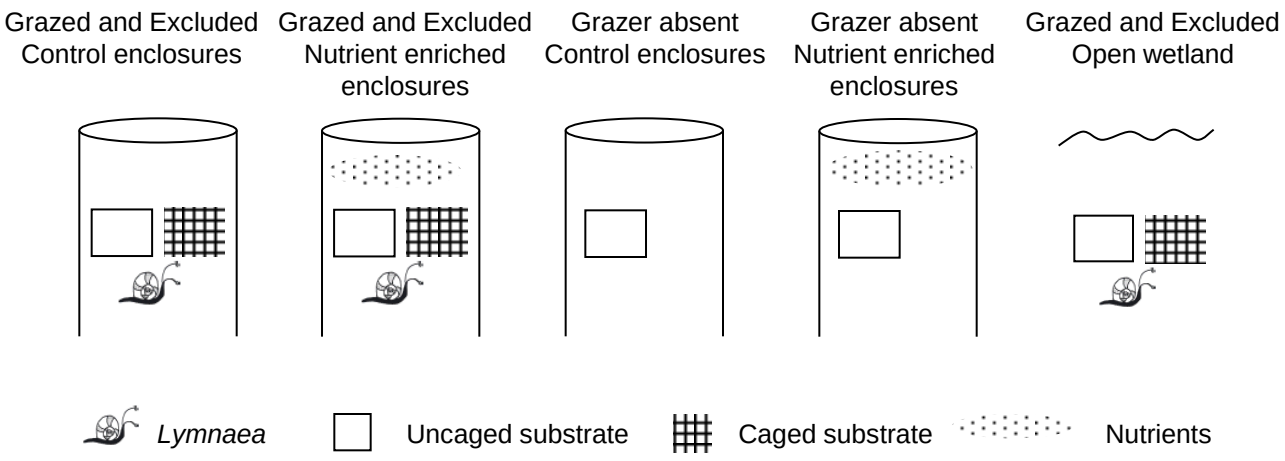

Figure 3.1 Schematic diagram of enclosure design. Enclosures were constructed of welded wire mesh (40 cm in diameter × 85 cm tall) and held ~60 L of water. The top 75 cm of each cylinder was wrapped with 0.1-mm clear window vinyl and embedded 10 cm into sediments with an open top extending 15 cm above the water column. I suspended all substrates attached to frames that maintained a consistent depth of 5 cm below the water surface. I 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.

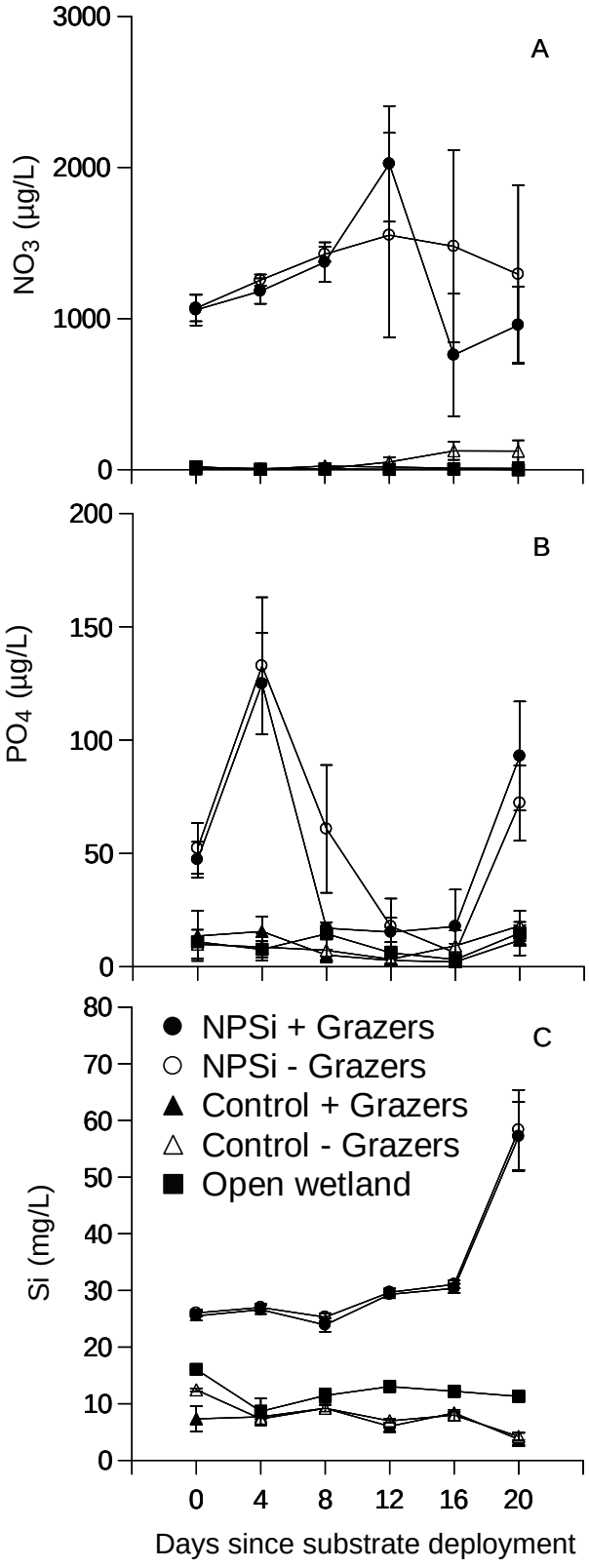

Figure 3.2 Dissolved nutrient concentrations of NO_3 (A), PO_4 (B), and Si (C) in nutrient enriched, control, and open wetland enclosures with (+) and without (–) grazers.

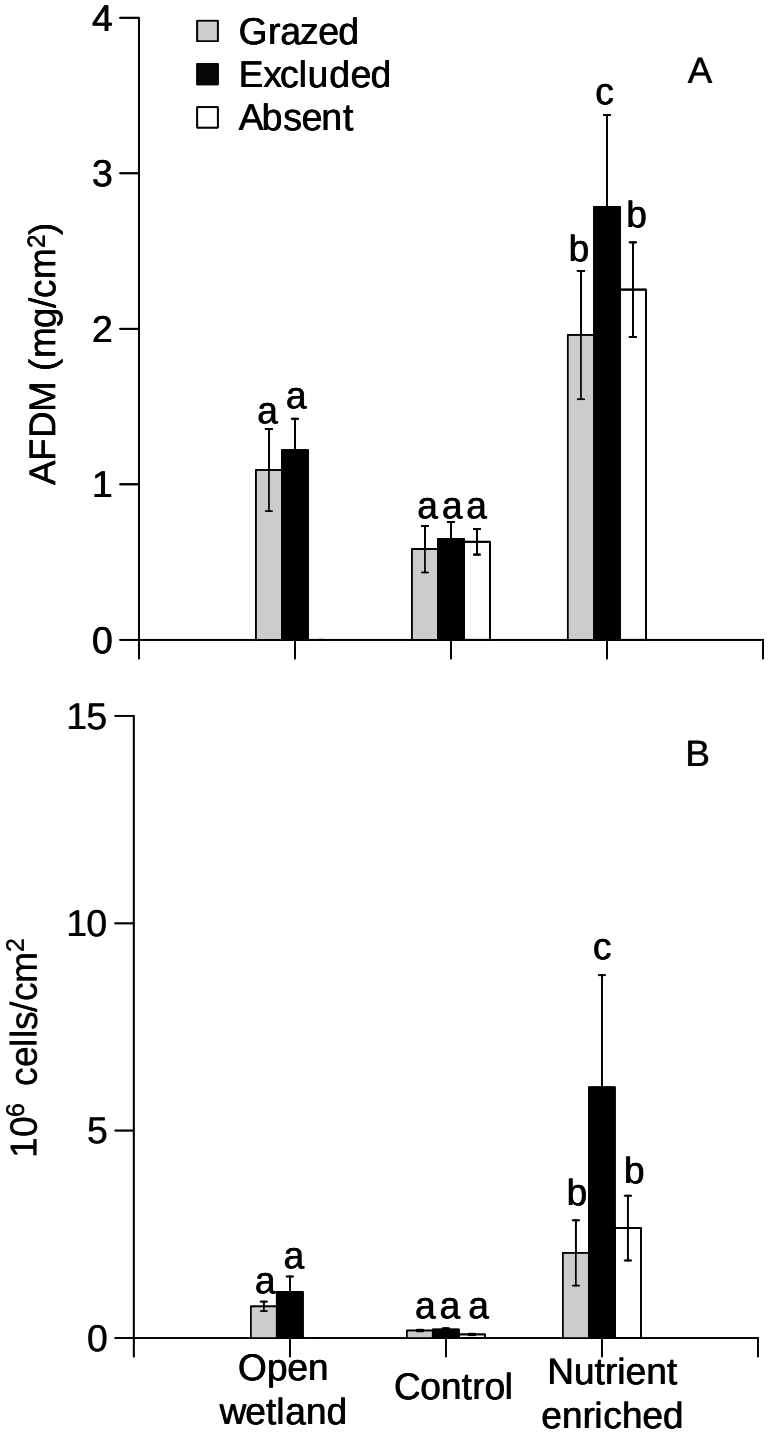

Figure 3.3 Mean (±1 SE; *n* = 4) ash-free dry mass (AFDM) (A) and cell density (B) in the open wetland, control, and nutrient-enriched enclosures with and without grazers. Bars with the same letter are not significantly different among treatments.

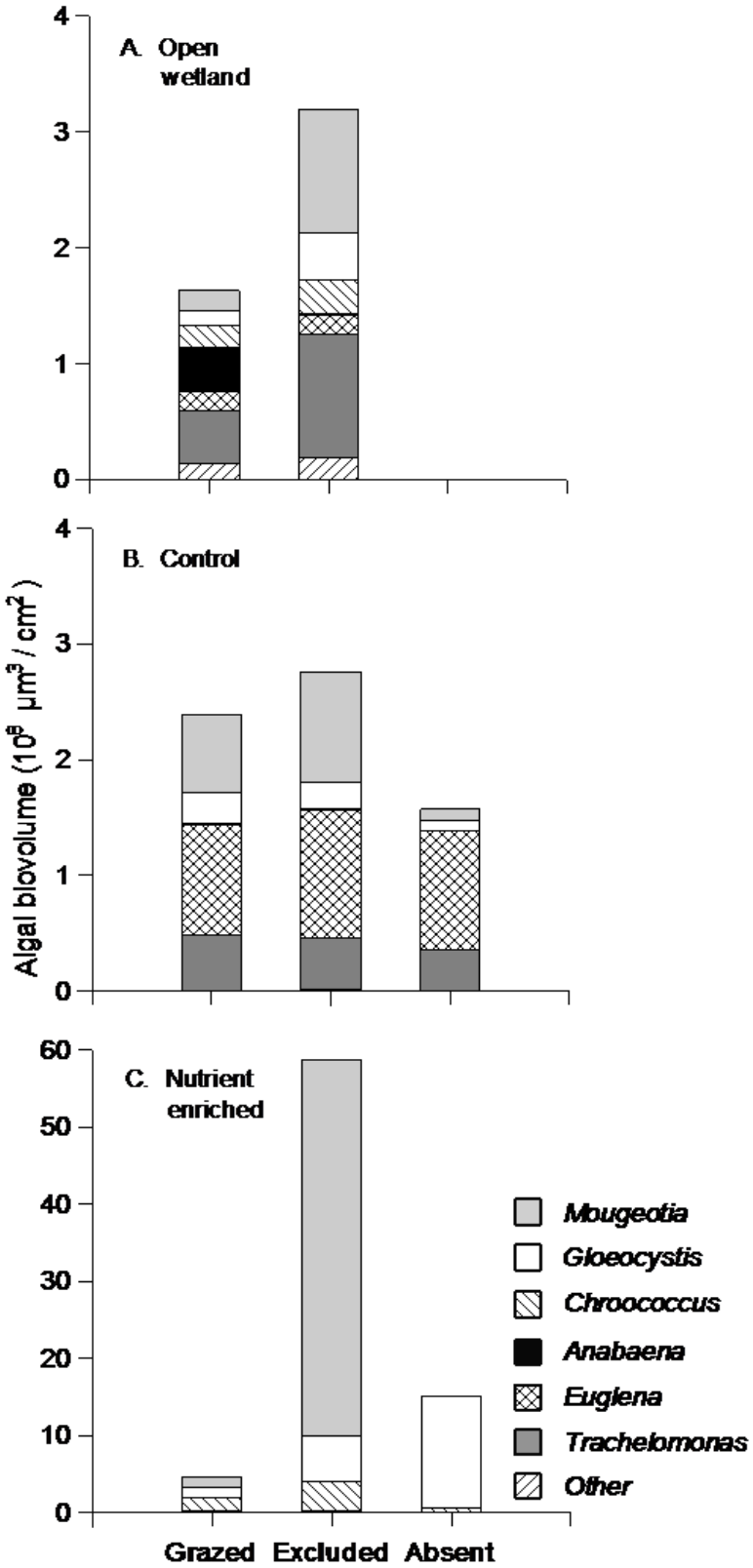

Figure 3.4 Taxonomic composition and total biovolume of algae with >5% relative abundance in the open wetland (A), control (B), and nutrient-enriched (C) enclosures with and without grazers.

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CHAPTER 4

THE ROLE OF LIGHT LIMITATION AND HERBIVORY ON ALGAL RESPONSE TO NUTRIENT INPUTS IN A BOREAL MARSH, ALASKA

4. 1 Introduction

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 influence dissolved oxygen concentrations (Browder et al. 1994, Richardson 2008), sediment formation (Gleason and Spackman 1974, McCormick et al. 1998), nutrient uptake and retention (Wetzel 1996, Gaiser et al. 2004), and can account for a significant amount of total primary production (Robinson et al. 1997, Richardson 2009, Wyatt et al. 2010). Despite their importance, we know relatively little about the factors that regulate algal communities in wetlands. This is particularly true for boreal regions, where wetlands are abundant and processes related to ongoing climate change are expected to have widespread impacts on aquatic ecosystems (Rouse et al. 1997, Schindler 1998).

Algal primary production is generally controlled by factors regulating from the bottom-up (light and nutrients) and from the top-down (herbivory). Even though these structuring forces are widely accepted to be interactive in both terrestrial (Hawkes and Sullivan 2001) and aquatic (Brett and Goldman 1997, Leibold et al. 1997, Hillebrand 2002) ecosystems, the degree to which each process influences producer biomass varies. Determining the hierarchy of regulatory factors on primary producers and the strength of their interaction is a fundamental goal for

ecologists (Hansson 1992, Rosemond et al. 2000), and the extent to which these regulatory processes operate in wetlands is largely unknown.

Light is required to carry out photosynthesis, therefore it is commonly considered the most important resource regulating algal communities (Hill 1996). Light conditions in wetlands are extremely dynamic. Not only are wetlands exposed to seasonal changes in incident radiation but light attenuation also varies with the degree of shading by overlying macrophytes (Robinson et al. 2000) because macrophytes are the primary substrate available for benthic algal colonization in wetlands. This poses an interesting problem for light limited algal primary production, especially in northern boreal wetlands that receive over 20 h of daylight during the summer growing season, resulting in rapid macrophyte growth (Chapin et al. 2006) and therefore decreased light availability to benthic algae. Furthermore, climate change processes which have led to a longer growing season (Magnuson et al. 2000, Chapin et al. 2006), with a subsequent increase and duration of macrophyte production.

In lakes and streams, insufficient light reduces the ability of algae to acquire and utilize essential nutrients (Hill et al. 1995, Hillebrand 2005, Liess et al. 2009). Therefore changes in light attenuation may affect the way benthic algae respond to nutrients (Grimshaw et al. 1997, Rosemond et al. 2000). This issue is particularly acute in boreal wetlands where changes in thermal regime are expected to increase the extent of seasonal ice thaw, which will probably promote nitrogen and phosphorus mineralization in the expanded active soil layer (Bridgham et al. 1995). An increase in nutrients is expected to increase algal primary production (Rouse et al. 1997). Understanding how changes in light attenuation will affect the ability of benthic algae to utilize nutrients is further complicated by food web interactions where grazers are free to

consume any increase in algal biomass, overwhelming the algal response to either changes in light, nutrients or both (Feminella and Hawkins 1995, Hill et al. 1995, Rosemond et al. 2000).

The aim of this study was to investigate *in situ* how differences in the relative availability of solar radiation in the presence or absence of grazing, alter the ability of benthic algae to respond to nutrient enrichment in a northern boreal wetland. I tested the following hypotheses: 1) nutrient enrichment stimulates algal accumulation, 2) grazers regulate algal responses to nutrients by suppressing algal accumulation, and 3) 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.

4.2 Methods

Study Site

I conducted this study in a freshwater marsh located on the floodplain of the Tanana River near the Bonanza Creek Experimental Forest, situated approximately 35 km southwest of Fairbanks, Alaska, U.S.A. (latitude 64.42° N, longitude 148.18° W) for three weeks from June 22 to July 8, 2008. The area has large fluctuations in daylight with more than 21 h on June 21 and less than 3 h on December 21. The low sun angle in both summer and winter limit the solar radiation that reaches the water surface. In Fairbanks (65°N) the maximum solar angle is 48.5° at the summer solstice, resulting in daily solar radiation of 22,375 $KJ/m^2/d$ in June (Hinzman et al. 2006). The study site is characteristic of other marsh habitats that occur in oxbows along the flood plain, 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 sp*., which is the most abundant grazer in the marsh (~30/m^2) throughout the summer growing season. Background concentrations of inorganic nutrients were generally low during the study and within the range of other wetlands and lakes in the region (see review in Wyatt et al. 2010). Mean ± SE dissolved organic carbon (DOC) concentration, measured biweekly from May to July, was 13.95 ± 2.4 mg/L and reduced photosynthetically active radiation (PAR) by approximately 20% at the surface.

Experimental design

I manipulated light, grazing, and nutrient concentrations *in situ* using 32 open-ended cylinder enclosures modified from the design described by Greenwood and Lowe (2006). I constructed enclosures by rolling welded wire mesh into a cylinder (40 cm in diameter) and lined the inside of each cylinder with a layer of 0.1 mm clear polyvinylidene film, which transmits 90% of PAR and 80-90% UV (Bothwell et al. 1993). I embedded each enclosure 10 cm into the sediment with the open top extending above the water column and placed them in areas with similar depth and open canopy. I placed four ceramic tiles (25 cm^2) into each enclosure as artificial substrates for algal colonization. I suspended all substrates attached to a wire frame that could be repositioned to maintain a consistent depth of 5 cm below the water surface.

I measured algal and macrophyte biomass over a five week period during the previous summer growing season to measure changes in algal biomass with deceasing light due to increasing macrophyte growth (Figure 4.1). The shaded treatment (75% blocked) simulated the low light levels measured at peak macrophyte biomass (Figure 4.1). The un-shaded treatment

(0% blocked) simulated the early growing season when macrophyte biomass is low (Figure 4.1). I used a factorial combination of nutrient enrichment (enriched or control), grazing (grazed or un-grazed), and light (shaded or un-shaded) with four replicates each (Figure 4.2). Un-shaded treatments received full sunlight. Shading was achieved using charcoal solar screening (New York Wire, Mt. Wolf, PA, U.S.A.) that blocked 75% of light. I adhered shade screen to 40 cm diameter rings made of pipe insulation, allowing all light treatments to float on the waters surface within each enclosure. This allowed the screen to move freely up and down with water level fluctuation, and also kept the screen suspended above the water so as not to disturb the substrates.

In a concurrent study, Wyatt et al. (2010) identified nitrogen (N) and phosphorous (P) as the nutrients most limiting to algal productivity at this study site. Therefore, I added a pre-weighed combination of N as $NaNO_3$ and P as Na_2HPO_4 evenly onto the waters surface in nutrient enriched enclosures every four days, for 16 days. I assumed these nutrient levels would saturate algal growth rates because they exceeded concentrations reported to be limiting for benthic algae in studies reviewed by Borchardt (1996). I began enrichment after the late spring thaw to simulate nutrient inputs from groundwater or surface water runoff (McDougal et al. 1997). I manipulated grazer access to periphyton on tiles inside nutrient enriched and control enclosures by nesting both caged (un-grazed treatment) and un-caged (grazed treatment) substrates together inside enclosures with natural abundances of the snail *Lymnaea* (Figure 4.2). Cages around substrata within mesocosm enclosures prohibited grazing but allowed algae access to nutrients. Cages were made of 1 mm clear polyethylene Nitex screen (Dynamic Aqua-Supply Ltd., Surrey, BC, Canada), which blocks approximately 5% PAR.

Sampling procedure

I measured average light during 15 second intervals every four days in each enclosure using a LI-COR submersible quantum sensor and LI-250 light meter (LI-COR, Lincoln, NE, U.S.A.) at peak sunlight. I collected and filtered water for dissolved nutrient analysis every four days using a 0.45 μm Millex®-HA syringe-driven filter unit (Millipore Corporation, Bedford, MA, USA). I determined concentrations of dissolved inorganic nitrogen (DIN) as nitrate + nitrite-N (cadmium reduction method, APHA 1998) using a Skalar® auto-analyzer (Skalar Analytical, Breda, Netherlands), and of soluble reactive phosphorous (SRP) (ascorbic acid method, APHA 1998) using a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, UK). I measured water depth, water temperature, pH, and conductivity in each enclosure every four days using a calibrated 650 YSI meter (YSI incorporated, Yellow Springs, OH, U.S.A.).

Following completion of the study, I removed algal biomass on tiles from each enclosure with a toothbrush and split the resulting homogenous algal slurry volumetrically for analysis of ash-free dry mass (AFDM) and cell counts. I was not able to measure chlorophyll *a* because I could not preserve samples in this remote field location. Thus, algal biomass was measured as mg/cm^2 AFDM, cell density/cm^2, and total algal biovolume μm^3/cm^2. I determined AFDM after drying samples for 24 h at 105ºC and ashing for 1 h at 500ºC in pre-weighed aluminum pans to determine the difference between dry mass and ashed mass, respectively (APHA 1998). I preserved a whole water sample with a 2% formalin solution for algal community analysis. I used standard protocols to characterize algal biomass and dominant taxonomic composition by counting and identifying at least 300 algal cells or colonies per sample using a Palmer-Maloney nanoplankton counting chamber and identified algae to genus at 400x magnification (Charles et

al. 2002). I quantified benthic algal abundance (cells/cm^2 of substrate) using the formula provided in Lowe and Laliberte (2006). I calculated biovolume ($\mu m^3/cm^2$ of substrate) by multiplying algal cell density by the estimated cell volume using geometric formulae from Hillebrand et al. (1999).

Statistical Analyses

All data for statistical analyses were log + 1 transformed if necessary to correct for non-normal distribution and unequal variances among treatments prior to analysis. I used a 3-way analysis of variance (ANOVA) with light and nutrients as between subjects factors and grazing as a within subject factor to determine the effects of light manipulation, nutrient enrichment, and grazing on benthic algal biomass as AFDM, cell density, and total biovolume. I examined differences in biovolume of common genera (occurring at ≥ 5% relative abundance) among treatments with a 1-way ANOVA. I used repeated measures ANOVAs to determine effects of treatments on dissolved nutrients, water depth, water temperature, pH, and conductivity measured throughout the experiment. I used Tukey post-hoc comparison of means tests to discriminate between different factor levels. I performed all statistical analyses with SYSTAT (version 11, SYSTAT software inc. Point Richmond, CA, USA).

4.3 Results

Water chemistry

Mean ± SE inorganic N and P concentrations in the control enclosures were DIN = 2.63 ± 6.39 µg/L; SRP = 17.3 ± 8.60 µg/L and remained nearly constant over the 16 day experiment

(Figure 4.3). N and P concentrations in nutrient enriched enclosures (DIN = 2194 ± 1184 μg/L; SRP = 239 ± 306 μg/L) were significantly greater than the control enclosures ($p < 0.05$). Nutrient concentrations remained slightly higher in shaded treatments compared to un-shaded treatments, but differences were not statistically significant ($p > 0.05$). Depth (17.6 ± 0.57 cm), water temperature (17.8 ± 0.15 °C), pH (7.03 ± 0.03), and conductivity (0.29 ± 0.01 μS) varied during the experiment but did not differ among treatments ($p > 0.05$; data not shown). Mean PAR was 568 ± 85.0 μmol quanta/m^2/s in un-shaded treatments, 63.0 ± 12.0 μmol quanta/m^2/s in shaded treatments, and 638.7 ± 75.4 μmol quanta/m^2/s in the open wetland.

Algal biomass

Grazing significantly decreased AFDM ($F_{1,11} = 40.5$, $p < 0.0001$; Figure 4.4; Table 4.1), cell density ($F_{1,11} = 39.4$, $p < 0.0001$; Figure 4.4; Table 4.1), and total biovolume ($F_{1,11} = 18.6$, $p = 0.001$; Figure 4.5; Table 4.1) compared to un-grazed treatments in control and nutrient enriched enclosures, under all light conditions. Grazers decreased algal biomass in nutrient enriched enclosures to levels that were not significantly different from grazed biomass in control enclosures ($p > 0.05$) under all light conditions. Algal biomass was greater in un-grazed nutrient enriched enclosures compared to control enclosures under all light conditions but differences were not significant ($p > 0.05$; Table 4.1). There was a significant effect of light on AFDM ($F_{1,11} = 9.21$, $p = 0.01$; Table 4.1), but not on cell density or total biovolume ($p > 0.05$).

There was a significant two way interaction between nutrients and grazing for AFDM ($F_{1,11} = 4.77$, $p = 0.05$; Table 4.1), cell density ($F_{1,11} = 11.04$, $p = 0.007$; Table 4.1), and total

biovolume ($F_{1,11} = 4.07$, $p = 0.069$; Table 4.1). 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) where nutrient enrichment increases algal biomass and grazing reduces the effect of nutrients. The interaction between light and nutrients was not significant for any of the biomass parameters ($p > 0.05$). The interaction between light and grazing was not significant for any of the biomass parameters ($p > 0.05$). The three way interaction between light, nutrients, and grazing was not significant for any of the biomass parameters ($p > 0.05$; Table 4.1).

Community composition

Shading did not affect algal community composition, but grazing and nutrient enrichment did. Of the ten taxa that were present in greater than 5% relative abundance, none of the taxa responded to changes in light (Figure 4.5). Green algae, especially *Gloeocystis*, comprised 54-68% of the of the total cell density in all treatments. Diatoms, especially *Nitzschia*, were more abundant in nutrient enriched enclosures compared to the control. Grazing decreased *Nitzschia* ($F_{7,22} = 2.204$, $p = 0.074$) compared to un-grazed treatments in both nutrient enriched and control enclosures regardless of light manipulation. Nutrient enriched enclosures had a greater abundance of the filamentous green algae *Ulothrix* compared to control enclosures. Grazing significantly decreased *Ulothrix* ($p = 0.05$) compared to un-grazed treatments in both nutrient enriched and control enclosures regardless of light manipulation. The basal cells of *Stigeoclonium* were more abundant on grazed than un-grazed substrates in nutrient enriched enclosures. Un-shaded nutrient enriched enclosures had a significantly lower abundance of *Gloeocapsa* (cyanobacteria) ($F_{7,22} = 5.575$, $p = 0.001$) and *Stigeoclonium* (chlorophyta) ($F_{7,22} =$

4.118, $p = 0.005$) independent of grazing, compared to any of the other nutrient or light treatments. Taxa from Euglenophyceae (*Trachelomonas*), Chrysophyceae (*Ophiocytium*), and Cyanophyceae (*Aphanocapsa* and *Chroococcus*) were unaffected by either light, nutrient or grazer manipulations.

4.4 Discussion

Grazing and nutrients were more important regulatory factors determining algal biomass and community composition than light. The addition of nutrients increased benthic algal biomass and grazers suppressed algal accumulation, supporting my first two hypotheses. These interacting and opposing influences of nutrients and grazing are consistent with 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. 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), where the positive effect of nutrients is decreased in the presence of grazers. However, my results indicate that the relative strengths of top-down versus bottom-up control were not equivalent. Since my experimental design allowed me to examine both the independent and interactive effects of nutrients and grazing, I was able to determine that grazers had a consistently greater effect on both algal biomass and taxonomic composition, indicating that grazing was the stronger regulatory factor during this study. The significant interaction between nutrients and grazers is consistent with results from a concurrent study (Rober et al. 2011). However, the shift in the primary regulatory factor from nutrients in the 2007 study to

grazers in this 2008 study suggests that the degree to which either factor regulates algal biomass and community composition may be influenced by interannual variability.

In the Florida Everglades increased nutrient inputs caused an increase in macrophyte abundance, which in turn reduced periphyton abundance due to light limitation (Grimshaw et al. 1997, McCormick et al. 1998). While the results of my survey of macrophyte growth in the Tanana River floodplain showed a similar trend of decreasing algal biomass with increasing macrophyte density (see Figure 4.1), experimentally manipulating light availability did not produce this same effect. While these results largely do not support the hypothesis that shading by macrophytes reduces the ability of algae to respond to nutrient enrichment, there was some evidence to support this. Water column nutrient concentrations remained slightly higher in shaded treatments compared to un-shaded treatments, suggesting that the algal community was not able to utilize nutrients in the shaded treatment as well as in the un-shaded treatment. Furthermore, algal biomass measured as AFDM was slightly lower in all shaded treatments compared to un-shaded treatments, which complements the greater uptake of nutrients in the un-shaded treatment.

The lack of a response by the algal community to light manipulation suggests that light was not as limiting as expected. High latitude ecosystems receive light nearly 20 h per day during the growing season, therefore algal communities in northern latitude ecosystems may receive sufficient light despite large seasonal changes in macrophyte cover. Active net photosynthesis is common at less than 10 µmol/m^2/s (Carlton and Wetzel 1987; 1988, Wetzel 2006). My study site received on average 638.7 µmol quanta/m^2/s during peak daylight hours just below the water surface and an average of 384.8 µmol quanta/m^2/s penetrated to the

sediments in un-shaded areas. This is a sufficient amount of light to saturate photosynthesis (Hill 1996). Furthermore, previous research suggests that algal growth may be less sensitive to reductions in light than photosynthesis (Rier et al. 2006). Therefore a 75% reduction in PAR which resulted in an average of 63 μmol quanta/m^2/s in shaded treatments had little effect on algal biomass. These results are consistent with those reported by Thomas et al. (2006) which found no effect of experimentally reducing light availability on periphyton primary production or community composition in the Everglades, and attributed this to the ability of algal communities to maintain efficient photosynthetic rates within their acclimated irradiance regime.

Algal taxonomic composition was largely the same in nutrient and light treatments. These results suggest 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 suggest that there are trade-offs between herbivore resistant and resource competitive species. This is consistent with literature from lakes (Marks and Lowe 1989), streams (McCormick and Stevenson 1991, Steinman 1996, Rosemond et al. 1993, 2000), and coastal environments (Lubchenco 1978) where grazer resistant species are overgrown by faster growing species when herbivores are removed. Thus, algal taxa with high growth potential, such as the dominant diatom taxa (*Nitzschia*) observed in un-grazed treatments in this study, could respond to increases in resources, but only when grazers were excluded. Basal filaments of *Stigeoclonium* were more abundant in grazed treatments, likely because their low profile growth form is considered resistant to grazing and they are commonly abundant under grazed conditions (Marks and Lowe 1989, McCormick and Stevenson 1991, Steinman 1996). Although small in size, *Gloeocystis* comprised approximately 50% or more of the total algal biovolume in all treatments. The abundance of this green alga may be due to its ability to exploit available nutrients and

outcompete other taxa for light and space (Graham et al. 1996). Furthermore, their small size and gelatinous sheath may protect them to from consumption or passage through the gut (Cuker 1983, Peterson et al. 2002).

The relative availability of light compared with nutrients in aquatic environments has been identified as a key factor regulating primary producers and their interactions with other trophic levels (Sterner et al. 1997, Berman-Frank and Dubinsky 1999). In this study, I found stronger effects of grazers and nutrients compared to light on benthic algae in a northern boreal wetland. My findings suggest that an increase in N and P availability with increased soil weathering and organic matter mineralization expected for the region with climate change processes (Bridgham et al. 1995, Rouse et al. 1997) will probably increase benthic algal biomass in northern boreal wetlands. The ability of grazers to suppress algal accumulation following enrichment suggests that, much like lake and stream ecosystems (Hansson 1992, Feminella and Hawkins 1995, Steinman 1996, Hillebrand 2002), benthic grazers can constrain benthic algal biomass to low accumulation in northern boreal wetlands even in conditions of elevated resource availability. Therefore grazing may play an increasingly important role in regulating benthic algal communities in northern boreal wetlands as nutrient inputs increase with climate change. Furthermore, the results from this study suggest that although the summer growing season is lengthening due to climate change processes (Magnuson et al. 2000, Chapin et al. 2006), the subsequent decrease in light attenuation due to an increase in the duration of macrophyte production may have little influence on algal biomass or taxonomic composition.

Table 4.1 Analysis of variance table showing the responses of benthic algal biomass measured as ash-free dry mass (AFDM), algal cell density, and total algal biovolume to manipulations of light, nutrients, and grazing.

Effect	df	SS	F	P
AFDM				
Light	1	0.017	9.212	**0.011**
Nutrient	1	0.003	1.824	0.204
Grazer	1	0.180	40.51	**<0.0001**
Light x Nutrient	1	0.002	0.901	0.363
Light x Grazer	1	0.003	0.009	0.927
Nutrient x Grazer	1	0.021	4.770	**0.052**
Light x Nutrient x Grazer	1	0.002	0.385	0.548
Cell Density				
Light	1	0.001	0.078	0.785
Nutrient	1	0.023	1.309	0.277
Grazer	1	1.129	39.40	**<0.0001**
Light x Nutrient	1	0.026	1.492	0.247
Light x Grazer	1	0.029	1.006	0.337
Nutrient x Grazer	1	0.316	11.042	**0.007**
Light x Nutrient x Grazer	1	0.024	0.847	0.337
Biovolume				
Light	1	0.116	1.341	0.271
Nutrient	1	0.013	0.147	0.709
Grazer	1	0.777	18.58	**0.001**
Light x Nutrient	1	0.098	1.135	0.309
Light x Grazer	1	0.044	1.044	0.329
Nutrient x Grazer	1	0.170	4.073	**0.069**
Light x Nutrient x Grazer	1	0.073	1.744	0.213

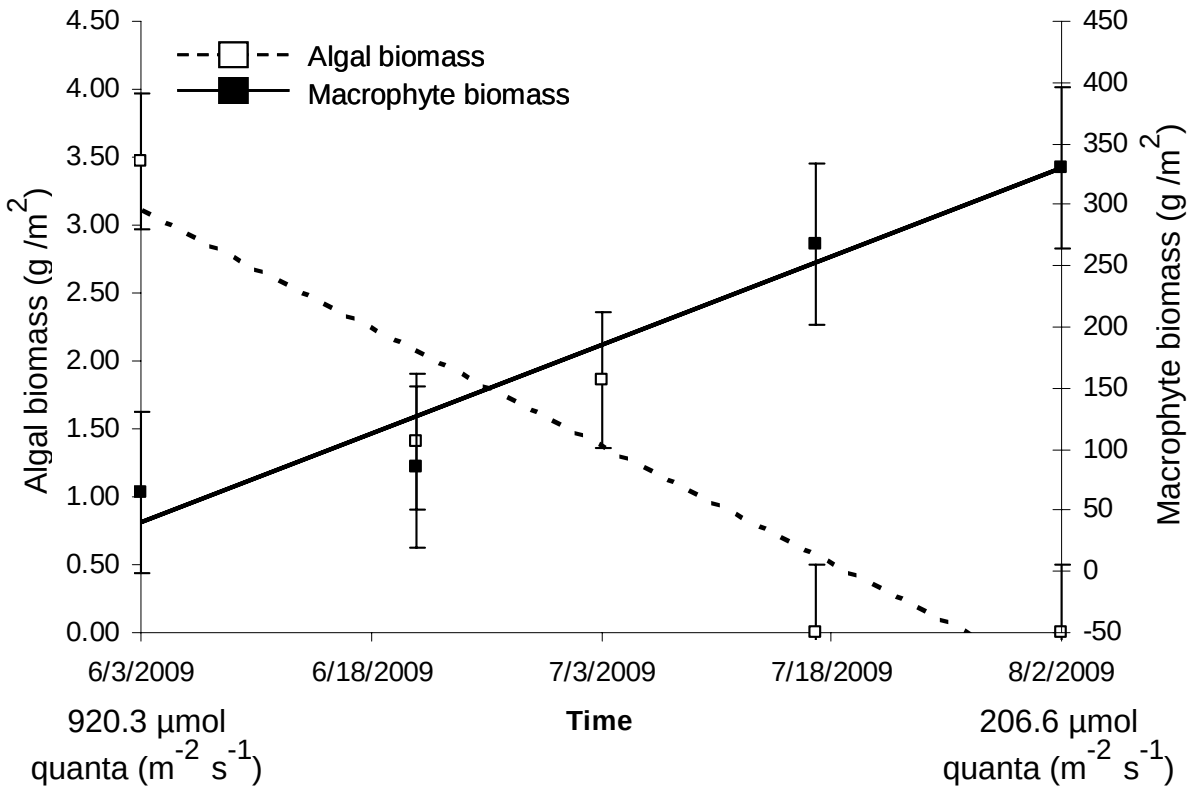

Figure 4.1 Algal biomass measured as ash-free dry mass versus above ground macrophyte biomass over a five week period during the summer growing season. Underwater PAR during the first week of sampling when macrophyte biomass was lowest and algal biomass was highest was 920.3 µmol quanta/m^2/s. Underwater PAR during the last week of sampling when macrophyte biomass was highest and algal biomass was lowest was 206.6 µmol quanta/m^2/s which was approximately 67% of available light.

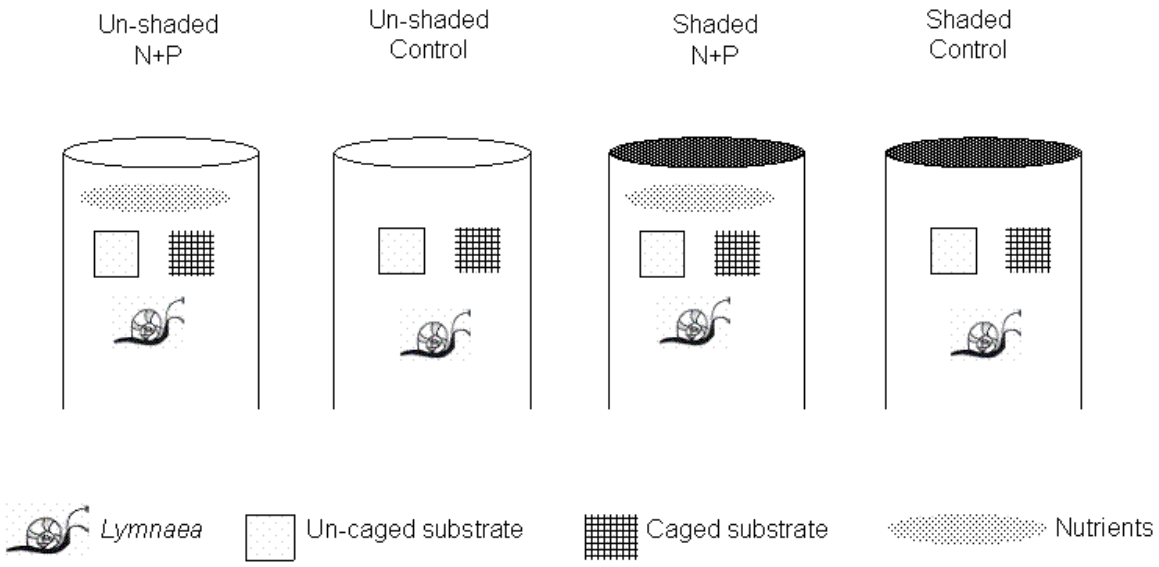

Figure 4.2 Graphic of enclosure design. Enclosures were constructed of welded wire mesh (40 cm in diameter and 85 cm tall), and held approximately 60 L of water. The top 75 cm of each cylinder was wrapped with 0.1 mm clear window vinyl and embedded 10 cm into sediments with an open top extending 15cm above the water column. I suspended all substrates attached to wire baskets and maintained a consistent depth of 5 cm below the water surface. I nested caged and un-caged substrates inside enclosures and added natural abundances of snails. Un-shaded treatments received full sunlight and 75% of light was blocked in shaded treatments.

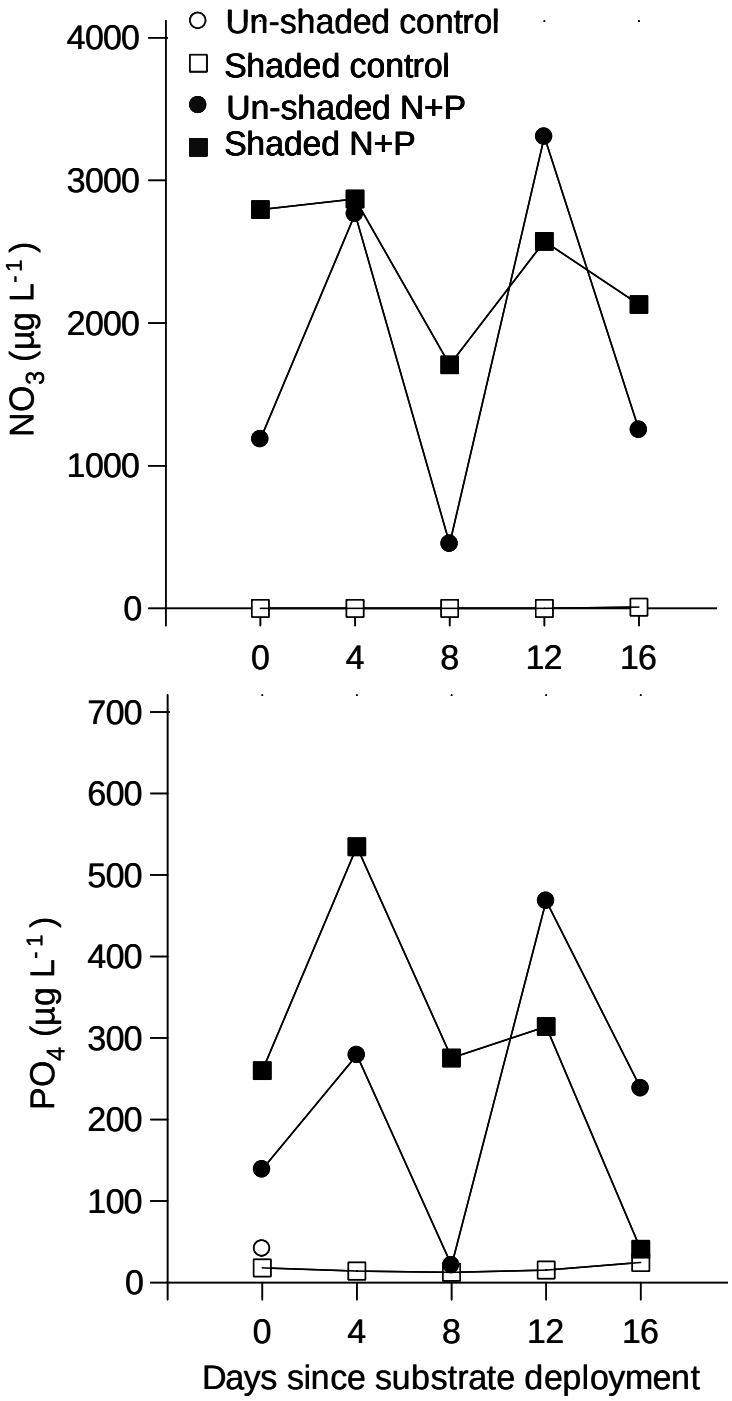

Figure 4.3 Dissolved nutrient concentrations of NO_3 and PO_4 in shaded and un-shaded nutrient enriched and control enclosures.

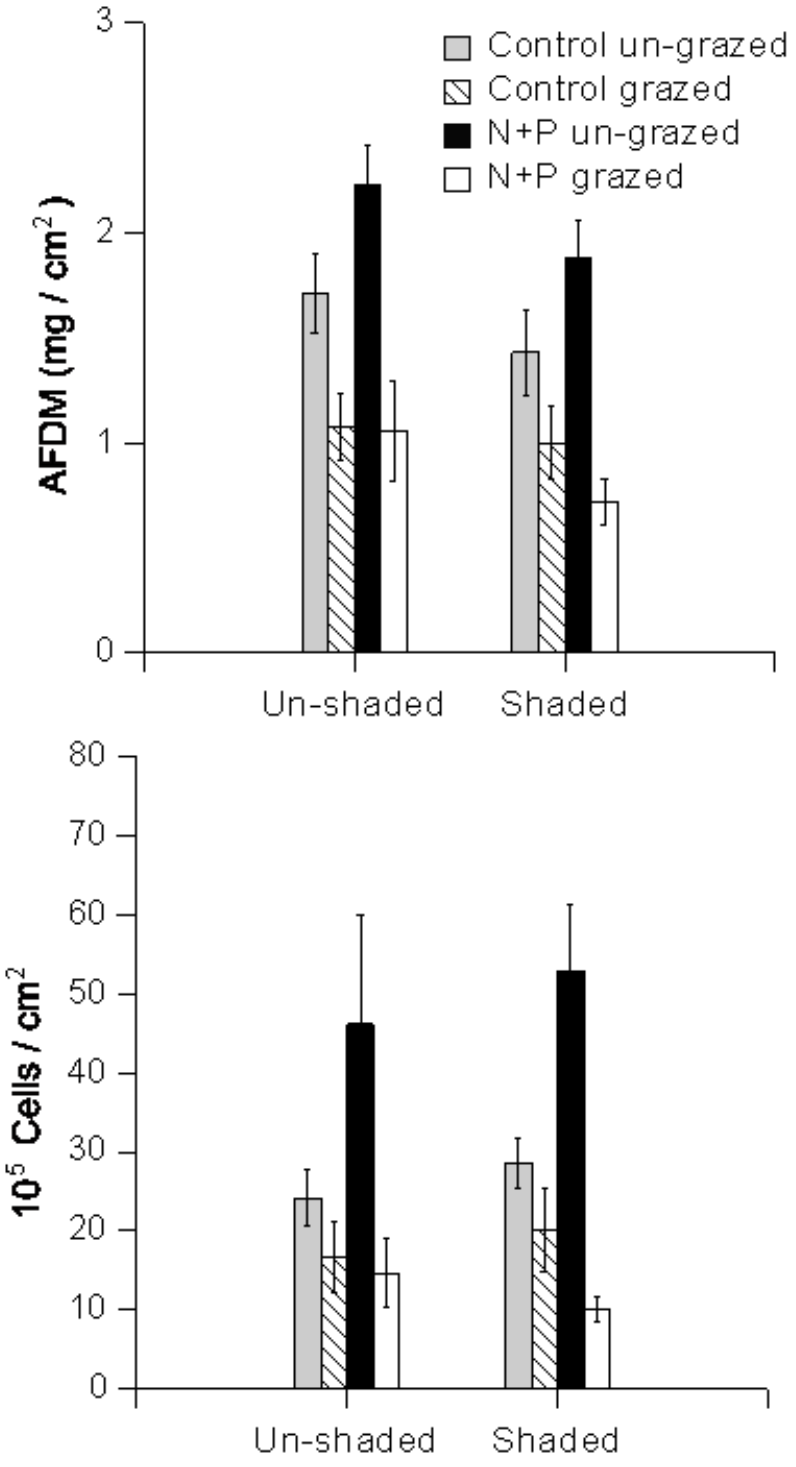

Figure 4.4 Benthic algal biomass measured as ash-free dry mass (AFDM) and cell density in control and nutrient enriched enclosures with and without grazers in shaded and un-shaded treatments. Bars represent the mean of four replicates ± SE.

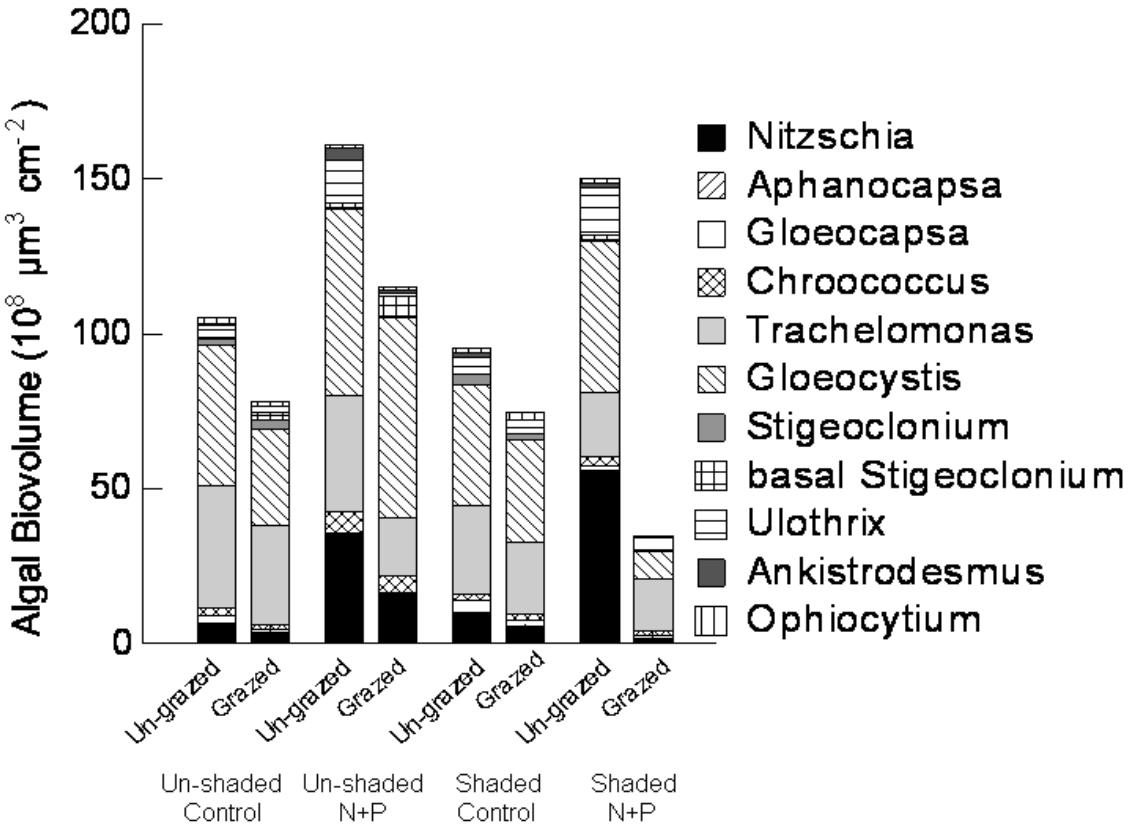

Figure 4.5 Grazed and un-grazed algal taxonomic composition and total algal biovolume in shaded and un-shaded nutrient enriched and control enclosures based on taxa comprising > 5% relative abundance.

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CHAPTER 5

ALGAL COMMUNITY RESPONSE TO EXPERIMENTAL AND INTERANNUAL VARIATION IN HYDROLOGY IN AN ALASKAN BOREAL FEN

5.1 Introduction

Algae can be abundant in wetlands and contribute significantly to many of the physical, chemical, and biological processes that characterize wetland ecosystems (Goldsborough and Robinson 1996, Wetzel 2006). Many of the processes carried out by algae in wetlands (e.g., nitrogen-fixation, soil formation) are related to taxonomic composition (Goldsborough and Robinson 1996, Inglett et al. 2004). Despite literature describing the importance of algae for wetland ecosystem processes (Vymazal 1995, Robinson et al. 2000, Richardson 2010), and known differences in algal functions related to taxonomic composition (Graham et al. 2009), relatively little is known about the factors that regulate algal communities in wetlands. This issue is particularly significant 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).

Hydrology is perhaps the single most important factor regulating the establishment and maintenance of wetland ecosystems (Mitsch and Gosselink 2006). Frequent water level fluctuations influence many of the physical and chemical factors characteristic of wetland habitats (e.g., nutrients, light, temperature, substrate availability), and therefore algal communities (Goldsborough and Robinson 1996). Research examining how algae respond to changes in hydrology has come mainly from the work conducted in the Florida Everglades (i.e.,

McCormick et al. 1998, Gottlieb et al. 2005, 2006, Iwaniec et al. 2006), where wetland hydrology has been significantly altered by human development (Sklar et al. 2005). The effects of hydrology on wetland algal communities at northern latitudes have been less studied. Changes in wetland hydrology in boreal regions are particularly significant, in part because temperatures that have constrained water at or near the surface of permanently frozen soils in the region are increasing rapidly. Furthermore, climate models predict that temperatures in the region will continue to increase during this century (Serreze et al. 2000, Hinzman et al. 2005, McGuire et al. 2007).

Peatlands may be particularly sensitive to global change because water level is highly dependent on changes in rates of precipitation and evapotranspiration (Hinzman et al. 2006, Sulman et al. 2010). Peatlands cover extensive portions of interior Alaska where the surface areas of open water bodies in wetland-rich landscapes are already declining, likely due to increased evapotranspiration with longer, drier growing seasons (Serreze et al. 2000, Euskirchen et al. 2006), drainage after permafrost thaw (Hinzman et al. 2005, Riordan et al. 2006), and/or encroachment of wetland vegetation (Roach et al. 2011). However, some wetland areas in Alaska are expanding due to hydrologic upwelling and increased flooding from melt-water runoff from surrounding uplands (Osterkamp et al. 2000).

Increased frequency of drought and flooding events associated with climate change will likely alter the physical and chemical conditions of aquatic ecosystems in the boreal region, including the movement of limiting nutrients into and out of wetlands (Rouse et al. 1997). Seasonal drought and exposure of sediments will likely oxygenate anaerobic soils and stimulate microbial decomposition facilitating nutrient remineralization, while flooding of previously dried soils may release available nutrients into the overlying water column (Boon 2006, Thomas et al.

2006). Algae in shallow wetlands are sensitive to changes in hydrology as well as water chemistry, and thus, even small changes in water depth can result in desiccation (Thomas et al. 2006) or expose algal communities to environmental conditions that may induce significant changes in community structure.

In this study, I monitored changes in algal community composition in response to an ecosystem-scale water table manipulation that included both drought (lowered water table treatment) and flooding (raised water table treatment) conditions in a rich fen in interior Alaska. Although surface water conditions would only typically allow for continuous algal colonization in the raised water table treatment, a significant flooding event provided a unique opportunity to examine algal community response at sites previously exposed to long-term drought as well. I investigated how much ecosystem memory of the antecedent water table manipulations regulated the ability of taxa to recolonize sites following prolonged drought compared to sites that had been continuously flooded. In a concurrent study, we reported on surface water chemistry and algal community metabolism following rewetting (Wyatt et al. 2012). Here, I evaluate the effects of rewetting on algal community structure.

5.2 Methods

Study site and experimental design

The APEX (Alaska Peatland Experiment) site is located within the Tanana River floodplain just outside the Bonanza Creek Experimental Forest, approximately 35 km southeast of Fairbanks, Alaska (64°82′N, 147°87′W). This region within interior Alaska has large fluctuations in temperature, with a mean annual temperature of -2.9°C, and low levels of

precipitation (269 mm/y) (Hinzman et al. 2006). The growing season is relatively short (135 days or less) and experiences more than 21 h of light per day in June. The APEX site utilized in this study is a rich fen which receives water from surface water runoff and precipitation, and to a small extent, groundwater. The APEX site is dominated by brown moss, *Sphagnum*, and emergent vascular flora, including *Equisetum*, *Carex*, and *Potentilla*.

Within the rich fen, three treatment plots were established in 2005 including a control, lowered, and raised water table treatment (Conlin 2008, Turetsky et al. 2008). Treatment plots are 120 m^2 in area and are located approximately 25 m apart. Each treatment plot is surrounded by a permanent, raised boardwalk. Prior to the initiation of the APEX water table manipulation in 2005, early growing season water table position and plant species composition were not significantly different between treatments (Turetsky et al. 2008). Water table is manipulated through a series of drainage canals (40 cm wide, 1 m deep) that divert water away from the lowered water table treatment. Surface water from a nearby well is pumped into the raised water table treatment at a rate of approximately 10 cm/d using solar powered bilge pumps. The chemistry of water additions to the raised water table treatment is similar to ambient pore water, with no significant differences in pH, electrical conductivity, and concentrations of anions-cations or organic acids (Turetsky et al. 2008). A datalogger communication system maintains natural fluctuations in water table levels in the experimental treatments based on fluctuations in the control treatment associated with precipitation and seasonal drying trends.

Throughout all four years of manipulation, the lowered water table treatment had a consistently lower mean water table height relative to the surface of the peat than the control treatment, and the raised water table treatment was consistently wetter (Figure 5.1; Kane et al. 2010). The mean (± SE) monthly water table position across all four years of manipulation

during the growing season for the control and lowered treatments was 7.2 ± 3.2 and 10.0 ± 3.8 cm beneath the surface of the peat, respectively, whereas the raised treatment had water 0.1 ± 2.2 cm above the peat surface on average. The water table position in the lowered treatment was also generally more variable than in the control, whereas experimentally raising the water table height in the raised treatment reduced fluctuations in water table height within the months of June, July and August (Figure 5.1; Kane et al. 2010).

However, from May-July 2009, water table height in treatment plots was not well regulated by experimental manipulation, but instead by a flood which occurred at the end of the summer in 2008. Between the months of May and October 2008, over 275 mm of precipitation fell in interior Alaska (National Atmospheric Deposition Program, station AK01). Therefore, all three treatments were flooded in August-September 2008 and remained flooded during the spring thaw in 2009 (Figure 5.1). Water table height above the peat surface decreased with time across all water table treatments following the spring snowmelt, but it was not significantly different between plots ($p > 0.05$; Figure 5.1). Following the spring flood, water column nutrient concentrations peaked in early June in each water table treatment and then decreased sharply (Figure 5.2A,B). Averaged across all sampling dates (mean ± SE), dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) were consistently greater in the lowered water table treatment (SRP = 2.86 ± 0.24 µg/L; DIN = 17.12 ± 2.05 µg/L) compared to raised (SRP = 1.07 ± 0.09 µg/L; DIN = 12.9 ± 0.84 µg/L) or control (SRP = 1.38 ± 0.16 µg/L; DIN = 12.4 ± 1.54 µg/L) water table treatments ($p < 0.0001$; Figure 5.2A,B; Wyatt et al. 2012).

Benthic algal biomass measured as chlorophyll *a* and ash-free dry mass (AFDM) peaked following the maxima in nutrient concentrations (Wyatt et al. 2012). Averaged across all sampling dates (mean ± SE), chlorophyll *a* concentration and AFDM were higher in the lowered

treatment (chl *a* = 23.3 ± 3.69 mg/m^2; AFDM = 2.889 ± 0.30 g/m^2) than in the control (chl *a* = 2.46 ± 0.44 mg/m^2; AFDM = 0.84 ± 0.09 g/m^2) or raised (chl *a* = 2.42 ± 0.43 mg/m^2; AFDM = 0.78 ± 0.06 g/m^2) water table treatments ($p < 0.0001$).

Sampling methods

In May 2009, I began monitoring algal parameters within each of the water table treatments weekly, and then every two weeks beginning in July until August to evaluate algal responses to altered water table position. I sampled algae at eight randomly selected locations in each of the water table treatments for estimates of algal density, biovolume, and taxonomic composition. Because the APEX site is part of a long-term study, I used non-destructive methods of removing algae from submersed surfaces. Each sample consisted of four 25 cm^2 subsamples collected from peat surface and the submersed portions of four stems of the dominant emergent macrophyte. I used a plastic syringe to remove algae from each 25 cm^2 quadrat until there were no loosely attached algae or biofilms present on the peat surface. In cases where algae were attached to erect plant stems, I scraped the submersed portion of four stems clean with a plastic spoon, and adjusted the surface area in calculations. Each composite sample, which included algal material from stems and from the peat surface, was diluted to a measured volume with filtered water and gently inverted several times before separating for subsequent analyses. Each algal sample was preserved with 2% formalin for algal taxonomic analysis. I used standard protocols to characterize algal taxonomic composition by counting and identifying at least 300 natural units or colonies per sample using a Palmer-Maloney nanoplankton counting chamber and identified algae to genus at 400X magnification (Charles et

al. 2002). For diatom compositional analysis, I acid cleaned an aliquot of each sample and mounted cleaned diatoms to a microslide using NAPHRAX® mounting medium. I identified and enumerated diatom valves at 1000X magnification. I quantified benthic algal abundance (cells/cm^2 of substrate) using the formula provided in Lowe and Laliberte (2006) and calculated biovolume ($\mu m^3/cm^2$ of substrate) by multiplying algal cell density by the estimated cell volume using geometric formulae from Hillebrand et al. (1999).

Data analysis

I log (x + 1) transformed data if necessary for statistical analyses to correct for nonnormal distribution and unequal variances among treatments prior to analysis. I used repeated measures ANOVAs with an adjusted Bonferroni significance level and Tukey's test for post hoc comparison of means to test the null hypothesis that water table treatment had no effect on algal cell density, biovolume, and taxonomic composition. I identified a total of 78 genera that were included in statistical analyses for cell density within phyla but individual taxa were only included in analyses when present at > 5% relative abundance. Biovolume was only calculated for taxa present at > 5% relative abundance. Water temperature (21.1 ± 0.3 °C), DO (9.52 ± 0.2 mg/L), and pH (6.51 ± 0.03) varied among treatments during the experiment but were not significant predictors of algal biomass or taxonomic composition within treatments ($p > 0.05$; data not shown). A detailed description of the physical and chemical variables in the APEX site during this study is reported in Wyatt et al. (2012). Statistical analyses were performed using general linear models in SPSS 18 (SPSS inc., Chicago, Illinois).

5.3 Results

Algal taxonomic composition

Mean algal cell density (10^4cells/cm^2) peaked immediately following the maxima in nutrient concentrations, and was nearly 3-fold higher in the lowered water table treatment (21.14 ± 2.9) compared to control (6.76 ± 1.31) or raised (8.39 ± 1.02) water table treatments ($F_{2,15}$ = 8.88, p = 0.003; Figure 5.3A). The absolute abundance of almost all taxa was greater in the lowered water table treatment due to greater overall biomass, however the relative abundance of taxa differed between treatments ($F_{22,180}$ = 5.95, p < 0.0001; Figure 5.4A-C).

Chrysophytes were significantly more abundant in the control water table treatment compared to lowered or raised water table treatments ($F_{2,75}$ = 36.525, p < 0.0001; Figure 5.4A). *Dinobryon* was the dominant chrysophyte in the control treatment ($F_{2,180}$ = 68.18, p < 0.0001; Figure 5.5A). Cyanobacteria comprised a greater proportion of total cell density in the raised (22–62%) and control (22–53%) water table treatments compared to the lowered (10–48%) water table treatment ($F_{2,75}$ = 11.21, p < 0.0001; Figure 5.4). *Nostoc* was the dominant cyanobacteria in all water table treatments and increased in abundance as nutrient concentration and water table position declined (Figure 5.5A-C, 5.5D-F). Diatom relative abundance peaked in the middle of the growing season in all treatments, but was consistently greater in the raised water table treatment (9–28%) compared to lowered (7–10%) or control (1–19%) treatments ($F_{2,75}$ = 13.75, p < 0.0001; Figure 5.4). The increase in diatom relative abundance in all treatments was driven by an increase in the abundance of *Tabellaria*, which was greater in the raised water table treatment compared to lowered or control treatments ($F_{2,180}$ = 25.13, p < 0.0001; Figure 5.5C).

The green algae (Chlorophyta) were more abundant in the lowered treatment compared to raised or control water table treatments ($F_{2,75} = 54.42$, $p < 0.0001$; Figure 5.5B). The lowered water table treatment was dominated by large filamentous green algae *Oedogonium* ($F_{2,180} = 6.62$, $p = 0.002$; Figure 5.5B), *Spirogyra* ($F_{2,180} = 9.37$, $p < 0.0001$; Figure 5.5B), and *Microspora* ($F_{2,180} = 5.54$, $p = 0.005$; Figure 5.5B). Small coccoid taxa comprised the greatest proportion of green algae in raised and control water table treatments, many of which were present at < 5% relative abundance (Figure 5.5A,C). The green algae *Gloeocystis*, *Bambusina*, *Ulothrix,* and *Zygnema* did not differ significantly between treatments at anytime during the study (Figure 5.5A-C). Of the 78 genera identified, 76% were present in all three water table treatments.

Algal biovolume

Total algal biovolume was significantly greater in the lowered water table treatment compared to raised or control water table treatments ($F_{2,15} = 25.89$, $p < 0.0001$; Figure 5.3B). Greater biovolume in the lowered water table treatment was driven by *Oedogonium* ($F_{2,180} = 12.9$, $p < 0.0001$; Figure 5.5E), *Spirogyra* ($F_{2,180} = 9.9$, $p < 0.0001$; Figure 5.5E), and *Microspora* ($F_{2,180} = 4.6$, $p = 0.011$; Figure 5.5E). Although filamentous green algae did not constitute a large proportion of the relative abundance of the algal community in raised or control water table treatments (Figure 5.5A,C), they had larger cell sizes compared to many of the diatoms, chrysophytes, and cyanobacteria that were present in greater relative abundance. Therefore, despite the low abundance of *Oedogonium*, *Spirogyra*, and *Bambusina* in raised and control water table treatments (Figure 5.5A,C), they comprised a significant portion of total algal

biovolume ($p < 0.05$; Figure 5.5D,F). These results are limited to the high biovolume taxa (i.e., filaments), because they comprised a portion of the cell density in all treatments (Figure 5.4D-F) and have much greater cell sizes compared to many of the smaller taxa.

5.4 Discussion

Algal community structure was significantly different among water table treatments, even when all treatments were flooded. Differences in community composition were manifested mostly by changes in relative abundance rather than the presence/absence of individual taxa. The presence of most taxa in all three treatments suggests that the long-term natural variation in water table position that occurs within both the control and experimental plots with spring flooding, precipitation events, and seasonal drawdown as well as similar regional environmental conditions, regulates species membership of the algal community (*sensu* Pickett et al. 1989, Stevenson 1997). However, altered nutrient dynamics associated with rewetting of previously dried soils likely regulates the density and relative abundance of taxa that were available to colonize substrates. Thus, antecedent conditions are likely acting on the algal community in two ways, first by limiting the taxa that are available in the seed bank to colonize substrates and then by increasing nutrient concentrations after rewetting, which shapes the relative abundance of taxa present on the peat surface.

The abundance of green algae across all water table treatments is consistent with the literature from a survey of North American peatlands (Yung et al. 1986). Many species of green algae have an affinity for low pH conditions (Graham et al. 1996, Greenwood and Lowe 2006, Wyatt and Stevenson 2010), making them well adapted to acidic conditions in peatland ecosystems. The presence of filamentous green algae in Alaskan wetlands has also been

attributed to their ability to tolerate the extreme fluctuations in temperature that occur at this latitude (Prescott 1963). The increase in filamentous taxa in the lowered water table treatment was likely the response to increased nutrient availability following the spring thaw, since some green algae are capable of exploiting available nutrients and outcompeting other taxa for light and space (Graham et al. 1996). These results are consistent with those reported in previous studies conducted within the Tanana River floodplain, where filamentous green algae increased in biomass following nutrient enrichment (Wyatt et al. 2010, Rober et al. 2011) and from Delta Marsh, Manitoba where filamentous green algae contributed approximately 87% of the total algal biomass after a wetland was re-flooded following an experimental drawdown (Robinson et al. 1997).

The increase in the abundance of *Nostoc* in all water table treatments as nutrient concentrations declined, suggests that it is able to survive in low nutrient environments. *Nostoc* is commonly found living endosymbiotically within moss tissues (Granhall and Selander 1973, DeLuca et al. 2002) and as epiphyton attached to moist moss surfaces in peatlands (Basilier 1980). *Nostoc* is capable of fixing atmospheric nitrogen (N) for moss and vascular plant growth and for microbial decomposition (DeLuca et al. 2002). N-fixation by cyanobacteria has been described as the most important source of N to many arctic and boreal regions, contributing as much as 80% of total annual ecosystem N (Solheim et al. 2006). While a considerable amount of research has been conducted within arctic and boreal regions to determine the importance of N-fixation in boreal forests (Uliassi and Ruess 2002, DeLuca et al. 2002, Hobara et al. 2006), to my knowledge none have quantified the N-fixation potential of peatland cyanobacteria under different water table regimes. My results suggest that changes in water table position will influence the abundance of N-fixing cyanobacteria and therefore likely the amount of N being

fixed under differing hydrologic conditions. This may be particularly significant under hydrologic conditions similar to those in the raised water table treatment, where continuously saturated soils reduce nutrient availability in the water column.

Diatoms are sensitive to desiccation stress, and the lower abundance of diatoms in the lowered water table treatment compared to the control and raised treatments is consistent with literature from the Everglades, where diatom abundance decreased in areas experiencing more frequent drought (Browder et al. 1981, Gottlieb et al. 2006). This may also explain the greater abundance of diatoms in the raised water table treatment, which had been flooded during the previous four growing seasons and consistently had less variability in water table position compared to the other treatments (Kane et al. 2010). Overall, diatoms did not contribute greatly to total cell abundance or biovolume in this study. This group of algae, which use silica (Si) to build their cell walls, may have been limited by Si concentrations which were below detection through much of the summer growing season (Wyatt et al. 2012). This is consistent with other studies which have shown that Si is an important limiting nutrient for algae in peatland ecosystems (Struyf and Conley 2009).

Chrysophytes are widely distributed and are commonly found in oligotrophic habitats, especially at northern latitudes (Wehr and Sheath 2003). The degree to which I observed chrysophytes in this study, particularly *Dinobryon,* is consistent with a previous study in Alaska (Hilliard 1968). This alga is mixotrophic, allowing it to switch between autotrophic and heterotrophic metabolism (Wehr and Sheath 2003). Therefore, it may be able to maintain metabolic activity in low light conditions or under ice (Wiedner and Nixdorf 1998), which may explain its abundance early in the growing season following the spring thaw. However, the lower abundance of *Dinobryon* in the raised and lowered water table treatments relative to the

control suggests that chrysophytes may be particularly sensitive to changes in hydrology and could decline in boreal peatlands as fluctuations in water table position become more frequent with climate change.

Since algal function within an ecosystem can be related to the overall abundance of a particular taxonomic group, I used estimates of algal abundance as an indication of their functional importance. In this study, filamentous green algae (*Oedogonium*, *Spirogyra*, *Microspora*) comprised a substantial proportion of the algal cell density in the lowered water table treatment and were dominant as measured by biovolume. Therefore, it is likely that filamentous green algae will play an increasingly important role in wetland ecosystem function with increasing frequency of drying and rewetting events. This may particularly true in shallow wetlands which we would expect to experience more frequent fluctuations in water table. This shift in community composition will likely have ecosystem level consequences given the significant amount of labile dissolved organic carbon that was released from filamentous green algae in the lowered water table treatment and its' utilization by bacterial communities (Wyatt et al. 2012).

Cell volume and abundance data were not consistent in raised and control water table treatments where cyanobacteria comprised a significant proportion of the algal community. These taxa (*Nostoc, Chroococcus,* and *Gloeocapsa*) are small coccoid cells, which have much smaller cell volumes compared to the filamentous green taxa present. Therefore, the dominance of filamentous green algae in measures of biovolume in raised and control water table treatments is disproportionate relative to their absolute abundance. This could mislead conclusions regarding the function of the algal community within these sites, where cyanobacteria, like *Nostoc*, may be important for ecosystem function.

Compared to the extensive literature on benthic algae in lakes and streams, there is little published information examining the benthic algal assemblages of freshwater wetlands or the factors that regulate their structure and function (Robinson et al. 2000). This discrepancy is particularly acute for northern boreal regions where wetlands are abundant and extremely vulnerable to disturbances associated with climate change. My results provide evidence that hydrology is an important factor regulating benthic algal community structure in a northern boreal peatland and adds to a growing literature on the role of algae in wetland ecosystems. The observed differences in algal taxonomic composition in response to fluctuations in water table suggests that increased frequency of drought and flooding events expected with climate change may significantly alter algal community structure and function in boreal wetlands from the expected natural peatland algal community (i.e., control treatment). My results suggest that this may be particularly important when hydrologic conditions influence nutrient mineralization and availability in surface soils. Furthermore, the similarity between taxa found in this study and those of other floristic studies in peatlands (i.e., Yung et al. 1986, Mataloni 1999, Greenwood and Lowe 2006), indicate that the effect of altered hydrology on algal community structure could be widely applicable to peatland ecosystems beyond those in Alaska.

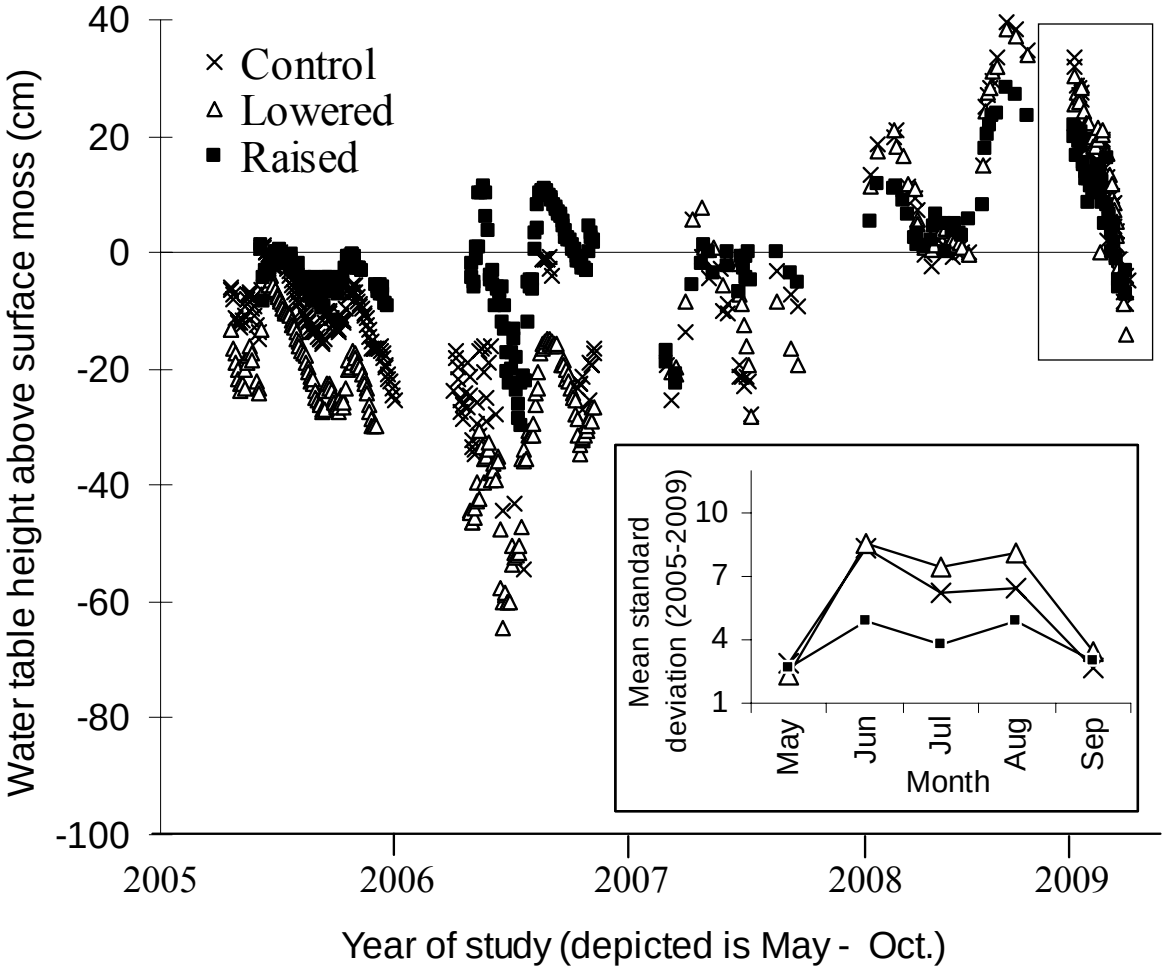

Figure 5.1 Long term seasonal trends in water table heights across the control, lowered, and raised water table treatments in interior Alaska (from Kane et al. 2010). Negative values indicate water table position below the surface of the peat. Outlined values indicate water table measurements made during this study. Inserted figure shows standard deviation in mean monthly water table position across the five years of study (total of 1938 individual water table measurements).

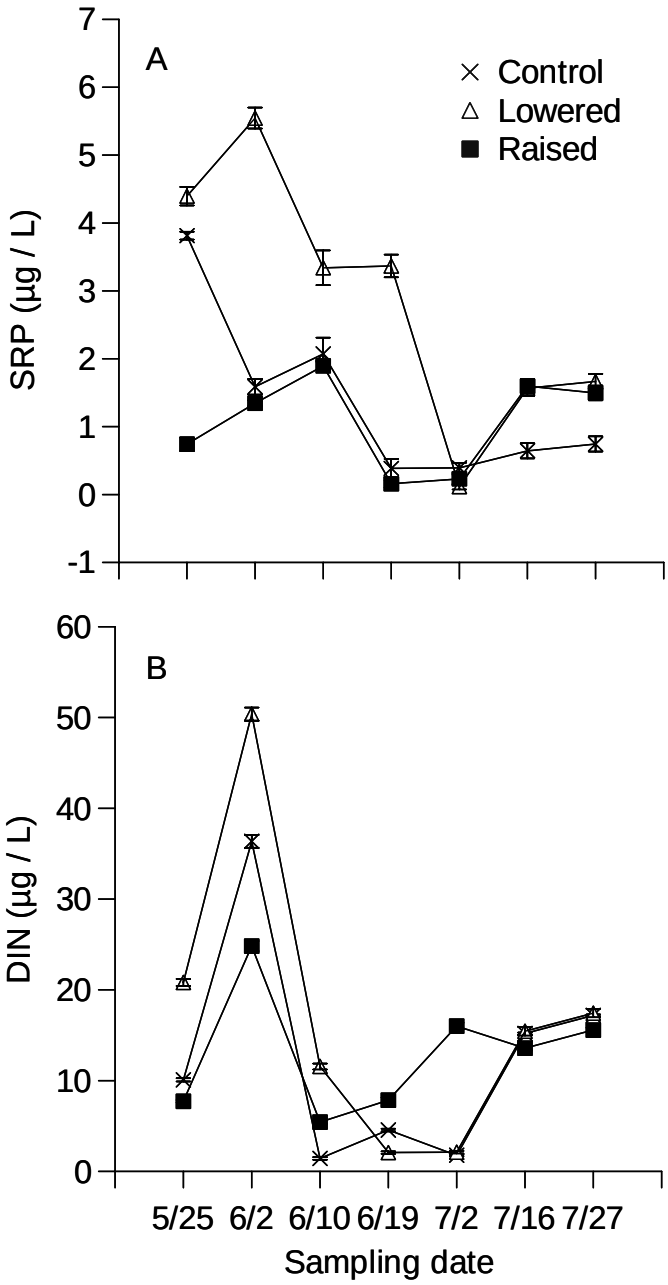

Figure 5.2 Mean (±1 SE; n = 8) (A) Soluble reactive phosphorus (SRP) and (B) dissolved inorganic nitrogen (DIN) concentrations in control, lowered, and raised water table treatments on each sampling date in the APEX fen during the summer growing season in 2009 (from Wyatt et al. 2012).

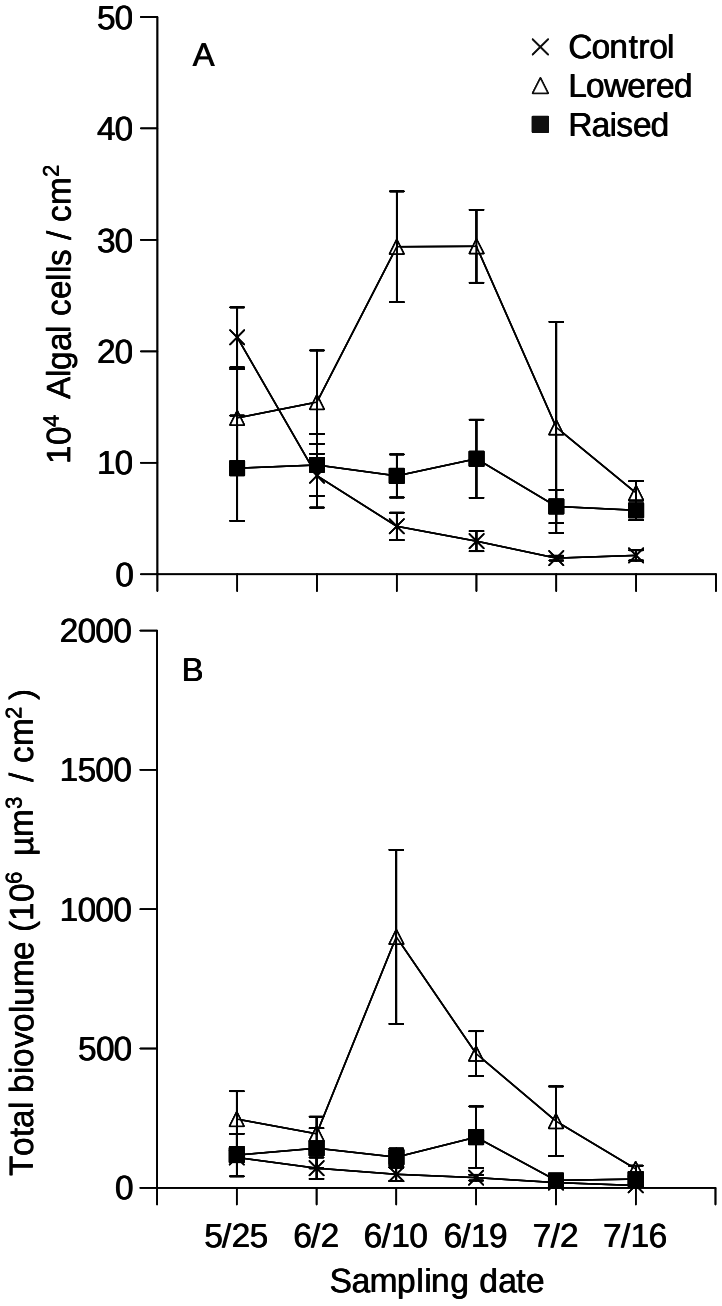

Figure 5.3 Mean (±1 SE; n = 8) algal cell density (A) and total biovolume (B) in the control, lowered, and raised water table treatments on each sampling date in the APEX fen during the summer growing season in 2009.

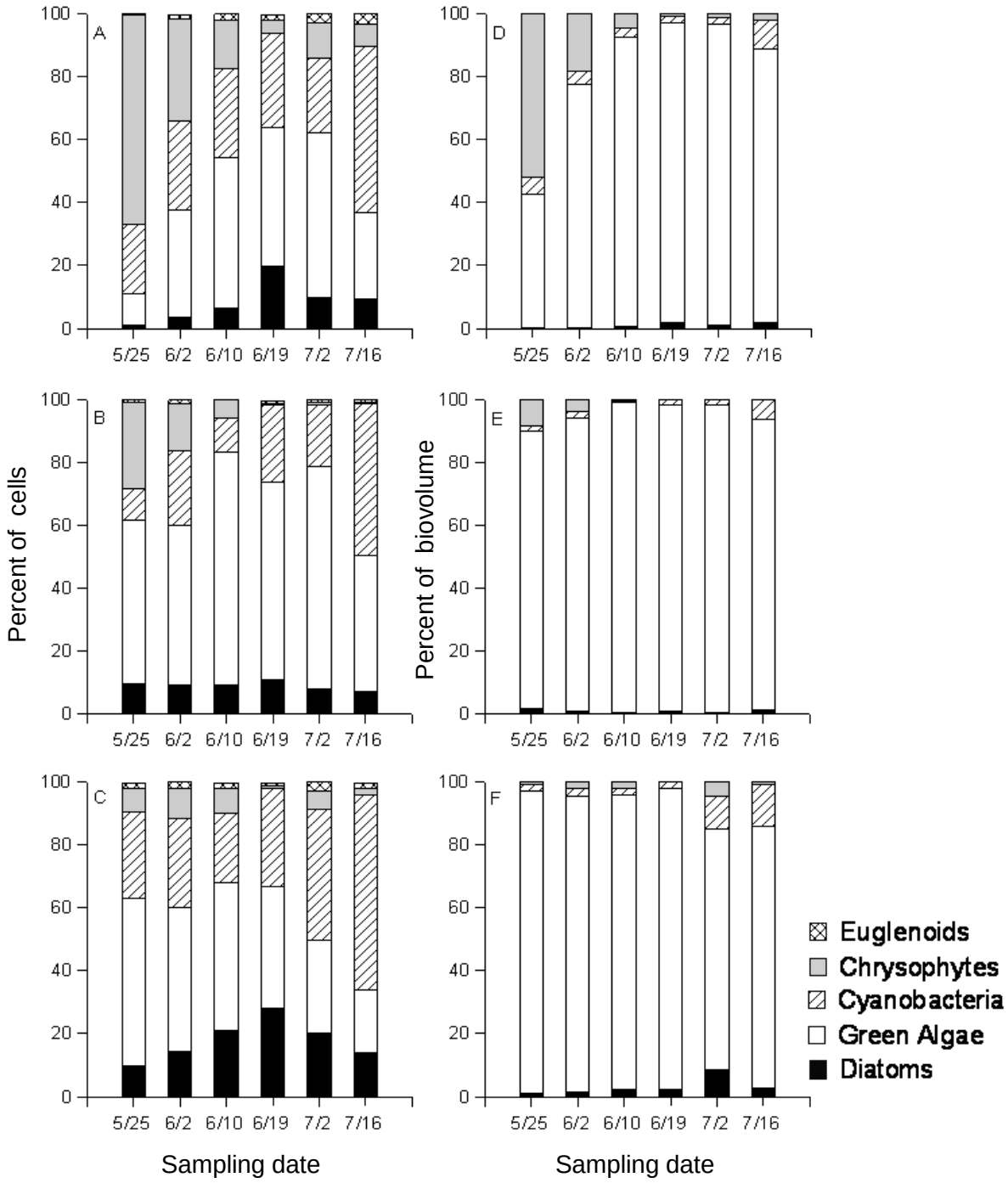

Figure 5.4 Percent of total cells (A-C) and total biovolume (D-F) in functional groups in the control (A, D), lowered (B, E), and raised (C, F) water table treatments on each sampling date in the APEX fen during the summer growing season in 2009.

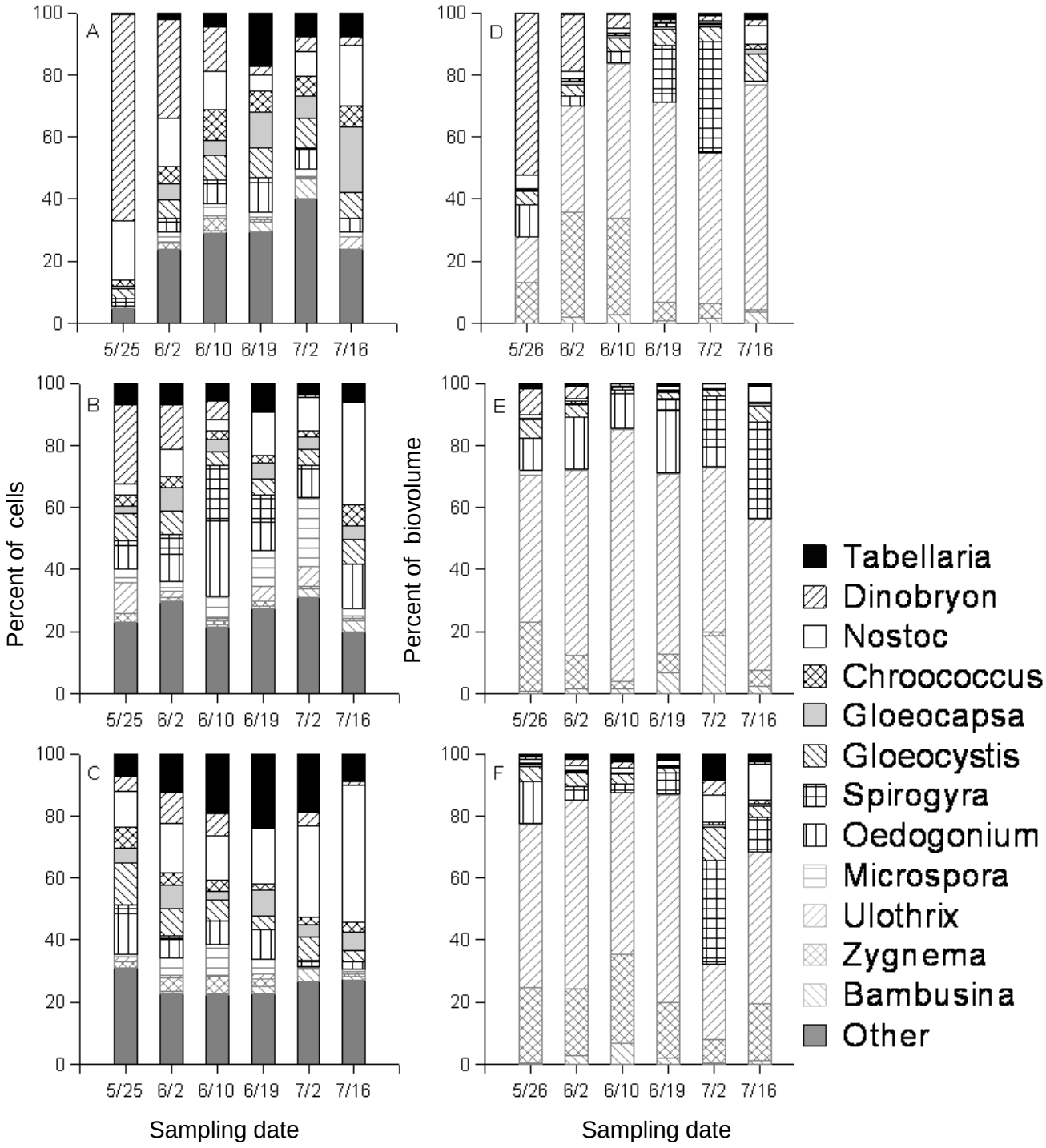

Figure 5.5 Algal taxonomic composition as relative abundance (A-C) and percent of total biovolume (D-F) of dominant algal genera in the control (A, D), lowered (B, E), and raised (C, F) water table treatments on each sampling date in the APEX fen during the summer growing season in 2009.

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CHAPTER 6

CONCLUSION

6.0 Summary

This dissertation research adds to a growing literature on the prevalence of algae in wetland ecosystems. The results of this dissertation improve our understanding of the abiotic and biotic factors that regulate benthic algal productivity and taxonomic composition in northern boreal wetlands and how this may be altered by processes related to ongoing climate change. My results indicate that algae are an ecologically important component of wetland ecosystems, aiding in wetland biogeochemical cycling and providing a labile food source for consumers. These results have important implications for energy flow in boreal wetlands and indicate that the current wetland structure and function may be altered by climate change.

6.1 Environmental controls on benthic algal structure and function

The work of Wyatt et al. (2010), Wyatt and Stevenson (2010), Rober et al. (2011), Wyatt et al. (2012), and Rober et al. (accepted) have contributed significantly to our understanding of the environmental controls on benthic algal structure and function in high latitude wetlands. Though little work had previously examined algal dynamics in northern boreal wetlands in interior Alaska, these studies have experimentally examined the role of nutrients, pH, grazers, light, and hydrology in regulating algal structure and function. Furthermore, my detailed documentation of spatial and temporal variation in algal abundance, productivity, and community composition is useful for understanding the natural distribution and abundance of

algae in boreal wetlands, which is necessary to predict how processes related to climate change will influence wetland primary production, biogeochemistry, and food-web structure.

Multiple lines of evidence indicate that nutrients are the most important environmental factor influencing algal abundance and taxonomic composition in these wetland ecosystems. Survey results showed that both N and P were strong predictors of algal taxonomic composition, influencing the community in the same direction and magnitude, indicating that both nutrients are co-limiting in these ecosystems. Results from *in situ* experimental nutrient enrichment showed the addition of a combination of N and P produced the greatest increase in algal productivity and altered taxonomic composition compared to the addition of either nutrient alone (Wyatt et al. 2010). Following long-term water table manipulation, rewetting of previously dried peatland soils released a pulse of nutrients into the water column which facilitated a spike in algal productivity (Wyatt et al. 2012) and altered taxonomic composition (Rober et al. accepted). Furthermore, nutrients excreted by snails were used by algae to regenerate biomass after consumptive losses (Rober et al. 2011). The mechanism by which nutrients enter these wetlands will likely differ, however the results from this work suggest that increased nutrient inputs will increase algal biomass and productivity and shift taxonomic composition.

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 (Rober et al. 2011). 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.

Hydrology was perhaps as important in regulating algal structure and function as nutrients. There is considerable seasonal variation in water depth within the wetlands of the Tanana River floodplain. During the course of this study water depth was consistently greater early in the growing season following snow melt, but prior to seasonal ice thaw in the soil, than late in the growing season. Algal abundance was also greatest during the early growing season with higher diversity of taxa compared to late season. In my survey of six wetlands within the floodplain I determined that hydrology was a significant factor influencing algal taxonomic composition. Furthermore, algal communities were directly affected by decreased water table position in the APEX water table manipulation, where only taxa that could tolerate periods of drought (e.g., *Nostoc*) were present at the end of the growing season when the water table had dropped below the peat surface (Rober et al. accepted).

Fluctuations in hydrology indirectly influence algal communities by influencing many of the physical and chemical factors within wetland habitats (e.g., nutrients, light, temperature, substrate availability) (Goldsborough and Robinson 1996). In several of our studies, hydrology indirectly influenced both algal biomass and taxonomic composition by influencing the movement and delivery of nutrients into the water column. Nutrient amendments added to mesocosms simulated nutrient inputs from groundwater or surface-water runoff following spring thaw and significantly increased algal biomass and influenced algal taxonomic composition (Wyatt et al. 2010, Rober et al. 2011). Furthermore, nutrients released from rewetted soils facilitated a significant increase in algal abundance and productivity (Wyatt et al. 2012), and favored the growth of filamentous green algae (Rober et al. accepted). Therefore, while nutrients have been shown to be the most important regulatory factor influencing algal communities, the mechanism by which nutrients enter the wetland is often determined by hydrologic processes.

Although I hypothesized that shading by macrophytes would limit light available for algal growth, the lack of a response by the algal community to light limitation in either the survey or light manipulation experiment, suggests that light was not as limiting as expected. High latitude ecosystems receive nearly 20 h per day of saturating light for the duration of the growing season, therefore algal communities in northern latitude ecosystems may receive sufficient light despite large seasonal changes in macrophyte cover. This may be especially true in wetlands where active net photosynthesis is common at less than 10 μmol/m^2/s (Carlton and Wetzel 1987, 1988, Wetzel 2006). My results are consistent with those from the Everglades where experimentally reducing light availability had no effect of on periphyton primary production or community composition, and was attributed to the ability of algal communities to maintain efficient photosynthetic rates within their acclimated irradiance regime (Thomas et al. 2006).

6.2 The contribution of algal productivity to total wetland primary production

Most estimates of wetland algal productivity have come from studies conducted in subtropical (Browder et al. 1994, Richardson 2008) and temperate regions (Goldsborough and Robinson 1996, Robinson et al. 2000). Given the importance of boreal wetlands as major stores of carbon, considerable effort has been made to quantify primary productivity in these ecosystems (cf. Thormann and Bayley 1997, Weltzin et al. 2000, Chivers et al. 2009). However, the majority of these studies have focused on macrophyte production (Wieder 2006) and have mostly ignored the potential role of algae in contributing to wetland primary production.

Mean productivity values among all wetland sites from my survey are within the range (0-500 g C/m^2/y) of values reported from in the literature of temperate freshwater marshes (see

review in Goldsborough and Robinson 1996). During peak productivity, my estimates of algal productivity fall within the lower range of productivity values reported for the subtropical Florida Everglades (300-600 g C/m^2/y; McCormick et al. 1998, Ewe et al. 2006). Assuming that peak macrophyte productivity among wetland sites (70-170 g C/m^2) is equivalent to annual net productivity (g C/m^2/y), my measured values of 30-230 g C/m^2/y for benthic algae (based on 135 day ice-free period) are equivalent, and in some cases higher, than macrophyte production.

My measurements of algal productivity in peatlands are among the few to be reported. My measures of algal productivity in a peatland are higher than many of the values reported for marshes and show that algae can contribute up to 50% of wetland primary production in peatland ecosystems. These results provide further support for the inclusion of algal primary production in estimates of total wetland gross primary production.

6.3 Role of algal taxonomic composition in wetland ecosystem function

Since algal function within an ecosystem can be related to the overall abundance of a particular taxonomic group, I used estimates of algal abundance as an indication of their functional importance. I found multiple lines of evidence for the functional importance of filamentous green algae in boreal wetland ecosystems. Filamentous green algae dominated the algal community following nutrient inputs in marshes and peatlands (Wyatt et al. 2010, Rober et al. 2011, Rober et al. accepted). The increase in filamentous green algae following enrichment likely has ecosystem level consequences given the significant amount of labile dissolved organic carbon that is released from filamentous green algae and its' utilization by bacterial communities (Wyatt et al. 2012). Increases in bacterial density in the presence of algal exudates could

increase the ability of the bacterial community to decompose more recalcitrant carbon substrates (i.e., Hamer and Marschner 2005), and thus influence wetland carbon cycling.

I found that grazers significantly reduced the filamentous green algae *Mougeotia* and *Ulothrix*, providing evidence for the importance of green algae to the wetland food web. Furthermore, the role of filamentous green algae in supporting fungal (Chapter 2) and bacterial communities (Wyatt et al. 2012) provides further support for utilization of algae in the microbial loop. Traditionally wetland food webs have been considered to be detritus based (Murkin 1989, Batzer and Wissinger 1996, Mitsch and Gosselink 2006), however detritus is a poor quality food source, and the extent to which detrital material is transferred from the microbial loop to higher trophic levels is unknown (Batzer et al. 2006). The concept that shredders of vascular plant matter dominate food web processes in streams may not apply to many non-wooded wetland types where shredders are relatively rare and microbial processes are primarily responsible for the breakdown of plant matter (Wissinger 1999, Hart and Lovvorn 2003). Additionally, stable isotope analyses indicate that invertebrates consume algae rather than macrophyte tissue (Neill and Cornwell 1992), and that assimilated detritus is also of algal origin rather than that of macrophytes (Hart and Lovvorn 2003). Although algae typically have lower standing stocks of biomass compared to wetland macrophytes, algal turnover rates are measured in days rather than years, and the edibility and nutritive value of algae makes them considerably more important to secondary production than living or non-living plant material (Campeau et al. 1994, Goldsborough and Robinson 1996, Robinson et al. 2000).

In both the survey of peatlands and marshes and in my study of algal community response to experimental water table manipulation I found significant quantities of N-fixing cyanobacteria, particularly *Nostoc*. *Nostoc* is commonly found living endosymbiotically within

moss tissues (Granhall and Selander 1973, DeLuca et al. 2002) and as epiphyton attached to moist moss surfaces in peatlands (Basilier 1980). *Nostoc* is capable of fixing atmospheric N for moss and vascular plant growth and for microbial decomposition (DeLuca et al. 2002). N-fixation by cyanobacteria has been described as the most important source of N to many arctic and boreal regions (Solheim et al. 2006). While a considerable amount of research has been conducted within arctic and boreal regions to determine the importance of N-fixation in boreal forests (Uliassi and Ruess 2002, DeLuca et al. 2002, Hobara et al. 2006), to my knowledge none have quantified the N-fixation potential of wetland cyanobacteria under different water table regimes. My results suggest that changes in water table position will influence the abundance of N-fixing cyanobacteria and therefore likely the amount of N being fixed under differing hydrologic conditions. Furthermore, potential increases in moss and macrophyte production facilitated by nutrients made available by N-fixing cyanobacteria could increase the carbon storage potential within boreal wetlands.

6.4 Implications of climate change on benthic algal structure and function

Climate models project that North American boreal regions will experience more warming than any other biome, with the greatest warming occurring in the continental interiors (National Research Council 2001). Interior Alaska is already experiencing large changes in climate including increases in surface annual temperatures (Hinzman et al. 2005, Houghton et al. 2001, McGuire et al. 2002; 2007, Serreze et al. 2000), increases in annual precipitation (Hinzman et al. 2005), longer growing seasons (Euskirchen et al. 2006, Goetz et al. 2005, Serreze et al. 2000), and altered snowpack dynamics (Dye 2002, Serreze et al. 2000). My results suggest that although the summer growing season is lengthening due to climate change processes

(Magnuson et al. 2000, Chapin et al. 2006), the subsequent decrease in light attenuation due to an increase in the duration of macrophyte production may have little influence on algal biomass or taxonomic composition.

In response to recent climatic change, the surface area of open water bodies within some wetland-rich landscapes in Alaska is declining, likely due to increased summer moisture deficits and permafrost degradation (Hinzman et al. 2005, Oechel et al. 2000, Riordan et al. 2006, Yoshikawa and Hinzman 2003). However, expansion of open water is occurring in wetlands in the Tanana Flats region of interior Alaska (Osterkamp et al. 2000), an area experiencing ongoing permafrost thaw and hydrologic upwelling as increased melt-water from the Alaska Range drains through the Tanana Flats. The differences in algal taxonomic composition I observed in response to fluctuations in water table suggests that increased frequency of drought and flooding events expected with climate change may significantly alter algal community structure and function in boreal wetlands. My results suggest that this may be particularly important when hydrologic conditions influence nutrient mineralization and availability in surface soils.

An increase in the extent of seasonal ice thaw is predicted to increase microbial decomposition and will probably promote N and P mineralization in the expanded active soil layer (Bridgham et al. 1995), as well as chemical weathering of parent rock material (Rouse et al. 1997). While regional variability of nutrient inputs may be significant, these changes are expected to have widespread impacts on nutrient concentrations of aquatic systems throughout the boreal forest (Rouse et al. 1997). My results suggest that this increase probably will increase benthic algal biomass in northern boreal wetlands. Furthermore, my results demonstrating the ability of grazers to suppress algal accumulation following enrichment, suggest that grazing may

play an increasingly important role in the regulation of algal abundance and taxonomic composition if nutrient inputs increase as expected with climate change.

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