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PRODUCTION OF VASCULAR AQUATIC PLANTS IN WETLANDS  
OF ALASKA: A COMPARATIVE STUDY

A  
THESIS

Presented to the Faculty  
of the University of Alaska Fairbanks  
in Partial Fulfillment of the Requirements  
for the Degree of

DOCTOR OF PHILOSOPHY

By  
Amy Sophia Larsen, B.S.

Fairbanks, Alaska

December 1997

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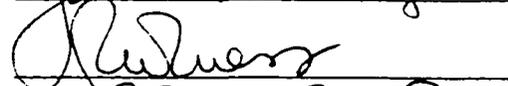
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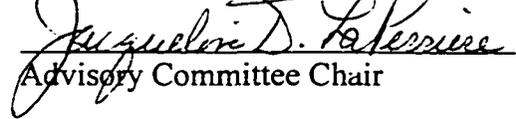
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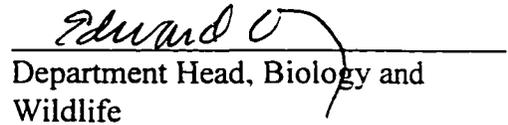








  
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## ABSTRACT

I examined the effects of climate and hydrology on aboveground biomass of macrophytes in wetlands across Alaska by investigating the effects of latitude, July mean air temperature, lake type (open, periodically inundated, and closed), hydrology, and water and sediment chemistry on emergent and submersed vascular plant biomass to determine environmental variables that influenced wetland plant growth.

I sampled aboveground biomass of macrophytes in four wetland complexes within Alaska: Kenai and Tetlin National Wildlife Refuges, Minto Flats State Game Refuge, and the Arctic Coastal Plain near Prudhoe Bay, Alaska. In addition to peak aboveground biomass, I also collected water and sediment samples from each lake that were analyzed for water temperature, color, alkalinity, turbidity, pH, orthophosphate,  $\text{NO}_3/\text{NO}_2\text{-N}$ ,  $\text{NH}_4^-$ , and total sediment C, N, and P.

I found a quadratic relationship between emergent plant biomass and latitude. Minto, the second most northern site, had the greatest plant biomass, Prudhoe Bay, the most northern site had the least, and Kenai and Tetlin had moderate levels of biomass. I found a positive linear relationship between emergent plant biomass and July mean temperature, suggesting that on-site summer condition is important in predicting biomass. Submersed plant biomass was better related to alkalinity, turbidity and sediment P than to latitude, which suggests that climate is not as important in predicting submersed plant biomass as it is in predicting emergent plant biomass.

Emergent plant biomass differed spatially and temporally, while submersed plant biomass showed no distinct patterns in variation across the landscape and with changes in hydrologic input. Many water and sediment chemistry variables differed among lake types and between flood regimes. Emergent plant biomass was associated with changes in water level as well as changes in water.

Plant species composition differed among lake types and tended to change with flood regime as well. A separate suite of species occupied closed lakes, while open and periodically inundated lakes tended to contain more similar plant species.

Both climate and hydrology appear to have a significant impact on emergent and submersed plant biomass and species composition in wetlands of Alaska. These spatial and temporal differences have direct influences on secondary producers living in wetlands of Alaska.

## TABLE OF CONTENTS

v

	<u>Page</u>
Abstract.....	iii
List of Figures .....	viii
List of Tables .....	x
Preface.....	xiii
Introduction.....	1
Chapter 1: Production of vascular aquatic plants in wetlands of Alaska: a latitudinal comparison.	
Abstract.....	4
Introduction.....	5
Study Site.....	6
Methods.....	8
Results.....	12
Discussion.....	13
Acknowledgments.....	18
Literature cited.....	18
Tables.....	24
Figures.....	27

Chapter 2: Influence of flooding on macrophyte biomass in a subarctic freshwater wetland.

Abstract .....	30
Introduction.....	32
Study area.....	34
Methods	
Results	
Chemical characteristics .....	38
Emergent biomass .....	39
Submersed biomass.....	40
Discussion	
Emergent biomass.....	42
Submersed biomass.....	43
Chemical characteristics .....	45
Ecology of Minto Flats .....	47
Literature cited .....	50
Tables.....	57
Figures.....	66

Chapter 3: The effects of flooding on species composition of macrophytes in a subarctic freshwater marsh.

Abstract .....	74
----------------	----

Introduction.....	75
Study site.....	76
Methods.....	77
Results.....	79
Discussion .....	81
Literature cited .....	86
Tables .....	89
Figures.....	92
<b>Overall Conclusions</b>	
A conceptual model of macrophyte biomass .....	94
A comparison of macrophyte biomass in subarctic and arctic wetlands of Alaska .....	97
Final comments.....	97
Literature cited .....	98
Figures.....	101

## LIST OF FIGURES

	<u>Page</u>
Chapter 1, Figure 1. Study site map of the four wetland complexes within Alaska. ....	27
Chapter 1, Figure 2. Regression analysis illustrating the relationship between emergent plant biomass and latitude in freshwater wetlands in Alaska. ....	28
Chapter 1, Figure 3. Regression analysis illustrating the relationship between emergent plant biomass and July mean temperature in freshwater wetlands in Alaska. ....	29
Chapter 2, Figure 1. Study site map of the lakes at Minto Flats, Alaska. Different degrees of shading indicate years of high and low water level. ....	66
Chapter 2, Figure 2. Mean (standard error) of emergent plant biomass in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems. ....	67
Chapter 2, Figure 3. Grass, sedge, broad-leaved, and rush biomass (mean and standard error) in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems. ....	68
Chapter 2, Figure 4. Mean (standard error) submersed plant biomass in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems. ....	70
Chapter 2, Figure 5. Biomass (mean and standard error) of finely dissected, floating-	

leaved, and pondweed submersed plants in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems.. .....	71
Chapter 2, Figure 6. A conceptual model of the interactions between macrophytes and climate, hydrology, and water and sediment chemistry .....	73
Chapter 3, Figure 1. Study site map of the lakes at Minto Flats, Alaska. Different degrees of shading indicate years of high and low water level. ....	92
Chapter 3, Figure 2. Map of the distribution of each lake based upon canonical discriminant function 1 (x-axis), which separates open and inundated lakes from closed lakes, and by discriminant function 2 (y-axis), which separates flooded from non-flooded years.....	93
Overall conclusions, Figure 1. A conceptual map of the interactions between macrophytes and climate, hydrology, and water and sediment chemistry.....	101

LIST OF TABLES

x

	<u>Page</u>
Chapter 1, Table 1. Mean emergent and submersed plant biomass (g dry weight · m <sup>-2</sup> ) for each of four wetland complexes.....	24
Chapter 1, Table 2. Mean and standard error values for each variable at each wetland.....	25
Chapter 1, Table 3. Significant ( $p \leq 0.05$ , and marginally significant $0.05 < p < 0.10$ ) variables detected in backwards multiple regression analysis for emergent and submersed plant biomass. ....	26
Chapter 2, Table 1. Plant species classified into plant groups utilized to make comparisons among the three lake types seen at Minto Flats.....	57
Chapter 2, Table 2. Analysis of variance of water and sediment chemical variables compared among lake types (open, inundated, and closed) and between flooding regime (flooded and non-flooded years).....	58
Chapter 2, Table 3. Means and standard errors for water and sediment chemical characteristics measured in open, inundated, and closed lake systems at Minto Flats during flooded and non-flooded years. ....	59
Chapter 2, Table 4. Results of a two-factor analysis of variance with interaction testing differences in plant biomass among lake types and between flooded and non-flooded years.....	60

Chapter 2, Table 5. Results of two factor analysis of variance with interaction testing differences in emergent plant group biomass among lake types and between flooded and non-flooded year. ....	61
Chapter 2, Table 6. Analysis of covariance describing relationships between plant group biomass and lake type, flooding regime, and water and sediment chemical characteristics. ....	62
Chapter 2, Table 7. Results of a two-factor analysis of variance with interaction testing differences in submersed plant biomass among lake types and between flooded and non-flooded years. ....	63
Chapter 2, Table 8. Results of two factor analysis of variance with interaction testing differences in submersed plant group biomass among lake types and between flooded and non-flooded year. ....	64
Chapter 2, Table 9. Analysis of covariance describing relationships between submersed plant group biomass and lake type, flooding regime, and water and sediment chemical characteristics. ....	65
Chapter 3, Table 1. Univariate test statistics (F) with 2 degrees of freedom among lake types and 1 degree of freedom between flood regimes. ....	89
Chapter 3, Table 2. Prediction results of canonical discriminant analysis. 92% of all cases were correctly classified using species abundance as the independent variable (results based on resubstitution). ....	90

Chapter 3, Table 3. Species dominance for species found in open, inundated,  
and closed lakes during years of flooding (F) and non-flooding (N)  
in the emergent and submergent vegetation zones.....91

## PREFACE

This thesis is written in three separate chapters that have been prepared for submittal to two separate journals. Chapter one has been prepared to be submitted to the *Canadian Journal of Fisheries and Aquatic Sciences*. Chapters two and three have been prepared to be submitted together to the *Canadian Journal of Botany*. Although these chapters are single authored, I received support and guidance from many people throughout this research. Without these interactions this endeavor would not have been as enjoyable or worthwhile.

This project has been funded by a wide variety of small grants, scholarships, assistantships, and fellowships that together allowed me to collect and analyze five years of field data and write my thesis. The University of Alaska Fairbanks Water Research Center, Angus Gavin Migratory Bird Research Fund, American Water Resources Association, Arctic Institute of North America, and University of Alaska Fairbanks Graduate Resource Fellowship all provided me with funds throughout this endeavor. I would especially like to thank the Department of Biology and Wildlife for always providing me with teaching assistantships when I wasn't able to secure outside funding.

I am forever indebted to my major advisor, Dr. Jacqueline LaPerriere (Dr. H<sub>2</sub>O) for her willingness to take me on as a student and share her knowledge with me. Jackie's door was always open to discuss my research and share her knowledge of biology, especially water chemistry (which she gently force-fed me over the years). Committee members Ron Barry, Mark Oswood, Roger Ruess, and James Sedinger also provided

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I owe a great deal of thanks to the staff at each of the refuges where I collected data. Terry Doyle, Rodney King, and Richard Machavenchy were particularly helpful in helping me acquire the necessary permits and helped me select lakes that would be suitable for sampling. The advice and guidance of these people made data collection within each of these areas (that I was not familiar with) much easier.

Thanks to my fellow graduate students, Burney Dunn, Maggie MacCluskie, Susan Sharbaugh, Mark Lindberg, Mike Eichholz, Scott Smidt, and Tom Simpson, who all helped me through problems that seemed to have no solution.

Most of all I thank my family who have supported me in all that I do. I especially thank my father, for his endless encouragement and my brothers for constantly picking on me. But mostly, I thank my sister Cindy and her husband Alec who picked me up and dusted me off whenever I needed it and provided me a home whenever I needed one. Finally, I would like to thank Mark Keech, my partner of four years, and my dog Kokanee (of three years) who made day to day life a joy even when life was throwing curve balls.

I would like to dedicate this thesis to the memory of my mother, Marie Larsen, who taught me to appreciate the beauty and splendor of the great outdoors.

## INTRODUCTION

Wetlands are transitional between terrestrial and aquatic ecosystems, and often contain some of the world's most productive plant communities (Westlake, 1963). Since wetlands occupy the interface between terrestrial and aquatic ecosystems, processes occurring in the terrestrial environment heavily influence them. In particular, wetlands are influenced by hydrologic inputs from the surrounding watershed. Fluctuations in precipitation over time, seasonally or interannually, have a direct influence on chemical inputs to the wetland (Mitsch and Gosselink, 1986) and vegetation within wetlands (van der Valk and Davis, 1978).

During periods of high water level, flood waters have been shown to import nutrients into wetland ecosystems (Gosselink and Turner, 1978). Additionally, lakes in Alaska open to hydrologic inputs have been shown to have higher nutrient concentrations, ionic regimes, alkalinity, and algal biomass than isolated lakes (Seppi, 1991; Murphy et al., 1984). Nitrogen and phosphorus are considered the nutrients most likely limiting macrophyte growth (Mitsch and Gosselink, 1986). Biomass of aquatic macrophytes, generally considered the dominant primary producers in inland freshwater marshes (Wetzel 1983, Kelly et al., 1983), is positively correlated with nutrient concentration (nitrogen and phosphorus) (Neely and Davis, 1985), suggesting that lakes that receive greater external inputs (additional nutrients) via flooding or hydrologic connections are likely to be more productive.

Macrophyte species composition also changes as water level changes through time in ponds in the prairie-pothole region of the North American mid-continent (van der Valk and Davis, 1978). Marshes cycle from a low water phase, during which mud-flat annual species are dominant, to the regenerating marsh phase when emergent plant species are dominant. The third phase of the marsh cycle is marked by the decline in emergent vegetation. The final phase of the cycle is the degenerating phase during which the majority of emergent plants have died and submerged and floating leaved plant species are dominant. These dramatic shifts in macrophyte species composition are dependent on water level fluctuations through time.

Nearly 50% of the state of Alaska is classified as wetland (Hall, 1994). Alaskan wetlands span 30° (52°N to 72°N) latitude. Thus, Alaskan wetlands are exposed to a wide variety of climatic conditions. Wetlands within Alaska also experience a diverse array of hydrologic regimes and fluctuations in water level due to the variable topography.

Annual primary productivity of macrophytes in arctic wetlands is low, generally less than 200 g · m<sup>-2</sup> dry weight (Alexander et al., 1980), two to three times less than temperate wetlands. Low primary productivity in northern latitude wetlands is due primarily to low temperatures, which are associated with low decomposition rates and subsequently low nutrient availability (Chapin, 1984). Brylinsky and Mann (1973) showed that phytoplankton production in freshwaters was negatively related to latitude. Schindler (1978) later concluded that global patterns of phytoplankton production could

better be explained by net annual phosphorus input into the water body and that nutrient input may be correlated with latitude.

This study investigated the influence of climate and hydrologic inputs (due to lake connectedness and flood regime) on plant biomass and water and sediment chemistry in subarctic and arctic wetlands of Alaska. This study had two major objectives. First, I investigated net annual aboveground biomass of vascular aquatic vegetation in Alaskan wetlands. Specifically, I compared plant biomass along a latitudinal gradient to determine if wetland plant biomass was negatively related to latitude. Additionally, I evaluated the influence of several water and sediment chemical characteristics on emergent and submerged plant biomass. Second, I investigated the relationship between wetland plant biomass and hydrology in a subarctic freshwater wetland. I compared wetland plant biomass, and water and sediment chemistry, and species composition among three lake types (open, temporarily inundated, and closed), and between three summers that were flooded and two summers that were not flooded. Additionally, I wanted to determine if there were any relationships between plant biomass and nutrient concentration and other water and sediment characteristics.

**Production of vascular aquatic plants in wetlands of Alaska: a latitudinal comparison<sup>1</sup>**

**Abstract**

Regression analysis was used to test for relationships between emergent and submersed plant biomass and latitude in freshwater wetlands in Alaska. A significant quadratic relationship was found between emergent plant biomass and latitude; however, no relationship was found between submersed plant biomass and latitude. Average July temperature (highest monthly mean temperature) was used as an index of summer climate. A significant positive linear relationship was found between emergent plant biomass and average July temperature. No significant relationship was found between submersed plant biomass and July temperature. Additional significant relationships were found between plant biomass, both emergent and submersed, and water and sediment chemistry. The results of this research suggest that localized differences in July temperature and water and sediment chemistry were more important in explaining variations in emergent plant biomass than latitude alone. Submersed plant biomass was positively related to alkalinity and turbidity and negatively related to sediment phosphorus.

<sup>1</sup>Prepared for submission to *Canadian Journal of Fisheries and Aquatic Sciences* as Larsen, A.S. Production of vascular aquatic plants in wetlands of Alaska: a latitudinal comparison

## **Introduction**

Wetlands are transitional between terrestrial and aquatic ecosystems and contain some of the world's most productive plant communities (Westlake, 1963). Aquatic macrophytes are generally considered the dominant primary producer in inland freshwater marshes (Kelly et al., 1983; Wetzel 1983). Additionally, macrophytes growing in wetlands provide a growing surface for epiphytes, which contribute substantially to community production. The state of Alaska currently contains 62.8% of the wetlands in the entire U.S. (Hall et al., 1994). Increased interest in the effects of global warming has resulted in a surge in research conducted on arctic and subarctic ecosystems. Current models of climactic change predict that northern latitudes may experience a 5-10°C rise in annual temperature in the early to mid-part of the next century (Manabe and Stouffer, 1979). Northern wetlands may be significantly altered by such a rise in temperature.

Global patterns in net primary productivity suggest that primary production decreases with increasing latitude in both terrestrial and aquatic ecosystems (Cooper 1975, Brylinsky and Mann 1973). On a global scale, primary production of phytoplankton has been shown to be highly correlated environmental variables (Brylinsky and Mann, 1973). On a regional level, however, Brylinsky and Mann (1973) considered nutrient concentration to be a better predictor of primary production of phytoplankton than energy-related variables. Schindler (1978) later concluded that global patterns of phytoplankton production could be better explained by net annual phosphorus

input into the water body and that nutrient input may be negatively correlated with latitude. Latitude is a composite variable that integrates the effects of several environmental conditions growing season length, sun's altitude, summer temperature maxima and minima, geochemical weathering, ice dynamics, and daylength. Thus it is not surprising that latitude accounts for a significant amount of global variation in primary production.

This study investigated biomass production of vascular aquatic vegetation in Alaskan wetlands. The objectives were to (i) test whether plant biomass differs across latitudes in freshwater wetlands of Alaska, and (ii) identify factors that might influence wetland plant biomass in Alaska. To accomplish these goals, peak seasonal aboveground biomass was harvested from four wetland complexes ranging over 10° latitude. Additional data were collected on water and sediment chemistry to determine variables that potentially influence wetland plant biomass.

### **Study site**

This study was conducted in four wetland complexes: Kenai National Wildlife Refuge, Minto Flats State Game Refuge, Tetlin National Wildlife Refuge, and the Arctic Coastal Plain near Prudhoe Bay (Figure 1). Weather data were obtained from the weather station nearest each wetland complex (within at least 60 km).

Kenai National Wildlife Refuge (60°34'N, 150°28'W) is located in south-central Alaska on the western half of the Kenai Peninsula. All samples collected from the Kenai NWR were collected within the Kenai Lowlands. The Kenai Lowlands are a portion of

the Cook Inlet-Susitna Lowlands and comprise approximately two-thirds of the refuge. This area contains thousands of lakes distributed throughout a vast area of muskeg. The lowland area is drained primarily by the Moose, Swanson, and the Chickaloon Rivers. The remaining portion of Kenai Refuge is mountainous with elevations from 990 to 1800 m above sea level (ASL). The climate of the refuge is considered transitional, between continental and maritime (Milner et al., 1997). Extended periods of temperatures below -18°C are rare, while summer temperatures rarely exceed 27°C. The majority of lakes are frozen from November to early May.

Tetlin National Wildlife Refuge (62°40'N, 141°07'W) is located in eastern interior Alaska, approximately 350 km southeast of Fairbanks, Alaska. The Tetlin NWR (USFWS, 1987) lies in the lower Chisana and Nabesna river drainages at the head of the Tanana River valley. The Tetlin NWR is bounded on the north by the Alaska Highway, on the south by Wrangell-St. Elias National Park and Preserve, on the east by the Canadian border, and on the west by the Tetlin Reserve. The Tetlin NWR lies within the "cold triangle" of Alaska where winter temperatures as low as -57°C have been recorded. Temperatures often stay below -40°C for extended periods during winter months, while summer temperatures are usually warm, typically ranging from 5°C – 27°C. Temperatures occasionally reach 32°C. The Tetlin NWR is underlain by discontinuous permafrost. The major rivers within the refuge freeze in October with ice break-up in early May. The large deep lakes in the refuge generally break up in late May or early June.

Minto Flats (64°50'N, 148°50'W) is a subarctic freshwater wetland located approximately 54 km west of Fairbanks, Alaska (ADF&G, 1991). Minto Flats is bounded on the north by the Tolovana River, to the south by Tanana River, to the east by low rolling hills and to the west by the Tanana and Tolovana Rivers. This 4100 km<sup>2</sup> lowland contains hundreds of lakes and ponds underlain by discontinuous permafrost. Summer temperatures generally range from 4°C to 22°C but may reach as high as 37°C. Winter temperatures generally range from -30°C to -4°C, although extended periods below -29°C often occur. Ponds and smaller lakes within this area generally freeze in October and break up in mid-May.

Prudhoe Bay (70°16'N, 148°54'W) lies on the Arctic Coastal Plain, a strip of land that borders the entire length of the Beaufort Sea and a small portion of the Chukchi Sea. The width of the plain varies from 16 km near the Canadian border to approximately 160 km south of Point Barrow. Thousands of thaw pond/lakes dominate the topography of the Arctic Coastal Plain (Hobbie, 1980). The entire area is underlain by a thick layer of continuous permafrost. Summer temperatures ranging from -1°C to 8°C are common, although temperatures occasionally reach 24°C. Winter temperatures are generally between -3°C and -21°C. Extreme winter temperatures may reach -45°C.

### **Methods**

During the period of peak aboveground biomass (July 15- August 5) in 1994 and 1995, vegetation was harvested from 90 ponds and lakes within the four wetland complexes described above (hereafter, Kenai, Tetlin, Minto, and Prudhoe). Biomass

samples were collected late in the growing season to reduce the variation in biomass among sites due to phenology. Sampling began at Kenai in mid-July and progressed northward following flowering phenology, ending at Prudhoe in the first week of August. Once during the course of each field season, ten lakes were sampled from each of the four wetland complexes, with the exception of Minto Flats State Game Refuge where 20 lakes were sampled during the 1995 field season. Each field season I sampled different lakes to increase my sample size. Lakes were selected based on logistic accessibility (less than 2.5 km from river/slough or road access), and all were geomorphologically similar (shallow basins with a well-developed emergent vegetation zone). Only vascular plants were collected because of the difficulties with accurately collecting mosses.

From each pond/lake, all aboveground biomass was removed from ten 0.25 m<sup>2</sup> quadrats. Five samples were randomly collected from within the emergent vegetation zone and five from within the submersed vegetation zone. Sampling sites were located from the most central point in the lake and compass readings were randomly selected for each sampling site. Areas within the lake with no emergent or submersed vegetation were not sampled and another random location was selected. Samples were sorted to species, with nomenclature following Hultén (1968) and dried at 65°C to a constant weight (weighed to the nearest 0.01 g). Aboveground biomass of each quadrat (weights of all species summed) was computed as g · m<sup>-2</sup> dry weight.

Once during each summer, during the period of vegetation sampling, three surface water samples from each pond/lake were collected within the area in which vegetation

was collected. Samples were collected from the top 30 cm of the water column prior to vegetation sampling to limit resuspension of sediment into the water column. Total alkalinity was determined by titration with a strong acid using a HACH digital titrator in combination with phenolphthalein and brom-cresol green methyl-red as end point indicators. Turbidity was measured in nephelometric turbidity units, using a HACH 16800 turbidimeter. Inorganic nitrogen (mg/L) and orthophosphate (mg/L) were determined using a HACH DR-EL/4 portable lab. NitraVer5 nitrate reagent accuvacs and PhosVer3 phosphate reagent accuvacs were used to determine  $\text{NO}_3/\text{NO}_2\text{-N}$  and orthophosphate colorimetrically. Nessler's reagent in combination with a HACH ammonia test kit (model NI-8) was used to measure  $\text{NH}_4^+$  (mg/L) in the water column. Apparent water color, measured in APHA platinum cobalt units, was determined using a HACH water color test kit (model CO-1). A HACH wide-range pH test kit (model 17-N) was used to determine pH of each water sample.

Once each year, five sediment cores, 5 cm in diameter and 30 cm in length, were collected from each lake. A single core was taken from five randomly selected quadrats where vegetation had been harvested. Samples were dried at  $65^\circ\text{C}$  until a constant weight was obtained, and ground in a mill with a 40 mesh screen prior to analysis. Sediment samples were analyzed for percent P, C, and N. A LECO Combustion Analyzer CHN-600 was used to determine total carbon, hydrogen, and nitrogen (LECO, 1996). Total sediment phosphorus was determined colorimetrically after perchloric acid digestion (Olsen and Sommers, 1982). Mean elemental composition (% C, N, and P) of sediments

was calculated for each waterbody. The C:N and N:P ratios were calculated for each sediment sample.

Latitude was determined by using a Sony PYXIS global positioning systems unit. For statistical analyses, latitude was rounded to the nearest degree. Average monthly temperatures for the past thirty years were acquired from the weather station nearest each wetland complex (National Oceanic and Atmospheric Administration, U.S. Weather Service 1996). Weather data for Kenai, Tetlin, Minto and Prudhoe were collected from airports in: Kenai, Northway, Fairbanks, and Prudhoe Bay/ARCO respectively. All weather stations were within 60 km of the lakes sampled. For each wetland, mean July temperature, the warmest month during summer, was used to represent summer temperature at each wetland.

Biomass data from both years were pooled due to insignificant ( $p > 0.05$ ) differences between years in biomass within an area. Regression was used to test for relationships between latitude or summer temperature and plant biomass. The best model relating biomass to water and sediment variables was found using backwards stepwise multiple regression. Analysis of the residuals showed no site-specific patterns of variation. All analyses were performed using procedures of SAS general linear models (GLM) (SAS Institute Inc. 1996).

## Results

Emergent plant biomass differed significantly among wetlands ( $p = 0.0001$ ), while submersed plant biomass did not ( $p = 0.49$ ). Tukey pairwise comparison of emergent plant biomass among wetlands showed that Kenai and Tetlin were not significantly different, while all other pairwise combinations were significantly different (Table 1). Mean emergent plant biomass was greatest at Minto and least at Prudhoe.

Biomass of submersed vegetation was similar among the three wetlands (Minto, Tetlin, and Kenai) where submersed species were collected. None of the lakes sampled at Prudhoe Bay contained submersed vascular plants. I observed a few ponds with submersed vegetation; however, these ponds were not sampled. Many of the ponds did have mosses growing in deeper portions.

A second order polynomial regression analysis showed a quadratic relationship between emergent plant biomass and latitude [emergent biomass =  $-9014.826 + 282.653(\text{latitude}) - 2.1(\text{latitude})^2$ ] ( $r^2 = 0.41$ ,  $p = 0.001$ ) (Figure 2). Emergent plant biomass was significantly related to mean July air temperature [emergent biomass =  $-19.677 + 7.732(\text{July temperature})$ ] ( $r^2 = 0.41$ ,  $p = 0.001$ ) (Figure 3). Submersed plant biomass was not correlated with either latitude ( $p = 0.57$ ) or mean July air temperature ( $p = 0.38$ ).

Backwards stepwise multiple regression analysis was used to determine which combinations of variables explained the greatest proportion of variation in emergent and submersed plant biomass (Table 3). July mean air temperature, alkalinity and orthophosphate in the water column were the three variables (Table 3) that collectively

explained the most variation in emergent plant biomass ( $r^2 = 0.44$ ,  $p = 0.0001$ ). I found a positive relationship between emergent plant biomass and alkalinity and a negative relationship between emergent plant biomass and orthophosphate in the water column. July mean temperature explained 41% of the variation in emergent plant biomass. Alkalinity and turbidity each explained an additional 4% of the variation.

July mean temperature, alkalinity, turbidity, and sediment % P were the variables that gave the best prediction of submersed plant biomass ( $r^2 = 0.38$ ,  $p = 0.0001$ ) (Table 3). Submersed plant biomass was positively correlated with both alkalinity and turbidity, while submersed plant biomass was negatively related to total phosphorus in the sediment. Sediment % P explained 23% of the variation in submersed plant biomass, alkalinity 17%, turbidity 3%, and highest monthly mean temperature 1%.

### **Discussion**

The most significant result of the study is the curvilinear relationship found between emergent plant biomass and latitude. Brylinsky and Mann (1973) considered latitude and mean annual air temperature to be the two most important energy-related variables in explaining global variation in phytoplankton productivity. However, on-site summer temperature, length of growing season, and winter extremes have been found to be more important than mean annual air temperature in understanding terrestrial vegetation-temperature relationships (Viereck and Van Cleve, 1984). My data suggest that wetland areas experiencing warmer summer temperatures, regardless of latitude, have higher net annual aboveground biomass than cooler areas (Figure 3). This is in

agreement with Billings and Mooney (1968), who concluded that Arctic ecosystems are temperature-limited.

Phosphorus is considered to be one of the major limiting nutrients in freshwater marshes (Klopatek and Stearns, 1978). In the water column, it is generally unavailable for vascular plant uptake because it is adsorbed to clay particles and organic peat, as well as being bound to ferric iron, calcium and aluminum under aerobic conditions (Mohanty and Dash, 1982). I found that emergent plant biomass was negatively correlated with orthophosphate in the water column and submersed plant biomass was negatively correlated with sediment P. One possible explanation for these relationships may be that the vegetation is reducing P pools in the sediment and the water column, with greater plant biomass reducing P pools proportionally. A large body of evidence has indicated that the sediment is the primary site of uptake of both nitrogen and phosphorus by emergent and submersed aquatic macrophytes (Barko et al., 1991; Sculthorpe, 1967). Algae remove orthophosphate directly from the water column. Rapid uptake of phosphorus by epiphytic periphyton may therefore contribute to reduced levels of orthophosphate in areas where macrophyte biomass is high. An alternative explanation for the negative correlation between emergent biomass and orthophosphate is that dense stands of vegetation have been shown to significantly reduce water flow through wetlands (Madsen and Warnecke, 1983) thereby allowing suspended solids, and associated P, to settle out of the water column and be deposited in the sediment (Klopatek and

Stearns, 1978). Increased residence time, as a result of dense patches of vegetation, results in greater nutrient uptake by heterotrophs as well as autotrophs.

I found that both emergent and submersed plant biomass was positively correlated with alkalinity. Primary productivity of phytoplankton has repeatedly been shown to be positively correlated with alkalinity (Hayes and Anthony, 1964, Carlander, 1955). Sand-Jensen (1983) showed that before reaching maximum photosynthetic rates under light-saturated conditions, submersed plants became carbon limited. Growth rate of *Elodea canadensis* was reduced in low concentration of dissolved inorganic carbon (DIC) and stimulated once DIC was increased (Madsen and Sand-Jensen, 1987). One might expect carbon limitation to occur in shallow, highly productive lakes where pH is increased by depletion of dissolved  $\text{CO}_2$  during photosynthesis and  $\text{HCO}_3^-$  becomes the dominant carbon source for plants (Madsen and Sand-Jensen, 1987). Many species of submersed plants are unable to utilize  $\text{HCO}_3^-$ , while other species have adapted to uptake  $\text{HCO}_3^-$  under low  $\text{CO}_2$  levels (Sand-Jensen and Gordon, 1986). Diurnal shifts in photosynthetic pathway – from the  $\text{C}_3$  pathway early in the morning when  $\text{CO}_2$  is available to CAM during the night when nocturnal respiration is occurring – have also been observed in submersed aquatic plants (Keely and Sandquist, 1991; Madsen, 1987). Additionally, dissolved inorganic carbon concentration is highly correlated with the distribution of submersed plants (Steemann-Nielsen, 1960; Raven, 1970). In lakes of low alkalinity, I mostly found floating leaved species such as *Nuphar polysepalum*, *Potamogeton natans*, and *Sparganium hyperboreum* which are able to use atmospheric  $\text{CO}_2$ . I also detected a

significant positive relationship between biomass of emergent vegetation and alkalinity, suggesting that alkalinity is probably correlated with another factor that I didn't measure which limits both emergent and submersed plant biomasses.

I found a positive relationship between submersed plant biomass and turbidity. Likewise, Lind et al. (1992) found that phytoplankton productivity is higher in more turbid areas within Lake Chapala. Turbidity of lakes sampled in my research was never so high as to limit light penetration (turbidity never exceeded 12.5 NTU) (Van Nieuwenhuysse, 1983). Nutrients associated with mineral turbidity have been implicated in the positive relationship between phytoplankton productivity and turbidity (Lind et al., 1992). Concerning aquatic vascular plants, turbidity may simply be a measure of the source of sediment-bound phosphorus when it is suspended in the water column.

Schindler (1978) concluded that global patterns of phytoplankton production could better be explained by net annual phosphorus input into lakes than by energy-related variables such as latitude. On a regional level, Brylinsky and Mann (1973) also concluded that nutrient availability assumes a greater importance in explaining patterns in production of phytoplankton than energy-related variables or inorganic carbon availability. I suggest that high latitude conditions lead to a somewhat different model than that posed by Brylinsky and Mann (1973) or Schindler (1978). I found that under conditions of prolonged daylight (nearly 24 hours daily) high rates of primary productivity (with little nocturnal regeneration of CO<sub>2</sub> by respiration) lead to inorganic carbon limitation prior to nutrient limitation. This is demonstrated by the positive

relationships found between emergent and submersed plant biomass and alkalinity (a measure of the inorganic carbon source). In most aquatic ecosystems inorganic carbon is seldom limiting; however, in subarctic and arctic ecosystems seasonal eccentricities of light may lead to high rates of primary production and subsequently rapid uptake of inorganic carbon. Additionally, with the extended periods of daylight there is little nocturnal regeneration of  $\text{CO}_2$  by respiration, suggesting that inorganic carbon becomes limiting before the vegetation is able to deplete sediment nutrients.

The quadratic relationship I found between latitude and emergent plant biomass, in which Prudhoe had the lowest mean biomass, Kenai and Tetlin have intermediate biomass, and Minto had the greatest biomass, suggests that summer temperature, rather than latitude, per se, is controlling plant biomass. Although phosphorus was an important nutrient in explaining variation in emergent and submersed plant biomass in Alaska, the linear relationship found between emergent plant biomass and July mean temperature suggests that temperature during the growing season is the dominant factor controlling emergent plant biomass. Temperature directly affects plant growth and is relatively easy to manipulate, while latitude is a complex composite variable that can not be manipulated. Warmer temperatures, due to global warming, are expected to increase several temperature-dependent processes in arctic ecosystems including thaw depth (Goodwin et al., 1984; Ostercamp 1984), decomposition rate, chemical weathering, growing season length, nitrogen fixation rate, and nutrient availability (Chapin, 1984). I

suggest that these temperature-dependent processes have a direct link to increased productivity of aquatic vascular plants in arctic and subarctic wetlands.

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## Tables

Table 1. Mean emergent and submersed plant biomass (g dry weight · m<sup>-2</sup>) for each of four wetland complexes. The Tukey multiple comparison test was used to examine differences in emergent or submersed plant biomass between wetland pairings. Wetlands sharing the same letter were not significantly different ( $P \geq 0.05$ ) from one another.

Area	<u>Emergent plant biomass</u>		<u>Submersed plant biomass</u>	
	Mean	SD	Mean	SD
Kenai	310.20 <sup>a</sup>	190.24	159.52 <sup>a</sup>	83.24
Tetlin	349.04 <sup>a</sup>	123.44	133.28 <sup>a</sup>	81.28
Minto	458.68 <sup>b</sup>	123.16	161.36 <sup>a</sup>	84.72
Prudhoe Bay	162.60 <sup>c</sup>	54.36		

Table 2. Mean and standard error values for each variable at each wetland. Data from (15 July- 5 August); 3 replicates for surface water determinations, 5 replicates for sediment chemistries.

	Prudhoe		Kenai		Tetlin		Minto	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Water Temperature (°C)	11.78	0.75	18.31	0.44	20.30	0.44	18.1	0.42
Color (ptu)	23.94	2.06	26.30	3.39	84.00	10.13	76.43	4.64
Alkalinity (mg/L)	191.95	6.68	28.57	4.77	67.12	7.69	41.09	3.85
Turbidity (NTU)	1.86	0.13	2.30	0.46	2.34	0.28	2.81	0.30
pH	8.09	0.10	7.22	0.15	8.02	0.23	7.81	0.16
PO <sub>4</sub> (mg/L)	0.07	0.01	0.19	0.02	0.20	0.04	0.14	0.02
NO <sub>3</sub> /NO <sub>2</sub> -N (mg/L)	2.18	0.20	1.01	0.08	1.52	0.13	1.72	0.15
NH <sub>4</sub> <sup>+</sup> (mg/L)	0.55	0.03	0.71	0.08	0.92	0.08	0.77	0.03
Sediment C (%)	15.05	1.83	10.93	1.56	12.38	2.30	9.95	1.11
Sediment N (%)	0.95	0.14	0.66	0.10	0.89	0.16	0.78	0.08
Sediment P (%)	0.07	-	0.05	-	0.09	-	0.09	-
Sediment N:P	12.92	1.57	12.11	2.11	9.08	1.36	8.12	0.78
Sediment C:N	17.35	0.97	16.85	0.49	14.74	0.63	12.68	0.25

Table 3. Significant ( $p \leq 0.05$ ; and marginally significant  $0.05 < p < 0.10$ ) variables detected in backwards multiple regression analysis for emergent and submersed plant biomass.

Source	Emergent		Submersed	
	Parameter estimate	p-value	Parameter estimate	p-value
Intercept	-50.01	0.0133	38.18	0.0001
Mean July air Temperature (°C)	9.49	0.0001	2.56	0.0620
Alkalinity	0.24	0.0271	0.33	0.0001
Orthophosphate	-47.33	0.0648		
Turbidity			4.03	0.0035
Sediment P			-403.65	0.0001

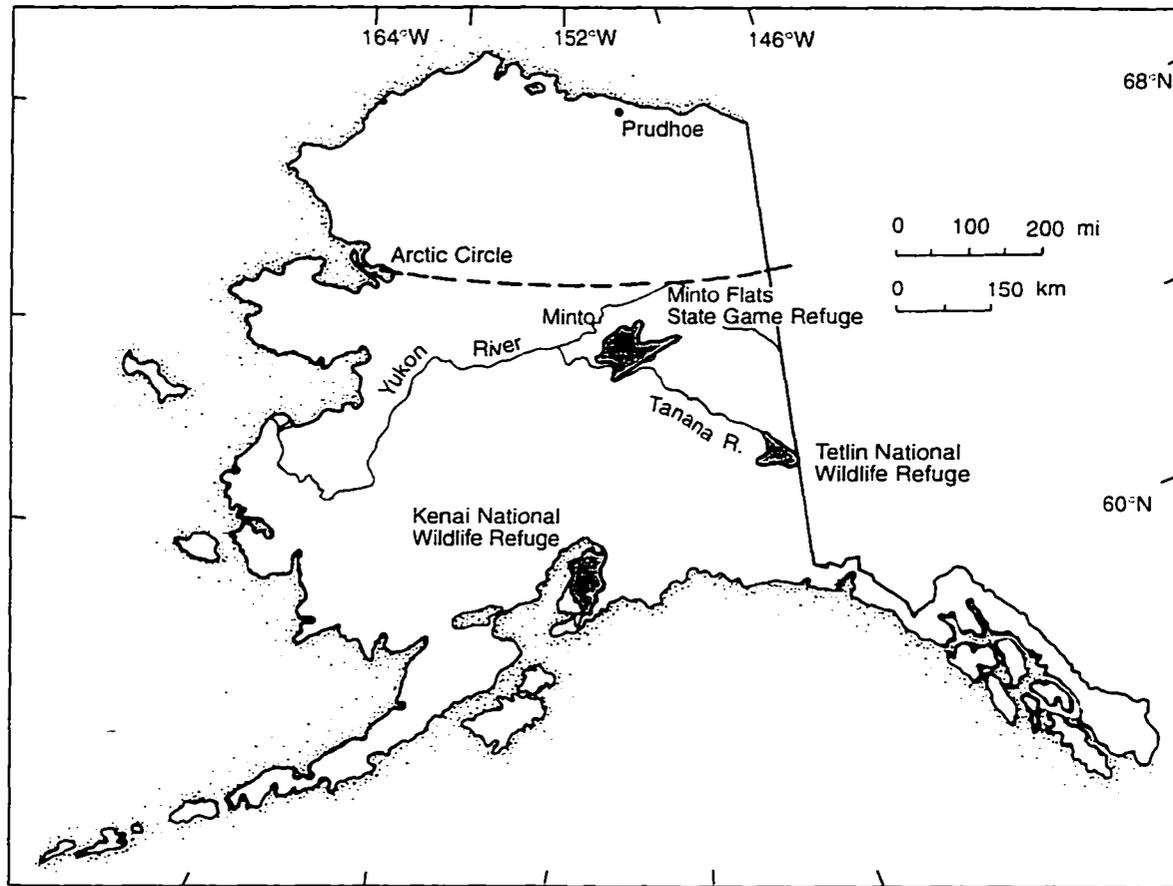


Figure 1. Study site map of the four wetland complexes within Alaska.

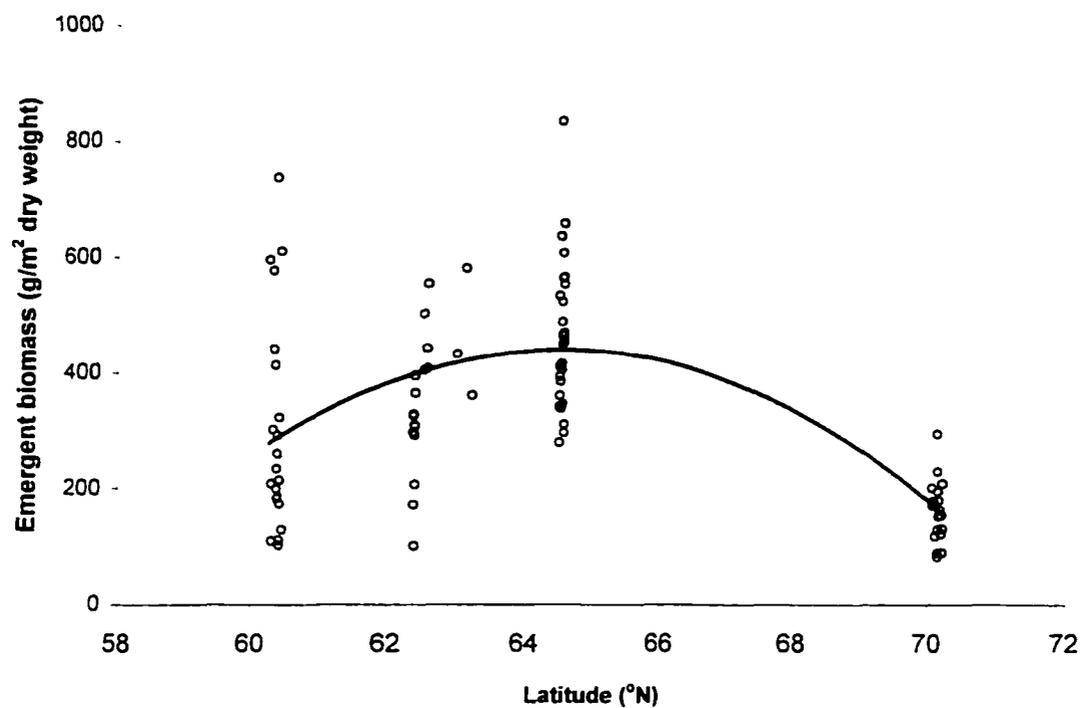


Figure 2. Regression analysis illustrating the relationship between emergent plant biomass and latitude in freshwater wetlands in Alaska.

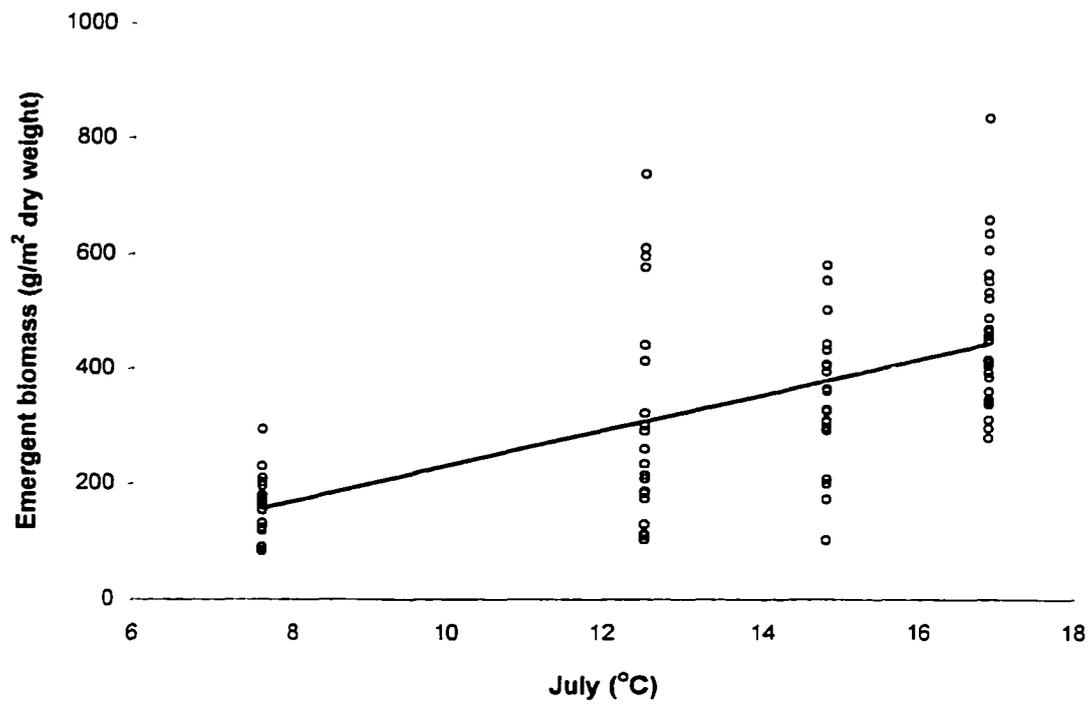


Figure 3. Regression analysis illustrating the relationship between emergent plant biomass and July mean temperature in freshwater wetlands in Alaska.

**Influence of Flooding Regime on Macrophyte Biomass in a Subarctic Freshwater  
Wetland<sup>1</sup>**

**Abstract**

I investigated the influence of flooding and lake type (open, inundated, or closed) on emergent and submersed plant biomass and water and sediment chemistry in a subarctic wetland in interior Alaska. Emergent plant biomass differed significantly among lake types but not between flood regimes. A significant interaction between lake type and flood regime suggests that biomass within each lake type is differentially influenced by flooding. Submersed plant biomass did not differ among lake types or between flooded and non-flooded years.

Water chemistry was significantly different among the three lake types for several characteristics: alkalinity, pH, turbidity, and total carbon in the sediment. Water color and total nitrogen in the sediment showed marginally significant differences among lake types. Water temperature, color, alkalinity, turbidity,  $\text{NO}_3/\text{NO}_2\text{-N}$ , and total carbon and nitrogen in the sediment were significantly different between flooded and non-flooded years.

Morphologically similar emergent and submersed plant species were grouped to facilitate data analysis. Biomass of rushes, grasses, sedges, and broad-leaved emergents

was differentially influenced by water and sediment characteristics. The biomass of submersed plant groups was related to alkalinity, turbidity and water color.

From these data I constructed a conceptual model that integrates the effects hydrology, both lake type and flood regime, and water and sediment chemistry have on macrophyte biomass. The model suggests that prior to nutrient limitation macrophytes growing at Minto become carbon limited. I suggest that this is due to the long summer day-lengths combined with the shallow nature of the wetland complex.

<sup>1</sup>Prepared for submission to the *Canadian Journal of Botany* as Larsen, A.S. Influence of Flooding regime on Macrophyte Biomass in a Subarctic Freshwater Wetland.

## Introduction

Hydrology is generally considered a critical determinant of wetland productivity (Mitsch and Gosselink, 1986). In subarctic Alaska, many freshwater wetlands undergo seasonal inundation due to spring snow-melt (Ford and Bedford, 1987). Heavy winter snow pack and rapid spring break-up are generally responsible for annual fluctuations in these wetlands. Ponds and lakes in wetland areas can be differentially influenced by water level fluctuations. Lakes open to hydrologic inputs are heavily influenced by flood events; however, nutrient retention is reduced due to the rapid hydraulic turnover. Hydrologically isolated lakes generally receive low nutrient inputs from surface flow, and little variation in shoreline extent reduces wet-dry cycles and hence nutrient release from the sediment. Lakes adjacent to sloughs and flowing waterways often become temporarily inundated during high water. Wetlands experiencing intermediate levels of inundation are generally more productive than continuously flowing or stagnant waters (Mitsch and Gosselink, 1986). Increased nutrient levels due to external inputs combined with periods of drying are considered the dominant reasons for this increased productivity. Data from ephemeral wetlands, such as those found in the prairie-pothole region of North America, suggest that nutrient availability is enhanced during periods of drawdown when increased oxygen concentration increases decomposition rates (Zak and Grigal, 1991). Flood waters bring nutrient-rich sediments into river floodplains (Gosselink and Turner, 1978) and adjacent wetlands (Mitsch and Gosselink, 1986).

Primary production in the arctic and subarctic is thought to be limited by nutrient availability (Alexander et al., 1980; Chapin, 1980), and consequently subarctic wetlands which receive external nutrient inputs (e.g., from riverine inputs) would be expected to have increased primary production. Nitrogen and phosphorus generally limit wetlands dominated by emergent plants (Neely and Davis, 1985). Nutrient and ionic regimes have been shown to be significantly different between hydrologically connected and hydrologically isolated wetlands in subarctic Alaska (Seppi, 1991; Murphy et al., 1984). Murphy et al. (1984) found that both phosphate and nitrite concentration in the water column was higher in connected wetlands than in isolated wetlands. Hydrologically connected wetlands also had higher alkalinity, pH, total phosphorus, calcium, and magnesium (Seppi, 1991). Seppi (1991) also found algae chlorophyll *a* concentrations were greater in connected oxbows than in isolated wetlands. To date, no one has investigated the effects that these differences in hydrologic connectedness (and hence periodic water level fluctuations) have on subarctic wetland vegetation. It has been suggested (Patricia Heglund, pers. comm. 1992. Alaska Science Center, Anchorage, Alaska) that primary production of vascular aquatic plants is greater in hydrologically connected wetlands than isolated wetlands.

Hydrology has also been shown to influence waterfowl use of wetlands. Murphy et al. (1984) showed that ducks used hydrologically connected wetlands significantly more than isolated lakes. Seppi (1991) found that invertebrate biomass (potential prey for waterfowl) was also greater in connected oxbows than in isolated oxbows. Primary

production of aquatic vegetation has both direct and indirect effects on waterfowl that use wetland vegetation for cover, nesting habitat, foraging habitat (Voigts, 1976; Krull, 1970), and food (Burris, 1991; Debruckyere, 1988; Krapu and Swanson, 1975; Bartonek and Hickey, 1969).

This investigation attempts to correlate differences in water chemistry and hydrologic connectedness to plant biomass. For the purposes of this research a lake was classified as “open” if it was hydrologically connected to a slough, “inundated” if the lake was temporarily inundated with flood waters, and “closed” if the lake was not hydrologically connected and was never flooded with overland water flow (potentially influenced by groundwater flow). I investigated the influence of hydrology on wetland plant biomass in a subarctic freshwater wetland complex in interior Alaska. The study had three specific objectives: to determine *i*) if wetland plant biomass differs among hydrologically connected, inundated, and closed lake systems, *ii*) if flooding influences wetland plant biomass, and *iii*) if water chemistry was correlated to plant biomass. I accomplished this by harvesting (at peak biomass in summer) aboveground plant biomass in hydrologically open, inundated, and closed lakes at Minto Flats, Alaska, over a 5 year period during which water levels fluctuated annually.

#### **Study area**

The study was conducted at Minto Flats State Game Refuge (ADF&G, 1991), (64°50'N, 148°50'W) a large subarctic freshwater wetland (Figure 1) 54 km west of Fairbanks, Alaska. Minto Flats is situated in a low-lying area that is highly susceptible

to flooding. This wetland complex is bordered on the east by low rolling hills covered with coniferous trees, including white spruce (*Picea glauca*) and black spruce (*Picea marianna*), on the north by the Tolovana River, on the south by the Tanana River, and on the west by the Tanana and Tolovana Rivers. The majority of research was conducted in the Minto lakes region of the flats which is located in the south-eastern corner of the refuge. This portion of the refuge contains numerous small lakes and ponds that are interconnected by a system of sloughs. During the years 1992-1994, high water levels in the Chatanika River, a fifth order tributary (Strahler, 1957; Horton, 1945) to the Tolovana River, flooded low-lying lakes within the Minto Lakes portion of the flats. In the 1995-1996 water levels were considerably lower throughout the summer.

### Methods

I collected data on 8–20 lakes each year in 1992–1996 at Minto Flats. I sampled a total of 24 lakes; eight of the lakes were sampled each year to determine annual variation in plant biomass. I classified each lake, based upon hydrologic connectedness, as open, inundated, or closed. A lake was classified as open if it had a slough/river that drained into or out of the lake. Lakes that experienced periodic inundation from a river during a flood event were classified as inundated. Lakes that were completely isolated from any overland water flow were classified as closed. Each year, I randomly collected 10, 0.25 m<sup>2</sup> vegetation samples from each lake. Sampling units were located from the most central point in the lake and randomly selected compass readings (1-360 °) were assigned to each quadrat. At each randomly selected location (compass reading) a single quadrat was

sampled within either the emergent or submersed vegetation zone. I collected 5 vegetation samples from within the emergent vegetation zone and 5 from within the submersed vegetation zone. I collected only emergent and submergent vascular plant species because of difficulties associated with accurately collecting mosses. I harvested all aboveground biomass rooted within a 0.25 m<sup>2</sup> quadrat during the last two weeks of July, the period of peak standing crop for the majority of species at Minto Flats. Live and dead plant biomass was separated, and the live biomass was sorted by species, dried at 65°C to a constant weight, and weighed. Morphologically similar species were grouped to facilitate comparisons among the three lake types (Table 1).

At the time of plant sampling, I randomly collected surface water (top 30 cm) samples from each lake in triplicate and analyzed each sample for several water quality characteristics. Total alkalinity was measured by titration with a strong acid using a HACH digital titrator in combination with phenolphthalein and brom-cresol green methyl-red as end-point indicators. Turbidity was measured in nephelometric turbidity units, using a HACH 16800 turbidimeter. Inorganic nitrogen (mg/L) and orthophosphate (mg/L) were determined using a HACH DR-EL/4 portable lab. HACH Company's NitraVer5 nitrate reagent AccuVacs™ and PhosVer3 phosphate reagent AccuVacs™ were used to colorimetrically determine NO<sub>3</sub>/NO<sub>2</sub>-N and orthophosphate. Nessler's reagent in combination with a HACH ammonia test kit (model NI-8) was used to estimate NH<sub>4</sub><sup>+</sup> (mg/L) in the water column. Apparent (unfiltered) water color, measured in APHA platinum cobalt units, was determined using a HACH water color test kit (model CO-1).

A HACH wide-range pH test kit (model 17-N) was used to determine pH of each water sample.

I randomly collected five sediment cores, 5 cm in diameter and 30 cm in length, from each lake at the time of plant sampling. Sediment samples were dried at 65°C to constant weight, and ground in a mill with a 40 mesh screen prior to analysis. Sediment samples were analyzed by combustion for total C and N using a LECO auto analyzer (CHN-600) (LECO, 1996). Total sediment phosphorus was determined colorimetrically after perchloric acid digestion (Olsen and Sommers, 1982).

I used a two-factor analysis of variance to test for differences in plant biomass, and water and sediment chemical characteristics among lake types and between flooded and non-flooded years. Multiple regression was used to test for relationships between plant biomass and water and sediment chemical characteristics. Analysis of covariance was used to test for differences among lake types and flooding regime by controlling for variation due to the covariates. Water temperature, color, alkalinity, turbidity, pH, orthophosphate,  $\text{NO}_3/\text{NO}_2\text{-N}$ ,  $\text{NH}_4^-$ , and sediment N, C and P were included in the analysis as covariates. Analyses were performed using the general linear models (GLM) procedures of SAS (SAS institute Inc. 1996). Analysis of the residuals showed no site-specific patterns of variation.

## Results

### Chemical characteristics

Water temperature, color, alkalinity, turbidity,  $\text{NO}_3/\text{NO}_2\text{-N}$ , and carbon and nitrogen content of the sediment were all significantly different between years in which the wetland was flooded and not flooded (Tables 2 and 3). Orthophosphate was marginally higher ( $p = 0.06$ ) in flooded than in non-flooded years. Water temperature was fairly stable among the three wetland types; however, in flood years, water temperatures were significantly warmer than in non-flooded years. During flood years water color and orthophosphate were also significantly greater while, alkalinity, turbidity and  $\text{NO}_3/\text{NO}_2\text{-N}$  were significantly less.

Alkalinity, turbidity, pH, orthophosphate, and total sediment C (%) and P (%) were influenced by lake type (Tables 2 and 3). Marginally significant differences among lake types were found for water color ( $p = 0.06$ ) and sediment N (%) ( $p = 0.08$ ). Turbidity, alkalinity, and orthophosphate tended to decrease as lake openness decreased and pH increased with lake openness. Water color was considerably greater in open and inundated lakes, especially during flooding, than in closed lake systems. Phosphorus in the sediment tended to increase with lake openness while sediment N and C decreased. Sediment C and N were highly correlated ( $r = 0.98$ ), but neither were correlated with sediment P.

### Emergent biomass

Lake type had a significant effect on emergent plant biomass ( $p = 0.03$ ). A significant interaction ( $p = 0.03$ ) between lake type and flooding regime showed that emergent biomass within each lake type was differentially influenced by flooding regime (Table 4 and Figure 2). Responses of plant groups to flooding and lake type varied greatly due to the different ecological niches occupied by each plant group (Table 5 and Figure 3). Grasses and sedges had consistently greater biomass in non-flooded years in all lake types. Closed lake systems had significantly more biomass of rushes than open or inundated lakes irrespective of flooding ( $p = 0.03$ ). Sedge biomass did not vary significantly ( $p < 0.05$ ) between flooded and non-flooded years, but differed significantly among the three lake types, with greatest biomass in open lakes and least in closed lakes ( $p = 0.01$ ). Broad-leaved emergents did not vary significantly in biomass among lake types or between flood regimes.

Lake type and flood regime were used as main effects, with water and sediment chemical characteristics specified as covariates, in an analysis of covariance, to determine the influence of each variable on biomass of each plant group (Table 6). Each plant group showed different relationships with water and sediment characteristics. After controlling for differences in water and sediment chemistry I found significant differences in rush biomass between flooded and non-flooded years and an interaction between lake type and flood regime. This suggests that reducing variation accounted for by differences in water and sediment chemistry enabled me to detect significant differences

between flooded and non-flooded years and the interaction between lake and type flood regime. Water temperature,  $\text{NO}_3/\text{NO}_2\text{-N}$  in the water, sediment nitrogen and phosphorus, and to some extent water color accounted for the variation that was previously explained by lake type. Rush biomass was negatively related to water temperature,  $\text{NO}_3/\text{NO}_2\text{-N}$ , and sediment P, and positively related to water color and sediment N. Grass biomass differed significantly among lake types (after controlling for differences in water and sediment chemistry), was inversely correlated with sediment P, and increased with increasing water color and sediment N. Water temperature and  $\text{NO}_3/\text{NO}_2\text{-N}$  ( $p = 0.06$ ) showed marginally significant positive relationships with grass biomass. The significant differences in grass biomass in flooded and non-flooded years detected in the ANOVA (Table 5) are explained in the analysis of covariance by variation in water color, sediment N and P, water temperature, and  $\text{NO}_3/\text{NO}_2\text{-N}$ . After controlling for water and sediment chemistry, sedge biomass varied significantly among lake types. A significant negative relationship between sedge biomass and orthophosphate accounted for variation previously explained by flood regime. ANCOVA was not successful in detecting differences in broad-leaved biomass among lake types or between flood regimes. As well as not being significantly different among lake types and not affected by flooding, biomass of broad-leaved emergents was not significantly related to any of the water or sediment characteristics.

#### Submersed biomass

Overall, submersed plant biomass did not vary significantly among lake types or between flooding regimes (Table 7 and Figure 4). Neither lake type nor flooding regime

had a significant impact on the biomass of pondweeds or floating-leaved plants (Table 8 and Figure 5). However, finely dissected plants had much higher plant biomass in non-flooded years ( $p = 0.001$ ) (Table 8 and Figure 5). Lake type also had a significant effect on biomass of finely dissected plants ( $p = 0.001$ ). Open lakes had the greatest biomass, closed the least and inundated a moderate biomass.

Maintaining lake type and flood regime as the main effects, analysis of covariance was used to control for water or sediment chemical variables to better detect differences in submersed plant biomass due to the main effects. Total submersed plant biomass was significantly (and positively) related to alkalinity and turbidity. However, no significant relationships were found between biomass of pondweed and finely dissected plants and any of the main effects or covariates. Due to missing data, it was not possible to use ANCOVA to test for differences in floating-leaved plant biomass among lake types and between flood regimes with all the covariates included.

Stepwise multiple regression was used to determine if biomass of pondweed, floating-leaved, or finely dissected plants was related to water or sediment chemistry. I detected significant ( $p = 0.01$ ) negative relationships with floating-leaved plant biomass and water color and alkalinity [plant biomass =  $76.23 - 0.42$  (water color) -  $0.60$  (alkalinity)] ( $r^2 = 0.74$ ,  $p = 0.01$ ). Water color explained 37% of the variation of floating-leaved plant biomass and total alkalinity explained an additional 37% of the variation. Biomass of finely dissected plants was positively related to turbidity and alkalinity [plant

biomass =  $-50.89 + 1.71 (\text{alkalinity}) + 20.46 (\text{turbidity})$ ] ( $p = 0.0003$ ,  $r^2 = 0.52$ ). Turbidity explained 41% of the total variation and alkalinity an additional 11%.

## **Discussion**

### Emergent biomass

The response of plants in the lakes at Minto Flats to flooding paralleled the zonation patterns of freshwater marshes i.e., response to flooding was greatest in plants occupying the most xeric habitats and least in the most hydric habitats. Typical marsh zonation patterns (van der Valk and Davis, 1978) follow a regular shift in species of plants from xeric to hydric conditions. Lowland grasses occupy moist meadows, sedges are in slightly deeper water and, broad-leaved emergents occupy moderately deep sites. Rushes are the emergent plant species occupying the most hydric conditions and were least effected by changes in flood regime. Plants most influenced by flooding in this study were grasses. Biomass of grasses was 2.5 and 1.5 times greater during non-flooded years, in hydrologically connected and temporarily inundated lakes, respectively. Flooding in connected lake systems where variation in water level was the greatest only reduced biomass of sedges and broad-leaved emergents. The pattern of variation in biomass of plant groups at Minto suggests that plant groups occupying hydric sites are generally less effected by flooding than those plant groups in more xeric areas in the marsh.

Repeatedly aquatic macrophytes have been shown to influence nutrient cycling within lakes (van Donk et al., 1993; Zak and Grigal, 1991; Graneli and Solander, 1988).

Currently, there are two conflicting views (Graneli and Solander, 1988) on how macrophytes influence nutrient cycling in wetlands: 1) littoral plant communities function as net sinks for nutrients, and 2) rooted macrophytes mediate a net transport of nutrients from the sediment to the water column. Relative to terrestrial plant communities, phosphorus is abundant in wetland sediments. It is generally accepted that aquatic macrophytes acquire the majority of their nutrients from the sediment (Wetzel, 1983, Barko et al., 1991). I found that biomass of rushes and grasses was greatest in lakes with the lowest sediment phosphorus, suggesting high densities of emergent plants may be depleting sediment phosphorus levels. Phosphorus is not generally limiting in wetland ecosystems because anaerobic conditions facilitate the release of phosphorus adsorbed to clay particles and organic peat, as well as phosphate bound to ferric iron, calcium, and aluminum during aerobic conditions (Mohanty and Dash, 1982). Phytoplankton and epiphytic algae quickly take up the little phosphorus that is available in the water column. Rapid uptake by algae may explain the negative relationship I found between sedge biomass and orthophosphate in the water column.

#### Submersed biomass

Submersed plant biomass was unrelated to lake type and flooding regime, perhaps due to plant beds shifting toward the shore during flood events. I sampled submersed plants where they were present each year. Submersed aquatic plants are very brittle and can easily be broken up by strong winds or rapid currents, which also act to distribute vegetation within the lake (Sculthorpe, 1967). If the fragmentary material includes a bud

or a part of a node it can quickly generate a new individual. The brittle nature of submersed aquatics may increase their survival during water level disturbances.

Light conditions have repeatedly been found to influence the distribution and biomass of submersed plants (Spence, 1969). Finely dissected plant biomass was positively correlated with greater turbidity in the water column. Turbidity within the lakes at Minto never exceeded 12 NTU, so light was never significantly reduced by high turbidity. Van Nieuwenhuyse (1983) showed that 75-80% of incident light penetrated 0.1 m of water with turbidity of 0.5-10 NTU.

Turbidity at Minto Flats is likely due to resuspension of sediment during storms. High winds resuspended sediment deposited during years in which the major tributaries were dredge-mined for gold (Wolf, 1982). Over one million cubic yards of sediment was deposited in the lakes of Minto Flats as a result of mining activity (Shepherd and Mathews, 1985). These recirculation events may represent a large flux of soluble phosphorus from the sediments into the water column. Rapid uptake of these nutrients by primary producers makes it difficult to get accurate measurements of phosphorus availability. However, particulate matter remains suspended for a considerably longer period of time and is quite easy to measure. Thus turbidity, with associated phosphorus, is probably a good surrogate for orthophosphate in these wetlands.

Biomass of finely dissected plants tended to be greater in lakes with greater alkalinity. Primary productivity of phytoplankton has repeatedly been shown to be positively correlated with alkalinity (Hayes and Anthony, 1964, Carlander, 1955) and

stream benthic algae (LaPerriere, 1983). Additionally, carbon limitation has been shown for several aquatic plant species (Sand-Jensen, 1983). Several mechanisms have developed in aquatic plant species to reduce carbon limitation. Some aquatic plants have adapted to taking up  $\text{HCO}_3^-$  under low  $\text{CO}_2$  levels (Sand-Jensen and Gordon, 1986) while other species shift from  $\text{C}_3$  to CAM photosynthesis to reduce carbon limitation. These plants use  $\text{C}_3$  photosynthesis during the morning when  $\text{CO}_2$  is still available and CAM photosynthesis during the night (Keely and Sandquist, 1991; Madsen, 1987), when respiration rates are high and  $\text{CO}_2$  is abundant.

#### Chemical characteristics

Nitrogen is generally considered the nutrient most likely to be limiting in wetland ecosystems (Gambrell and Patrick, 1978). Nitrogen limitation has been observed in freshwater wetlands (Klopatek, 1978), freshwater tidal marshes (Simpson et al., 1978), and salt marshes (Sullivan and Daiber, 1974; Valiela and Teal 1979). Several groups of microorganisms that perform differently in the presence or absence of oxygen mediate nitrogen transformations within the sediment. Anaerobic conditions due to flooding result in higher concentrations of  $\text{NH}_4^+$ -N in the sediment (Neill, 1995; Kadlec, 1986); this is likely due to lower microbial N immobilization during flooding rather than increased mineralization rates (Neill, 1995). I found increased  $\text{NH}_4^+$ -N in surface water of inundated lakes when flooded; however, closed and open lakes had relatively stable concentrations of  $\text{NH}_4^+$ . This increase is likely due an increase in the area of lake sediment, which results in a larger area of the lake in contact with the thin layer of

oxidized sediment, where  $\text{NH}_4^+$ -N concentration is low, which facilitates the upward diffusion of  $\text{NH}_4^+$ -N, from the deeper reduced sediments into the water column. After water levels returned to near normal,  $\text{NO}_3^-/\text{NO}_2^-$ -N increased substantially in each of the three lake types. Pinay and Naiman (1991) also saw increased  $\text{NO}_3^-$ -N following drawdown within beaver-dominated sedge and grass wetlands. This increase in  $\text{NO}_3^-/\text{NO}_2^-$ -N is likely due to increased nitrification rates due to increased oxygen available to decomposers (Neill, 1995). Rushes and grasses at Minto were positively related to sediment N. However, pondweed biomass was greater in lakes with low sediment N. Different responses to nitrogen availability by the various plant groups may simply be a result of reduced diffusion rates in flooded waters. Grass meadows at Minto were water-free late in the growing season when samples were collected. Less water in the sediment may have led to oxygenated conditions which in turn led to increased nitrification rates. This hypothesis is supported by increased  $\text{NO}_3^-/\text{NO}_2^-$ -N during non-flooded years at Minto. Decreased denitrification rates during low water years may also lead to increased nitrogen availability (Mitsch and Gosselink, 1986).

Water color increased substantially during flooded years. This increase was likely due to increased inputs of organic matter from the surrounding uplands (allochthonous inputs) (Wetzel, 1983). Humates, which are largely responsible for the dark coloration of the water within these wetlands, accumulate in runoff as it percolates through organic-rich strata (McDowell and Likens, 1988). Water color may help explain the variation in water temperature between flooded and non-flooded years. Dissolved organic matter that

tints the water absorbs incident light; the more colored the water the more light is absorbed, increasing water temperature (James and Birge, 1938). Flood waters are also responsible for exporting organic and inorganic material (Mitsch and Gosselink, 1986). Both sediment C and N were reduced during flooded years of my study, indicating possible exportation of organic material or importation of inorganic material.

#### Ecology of Minto Flats

In general, nutrient concentrations were considerably higher in the Minto Flats wetland complex than in other lakes in subarctic Alaska (Rae, 1986) and were more similar to temperate lakes (Kadlec, 1986). Orthophosphate ranged from 0.09 to 0.30 mg/L in ponds at Minto. Orthophosphate measured in small upland ponds near Fort Greely, Alaska (63°58' N, 145°45' W) was considerably lower ranging from 0.002 mg/L in mid-July to 0.034 mg/L in mid-August (Rea, 1986). Total phosphorus at Harding Lake, a large subarctic lake in interior Alaska (64°25' N, 146°50' W), ranged from 0.006-0.020 mg/L (LaPerriere et al., 1978). Inorganic nitrogen in the water column was also considerably greater at Minto (0.67-1.69 mg/L) than at ponds near Fort Greely, ranging from 0.006-0.230 mg/L NO<sub>3</sub>/NO<sub>2</sub>-N (Rea, 1986). Nitrate/nitrite nitrogen was undetectable during summer at Harding Lake and reached a maximum of 0.025 mg/L in April beneath the ice sheet (LaPerriere et al., 1978).

Plant biomass is considerably greater in subarctic freshwater wetlands than in arctic wetlands. Estimates of overall emergent plant biomass at Minto ranged from 360 to 556 g · m<sup>-2</sup>, two to three times as much as in arctic wetlands (200 g · m<sup>-2</sup>) (Alexander et

al., 1980). It is difficult to compare biomass of submersed vegetation in subarctic wetlands and arctic wetlands because these measurements have not been made in the arctic. Emergent and submersed plant biomass at Minto is comparable to that in more temperate regions. Emergent plant biomass is 503-637 g · m<sup>-2</sup> at Eagle Lake, a prairie glacial marsh in Iowa (van der Valk and Davis, 1978), where submersed plant biomass is 200 g m<sup>-2</sup> (van der Valk and Bliss, 1971). Long summer day-lengths appear to compensate for the reduced length of the growing season in subarctic Alaska. Additionally, high nutrient availability in Minto Flats lakes possibly reduces the limitation to growth of wetland plants likely often experienced in other subarctic and arctic ecosystems with lower nutrient availability. Defecation by high densities of waterfowl at Minto may add additional nutrient inputs into the water column. Both past mining and defecation by high densities of waterfowl have essentially served as fertilization events, increasing plant biomass.

Using the results of this research I have constructed a conceptual model (Figure 6) to illustrate the interactions between macrophytes growing at Minto and hydrology and water and sediment chemistry. The model attempts to illustrate the most important relationships found in this research. Hydrological differences, among lake types and between flood regimes, were related to macrophyte biomass and, water and sediment chemistry. Emergent and submersed plant biomasses were both positively related to alkalinity, a measure of carbon availability. The shallow nature of Minto in combination with high measurements of pH have led me to speculate that carbon limitation may occur

in arctic and subarctic wetlands where long summer day-lengths, and subsequently high photosynthetic rates, combined with reduced nocturnal respiration limit carbon availability. In short, carbon is limiting photosynthesis. I have also speculated that carbon limitation occurs prior to nutrient limitation in this nutrient rich wetland. This idea is supported by the negative relationship I found between submersed plant biomass and sediment P; lakes with the least sediment P had the greatest submerged plant biomass. Within this system I suggest that submerged macrophytes are acting as a net nutrient sink, removing readily available sediment P and storing it in aboveground biomass. This model suggests that due to the short, but intense summer macrophyte growth is limited not by nutrients but by carbon.

The relatively high levels of plant biomass at Minto have important implications to secondary consumers in the area. Aquatic plants are an important source of energy and nutrients for invertebrate and vertebrate populations living in marsh habitats, especially fish and waterfowl. Minto Flats supports densities of nesting waterfowl comparable to those in the mid-continent prairies (Conant and Hodges, 1985). Both the leaves (Bartonek and Hickey, 1969) and the seeds (Burris, 1991; Debruckyere, 1988; Krapu and Swanson, 1975) of emergent and submergent plants are important foods for ducks. Hydrophytes are also important to waterfowl production because they harbor large quantities of macroinvertebrates (Voigt, 1976; Krull, 1970) which provide a source of animal protein. In addition to providing a direct nutrient source for some waterfowl, macrophytes provide a substrate for epiphytic periphyton that in turn is used by invertebrates as a food source.

Moreover, decaying macrophytes in this system drive the detrital food web by annually contributing large quantities of energy to the detrital economy of the lake. Understanding the factors determining productivity of subarctic wetland vegetation is critical in understanding trophic interactions within these complex ecosystems.

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**Tables**

Table 1. Plant species classified into plant groups utilized to make comparisons among the three lake types studied at Minto Flats.

Emergent Plant Groupings	
<u>Rushes</u> <i>Equisetum fluviatile</i> <i>Eleocharis palustris</i> <i>Scirpus validus</i>	<u>Sedges</u> <i>Carex limosa</i> <i>Carex aquatilis</i> <i>Carex Rostrata</i> <i>Eriophorum angustifolium</i>
<u>Grasses</u> <i>Glyceria maxima</i> <i>Acorus calamus</i> <i>Arctophyla fulva</i> <i>Typha latifolia</i>	<u>Broad-leaved</u> <i>Menyanthes trifoliata</i> <i>Potentilla palustris</i> <i>Calla palustris</i> <i>Sparganium angustifolium</i> <i>Hippuris vulgaris</i>
Submersed Plant Groupings	
<u>Pondweeds</u> <i>Potamogetan zosterfolius</i> <i>Potamogetan gramineus</i> <i>Potamogetan praelongus</i> <i>Potamogetan perfoliatus</i> <i>Potamogetan pectinatus</i> <i>Potamogetan vaginatus</i> <i>Potamogetan foliosus</i> <i>Potamogetan friesii</i> <i>Potamogetan bechtoldi</i> <i>Potamogetan robinsii</i>	<u>Floating-Leaved</u> <i>Nuphar polysepalum</i> <i>Nymphaea tetragona</i> <i>Polygonum amphibia</i> <i>Potamogetan natans</i> <i>Sparganium hyperboreus</i> <i>Lemna trisulca</i> <i>Lemna major</i>
<u>Finely dissected</u> <i>Utricularia vulgaris</i> <i>Myriophyllum spicatum</i> <i>Ceratophyllum demersum</i> <i>Ranunculus tricophylus</i>	

Table 2. Analysis of variance of water and sediment chemical variables compared among lake types (open, inundated, and closed) and between flooding regimes (flooded and non-flooded years.) Degrees of freedom for lake type = 2 and for flood regime =1.

Source	Lake Type			Flood Regime		
	SS	F	p	SS	F	p
Temperature (°C)	1.91	0.31	0.73	78.25	25.58	0.0001
Color (ptu)	40850.00	2.91	0.06	82181.59	25.98	0.0001
Alkalinity (mg/L)	8256.91	22.44	0.0001	1245.22	6.77	0.01
Turbidity (NTU)	42.49	4.93	0.01	23.22	5.39	0.02
pH	7.04	6.65	0.003*	0.03	0.28	0.60*
Orthophosphate (mg/L)	0.17	3.09	0.05	0.10	3.59	0.06
NO <sub>3</sub> /NO <sub>2</sub> -N (mg/L)	0.34	0.21	0.81	6.57	7.72	0.007
NH <sub>4</sub> <sup>+</sup> (mg/L)	0.01	0.04	0.95	0.05	1.12	0.29
Sediment C (%)	212.28	4.45	0.01	126.45	5.31	0.02
Sediment N(%)	0.66	2.62	0.08	0.81	6.31	0.01
Sediment P (%)	0.01	3.33	0.05*	0.01	1.54	0.22*

\* Indicates a significant ( $p \leq 0.05$ ) interaction between lake type and flood regime.

Table 3. Means and standard errors for water and sediment chemical characteristics measured in open, inundated, and closed lake systems at Minto Flats during flooded and non-flooded years.

	Connected				Inundated				Closed			
	Flooded		Non-Flooded		Flooded		Non-Flooded		Flooded		Non-Flooded	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Temperature °C	19.71	0.42	18.33	0.91	20.25	0.47	16.66	0.65	21.00	0.57	16.60	0.97
Color	204.60	29.92	84.18	6.18	229.11	44.03	69.30	6.47	114.63	23.42	63.57	9.31
Alkalinity (mg/L)	47.33	2.65	62.83	1.72	33.00	4.49	42.33	7.15	19.54	3.28	25.20	7.46
Turbidity (NTU)	2.81	0.31	5.54	1.03	0.69	-	3.36	0.42	1.07	0.07	2.11	0.15
pH	8.03	0.23	8.49	0.25	7.50	0.34	7.76	0.21	7.92	0.26	6.87	0.17
Orthophosphate (mg/L)	0.30	0.05	0.24	0.03	0.29	0.14	0.09	0.01	0.14	0.05	0.13	0.04
NO <sub>3</sub> /NO <sub>2</sub> -N (mg/L)	0.75	0.27	1.26	0.24	0.67	0.28	1.69	0.40	0.85	0.30	1.48	0.25
NH <sub>4</sub> <sup>+</sup> (mg/L)	0.82	0.06	0.79	0.06	0.89	0.12	0.70	0.05	0.80	0.08	0.83	0.07
Sediment C (%)	7.19	0.86	6.65	0.93	7.85	1.48	10.43	1.39	8.27	1.49	16.62	4.83
Sediment N (%)	0.60	0.07	0.58	0.07	0.63	0.09	0.83	0.10	0.58	0.10	1.22	0.34
Sediment P (%)	0.11	0.01	0.09	0.005	0.07	-	0.10	0.00	0.06	0.006	0.08	0.008

Table 4. Results of a two-factor analysis of variance with interaction testing differences in plant biomass among lake types and between flooded and non-flooded years.

Source	df	SS	F	P
Lake Type	2	8858.11	3.69	0.03
Flood Regime	1	2450.43	2.04	0.16
Type*Flood Regime	2	9182.30	3.82	0.03
Error	57	68434.69		

Table 5. Results of two factor analysis of variance with interaction testing differences in emergent plant biomass among lake types and between flooded and non-flooded years.

	Rush			Grass			Sedge			Broad-leaved		
	SS	F	P	SS	F	P	SS	F	P	SS	F	P
Lake Type	249879	3.78	0.03	155947	1.90	0.17	552035	5.18	0.01	34110	1.71	0.19
Flood regime	21354	0.65	0.43	459055	11.17	0.00	198019	3.71	0.06	951	0.10	0.75
Lake type*flood regime	100666	1.52	0.23	133783	1.63	0.21	171440	1.61	0.21	46489	2.37	0.10
Error	1320375			1273978			1760064			382887		
Error DF	40			31			33			39		

Table 6. Analysis of covariance describing relationships between plant group biomass and lake type, flooding regime, and water and sediment chemical characteristics. Degrees of freedom for lake type = 2, flood regime = 1, lake type \* flood regime = 2, and the remaining variables have 1 degree of freedom. An asterisk marks covariates which explain a significant ( $p \leq 0.05$ ) amount of variation (results based upon type III SS).

	Rush			Grass			Sedge			Broad-leaved		
	SS	F	P	SS	F	P	SS	F	P	SS	F	P
Lake type	8150	1.71	0.29	246368	10.97	0.01	523208	6.67	0.05	47458	2.09	0.23
Flood Regime	24034	10.08	0.03	12530	1.12	0.33	15623	0.40	0.56	1180	0.10	0.76
Lake * Flood regime	51837	10.87	0.02	2504	0.11	0.89	51275	1.31	0.31	538	0.05	0.83
Water Temperature °C	18703	7.84	0.04*	64489	5.74	0.06	20611	0.53	0.50	5608	0.49	0.52
Water Color	13939	5.84	0.07	102655	9.14	0.02*	5110	0.13	0.73	6059	0.53	0.50
Alkalinity (mg/L)	2034	0.85	0.40	963	0.09	0.78	21	0.00	0.98	20304	1.79	0.25
Turbidity (NTU)	4123	1.73	0.25	1	0.00	0.99	30407	0.77	0.42	9363	0.82	0.41
pH	8827	3.70	0.12	127	0.01	0.91	111479	2.84	0.16	7613	0.67	0.45
Orthophosphate (mg/L)	32	0.01	0.91	7926	0.71	0.43	281593	7.18	0.05*	7632	0.67	0.45
Nitrogen (mg/L)	25285	10.60	0.03	61618	5.49	0.06	43178	1.10	0.35	454	0.04	0.85
NH <sub>4</sub> <sup>+</sup> (mg/L)	2063	0.87	0.40	395	0.04	0.85	49089	1.25	0.32	3311	0.29	0.61
Sediment N (%)	74962	31.43	0.01*	79646	7.09	0.04*	347	0.01	0.92	4296	0.38	0.57
Sediment P (%)	32980	13.83	0.02*	88118	7.84	0.03*	10025	0.26	0.63	3042	0.27	0.63
r <sup>2</sup>		0.96			0.94			0.91			0.80	

Table 7. Results of a two-factor analysis of variance with interaction testing differences in submersed plant biomass among lake types and between flooded and non-flooded years.

Source	df	SS	F	P
Lake type	2	1636.38	0.52	0.60
Flood regime	1	655.21	0.21	0.65
Type* Flood	2	61.05	0.02	0.98
Error	53	167048.41		

Table 8. Results of two factor analysis of variance with interaction testing differences in submersed plant biomass among lake types and between flooded and non-flooded years.

	Floating-leaved			Pondweeds			Finely-dissected		
	SS	F	P	SS	F	P	SS	F	P
Lake type	647	1.19	0.32	14325	0.13	0.87	84509	11.85	0.0001
Flood Regime	3	0.01	0.92	11946	0.22	0.64	117462	32.93	0.0001
Lake type * flood regime	598	1.06	0.36	7837	0.07	0.93	67131	9.41	0.0003
Error		6213			2232074			174767	
Error DF		22			41			49	

Table 9. Analysis of covariance describing relationships between plant group biomass and lake type, flooding regime, and water and sediment chemical characteristics. Degrees of freedom for lake type = 2, flood regime = 1, lake type \* flood regime = 2, and the remaining variables have 1 degree of freedom.

Source	Pondweeds			Finely dissected			Submersed		
	SS	F	P	SS	F	P	SS	F	P
Lake type	11225	1.32	0.43	6386	0.67	0.53	295	0.77	0.48
Flood regime	1113	0.26	0.66	169	0.04	0.85	12	.06	0.80
Lake type * flood regime	5013	0.59	0.62	26446	2.79	0.11	45	.12	0.88
Water temperature (°C)	399	0.09	0.78	6746	1.42	0.26	219	1.15	0.30
Color	2	0.00	0.98	2319	0.49	0.50	100	0.53	0.48
Alkalinity (mg/L.)	1577	0.37	0.60	2706	0.57	0.46	1082	5.95	0.03
Turbidity (NTU)	3494	0.82	0.46	14671	3.09	0.11	1503	7.86	0.02
pH	465	0.11	0.77	6363	1.34	0.27	206	1.08	0.31
PO <sub>4</sub> <sup>-3</sup> (mg/L.)	2854	0.67	0.49	2486	0.52	0.48	381	2.00	0.18
NO <sub>3</sub> /NO <sub>2</sub> -N	1215	0.29	0.64	10753	2.27	0.16	49	0.26	0.62
NH <sub>4</sub> <sup>+</sup>	437	0.10	0.77	84	0.02	0.89	26	0.14	0.71
Sediment N (%)	981	0.23	0.67	861	0.18	0.68	136	0.71	0.41
Sediment P (%)	1803	0.42	0.58	178	0.04	0.85	596	3.12	0.10

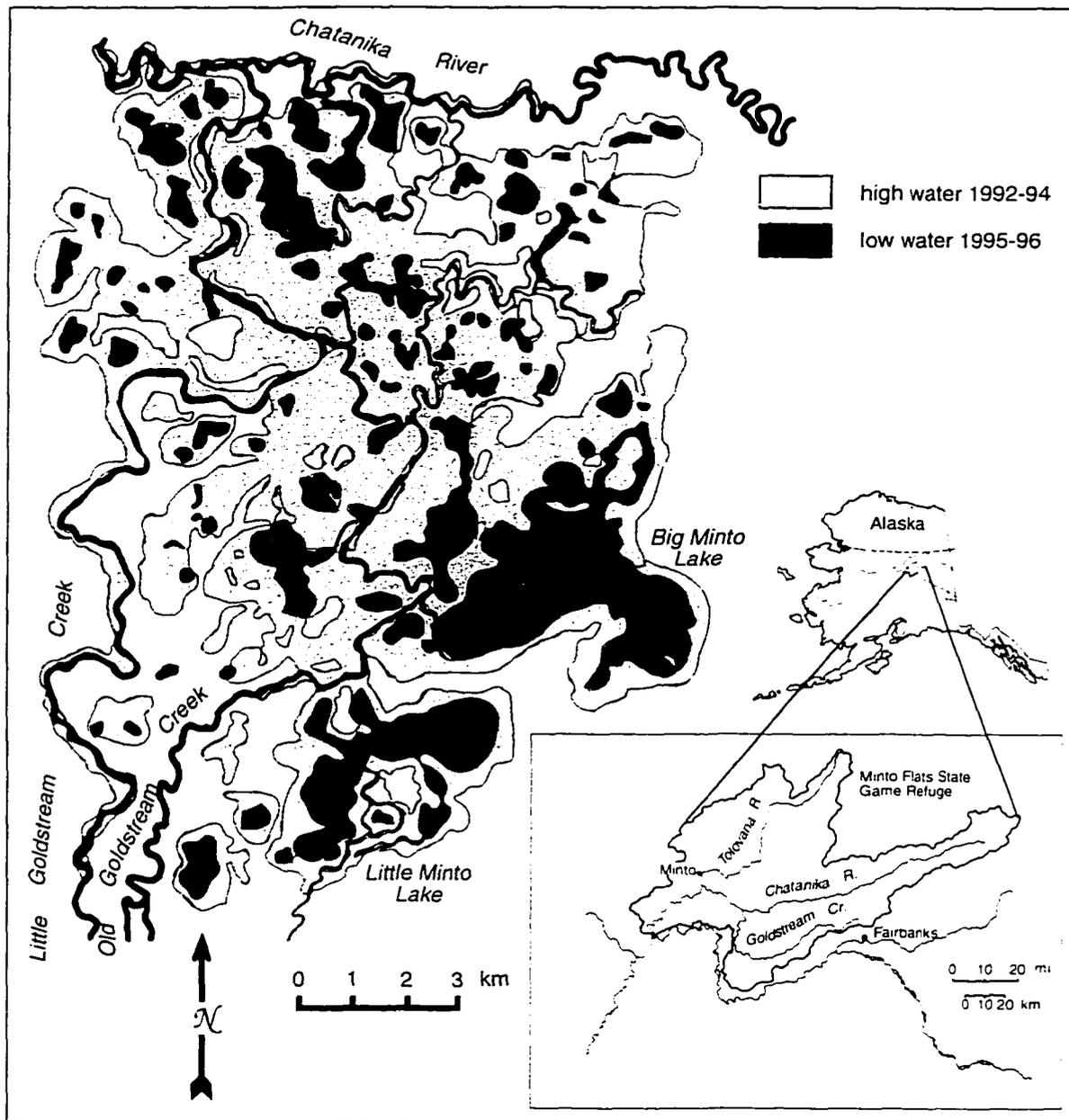


Figure 1. Study site map of the lakes at Minto Flats, Alaska. Different degrees of shading indicate years of high and low water level.

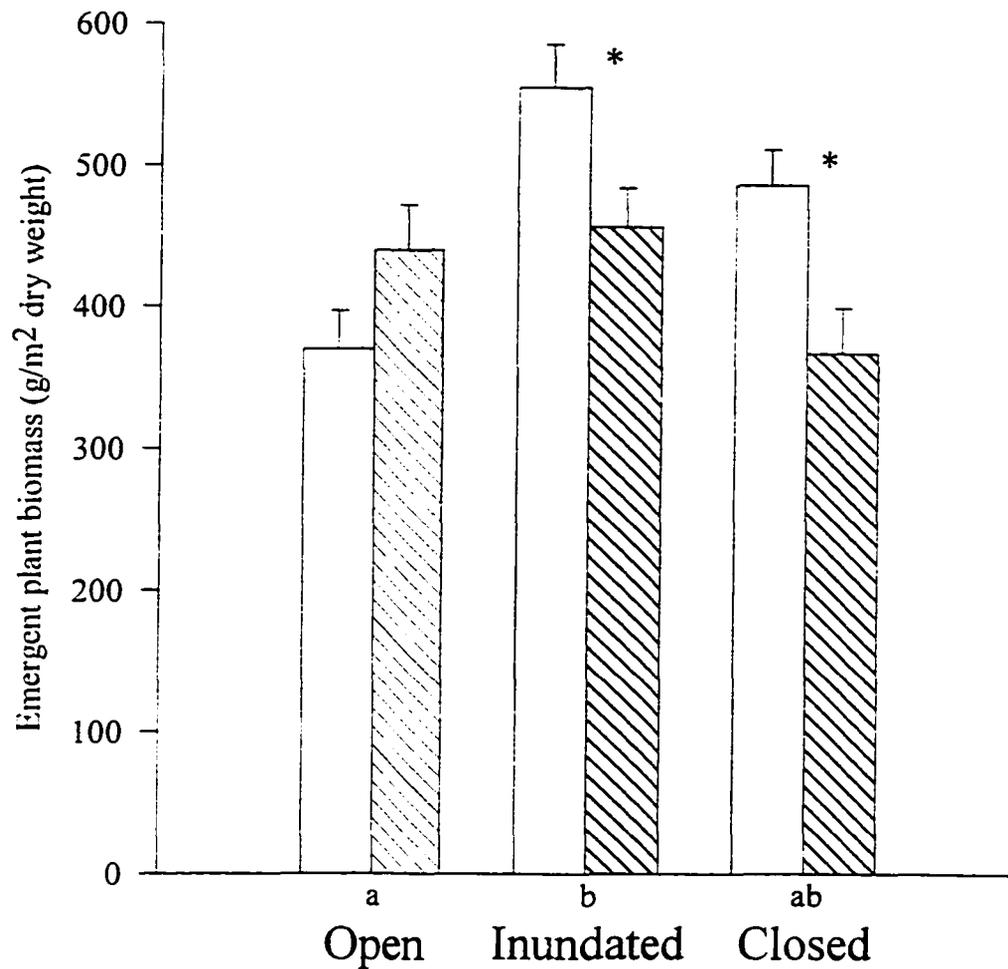


Figure 2. Mean (+ standard error) of emergent plant biomass in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems. Lake types sharing the same letter are not significantly different ( $P \geq 0.05$ ) from one another. Lake types which differ significantly ( $p < 0.05$ ) between flooded and non-flooded years are marked with an asterisk.

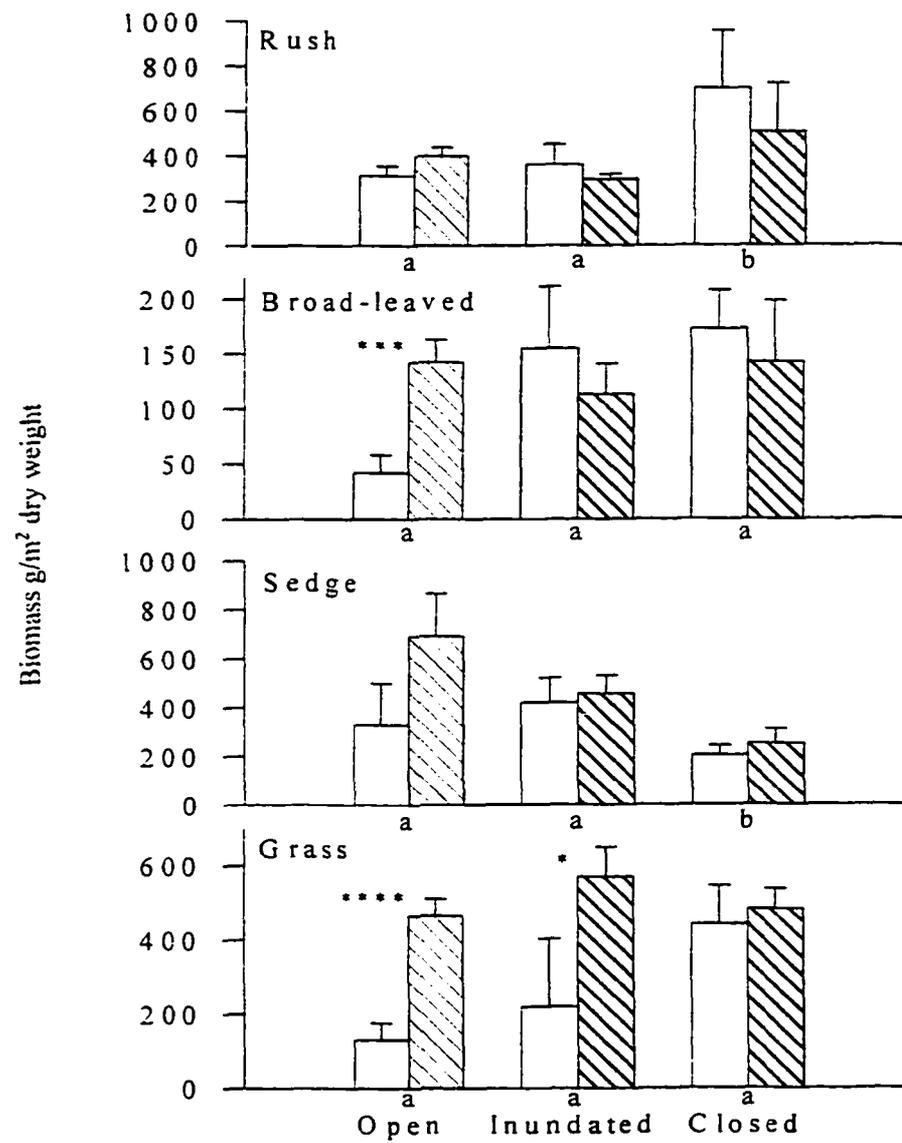


Figure 3. Grass, sedge, broad-leaved, and rush biomass (mean and standard error) in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems. Lake types sharing the same letter are not significantly different ( $P \geq 0.05$ ) from one another. Lake types which differ significantly between flooded and non-flooded years are marked with an \* if significant at the 0.10 level, \*\* if significant at the 0.01 level, \*\*\* if significant at the 0.001 level, and \*\*\*\* significant at the 0.0001 level.

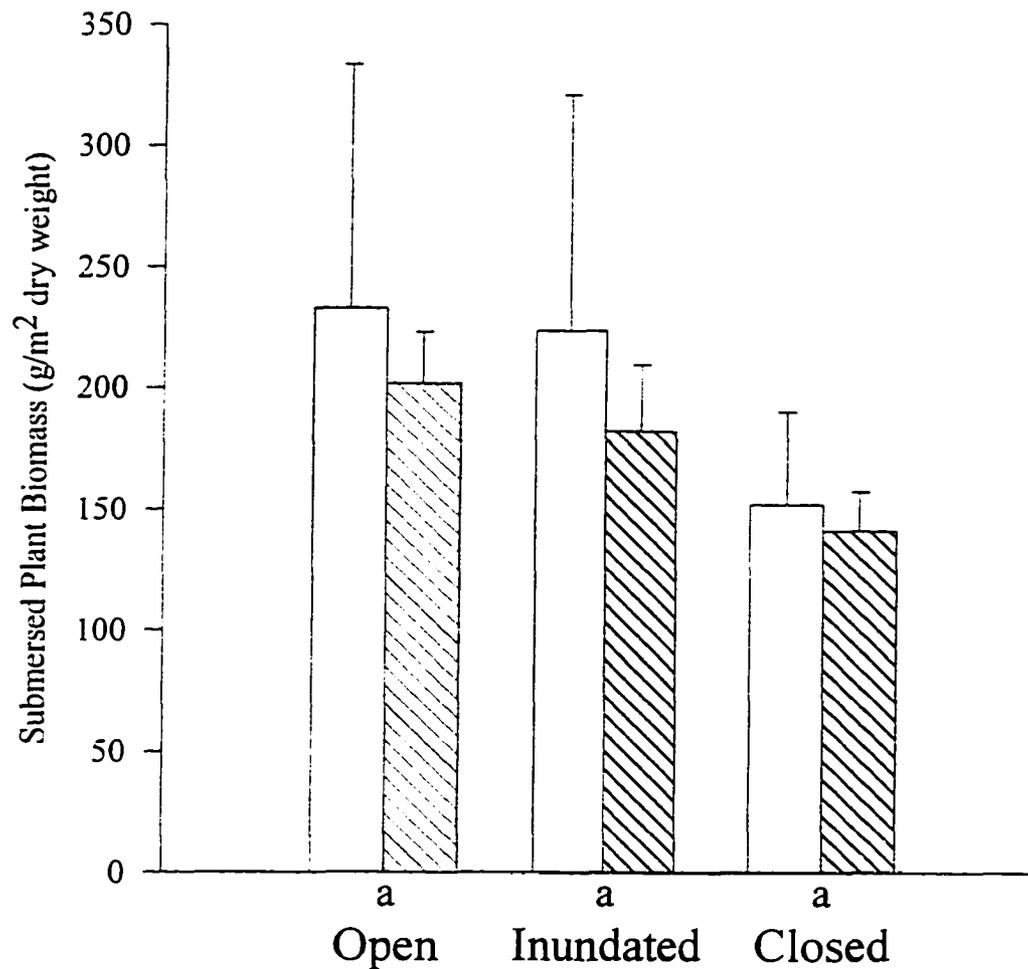


Figure 4. Mean (standard error) submersed plant biomass in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems. Lake types sharing the same letter are not significantly different ( $p \geq 0.05$ ) from one another. Lake types did not differ significantly ( $p > 0.05$ ) between flooded and non-flooded year.

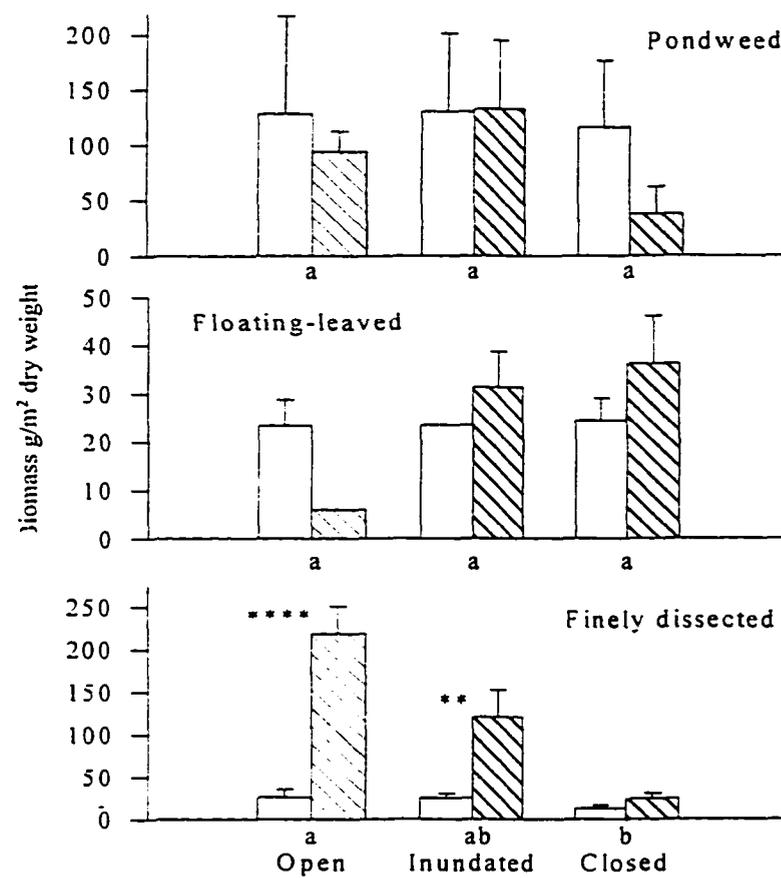


Figure 5. Biomass (mean and standard error) of finely dissected, floating-leaved, and pondweed submersed plants in flooded (clear bars) and non-flooded (hatched bars) years at Minto Flats in open, temporarily inundated, and closed lake systems. Lake types sharing the same letter are not significantly different ( $P \geq 0.05$ ) from one another. Lake types which differ significantly between flooded and non-flooded years are marked with an \* if significant at the 0.10 level, \*\* if significant at the 0.01 level, \*\*\* if significant at the 0.001 level, and \*\*\*\* if significant at the 0.0001 level.

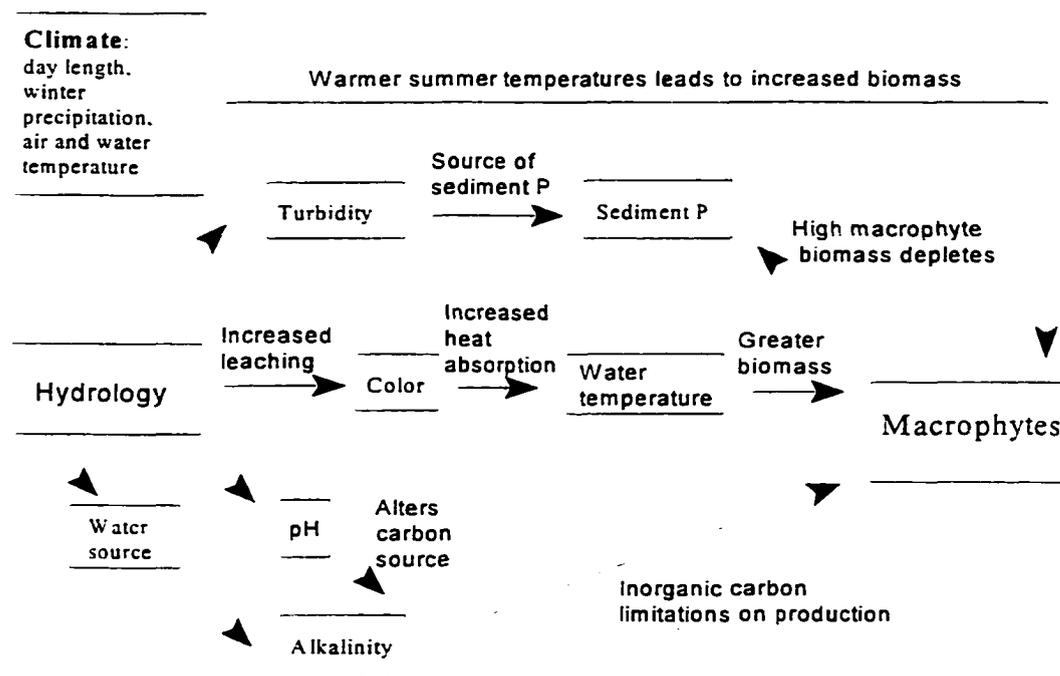


Figure 6. A conceptual model of the interactions between macrophytes and climate, hydrology, and water and sediment chemistry.

**The effects of flooding on species composition of macrophytes in a subarctic  
freshwater marsh<sup>1</sup>**

**Abstract**

Species composition of macrophytic vegetation in 13 subarctic lakes, differing in hydrologic input (open, temporarily inundated, and closed), was evaluated over a 5 year period during which time water levels fluctuated from flooded to near normal. Thirty-three plant species were found in the lakes. Results from MANOVA showed that species composition was significantly different among lake types and between years that experienced different flood regimes. A large proportion of species found in the lakes did not occur in both open and closed lake systems; however, over the course of the study many of these species did occur in inundated lakes. Canonical discriminant analysis was used to determine if plant species composition could be used to classify lakes according to lake type and flood regime. Species composition was highly successful in classifying lakes: 92% of the lakes were successfully classified. Mahalanobis distances showed clear separation of open and inundated lakes from closed lakes; however, the model was not very successful in separating lakes that underwent compositional changes due to flooding. The results of this study indicate that species composition is heavily influenced by lake type and to some extent by flood regime.

<sup>1</sup>Prepared for submission to the Canadian Journal of Botany as Larsen, A.S. The effects of flooding on species composition of macrophytes in a subarctic freshwater marsh.

## Introduction

Species composition of macrophytic vegetation within wetland habitats is generally thought to be controlled by hydrology (Mitsch and Gosselink, 1986). In northern prairie wetlands dramatic fluctuations in water level over time (5-30 years) are associated with large shifts in species composition (van der Valk and Davis, 1978). Which follow a successional series that has four phases: dry, regenerating, degenerating, and open marsh (van der Valk and Davis, 1978). Mud flat annuals dominate the dry marsh phase. The drying of the marsh sediment stimulates germination of emergent plant species that persist and become dominant in the regenerating phase. The degenerating phase is marked by a rapid decline of emergent plant species and an increase in submersed plant species. Finally, the open marsh phase is characterized by high water levels which eliminate emergent vegetation and enhance growth of submersed and floating aquatics (van der Valk and Davis, 1978). Below-average water levels return the cycle to the dry marsh phase. These successional processes suggest that species composition is dependent on differential susceptibility of various species to water level fluctuations.

Interior Alaska wetlands water level fluctuations are driven by levels of winter precipitation (snow) and rate of spring melt (Ford and Bedford, 1987), but little is known about the effects that water level fluctuations have on plant species composition. However, several authors have evaluated the effects of hydrologic connectedness on duck

use (Seppi, 1991, Murphy et al., 1984), invertebrate abundance (Seppi, 1991), water chemistry (Larsen, unpublished manuscript; Seppi, 1991; Murphy et al., 1984), and plant biomass (Larsen unpublished, 1997) in subarctic wetlands. Lakes open to hydrologic inputs are heavily influenced by flood events. Isolated lakes are generally closed to overland water flow; however, increased groundwater inputs due to flooding are likely. Closed lakes adjacent to sloughs receive overland flooding due to high water levels. This paper explores the dynamics of species composition in relation to hydrologic regime. I investigated the influence of lake type and flooding regime on wetland plant species composition in a large subarctic marsh. This study had two objectives: *i*) to determine if plant species composition differs among hydrologically open, temporarily inundated, and hydrologically closed lake types, and *ii*) to determine if species composition of vascular plants differs in flooded and non-flooded years. I accomplished these objectives by evaluating differences in species abundance among open, temporarily inundated, and closed lake systems during 3 flooded and 2 non-flooded years.

### **Study Site**

During the summers of 1992-1996 plant species composition of aquatic macrophytes was recorded from 13 lakes within the Minto Flats State Game Refuge (MFSGR), hereafter "Minto". Minto is a large subarctic wetland located in interior Alaska (64°50'N, 148°50'W) (Figure 1). Minto contains a diverse array of lake types formed primarily by fluvial activity (ADFG, 1991). This area experiences seasonal and interannual fluctuations in water level due primarily to variability in winter precipitation.

Lakes sampled for this research were restricted to the south-eastern corner of the refuge. This portion of the refuge is drained by Goldstream Creek, the flow of which is reversed during years of high winter precipitation or rapid spring melt, causing high water levels in this portion of Minto. During these high water periods, Minto acts as a large reservoir, slowly draining as water levels decline on the Tanana River (the major river draining the area). High precipitation (snow) in the preceding winter resulted in high water levels in the summers of 1992, 1993, and 1994. Average winter precipitation 1994-95 and 1995-96 led to near normal water levels at Minto.

Minto supports high densities of breeding waterfowl (Conant and Hodges, 1985). There are 12 species of ducks which nest in the Minto Flats State Game Refuge (Petrula, 1994). Dominant species include northern shovelers (*Anas clypeata*), lesser scaup (*Aythya affinis*), northern pintail (*Anas acuta*), mallards (*Anas platyrhynchos*), and American wigeon (*Anas americana*). Gadwalls (*Anas strepera*) are present in much smaller numbers.

### **Methods**

Data were collected from 13 ponds/lakes within the MFSGR. Each lake was sampled at least twice from 1992 to 1995, and eight were sampled annually to determine changes in species composition among years. Species richness was determined for 10 randomly selected quadrats (0.25m<sup>2</sup>) within each water body. Vegetation was harvested from five quadrats located within the emergent vegetation zone and five in the submersed vegetation zone. Vascular plants were identified to species; nomenclature conforms to

Hulten (1968) (Table 1). Species abundance was determined as the total number of times each species occurred within each lake.

Each lake/pond was classified as open, inundated, or closed based on its hydrologic regime and susceptibility to flooding. A lake was classified as “open” if it was hydrologically connected to a slough or river and was always influenced by annual flooding cycles, “inundated” if it was only occasionally inundated with flood waters via overflow or changes in water table, and “closed” if it was not hydrologically connected and was never flooded.

MANOVA (SAS Institute Inc. 1996) was used to test for differences in species abundance and composition among lake types and between flooded and non-flooded years. Canonical discriminant analysis (CDA) (SAS Institute Inc. 1996) was used to determine if species composition could be used to accurately classify each lake based upon species composition. For CDA, each lake type was first classified as open, inundated or closed and subclassified as flooded or non-flooded based on spring water conditions (and winter precipitation levels), for a total of six classes. The success of the classification prediction was analyzed to determine how useful species composition is in classifying lakes. Mahalanobis distances were then compared to determine if there was significant separation among lake types and between flood regimes (SAS Institute Inc. 1996).

Species dominance (presence/absence of each species within a quadrat) was determined for the emergent and submergent vegetation zones of each wetland class.

Dominance was calculated as the total number of quadrats in which the species was present relative to the total number of quadrats from each lake type (shown as percent).

### Results

Results of MANOVA showed significant differences in species abundance among lake types (Wilk's Lambda  $p = 0.0001$ ,  $F_{64, 34} = 8.24$ ) and between flooded and non-flooded years (Wilk's Lambda  $p = 0.01$ ,  $F_{32, 17} = 2.82$ ). Two-factor analysis of variance for individual species showed that presence values of 15 species were not significantly different among lake types or between flooded and non-flooded years (Table 1). Presence values of 11 species were significantly different among lake types but not between flooded and non-flooded years. *Glyceria maxima*, *Potamogetan perfoliatus*, *Myriophyllum spicatum*, and *Utricularia vulgaris* were significantly different between flooded and non-flooded years but not among lake types (*Glyceria maxima* and *Utricularia vulgaris* were marginally different among types ( $p = 0.06$ )), while *Equisetum fluviatile*, *Polygonum amphibium*, and *Potamogetan gramineus* were significantly different both among lake types and between flooded and non-flooded years.

Thirty-three plant species were included in the canonical discriminant analysis. Success of classification prediction was evaluated by examining the number of lakes in which species abundances were able to successfully classify the lake type/flood regime (Table 2). Based on resubstitution, 92% of the samples were correctly classified using species abundance. Mahalanobis distance between groups showed significant ( $p \leq 0.0001$ ) separation between open and closed lakes irrespective of flood regime.

Inundated lakes were also significantly ( $p \leq 0.0001$ ) different from closed lakes. A significant ( $p = 0.05$ ) difference was also detected between inundated lakes that were flooded and open lakes that were not, suggesting that differences in species composition do occur between open and inundated lake types. Group separation was more easily seen when discriminant function 1 was plotted against discriminant function 2 (Figure 2). Results from the CDA showed that the first discriminant function explained 87.6% of the variation and the second discriminant function explained an additional 6.9% of the variation. *Equisetum fluviatile*, *P. gramineus*, *Arctophyla fulva*, *Polygonum amphibium*, *Ceratophyllum demersum*, *Sparganium multipedunculatum*, *Callitriche hermaphroditica*, and *Glyceria maxima* loaded heavily on the first axis. *P. Zosterfolius*, *P. gramineus*, *Carex aquatilis*, *Utricularia vulgaris*, *Hippuris vulgaris*, *Cicuta mackenzianna*, *P. foliosus*, and *P. Freesii* loaded heavily on the second axis. Figure 2 illustrates the clear separation of open and inundated lakes from closed lakes along axis 1 (x-axis). There also appear to be differences in species composition between open lakes under the two flood regimes along axis 2 (y-axis); however, the differences are not significant ( $p = 0.14$ ).

Species dominance was calculated for each species within the emergent vegetation zone and the submersed vegetation zone (Table 3). *Equisetum fluviatile* was the dominant emergent species in open and inundated lakes during both flooded and non-flooded conditions. *Menyanthes trifoliata* was the dominant emergent in closed lakes. *Potamogeton gramineus* and *Polygonum amphibium* were the dominant submersed plants

in open lakes during flooding and *Utricularia vulgaris* was dominant in inundated lakes during flooding. *Myriophyllum spicatum* and *Potamogeton perfoliatus* were the dominant species in both open and inundated lakes during non-flooded years. *Potamogeton natans* and *Utricularia vulgaris* were the dominant species in closed lakes during flooded years and *Potamogeton natans* was dominant during non-flooded years.

Twenty of the 33 species found in lakes at Minto showed little overlap between open and closed lake systems. *Menyanthes trifoliata*, *Typha latifolia*, *Potentilla palustris*, *Calla palustris*, *Potamogeton natans*, *Sparganium hyperboreum*, *Carex limosa*, *Potamogeton foliosus*, *Potamogeton Freesii*, *Nuphar polysepalum*, *Nymphaea tetragona*, and *Eleocharis palustris* occurred in closed lake systems, infrequently in inundated lake systems, and never in open lakes. *Arctophyla fulva*, *Polygonum amphibium*, *Lemna major*, *Lemna trisulca*, *Callitriche hermaphroditica*, *Glyceria maxima*, and *Carex rostrata* occurred in open and inundated lakes but not in closed lakes.

### Discussion

Plant species abundance was significantly ( $p \leq 0.05$ ) different among lake types for 42% of the species found in lakes at Minto. However, only 18% of the species showed significant ( $p \leq 0.05$ ) differences between flooded and non-flooded years. A large proportion (61%) of the plant species found at Minto were restricted in their distribution (i.e., they occurred either in open or closed lakes not in both). Inundated lakes contained species that were dominant in both open and closed lake systems (as might be expected).

Discriminant analysis was highly successful at separating each lake into the appropriate class based upon abundance of the 33 vascular plant species. In particular, species composition in closed lakes was distinctly different from both open and inundated lakes. There also appeared to be marginally significant differences between open and inundated lakes. These differences suggest that species composition is substantially different in each type of lake.

Species composition in open and inundated lakes experiencing the same flood regime was not significantly different. However, open flooded lakes and inundated non-flooded lakes were significantly different from one another in species composition. The similarities between open and inundated lakes in species composition, during years of similar hydrologic regime (flooded or non-flooded), illustrate the coupling of species composition and hydrology. Further evidence of the coupling between species composition and hydrology is the presence of *Menyanthes trifoliata* and *Potentilla palustris*, which were dominant in closed lakes, but present in inundated lakes during extremely low water years after prolonged isolation from flood waters. These species likely became established during prolonged isolation (low water years) and then persisted during the first years of inundation, after which they were eliminated. Water levels at Minto prior to the study had been low for an extended period (Rod King, pers. comm. 1994. Fairbanks, AK, United States Fish and Wildlife Service). Thus, it appears that after prolonged isolation, inundated lakes experience a shift to a species composition that more closely resembles that of closed lakes.

Analysis of variance showed that many plant species found at Minto were influenced by lake type, flood regime, or both. These univariate analyses suggest two patterns in species composition demonstrating that species composition is dependent upon hydrology. First, species which primarily occur in closed lakes did not differ in abundance between flooded and non-flooded years. Second, species composition in open lakes was transient as shown by the many significant differences in species abundance found between flooded and non-flooded years.

These results suggest that subarctic freshwater wetlands, much like northern prairie wetlands, are highly dynamic. Species composition in open and inundated lake systems changes in response to flooding. The diverse composition of the seed bank in northern prairie wetlands is thought to enable changes in species composition over time and with water level (van der Valk and Davis, 1978). No research has been conducted on the seed banks of subarctic freshwater wetlands. However, large rafts of seeds seen windrowed against the shore in lakes within Minto Flats suggest that seeds are distributed over a wide area (personal observation). Many seeds have been shown to remain viable in the sediment for extended periods (Sculthorpe, 1967); seeds of several aquatic plant species remain viable for over 50 years (Mayer and Poljakoff-Mayber, 1982). Perennial species may be able to withstand periods of inundation by drawing on stored reserves (Sculthorpe, 1967). Additionally, many submersed plants have perennating organs that remain dormant in the sediment until favorable environmental conditions cause breakage of dormancy (Sculthorpe, 1967). Propagules of submersed plant species are the principal

means of regeneration (Sculthorpe, 1967). These adaptations may help foster the dynamic nature of plant communities in open and inundated lakes in subarctic Alaska.

Spatial differences in species composition potentially have large impacts on secondary consumers using subarctic wetlands, in particular waterfowl which migrate long distances to nest in these areas (Sedinger, 1997). Many of the plant species present in the lakes at Minto are important food resources for ducks nesting and molting there. American wigeon and gadwall are considered the most vegetarian of the dabbling ducks (Krapu and Reinecke, 1992), feeding primarily on the stems and leafy parts of aquatic plants (Bellrose, 1980). Pondweeds (*Potamogeton* spp.), coontail (*Ceratophyllum demersum*), and smartweed (*Polygonum* spp.) are commonly eaten by wigeon (Bellrose, 1980). Diets of American wigeon nesting in subarctic Alaska consist primarily of plant matter, (100% prelaying, 72% laying, and 92% postlaying) (Debruyckere, 1988). *Equisetum* spp. was a dominant food item consumed by more than 42% of all females, and it made up 33% of the diet of males (Debruyckere, 1988). *Equisetum* is a dominant plant species in open and inundated lakes during both flooded and non-flooded conditions. *Potamogetan* spp. and *Cicuta mackenziana* accounted for 27.7% of the diet of postlaying female wigeon. Other important plant foods of wigeon include *Carex* spp., *Sparganium* spp., and *Potamogeton* spp. Additionally, wigeon (Debruyckere, 1988) and northern pintails (Burriss, 1991) rely heavily on seeds of many aquatic and semi-aquatic plant groups. Callitrichaceae seeds are an important food resource for female northern pintails arriving at and rearing broods at Minto Flats (Burriss, 1991). Other important

seeds in the diets of female northern pintails at Minto include Haloragaceae, Sparganaceae, and Cyperaceae (Burris, 1991), all of which are plants found in open, closed and inundated lakes at Minto. Identification of seeds to species is extremely difficult and often impossible. Thus, making generalizations about habitat quality, based upon macrophyte species composition, is difficult. However, many of the plant species found in open lake systems are important food resources for ducks nesting in subarctic Alaska. Two food resources important to several species of ducks nesting at Minto, *Equisetum* and Callitrichaceae seeds, are found only in open and inundated lake systems. I suggest that open and inundated lake systems provide important food resources for ducks nesting in subarctic Alaska.

In subarctic Alaska, Murphy et al. (1984) and Seppi (1991) showed that duck use of open lake systems was significantly greater than use of isolated lake systems. Seppi (1991) found that duck brood density was best predicted by total phosphorus and algae chlorophyll *a* concentration (amongst an array of limnologic characteristics). It is unlikely that returning birds directly assess food resources at any given location (Seastedt and MacLean, 1979), instead they probably are using more stable but indirect (proximate) measures of habitat quality. Plant species composition may not be the proximate measure by which ducks evaluate a given wetland. However, I suggest that open and inundated lake systems are ultimately more attractive to ducks (regardless of proximate cues) not only because they receive larger nutrient inputs but also because they contain important forage species of plants.

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## Tables

Table 1. Univariate test statistics (F) with 2 degrees of freedom among lake types and 1 degree of freedom between flood regimes for the major species of Minto Flats State Game Refuge 1992-1996.

Species	Lake type		Flood regime	
	F	P	F	P
<i>Equisetum fluviatile</i> L. ampl. ehrh.	32.57	0.001	7.89	0.007
<i>Menyanthes trifoliata</i> L.	44.73	0.001	2.12	0.15
<i>Glyceria maxima</i> (Hartm.)	2.91	0.06	16.51	0.001
<i>Potamogeton natans</i> L.	17.55	0.001	0.33	0.56
<i>Polygonum amphibium</i> L.	6.69	0.002	8.36	0.005
<i>Sparganium hyperboreum</i> Laest.	14.57	0.001	0.88	0.353
<i>Carex limosa</i> L.	16.11	0.001	0.00	1.0
<i>Sparganium multipedunculatum</i> (Morong) Rydb.	10.87	0.001	1.07	0.305
<i>Utricularia vulgaris</i> L.	2.74	0.074	16.11	0.001
<i>Potamogeton gramineus</i> L.	4.43	0.017	10.13	0.003
<i>Nuphar polysepalum</i> Engelm.	3.32	0.044	2.74	0.105
<i>Typha latifolia</i> L.	7.52	0.001	0.36	0.549
<i>Carex aquatilis</i> Wahlenb.	4.61	0.014	2.75	0.103
<i>Potamogeton perfoliatus</i> L.	0.74	0.480	6.36	0.015
<i>Myriophyllum spicatum</i> L.	1.36	0.266	6.60	0.013
<i>Potentilla palustris</i> (L.) Scop.	4.64	0.014	0.73	0.396
<i>Arctophila fulva</i> (Trin.)	2.12	0.131	3.28	0.076
<i>Hippuris vulgaris</i>	4.15	0.021	0.14	0.706
<i>Carex rostrata</i> Stokes	0.87	0.426	2.98	0.090
<i>Potamogetan pectinatus</i> L.	0.89	0.415	3.28	0.076
<i>Nymphaea tetragona</i> Georgi	3.84	0.028	0.03	0.873
<i>Calla palustris</i> L.	2.05	0.140	0.67	0.418
<i>Cicuta mackenzieana</i> Raup	0.95	0.392	2.20	0.144
<i>Callitriche hermaphroditica</i> L.	1.60	0.211	1.00	0.323
<i>Ceratophyllum demersum</i> L.	2.29	0.112	0.67	0.418
<i>Potamogeton foliosus</i> Raf.	1.03	0.364	1.16	0.287
<i>Eleocharis palustris</i> (L.)	1.14	0.328	0.61	0.438
<i>Potamogetan Friesii</i> Rupr.	0.89	0.416	0.93	0.339
<i>Potamogetan Berchtoldi</i> Frieb.	0.69	0.508	1.72	0.195
<i>Potamogetan zosterifolius</i> Schum.	0.03	0.966	1.89	0.175
<i>Lemna minor</i> L.	0.59	0.560	0.68	0.413
<i>Lemna trisulca</i> L.	0.59	0.560	0.68	0.413
<i>Potamogeton alpinus</i> Balb	0.41	0.665	1.31	0.258

Table 2. Prediction results of canonical discriminant analysis. 92% of all cases were correctly classified using species abundance as the dependant variable, results based on resubstitution.

	Open		Inundated		Closed	
	Flooded	Non-flooded	Flooded	Non-flooded	Flooded	Non-flooded
Open flooded	14	0	1	0	0	0
Open non-flooded	0	9	0	1	0	0
Inundated flooded	1	0	7	0	0	0
Inundated non-flooded	0	0	0	3	0	0
Closed flooded	0	0	0	0	9	1
Closed non-flooded	0	0	0	0	0	6

Table 3. Species dominance, calculated as the total number of quadrats in which the species was present relative to the total number of quadrats from each lake type (shown as percent), for species found in open, inundated, and closed lakes during years of flooding (F) and non-flooding (N) in the emergent and submergent vegetation zones.

Species	Open		Inundated		Closed	
	F	N	F	N	F	N
<b>Emergent species</b>						
<i>Arctophila fulva</i>	17.2	0	2.3	0	0	0
<i>Calla palustris</i>	0	0	0	0	7.8	1.8
<i>Carex aquatilis</i>	4.1	3.3	23.9	5	15.6	10.7
<i>Carex limosa</i>	0	0	0	0	14.2	21.4
<i>Carex rostrata</i>	0	5.0	0	0	0	0
<i>Cicuta mackenzieana</i>	0.8	0	3.4	0	2.8	0
<i>Eleocharis palustris</i>	0	0	0	0	0.7	0
<i>Equisetum fluviatile</i>	61.5	38.3	44.3	75.0	2.1	3.6
<i>Glyceria maxima</i>	0	23.3	0	10	0	0
<i>Hippuris vulgaris</i>	0.8	0	4.5	5.0	0.7	1.8
<i>Menyanthes trifoliata</i>	0	0	14.8	0	27.0	34.0
<i>Potentilla palustris</i>	0	0	6.8	0	6.4	7.1
<i>Sparganium hyperboreum</i>	0	0	0	0	12.8	10.7
<i>Sparganium multipedunculatum</i>	15.6	30.0	0	5.0	0	0
<i>Typha latifolia</i>	0	0	0	0	9.9	8.9
<b>Submersed plant species</b>						
<i>Callitriche hermaphroditica</i>	0.6	3.2	0	0	0	0
<i>Ceratophyllum demersum</i>	11.8	11.3	2.7	0	0.9	0
<i>Lemna minor</i>	0.6	0	0	0	0	0
<i>Lemna trisulca</i>	0.6	0	0	0	0	0
<i>Myriophyllum spicatum</i>	0	25.9	1.4	23.5	11.5	15.9
<i>Nuphar polysepalum</i>	0	0	0	0	0.9	11.4
<i>Nymphaea tetragona</i>	0	0	0	0	1.8	2.3
<i>Polygonum amphibium</i>	24.7	1.6	5.4	11.8	0	0
<i>Potamogeton alpinus</i>	1.2	0	0	0	1.8	0
<i>Potamogeton Berchtoldi</i>	1.8	0	0	0	3.5	0
<i>Potamogeton foliosus</i>	0	0	6.8	0	5.3	0
<i>Potamogeton Friesii</i>	0	0	1.4	0	0.9	0
<i>Potamogeton gramineus</i>	29.4	6.5	18.9	0	3.5	0
<i>Potamogeton natans</i>	0	0	0	0	17.7	36.4
<i>Potamogeton pectinatus</i>	2.4	11.3	2.7	0	0	6.8
<i>Potamogeton perfoliatus</i>	1.2	29.0	5.4	47.1	13.3	13.6
<i>Potamogeton zosterifolius</i>	7.1	11.3	13.5	0	9.7	0
<i>Utricularia vulgaris</i>	18.8	0	41.9	17.6	29.2	13.6

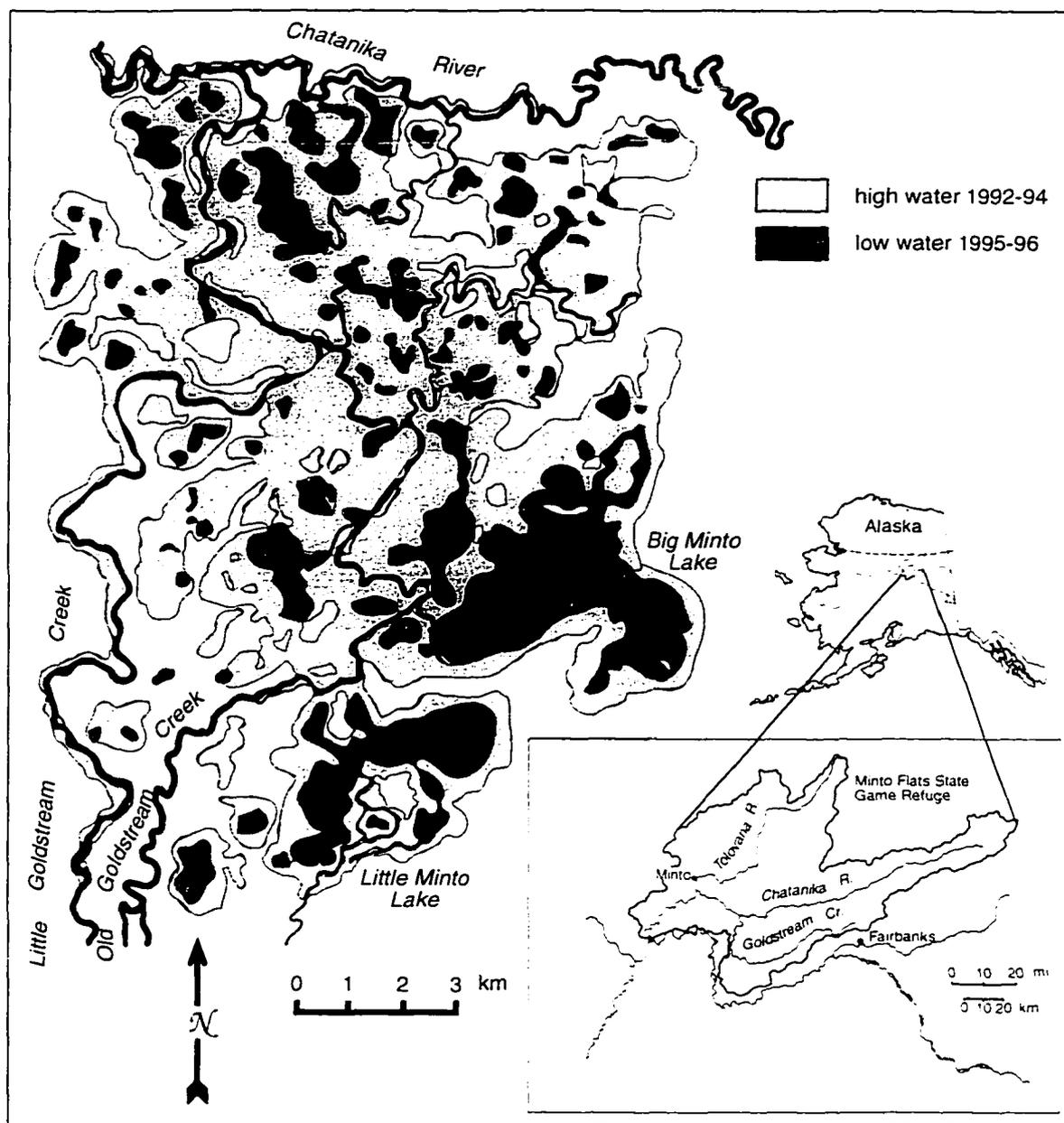


Figure 1. Study site map of the lakes at Minto Flats, Alaska. Different degrees of shading indicate years of high and low water level.

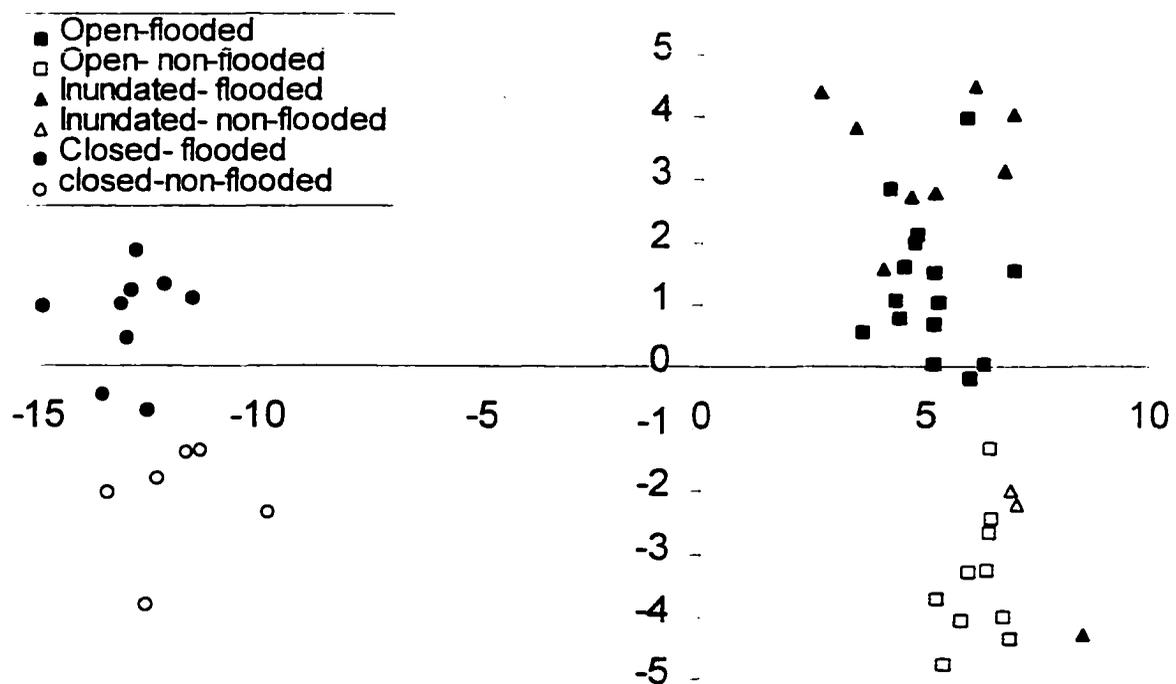


Figure 2. Map of the distribution of each lake based upon canonical discriminant function 1 (x-axis), which separates open and inundated lakes from closed lakes, and by discriminant function 2 (y-axis), which separates flooded from non-flooded years.

## OVERALL CONCLUSIONS

### **A conceptual model of macrophyte biomass**

Using data and information presented in each of the three chapters of my thesis I was able to construct a model (Figure 1) that depicts the relationships between wetland macrophytes and climate and hydrology. This model will hopefully serve as a framework upon which future experiments will be developed to test the various relationships and interactions between macrophytes and their environment. The remaining paragraphs represent a description of the model (with supporting evidence) and links to secondary producers.

Brylinsky and Mann (1973) documented the negative relationship between phytoplankton production and latitude. Their research showed that latitude and mean annual air temperature were the two most important energy-related variables in explaining global variation in phytoplankton productivity. Other variables (on-site summer temperature, length of growing season, and winter extremes) have been shown to be more predictive of terrestrial production than latitude or mean annual air temperatures (Viereck and Van Cleve, 1984). Latitude essentially integrates the effects of day-length, length of the growing season, incident solar radiation, geochemical weathering, and annual temperature into a single variable that can not be experimentally manipulated. My data suggest that July mean temperature (a surrogate for on-site summer temperature) is a better predictor of macrophyte biomass in arctic and subarctic wetlands than latitude. This is in agreement with Billings and Mooney (1968) who concluded that Arctic

ecosystems are temperature-limited systems. My data and data shown by Brylinsky and Mann (1973) have established the link between primary production (in aquatic ecosystems) and climate. Furthermore, it would be much easier to manipulate temperature than the bollix of other variables associated with latitude to experimentally test these relationships.

Nutrient availability has also been shown to be important in predicting phytoplankton production. Schindler (1978) showed that global patterns of phytoplankton production were better explained by net annual phosphorus input into lakes than by energy-related variables such as latitude. On a regional level, Brylinsky and Mann (1973) also concluded that nutrient availability assumes a greater importance in explaining patterns in primary production of phytoplankton than energy-related variables. Although phosphorus was an important nutrient in explaining variation in emergent and submersed plant biomass in Alaska, the relationships were opposite of those found by Shindler (1978) and Brylinsky and Mann (1973). Submerged plant biomass tended to be greater where sediment P was the least, and emergent plant biomass was greatest in lakes with the lowest orthophosphate. I have suggested that submerged macrophytes are acting as a net nutrient sink, removing readily available sediment P and storing it in aboveground biomass. The negative relationship between emergent plant biomass and orthophosphate may be due to the increase in surface area (increased emergent plant biomass) on which biofilm (epiphytic periphytes, bacteria, and fungi) grows, which in turn removes orthophosphate proportionally.

Primary productivity of phytoplankton has repeatedly been found to be positively correlated with alkalinity (Hayes and Anthony, 1964, Carlander, 1955). Sand-Jensen (1983) showed that before reaching maximum photosynthetic rates under light-saturated conditions, submersed plants became carbon limited. I hypothesize that carbon limitation may occur in arctic and subarctic wetlands where long summer day-lengths, and subsequently high photosynthetic rates, combined with reduced nocturnal respiration limit carbon availability.

My results suggest that subarctic freshwater wetlands, much like northern prairie wetlands, are highly dynamic. Species composition in open and inundated lake systems changed in response to flooding. The diverse composition of the seed bank in northern prairie wetlands is thought to enable changes in species composition over time and with water level (van der Valk and Davis, 1978) and there are likely parallels in subarctic wetlands.

Based on the results of my research, hydrology also had a direct impact on emergent plant biomass and water and sediment chemistry. Heavy winter precipitation is responsible for flooding major rivers in Alaska (Ford and Bedford, 1987), which causes water levels to change within wetlands adjacent to these rivers. The response of plants in the lakes at Minto Flats to flooding disturbance parallels the zonation patterns of freshwater marshes (i.e., growth response to flooding was greatest in plants occupying the most xeric habitats and least in the most hydric habitats). Water level changes influenced not only macrophyte biomass but also water and sediment chemistry. In addition to

changes in plant biomass with changes in hydrology, species composition also varied with hydrologic connectedness (lake type) and flood regime.

### **A comparison of Macrophyte biomass in subarctic and arctic wetlands of Alaska**

In general, plant biomass is considerably greater in subarctic freshwater wetlands than in arctic wetlands. Overall emergent plant biomass was two to three times higher at Minto than in arctic wetlands ( $200 \text{ g} \cdot \text{m}^{-2}$ ) (Alexander et al., 1980). It is difficult to compare biomass of submersed vegetation in subarctic wetlands to that in arctic wetlands because the biomass of submersed plants has not been measured in the arctic. Emergent and submersed plant biomass at Minto is comparable to that in more temperate regions. At Eagle Lake, a prairie glacial marsh in Iowa emergent plant biomass is  $503\text{-}637 \text{ g} \cdot \text{m}^{-2}$  (van der Valk and Davis, 1978), and submersed plant biomass is  $200 \text{ g} \cdot \text{m}^{-2}$  (van der Valk and Bliss, 1971). Long summer day-lengths appear to compensate for the reduced length of the growing season in subarctic Alaska. Nutrient inputs from past gold-dredge mining and rapid nutrient cycling by waterfowl serve to fertilize lakes at Minto. This high nutrient availability in Minto Flats lakes possibly reduces the limitation to growth of wetland plants likely often experienced in other subarctic and arctic ecosystems with lower nutrient availability.

### **Final comments**

The information presented in this thesis provides the background information necessary for future research. The model itself presents a labyrinth of questions that can now be tested experimentally. Understanding the factors determining productivity of

subarctic wetland vegetation is critical in understanding trophic interactions within these complex ecosystems. Moreover, understanding the role that macrophytes play in the detrital food web by annually contributing large quantities of energy to the detrital economy of the lake is critical in understanding wetland trophic interactions.

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Figures

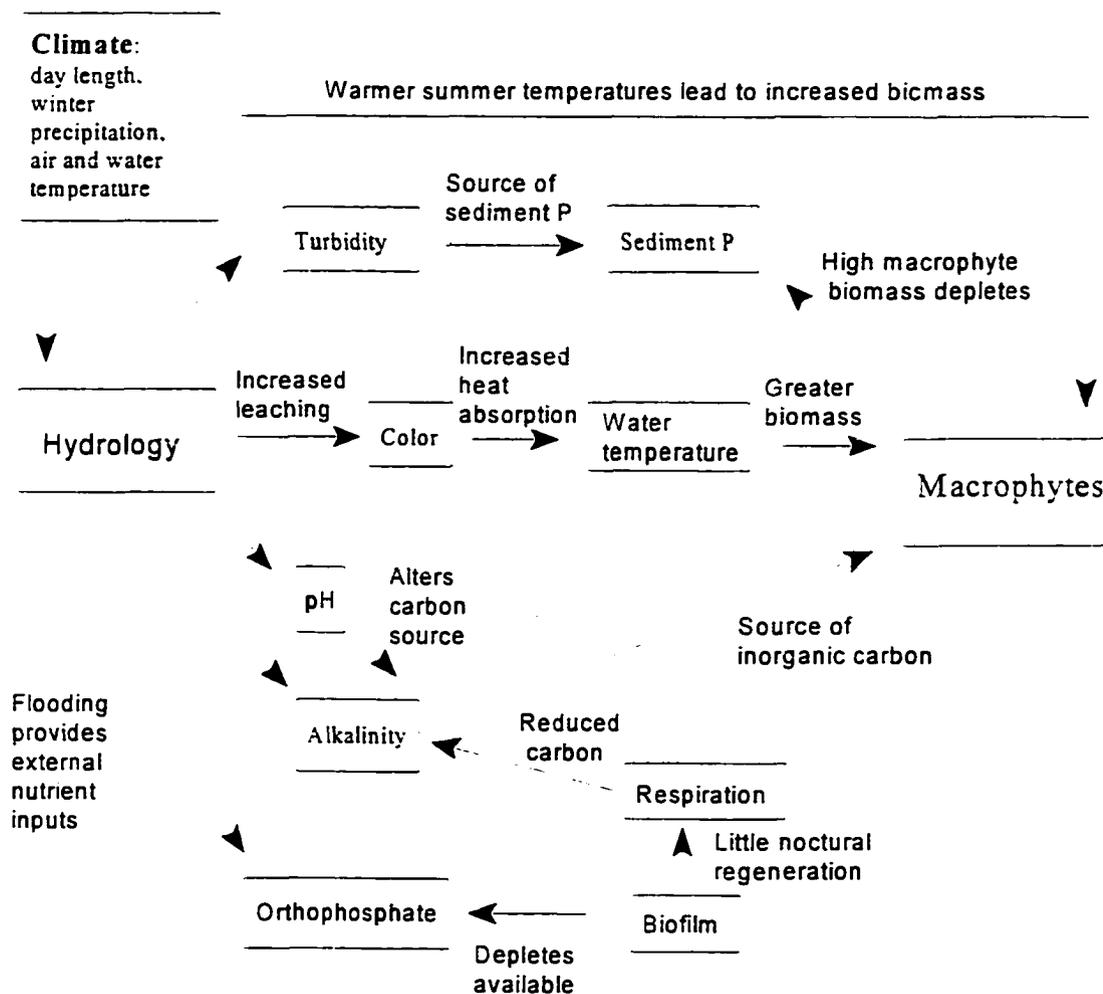


Figure 1. A conceptual model of the interactions between macrophytes and climate, hydrology, and water and sediment chemistry.