

2015-01-01

Monitoring And Understanding Decadal Scale Changes In Hydrology, Productivity And Carbon Balance In Arctic Tundra Ponds

Christian Gerardo Andresen

University of Texas at El Paso, cgandresen@gmail.com

Follow this and additional works at: https://digitalcommons.utep.edu/open_etd



Part of the [Climate Commons](#), and the [Environmental Indicators and Impact Assessment Commons](#)

Recommended Citation

Andresen, Christian Gerardo, "Monitoring And Understanding Decadal Scale Changes In Hydrology, Productivity And Carbon Balance In Arctic Tundra Ponds" (2015). *Open Access Theses & Dissertations*. 1198.
https://digitalcommons.utep.edu/open_etd/1198

This is brought to you for free and open access by DigitalCommons@UTEP. It has been accepted for inclusion in Open Access Theses & Dissertations by an authorized administrator of DigitalCommons@UTEP. For more information, please contact lweber@utep.edu.

MONITORING AND UNDERSTANDING DECADEAL SCALE CHANGES
IN HYDROLOGY, PRODUCTIVITY AND CARBON
BALANCE IN ARCTIC TUNDRA PONDS

CHRISTIAN GERARDO ANDRESEN

Environmental Science and Engineering Doctoral Program

APPROVED:

Vanessa Lougheed, Ph. D., Chair

Craig E. Tweedie, Ph. D.

Jose M. Hurtado, Ph. D.

Michael L. Moody, Ph.D.

Charles Ambler, Ph.D.
Dean of the Graduate School

Copyright ©

by

Christian G. Andresen

2014

MONITORING AND UNDERSTANDING DECADEAL SCALE CHANGES
IN HYDROLOGY, PRODUCTIVITY AND CARBON
BALANCE IN ARCTIC TUNDRA PONDS

by

CHRISTIAN GERARDO ANDRESEN, B.Sc.

DISSERTATION

Presented to the Faculty of the Graduate School of
The University of Texas at El Paso
in Partial Fulfillment
of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

Environmental Science and Engineering Doctoral Program

THE UNIVERSITY OF TEXAS AT EL PASO

December 2014

Acknowledgements

This research project was accomplished with the input and support of many people. First, the guidance and help of my graduate advisor and friend, Dr. Vanessa L. Lougheed, was incommensurable. I would not have accomplished this dissertation without her guidance and support; thank you for making me the scientist and person that I am today, I will always be indebted. Second, I would like to thank my family for all their moral support, in particular to my parents, Karsten Juan Andresen and Maria de los Angeles Soto, I am truly blessed for having them as my parents. Also, thanks to my dissertation committee: Dr. Tweedie, Dr. Hurtado and Dr. Moody for their insight and feedback. To my UTEP colleagues Sergio A. Vargas, Dr. Mark J. Lara, Dr. Sandra Villarreal, Dr. David Lin and Ryan Cody for sharing great moments and always being there at times of urgent need. Acknowledgements to my lab and field assistants Frankie Reyes, Christina Hernandez, Nicole Gallegos, Gabriela Tarin-Contreras, David Hernandez and Mariana Vargas for their help with thousands of samples and long days of work. In addition, I would like to recognize John E. Hobbie, Vera Alexander and all the International Biological Program (IBP) tundra ponds team from the 1970s for producing invaluable historical research records on which a significant portion of this study was based.

This project was funded almost entirely by the National Science Foundation (NSF), through both an NSF Graduate Research Fellowship and the Louis Stokes Alliance for Minority Participation (LSAMP) NSF bridge-to-the-doctorate fellowship. Also thanks to Dr. Diana Natalicio, a person that I deeply admire, for her economic support at the final stage of this dissertation through the Dr. Natalicio Presidential Dissertation Fellowship. The NSF grant ARC-0909502 to Dr. Lougheed also provided financial support for travel to and lodging in Barrow, AK, undergraduate assistants and lab supplies. Finally, I am grateful to CH2MHill Polar Services, UMIAQ and BASC for their logistical field support.

Dissertation Abstract

The Arctic is known for containing large stocks of soil organic carbon, which exists frozen in permafrost in a greenhouse inert state. With predicted future warming in these high northern latitudes, the mobilization of stored soil organic carbon and release to the atmosphere may increase and induce further positive climatic feedbacks. Previous studies have shown that Arctic wetlands and ponds cover a large percentage of the Arctic Coastal Plain and contribute large amounts of carbon to the atmosphere; however, it remains largely unknown how these systems are responding to a warming climate and how this change will impact regional carbon budgets. Therefore, it is of urgent interest to better assess and monitor the effects of climate change on Arctic wetlands and their role in the fate and transport of carbon to the atmosphere.

The overall focus of this dissertation is to identify decade time scale changes in the structure and function of Arctic tundra ponds, to understand how these changes are driven by warming and nutrient enrichment, and to advance new technologies to remotely track environmental change. Specifically, this study aims to:

- Assess decadal time scale changes in surface hydrology of tundra wetland ponds and its relationship with landscape geomorphological evolution.
- Determine decadal time scale changes in methane emissions through modeling of environmental drivers of methane efflux from aquatic vegetation.
- Develop and evaluate novel near-surface remote sensing tools for monitoring phenology and productivity of Arctic aquatic macrophytes.
- Investigate the impacts of nutrient enrichment on Arctic aquatic plant productivity and spectral properties.

Our study was carried out on the Arctic coastal plain, more specifically on the Barrow Peninsula, Alaska. This region is underlain by continuous permafrost and dominated by drained thaw lake basins

containing numerous wetland ponds. The comparison of historical aerial imagery from 1948 to modern high resolution satellite imagery revealed a net decrease in area and number of ponds. This contradicts geomorphological succession processes in the Arctic coastal plain and provides evidence that climate change can reverse millennial-scale processes affecting landscape evolution and surface energy balance for this region.

During the summers of 2010-2013, re-sampling of historical research sites established in the 1970's demonstrated a deepening of the active layer and an increase in aboveground biomass and cover of the dominant aquatic plants *Carex aquatilis* and *Arctophila fulva*. This is attributed to an increase in nutrients and warmer, longer growing seasons. Plant-mediated methane efflux was observed to be a function of thaw and water depth for *C. aquatilis* and plant biomass for *A. fulva*. Based on the increase in biomass and thaw depth, we modeled past and present methane emissions and estimated an increase efflux of 240% for *C. aquatilis* and 80% for *A. fulva* over the past 40 years. Although both plant species only cover 11% of the land surface in the Barrow peninsula, we found that they account for approximately 78% of the total estimated methane emissions for this region. These results emphasize the effects of climate change on soil-atmosphere methane emissions and the importance of *C. aquatilis* and *A. fulva* as key species for methane efflux.

Timing and intensity of plant primary production and phenology has implications for land-atmosphere carbon exchange. The need for high-frequency monitoring of plant phenology and productivity in Arctic wetlands motivated the development of a novel technology that employs digital repeat photography as a near-surface remote sensing method to track seasonal plant biomass and phenology. We took advantage of the red, green and blue (RGB) color space of commercial digital cameras to estimate seasonal greenness based on a multi-channel RGB index. Digital repeat photography observations at 9 sites over 4 growing seasons (2010-2013) revealed (i) interannual variation in greening, (ii) species-specific and (iii) site-specific greening patterns. Nutrient availability

and temperature determined the timing and magnitude of aquatic plant green-up. This novel automated method proven to be a reliable and cost-effective alternative for continual monitoring of productivity in aquatic plants, important for assessing carbon and energy balance in arctic wetlands.

Nutrient release from thawing permafrost and warming soils likely has significant effects on primary productivity in aquatic systems and thus, carbon exchange. However, no studies have assessed how Arctic aquatic plants vary in nutrient status among sites with different levels of nutrient enrichment, and how this may impact spectral responses important for remote sensing monitoring. We sampled water, plant and soil nutrients as well as plant biomass and spectral reflectance in (i) relatively pristine reference ponds and (ii) urban and thermokarst ponds as our nutrient enriched sites. Multivariate analyses indicated that measures of greenness were strongly related to gradients in nutrient enrichment and plant nutrients.

Combined these findings reveal substantial changes in the structure and function of Arctic tundra ponds over the past 40 or more years, which have major implications for carbon efflux as thawing of permafrost continues enriching aquatic ecosystems. They also demonstrate the utility of remote sensing technologies, including novel near-surface methods, in monitoring key components of Arctic tundra ecosystems such as: pond extent and productivity.

Table of Contents

Acknowledgements.....	iv
Dissertation Abstract	v
List of Tables	x
List of Figures.....	xi
Chapter 1: Introduction.....	1
1.1. Rationale for this dissertation	1
1.2 Current research challenges.....	8
1.3 Goals and objectives	9
1.4 Study area	10
1.5 Structure of this Dissertation	12
Chapter 2: Disappearing Arctic tundra ponds: Fine-scale analysis of surface hydrology in drained thaw lake basins over a 65 year period (1948-2013).....	13
2.1 Abstract.....	13
2.2 Introduction.....	14
2.3 Methods	16
2.4 Results.....	21
2.5 Discussion.....	30
2.6 Conclusion	35
Chapter 3: Decadal changes in thaw depth and aquatic emergent macrophyte biomass in Arctic tundra ponds: Implications for methane flux.....	37
3.1 Introduction.....	37
3.2 Methods	38
3.3 Results.....	44
3.4 Discussion.....	51
3.5 Conclusion	56
Chapter 4: Applications of digital repeat photography to track seasonal plant phenology and biomass of aquatic plants in Arctic wetlands.....	57
4.1 Introduction.....	57
4.2 Data and Methods	58
4.3 Results.....	63
4.4 Discussion.....	69

4.5 Conclusion	74
Chapter 5: The relationship between nutrient enrichment of Arctic aquatic plants and their biomass and optical properties.....	76
5.1 Introduction.....	76
5.2 Methods	77
5.3 Results.....	80
5.4 Discussion.....	85
5.5 Conclusion	89
Chapter 6: General Discussion	90
6.1 Key research findings	90
6.2 Broader implications.....	92
6.3 Future Research Priorities.....	94
References.....	95
Biographical Sketch.....	108

List of Tables

Table 1. Imagery details.	18
Table 2. Average pond area and number for the DTLB analyzed.	24
Table 3. Correlation coefficients (r) between climatic factors and biomass and thaw depth (n=6 years). ..	48
Table 4. Summary of modern (2010-2013) peak-season plot-based means of CH ₄ controlling factors and modeled CH ₄ flux (C-CH ₄ mg m ⁻² hr ⁻¹) for the Barrow Peninsula by plant species. Uncertainty estimates represent 95% confidence intervals.	50
Table 5. Location and classification of sites sampled in this study. Plant types include <i>Arctophila fulva</i> (A) and <i>Carex aquatilis</i> (C).	59
Table 6. Summary of sites sampled in this study	78
Table 7. Nutrients and detection limits analyzed from live plant tissue.	79
Table 8. Range of environmental variables by vegetation type from 17 ponds in Barrow and Atkasuk, Alaska. p-values are for paired t-test between <i>Arctophila fulva</i> and <i>Carex aquatilis</i>	81
Table 9. Correlation coefficients between PC axes and leaf nutrients for <i>Carex aquatilis</i> (right) and <i>Arctophila fulva</i> (left).	84
Table 10. PC axes correlations with environmental variables.	85

List of Figures

Figure 1. (Left) Map of the upper Barrow Peninsula depicting DTLB analyzed in this study colored by geomorphic age. (Right) Oblique aerial view of the polygonal landscape inside the IBP DTLB.	17
Figure 2. Example of inter-annual variability in pond area and number at the IBP site (71°17'N, 156°41'W) from 1948-2013. White contours indicate pond margins.....	21
Figure 3. Net change in pond area (top) and number (bottom) over the study period.	22
Figure 4. Frequency distribution of pond sizes (<10,000m ²) for the initial (1948) and the last year (2010) of analysis.	22
Figure 5. Comparison of medium, old and ancient DTLB with respect to (a) total pond area (2010 only), (b) number (2010 only), (c) percent change in pond area (1948 versus 2010), (d) percent change in pond numbers (1948 versus 2010) (statistical differences indicated at p<0.05, Tukey HSD).	23
Figure 6. Comparison of area estimates made with detailed low-altitude KAP and satellite-based imagery.	25
Figure 7. (Top) Typical pond profile from IBP Pond J in mid-August (mean of 2010-13 ± SE) indicating areas covered with <i>Carex aquatilis</i> , <i>Arctophila fulva</i> and open water, along with the pond area delineated in this study. (Bottom) detail aerial image with satellite-based pond delineation (white line) and pond profile transect (black line).	26
Figure 8. Average pond area change through time, based on multiple analyses of seven historical IBP tundra ponds. Data includes delineation of satellite and aerial imagery, published estimates by Miller et al., (1980) and delineation of low-altitude KAP images.	27
Figure 9. Comparison of water and thaw depths between 1970's and 2010's across a polygon transect in IBP Pond C in late August.....	28
Figure 10. Relationship between surface area lost (1948-2010) and average water depth for 7 IBP tundra ponds.....	28

Figure 11. Trendlines for summer (July-August) (a) average temperature ($p < 0.001$) and (b) total precipitation ($p > 0.05$) between 1949 and 2013 for Barrow Alaska (data source: Alaska Climate Research Center).	29
Figure 12. Study area and ponds sampled in this study. Historical sites were re-sampled for biomass, thaw depth and water depth. Synoptic sites distributed across the Barrow region were sampled for comparative purposes to IBP sites.	40
Figure 13. Allometric relationships between plant dry weight and morphological measurements for <i>A. fulva</i> (left) and <i>C. aquatilis</i> (right).	45
Figure 14. Relationship between predicted dry weight (measured by allometry) and harvested dry weight for <i>C. aquatilis</i> and <i>A. fulva</i> plots (20x50cm). A 1:1 relationship is illustrated by the solid black line. Dashed lines indicate regression lines for <i>C. aquatilis</i> (small dashes) and <i>A. fulva</i> (large dashes).	45
Figure 15. Comparison of weekly seasonal aboveground dry weight biomass (\pm SE) between 1970's and 2010's for <i>A. fulva</i> and <i>C. aquatilis</i> at three sites (IBP Pond 10, C, J).	47
Figure 16. Repeat photography (1976-2012) depicting increased cover of <i>A. fulva</i> off the dock in IBP Pond J. Historical photo courtesy of Dr. Malcolm Butler (North Dakota State University).	47
Figure 17. Regression models developed for <i>A. fulva</i> (left panel) and <i>C. aquatilis</i> (right panel), for retrogressive analysis. Uncertainty ranges correspond to 95% confidence intervals.	49
Figure 18. Modeled CH ₄ flux (\pm 95% CI) comparison between <i>C. aquatilis</i> and <i>A. fulva</i> in 1970s and 2010s of historic ponds sites and 2010's in ponds across the Barrow region.	50
Figure 19. Near-surface, oblique camera mounted on a tripod facing north towards IBP Pond J (left) and a sample photo taken from this system (right) in early summer 2010.	62
Figure 20. Average seasonal GEI trends of 2013 reference sites for <i>C. aquatilis</i> and <i>A. fulva</i> and environmental characteristics. Seasonal photographs are for site IBP Pond 10 (2013), with <i>A. fulva</i> (left) and <i>C. aquatilis</i> (right) of each image.	65

Figure 21. Multi-annual (2010-2013) seasonal patterns in GEI of <i>Carex aquatilis</i> and <i>Arctophila fulva</i> measured in multi-annual sites using digital repeat photography.	66
Figure 22. Responses of GEI and NDVI to aboveground dry biomass for <i>Arctophila fulva</i> (circles) and <i>Carex aquatilis</i> (triangles).	67
Figure 23. .Seasonal variability of average GEI among site types for <i>Carex aquatilis</i> (top) and <i>Arctophila fulva</i> (bottom) in 2013.	68
Figure 24. Multi-annual (2010-2013) daily average temperature effects on daily average GEI observations of sites (Pond-C, Pond-J and Pond-10) for (a) <i>Carex aquatilis</i> and (b) <i>Arctophila fulva</i> . Vertical solid lines represent the threshold points of greening, as determined by regression trees, while dashed horizontal lines are the means for each partition.	69
Figure 25. Relationship between dry weight aboveground biomass of <i>Carex aquatilis</i> (left) and <i>Arctophila fulva</i> (right) with P content of leaves. <i>Arctophila fulva</i> Biomass = $46.519361 + 839.79717 * P\% \text{ Leaves}$ ($r^2=0.32$, $p=0.04$). <i>Carex aquatilis</i> Biomass = $-13.80174 + 1103.8418 * P\% \text{ Leaves}$ ($r^2=0.37$, $p=0.02$).	82
Figure 26. Plots of PCA site scores for <i>Carex aquatilis</i> (left) and <i>Arctophila fulva</i> (right) plant nutrient data. Environmental variables associated to each axes are depicted along dashes lines.	84

Chapter 1: Introduction

1.1. RATIONALE FOR THIS DISSERTATION

It has been well documented that atmospheric greenhouse gases play a key role in global radiative forcing with the potential to alter the state of the earth's climate (IPCC 2007). Increasing trends of atmospheric greenhouse gases over the past few decades have been attributed to anthropogenic activities. Consequently, global atmospheric and oceanic average temperatures have increased (IPCC 2007) changing the global system with the most pervasive effects in higher northern latitudes, particularly in the Arctic (ACIA 2005).

The Arctic has changed dramatically over recent decades as a result of the amplification of global warming. Between 1875 and 2008, Arctic temperature has warmed 1.6 times the rate of lower latitudes (Bekryaev et al. 2010) unraveling a multitude of substantial environmental effects including: thinning and melting of the sea ice and polar ice sheets (Stroeve et al. 2007), warming and thawing permafrost (Osterkamp and Romanovsky 1999, Shiklomanov et al. 2010), changes in surface hydrology (Smith et al. 2005, Carroll et al. 2011, Bouchard et al. 2013) and increased biomass and primary productivity (Bhatt et al. 2010, Walker et al. 2012b, Epstein et al. 2012). The Arctic region is characterized by containing a significant portion of the global stores of soil organic carbon (Tarnocai et al. 2009). With increasing temperatures, the future state of this organic carbon pool is of concern given the implications of its potential release to the atmosphere enhancing future positive warming feedbacks (Schaphoff et al. 2013, Schuur et al. 2013). Therefore is of urgent concern assess any changes in the Arctic system that may alter future climatic feedbacks.

To advance the knowledge on the complexity and sensitivity of the Arctic system to climate change and to better predict its future state, it is necessary to understand this system over decadal time scales. The use of historical records provides a unique opportunity to address long-term changes in ecosystem structure and function (Callaghan et al. 2011, Lara et al. 2012, Villarreal et al. 2012) and its

relationship with climate change. In addition, the development of new technology to track environmental change, allows more accurate observations of these remote and enigmatic systems (Stow et al. 2004). This study explores decadal time scale changes in structure and function in Arctic wetlands and develops new tools to remotely monitor and understand these systems.

1.1.1 Arctic ecosystems are changing

The Arctic is spatially defined by its location north of 66.5 °N latitude, and characterized by its low temperatures due to the relatively low levels of solar radiation compared to equatorial regions. The Arctic Ocean is surrounded by several continents whose northern terrestrial systems are dominated by tundra underlain by continuous permafrost. This Arctic system is spatially and temporally complex with all components interrelated and interconnected (Figure 1) both within the Arctic itself and to the global system. Some of the most widespread and impactful changes in this system have to do with a reduction in the extent of sea ice and permafrost.

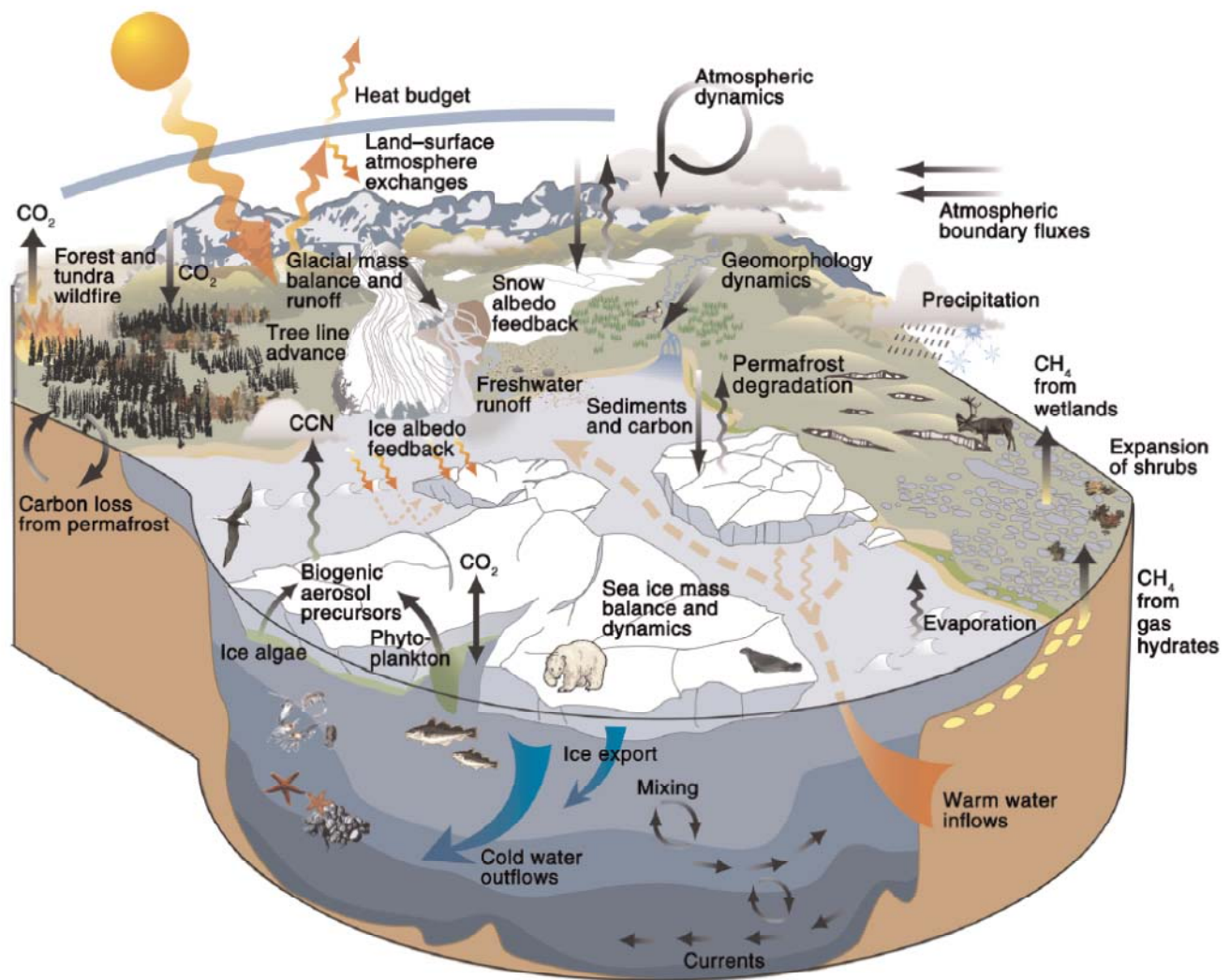


Figure 1. The complex Arctic system is strongly influenced by feedbacks from each subsystem as well as from global processes (from Hinzman et al. 2013).

Satellite data has shown that Arctic sea ice extent has been declining considerably over the past decade (Stroeve et al. 2007). 2012 showed the lowest sea ice extent on record since 1979, with the past 8 years having the lowest extents during that same time period (source: NSIDC). This reduction in sea ice will continue to decrease albedo and consequently increase warming of the Arctic Ocean, thus promoting a positive feedback with further reduction of sea ice extent. This phenomenon also shows a strong association with change in Arctic terrestrial coastal systems (Wendler et al. 2009, Bhatt et al. 2010).

Similarly to sea ice extent, permafrost is beginning to warm and thaw across its range in the Arctic region (Osterkamp and Romanovsky 1999, Schuur et al. 2008), with most notable changes along

coastal Arctic areas (Romanovsky et al. 2010). The thawing of permafrost has resulted in a wide range of ecosystem-level responses including changes in plant community structure and function (Sturm et al. 2001, Lara et al. 2012, Villarreal et al. 2012), thermokarst and talik events (Yoshikawa and Hinzman 2003), leaching of nutrients (Reyes and Lougheed n.d., Frey and McClelland 2009) and surface hydrology (Smith et al. 2005, Arp et al. 2011).

1.1.2 Surface hydrology

Hydrology in the Arctic plays a key role in surface energy balance (Liljedahl et al. 2011), land-atmosphere carbon fluxes (Torgersen and Branco 2008, Zona et al. 2009, Lara et al. 2012), geomorphic processes (Hinkel et al. 2003, Yoshikawa and Hinzman 2003, Arp et al. 2011), and ecosystem structure and function (Lara et al. 2012, Villarreal et al. 2012). Hydrology is strongly influenced by patterns of freeze and thaw in the Arctic, where lakes and ponds form within thaw depressions in the landscape. Consequently, greater than one-half of the Arctic coastal plain landscape in north Alaska is dominated by thaw lakes and drained thaw lake basins (DTLB) (Frohn et al. 2005b, Wang et al. 2012), which often contain numerous tundra ponds (Hinkel et al. 2003). With warming temperatures, permafrost degradation along with the intensification of the hydrological cycle (Rawlins et al. 2010), may increase freshwater discharge to the ocean (Lawrence and Slater 2005), increase the relative importance of sub-surface flow paths (Frey and McLelland, 2009), release stored soil nutrients into freshwater environments (Hobbie et al. 1999, Frey and Smith 2005, Schindler and Smol 2006a, Frey et al. 2007, Keller et al. 2007, 2010, McClelland et al. 2007, Lougheed et al. 2011b, Lewis et al. 2012) and continue to shape lake and pond distribution and thus the Arctic landscape (Andresen and Lougheed accepted, Smith et al. 2005, Riordan et al. 2006).

1.1.3 Changes in ecosystem structure and function of Arctic tundra ponds

Productivity in Arctic tundra vegetation is generally constrained by temperature, light and nutrients (Chapin et al. 1975, Chapin, FS et al. 1995, Shaver et al. 1998). The observed circum-arctic plant biomass increase over recent decades has been attributed to warming temperatures (Bhatt et al. 2010) but the direct and indirect effects of temperature on productivity remains unclear. Experimental studies have indicated that nutrients, not temperature, promoted greening and higher production of biomass (Shaver et al. 1998, Boelman et al. 2003). Most of the existing studies have focused on non-aquatic systems; however, in Arctic freshwaters there may be a stronger link between warming and nutrient enrichment and these drivers of production may be difficult to elucidate.

Wet tundra macrophyte communities are one of the most productive landscape units in the Arctic but have also undergone among the most dramatic changes in recent times (Lara et al. 2012, Villarreal et al. 2012, Lin et al. 2012). For example, Lin et al (2012) found an overall increase of dry and moist communities and a decrease of open water over the past 60 years in the Barrow area. This change can be associated with substantial impacts on effluxes of carbon from the landscape and increased nutrient content of associated water bodies. For example, even a short-term pulse in nutrient release from sediment or water has the potential to substantially increase algal production in high latitude environments (Eichel et al. 2014).

Arctic wetlands are known to be responsible for significant contribution of carbon fluxes to the atmosphere, especially methane (Reeburgh and Whalen 1992), a significant greenhouse gas with a warming potential 25 times greater than CO₂. Recently, methane in Arctic wetlands has been noted to be controlled by surface hydrology (e.g. water depth) (Kutzbach et al. 2004), active layer thickness (von Fischer et al. 2010) and aquatic vascular plant biomass. Aquatic graminoids, in particular, have been recognized to regulate methane flux in wetlands by acting as a methane transport pathway from the soil to the atmosphere through aerenchyma, or air channels, in their stems. However, few studies have

addressed the role of Arctic aquatic plants in methane emissions and species-level regional contributions have been not quantified.

1.1.4 Ecology of *Carex aquatilis* and *Arctophila fulva*

In the Arctic coastal plain, the dominance of ponds and lakes provides habitat for several vascular aquatic emergent plants. In particular, wetlands on the Barrow Peninsula contains aquatic rooted plants such as *Carex aquatilis*, *Arctophila fulva* and *Ranunculus palasii* (McRoy and Leue 1973); however, *C. aquatilis* and *A. fulva* are the most abundant aquatic species in the Barrow area (Hobbie 1980, Villarreal et al. 2012). These perennial species usually grow in pure stands and are the most important primary producers in Barrow tundra ponds (McRoy and Leue 1973). They are adapted to local conditions of short growing season (2-3 months) and cold temperatures (4 °C summer average) with the ability to photosynthesize and translocate carbohydrates at similar rates compared to temperate plants (Tieszen 1973). Both *C. aquatilis* and *A. fulva* contain aerenchyma, an internal air conduit within the vegetative organs, acting as a gas pathway facilitating CH₄ diffusion from anoxic soils (Kutzbach et al. 2004). Recently, these species have gained attention as important soil-atmosphere CH₄ pathway in ponds (von Fischer et al. 2010, Lara et al. 2012)

C. aquatilis (Wahlenb) is known for its wide distribution across the northern hemisphere including the Arctic and boreal regions. This sod-forming perennial water sedge (Cyperaceae family) usually occurs in monoculture stands, arising singly or in groups connected by thick, long rhizomes forming extensive systems of interconnected tillers. This species inhabits riparian habitats such as streams, lakes and ponds. *C. aquatilis* is adapted to cold temperatures as low as -20 °C and can be found from sea level to over 3,350 m in elevation (Chapin, FS and Chapin 1981). In the Barrow area, *C. aquatilis* grows in all polygon microhabitats (Shaver et al. 1979) and, in the 1970s, accounted for approximately 25-40% of the vascular plant production of the Barrow community (Tieszen 1972). In

contrast to *C. aquatilis* in other microhabitats, *C. aquatilis* in ponds contained the highest leaf sugar (glucose-equivalents) production rates and green-leaf weight, suggesting a high degree of carbon-fixing capacity (Shaver et al. 1979).

A. fulva (Trin.), commonly known as pendant grass (Poaceae family), is a tall emergent perennial aquatic grass with a wide distribution across Arctic and Boreal regions. It is known for growing in shallow, standing water or wet meadows often forming pure stands and prefers areas with limited competition by other species (Dobson 1989). *A. fulva* is characterized by having larger leaves at the top of the plant compared to the base and its distinctive reddish green coloration (Aiken and Buck 2002). In the Arctic, *A. fulva* inflorescences have been found to lack viable seeds in its northern limits (Kreivi et al. 2005) including northern Alaska (Dobson 1989). This species generally spreads clonally from perennial underground rhizomes and is known to re-grow from apparently dead, previous season's culms (Dobson 1989). It has been suggested that the main dispersal mechanism by *A. fulva* in its northern limits is by floating fragments of rhizomes and culms moved by water and wave action (Kreivi et al. 2005). In the Barrow area, *A. fulva* has been identified for its high methane efflux as compared to other vegetation types (Lara et al. 2012). This phenomenon is likely a result of its habitat preference inside ponds rich in organic soils and its structural morphology which is characterized by large air spaces in both shoots and rhizomes (Aiken and Buck 2002).

These two aquatic plant species have been found to be the most sensitive to change over the past decades in the Barrow area, as compared to vegetation in moist and dry land cover types (Villarreal et al. 2012, Lin et al. 2012). For example, Villarreal et al. (2012) observed an increase in cover of aquatic *C. aquatilis* over the past 40 years and a concurrent decrease in diversity, in particular bryophytes, in aquatic *Carex* graminoid community. Similarly, *A. fulva* was noted to increase in cover among aquatic communities by 20-25 % over recent decades in the Barrow area (Villarreal et al. 2012). However, the

factors responsible for these increases are largely unknown and their study is of importance as they are coupled with changes in ecosystem function (Lara et al. 2014).

1.1.4 Recent advances in remote sensing ecosystem monitoring

The use of remote sensing has revolutionized the monitoring of ecosystems from local to global scales. In particular, remote sensing has been widely employed to understand Arctic vegetation responses to climate change including monitoring of above ground biomass, plant community structure, distribution and phenology (Walker 2003, Boelman et al. 2003, Stow et al. 2004, Verbyla 2008, Epstein et al. 2012). Multispectral indices have been developed and highly utilized to characterize specific vegetation properties. The Normalized Difference Vegetation Index (NDVI) is the most commonly used vegetation index for assessing photosynthetic capacity and aboveground biomass in Arctic systems (Jia 2003, Stow et al. 2004, Zeng and Jia 2013). Satellite imagery is the most commonly used and diverse remote sensing platform. However, satellite observations are often limited temporally and spatially, mainly by the continuous cloud cover in the Arctic region. Recently, the integration of multilevel remote sensing in other ecosystems such as aerial and near-surface techniques have proven to greatly improve spatial and temporal sampling. Therefore, it is imperative to test these remote sensing tools in the Arctic landscape to better characterize the effects of climate change on polar ecosystems.

1.2 CURRENT RESEARCH CHALLENGES

Given its rapid warming compared to the southern ecosystems and its significant role in global climatic feedbacks (Wendler et al. 2002, Cornelissen et al. 2007), research in the Arctic is of urgent concern. More specifically, there is an increasing need to understand how Arctic aquatic systems are responding to global change, the drivers of change in these predominant landscape units, and the implications of any alterations to the systems at local to global levels. The Arctic is a relatively slow-growing ecosystem where changes in ecosystem structure and function can take several decades to be

observed and monitoring ecosystem change can be difficult without long-term datasets. Most studies that addressed climate effects in Arctic ecosystems are typically based in experimental settings (Chapin, FS et al. 1995, Shaver et al. 1998, Boelman et al. 2003, Mack et al. 2004) or based on remote sensing (e.g. Bhatt et al. 2010) with a high degree of uncertainty given the diversity and complexity of environmental factors involved in ecosystem changes. Furthermore, the Arctic system has a high degree of year-to-year environmental variability mainly associated to interannual climatic variation. Structural (Villarreal et al. 2012, Lin et al. 2012) and functional (Lara et al. 2012) studies have shown that multi-annual variability can be problematic when comparing long-term datasets and careful examination of the climate record and multi-year sampling is required to avoid inter-annual uncertainty. Therefore there is an urgent need to rescue and revisit historical research sites, and use other long-term fine-scale data resources, to better assess long-term ecosystem structural and functional changes.

1.3 GOALS AND OBJECTIVES

This study addresses the following overarching question:

“How have surface hydrology, productivity, and carbon fluxes in arctic ponds changed in response to climate change over decadal time scales”

The overall focus of this dissertation is to identify decadal time scale changes in the structure and function of Arctic tundra ponds, to understand how these changes are driven by warming and nutrient enrichment, and to advance new technologies to remotely track environmental change. Specifically, this study aims to:

- Assess decadal time scale changes in surface hydrology of tundra wetland ponds and its relationship with landscape geomorphological evolution.
- Determine decadal time scale changes in methane emissions through modeling of environmental drivers of methane efflux from aquatic vegetation.

- Develop and evaluate novel near-surface remote sensing tools for monitoring phenology and productivity of Arctic aquatic macrophytes.
- Investigate the impacts of nutrient enrichment on Arctic aquatic plant productivity and spectral properties.

1.4 STUDY AREA

This study was completed on the northern Barrow peninsula, on the Outer Arctic coastal plain of Northern Alaska (Frohn et al. 2005b, Wang et al. 2012), within and near the village of Barrow, AK, USA (Figure 2). The area is characterized by its strong maritime climate influenced by the Arctic Ocean (Wendler et al. 2002) and is underlain by continuous permafrost and shallow active layer (Streletskiy et al. 2007). This region has been generally described by Brown et al. (1980) and Hinkel et al. (2003). The Barrow area represents a flagship for Arctic studies with research initiated in the 1940's at the Naval Research Laboratory. Since that time, innumerable environmental studies have documented important regional features, such as plant community structure (Villarreal et al. 2012, Lin et al. 2012), ecosystem function (Zona et al. 2009, von Fischer et al. 2010, Lara et al. 2012), hydrology (Hinkel et al. 2007, Liljedahl et al. 2011), geomorphology (Hinkel et al. 2003, Wang et al. 2012), aquatic ecology (Lougheed et al. 2011) and climate (Wendler et al. 2009). There is, however, conflicting information on how cover of lakes and ponds will change with permafrost degradation (e.g. Smith et al. 2005, Riordan et al. 2006, Hinkel et al. 2007, Plug et al. 2008, Labrecque et al. 2009, Sannel and Kuhry 2011, Jones et al. 2011, Carroll et al. 2011). Understanding of the relationship between permafrost, climate and surface hydrology is an ongoing challenge and future further research need.

Despite the fact that about 22% of the land area on the Arctic Coastal Plain is covered with lakes, and more than 65% is marked by former lake basins filled with ponds (Hinkel et al. 2003; Frohn et al. 2005), relatively little limnological research has occurred in Barrow since the late 1970s. Small ponds less than one hectare, in particular, remain poorly studied despite their predominance in the landscape

and have unique characteristics. Physically, they are small (30 x 40 m), shallow (<0.5 m deep) ponds occupying low-centered ice wedge polygons and surrounded by wet tundra within a large thaw-lake basin. Pond margins are dominated by the aquatic graminoids *Carex aquatilis* and *Arctophila fulva*. Ponds freeze to the bottom each winter and thaw for only a few months in summer (Stross et al. 1980), when water from snow melt fills the ponds and flows between them for only a few days in spring. During the summer, most water is lost from the ponds through evaporation; however, this is largely balanced by precipitation. Ponds are characterized by circumneutral pH, low conductivity and dissolved gasses near saturation (Sheath, 1986; Hobbie 1980). Recent studies revisited tundra ponds first sampled in the 1970s as part of the International Biological Program (IBP) and reported increases in water temperature, phosphorus, nitrate, ammonia, and algal biomass over the past 40 years (Lougheed et al. 2011a). In addition to these changes in nutrients, tundra pond margins have experienced large increases in macrophyte cover in recent decades (Lougheed et al. 2011a, Villarreal et al. 2012, Lin et al. 2012).

Specific study and sampling locations are later described in each chapter of this dissertation.

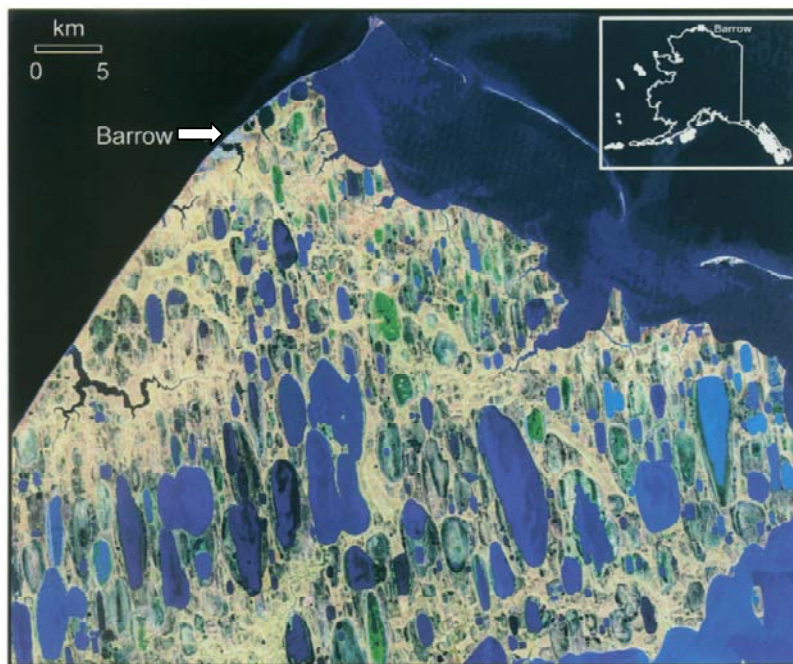


Figure 2. Satellite image of the Barrow peninsula located in the outer coastal plain of northern Alaska (adapted from (Hinkel et al. 2003)).

1.5 STRUCTURE OF THIS DISSERTATION

The dissertation presented in this manuscript is composed of a total of six chapters, where four chapters (2-5) are composed of distinct technical datasets (Table 1). The author of this dissertation (Christian G. Andresen) is the lead author and analyst of each chapter presented in this document. In addition to the work presented in this dissertation, the author has contributed to different manuscripts as a co-author including two Arctic land-cover change studies (Lin et al., 2012, Tweedie et al., in prep), one aquatic nutrient limitation study (Lougheed et al submitted) and one remote sensing methodological note (Andresen et al. 2014).

Table 1. Publication status of the chapters presented in this study.

Chapter	Title and planned publications
1	Introduction C. G. Andresen No submission intended
2	Disappearing Arctic tundra ponds: Fine-scale analysis of surface hydrology in drained thaw lake basins over a 65 year period (1948-2013). Authorship: C. G. Andresen, V. L. Lougheed Journal: Journal of Geophysical Research, Biogeosciences Accepted with revisions (Nov. 2014)
3	Decadal changes in thaw depth and aquatic emergent macrophyte biomass in Arctic tundra ponds: Implications for methane flux. Authorship: C. G. Andresen, M. J. Lara, C. E. Tweedie, V. L. Lougheed Target Journal: Global Change Biology Estimated date of submission: January 2015
4	Applications of digital repeat photography to track seasonal plant phenology and biomass of aquatic plants in Arctic wetlands. Authorship: C. G. Andresen, C. E. Tweedie, V. L. Lougheed Target Journal: Ecological Applications
5	The relationship between nutrient enrichment of Arctic aquatic plants and their biomass and optical properties. Authorship: C. G. Andresen, V. L. Lougheed Target Journal: Arctic, Antarctic and Alpine Research
6	Conclusion C. G. Andresen No submission intended

Chapter 2: Disappearing Arctic tundra ponds: Fine-scale analysis of surface hydrology in drained thaw lake basins over a 65 year period (1948-2013).

2.1 ABSTRACT

Long-term fine-scale dynamics of surface hydrology in Arctic tundra ponds less than one hectare is largely unknown; however, these small systems may contribute substantially to carbon fluxes, energy balance and biodiversity in the Arctic system. The combination of rare historical imagery and historic field datasets provides a unique opportunity for understanding long-term changes in hydrology of these small but significant freshwater systems. Change in pond area and abundance across the upper Barrow Peninsula, Alaska was assessed by comparing historic aerial imagery (1948) and modern sub-meter resolution satellite imagery (2002, 2008, 2010). Photogrammetric analysis was aided by field observations (2010-2013) of pond water and thaw depth transects and seasonal low-altitude aerial imagery in 7 ponds of the International Biological Program (IBP) historic research site. Over 2,800 ponds in 22 drained thaw lake basins (DTLB) with different geological ages were analyzed. We observed a net decrease of 30.3% in area and 17.1% in number of ponds over the 62 year period. The inclusion of field observations of pond areas in 1972 from a historic research site confirms the linear downward trend in area. Pond area and number were dependent on the age of DTLB; however, changes through time were independent of DTLB age, contradictory to the hypothesized geomorphologic landscape succession of the thaw lake cycle. These losses were coincident with increases in air temperature, active layer and density and cover of aquatic emergent plants in ponds. Increased evaporation due to warmer and longer summers, permafrost degradation and transpiration from encroaching aquatic emergent macrophytes are likely the factors contributing to the decline in surface area and number of ponds.

2.2 INTRODUCTION

The Arctic coastal plain landscape in north Alaska is dominated by thaw (thermokarst) lakes and associated drained thaw lake basins (DTLB) (Frohn et al. 2005b, Wang et al. 2012) containing numerous tundra ponds (Hinkel et al. 2003). However, little is known about the surface hydrology of Arctic tundra ponds over the past century, when unprecedented changes in climate have been observed for this region (IPCC 2007, Duarte et al. 2012, Hinzman et al. 2013). Ponds are excellent indicators of climate change given their hydrological isolation, small water volumes and large surface area-to-depth ratios (Riordan et al. 2006, Smol and Douglas 2007). Furthermore, hydrology in the Arctic landscape, in particular surface water area, is a fundamental aspect governing ecosystem structure (Villarreal et al. 2012), function (Zona et al. 2009, Olivas et al. 2010, Lara et al. 2012) and energy balance (Liljedahl et al. 2011). Global Climate Models suggest that the hydrological cycle will intensify due to an increase of Arctic temperatures (Rawlins et al. 2010) greatly affecting these systems, which will be key in understanding future climatic feedbacks. Therefore, understanding of changes in surface hydrology in response to a changing climate is imperative.

Previous long-term analyses of changes in lake and large pond hydrology across the Arctic and boreal regions have shown differing trends. Several studies from areas of discontinuous and sporadic permafrost agree in a general reduction in area and number of ponds (Yoshikawa and Hinzman 2003, Smith et al. 2005, Riordan et al. 2006, Sannel and Kuhry 2011) mainly attributed to permafrost degradation, resulting in lateral and subsurface drainage. However, studies in deep, continuous permafrost are more ambiguous with diverse responses to the effects of climate including lake area increases (Smith et al. 2005, Jones et al. 2011), decreases (Carroll et al. 2011), both increases and decreases (Plug et al. 2008, Labrecque et al. 2009) or shows null or small changes (Riordan et al. 2006, Hinkel et al. 2007, Sannel and Kuhry 2011). This ambiguity can be attributed primarily to regional differences in climate and geomorphology (i.e. water balance, permafrost ice content, etc.), but also to

differences in temporal and spatial scale of analyses, where different time periods can reflect distinct trends in area change (Plug et al. 2008) and waterbody size may determine responses (Labrecque et al. 2009, Jones et al. 2011).

Thaw lakes and basins are abundant landscape features across the Arctic in Alaska (Hopkins 1949, Frohn et al. 2005b, Wang et al. 2012), Canada (Mackay 1988, Plug et al. 2008, Marsh et al. 2009) and Russia (Grosse et al. 2008, Karlsson et al. 2012), and are hypothesized to form and cycle over thousands of years (Hopkins 1949, Carson and Hussey 1962, Billings and Peterson 1980). The thaw-lake cycle suggests that following drainage, water bodies will reform as a result of a progressive development of ponds in ice-wedge troughs and thermokarst. Thaw subsidence and wind-driven wave erosion continue to enlarge bodies of water resulting in the re-formation of a lake (Livingstone 1954, Hinkel et al. 2003, Jorgenson and Shur 2007). Wang et al. (2012) estimated a combined cover of 57% for thaw lakes and DTLB in the Arctic coastal plain in Alaska. Given that ponds in thaw lake basins represent a fundamental aspect of the thaw lake evolution, and therefore, the Arctic coastal plain landscape, it is imperative to assess any changes in these small ecosystems.

In the Arctic coastal plain, small closed-basin tundra ponds (< 1 ha) have been overlooked in terms of long-term hydrological change (i.e. Hinkel et al., 2007) and underestimated in surface hydrology inventories (i.e. Frohn et al., 2005; Wang et al., 2012), largely due to the inadequate image spatial resolution (e.g. Landsat, 30m) employed in analyses. *Hinkel et al.*, (2003) estimated less than 1% of area on the Barrow Peninsula, Alaska was covered by ponds smaller than 1 ha. However, field observations and preliminary spatial analyses suggest a greater coverage of these smaller water bodies in this region. Therefore, improvement in the spatial resolution is emphasized to adequately assess landscape surface hydrology.

Aerial imagery acquired in 1940's across the Barrow Peninsula, Alaska, is a rare example of very-high spatial resolution historical imagery and an invaluable tool for assessing long-term changes in

surface hydrology at the polygon level. In addition, recent advances in commercial satellite imagery (e.g. Quickbird, Worldview) has made available sub-meter resolution panchromatic imagery, which combined with historic aerial photographs, can provide new means to assess decadal-scale changes in surface hydrology of tundra ponds at a very fine spatial scale. The objectives of this study are to: (i) assess the long and short-term inter-annual spatial extent variability of tundra ponds, (ii) evaluate the role of DTLB age in these changes, (iii) help understand the biogeomorphological drivers of pond areal extent, and (iv) validate the methodology used in this study for pond delineation.

2.3 METHODS

2.3.1 Study Area

The study area is located in the upper Barrow peninsula within the Alaskan Arctic Outer Coastal Plain. It extends 300 km² north from Walakpa Bay and Iko Bay to the shores of Elson Lagoon and the Chukchi Sea. This relatively low-relief landscape (0-10m above sea level) is characterized by its deep continuous permafrost (>400 m) and a thin active layer (~0.3-0.4 m)(Brown et al. 1980). This area is dominated by DTLB (Hinkel et al. 2003, Wang et al. 2012) which can contain hundreds of closed-basin tundra ponds (see Figure 1). Winters are long and cold averaging -12°C, while summers are short and cool averaging 4°C. The mean annual precipitation averages 11 cm/year, with a snow pack of 20-40 cm/year (climate data from ACIS, 2013).

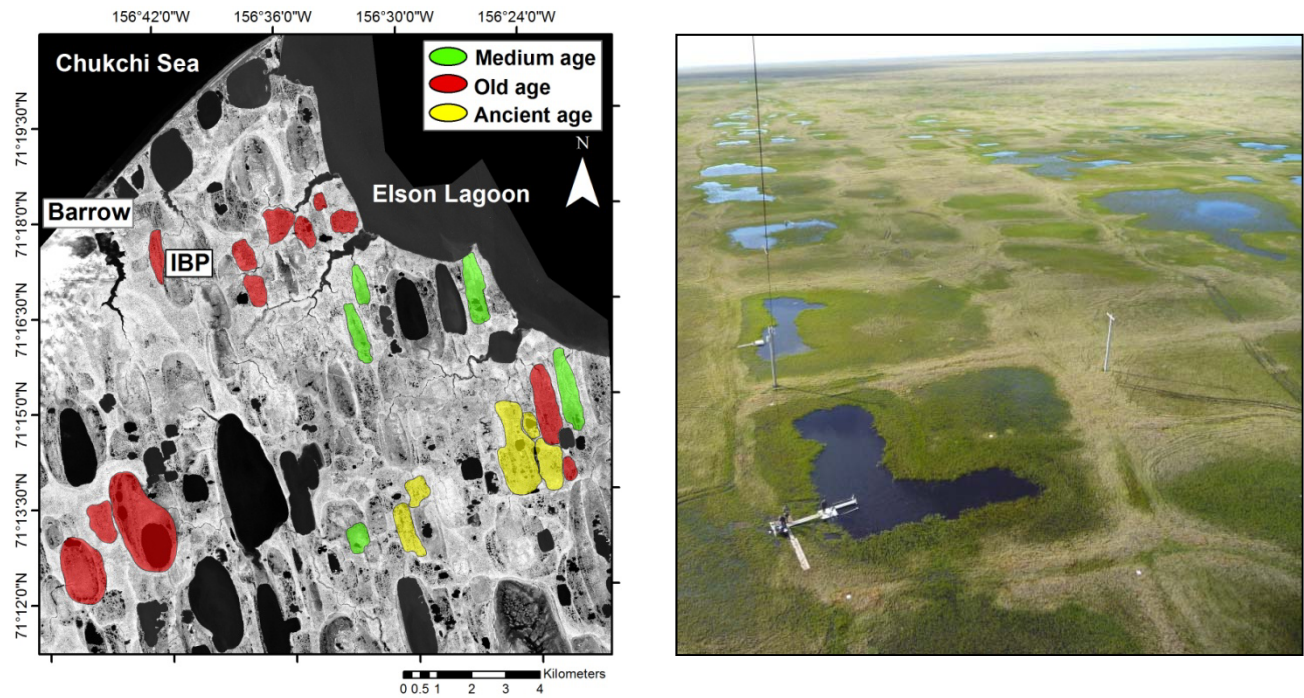


Figure 1. (Left) Map of the upper Barrow Peninsula depicting DTLB analyzed in this study colored by geomorphic age. (Right) Oblique aerial view of the polygonal landscape inside the IBP DTLB.

2.3.2 Image Analysis

To allow a quantitative interpretation of the spatial and temporal changes on the areal extent of Arctic ponds, we compared high spatial resolution historic aerial photographs to modern satellite imagery. Historical aerial black and white film photographs were scanned at 1200 dots per inch, with an output spatial resolution of approximately 0.7m/per pixel. Modern very-high-resolution panchromatic Quickbird and Worldview imagery was employed not only to assess the long-term change in surface water extent of ponds but to understand recent inter-annual variability in pond areas. All imagery including scanned historical imagery was re-sampled to a spatial scale of 0.7m and registered using a nearest neighbor second-polynomial-degree transformation to a rectified, ortho-corrected Quickbird scene maintaining a root mean square error (RMSE) < 1.0. The images used in this study were selected due to a) parallel acquisition dates, b) high-spatial resolution (0.5-0.7 m), c) common footprint d) and similar spectral qualities (Table 1).

Table 1. Imagery details.

Image year	Date	Sensor	Spatial resolution
1948	August 4 th	Aerial film, black and white	0.7 m
2002	August 2 nd	Quickbird Panchromatic	0.7 m
2008	July 30 th	Quickbird Panchromatic	0.7 m
2010	August 10 th	World-View Panchromatic	0.5 m

For consistency, all images were acquired during a 2-week period at the end of July – beginning of August, which corresponds to peak growing season in the region. The historic aerial imagery from 1948 is not only the oldest imagery on record for this area but has a broad areal coverage across the Barrow Peninsula with a very high spatial resolution suitable for this analysis. Although some additional historical images exist between 1948 and 2002, at least one of the following disadvantages made these data unsuitable for analyses: a) poor spatial resolution, which did not allow accurate delineation of the smaller and common ponds (<100 m²), b) early summer acquisition dates, which were not directly comparable to peak season images. The inclusion of multiple images acquired in recent years (2002, 2008, 2010) was made to account for any short-term interannual variability in pond area.

On the Barrow Peninsula, Arctic tundra ponds are well discerned features in the landscape and are characterized by a sharp edge and flat bottoms, and are dominated by *C. aquatilis* in the shallow marsh of pond margins and *A. fulva* in deeper water inside ponds (Villarreal et al. 2012). To delineate and extract the areal extent of ponds, we took advantage of clear differentiation of pond margins by sedges (e. g. *C. aquatilis*) during peak season and delineated deeper water where sedges are not found. *A. fulva*, growing in deeper water, was considered as part of pond area.

Pond delineation was performed using an object-oriented classification (a.k.a. feature extraction) in Environment for Visual Images Software (ENVI v4.2). Object oriented classification considers not only spectral properties in a scene, but the spatial heterogeneity of pixels resulting in clusters of pixels that form objects, in this case ponds. This method has been shown to improve accuracy and detail of classifications compared to single pixel classification (Laliberte et al. 2004) and has been used in

previous studies to extract lake and pond areas for Arctic systems (Frohn et al. 2005b, Jones et al. 2011, Wang et al. 2012, Karlsson et al. 2012). Each DTLB frame was processed employing the ENVI feature extraction extension with segmentation at a scale level of 45 and merging of 90. Pond areas were defined based on conservative threshold values from typical ponds sites. The vectors extracted from the automated object-oriented classification were reviewed and corrected for evident misclassifications and delineation errors in ArcGIS© v10. Although quality control has a high degree of subjectivity, human error was minimized by careful examination of pan-sharpened color Quickbird imagery or historical aerial photographs as reference, and corrections were performed by a single reviewer for consistency. We limited mapping to pond areas greater than a conservative 16 m² (44 pixels) to maintain precision.

We focused on closed-basin ponds contained in 22 DTLB (Figure 1), selected based on the quality of the historic imagery (e.g. cloud free, outside of photo vignetting areas). DTLB ages were extracted from Hinkel et al. 2003, and for the purpose of this study, we focused on medium, old and ancient DTLB given that young-age basins rarely contain ponds (Hinkel et al. 2003).

2.3.3 Delineation precision assessment

To assess the methodological precision of delineation of ponds, we calculated edge precision error (Persello et al. 2010) by comparing areas derived from the object-oriented classification to the areas from high resolution aerial photographs. The precision error, defined as the accuracy of reproducing the same geometry, was assessed using the edge location error equation in Persello et al. (2010) before review and correction was performed in delineations. The error value ranges from 0 to 1 where 0 error is a perfect geometric match.

High-spatial resolution (1-2cm), low-altitude (100-130m) RGB nadir-view images of 34 ponds (including the IBP site ponds, described below) in the study area were acquired between July 28th and August 6th in 2010 using a small-format kite aerial photography (KAP) system (Aber et al. 2006). Images acquired by KAP were geometrically registered using ground control points measured by

Differential Geographic Positioning System (DGPS). Although methodological validation of the object oriented classification was performed for 2010, we assumed the accuracy obtained will be comparable with the accuracy for the 1948, 2002 and 2008 imagery given identical image analysis.

2.3.4 Historical data and physical surveys

The historical International Biological Program (IBP) tundra ponds were studied in great detail in the early 1970s (Hobbie 1980) (Figure 1). To provide a mid-point surface area estimate between 1948 and 2002 images, we used estimates of areal extent determined by Miller et al., (1980) in 1972 at 7 IBP ponds. Miller et al., (1980) defined pond area as that extending from the open water into the flooded sedges “marsh” (presumably *C. aquatilis*) deeper than 10cm, which coincides with the area delineated in this study, as described below. In addition, KAP images were acquired from these same 7 ponds in late August 2010-2013, in order to provide additional evidence for changes in pond areal extent.

Cross-polygon transects of thaw depth and water depth were also completed every 2-m across multiple ponds in the early 1970s (Barsdate and Prentki 1973) and 2011-13 using a metal rod calibrated in cm. Here we present thaw depth and water depth data from IBP Pond C (71.2946 N, 156.70210 W) comparing historical data (August 1970-2) to current data (August 2011-3) collected using similar methods. We also present depth in IBP Pond J (71.293626 N, 156.70144 W) collected along a cross-polygon transect in August 2011-3. For the remaining 5 IBP ponds, average water depth was determined from a 5x5 m grid throughout each pond.

Climate data from the Barrow Airport (1949-2013) was retrieved from The Alaska Climate Research Center website (<http://climate.gi.alaska.edu/>). Climate data for the years 1945-1948 are missing for the Barrow Area (Alaska Climate Research Database).

2.4 RESULTS

2.4.1 Pond surface area change analysis

Pond delineation through time showed both a loss of pond area and number (Figure 2). A total maximum of 2,855 ponds covering more than 162.3 ha in 22 DTLB were identified in 1948 (Figure 3). Compared to 1948, we calculated an overall decrease of 29-31% in total pond area and a net decrease of 13-17% in number of ponds over a 54-62 year period. Minimal inter-annual change in area (3%) was observed between 2002, 2008 and 2010. Average pond size was 476 m², and the most dramatic change was seen in ponds smaller than 200 m² (Figure 4).

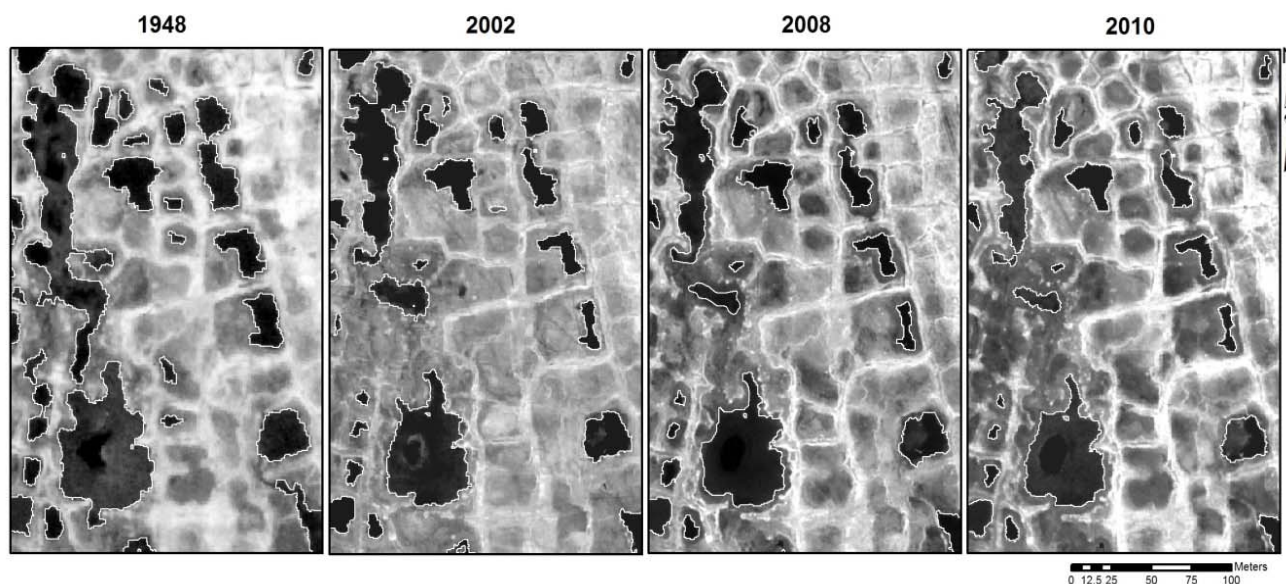


Figure 2. Example of inter-annual variability in pond area and number at the IBP site (71°17'N, 156°41'W) from 1948-2013. White contours indicate pond margins.

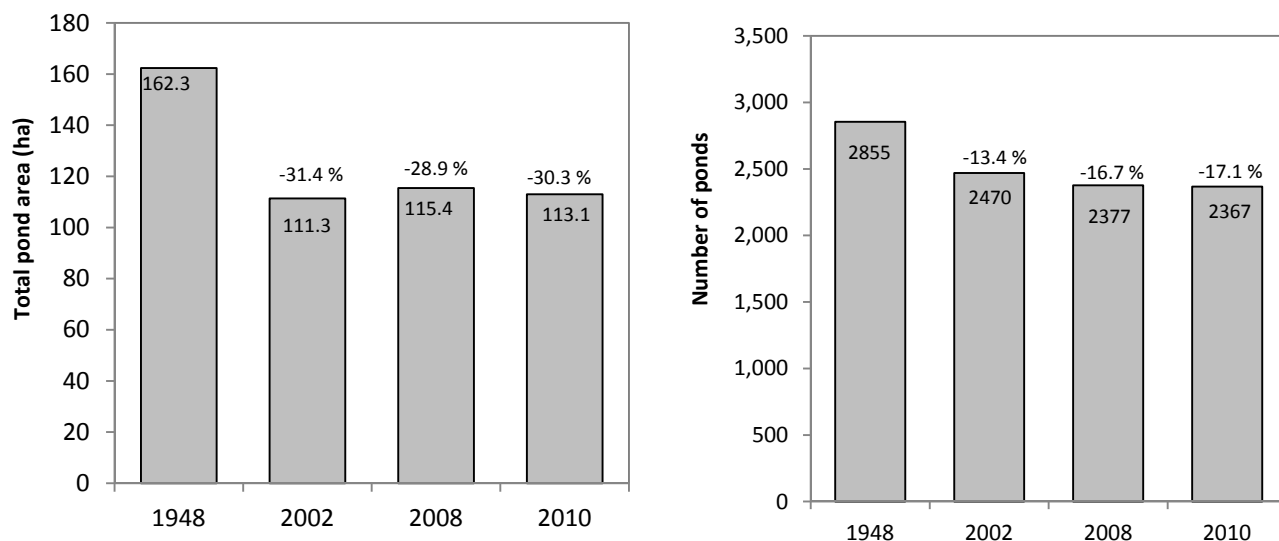


Figure 3. Net change in pond area (top) and number (bottom) over the study period.

Based on the combination of our average pond area and number estimates from 2010 and the DTLB age classification map from Hinkel et al. (2003), we estimate that approximately 50,000 ponds (< 1 ha) are located within DTLB on the Barrow Peninsula, accounting for approximately 3% of the total DTLB area and 1.9% of the Barrow peninsula.

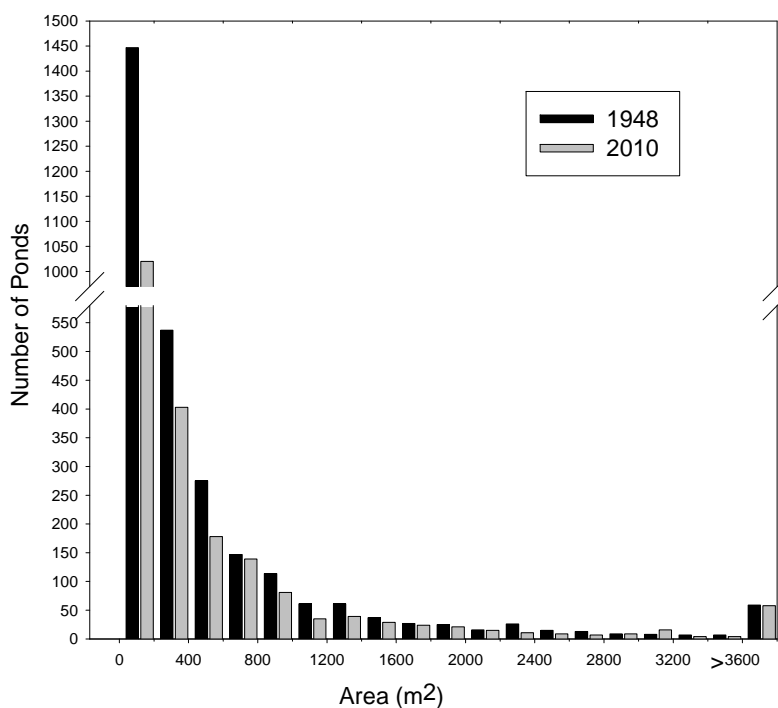


Figure 4. Frequency distribution of pond sizes (<10,000m²) for the initial (1948) and the last year (2010) of analysis.

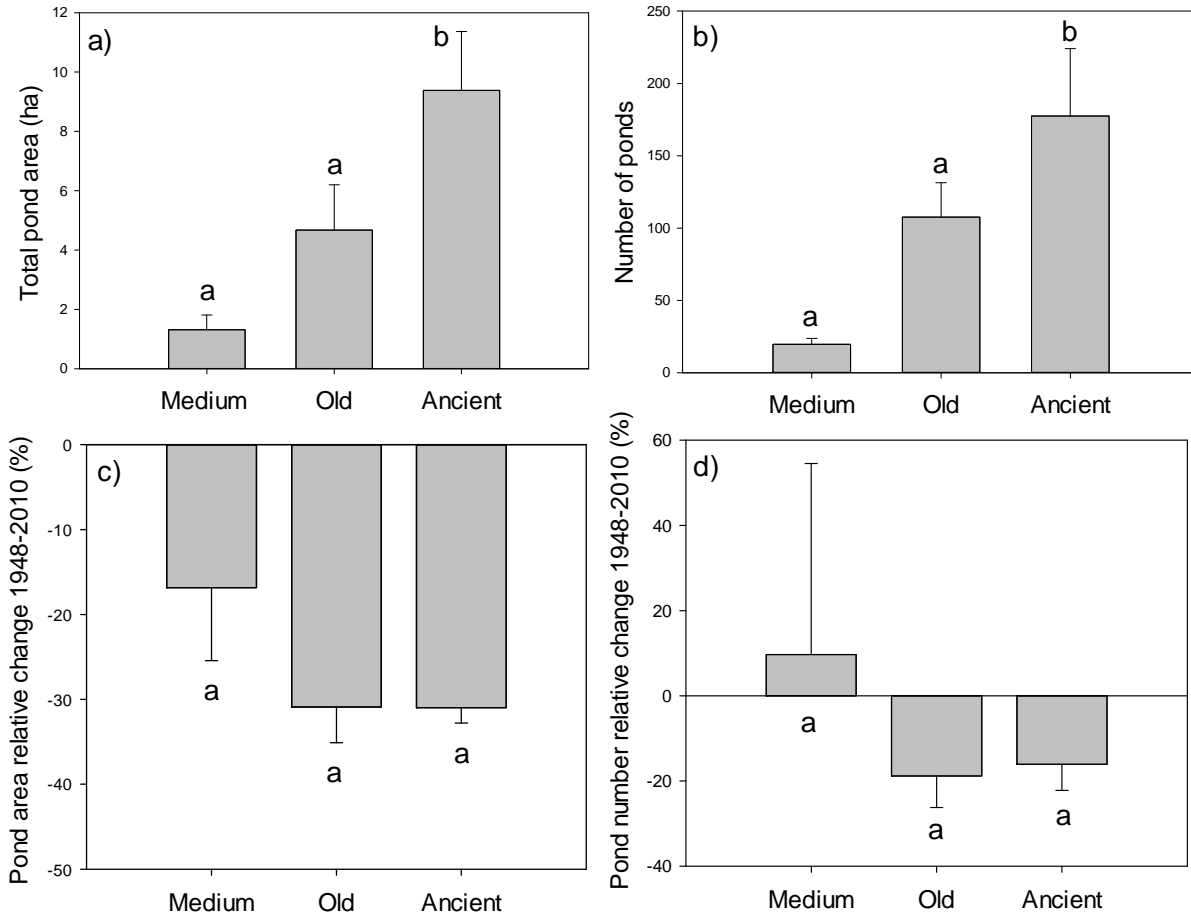


Figure 5. Comparison of medium, old and ancient DTLB with respect to (a) total pond area (2010 only), (b) number (2010 only), (c) percent change in pond area (1948 versus 2010), (d) percent change in pond numbers (1948 versus 2010) (statistical differences indicated at $p < 0.05$, Tukey HSD).

2.4.2 Effect of DTLB age

Analyzed DTLB areas ranged from 15.5 to 318.6 ha with a mean area value of 76.6 ha, and contained from 8 to 470 ponds with a mean of 108-130 per DTLB, depending on the year (Table 2). Total pond surface area (for water bodies <1.0 ha) varied from 0.7% to 17% of the total DTLB area with a mean of 8%. Larger DTLB tended to hold more ponds and a greater total ponded area. For 2010, there was a significant positive correlation of DTLB size with pond area ($r=0.62$, $p < 0.01$) and number of ponds ($r= 0.43$, $p < 0.05$). This relationship also held among past years.

In any given year, pond area and number were related to DTLB age. For example, in 2010 there was significantly greater cover and number of ponds in ancient basins compared to medium- and old-age DTLB (Figure 5a & 5b); similar trends were seen for all other study years. While the percent of total pond area decreased for all DTLB types over the period of study (Figure 5c), there was no significant difference in this percent change among medium, old and ancient DTLB. The number of ponds observed in old and ancient DTLB decreased by an average of 15-25% and, while there was a slight non-significant increase in ponds in medium-age DTLB, a high degree of variability in change in number of ponds was observed (Figure 5d).

Table 2. Average pond area and number for the DTLB analyzed.

Age	Number of DTLB	Average DTLB Area (ha)	Average net pond area (ha)				Average number of ponds			
			1948	2002	2008	2010	1948	2002	2008	2010
Medium	4	75.92	1.59	1.33	1.35	1.32	18	20	20	20
Old	13	75.39	6.77	4.45	4.76	4.68	133	113	108	108
Ancient	5	80.37	13.60	9.64	9.63	9.38	212	185	178	178
All Basins	22	76.62	7.38	5.06	5.25	5.14	130	112	108	108

2.4.3 Assessment of methodology

The comparison of satellite-based pond delineation with low-altitude KAP delineation from 34 ponds in 3 different DTLB revealed a good geometric accuracy with a mean precision error (edge location error) of 0.074 (or 7.4%). A statistical linear comparison also revealed a near-perfect relationship among the two methods (Figure 6).

Comparison of high-resolution KAP delineation to concurrent transect data indicated that the classification method clearly delineated the edge of the aquatic sedges (*C. aquatilis*) occurring at less than 10 cm depth (Figure 7a & 7b). On average, depth within the aquatic sedge (*C. aquatilis*) in this

pond was 4.5 cm, which was significantly lower than the water depth in both the *A. fulva* populations (16.2 cm) and open water (22.0 cm).

The downward trend in areal cover of ponds observed from satellite imagery is also supported by additional sources of data collected at IBP ponds, including ground-based historic area measurements from 1972 (Miller et al. 1980) and low-altitude KAP photography in 2011-2013 (Figure 8). The linear fit in Figure was used as a correction factor when comparing satellite to KAP-derived areas in Figure 8. Pond area in the IBP sites declined steadily by 3.8 m² per pond per year ($p < 0.001$, $R^2 = 0.24$), which corresponds to an average areal decrease of 0.5-1% per year or 39% change between 1948 and 2010. These values agree with the percent loss of similarly sized ponds throughout the upper Barrow peninsula.

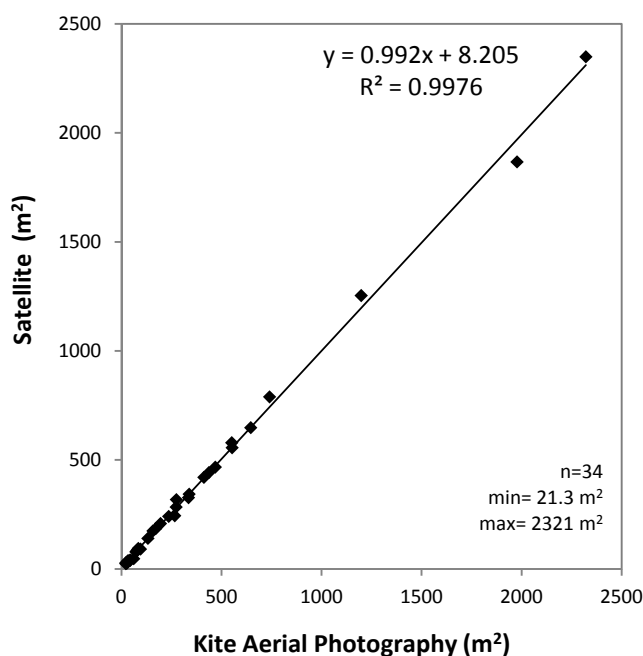


Figure 6. Comparison of area estimates made with detailed low-altitude KAP and satellite-based imagery.

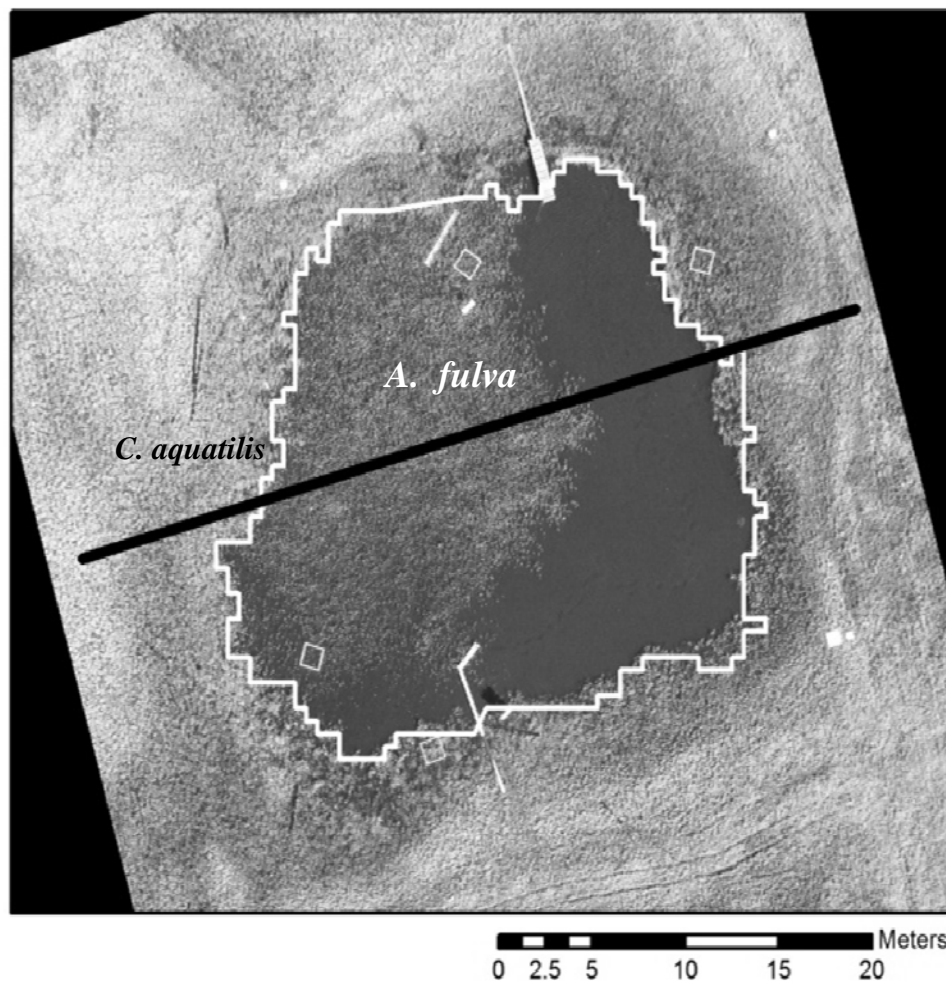
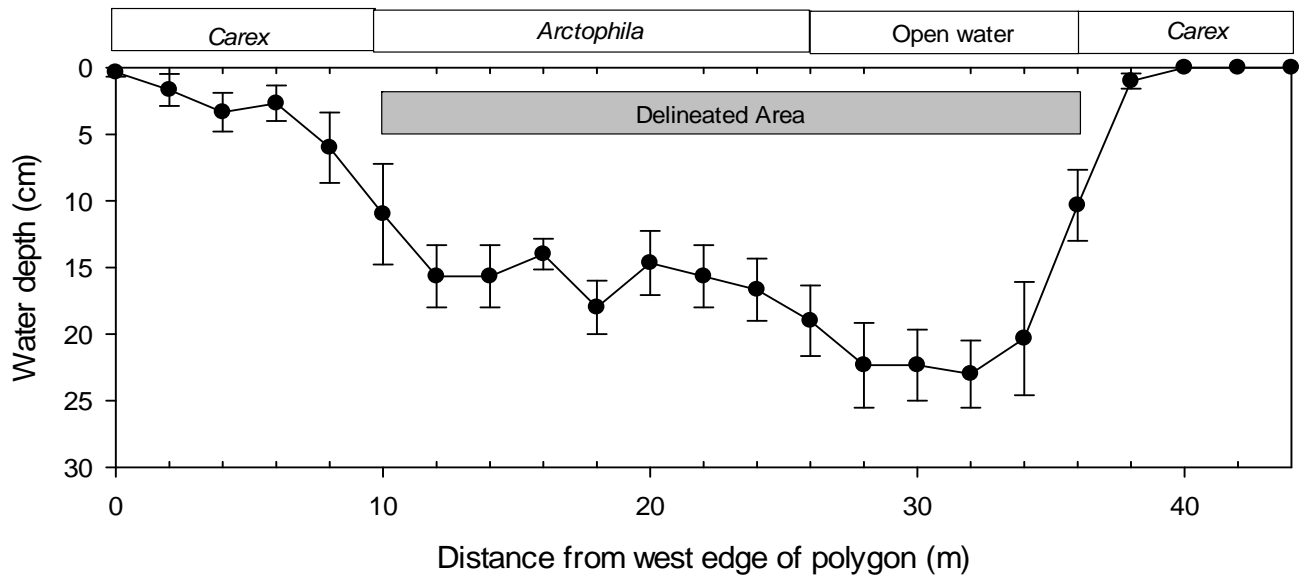


Figure 7. (Top) Typical pond profile from IBP Pond J in mid-August (mean of 2010-13 \pm SE) indicating areas covered with *Carex aquatilis*, *Arctophila fulva* and open water, along with the pond area delineated in this study. (Bottom) detail aerial image with satellite-based pond delineation (white line) and pond profile transect (black line).

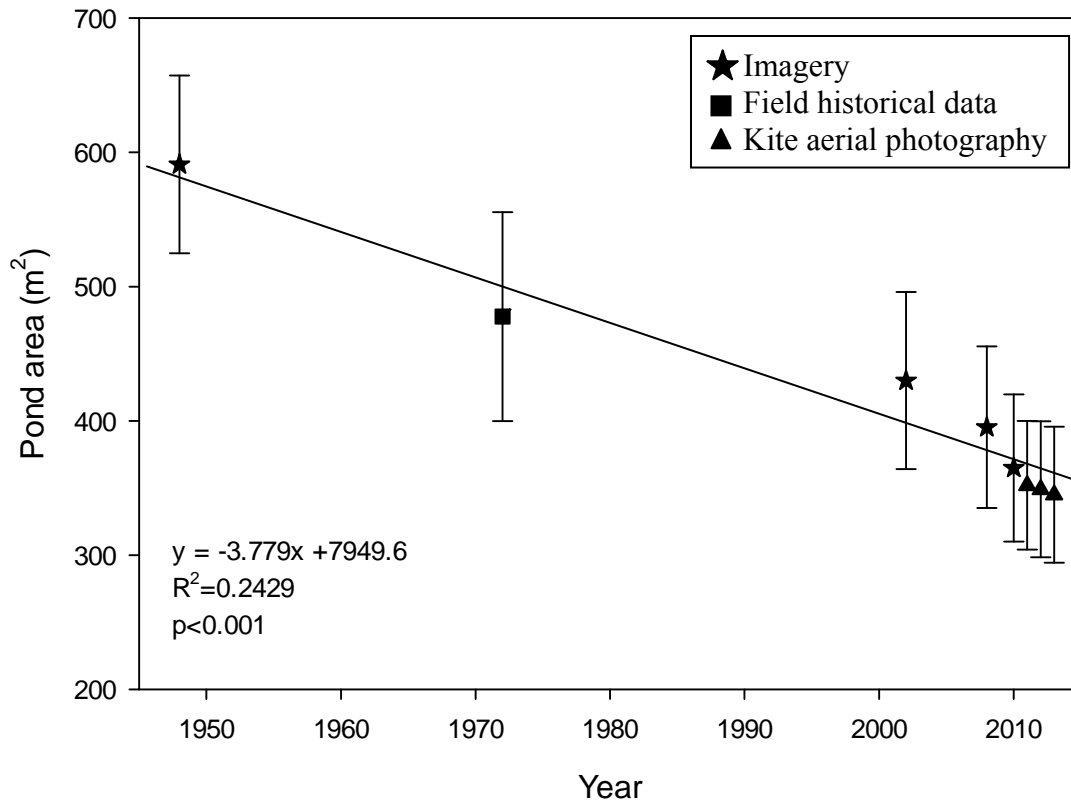


Figure 8. Average pond area change through time, based on multiple analyses of seven historical IBP tundra ponds. Data includes delineation of satellite and aerial imagery, published estimates by Miller et al., (1980) and delineation of low-altitude KAP images.

2.4.4 Environmental drivers of change

Despite this decrease in pond area, no statistically significant changes in water depth were found between 1970's and 2010's in IBP Pond C (Figure 9). However, thaw depth was on average 11cm deeper by the end of August in 2011-2013 compared to 1970-1972 (paired t-test; $p < 0.001$) (Figure 9). A negative relationship was observed between average pond depth and area lost in 7 IBP ponds, with an average loss of 9.6 m² per cm of depth ($R^2 = 0.49$, $p < 0.01$, Figure 10), suggesting that deeper ponds were more resistant to areal loss compared to shallower systems.

The net reduction in pond area and number across the 22 DTLB analyzed may be attributed partly to changes in climate. Summer air temperature in the Barrow peninsula has increased at a rate of 0.032°C/year, with an overall increase of 2°C since 1949. While summer precipitation has remained steady, contributing to an increased deficit in water balance for the region (Figure 11).

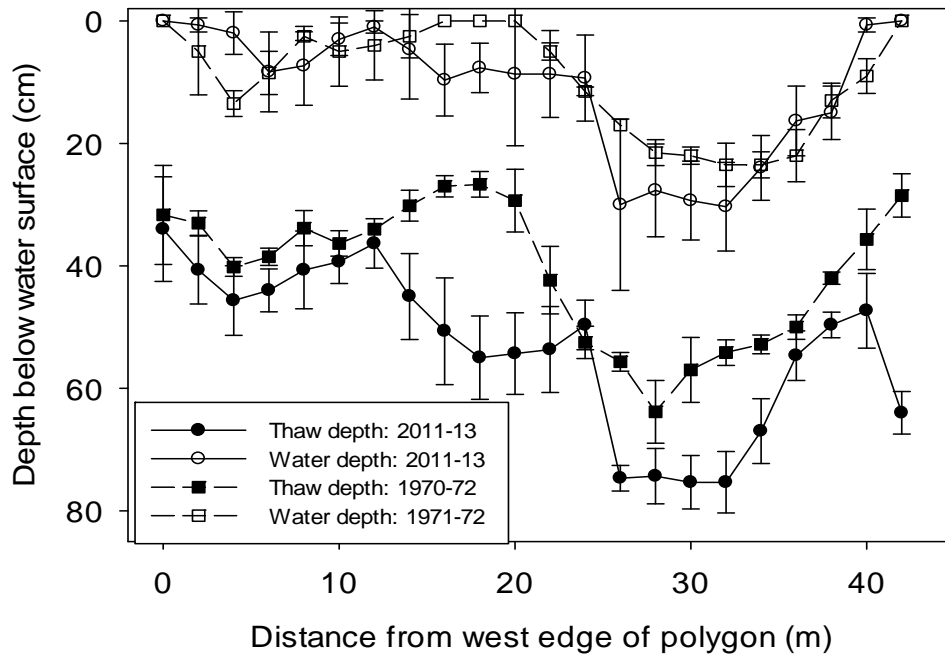


Figure 9. Comparison of water and thaw depths between 1970's and 2010's across a polygon transect in IBP Pond C in late August.

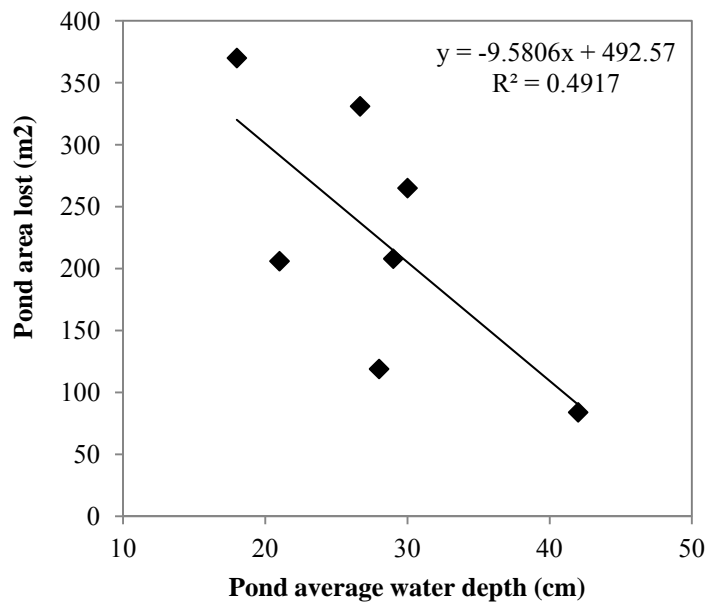


Figure 10. Relationship between surface area lost (1948-2010) and average water depth for 7 IBP tundra ponds.

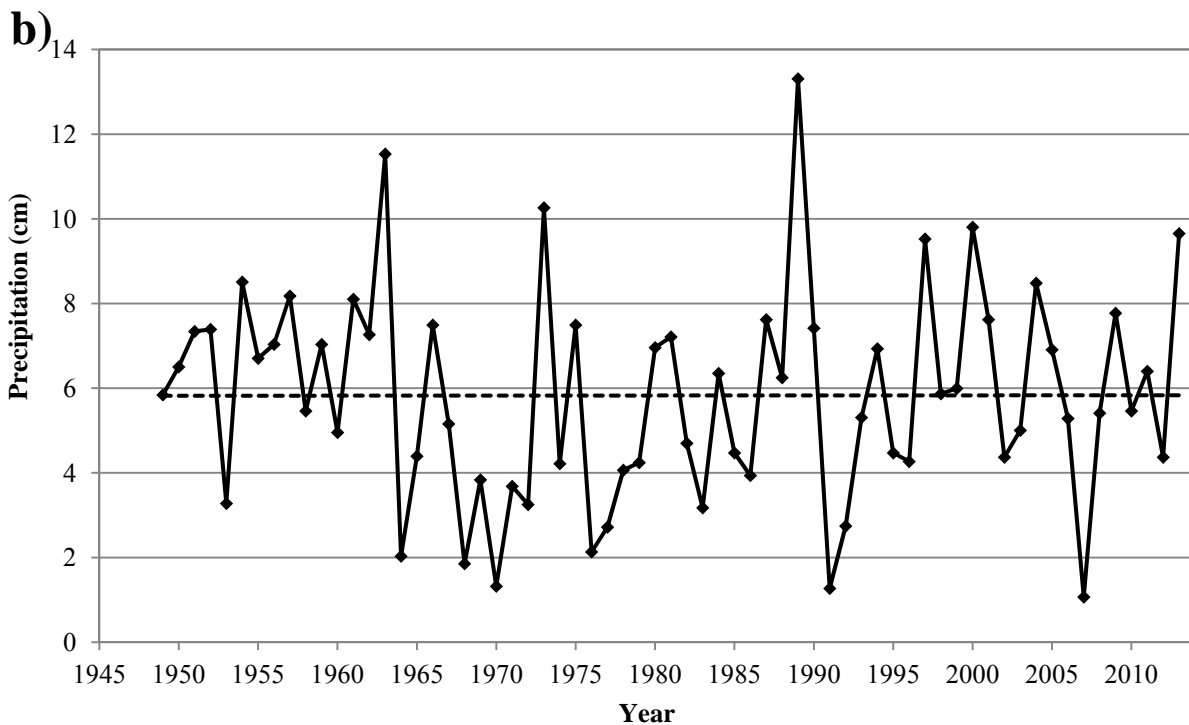
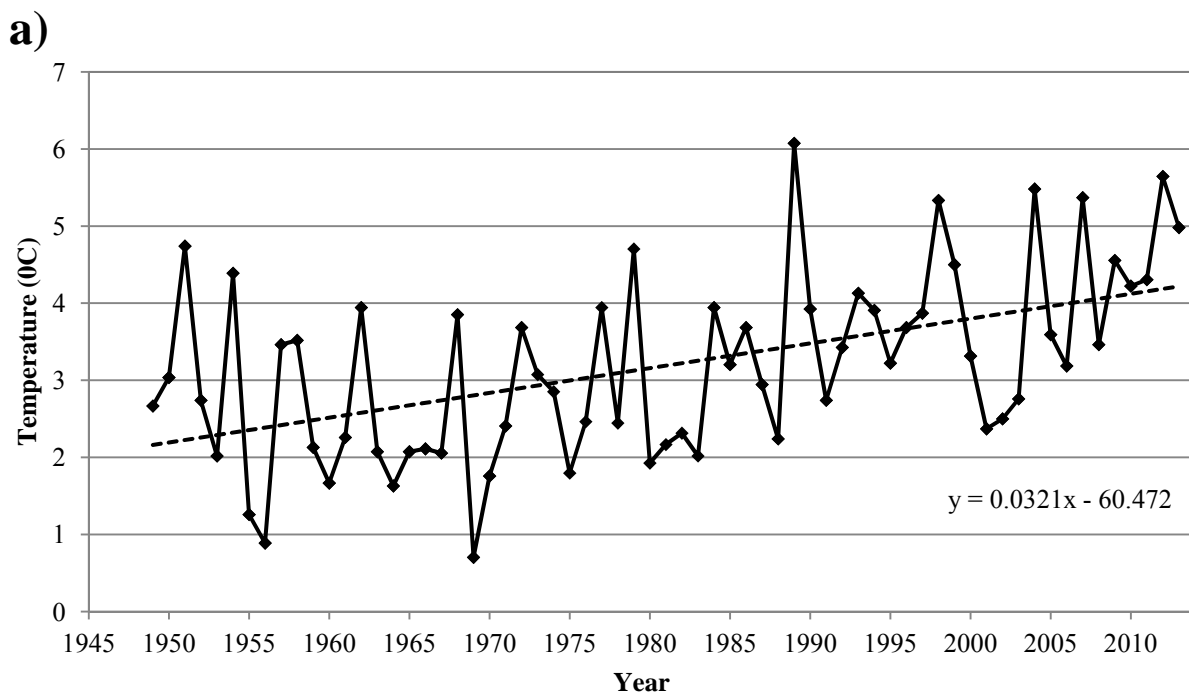


Figure 11. Trendlines for summer (July-August) (a) average temperature ($p < 0.001$) and (b) total precipitation ($p > 0.05$) between 1949 and 2013 for Barrow Alaska (data source: Alaska Climate Research Center).

2.5 DISCUSSION

Multiple lines of evidence lend support to three major themes regarding climate driven effects on tundra ponds in DTLB. First, tundra ponds in the Arctic coastal plain area of the upper Barrow Peninsula, Alaska, have significantly decreased in size and number between 1948 and 2000-2013. Second, historic and current field surveys suggest that increased thaw depth, temperature and vegetation cover play an important role in this change. Three, reduction in area and number of ponds was observed evenly regardless of DTLB age, contradictory to the typical DTLB cycle hypothesis. Although changes in lake and large pond area have been previously documented across the Arctic region (e.g. Smith et al. 2005, Riordan et al. 2006, Smol and Douglas 2007, Jones et al. 2011) this is the first study to examine the long-term hydrological dynamics of closed-basin ponds at a very fine spatial scale in continuous permafrost. Because hydrology, in particular surface water area, is a key factor influencing land-atmosphere carbon fluxes (Zona et al. 2009, Olivas et al. 2010) and energy balance (Liljedahl et al. 2011) in the Arctic coastal tundra, it is essential to understand changes in pond areas in response to a warming climate.

2.5.1 Trends and drivers of pond surface area change

A decrease in the surface area of Arctic tundra ponds agrees with current (Schindler and Smol 2006b, Smol and Douglas 2007, White et al. 2007) and projected (Prowse et al. 2006, IPCC 2007, Avis et al. 2011) climate driven effects on Arctic wetlands related to longer ice-free seasons, higher water temperatures, enhanced water loss and increased infiltration due to permafrost thaw. Findings from this study agree with others by Lin et al. (2012) who found a reduction of surface water in the Barrow area and Carroll et al. (2011) who recorded decreased lake area in northern Canada, but were not consistent with other similar analyses on larger ponds and lakes in continuous permafrost that observed an increase (Smith et al. 2005, Jones et al. 2011) or minimal change (Riordan et al. 2006, Hinkel et al. 2007, Sannel and Kuhry 2011) in surface area. However, most of these studies are based on coarse satellite imagery

(e.g. MODIS, Landsat) making direct comparison to our study difficult given the different spatial resolution of the analyses.

The observed trends of pond disappearance in our study area could be attributed to several climate-driven factors including (i) negative water balance, (ii) vegetation in-filling, and (iii) permafrost degradation.

Over the past 50 years, the Barrow area has undergone a significant increase in summer temperature with minimal increase in precipitation. This deficit could adversely affect hydrologic budgets in the region (Hinzman et al. 2005) and may play an important role on the fate of small tundra ponds with large area-to-depth ratios. However, Liljedahl et al. (2011) found that Arctic coastal wetlands have a strong hydrologic resistance to drying favored by vapor pressure deficits from a maritime climate, mitigating warmer conditions, which is corroborated by our findings of minimal changes in water depth at IBP ponds over the past 40 years. A relatively stable water depth also suggests that changes in pond area are not purely attributable to changes in evaporation and/or evapotranspiration as other Arctic studies have suggested (Smol and Douglas 2007).

Substantial changes in vegetation communities have also occurred in the Barrow region within the last half century. In particular, the cover of aquatic macrophytes has increased in tundra ponds (Lougheed et al. 2011b) and pond margins (Villarreal et al. 2012) with significant effects on ecosystem function (Lara et al. 2012). Macrophyte expansion may be attributed to (i) a lengthening of the growing season with an increase in the number of snow-free days (Stone et al. 2002), (ii) increased water temperature of ponds (Lougheed et al. 2011b), which may enhance productivity, and (iii) increased pond nutrient concentrations (Lougheed et al. 2011b) related in part to permafrost thaw (Reyes and Lougheed n.d.) which may stimulate macrophyte growth.

Pond shrinkage as a result of infilling by vegetation has previously been noted in a few studies across the Arctic (Jorgenson and Shur 2007, Grosse et al. 2008, Sannel and Kuhry 2011). Our

delineation method clearly demarcated the edge of the shallow *C. aquatilis* sedge community surrounding the ponds, where temporal inward progression is evident. In agreement with our observations, Villarreal et al., (2012) also documented an increase cover of the dominant wetland plant species (*C. aquatilis* and *A. fulva*) in pond margins over the past 40 years in the IBP sites and other parts of the upper Barrow Peninsula. In addition, they also noted a consistent increase in the cover of the shallow facultative wetland plant *Dupontia fisheri* at the expense of deep-water *A. fulva* at a small pond near our IBP pond sites, which is a phenomenon that we are also likely capturing in our analyses. In-filling is also supported by the observed relationship between areal loss and pond depth in the IBP site, where shallow ponds tend to be less resistant to decreases in area compared to deeper ponds. Deeper ponds are likely less easily colonized by shallow-water species, such as *Carex aquatilis* and *Dupontia fisheri*.

Permafrost it is known to have an important role in the hydrology of closed-basin systems. Surface area shrinkage observed in ponds (Riordan et al. 2006, Sannel and Kuhry 2011) and lakes (Smith et al. 2005) in discontinuous and sporadic permafrost regions has been largely attributed to lateral and sub-surface drainage as a result of permafrost thaw (Yoshikawa and Hinzman 2003). On the other hand, permafrost degradation in continuous permafrost has been associated with enlarging thermokarst lakes (Jones et al. 2011), and is predicted to lead to a transition in Arctic freshwater systems from a surface water-dominated to groundwater-dominated (Frey and McClelland 2009). Our observed increase in active layer below tundra ponds, likely related to a significant increase in summer water temperature over the past 40 years (Lougheed et al. 2011b), suggests that lateral drainage and pond deepening due to thermal erosion may be occurring.

It is clear that the fate of small tundra ponds is not being controlled by a single factor such as evaporation (Smol and Douglas 2007) or permafrost degradation (Yoshikawa and Hinzman 2003) as other studies have suggested, but rather by a combination of different environmental factors. We

propose that a negative water balance combined with vegetation infilling and permafrost thaw play a complex role in the reduction in area and number of tundra ponds in the Barrow Peninsula. Increased evaporation as a result of warmer air and water temperatures is negatively impacting the water budget of ponds. With reduced water level relative to the ground surface, aquatic vegetation is able to encroach into the ponds, further contributing to water loss via evapo-transpiration. However, permafrost degradation and active layer subsidence (e.g. Streletskiy et al., 2007), are likely acting as a compensatory mechanism maintaining water depth in the open water areas. Although the relationship between hydrology, temperature, vegetation and permafrost is highly complex and requiring further study, this study provides strong evidence for their role in pond area reduction.

2.5.2 Effect of DTLB age on areal change

The “thaw lake cycle” model, initiated by Cabot (1947) then articulated by Hopkins (1949), Britton (1957), Carson and Hussey (1962), Carson (1968), Billings and Peterson (1980) and more recently discussed by Hinkel et al., (2003, 2007) and Jorgenson and Shur, (2007) identify ponds as key elements for the initiation of the thaw lake evolution. As the DTLB begins to age after a drainage event, ponding of water is promoted by ground thaw and thermokarst, followed by expansion and coalescence into larger bodies of water, increasing the total pond area in a DTLB. In agreement with this hypothesis, our study found greater area and number of ponds in older DTLB. At the decadal time-scale, we expected DTLB would experience an increase in pond areas and merging of individual ponds; however, observed changes of decrease in total pond area and number were independent of DTLB age. The significant decrease in pond area in basins of all ages over the relatively short period of time suggests that millennial succession processes such as DTLB evolution, may be overridden by factors related to changes in the Arctic climate.

The high variability of percent change in number of ponds observed for medium-age basins (Figure 5d) is attributed to the appearance of new small ponds, likely as a result of thermokarst activity

and ground subsidence at this early stage of the DTLB cycle (Billings and Peterson 1980). It should be noted that estimates of pond number may be biased given their tendency to coalesce or divide over time (Riordan et al. 2006), making pond area a better proxy for change.

Our results indicate that thaw lake evolution is more stable and not as cyclic as previously thought. Assumptions of a “cycle” were originally based on observations substituting time for space (e.g. Billings and Peterson, 1980) and has recently been challenged by lack of evidence supporting repeated thaw-lake cycles (Hinkel et al. 2003, 2007, Jorgenson et al. 2006). Minimal change in total lake area and low rates of drainage have been documented for our study region (Hinkel et al. 2007) and other areas in the Arctic coastal plain in Alaska (Riordan et al. 2006, Jorgenson and Shur 2007), suggesting a relatively stable landscape compared to similar Arctic regions (Mackay 1988, Plug et al. 2008). However, our study period represents a snapshot compared to the hypothesized thaw lake cycle of 3000-5000 years (Hinkel et al. 2003), and rates of change for DTLB are controversial and difficult to assess at this time. Further review of the DTLB evolution for this region will provide better insight into the causes and consequences of pond area reduction and their role in the thaw lake cycle.

2.5.3 Methodological assessment

Two major sources of methodological uncertainty are identified and addressed in our study: (i) short-term inter-annual effects on water extent and (ii) detection and geometric accuracy of automated classification. Low-altitude aerial photography of Arctic tundra ponds acquired in four consecutive years (2010-2013) demonstrated a continual decline in area during peak season, eliminating the possibility that estimates of long-term change have been greatly affected by inter-annual variability. Regarding the classification algorithm, we reported a geometric precision delineation error of 0.074 (7.4%). This error, also depicted by the regression model in Figure 6, is likely attributed in part to a slight overestimation of pond area by satellite imagery as a result of boundary pixels containing a mix of land and water, where the spectral signature of the pixel is often dominated by the strong mid-infrared absorption of water (e.g.

Riordan et al., 2006). Although our accuracy assessment was derived from a small pool of ponds (n=34), it was undertaken in a conservative fashion and was based on a variety of tundra ponds located across the study region with different sizes and depths.

It is important to note that the restricted footprint of historical imagery summed with the relative rarity of medium and ancient age DTLB across the upper Barrow peninsula may have limited our ability to fully characterize pond size dynamics in DTLBs of varying ages. Further analysis of medium and ancient age DTLB may give better insight into the role of ponds in thaw lake evolution. In addition, basin age estimates were provided from Hinkel et al., (2003), derived using extrapolation of ground measurements by remote sensing methods, and uncertainty in accuracy should be considered. Further ground observations may be needed to fully ascertain the age of the basins analyzed in this study.

2.6 CONCLUSION

This study explored the surface hydrological dynamics of open water of tundra ponds at a fine spatial scale in drained thaw lake basins across the Barrow peninsula, Alaska over a 65 year period. Our study is the first of its kind to look at ponds within low-center polygons, using sub-meter aerial and satellite imagery, and uses one of the oldest historical imagery datasets for the Arctic circa 1948. In addition, our analysis was aided by historic and current field observations of permafrost thaw depth and water depth of ponds to better understand changes in pond area and number over the study period.

The mechanisms behind reduction of pond size and number are attributed to a combination of negative water balance, deepening of the active layer and an increase in biomass density and cover of aquatic sedges in ponds. This change was independent of basin age and size, contradictory to the hypothesized “thaw lake cycle” for this region, suggesting a landscape highly dependent to changes in climate.

The decrease of pond size and number across the Barrow peninsula not only has major implications for surface energy balance and land-atmosphere carbon exchange but is of ecological

importance for the fauna in the Arctic coastal plain (e.g. decrease habitat for threatened and endangered waterfowl, nesting and feeding grounds, etc.) and the native communities that depend on these wetlands for their sustainable lifestyle. In addition, concerns for future climatic projections on water and energy budgets for the Arctic coastal plain should consider wetland ponds given their dominance on the Arctic landscape and the important role they play in the Arctic hydrological system.

Chapter 3: Decadal changes in thaw depth and aquatic emergent macrophyte biomass in Arctic tundra ponds: Implications for methane flux.

3.1 INTRODUCTION

Vast expanses of the permafrost influenced areas of the Arctic are covered with freshwater ecosystems, including vegetated ponds and wetlands (Hinkel et al. 2003, Frohn et al. 2005a, Smith et al. 2007). Arctic wetlands in high northern latitudes produce large amounts of CH₄, which may account for approximately 10% of the global atmospheric CH₄ sources (Reeburgh and Whalen 1992). In Arctic wetlands, CH₄ flux has been observed to be controlled by a variety of factors including soil temperature, water table depth (Kutzbach et al. 2004), thaw depth (von Fischer et al. 2010) and vegetation type. Plants play an important role in CH₄ production (Sutton-Grier and Megonigal 2011), consumption (i.e. oxidation) (Segers 1998) and release (Morrissey et al. 1992, King et al. 1998). Aquatic emergent vascular plants serve as a key CH₄ release pathway through aerenchymatous tissue (i.e. Kutzbach et al., 2004) that acts as a gas conduit and allows CH₄ to be ventilated from the soil to the atmosphere, avoiding oxidation in aerobic layers. The long-term effects of climate warming on the distribution of these plants have been poorly understood in the Arctic. Therefore, it is imperative to assess any biomass changes of these key CH₄ species that can alter soil-atmosphere CH₄ flux and can potentially induce positive greenhouse feedbacks.

For the Arctic coastal plain in northern Alaska, recent studies and preliminary data have associated relatively large rates of CH₄ flux to the dominant aquatic emergent vascular plants: *Carex aquatilis* and *A. fulva* (von Fischer et al. 2010, Lara et al. 2012). Both species contain aerenchyma that may act as gas conduits (Aiken and Buck 2002, Kutzbach et al. 2004) and account for the highest CH₄ flux compared to other vegetation communities in the Arctic coastal plain (Lara et al. 2012). However, there is uncertainty on the structural and functional responses of these CH₄-important species to recent warming and permafrost thaw due in part to a lack of long-term datasets for the Arctic. The International Biome Project (IBP) in Barrow, Alaska, is one of the only detailed historical datasets (circa 1970) on

Arctic aquatic production (Hobbie 1980) that contains records of macrophyte biomass, thaw depth and water depth among other important drivers of CH₄ flux in tundra wetlands. Comparing current to historical records from the IBP allows quantification of decadal-scale changes of methane-controlling factors and estimation of the associated effects on CH₄ flux.

This study aims to:

- (i) Establish a method for estimating biomass of dominant aquatic plant species (*Carex aquatilis* and *Arctophila fulva*) in tundra ponds using allometry and photo analysis of leaf area index (LAI);
- (ii) Assess decadal-scale changes in water depth, thaw depth and biomass of both *C. aquatilis* and *A. fulva*;
- (iii) Identify the species-specific drivers of CH₄ flux from aquatic macrophytes;
- (iv) Model changes in CH₄ flux over decadal-time scales and at regional level.

3.2 METHODS

3.2.1 Site Description

This study was conducted on an Arctic Coastal Plain tundra landscape near Barrow, Alaska, USA. This area is underlain by continuous permafrost with a shallow active layer depth ranging from 20-80 cm (Streletskiy et al. 2007). Winters are long and cold and summers are short and cool with average temperatures of -19 and 3.9° C, respectively. The snow free season usually starts in early June and lasts until early September. This tundra environment is characterized by drained thaw lake basins containing numerous tundra ponds formed by ice wedges and thermokarst processes (Billings and Peterson 1980, Hinkel et al. 2003). The region is characterized by acidic soils, rich in organic matter produced as a result of plant detritus accumulation (Brown et al. 1980).

Vegetation in tundra ponds is dominated by two aquatic emergent graminoids: *Carex aquatilis* and *Arctophila fulva*, commonly found in pure stands, dominating unique wet tundra communities (Villarreal et al. 2012), and accounting for approximately 11% of the land cover in the Upper Barrow Peninsula area (Tweedie et al in prep). However, other less common plant species occur within these communities, including *Ranunculus pallasii*, *Dupontia fisherii*, and some species from the *Eriophorum* genus such as *E. angustifolium*, *E. russeolum*, *E. scheuchzeri*. Our target taxa in this study, *C. aquatilis* and *A. fulva*, are rooted aquatic emergent monocots that usually form clonal colonies in ponds (Johnson and Tieszen 1973), with *A. fulva* found in deeper water than *C. aquatilis* (Andresen & Loughheed, accepted).

3.2.2 Climate Analysis

To better understand drivers of biomass, thaw depth and water depth change between the 1970's and 2010's, we retrieved long-term climate records of the Barrow Airport, National Weather Service (1949-2013) from The Alaska Climate Research Center website (<http://climate.gi.alaska.edu/>). Monthly summer averages (June-August) were calculated for study years, and long term (30 yr) averages were calculated for the years prior to 1972 and 2013. In addition, degree days of thaw (TDD), referred here as the days with mean temperature above the freezing point before September 1st, were calculated for sampled years.

3.2.3 Past Biomass, Thaw Depth and Water Depth Sampling

In 1971 and 1972, aboveground biomass of *C. aquatilis* and *A. fulva* was harvested every 10 days from 3 ponds at the IBP historical research site near the town of Barrow, Alaska, (71°17'N, 156°41'W) (McRoy and Leue 1973) (Figure 12). IBP Pond J (71.293626N, -156.70144W) was harvested for both *C. aquatilis* and *A. fulva* biomass. IBP Pond C (71.2946N, -156.70210W) was monitored for *C. aquatilis* only and IBP Pond 10 (71.2945N, -156.70324W) (a.k.a IBP Pond L) for *A. fulva* only given

the absence or near-absence of the other species. Aboveground biomass samples consisted of paired 50 x 20 cm rectangular quadrats along a transect covering shallow (0-3 cm), mid-depth (3-8 cm) and deep water (8-13 cm). Live versus dead biomass material was separated and oven-dried for 24 hrs at 95 °C. Historical biomass McRoy and Leue (1973) were published as averages for each sampling date (with no standard deviation). In addition, thaw depth and water depth were collected along cross-polygon transects at IBP ponds C and E (71.29422N, -156.70172W) during late August in 1971 and 1972 by Miller et al., (1980).

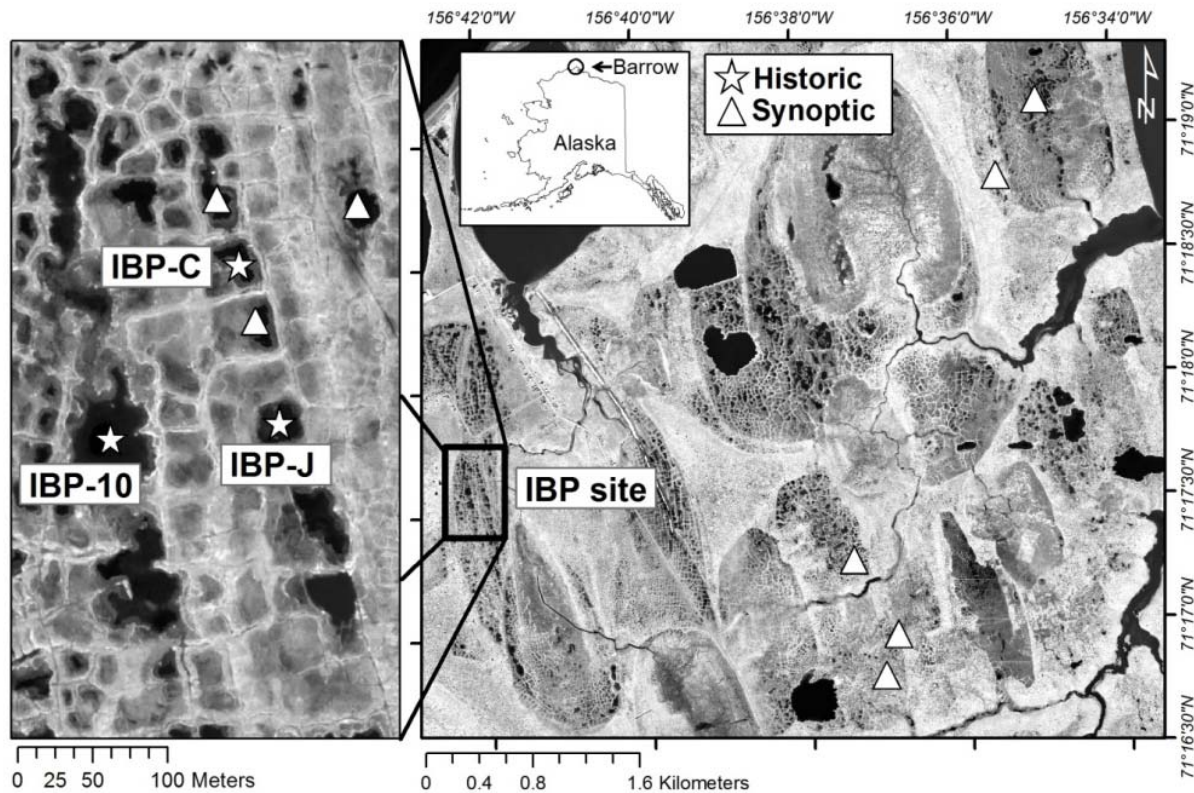


Figure 12. Study area and ponds sampled in this study. Historical sites were re-sampled for biomass, thaw depth and water depth. Synoptic sites distributed across the Barrow region were sampled for comparative purposes to IBP sites.

3.2.4 Present-day Biomass, Thaw Depth and Water Depth Sampling

In 2010-2013, these same ponds (IBP Pond C, J, 10) were re-sampled. To limit disturbance due to biomass clipping, we developed allometric relationships that allowed repeat, non-destructive seasonal monitoring of live aboveground biomass of *C. aquatilis* and *A. fulva*. In 2010, allometric relationships

were created from the aboveground tissues of 10-15 individuals of each plant species, collected from multiple ponds every 10-days over the growing season. Multiple morphometric characteristics of plants (e.g. internode length, leaf length, plant height, leaf number, etc.) were measured to identify the variables that best explained plant dry weight. Harvested tissues were then oven dried (95° C) and weighed. Multiple regression models were created relating weight to morphometrics and the best-fits were selected to predict biomass. Following 2010, only the variables that best explained plant dry weight, which were plant height for *A. fulva* and sum of leaf lengths for *C. aquatilis*, were measured. Additional plants were regularly collected, measured and dried from various ponds and dates throughout the study period to ensure the relationships held through time. To assess accuracy of the allometric plot estimates, each year we harvested 5-10 biomass plots at peak growing season after harvests, to compare allometric estimates with actual weights.

In 2010-2012, IBP Pond J, Pond C, and Pond 10 were visited every 10 days during the growing season (June 10th-August 20th); these are referred to as “Historic” sites (Figure 12). In addition, eight other reference or “Synoptic” sites (Figure 12) that include additional ponds in the IBP and ponds distributed across the Barrow area were sampled at peak growing season (first week of August 2010-12) to understand the spatial variability of macrophyte biomass across the region and to verify trends in biomass at a larger spatial scale. The IBP ponds were also sampled once during peak growing season in 2013. In addition to biomass, water and soil thaw depth were measured at each plot.

To determine whether total plant biomass has changed over time, we compared weekly averaged dry weight between 1971-1972 and 2010-2013 using a paired t-test following assessment of normality (Shapiro-Wilk test). Similarly, to estimate changes in thaw depth and water depth between the 1970s and 2010s, we compared peak growing season water depth and thaw depths from cross-polygon transects in IBP Pond C and E using a paired t-test. Drivers of plant biomass and thaw depth were

assessed by simple linear regressions. Independent variables included in the analyses were average summer temperatures (July-August) and thaw degree days (TDD).

3.2.5 Methane Fluxes

Land atmosphere CH₄ fluxes were measured *in situ* near Barrow, 42 ~0.25m² plots using the closed chamber technique (i.e. Lara et al., 2012). All fluxes were measured using a photo-acoustic multi-gas analyzer (INNOVA 1312 AirTech Instruments A/S, Denmark), during the 2008-2010 peak growing seasons (August 3rd through 15th). Flux sites were selected to represent a range of vegetation and soil characteristics within aquatic habitats, including gradients in vegetation density, thaw depth, and water table depth. Generally, all sites were distributed within 2 km² of the historic IBP ponds, and clustered in groups of three plots.

To determine vegetation biomass within the chamber plots, vegetation was harvested only from plots outside IBP legacy sites to minimize long-term disturbance. For IBP legacy sites, we estimated biomass for unharvested plots using a regression model between dry weight biomass and LAI estimated from *A. fulva* and *C. aquatilis* chamber plot nadir-view pictures (n=14 and n=20 respectively) using an image by brightness threshold image classification technique in Image J software (v1.43u). For a subset of plots for each plant species, plot photos were acquired for determination of LAI prior to harvest and drying of all live aboveground biomass. Then, a linear regression model was employed to associate LAI and plant biomass.

We used stepwise regression models to identify the simplest species-specific (i.e. *A. fulva* or *C. aquatilis*) multiple regression models relating CH₄ flux to important known environmental drivers of flux. Input variables included vegetation biomass, water depth, thaw depth, and soil temperature (1 cm depth). Overall variance in model parameters were determined by bootstrapping parameter estimates over 1000 iterations. Prior to statistical analysis, data were checked for normality and natural log transformed, where applicable. Statistical analyses were performed in JMP Pro version 11.

To estimate long-term changes in peak growing season CH₄ flux between 1970's and 2010's at the historic IBP ponds site, we modeled peak-season CH₄ flux for each plant species based on peak-season biomass data from plots while water depth and thaw depth data were derived from cross-polygon transect data measured in both the 1970s and 2010s at these historic IBP sites. This retrogressive analytical approach assumes that drivers of CH₄ flux identified based on data collected in the early 2010s, will be constant over time (i.e. in the 1970s) and among similar pond ecosystems.

We assessed modern CH₄ flux of *C. aquatilis* and *A. fulva* for the Barrow Peninsula by scaling-up peak season CH₄ flux based on recent land cover determinations. Modern peak-season CH₄ flux was modeled for each plant species based on plot-level observations of the primary drivers of CH₄ flux (i.e. biomass, thaw depth, water table depth) collected in both the historic IBP and synoptic sites over a four year period (2010-2013) to incorporate the widest and most representative range of conditions. Then, average modeled CH₄ flux for each plant species was multiplied by area cover of communities dominated by *C. aquatilis* and *A. fulva*. Areal cover of *C. aquatilis* and *A. fulva* was estimated based on a high-spatial resolution (0.7m) geobotanical map of a 428 km² northern subsection of the Barrow Peninsula developed by Tweedie et al. in prep. This area represents approximately 27% of the 1,800 km² area defined as the Barrow Peninsula by Hinkel et al. (2003) .

In brief, the land cover characterization was undertaken employing a supervised classification (minimum-distance algorithm) of Quickbird satellite imagery using plant species cover estimates collected in 388 plots associated with long-term ecological studies in the area as training sites. The final land cover map described 9 distinct vegetation communities associated with a moisture and microtopographic gradient with an overall map accuracy of 83%. The percentage cover area for communities dominated by aquatic *C. aquatilis* and *A. fulva* represented 8.5% and 3%, respectively, of the region. Although the mapped subsection represented approximately only one-third of the total peninsula area, we assumed percent cover estimates to be representative of the entire Barrow Peninsula.

3.3 RESULTS

3.3.1 Climate Analysis

Long-term climate records of the Barrow Airport (1949-2013) revealed warmer summer conditions and longer growing seasons for years 2010-2013 compared to 1971-72. The mean summer (Jun-Aug) air temperature in 2010-2013 was 1.7 °C warmer compared to 1971-1972 (3.0 °C). 1971 was a normal year, while 1972 was a relatively warm year with temperatures 1.1 °C above the previous 30-year long term mean of 2.6 °C. More recently, 2010 and 2011 were similar to the long-term mean, while 2012 and 2013 were warmer years, 1.8 °C and 1.1 °C, respectively, above the long-term mean of 3.8 °C. Thaw degree days (TDD) increased on average by 13.8 days between 1971-72 and 2010-13. 1971 had a short TDD of 62 days, while 1972 had a relatively large TDD (77). 2010-2013 years were similar with an average of 83 TDD.

3.3.2 Allometry and Leaf Area Index

Second-order polynomial relationships were found relating macrophyte dry weight to morphological variables. The sum of leaf lengths of *C. aquatilis* explained 87% of the variation in plant dry weight, while *A. fulva* plant height explained 80% of variation in plant weight (Figure 13). Harvested plot biomasses of both *A. fulva* and *C. aquatilis* agreed well with weights predicted from allometry (Figure 14). Similarly, LAI and dry weight had a strong positive association for both *C. aquatilis* ($y=0.1181x-0.4335$, $R^2=0.93$, $p<0.0001$) and *A. fulva* ($y=0.0648x-0.148$, $R^2=0.96$, $p<0.0001$).

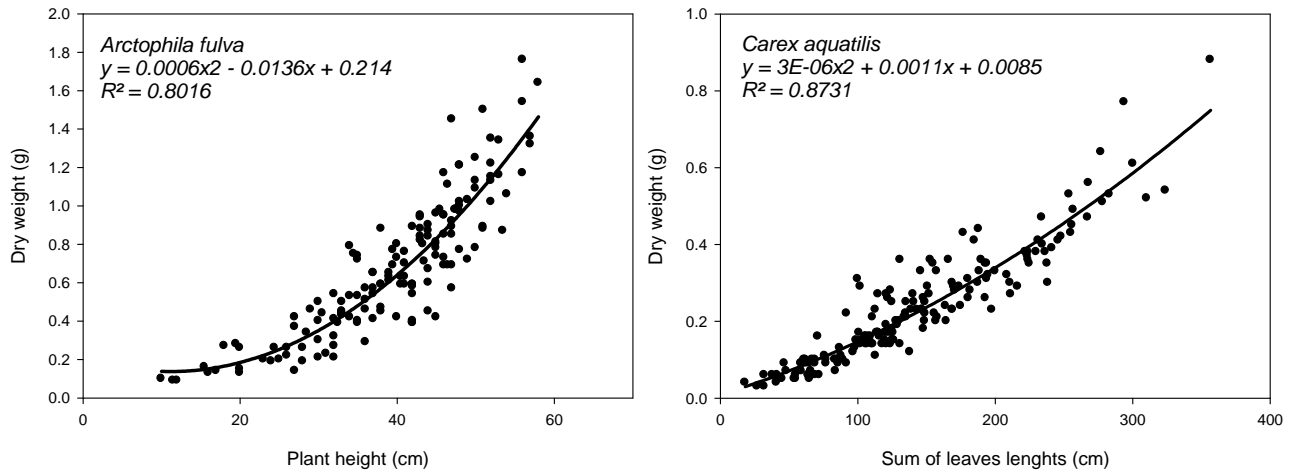


Figure 13. Allometric relationships between plant dry weight and morphological measurements for *A. fulva* (left) and *C. aquatilis* (right).

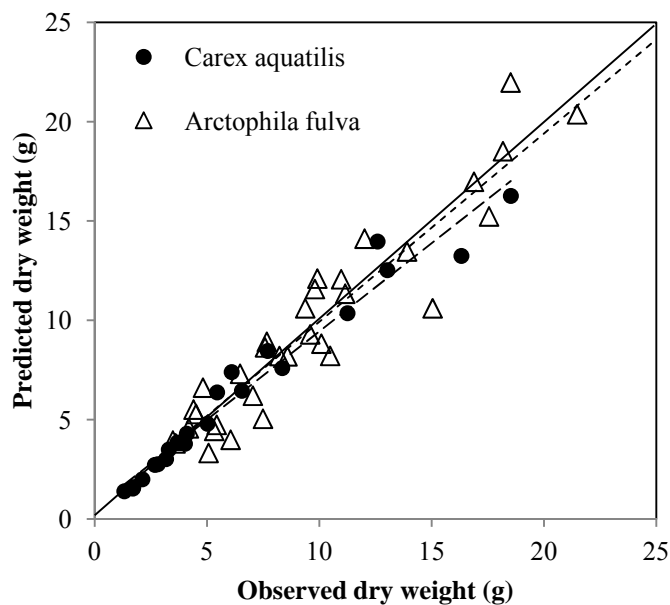


Figure 14. Relationship between predicted dry weight (measured by allometry) and harvested dry weight for *C. aquatilis* and *A. fulva* plots (20x50cm). A 1:1 relationship is illustrated by the solid black line. Dashed lines indicate regression lines for *C. aquatilis* (small dashes) and *A. fulva* (large dashes).

3.3.3 Biomass change

Seasonal above-ground biomass was significantly higher ($p < 0.05$) in 2010's compared to 1970's for both *A. fulva* and *C. aquatilis* for most sites. In IBP Pond J, however, *C. aquatilis* 1970s peak-season

biomass approached that observed in the 2010s ($p=0.116$) (Figure 15), largely due to higher *C. aquatilis* biomass in 1972 (not shown). Although there was some seasonal variability of biomass among consecutive years (e.g. 2010-2013; 1971-1972), no significant differences were found (ANOVA, Tukey KSD, $p>0.05$). Although only these 3 sites were sampled in the 1970s, plant biomass in the IBP sites appears to be conservatively representative of ponds in the region. Modern peak growing season biomass of both *C. aquatilis* and *A. fulva* at IBP ponds fell within one standard deviation of the range of biomass estimates observed at modern synoptic sites across the Barrow area (*C. aquatilis*: 168 ± 51 g/m², *A. fulva*: 123 ± 48 g/m², mean \pm SD).

Concomitant with biomass, cover of both aquatic macrophyte species appears to have increased in IBP ponds over the past 40+ years. Repeat photography indicates that *A. fulva* in IBP pond J increased substantially in cover from 1975 to 2012 (Figure 16). In addition, IBP pond B experienced a marked increase in *C. aquatilis* cover (Figure 5 in Lougheed et al., 2011) and colonization by *A. fulva* at the north end of the pond.

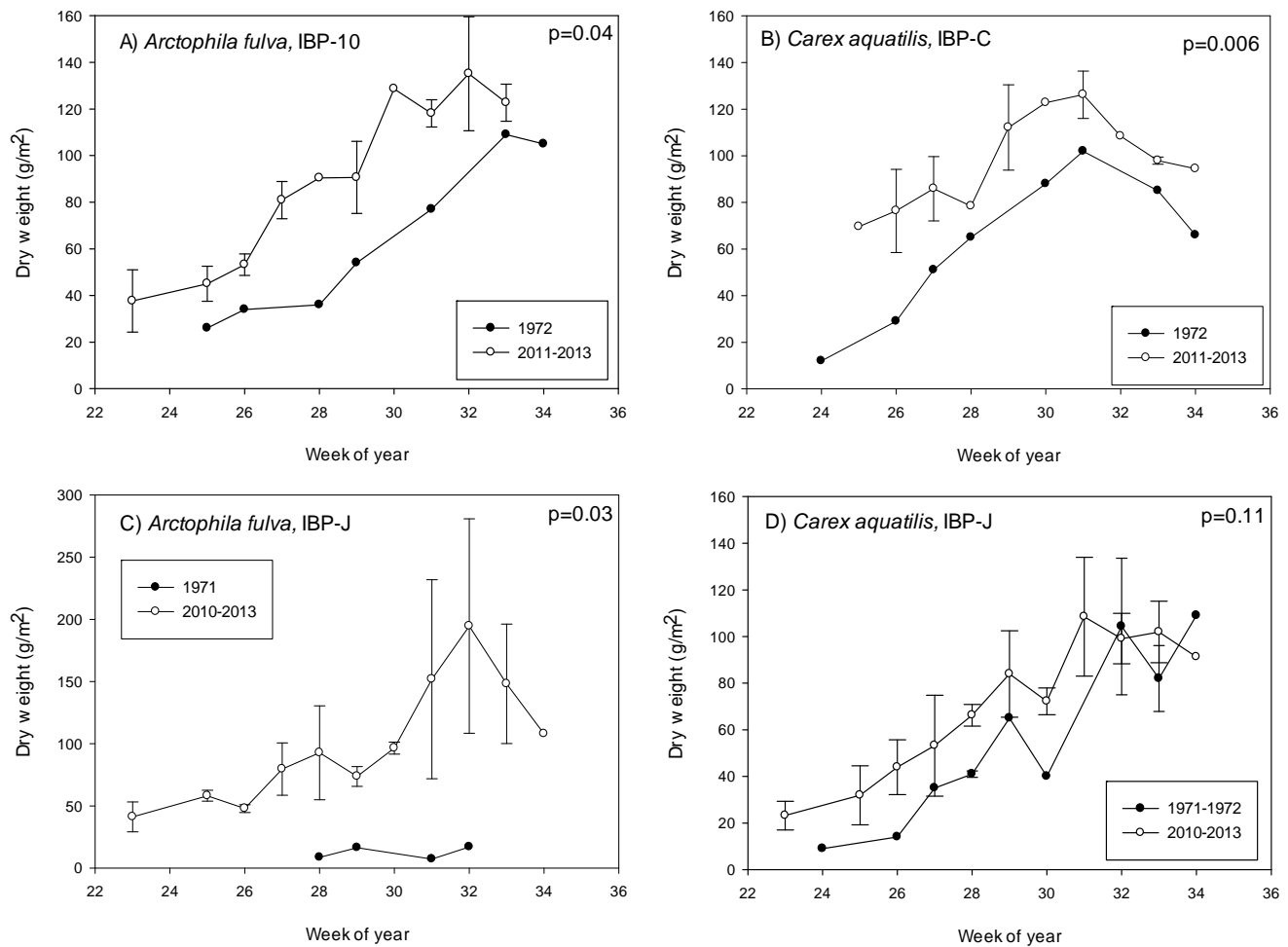


Figure 15. Comparison of weekly seasonal aboveground dry weight biomass(\pm SE) between 1970's and 2010's for *A. fulva* and *C. aquatilis* at three sites (IBP Pond 10, C, J).



Figure 16. Repeat photography (1976-2012) depicting increased cover of *A. fulva* off the dock in IBP Pond J. Historical photo courtesy of Dr. Malcolm Butler (North Dakota State University).

3.3.4 Thaw Depth and Water Depth

Average cross-polygon thaw depth increased significantly between the 1970's ($31.54 \pm$ SD 5.9cm) and 2010's ($43.6 \pm$ SD 7.9cm), with an average increase of 12cm (paired t-test; $p < 0.0001$). Contrary to thaw depth, we observed no significant changes in water depth between 1970's and 2010's for the same time period ($p = 0.62$).

3.3.5 Drivers of Biomass and Thaw Depth Change

Peak growing season biomass and thaw depth were associated with warmer and longer growing seasons. However, only TDD had significant relationships with peak-season thaw depth and biomass for both plant species (Table 3).

Table 3. Correlation co-efficients (r) between climatic factors and biomass and thaw depth (n=6 years).

	Summer Temperature	TDD
Thaw depth	0.8181	0.8625*
<i>A. fulva</i> biomass	0.695	0.8221*
<i>C. aquatilis</i> biomass	0.7106	0.8551*

(*) represent values significant at the $p < 0.05$ level.

3.3.6 Methane Flux

CH₄ flux was strongly associated with *A. fulva* biomass ($\text{CH}_4 = 0.0694(\text{biomass}) + 2.08$, $R^2 = 0.8$, $p < 0.001$), with no other variable contributing significantly to flux. Conversely, CH₄ flux for *C. aquatilis* was best explained by both thaw depth and water depth ($R^2 = 0.57$, $p = 0.0064$) using a multivariate model ($\ln \text{CH}_4 = -3.226 + 0.112(\text{thaw depth}) - 0.077(\text{water depth})$). Based on estimates using these models, average modeled peak growing season CH₄ flux varied substantially among species. *A. fulva* average

CH₄ flux of 13.10 ± 1.69 mg C-CH₄ m⁻²hr⁻¹ was several-fold higher than *C. aquatilis* flux of 2.31 ± 0.77 mg C-CH₄ m⁻²hr⁻¹.

These models also allowed us to estimate forty years (1970's-2010's) of CH₄ flux change in IBP ponds. CH₄ flux increased by 81% on average for *A. fulva* and by 240% for *C. aquatilis*. These percentages correspond to changes in fluxes from 7.9 ± 2.4 to 14.3 ± 5.7 mg C-CH₄ m⁻²hr⁻¹ for *A. fulva* and from 0.71 ± 0.32 to 2.44 ± 0.79 mg C-CH₄ m⁻²hr⁻¹ for *C. aquatilis* (Figure 18). Combining fluxes from both *C. aquatilis* and *A. fulva* indicates that CH₄ fluxes have doubled over the past 40 years from 8.6 mg C-CH₄ m⁻²hr⁻¹ to 16.8 mg C-CH₄ m⁻²hr⁻¹.

Finally, we estimated peak-season wetland CH₄ flux to be 963.92 C-CH₄ kg/hr for both species across the Barrow Peninsula by considering biomass, thaw and water depth measured in plots across the region (Table 4). Even though *A. fulva* had lower areal cover (3.1%) compared to *C. aquatilis* (8.5%), it dominated regional aquatic CH₄ flux with more than double the flux (649.76 ± 84 mg C-CH₄ m⁻²hr⁻¹), as compared to *C. aquatilis* (314.16 ± 105 mg C-CH₄ m⁻²hr⁻¹).

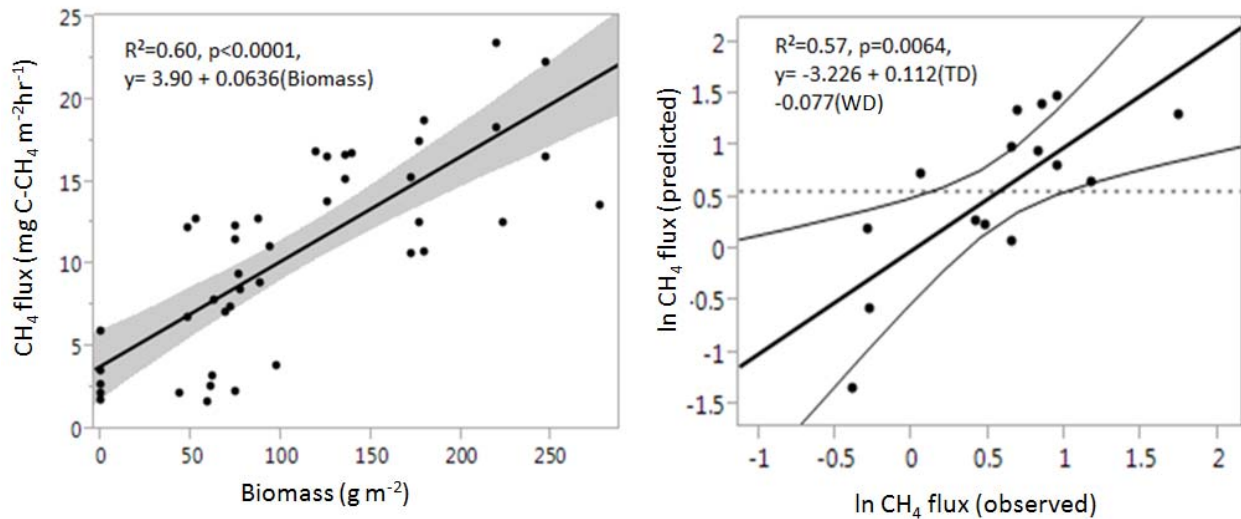


Figure 17. Regression models developed for *A. fulva* (left panel) and *C. aquatilis* (right panel), for retrogressive analysis. Uncertainty ranges correspond to 95% confidence intervals.

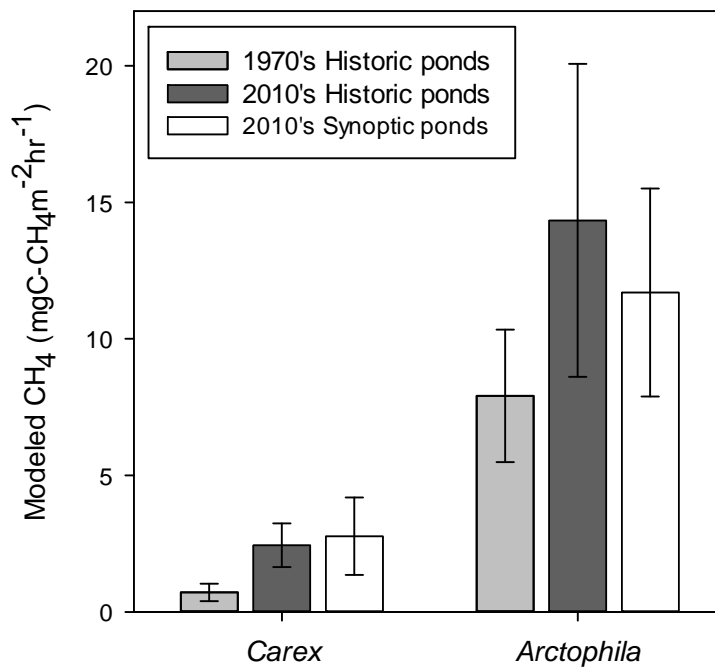


Figure 18. Modeled CH₄ flux (\pm 95% CI) comparison between *C. aquatilis* and *A. fulva* in 1970s and 2010s of historic ponds sites and 2010's in ponds across the Barrow region.

Table 4. Summary of modern (2010-2013) peak-season plot-based means of CH₄ controlling factors and modeled CH₄ flux (C-CH₄ mg m⁻²hr⁻¹) for the Barrow Peninsula by plant species. Uncertainty estimates represent 95% confidence intervals.

Plant species	Biomass (g/m ²)	Thaw depth (cm)	Water depth (cm)	Modeled† CH ₄ flux	Area* Barrow Peninsula (km ²)	Barrow Peninsula CH ₄ (10 ³ gC-CH ₄ hr ⁻¹)
<i>Arctophila fulva</i>	144.7±27	49±7.1	25.2±4.6	13.10±1.69	49.6 (3.1%)	649.76±84
<i>Carex aquatilis</i>	154.2±19	41±2.98	10.3±3.22	2.31±0.77	136 (8.5 %)	314.16±105
Totals					185.6(11.6%)	963.92

* Estimated from percentages by Tweedie et al (in prep).

† Average of modeled CH₄ species plots

3.4 DISCUSSION

This study represents the first effort to quantify decadal-scale changes in biomass, thaw depth and CH₄ flux of the two dominant aquatic emergent plants in the Arctic coastal plain: *Arctophila fulva* and *Carex aquatilis*. The comparison between historical datasets and modern observations revealed an increase in thaw depth and biomass for both aquatic emergent species over a 40 year period, which may have important consequences for an increase in CH₄ flux for the same time period (*sensu* Lara et al. 2012). Changes in thaw depth and biomass are concomitant with changes in air and water temperature, as well as increased nutrient levels observed in ponds over recent decades in the Barrow area (Wendler et al. 2009, Loughheed et al. 2011b). This study underlies the importance of aquatic *A. fulva* and *C. aquatilis* as key soil-atmosphere CH₄ pathways, as they may account for approximately 78% of the regional CH₄ flux while covering a small portion (11%) of the landscape (Tweedie et al. in prep, Lara et al. 2014).

3.4.1 Allometry

Plant allometry is commonly employed for estimating biomass of shrubs and trees (Niklas 1995, Schafer and Mack 2014). This study supports plant allometry as an alternative method for non-destructive estimation of biomass in aquatic graminoids. These allometric equations for *C. aquatilis* and *A. fulva* biomass will facilitate future studies on these dominant emergent aquatic plants on the Arctic coastal plain. Allometry estimates proved to be conservative and accurate in predicting aboveground biomass with a slight underestimation of denser biomass plots (Figure 14). Therefore estimates reported in this study using allometry at peak growing season are not likely overestimated and differences in biomass between 1971-1972 and 2010-2013 are thus conservative.

3.4.2 Causes of biomass and thaw depth increase

The increase in biomass of both species over time agrees with other long-term plot-level studies in wet sedge tundra (Hill and Henry 2011) and dry High-Arctic heath tundra (Hudson and Henry 2009). Increased biomass has also been indirectly observed with broad-scale greening satellite-derived observations (Bhatt et al. 2010, Walker et al. 2012b, Epstein et al. 2012) and modeling studies (Epstein et al. 2000, Euskirchen et al. 2009). Although attribution of change to specific factors is complicated in non-controlled settings, we primarily attribute changes in biomass to increasing temperatures (Wendler et al. 2009) and longer growing seasons (Stone et al. 2002), as reflected in TDD in this study. Both are known to alter Arctic tundra productivity from experimental and observed studies in wet sedge tundra communities (Chapin, FS et al. 1995, Shaver et al. 1998, Hill and Henry 2011). However, other important warming-related factors are also likely enhancing biomass production including increased nutrient availability (Lougheed et al. 2011b) released from permafrost thaw (Reyes and Lougheed, n.d.). Notably, temperature and nutrients have been observed to be a strong predictor of biomass in experimental treatments in wet sedge tundra (Shaver et al. 1998, Boelman et al. 2003, Walker et al. 2006) and they have been found to alter CH₄ biomass and fluxes in *A. fulva* (Lara 2012).

The increase in *A. fulva* cover observed in this study agrees with observations by (Villarreal et al. 2012) in the Barrow area, who reported increase of 20-25% in relative cover of *A. fulva* in aquatic communities in the Barrow area between 1972 and 2010. In line with Villarreal et al. (2012), we found *A. fulva* has increased in cover, and even newly colonized ponds, in the IBP site. For example, in the 1970s, McRoy and Leue (1973) reported that *A. fulva* was only a minor component of the vegetation cover in IBP Pond J; however, today, *A. fulva* covers nearly a third of the pond area. This may help explain the drastic differences of IBP Pond J *A. fulva* biomass observed between 1971 and 2010s (Figure 4c), where *A. fulva* was perhaps only starting to colonize IBP Pond J in the 1970s and thus exhibited low biomass. In addition, another pond, IBP Pond B, was devoid of *A. fulva* 40 years ago and is currently

being colonized by this plant at the north end. Within the primary IBP ponds, only IBP Pond C continues to be absent of such species and the drivers of *A. fulva* colonization in this area remain unclear.

Thickening of the active layer (a.k.a thaw depth) has been widely observed across the Arctic, including the Barrow area (e.g. Streletskiy et al. 2007). However, our studies are, to our best knowledge, the first to assess changes in active layer over 40+ years within the open water of ponds and fringing aquatic vegetation (Andresen & Loughheed, accepted). We consider our estimates of thaw depth to be conservative due to the ice-rich stratum in the permafrost for this region, which reduces the apparent permafrost thaw depth. Previous studies attribute the thickening of the active layer to increased temperature and the duration of the thawing period (e.g. Streletskiy et al. 2007). We have similarly found that thawing period has a significant linear relationship with peak-season average thaw depth. These trends have important implications for carbon flux, given the observed relationships between thaw depth and CH₄ release in this study and others (Johansson et al. 2006, von Fischer et al. 2010).

3.4.3 Methane flux

In agreement to other studies, our study found that (i) aboveground biomass, thaw depth and water depth are strong predictors of CH₄ flux and that (ii) CH₄ rates vary among species (Kao-Kniffin et al. 2010, Ström et al. 2012). CH₄ flux responded linearly to biomass increase of *A. fulva*, consistent with previous studies on other aquatic plants (Joabsson et al. 1999, Joabsson and Christensen 2001). *C. aquatilis*, on the other hand, had a strong response of CH₄ flux to a combination of thaw depth and water depth. We suspect that the shallow water habitat preference by *C. aquatilis* results in greater susceptibility to microscale spatial variability of known methane-controlling factors including differences in soil temperature (Morrissey et al. 1992, Sachs et al. 2010) and plant morphology (Kutzbach et al. 2004, von Fischer et al. 2010). Similar to our results, von Fischer et al (2010) found that *C. aquatilis* growing in deeper thaw depths had higher rates of CH₄ flux, suggesting that plants could

have greater CH₄ transport capacity through deeper below ground biomass with greater access to methanogenic substrates and labile carbon sources compared to plants in thinner active layer habitat.

CH₄ rates reported in this study for both *C. aquatilis* and *A. fulva* fall within the range of previously observed measurements from flux chamber plots in aquatic tundra (von Fischer et al. 2010) and wet tundra in the Barrow area (Morrissey et al. 1992, 1993, von Fischer et al. 2010, Lara et al. 2014), as well as other Arctic locations (Kutzbach et al. 2004, Sachs et al. 2010). Our flux measurements were carried out across a variety of ponds, at different plant densities, water depths and thaw depths, providing a good representation of spatial variability within vegetated pond margins in the region. In addition, we consider that our single measurements during peak growing season are representative of overall peak growing season trends given the low diurnal variability of CH₄ flux previously observed in the study area using both closed plot chambers (von Fischer et al. 2010) and eddy covariance (Zona et al. 2009). Repeated plot CH₄ flux rates observations by von Fischer et al., (2010) revealed a coefficient of variation of 16% for peak growing season, which suggests a temporal stability of CH₄ flux. It is important to note that CH₄ flux rates in this study are likely underestimated as CH₄ gas ebullition and diffusion from biologic and geologic sources (e.g. Anthony et al., 2012) were not quantified. However, these pathways should be further investigated temporally and spatially given their potential as CH₄ source.

Our species-specific retrogressive CH₄ models demonstrated a two-fold increase in CH₄ flux from both *A. fulva* and *C. aquatilis* between 1971-1972 and 2010-2013, modeled and estimated based on changes in biomass, thaw depth, and water depth. Similarly, studies employing CH₄ modeling based on vegetation change have also predicted increased CH₄ fluxes over decadal- time scales. Lara et al. (2012) showed increased CH₄ fluxes over decade-time scales in an aquatic pond margin community in the Barrow area based on CH₄ modeling of plant community changes. Also, Johansson et al. (2006) documented decadal scale increase in CH₄ fluxes in sub-arctic peatlands as a result of permafrost thaw.

The extrapolation of CH₄ estimates of *A. fulva* and *C. aquatilis* is, to our best knowledge, the first effort to quantify and understand regional CH₄ budgets of these dominant Arctic aquatic plant species. Estimates in this study represent approximately 78% of the total peak growing season CH₄ flux of $1,247 \times 10^3$ gC-CH₄ hr⁻¹ reported by Lara et al. (2014) for the Barrow Peninsula, even though *A. fulva* and *C. aquatilis* represent only ~11% of the land area. However, we consider that estimates reported by Lara et al (2014) may have underestimated CH₄ flux as a result of the lack of discrimination among these species, which vary in cover and density among different geomorphic types. In particular, the underestimation of *A. fulva* cover, which as shown in this study has 5-fold higher CH₄ fluxes compared to *C. aquatilis*, likely contributed to an overall underestimate of regional flux by Lara et al. (2014). Our results demonstrate that *A. fulva* dominates CH₄ contributions at a regional scale compared to *C. aquatilis* and other plant species (von Fischer et al. 2010, Lara et al. 2012). We attribute this to *A. fulva*'s unique adaptation to colonize deep water (Andresen and Loughheed accepted), which allows the plant to potentially extend roots in new stocks of labile carbon without competition, allowing CH₄ to be ventilated straight from the soil of these aquatic systems and into the atmosphere (Joabsson and Christensen 2001, Kutzbach et al. 2004).

The regional methane contributions of both *C. aquatilis* and *A. fulva* reported in this study (963×10^3 gC-CH₄ hr⁻¹) correspond to an efflux to the atmosphere of $23,112 \times 10^3$ gC-CO₂ hr⁻¹, assuming a CO₂ equivalence of 23-fold methane warming potential. This carbon flux negates approximately half of the total Net Ecosystem Exchange ($-42,658 \times 10^3$ gC-CH₄ hr⁻¹) reported by Lara et al. (2014) for the Barrow Peninsula, Alaska. Expansion of aquatic macrophytes, as suggested in Chapter 1, could further reduce the carbon sink capacity of the Arctic tundra.

3.5 CONCLUSION

Re-sampling of historical research sites established in 1970's demonstrated a deepening of the active layer depth and an increase in methane fluxes and aboveground biomass and cover of the dominant aquatic plants *C. aquatilis* and *A. fulva* over the past 40 years. Although both plant species only cover 11% of the land surface in the Barrow peninsula, we found that they account for approximately 78% of the total estimated methane emissions for this region (Lara et al. 2014). These results emphasize the effects of climate change in soil-atmosphere methane emissions and the importance of *C. aquatilis* and *A. fulva* as key methane-mediator species.

The increase in biomass and thaw depth not only has major implications for hydrology, geomorphology and energy balance (Andresen and Loughheed accepted, Hinkel et al. 2003, Swann et al. 2010, Shiklomanov et al. 2010, Liljedahl et al. 2011) but is of ecological significance for CH₄ flux as observed in this study. The increase in CH₄ fluxes in this study provides further evidence for positive climatic warming feedbacks from Arctic wetlands. In addition, the increase of methane will continue enhancing the forcing towards a warmer climate in the future for the Arctic region.

Chapter 4: Applications of digital repeat photography to track seasonal plant phenology and biomass of aquatic plants in Arctic wetlands.

4.1 INTRODUCTION

In the Arctic, timing, extent, and intensity of plant primary productivity is of ecological significance influencing hydrology, carbon fluxes and energy balance (Andresen and Loughheed accepted, Prowse et al. 2006, Westergaard-Nielsen et al. 2013). Arctic wetlands in particular, play a key role in the global carbon cycle and have recently been highlighted as key areas for study given their potentially changing function as carbon sinks or sources (Sitch et al. 2007, McGuire and Anderson 2009). Therefore, documenting wetland plant phenological responses to a changing climate in the Arctic is essential for assessing potential climatic feedbacks at a global scale.

Plot-scale phenological measurements can provide detailed observations on seasonal trends and changes at the species-level (e.g. Oberbauer et al. 2013). However, plot-level measurements are often labor-intensive and logistically difficult in the Arctic. Spectral vegetation indices from satellite-based remote sensing, such as the Normalized Difference Vegetation Index (NDVI), have proven to be a reliable method for estimating regional and continental scale changes in aboveground biomass and phenology in the Arctic (Bhatt et al. 2010, Epstein et al. 2012, Walker et al. 2012a). However, the limited temporal coverage added to the continual cloud cover for the Arctic limits detailed seasonal satellite observations (Stow et al. 2004). Therefore there is a need to develop mid-scale remote sensing methods to track plant biomass and bridge the gap between plot and satellite-level observations.

Digital repeat photography has recently been developed as an alternative near-surface remote sensing method for high temporal resolution in the characterization of plant greenness to track plant phenology based on indices derived from the red, green and blue (RGB) color spaces (e.g. Richardson et al. 2009, Elmore et al. 2012, Saitoh et al. 2012). Previous studies have employed commercial digital cameras to assess seasonal and inter-annual greening trends in a wide range of ecosystems including desert scrublands (Kurc and Benton 2010, Gonzalez 2012), subalpine grassland (Migliavacca et al.

2011), low Arctic tundra (Westergaard-Nielsen et al. 2013) and forests (Richardson et al. 2009, Elmore et al. 2012, Keenan et al. 2014). Greenness indices derived from RGB color space such as the green excess index (GEI) and the green chromatic coordinate (G%) have proven to be good indicators of gross primary production (GPP) and leaf area index (LAI) (Richardson et al. 2009, Ahrends et al. 2009, Saitoh et al. 2012b, Keenan et al. 2014). However, to our knowledge, no studies have directly linked RGB indices to aboveground biomass nor tested its potential in vegetated aquatic systems (e.g. wetlands). In addition, the technology has not been used for assessing plant phenological responses to different environmental conditions such as gradients of temperature and nutrients, key limiting factors in Arctic tundra plant communities with implications for carbon balance (Chapin, FS et al. 1995, Shaver et al. 1998). The spectral responses of these factors in non-experimental settings are also poorly understood (Jia 2003, Boelman et al. 2005). The monitoring of nutrient enriched sites as well as warmer, southern latitude sites will provide a better insight into the effects of nutrients and temperature in seasonal plant phenology, and thus, help understand seasonal dynamics in land-atmosphere carbon exchange.

This study will evaluate the effectiveness of digital repeat photography, a novel automated and cost-effective method to assess (i) inter-annual patterns in greenness of aquatic emergent macrophytes, (ii) the effects of latitude and nutrient gradients on seasonal greenness and (iii) the relationship between greenness, biomass and ground-based NDVI.

4.2 DATA AND METHODS

4.2.1 Research Site

This study was based in the Arctic coastal plain area near Barrow and Atkasuk, Alaska. This region is characterized by its low-relief, shallow thaw depth, deep permafrost and the dominance of thaw lakes and basins that contain numerous ponds (Andresen and Loughheed accepted., Hinkel et al. 2003). This Arctic landscape (~72 latitude) is known for its short growing season lasting approximately

three months from early June to the beginning of September with an average summer temperature of 4 °C. The annual growing cycle starts with warmer temperatures and 24 hours of light in late May-early June triggering snow melt, and thawing of the active layer, suitable conditions for plant growth. Peak growing season is usually reached in late July-early August followed by senescence and decreasing temperature and daylight hours. In late September, snow starts covering the vegetated areas and ice develops gradually freezing these shallow pond systems throughout the water column.

For the purpose of this study, we monitored a total of nine tundra pond sites (Table 5). This included five sites that were representative reference sites for Barrow, AK (IBP-J, IBP-C, IBP-10, ITEX-N, WL3), one enriched thermokarst pond (TK3), one enriched urban pond (BOXER) and two ponds located approximately 100 km south of Barrow near the village of Atqasuk, AK (ATQ-E, ATQ-W). Given that Barrow air temperature is expected to continue its upward trajectory over the next century, we used sites in Atqasuk as a proxy for the future state of Barrow ponds in regards to temperature effects in aquatic vegetation seasonal phenology. The mean summer (Jun-Aug) temperature in Atqasuk is ~8 °C, and twice as warm as Barrow (4 °C). All ponds contained the two dominant Arctic aquatic graminoids, *A. fulva* and *C. aquatilis*, except for ponds IBP-C and TK3, which contained only *C. aquatilis*. Three representative sites (IBP-C, J, 10) were monitored for three or four consecutive years, while the remaining sites were only monitored in 2013.

Table 5. Location and classification of sites sampled in this study. Plant types include *Arctophila fulva* (A) and *Carex aquatilis* (C).

Site	Type	Latitude	Longitude	Plant type	Season
IBP-10	Reference	71.2935	-156.70433	A, C	2011-2013
IBP-J*	Reference	71.29363	-156.70144	A, C	2010-2013
IBP-C*	Reference	71.2946	-156.70210	C	2010-2013
ITEX-N	Reference	71.31814	-156.58322	A, C	2013
WL03	Reference	71.2823	-156.61625	A, C	2013
TK3	Enriched/Thermokarst	71.27398	-156.636431	C	2013
BOXER	Enriched/Urban	71.30362	-156.752594	A, C	2013
ATQ-E	Lower Latitude	70.447892	-157.362756	A, C	2013
ATQ-W	Lower Latitude	70.457525	-157.401083	A, C	2013

* Sites with BirdCam; all others sites used TimeLapseCam

4.2.2 Digital cameras and set-up.

We employed inexpensive time-lapse cameras as a near-surface remote sensing method to continuously acquire photographs and monitor plant phenology and biomass of *C. aquatilis* and *A. fulva*. The cameras used in this project were either a Wingscapes WSCA02 BirdCam 2.0 (8 megapixels) or Wingscapes TimeLapseCam 8.0 (8 megapixels). All sites used the TimeLapseCam except IBP-J and IBP-C which used the BirdCam. Both cameras output 8-bit JPG files within the RGB range, although specific spectral responses are unknown. Each image is imbedded with site, date and time information. These cameras were selected because of their: (a) time-interval configuration, (b) freeze proof and water resistant design and (c) low cost (approximately US \$100-\$150).

Cameras were mounted on heavy-duty tripods 2.5m above ground and positioned pointing North at a downward angle of approximately -30 degrees from the horizon for consistency (Figure 19). The cameras were programmed to trigger at 30 minute intervals during the growing season from early June to late August-September. In some cases, technical difficulties with battery life or camera error limited some seasonal observations, and thus resulted in missing GEI values. The yearly end dates of image acquisition varied depending on access to remote sites by local volunteers. Cameras were operated with automatic exposure adjusting to different light conditions, therefore, the output pixels represent relative brightness for each channel as opposed to total radiance values. Conversely, white balance was fixed to “Sunlight” to minimize influences of automatic camera settings in scene illumination improving consistency in RGB brightness values from changing weather and lighting conditions (Richardson et al. 2009).

4.2.3 Image Processing

Images were analyzed for seasonal changes in the relative brightness of the Red, Green and Blue channels using a MATLAB script. User-defined regions of interest (ROIs) in the scene were selected to understand changes in channel brightness for areas dominated by different taxa (i.e. *C. aquatilis* or *A. fulva*). For these regions, we averaged all pixels for each channel and calculated channel chromatic coordinates (channel percentage) and the “green excess” index (GEI) (Richardson et al. 2009). The GEI index was calculated using the formula: $[2 \cdot G - (R + B)]$ where G is the brightness value in the green channel, R is the brightness value in the red, and B is the brightness value in the blue.

Daily averages were computed using only photos acquired within 6 hours of solar noon (14:00 hrs ADT) in order to capture the highest incident solar radiation on plants. Daily averages were also used to minimize diurnal changes in light and weather conditions on vegetation. We excluded images affected by water condensation on the lens, which represented less than 5% of all images.

To enable inter-comparison of RGB values among cameras, we assessed differences in RGB channel brightness by repeatedly photographing a gray calibration card commonly used for film, video and printer calibration (Digital Kolor Kard) under identical sunny conditions. We determined the average offset factor in each channel from an assumed half-tone gray brightness value of 127 in an 8-bit RGB scale of 0-255. Cameras gray calibration card brightness resulted on an average (\pm SD) of 108 ± 10 , 126.6 ± 10.4 and 127.8 ± 13.6 for Red, Green and Blue channels respectively. Both camera types showed similar channel brightness variability. After image processing, calculated RGB values were then corrected using the offset factor obtained for each camera.

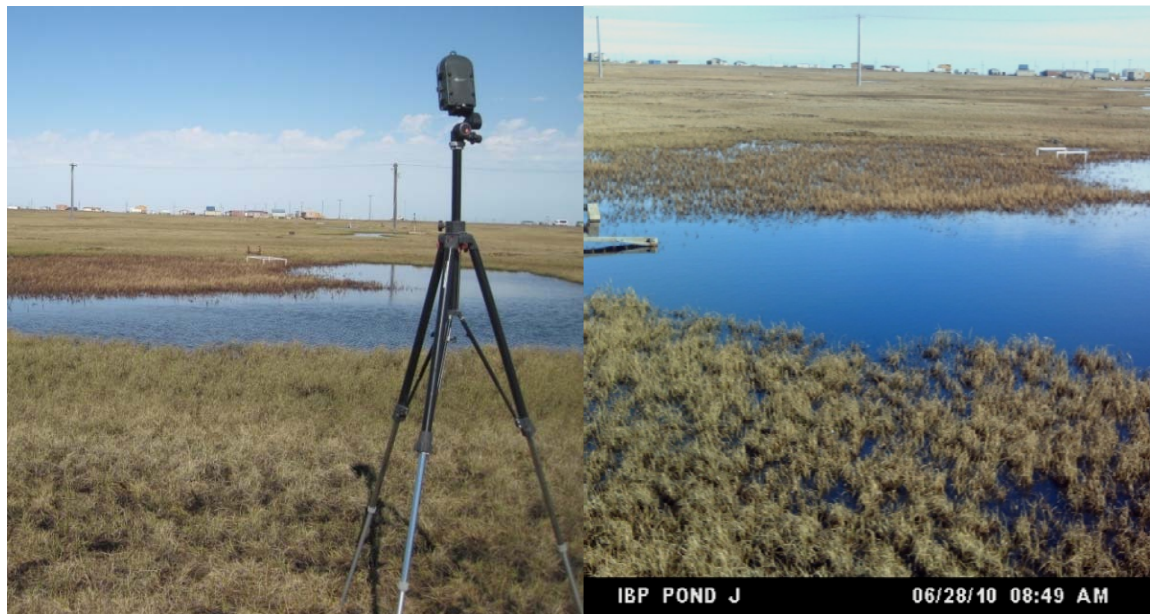


Figure 19. Near-surface, oblique camera mounted on a tripod facing north towards IBP Pond J (left) and a sample photo taken from this system (right) in early summer 2010.

4.2.4 Ancillary observations

Using methods described in Andresen et al. (In prep, see Chapter 3), we measured plant biomass of *C. aquatilis* (IBP-C, IBP-J) and *A. fulva* (IBP-J, IBP-10) in the footprint of the cameras every 10 days over the growing season (June-August) of years 2010-2013. In brief, to avoid harvesting plants from the study site, we estimated aboveground dry-weight biomass using allometric relationships that related plant dry weight to the sum of leaf lengths for *C. aquatilis* and plant height for *A. fulva*.

Field reflectance was collected from early June to late August of years 2011-2012 employing a single channel portable spectrometer (JAZ, Ocean Optics) that measured radiance (radiation from target) of vegetation. Radiance from the target was cross-calibrated at every site using a 99% reflective white calibration panel, allowing the estimation of reflectance by dividing the target radiance over the calibration panel radiance. Reflectance measurements were acquired for each biomass plot (described above) with a circular footprint of ~50cm in diameter. The Normalized Difference Vegetation Index

(NDVI) is a widely used multispectral index and has been commonly employed in Arctic vegetation to track plant productivity and biomass from plot-level (Boelman et al. 2005, Soudani et al. 2012, Gamon et al. 2013) to regional and global scales (Jia 2003, Bhatt et al. 2010, Walker et al. 2012a, Zeng and Jia 2013). NDVI was estimated from reflectance values in the red and infrared wavelengths using the formula: $NDVI = (800nm-680nm)/(800nm+680nm)$. Then, we averaged reflectance values of each sampled date at each site. In most instances, biomass and reflectance were collected within the field view of the time-lapse cameras, matching the photo's ROI used to extract GEI to allow comparison between biomass, GEI and NDVI. To better understand the relationships between NDVI, biomass and GEI, as well as the association of greening trends (e.g. GEI) to climate data, we used simple linear regressions as well as a partitioning analysis (i.e. regression tree) to identify non-linear interactions (Keenan et al. 2014). Green-up date was determined using a regression tree analysis performed in JMP 11. Climate data, including air temperature, precipitation, photosynthetic active radiation (PAR), wind speed and direction were measured using a HOBO® portable weather station operated near IBP Pond C from mid-June to mid-August.

4.3 RESULTS

Repeat photography appeared to accurately portray seasonal trends in greening and senescence for both *C. aquatilis* and *A. fulva* across the growing season and also distinguished unique seasonal greening patterns among species (Figure 20). *C. aquatilis* greened gradually over the course of the summer, with an average greening day, determined with regression tree analysis, of 189. Conversely, *A. fulva* greened abruptly starting in mid-July after a dip in GEI observed between days 190 and 200 as a result of the plant reddening and a resulting peak in the red channel. The average greening day for *A. fulva* was 199. Both *C. aquatilis* and *A. fulva* reached peak greenness in mid to late July, between days 200 and 210. Peak-season GEI values were different among plant species reaching values of 30-50 for *C. aquatilis* and 10-20 for *A. fulva*. Both species started to senesce on approximately the same date in

early August with *C. aquatilis* senescing gradually and *A. fulva* more rapidly reaching maximum red on days 250-260. GEI then approached a value near zero as winter approached (Figure 20).

Multi-year analysis of GEI from digital repeat photography revealed inter-annual variation in greening for both *C. aquatilis* and *A. fulva* in all multi-year sampled sites (n=3) (Figure 21). 2010 had the latest green-up dates (206 and 205 for *C. aquatilis* & *A. fulva*, respectively. While 2012 had the earliest green-up date for both *C. aquatilis* (180) and *A. fulva* (192). We found that June mean temperature was the best predictor of *C. aquatilis* green-up date ($r^2 = 0.34$, $p=0.04$, Green-up date= $201.573-4.711*(\text{June})$) while for *A. fulva* the relationship was non-significant ($r^2 = 0.21$, $p=0.24$, Green-up date= $203.478-1.776*(\text{June})$). The number of years (n=4) sampled in this study limited statistical predictions based on mean annual temperatures.

GEI was strongly related to more traditional measures of greening, such as aboveground biomass and ground-based NDVI. GEI was strongly associated with aboveground biomass for *A. fulva* ($r^2=0.89$, $p<0.001$) and *C. aquatilis* ($r^2=0.95$, $p<0.001$). Similarly, NDVI was also well associated with biomass for *A. fulva* ($r^2=0.58$, $p<0.01$) and *C. aquatilis* ($r^2=0.78$, $p<0.001$). GEI and NDVI also had a good agreement in both *C. aquatilis* ($r=0.93$, $p<0.001$) and *A. fulva* ($r=0.74$, $p<0.01$) (Figure 22).

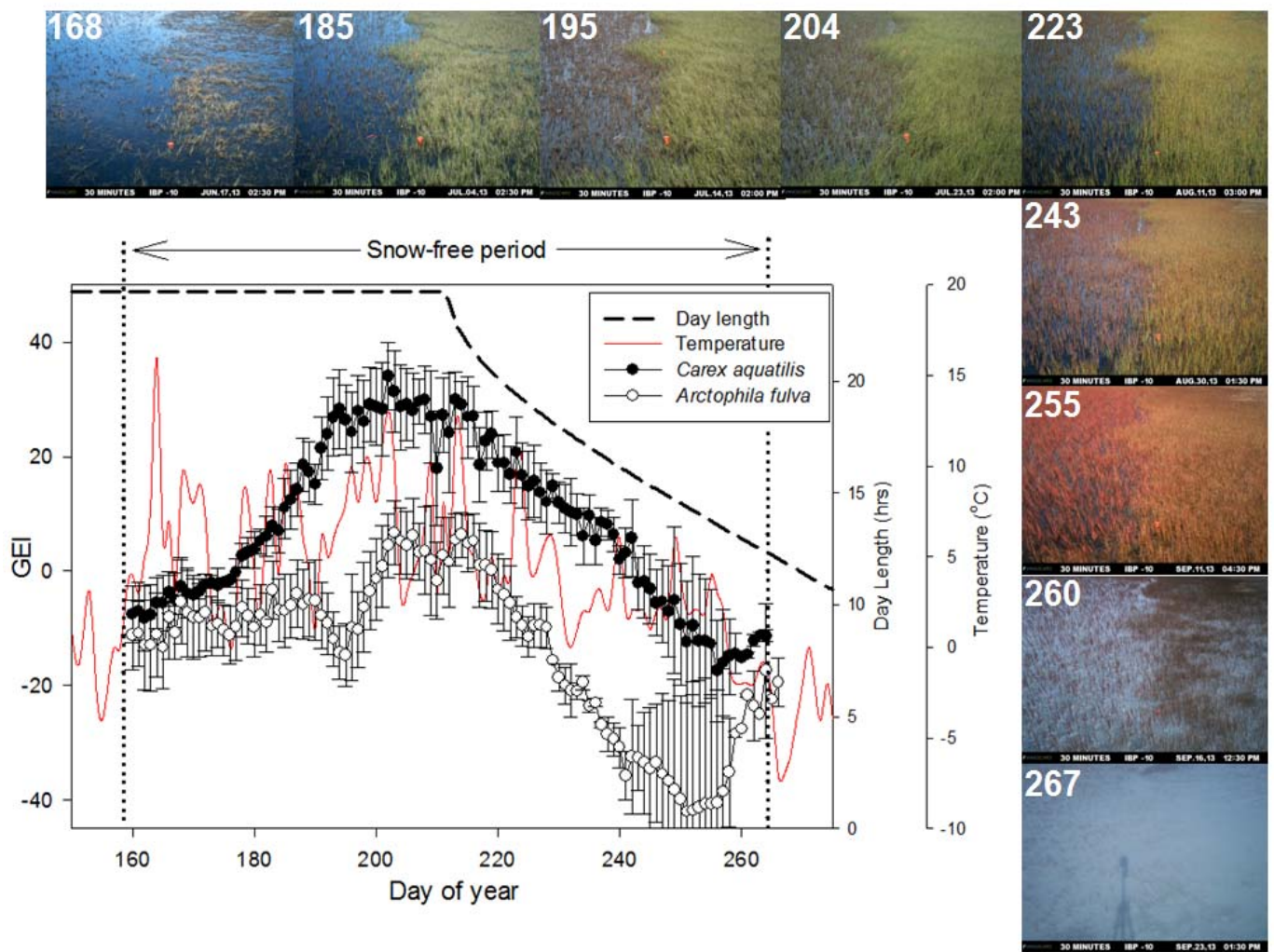


Figure 20. Average seasonal GEI trends of 2013 reference sites for *C. aquatilis* and *A. fulva* and environmental characteristics. Seasonal photographs are for site IBP Pond 10 (2013), with *A. fulva* (left) and *C. aquatilis* (right) of each image.

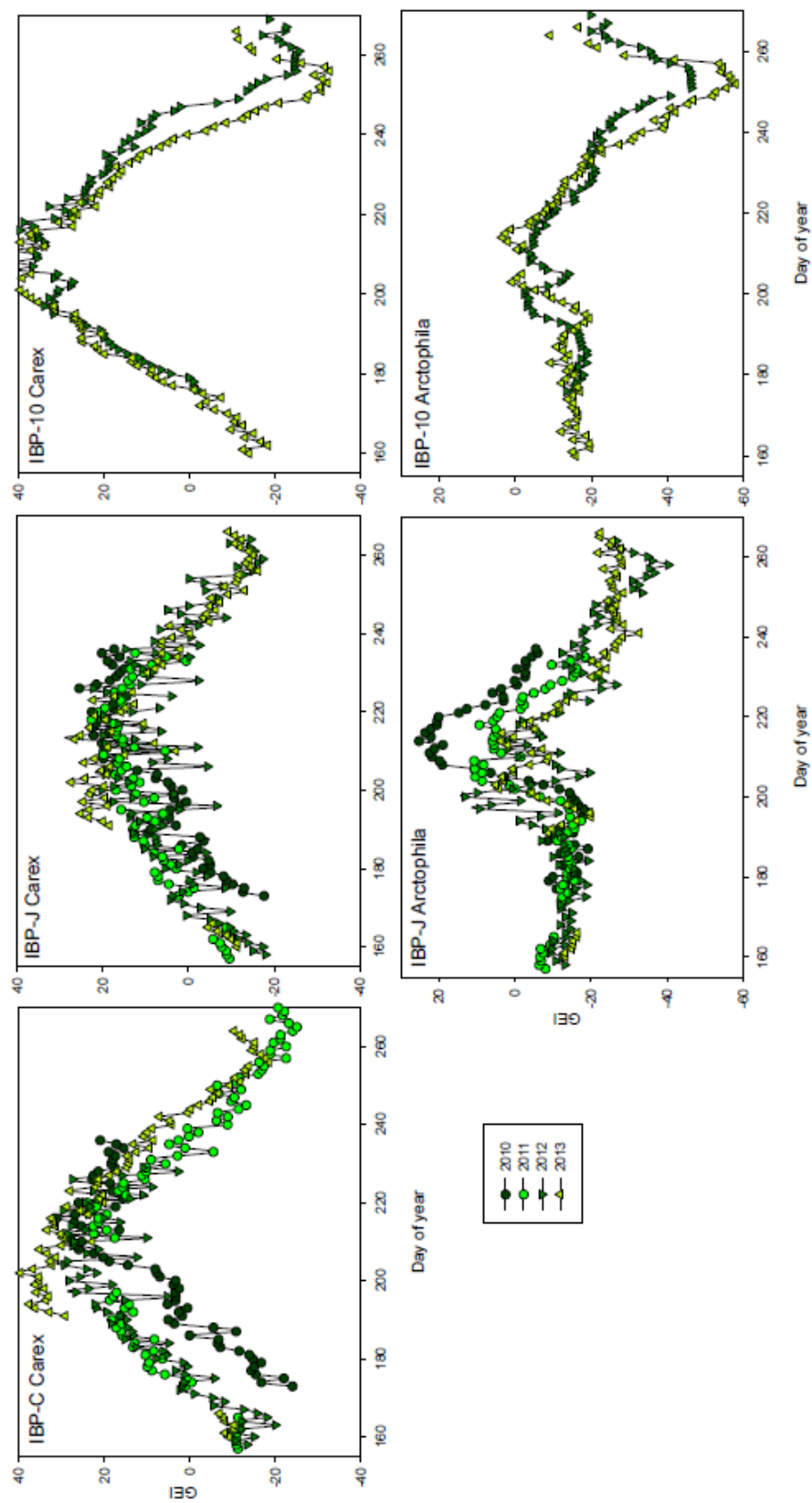


Figure 21. Multi-annual (2010-2013) seasonal patterns in GEI of *Carex aquatilis* and *Arctophila fulva* measured in multi-annual sites using digital repeat photography.

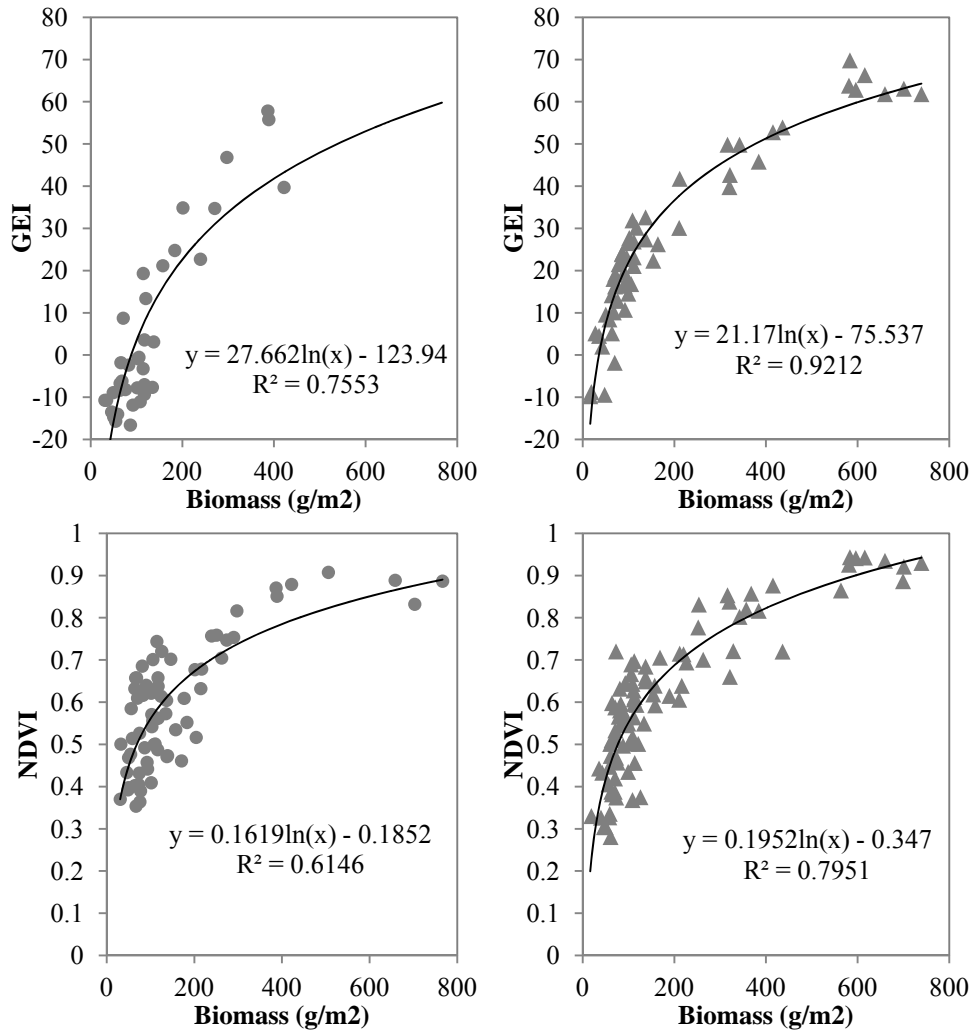


Figure 22. Responses of GEI and NDVI to aboveground dry biomass for *Arctophila fulva* (circles) and *Carex aquatilis* (triangles).

4.3.1 Environmental controls of greening.

Multi-annual (2010-2013) summer mean daily greenness measured by GEI was associated to daily mean temperature for both *C. aquatilis* ($r=0.48$ $p<0.0001$) and *A. fulva* ($r=0.37$ $p<0.0001$). Regression tree analysis indicated that greening was triggered by different threshold temperatures in each species. *C. aquatilis* GEI was observed to respond after 3.3 °C while *A. fulva* GEI responded to a warmer temperature of 6.5 °C (Figure 24).

Seasonal trends in GEI among reference sites (IBP-J, IBP-C, IBP-10, ITEX-N, WL3) were similar while cameras situated in enriched systems (BOXER,TK3) and lower latitude sites (ATQ-E, ATQ-W) showed the highest levels of GEI for both plant species (Figure 23). On average, *C. aquatilis* green-up two days earlier (day 185) in lower latitude sites compared to the sites located near Barrow (day 187) while *A. fulva* showed no difference in green-up date among site types (day 199). We observed a prolonged period of peak greenness of approximately 10 days in the enriched sites for *C. aquatilis*.

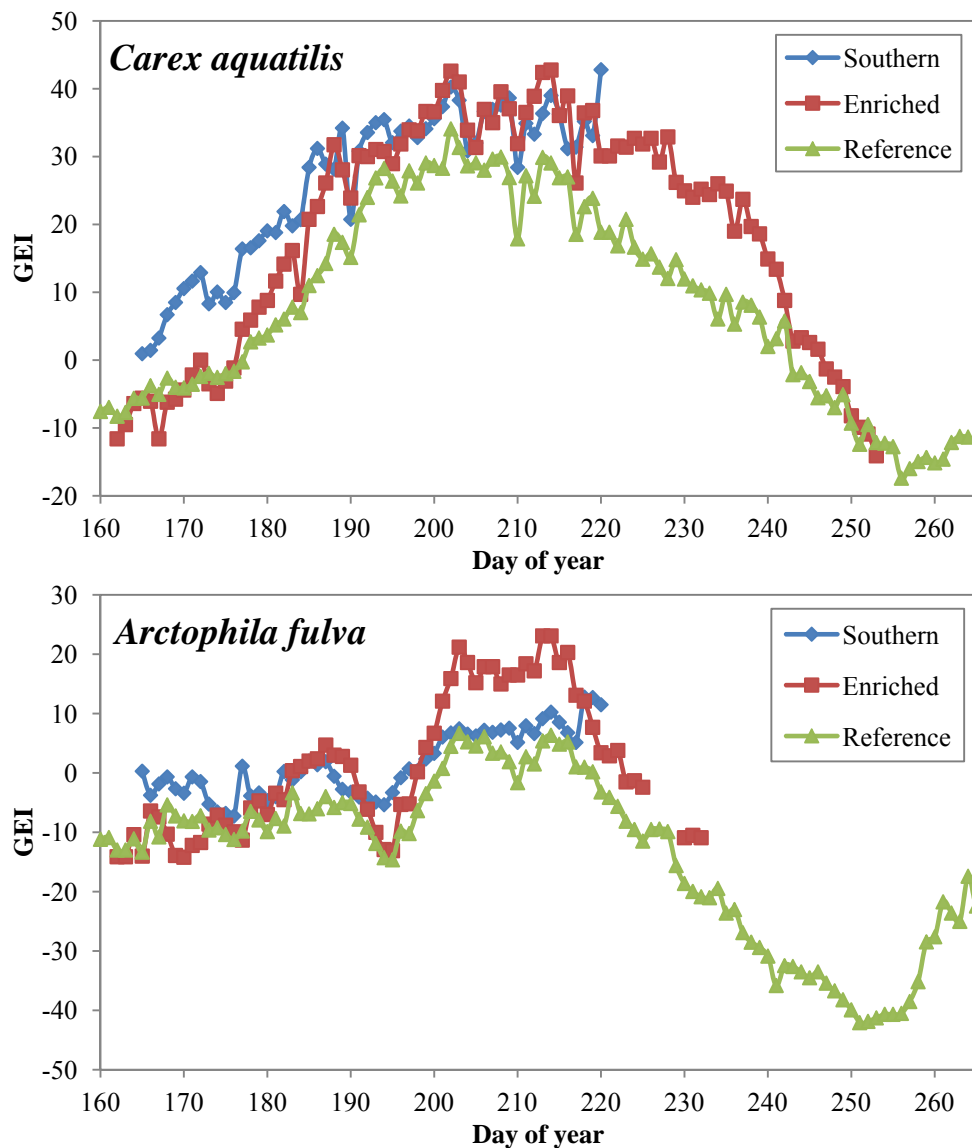


Figure 23. Seasonal variability of average GEI among site types for *Carex aquatilis* (top) and *Arctophila fulva* (bottom) in 2013.

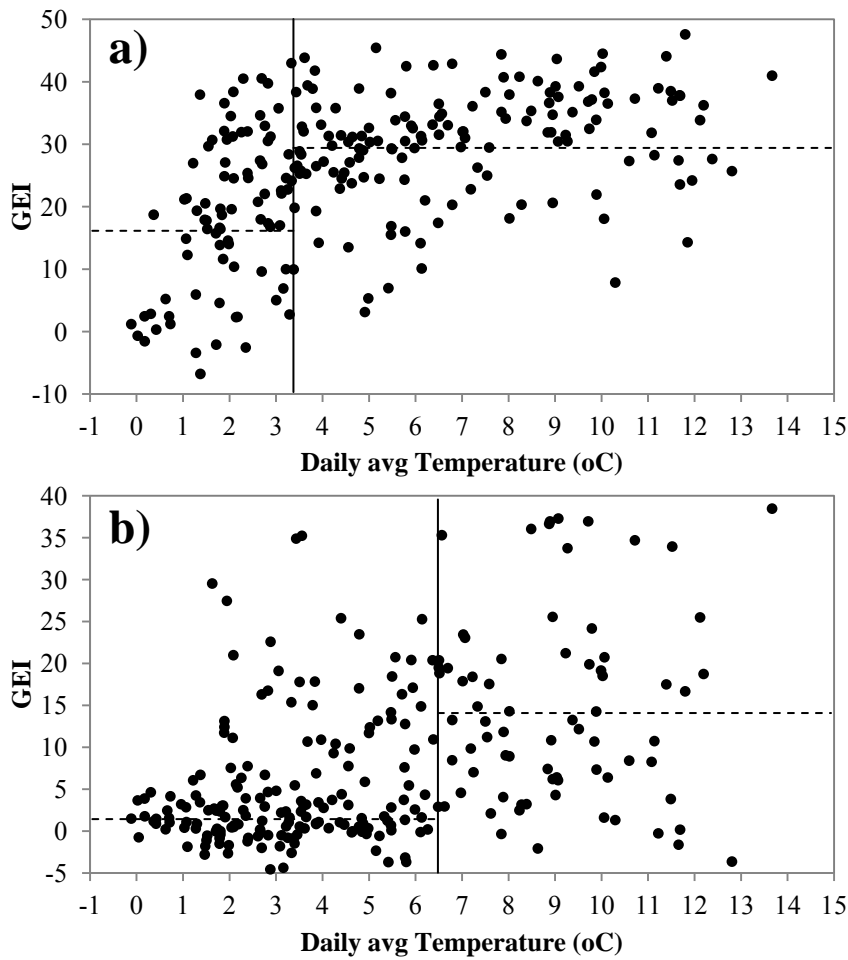


Figure 24. Multi-annual (2010-2013) daily average temperature effects on daily average GEI observations of sites (Pond-C, Pond-J and Pond-10) for (a) *Carex aquatilis* and (b) *Arctophila fulva*. Vertical solid lines represent the threshold points of greening, as determined by regression trees, while dashed horizontal lines are the means for each partition.

4.4 DISCUSSION

This study evaluated the potential of near-surface digital repeat photography as an inexpensive and automated method to (i) track inter- and intra-annual trends in plant phenology and biomass of aquatic emergent plants in remote Arctic wetlands and (ii) assess the effects of temperature and nutrients on seasonal phenology. Four years of summer phenology monitoring using digital repeat photography effectively identified variability in timing of greening among plant species, where temperature and nutrients play an important role in timing and peak intensity of greenness.

4.4.1 *Arctophila fulva* and *Carex aquatilis* phenology

The unique greening trends observed among different taxa (i.e. *C. aquatilis* and *A. fulva*) concurs with other studies that show taxa-specific greening timing (Richardson et al. 2009, Ide and Oguma 2010). *C. aquatilis* demonstrated an early and gradual increase in greening after snowmelt attributed to the characteristic sequential leaf growth in *C. aquatilis* and other sedges (Tieszen 1972, McRoy and Leue 1973). On the other hand, *A. fulva* had a delayed but abrupt green-up produced by the emergence of the plant from the water. Although *C. aquatilis* and *A. fulva* had different green-up patterns, both species reached maximum greening during the same time period in late July. The overall lower GEI values observed for *A. fulva* compared to *C. aquatilis* are likely attributable to the red pigmentation and low chlorophyll concentrations characteristic of *A. fulva* (Tieszen 1973).

The observed *A. fulva* green-up date was on average 10 days after *C. aquatilis* suggesting a higher temperature optima compared to *C. aquatilis*. Cold events in mid-summer greatly affected plant greenness in *A. fulva* likely associated to physiological plant stress (Chapin 1991) due to the reduction of photosynthesis as observed by the decrease in greenness, and thus, leaf nitrogen. We observed a decrease in GEI in 2011, 2012 and 2013 during peak season after cold fronts with the magnitude of change in GEI depending on the severity of the temperature decrease. Although greenness in *A. fulva* generally increased within ~5 days of a cold event, it never did recover completely to pre-event GEI greenness. *C. aquatilis* also showed decreases in greening after cold events during peak season but these dips were smaller than those observed for *A. fulva*. These observations suggest that *A. fulva* may be more sensitive to cold temperatures as compared to *C. aquatilis*.

Lengthening of growing season and a warming climate are factors known to influence plant species distribution (Grabherr et al. 1994, Walther et al. 2002). The observed higher temperature optima of *A. fulva* may help explain the recent increase in biomass and cover of this species over the past 40 years in the Barrow area (Andresen et al. in prep). Summer (June-August) mean temperature in the

coastal region of Barrow, Alaska has increased by about 3 °C over the past 60 years (Andresen and Loughheed accepted.) while degree days of thaw have also increase by 13 days over the past 40 years (Andresen in prep, Chapter 3). These warming trends are likely promoting the success of this species. In addition, *A. fulva* largely lacks any competition for habitat due to its adaptation to deep water, allowing colonization of new, untouched habitat and access to greater sources of nutrient supplies.

Temperature, nutrients and latitude have been observed to effect plant phenology (Borner et al. 2008, Oberbauer et al. 2013, Zeng et al. 2013). Greater greenness and earlier onset observed in enriched areas and lower latitudes compared to the reference sites suggests that both temperature and nutrients play a key role in enhancing productivity of these aquatic species. The earlier onset for southern, warmer sites agrees with previous experimental studies on plant phenology of *C. aquatilis* (Oberbauer 2013) and satellite derived greening (Zeng et al. 2013). Enriched sites showed the highest greening followed by lower latitude sites, coincident with manipulation studies in wet sedges (Shaver et al. 1998, Boelman et al. 2003) that found the greatest change in fertilized treatments with little or null responses to warming treatments. In addition, we found that nutrient enriched sites exhibited extended peak greening in *C. aquatilis*, senescing on average 10 days later than reference sites. No differences were observed for senescing in *A. fulva*. Our results support previous observations that tundra vegetation is strongly nutrient limited (Shaver et al. 1998). This is also supported by the higher above-ground biomass found in nutrient enriched sites compared to southern and reference sites (Andresen and Loughheed in prep, Chapter 5)

4.4.2 Biomass, Green Excess Index and NDVI

Our study supports the use of color indices derived from digital repeat photography to assess plant biomass in aquatic emergent plants. We found that the GEI performed better at higher plant biomass compared to NDVI. Although both NDVI and GEI asymptotically approached saturation with high biomass, GEI maintained a higher slope compared to the widely used NDVI (Gao et al. 2000, Viña

et al. 2011); this comparison was most obvious for *A. fulva*. Given that regional biomass estimates in aquatic systems for *C. aquatilis* and *A. fulva* averaged 154.2 ± 19 and 144.7 ± 27 g/m² respectively (Andresen et al in prep) and that these ranges are within the lower end of asymptotic curves, both GEI and NDVI are broadly suitable for these types of environments. However, differences among sites at the higher end of nutrient enrichment gradient may not be as easily distinguished with the industry standard NDVI.

It is important to note that the comparison among NDVI and GEI is based on different viewing angles, where NDVI was measured perpendicular to the ground (nadir view) while GEI was derived from an oblique angle ranging from 77°-85° off nadir view. Therefore, greenness was likely overestimated using the GEI, as compared to NDVI, due to the exposure of more leaves within the measured oblique angle footprint. Aerial nadir view GEI measurements of the timelapse cameras footprint demonstrated relatively low values of GEI compared to the obliquely derived GEI estimates from time lapse cameras (unpublished data). This suggests that GEI may not saturate compared to NDVI in high biomass conditions when measured from the same angle.

The strong correlation between GEI and NDVI for both plant species concurs with previous studies (Westergaard-Nielsen et al. 2013) indicating the potential of GEI for assisting as a mid-level remote sensing platform to track seasonal trends in plant phenology. However, in contrast to (Westergaard-Nielsen et al. 2013), we tested the performance of GEI along a range of plant biomass. This ability to accurately assess biomass and NDVI with the high observation frequency of this method will aid satellite based observations that are usually limited by coverage and cloud cover in this Arctic region (Stow et al. 2004).

4.4.3 Limitations of GEI

Shifts in incident solar radiation, changing weather conditions and wind-driven movement of the plants were observed to contribute to changes in color channel brightness within short periods of time

(e.g. minutes-hours). Our study minimized this variability by using “fixed white balance” and daily GEI averages, greatly reducing day-to-day variability and allowing better sensitivity to seasonal changes in vegetation greenness (Richardson et al. 2009). Therefore, we attribute seasonal GEI changes to direct changes in greenness of plants as opposed as illumination effects sensed by the camera.

Changes in water level are likely an important factor affecting GEI. Water level data (unpublished data) from four ponds across the Barrow area (IBP-J, IBP-B, ITEX-S, WL02) indicate a mean range in water level of 17 ± 7 cm for the ice-free season. These fluctuations may translate to the reduction or increment of the blue channel brightness sensed by the digital camera. Our study did not consider this phenomenon, which should be further investigated to provide a corrective methodology for such events.

As any other multichannel index, GEI might be problematic for characterizing color in specific objects or conditions (e.g. water, snow, vegetation) since different matter may reflect wavelengths differently but in a way that can produce a similar GEI value. For example, the GEI value of open water conditions at the beginning of the season is dominated by the blue signal over the green, while vegetation senescence at the end of the season is dominated by the red channel over the green. These two very different conditions produce the same GEI value. Therefore, we advise careful evaluation of GEI depending on the season period when the value was sensed.

It is important to note that commercial time lapse cameras are not scientific-grade instruments and signal may differ among sensors. In addition, the responses of the camera sensor to wavelengths in the red, green and blue portion of the spectrum are unknown. However, our methodology for inter-camera comparison may be an effective, non-technical approach for relating multiple sensors. Gray standard targets have previously been used for assessing color balance in cameras (Richardson et al. 2009) and, for this study, proved to be a useful and inexpensive calibration tool improving standardization for inter-site greenness comparisons. There is a lack of studies assessing how different

cameras can be used to accurately determine differences among sites (Sonnentag et al. 2011, 2012). Therefore, this study provides a preliminary method for assessing future dynamics of vegetation phenology obtained from RGB color brightness levels with multiple sensors at different sites.

Different models have been suggested for estimation of green-up and senescing dates depending mainly in the curve characteristics of seasonal greening trends. Curve fitting techniques such as quadratic functions have been employed for high Arctic regions given the short growing periods (Meltotte et al. 2008). Also, sigmoid curves have been widely employed in different environments (Richardson et al. 2009, Elmore et al. 2012, Granados et al. 2013) including the low Arctic (Westergaard-Nielsen et al. 2013). However, threshold-based estimation has proven to be more effective compared to curve-fitting models (Keenan et al. 2014). The threshold-based method used in our study proved to be an accurate system to identify mid-maximum GEI values that can be associated with key phenological changes for different species. Further comparison among curve-fitting and threshold approaches will provide a better insight into extracting phenological information from time series observations using digital repeat photography.

4.5 CONCLUSION

Timing and intensity of plant primary production and phenology has implications for land-atmosphere carbon exchange. The need for high-frequency monitoring of plant phenology and productivity in Arctic wetlands motivated the development of a novel system that employs digital repeat photography as a near-surface remote sensing method to track seasonal plant biomass and phenology. This novel automated method proved to be a reliable and cost-effective alternative for continual monitoring of biomass and greening in aquatic plants, as well as assessing nutrient and latitude effects in aquatic plant phenology, important factors influencing carbon and energy balance in arctic wetlands. In the future, the integration of near-surface observations with satellite-level remote sensing platforms

promises to greatly advance understanding of ecological systems, with the ultimate goal to further refine global coupled models and better predict future climatic scenarios.

Chapter 5: The relationship between nutrient enrichment of Arctic aquatic plants and their biomass and optical properties.

5.1 INTRODUCTION

In the Arctic, plant growth is limited by low temperatures, short growing-seasons and nutrients (Chapin et al. 1975, Shaver et al. 1998). Concurrent with warming temperatures, signs of increasing primary productivity of tundra vegetation across the Arctic have been observed in recent decades (Jia 2003, Walker et al. 2012b) with implications for global carbon and energy budgets (Walker et al. 2006, Oberbauer et al. 2007, Swann et al. 2010). Continued warming is expected for Arctic regions and will likely further stimulate plant productivity but the direct causes and consequences of increase productivity have been poorly studied.

Nutrients in particular play a key role influencing plant growth and the effects of climate change on nutrient availability are complex and diverse. Early work by Chapin et al., (1975) and Shaver et al., (1998) demonstrated that nutrients enhanced plant biomass and plant accumulated nutrients in wet tundra communities. Recent evidence suggests that nitrogen mineralization will be enhanced by increasing temperatures in Arctic soils (Weintraub and Schimel 2003, Uhlířová et al. 2007) and that this permafrost degradation from a warming Arctic may provide substantial nutrient inputs to freshwater ecosystems (Reyes and Loughheed n.d., Keuper et al. 2012). Therefore, it is of importance to assess the effects of these increased nutrients on plant productivity.

Our study builds on previous studies that examined nutrient impacts on wet tundra (Shaver et al. 1998, Boelman et al. 2003) by focusing on aquatic plant communities, which are relatively understudied in the Arctic. Arctic aquatic plants are known for their high productivity compared to terrestrial communities and contribute to a significant portion of methane fluxes (Andresen et al. in prep; Joabsson and Christensen, 2001; Lara et al., 2015). In recent decades, Arctic aquatic communities have increased in biomass and cover (Andresen and Loughheed accepted, Villarreal et al. 2012), likely attributed to an

increase in nutrients in their aquatic pond habitat (Lougheed et al. 2011b), but the impacts of nutrients on Arctic aquatic plant communities remain poorly understood.

Remote sensing has been used to detect and quantify plant productivity in Arctic systems based on multispectral indices such as the normalized vegetation index (NDVI). Boelman et al., (2003) showed the applicability of NDVI as a tool to track spectral responses of wet sedge tundra to nutrients in fertilization and warming experiments. Other studies employing digital repeat photography have successfully assessed plant phenology, biomass and productivity by evaluating vegetation color with indices in the visual spectral range (blue, green and red) (Richardson et al. 2007, Sonnentag et al. 2012, Saitoh et al. 2012b). However, no studies have investigated the plant spectral responses to nutrient enrichment in aquatic communities. Therefore, we investigate the spectral signals of aquatic plant communities to nutrients employing commonly used vegetation indices to improve monitoring of nutrient enrichment in Arctic aquatic landscapes.

The objectives of this study are to (i) assess the importance of environmental nutrient status on plant leaf nutrient concentrations, and (ii) the consequent spectral qualities of the dominant aquatic emergent vascular tundra plants in the Barrow area.

5.2 METHODS

5.2.1 Study Sites

A total of seventeen tundra ponds on the Barrow Peninsula, Alaska, were sampled in early August 2013 along a nutrient and latitudinal gradients. Sites were grouped in four categories according to their geographic location and nutrient source as: (i) enriched urban, (ii) enriched thermokarst, (iii) reference, and (iv) southern latitude (Figure 25, Table 6). Enriched urban ponds were located within the town of Barrow, AK and their source of nutrients was mainly from urban runoff. Enriched thermokarst ponds were situated within the Barrow Environmental Observatory (BEO), and their nutrient inputs

originate from permafrost slumping into ponds. Reference sites were located across the region in the historical International Biological Program (IBP) sites and in the BEO; but these sites were not experience accelerated permafrost slumping. Finally, southern latitude ponds were located 100 km south of Barrow near the town of Atqasuk, AK.

Table 6. Summary of sites sampled in this study

Site	Site type	Plant species	Latitude	Longitude
AHMA	Enriched/urban	A,C	71.303809	-156.741201
ATQ-E	Southern	A,C	70.447892	-157.362756
ATQ-W	Southern	A,C	70.457525	-157.401083
BOXER	Enriched/urban	A,C	71.303617	-156.752594
BOXER-2	Enriched/urban	A,C	71.304114	-156.748877
IBP-10	Reference	A,C	71.2935	-156.70433
IBP-B	Reference	A,C	71.294924	-156.702552
IBP-C	Reference	C	71.2946	-156.70210
IBP-D	Reference	A,C	71.294851	-156.700166
IBP-J	Reference	A,C	71.293626	-156.70144
IBP-X	Reference	A,C	71.295801	-156.699817
ITEX-N	Reference	A,C	71.318141	-156.58322
TK1	Enriched/thermokarst	C	71.27496	-156.632653
TK3	Enriched/thermokarst	C	71.273975	-156.636431
UTIQ	Enriched/urban	A,C	71.302004	-156.722267
WL02	Reference	C	71.2797	-156.61891
WL03	Reference	A,C	71.2823	-156.61625

5.2.2 Plant nutrients

For all sites, we collected live leaf and root tissue samples of *A. fulva* and *C. aquatilis* at peak growing season (1-8 August, 2013). Each sample consisted of 10-15 plants collected from different depths and multiple haphazardly selected locations in each pond. The collected plants were rinsed with distilled water, oven-dried at 60° C for 24 hrs inside open paper envelopes, then shipped to Utah State University Analytical Labs (USUAL) for immediate processing. Macro- and micro-nutrients in leaves of each plant were analyzed using an inductively-coupled plasma spectrometer (ICP-MS) (Table 7). Only nitrogen was analyzed by combustion analysis (HNO₃/H₂O₂ digestion, Leco Instrument). Although we

collected and analyzed both leaf and root tissue for this study, we focus only in leaf nutrients in this Chapter.

Table 7. Nutrients and detection limits analyzed from live plant tissue.

Element	Detection limit	Units	Element	Detection limit	Units
Al	0.05	mg/kg	Mn	0.05	mg/kg
As	0.05	mg/kg	Mo	0.05	mg/kg
B	0.05	mg/kg	N	0.01	mg/kg
Ba	0.05	mg/kg	Na	0.05	mg/kg
Ca	5.00E-06	%	Ni	0.05	mg/kg
Cd	0.05	mg/kg	P	0.00015	%
Co	0.05	mg/kg	Pb	0.05	mg/kg
Cr	0.05	mg/kg	S	0.00005	%
Cu	0.05	mg/kg	Se	1.25	mg/kg
Fe	0.05	mg/kg	Si	0.05	mg/kg
K	2.50E-05	%	Sr	0.05	mg/kg
Mg	5.00E-06	%	Zn	0.05	mg/kg

5.2.3 Additional observations collected

Concomitant with the collection of aquatic plants for nutrient analysis, we collected soil and water samples, measured aboveground plant biomass and spectral reflectance, and monitored most sites using time-lapse photography.

Soil samples from three separate locations at 10 cm depth within the roots of each plant species were combined in a plastic bag and frozen until analysis. In the lab, soil samples were air dried for 7 days given their high moisture and organic contents, then analyzed for physical and chemical factors (Table 8). Physical and chemical characteristics of the water were determined as described in (Lougheed et al. 2011b). In contrast to soil, which was sampled for each plant type, open water column properties were assumed to be representative of the whole pond, including both plant species.

Aboveground plant biomass was harvested within duplicate representative 50cm x 20cm quadrats for each species at each site. Similarly, 5-10 reflectance measurements with a circular footprint of ~50cm in diameter were acquired for each plant type in each site using a JAZ spectrometer (Ocean Optics). The Normalized Difference Vegetation Index (NDVI) was calculated from average plot

reflectance values. Using digital repeat photography in ponds (IBP-C, IBP-J, IBP-10, ITEX-N, WL03, TK3, BOXER, ATQ-E, ATQ-W), we calculated the “green excess” index (GEI) (Richardson et al. 2009) from peak season oblique images of each plant species using the formula: $[2 * G - (R + B)]$ where G is the brightness value in the green, R is the brightness value in the red, and B is the brightness value in the blue. For camera details and setup refer to Chapter 3.

5.2.4 Statistical analysis

Differences in environmental and biological characteristics among sites dominated by *C. aquatilis* and *A. fulva* were assessed using a paired t-test, with sites compared within each sampled ponds. We employed a principal components analysis (PCA) to generate linear combinations of the plant leaf nutrient data to describe the primary gradients in plant nutrient enrichment among the sites. PCA assumes linear relationships among variables, which was confirmed with scatterplots prior to analysis. Plant nutrient data was standardized to zero mean and unit variance and \log_{10} transformed where applicable to obtain a normal distribution. PCA axes were then associated to environmental data (i.e. soil and water nutrients, plant biomass, NDVI, GEI) using a Pearson correlation in JMP. Variables were log-transformed as required to meet the assumptions of normality. All statistical analyses were performed in SAS JMP software v4.0. Significance of the PC axes was confirmed in PC-ORD.

5.3 RESULTS

Soil chemistries within the ponds did not vary among locations dominated by different plant species (paired t-test, $p > 0.05$). However, there was a difference in green-up date and GEI ($p < 0.01$, Table 8). *A. fulva* greened later (day 198 vs. 182) and had lower GEI (9 vs. 33) as compared to *C. aquatilis*. There was no corresponding difference in NDVI or biomass among species ($p > 0.05$). We found significantly higher amounts of leaf Al, B, Ba, Mn, Na, Ni, Si and Zn in *C. aquatilis* compared to *A. fulva* ($p < 0.05$ level). The most abundant leaf element in both plant species was N, followed in

decreasing order by K, P, S and Mg for undisturbed ponds. Enriched ponds also showed a similar trend with N as the most abundant.

Examining the relationships between plant biomass and the macronutrient (N, P) content of the plant leaves, plant roots and soil revealed that plant leaf phosphorus content was a primary determinant of plant biomass, explaining approximately one-third of the variation in biomass for both species (Figure 25). There were no significant relationships between plant biomass and leaf nitrogen, nor between root nutrient content and soil nutrients. Furthermore, there were not significant relationships among the N and P contents of the plants with that of the soil. For subsequent analyses, we focus solely on leaf nutrient content.

Table 8. Range of environmental variables by vegetation type from 17 ponds in Barrow and Atkasuk, Alaska. p-values are for paired t-test between *Arctophila fulva* and *Carex aquatilis*.

Variable	<i>Arctophila fulva</i>		<i>Carex aquatilis</i>		p-value
	Mean	Range	Mean	Range	
Soil pH	5.23	4.7-6.3	5.14	4.7-6.3	0.63
Soil EC (dS/m)	0.86	0.26-2.75	0.589	0.12-2.67	0.34
Soil P, available (mg/kg)	4.78	2.1-10.5	5.625	2-21.3	0.63
Soil K, available (mg/kg)	42.82	19-80	44.188	11-109	0.88
Soil Nitrate-N (mg/kg)	1.87	0.01-7.6	1.2	0.01-3.8	0.35
Greening day (DOY)	198	198-199	182	175-191	0.001
GEI	8.57	0-18	33.44	29-37	0.001
NDVI	0.65	0.485-0.759	0.646	0.459-0.860	0.86
Biomass (g/m ²)	222.23	124-532	197.4	109-365	0.50
Leaf TN (%)	2.36	1.71-3.06	2.36	1.35-2.76	p>0.05
Leaf P (%)	0.2	0.1-0.32	0.2	0.012-0.28	p>0.05
Root TN (%)	1.1	0.67-1.45	0.96	0.69-1.2	p>0.05
Root P (%)	0.15	0.06-0.56	0.13	0.07-0.26	p>0.05

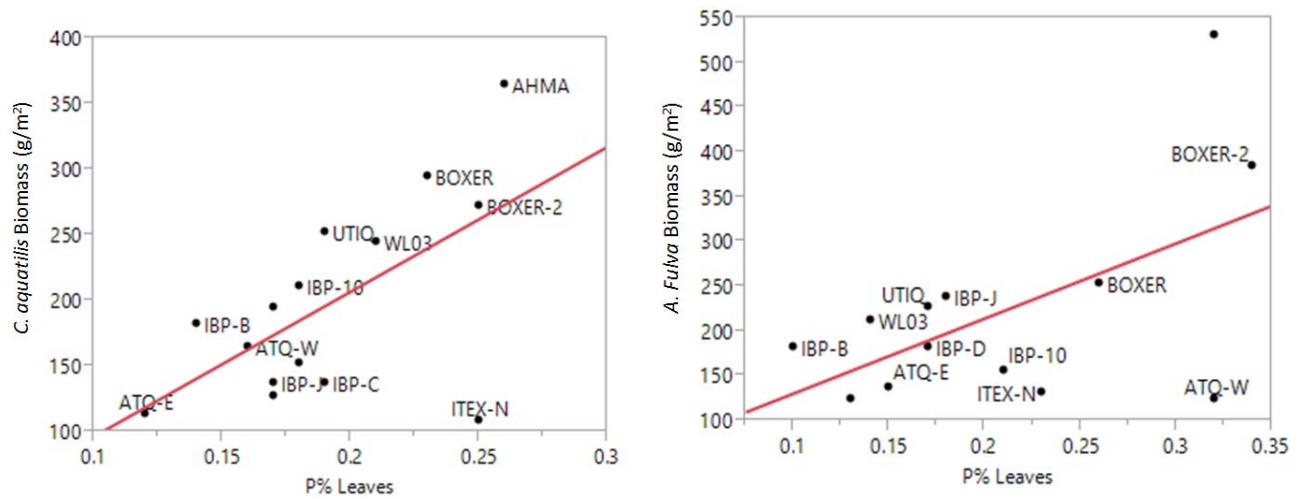


Figure 25. Relationship between dry weight aboveground biomass of *Carex aquatilis* (left) and *Arctophila fulva* (right) with P content of leaves. *Arctophila fulva* Biomass = $46.519361 + 839.79717 \cdot \text{P\% Leaves}$ ($r^2=0.32$, $p=0.04$). *Carex aquatilis* Biomass = $-13.80174 + 1103.8418 \cdot \text{P\% Leaves}$ ($r^2=0.37$, $p=0.02$).

5.3.1 *Arctophila fulva*

For *A. fulva*, the first four PC axes explained 72% of the variation in plant leaf nutrients. However, only axis 1 and 4 were significant ($p<0.05$). Axis 1 explained 29% of the variation and was positively correlated with the plant macronutrients N, P, K, Ca, Mg, S as well as other elements such as Al, B, Ba, Mn, S, Zn, and negatively correlated with Ni, Pb and Fe. On the other hand, PC axis 4 explained 13% of the variation and was positively correlated with As, Ca, Cr, Ni, Si, Zn. (Table 9).

Site types for *A. fulva* were clearly separated along axes PCA-1 and PCA-4 (Figure 26). Enriched urban systems were located on the upper left quadrant, coinciding with higher concentrations of many leaf nutrients and environmental variables such as soil P, EC, water P, Si, DOC, plant biomass and greener vegetation (e. g. NDVI, GEI). Conversely, reference sites and those at southern latitude were located in the opposite quadrants of the plot with a wider distribution along PCA-4 and thus, wider variability in leaf nutrients and environmental conditions. Southern sites for *A. fulva* showed a similar distribution to reference sites (Figure 26).

5.3.2 *Carex aquatilis*

C. aquatilis PC axis 1 and 2 explained 50% of the variation in the plant nutrient data. PC axis 1 (26%) showed positive relationships with important macronutrients N, P, and Mg and other elements such as Al, Ba, Co, Cu, Fe, Mo, Pb, Zn. PC axis 2 explained 24% of the variation in leave nutrients and was positively associated with Al, Ba, K, Mn, P, S, Sr, and negatively associated with Ni, Mo, Se, Zn (Table 9).

The *C. aquatilis* PC plot of axes 1 and 2 (Figure 26) also showed sites grouped by type. We observed a good separation along PCA-2 of enriched urban ponds as compared to reference, southern and enriched thermokarst. Similar to *A. fulva*, the enriched sites were found at the positive end of an axis that was positively associated with water nutrients, alkalinity, conductance, plant biomass, NDVI and soil K (Table 10). Environmental variables positively associated with the vertical distribution of sites along axis 1 included soil EC, water nutrients (TDP, SRP, NO₃), and negative correlations with water pH, alkalinity and *C. aquatilis* green-up date (Table 10). We noticed grouping of enriched thermokarst and reference sites for *C. aquatilis* in a portion of the plot associated with high electrical conductance and water TDP, SRP and NO₃. Conversely to *A. fulva*, the southern sites were clustered away from other sites, in the lower left quadrant, likely reflecting earlier green up, higher GEI, and lower soil and water nutrients.

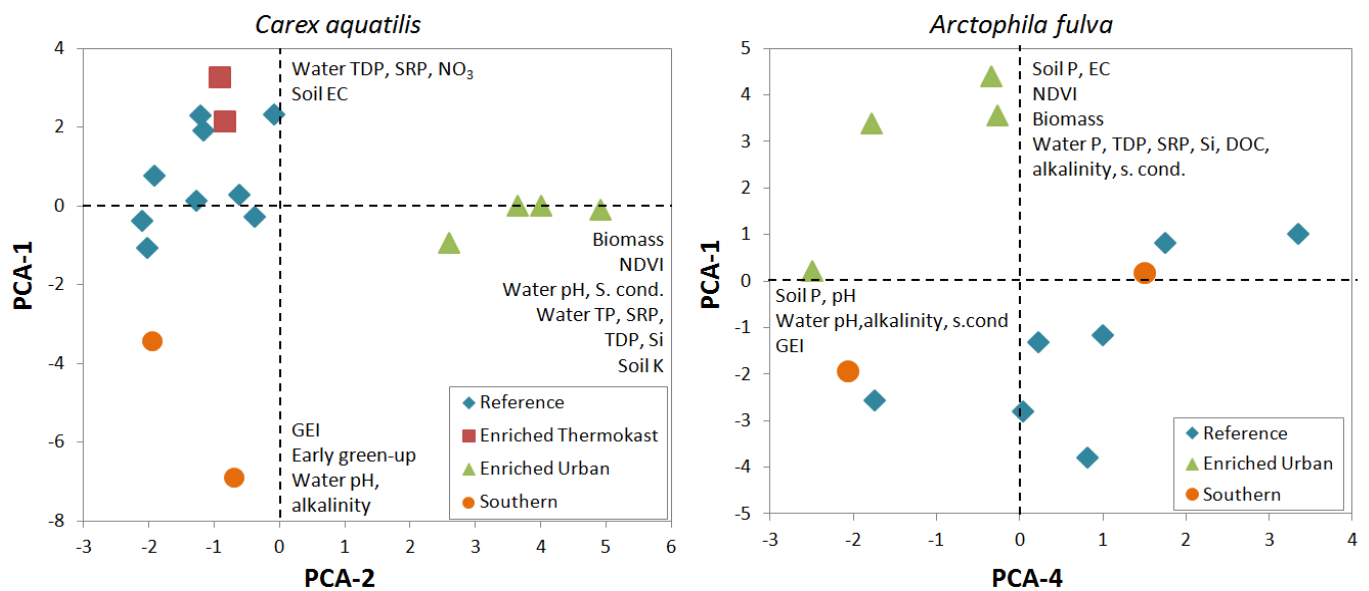


Figure 26. Plots of PCA site scores for *Carex aquatilis* (left) and *Arctophila fulva* (right) plant nutrient data. Environmental variables associated to each axes are depicted along dashes lines.

Table 9. Correlation coefficients between PC axes and leaf nutrients for *Carex aquatilis* (right) and *Arctophila fulva* (left).

<i>Carex aquatilis</i>						<i>Arctophila fulva</i>					
	Variance explained	Axis p-value	Leaf Nutrient	<i>r</i>	p-value		Variance explained	Axis p-value	Leaf Nutrient	<i>r</i>	p-value
PC axis 1	26%	0.001	TN	0.84	0.001	PC axis 1	29%	0.001	P	0.83	0.001
			Cu	0.72	0.001				Sr (log)	0.81	0.001
			Co (log)	0.66	0.019				K	0.80	0.001
			Na (log)	0.63	0.007				Al	0.76	0.003
			Mg	0.61	0.009				Mg	0.73	0.005
			Pb	0.58	0.016				B	0.71	0.007
			P	0.56	0.019				S	0.64	0.018
			Mo	0.54	0.024				Mn	0.63	0.021
			Zn	0.53	0.029				Ca (log)	0.53	0.061
			Fe	0.44	0.081				Ba (log)	0.51	0.076
			Al	-0.48	0.051				TN	0.50	0.079
			Ba (log)	-0.73	0.001				Ni	-0.53	0.063
			S	0.89	0.001				Pb	-0.54	0.057
			K	0.85	0.001				Fe (log)	-0.56	0.046
			Sr (log)	0.74	0.001	PC axis 2	15%	0.73	Se (log)	0.64	0.019
PC axis 2	24%	0.001	Mn	0.65	0.004				B	0.60	0.029
			Ba (log)	0.59	0.013				S	0.53	0.061
			P	0.56	0.020				Pb	0.53	0.065
			Al	0.43	0.084				Ba (log)	-0.67	0.013
			Se (log)	-0.48	0.052				Mo	-0.70	0.007
			Ni	-0.62	0.008	PC axis 3	14%	0.22	TN	0.62	0.025
			Mo	-0.63	0.007				As (log)	0.77	0.074
			Zn	-0.66	0.004				Co	0.67	0.012
			Ni (log)	-0.85	0.001				Cu	0.63	0.021
			Si	0.74	0.001				Se (log)	-0.65	0.017
PC axis 3	15%	0.004	Pb	0.60	0.010	PC axis 4	13%	0.053	Cr	0.86	0.001
			Na (log)	0.48	0.049				As (log)	0.80	0.054
			Mg	0.47	0.060				Zn	0.58	0.038
			Ba (log)	0.44	0.075				Ni	0.58	0.040
			Fe	-0.68	0.003				Ca (log)	0.50	0.080
			P	-0.47	0.056				Si	-0.53	0.061

Table 10. PC axes correlations with environmental variables.

<i>Carex aquatilis</i>				<i>Arctophila fulva</i>			
	Environmental Variable	<i>r</i>	<i>p</i> -value		Environmental Variable	<i>r</i>	<i>p</i> -value
PC axis 1	Green-up day	0.67	0.049	PC axis 1	Water Si	0.84	0.001
	Water TDP (log)	0.56	0.020		Water SRP (log)	0.83	0.000
	Water NO ₃ (log)	0.52	0.034		Water Sp. Conductance	0.80	0.003
	EC (log)	0.47	0.069		Water TDP (log)	0.79	0.001
	Water SRP (log)	0.44	0.076		Water Alkalinity	0.78	0.005
	Water Alkalinity (log)	-0.61	0.020		NDVI	0.70	0.008
	GEI	-0.62	0.078		Water DOC	0.69	0.019
	Water pH	-0.70	0.004		Water TP (log)	0.67	0.012
					EC (log)	0.66	0.027
PC axis 2	Water Sp. Conductance (log)	0.94	0.001	PC axis 2	Soil P (log)	0.61	0.045
	Water Alkalinity (log)	0.88	0.001		Biomass (log)	0.59	0.034
	Biomass	0.84	0.001		Water pH	0.53	0.096
	Water pH	0.73	0.002		Green-up day	0.69	0.084
	Water Si (log)	0.58	0.018		Water NO ₃	0.55	0.050
	NDVI	0.56	0.071	PC axis 4	Water pH	-0.68	0.021
	Water SRP (log)	0.54	0.024		GEI	-0.67	0.098
	Water TDP (log)	0.53	0.029		Soil P (log)	-0.67	0.025
	Soil K	0.50	0.050		Water Alkalinity	-0.62	0.044
	Water TP (log)	0.41	0.099		Water Sp. Conductance	-0.59	0.057
					Soil pH	-0.53	0.075
PC axis 3	Water NO ₃ (log)	-0.46	0.062				
	Water DOC (log)	-0.61	0.016				
	Water Light ext. (log)	-0.63	0.050				
PC axis 4	Soil pH	-0.60	0.014				

5.4 DISCUSSION

We explored the causes and consequences of nutrient enrichment in two aquatic tundra species. Plant leaf nutrients were a function of soil and water nutrients in Arctic tundra ponds. In addition, plant greenness, measured by NDVI and GEI, was dependent on leaf nutrient content in both plant species. However, among species, there were slight differences in regional trends. For both plant species, tundra ponds located in pristine, non-urbanized areas had unique biological, physical and chemical characteristics compared to ponds in developed, urban areas. In addition, *C. aquatilis* located in ponds in southern latitudes near Atkasuk appeared to be distinct in leaf nutrients as compared to ponds in the Barrow area.

5.4.1 Leaf nutrients

The environmental gradient investigated in this study was highlighted by the principal component analysis and allowed better understanding of the factors influencing leaf nutrients. Our

analysis, in line with other studies, demonstrated that soil and water nutrients in ponds have a major role influencing plant leaf nutrients and aboveground biomass (Chapin et al. 1975, Shaver et al. 1998). The Arctic in general is typically low in inorganic forms of N and P in both soil (Mack et al. 2004, Keuper et al. 2012) and surface waters (Rautio et al. 2011) and thus, nutrient limited. Arctic wet sedge in particular, has been noted to be P limited given the highly organic soil which enhances recycling of N by mineralization of soil organic matter (Shaver et al. 1998, Keuper et al. 2012). Primary productivity of phytoplankton and periphyton in tundra ponds in the Barrow area have been shown to be NP co-limited (Lougheed et al in prep). In line with other studies, aquatic *C. aquatilis* and *A. fulva* appear to be P limited (Chapin, FS et al. 1995, Boelman et al. 2003, Mack et al. 2004) as observed by the significant relationship between biomass and P leaf content (Figure 1). In fact, Lougheed et al (in prep) suggest that macrophytes may be outcompeting algae for available nitrogen, which may account for the N limitation of algae but N sufficiency of plants. Soil nutrients were similar among cover types which may explain the homogeneous leaf macronutrient concentrations among *C. aquatilis* and *A. fulva*. However, we observed higher micronutrients and other non-essential minerals in *C. aquatilis* compared to *A. fulva*. These disparities are likely attributed to differences in taxonomic groups and thus, taxa-specific seasonal nutrient dynamics (Chapin et al. 1975).

The nutrient concentrations reported in this study span the general range for northern wetlands (Edwards and Jefferies 2010). However, when compared to historical studies in the Barrow area, we found that the major plant macronutrients in *C. aquatilis* had increased since they were determined in 1970 by Chapin et al (1975). N, P and Ca plant percentage content increased from 2.18 ± 0.09 to 2.4 ± 0.2 , 0.15 ± 0.02 to 0.18 ± 0.03 , 0.08 ± 0.02 to 0.14 ± 0.08 respectively. However, K and Mg were lower compared to 1970. Calcium is known to accumulate as a result of high transpiration (Chapin 1980). The remarkable increase in Ca observed between 1970 and 2013 suggests that *C. aquatilis* may be experiencing higher evapotranspiration rates compared to 43 years ago, likely as a consequence of

modern warmer temperatures. It is important to note that *C. aquatilis* has been shown to have phenotypical differences across moisture gradients (Shaver et al. 1979). Thus, *C. aquatilis* sampled in wet meadows might have different physiological characteristics, and therefore, different nutrient composition compared to *C. aquatilis* in aquatic systems.

Higher plant nutrients may be a result of increased nutrient release from thawing permafrost (Reyes and Lougheed n.d., Keuper et al. 2012) which has also contributed to higher nutrient concentrations found in the ponds (Lougheed et al. 2011b). Increased nutrients in these systems is likely attributed to the degradation of permafrost in these tundra ponds as seen by Andresen and Lougheed (accepted, Chapter 1), which has been shown to release valuable nutrients from permafrost core thawing experiments (Reyes and Lougheed n.d.).

5.4.2 Plant nutrients, biomass, NDVI and GEI

In line with other studies in the Arctic, the spectral properties of plants, in particular NDVI, have been noted to be a function of biomass caused by increased nutrients (Boelman et al. 2003, 2005, Epstein et al. 2012, Raynolds et al. 2012). For example, Boelman et al. (2003) observed higher NDVI values in N and P fertilized treatments in wet sedge tundra communities compared to control treatments. In our study, we attribute the NDVI observations to be a function of both plant biomass and leaf greenness as a result of high plant productivity. This is expected assuming that more biomass exposed to the sensor will increase the NDVI signal as it will be less but more vigorous, greener plants. However, the distinction between plant biomass and leaf greenness is beyond the scope of this study and should be further investigated.

The overall increase in terrestrial productivity of the Arctic as observed from satellite NDVI measurements has been directly attributed to increasing temperatures. However, our study and others have shown that Arctic tundra greenness is a direct response from nutrient enrichment. In a temperature and fertilization experimental studies on wet sedge tundra using greenhouses, Shaver et al. (1998)

observed nutrients as the main limiting factor for biomass with non-significant responses to the increase in temperature by the greenhouse. In addition, spectral reflectance measurements of these experimental treatments by Boelman et al. (2003) confirmed higher NDVI for nutrient treatments and negligible differences between controls and greenhouse treatments. This supports that Arctic tundra is more strongly limited by nutrients as opposed to temperature, suggesting that the overall “greening” of the Arctic tundra observed from satellite sensors is likely an indirect result of temperature, as thawing of permafrost and the resulting increase in soil nutrient mineralization are enhancing biomass and thus, altering the optical properties of vegetation.

The spectral response of plants as a result of nutrient enrichment further supports the capacity to use remote sensing to monitor plant nutrient quality. Among the spectral indices used, the Normalized Difference Vegetation Index (NDVI) is a widely used multispectral index employed to remotely estimate primary productivity and biomass, and has been a common used for Arctic tundra ecosystems (Jia 2003, Stow et al. 2004, Bhatt et al. 2010, Zeng et al. 2013). In contrast, GEI is an emerging multiband index that has been strongly associated to gross primary production and phenology in vegetation (Ide and Oguma 2010, Migliavacca et al. 2011, Saitoh et al. 2012b, Keenan et al. 2014). However, it has not been tested for monitoring nutrient enrichment in aquatic plants. Our study is among the first to link variability in the nutrient content of Arctic aquatic plants with spectral responses measured using multispectral indices such as NDVI and GEI. With further refinement, the use of a digital repeat photography system could have the potential to improve monitoring and understanding of global change effects in aquatic communities at large temporal and spatial scales. The wide range of environmental nutrient status and the broad spatial sampling undertaken in this study provides a strong confidence on the use of these indices at a regional scale.

5.5 CONCLUSION

This study, one of the first to focus on Arctic aquatic vegetation, indicates that these important components of the Arctic coastal plain landscape are nutrient limited. We suggest that warming will not necessarily directly induce an increase in biomass, but the indirect results of warming, such as permafrost thaw and related biogeochemical inputs will provide the resources to enhance productivity in these systems. In addition, this study established baseline relationships between optical measurements and aquatic plant nutrient status across a nutrient gradient. This will enable a better understanding of nutrients enrichment impacts at larger spatial scales using remote sensing with the ultimate goal of advancing the understanding of climate change in tundra aquatic systems.

Chapter 6: General Discussion

The work presented in this dissertation was motivated by the urgent need to better understand the effects of global change on the structure and function of Arctic freshwater systems over decadal time-scales and their potential to affect global climatic feedbacks. Given the key role of the Arctic in the global carbon and energy balance, this study represents a significant contribution for assessing future state of the Arctic and the earth system. The effects of climate change on aquatic systems are complex, diverse and significant. This dissertation addresses key research challenges in regards to climate change consequences in Arctic aquatic systems over decadal time scales. Below, I present the summary of the key research findings of this dissertation, as well as broader implications and future research directions.

6.1 KEY RESEARCH FINDINGS

6.1.1 *How has surface hydrology of Arctic tundra ponds changed over the past 65 years?*

And what are the causes and consequences at the ecosystem level? (Chapter 2)

Fine spatial-scale analysis of surface hydrology in the Barrow peninsula revealed a decrease in pond area (30%) and number (17%) over the past 65 years (1948-2013). Losses were coincident with warmer air and water temperatures, increased active layer depth and density and cover of aquatic emergent plants in ponds. These observations agree with current (Schindler and Smol 2006b, White et al. 2007) and projected (Prowse et al. 2006, Avis et al. 2011) climate change effects on Arctic aquatic systems. We propose that the increased water loss from longer and warmer summers, permafrost degradation and transpiration of encroaching aquatic grasses in ponds are the major factors contributing to the decline in surface hydrology of ponds. In addition, the reduction in area and number of ponds was similar among drained thaw lake basin ages, contradicting the hypothesized geomorphological cycle of pond development and expansion in these basins (Billings and Peterson 1980, Hinkel et al. 2007). These

results strongly suggest that the geomorphological evolution of the Arctic landscape is highly dependent on changes in climate.

6.1.2 *How has aquatic plant biomass, thaw depth and methane flux changed over the past 40 years? And what is the current regional methane flux from aquatic vegetation? (Chapter 3)*

We observed a significant increase of thaw depth, aquatic emergent biomass and modeled methane efflux over the past 40 years in tundra ponds. These results agree with decadal time-scale studies on non-aquatic thaw depth (Streletskiy et al. 2007), vegetation biomass (Hill and Henry 2011) and modeled carbon fluxes (Lara et al. 2012). These increases are attributable to a warmer climate resulting in permafrost degradation and leaching of nutrients into ponds (Reyes and Loughheed n.d., Loughheed et al. 2011b), which have enhanced plant biomass and methane fluxes. We found aquatic emergent plants to contribute to approximately 78% of the methane contributions at the regional scale, while only covering 11% of the landscape. This study emphasizes the importance of aquatic tundra vegetation in methane fluxes and thus, land-atmosphere carbon release.

6.1.3 *How can we track seasonal plant biomass and phenology of aquatic vegetation using near-surface remote sensing? (Chapter 4)*

This study developed and evaluated the effectiveness of digital repeat photography as a novel, cost-effective tool to remotely monitor seasonal dynamics of plant biomass and phenology. Analysis of multi-year (2010-2013) observations of image-derived GEI (green excess index) revealed taxon-specific phenological trends, as well as inter-annual variability in greening, consistent with other phenological studies in temperate regions (Richardson et al. 2009, Saitoh et al. 2012a). We found temperature and nutrients to be the major drivers of seasonality (green-up date, senescence) and intensity of greening. *A. fulva* had a stronger greening response to warmer temperatures, suggesting that the increase in *A. fulva* biomass and cover observed over recent decades may be linked to the increasing temperature trends in

the Arctic . Biomass, ground-reflectance NDVI and GEI derived from cameras had a strong association, supporting the use of digital repeat photography as a mid-level remote sensing tool for fine-scale monitoring of greening and with potential applications for validating satellite-derived plant phenology trends.

6.1.4 *How aquatic plants respond to nutrient enrichment?* (Chapter 5)

This study demonstrates that greening and biomass of the dominant aquatic plants of tundra ponds, *C. aquatilis* and *A. fulva*, are (i) a function of plant nutrient content, (ii) likely P-limited, (iii) driven by changes in nutrient availability in both the soil and water. This study, one of the first to focus on Arctic aquatic vegetation, indicates that these important components of the Arctic coastal plain landscape are nutrient limited. We suggest that warming will not necessarily directly induce an increase in biomass, but the indirect results of warming, such as permafrost thaw and related biogeochemical inputs (Reyes and Loughheed, nd), will provide the resources to enhance productivity in these systems. In addition, this study established baseline relationships between optical measurements and aquatic plant biomass across a nutrient gradient. This will enable us to better understand nutrients at larger spatial scales using remote sensing with the ultimate goal of advancing the understanding of climate change in tundra aquatic systems.

6.2 BROADER IMPLICATIONS

An enhanced understanding of how the Arctic system, in particular the structure and function of freshwater ecosystems, is responding to climate change will provide a better insight into the future state of the Arctic and the global system as they continue to respond to warming. This study finds potentially contrasting impacts of warming on Arctic wetlands and their potential feedbacks of energy balance and land-atmosphere carbon exchange. The decrease of pond open water areas and expansion of aquatic vegetation observed in this investigation is likely promoting a negative climatic feedback by decreasing

surface albedo, and thus, reflecting solar energy back to space. This effect may be further stimulated by enhanced primary productivity of vegetation, driven by increased nutrients in aquatic systems from permafrost thawing and temperature-enhanced soil processes. While vegetation is often considered a carbon sink, others have shown that *C. aquatilis* and *A. fulva* in wet tundra are large sources of both CO₂ and CH₄ to the atmosphere (von Fischer et al. 2010, Lara 2012). The expansion of these aquatic graminoids are key to methane transport from the sub-surface to the atmosphere and may enhance carbon efflux as compared to the flux from open water; thus, acting as a positive climatic feedback. Therefore, the relative roles of these ecosystem processes to climatic feedbacks should be further assessed to better understand the direction of which the Arctic system will contribute to future climate.

Ecological research is experiencing a major technological revolution. While satellite-based remote sensing has allowed estimation of important decadal-scale trends in the Arctic, such as greening (e.g. Bhatt), land cover change (Lin et al. 2012), and hydrological changes (e.g. Hinkel et al. 2003). These methodologies remain limited by low frequency of image acquisition, access to cloud-free imagery, and relatively low spatial resolutions. The near-surface remote sensing tool presented in this study, with further refinement, has the power to monitor Arctic ecosystem structure and function from the species-level to communities with greater reliability, resolution and frequency compared to satellite-based methods, and with substantially less labor than traditional ecological surveys which are labor-intensive and logistically difficult.

The integration of near-surface observations with satellite-level remote sensing platforms promises to greatly advance understanding of ecological systems, with the ultimate goal to further refine global coupled models and better predict future climatic scenarios.

6.3 FUTURE RESEARCH PRIORITIES

The research presented in this dissertation has contributed to key findings in Arctic aquatic ecosystem ecology that scientists have largely failed to address as a result of the lack of long term datasets. Significant intellectual contributions have been made through this dissertation on the effects of global change in the Arctic system over decadal time-scales; however, we have identified further research priorities that should be addressed:

- Continue to rescue, resample and preserve historic as well as current research sites for further long-term monitoring, in particular in the Arctic region.
- Understand in detail the biogeochemical processes of production, uptake, transport and release of carbon by Arctic aquatic species in response to climate change.
- Nutrient enrichment in tundra ponds from permafrost thaw and nitrogen mineralization among other biogeochemical processes should be further investigated.
- Meta-analysis and synthesis of both historic and current research of ecosystem structure and function for the Arctic coastal plain is of urgent need.
- Develop formal protocols for evaluating, calibrating and validating satellite-based products using near-surface remote sensing with the ultimate goal to establish a regional and global scale monitoring system to track Arctic ecosystem responses to climate change.
- Incorporate the models developed in this study to global climatic coupled models to better understand the direction of climatic feedbacks under increased warming scenarios in the Arctic.

References

- Aber, J. S., S. W. Aber, F. Pavri, E. Volkova, and R. L. P. II. 2006. Small-format aerial photography for assessing change in wetland vegetation, Cheyenne Bottoms, Kansas. *Transactions of the Kansas Academy of Science* 109:47–57.
- ACIA. 2005. Arctic climate impact assessment scientific report. Cambridge University Press, Cambridge, UK.
- Ahrends, H., S. Etzold, W. Kutsch, R. Stoeckli, R. Bruegger, F. Jeanneret, H. Wanner, N. Buchmann, and W. Eugster. 2009. Tree phenology and carbon dioxide fluxes: use of digital photography for process-based interpretation at the ecosystem scale. *Climate Research* 39:261–274.
- Aiken, S., and R. Buck. 2002. Aquatic leaves and regeneration of last year's straw in the arctic grass, *Arctophila fulva*. *Canadian Field-Naturalist* 116.
- Andresen, C. G., and V. L. Lougheed. (n.d.). Disappearing Arctic tundra ponds: Fine-scale analysis of surface hydrology in drained thaw lake basins over a 65 year period (1948-2013). *Journal of Geophysical Research*.
- Andresen, C. G., S. A. Vargas, V. L. Lougheed, and C. E. Tweedie. 2014. Kite-based Aerial Photography (KAP): A Low Cost, Effective Tool for Wetland Research. *Wetlands Science and Practice*.
- Arp, C. D., B. M. Jones, F. E. Urban, and G. Grosse. 2011. Hydrogeomorphic processes of thermokarst lakes with grounded-ice and floating-ice regimes on the Arctic coastal plain, Alaska. *Hydrological Processes* 25:2422–2438.
- Avis, C. a., A. J. Weaver, and K. J. Meissner. 2011. Reduction in areal extent of high-latitude wetlands in response to permafrost thaw. *Nature Geoscience* 4:444–448.
- Barsdate, R. J., and R. T. Prentki. 1973. Nutrient Metabolism and Water Chemistry in Lakes and Ponds of the Arctic Coastal Tundra. U.S. Tundra Biome Data Report 73-27. Page 163.
- Bekryaev, R. V., I. V. Polyakov, and V. a. Alexeev. 2010. Role of Polar Amplification in Long-Term Surface Air Temperature Variations and Modern Arctic Warming. *Journal of Climate* 23:3888–3906.
- Bhatt, U. S., D. a. Walker, M. K. Raynolds, J. C. Comiso, H. E. Epstein, G. Jia, R. Gens, J. E. Pinzon, C. J. Tucker, C. E. Tweedie, and P. J. Webber. 2010. Circumpolar Arctic Tundra Vegetation Change Is Linked to Sea Ice Decline. *Earth Interactions* 14:1–20.
- Billings, A. W. D., and K. M. Peterson. 1980. Vegetational Change and Ice-Wedge Polygons through the Thaw-Lake Cycle in Arctic Alaska. *Arctic and Alpine Research* 12:413–432.
- Boelman, N. T., M. Stieglitz, K. L. Griffin, and G. R. Shaver. 2005. Inter-annual variability of NDVI in response to long-term warming and fertilization in wet sedge and tussock tundra. *Oecologia* 143:588–97.

- Boelman, N. T., M. Stieglitz, H. M. Rueth, M. Sommerkorn, K. L. Griffin, G. R. Shaver, and J. a Gamon. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia* 135:414–21.
- Borner, A. P., K. Kielland, and M. D. Walker. 2008. Effects of Simulated Climate Change on Plant Phenology and Nitrogen Mineralization in Alaskan Arctic Tundra Effects of Simulated Climate Change on Plant Phenology and Nitrogen Mineralization in Alaskan Arctic Tundra. *Arctic, Antarctic, and Alpine Research*. 40:27–38.
- Bouchard, F., K. W. Turner, L. a. MacDonald, C. Deakin, H. White, N. Farquharson, a. S. Medeiros, B. B. Wolfe, R. I. Hall, R. Pienitz, and T. W. D. Edwards. 2013. Vulnerability of shallow subarctic lakes to evaporate and desiccate when snowmelt runoff is low. *Geophysical Research Letters* 40:6112–6117.
- Britton, M. E. 1957. Vegetation of the arctic tundra. Pages 26–72 *in* H. H. P., editor. *Arctic Biology* (2nd ed.1967). Oregon State University Press.
- Brown, J., K. Hinkel, and F. E. Nelson. 1980. An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska. Dowden Hutchinson & Ross, Stroudsburg, PA.
- Cabot, E. C. 1947. The northern Alaskan Coastal Plain interpreted from aerial photographs. *Geographical review* 37:639–648.
- Callaghan, T. V., T. R. Christensen, and E. J. Jantze. 2011. Plant and Vegetation Dynamics on Disko Island, West Greenland: Snapshots Separated by Over 40 Years. *Ambio* 40:624–637.
- Carroll, M. L., J. R. G. Townshend, C. M. DiMiceli, T. Loboda, and R. a Sohlberg. 2011. Shrinking lakes of the Arctic: Spatial relationships and trajectory of change. *Geophysical Research Letters* 38:L20406.
- Carson, C. 1968. Radiocarbon dating of lacustrine strands in arctic Alaska. *Arctic*:12–26.
- Carson, C., and K. Hussey. 1962. The oriented lakes of arctic Alaska. *The Journal of Geology* 70:417–439.
- Chapin, F. I. 1980. The mineral nutrition of wild plants. *Annual review of ecology and systematics* 11:233–260.
- Chapin, F. I., K. Van Cleve, and L. Tieszen. 1975. Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. *Arctic and Alpine Research* 7:209–226.
- Chapin, F. S. 1991. Integrated responses of plants to stress. *BioScience* 41:29–36.
- Chapin, FS, I., and M. Chapin. 1981. Ecotypic differentiation of growth processes in *Carex aquatilis* along latitudinal and local gradients. *Ecology* 62:1000–1009.
- Chapin, FS, I., G. Shaver, and A. Giblin. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711.

- Cornelissen, J. H. C., P. M. van Bodegom, R. Aerts, T. V. Callaghan, R. S. P. van Logtestijn, J. Alatalo, F. S. Chapin, R. Gerdol, J. Gudmundsson, D. Gwynn-Jones, A. E. Hartley, D. S. Hik, A. Hofgaard, I. S. Jónsdóttir, S. Karlsson, J. a Klein, J. Laundre, B. Magnusson, A. Michelsen, U. Molau, V. G. Onipchenko, H. M. Quested, S. M. Sandvik, I. K. Schmidt, G. R. Shaver, B. Solheim, N. a Soudzilovskaia, A. Stenström, A. Tolvanen, Ø. Totland, N. Wada, J. M. Welker, and X. Zhao. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology letters* 10:619–27.
- Dobson, J. L. 1989. Autecology of aquatic and terrestrial growth forms of *Arctophila fulva*, an arctic tundra grass of northern Alaska. University of Idaho, Moscow, ID, US.
- Duarte, C. M., T. M. Lenton, P. Wadhams, and P. Wassmann. 2012. Abrupt climate change in the Arctic. *Nature Climate Change* 2:60–62.
- Edwards, K. a., and R. L. Jefferies. 2010. Nitrogen uptake by *Carex aquatilis* during the winter-spring transition in a low Arctic wet meadow. *Journal of Ecology* 98:737–744.
- Eichel, K. A., M. L. Macrae, R. I. Hall, L. Fishback, and B. B. Wolfe. 2014. Nutrient Uptake and Short-Term Responses of Phytoplankton and Benthic Algal Communities from a Subarctic Pond to Experimental Nutrient Enrichment in Microcosms. *Arctic Antarctic and Alpine Research* 46:191–205.
- Elmore, A. J., S. M. Guinn, B. J. Minsley, and A. D. Richardson. 2012. Landscape controls on the timing of spring, autumn, and growing season length in mid-Atlantic forests. *Global Change Biology* 18:656–674.
- Epstein, H. E., M. K. Reynolds, D. a Walker, U. S. Bhatt, C. J. Tucker, and J. E. Pinzon. 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters* 7:015506.
- Epstein, H. E., M. D. Walker, F. S. Chapin, and A. M. Starfield. 2000. a Transient, Nutrient-Based Model of Arctic Plant Community Response To Climatic Warming. *Ecological Applications* 10:824–841.
- Euskirchen, E. S., A. D. McGuire, F. S. Chapin, S. Yi, and C. C. Thompson. 2009. Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: implications for climate feedbacks. *Ecological applications* 19:1022–43.
- Von Fischer, J. C., R. C. Rhew, G. M. Ames, B. K. Fossick, and P. E. von Fischer. 2010. Vegetation height and other controls of spatial variability in methane emissions from the Arctic coastal tundra at Barrow, Alaska. *Journal of Geophysical Research* 115:G00I03.
- Frey, K. E., and J. W. McClelland. 2009. Impacts of permafrost degradation on arctic river biogeochemistry 182:169–182.
- Frey, K. E., D. I. Siegel, and L. C. Smith. 2007. Geochemistry of west Siberian streams and their potential response to permafrost degradation. *Water Resources Research* 43:W03406.

- Frey, K. E., and L. C. Smith. 2005. Amplified carbon release from vast West Siberian peatlands by 2100. *Geophysical Research Letters* 32:L09401.
- Frohn, R. C., K. M. Hinkel, and W. R. Eisner. 2005a. Satellite remote sensing classification of thaw lakes and drained thaw lake basins on the North Slope of Alaska. *Remote Sensing of Environment* 97:116–126.
- Frohn, R. C., K. M. Hinkel, and W. R. Eisner. 2005b. Satellite remote sensing classification of thaw lakes and drained thaw lake basins on the North Slope of Alaska. *Remote Sensing of Environment* 97:116–126.
- Gamon, J. a., K. F. Huemmrich, R. S. Stone, and C. E. Tweedie. 2013. Spatial and temporal variation in primary productivity (NDVI) of coastal Alaskan tundra: Decreased vegetation growth following earlier snowmelt. *Remote Sensing of Environment* 129:144–153.
- Gao, X., A. Huete, W. Ni, and T. Miura. 2000. Optical–biophysical relationships of vegetation spectra without background contamination. *Remote Sensing of Environment* 74:609–620.
- Grabherr, G., M. Gottfried, and H. Pauli. 1994. Climate effects on mountain plants. *Nature* 369:448.
- Granados, J. a., E. a. Graham, P. Bonnet, E. M. Yuen, and M. Hamilton. 2013. EcoIP: An open source image analysis toolkit to identify different stages of plant phenology for multiple species with pan-tilt-zoom cameras. *Ecological Informatics* 15:58–65.
- Grosse, G., V. Romanovsky, K. Walter, H. Lantuit, and S. Zimov. 2008. Distribution of Thermokarst Lakes and Ponds at Three Yedoma Sites in Siberia:551–556.
- Hill, G. B., and G. H. R. Henry. 2011. Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology* 17:276–287.
- Hinkel, K., W. Eisner, B. JG, F. E. Nelson, K. M. Peterson, and D. Xiaoyan. 2003. Spatial extent, age, and carbon stocks in drained thaw lake basins on the Barrow Peninsula, Alaska. *Arctic, Antarctic, and Alpine Research*. 35:291–300.
- Hinkel, K. M., B. M. Jones, W. R. Eisner, C. J. Cuomo, R. a. Beck, and R. Frohn. 2007. Methods to assess natural and anthropogenic thaw lake drainage on the western Arctic coastal plain of northern Alaska. *Journal of Geophysical Research* 112:F02S16.
- Hinzman, L. D., N. D. Bettez, W. R. Bolton, F. S. Chapin, M. B. Dyurgerov, C. L. Fastie, B. Griffith, R. D. Hollister, A. Hope, H. P. Huntington, A. M. Jensen, G. J. Jia, T. Jorgenson, D. L. Kane, D. R. Klein, G. Kofinas, A. H. Lynch, A. H. Lloyd, a. D. McGuire, F. E. Nelson, W. C. Oechel, T. E. Osterkamp, C. H. Racine, V. E. Romanovsky, R. S. Stone, D. a. Stow, M. Sturm, C. E. Tweedie, G. L. Vourlitis, M. D. Walker, D. a. Walker, P. J. Webber, J. M. Welker, K. S. Winker, and K. Yoshikawa. 2005. Evidence and Implications of Recent Climate Change in Northern Alaska and Other Arctic Regions. *Climatic Change* 72:251–298.

- Hinzman, L. D., C. J. Deal, a D. McGuire, S. H. Mernild, I. V Polyakov, and J. E. Walsh. 2013. Trajectory of the Arctic as an integrated system. Ecological applications : a publication of the Ecological Society of America 23:1837–68.
- Hobbie, J. E. 1980. Limnology of Tundra Ponds. Dowden, Hutchinson & Ross, Stroudsburg, PA.
- Hobbie, J. E., B. J. Peterson, N. Bettez, L. Deegan, W. J. O'Brien, G. W. Kling, G. W. Kipphut, W. B. Bowden, and A. E. Hershey. 1999. Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. Polar Research 18:207–214.
- Hopkins, D. 1949. Thaw lakes and thaw sinks in the Imuruk Lake area, Seward Peninsula, Alaska. The Journal of Geology 57:119–131.
- Hudson, J., and G. Henry. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 90:2657–2663.
- Ide, R., and H. Oguma. 2010. Use of digital cameras for phenological observations. Ecological Informatics 5:339–347.
- IPCC. 2007. Intergovernmental Panel on Climate Change.
- Jia, G. J. 2003. Greening of arctic Alaska, 1981–2001. Geophysical Research Letters 30:2067.
- Joabsson, A., and T. Christensen. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Global Change Biology 7:919–932.
- Joabsson, A., T. Christensen, and B. Wallén. 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Trends in Ecology & Evolution 14:385–388.
- Johansson, T., N. Malmer, P. M. Crill, T. Friborg, J. H. Åkerman, M. Mastepanov, and T. R. Christensen. 2006. Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. Global Change Biology 12:2352–2369.
- Johnson, P. L., and L. L. Tieszen. 1973. Vegetative research in arctic Alaska. Pages pp. 169–198. *in* M. E. Britton, editor. In Alaskan Arctic Tundra. Arctic Institute of North America Technical Paper 25.
- Jones, B. M., G. Grosse, C. D. Arp, M. C. Jones, K. M. Walter Anthony, and V. E. Romanovsky. 2011. Modern thermokarst lake dynamics in the continuous permafrost zone, northern Seward Peninsula, Alaska. Journal of Geophysical Research 116:G00M03.
- Jorgenson, M. T., and Y. Shur. 2007. Evolution of lakes and basins in northern Alaska and discussion of the thaw lake cycle. Journal of Geophysical Research 112:F02S17.
- Jorgenson, M. T., Y. L. Shur, and E. R. Pullman. 2006. Abrupt increase in permafrost degradation in Arctic Alaska. Geophysical Research Letters 33:L02503.
- Kao-Kniffin, J., D. S. Freyre, and T. C. Balser. 2010. Methane dynamics across wetland plant species. Aquatic Botany 93:107–113.

- Karlsson, J. M., S. W. Lyon, and G. Destouni. 2012. Thermokarst lake, hydrological flow and water balance indicators of permafrost change in Western Siberia. *Journal of Hydrology* 464-465:459–466.
- Keenan, T., B. Darby, and E. Felts. 2014. Tracking forest phenology and seasonal physiology using digital repeat photography: a critical assessment. *Ecological Applications* 24:1478–1489.
- Keller, K., J. D. Blum, and G. W. Kling. 2007. Geochemistry of soils and streams on surfaces of varying ages in arctic Alaska. *Arctic Antarctic and Alpine Research* 39:84–98.
- Keller, K., J. D. Blum, and G. W. Kling. 2010. Stream geochemistry as an indicator of increasing permafrost thaw depth in an arctic watershed. *Chemical Geology* 273:76–81.
- Keuper, F., P. M. van Bodegom, E. Dorrepaal, J. T. Weedon, J. van Hal, R. S. P. van Logtestijn, and R. Aerts. 2012. A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology* 18:1998–2007.
- King, J., W. Reeburgh, and S. Regli. 1998. Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment. *Journal of Geophysical ...* 103:29,083–29,092.
- Kreivi, M., P. Rautiainen, J. Aspi, and M. Hyvärinen. 2005. Genetic structure and gene flow in an endangered perennial grass, *Arctophila fulva* var. *pendulina*. *Conservation Genetics* 6:683–696.
- Kurc, S. a., and L. M. Benton. 2010. Digital image-derived greenness links deep soil moisture to carbon uptake in a creosotebush-dominated shrubland. *Journal of Arid Environments* 74:585–594.
- Kutzbach, L., D. Wagner, and E.-M. Pfeiffer. 2004. Effect of microrelief and vegetation on methane emission from wet polygonal tundra, Lena Delta, Northern Siberia. *Biogeochemistry* 69:341–362.
- Labrecque, S., D. Lacelle, C. R. Duguay, B. Lauriol, and J. Hawkings. 2009. Contemporary (1951-2001) Evolution of Lakes in the Old Crown Basin, Northern Yukon, Canada: Remote Sensing, Numerical Modeling, and Stable Isotope Analysis. *Arctic* 62:225–238.
- Laliberte, A. S., A. Rango, K. M. Havstad, J. Paris, R. Beck, R. McNeely, and A. Gonzalez. 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. *Remote Sensing of Environment* 93:198–210.
- Lara, M. 2012. Implications of decade time scale Arctic plant community change on ecosystem function. Doctoral Dissertation. University of Texas at El Paso.
- Lara, M. J., D. A. McGuire, E. S. Euskirchen, C. E. Tweedie, K. M. Hinkel, A. N. Skurikhin, V. E. Romanovsky, G. Grosse, and W. R. Bolton. 2014. Century time-scale change in peak growing season CO₂ and CH₄ flux in response to change in ice-wedge polygonal tundra , on the Barrow Peninsula in Arctic Alaska. *Global Change Biology*:1–50.
- Lara, M. J., S. Villarreal, D. R. Johnson, R. D. Hollister, P. J. Webber, and C. E. Tweedie. 2012. Estimated change in tundra ecosystem function near Barrow, Alaska between 1972 and 2010. *Environmental Research Letters* 7:015507.

- Lawrence, D. M., and A. G. Slater. 2005. A projection of severe near-surface permafrost degradation during the 21st century. *Geophysical Research Letters* 32.
- Lewis, T., M. J. Lafrenière, and S. F. Lamoureux. 2012. Hydrochemical and sedimentary responses of paired High Arctic watersheds to unusual climate and permafrost disturbance, Cape Bounty, Melville Island, Canada. *Hydrological Processes* 26:2003–2018.
- Liljedahl, a. K., L. D. Hinzman, Y. Harazono, D. Zona, C. E. Tweedie, R. D. Hollister, R. Engstrom, and W. C. Oechel. 2011. Nonlinear controls on evapotranspiration in Arctic coastal wetlands. *Biogeosciences Discussions* 8:6307–6344.
- Lin, D. H., D. R. Johnson, C. Andresen, and C. E. Tweedie. 2012. High spatial resolution decade-time scale land cover change at multiple locations in the Beringian Arctic (1948–2000s). *Environmental Research Letters* 7:025502.
- Livingstone, D. 1954. On the orientation of lake basins. *American Journal of Science* 252:547–554.
- Lougheed, V. L., M. G. Butler, D. C. McEwen, and J. E. Hobbie. 2011a. Changes in Tundra Pond Limnology: Re-sampling Alaskan Ponds After 40 Years. *Ambio* 40:589–599.
- Lougheed, V. L., M. G. Butler, D. C. McEwen, and J. E. Hobbie. 2011b. Changes in Tundra Pond Limnology: Re-sampling Alaskan Ponds After 40 Years. *Ambio* 40:589–599.
- Mack, M. C., E. a G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431:440–3.
- Mackay, J. 1988. Catastrophic lake drainage, Tuktoyaktuk Peninsula area, District of Mackenzie. Pages 83–90 *Current Research, Part D, Geological Survey of Canada, Paper 88-ID*.
- Marsh, P., M. Russell, S. Pohl, H. Haywood, and C. Onclin. 2009. Changes in thaw lake drainage in the Western Canadian Arctic from 1950 to 2000 158:145–158.
- McClelland, J. W., M. Stieglitz, F. Pan, R. M. Holmes, and B. J. Peterson. 2007. Recent changes in nitrate and dissolved organic carbon export from the upper Kuparuk River, North Slope, Alaska. *Journal of Geophysical Research-Biogeosciences* 112:G04S60.
- McGuire, A., and L. Anderson. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* 79:523–555.
- McRoy, C. P., and T. S. Leue. 1973. Productivity of Emergent Vascular Aquatic Plants in Tundra Ponds in 1971 and 1972. Data Report 73-8. 15 pp. U.S. Tundra Biome. Page 15.
- Meltofte, H., T. R. Christensen, B. Elberling, M. Forchhammer, and M. Rasch. 2008. High-Arctic ecosystem dynamics in a changing climate. Academic Press.
- Migliavacca, M., M. Galvagno, E. Cremonese, M. Rossini, M. Meroni, O. Sonnentag, S. Cogliati, G. Manca, F. Diotri, L. Busetto, A. Cescatti, R. Colombo, F. Fava, U. Morra di Cella, E. Pari, C. Siniscalco, and A. D. Richardson. 2011. Using digital repeat photography and eddy covariance data

to model grassland phenology and photosynthetic CO₂ uptake. *Agricultural and Forest Meteorology* 151:1325–1337.

Miller, P. C., R. T. Prentki, and R. J. Barsdate. 1980. Physics. Page 51 *in* J. E. Hobbie, editor. *Limnology of Tundra Ponds*. Dowden Hutchinson & Ross, Stroudsburg, PA.

Morrissey, L. A., G. P. Livingston, E. Systems, S. Division, and M. Field. 1992. Methane Emissions From Alaska Arctic Tundra: An Assessment of Local Spatial Variability. *Journal of Geophysical Research* 97:661–670.

Morrissey, L., D. Zobel, and G. Livingston. 1993. Significance of stomatal control on methane release from *Carex*-dominated wetlands. *Chemosphere* 26:339–355.

Niklas, K. 1995. Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of botany* 75:217–227.

Oberbauer, S. and others. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. *Philosophical Transactions of the Royal society*.

Oberbauer, S., C. Tweedie, J. M. Welker, J. T. Fahnestock, G. H. R. Henry, P. J. Webber, R. D. Hollister, D. A. Walker, A. Kuchy, E. Elmore, and G. Starr. 2007. Tundra CO₂ fluxes in response to experimental warming across latitudinal and moisture gradients. *Ecological ...* 77:221–238.

Olivas, P. C., S. F. Oberbauer, C. E. Tweedie, W. C. Oechel, and A. Kuchy. 2010. Responses of CO₂ flux components of Alaskan Coastal Plain tundra to shifts in water table. *Journal of Geophysical Research* 115:G00I05.

Osterkamp, T., and V. Romanovsky. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes*:17–37.

Persello, C., S. Member, L. Bruzzone, and S. Member. 2010. A Novel Protocol for Accuracy Assessment in Classification of Very High Resolution Images 48:1232–1244.

Plug, L. J., C. Walls, and B. M. Scott. 2008. Tundra lake changes from 1978 to 2001 on the Tuktoyaktuk Peninsula, western Canadian Arctic. *Geophysical Research Letters* 35:L03502.

Prowse, T. D., F. J. Wrona, J. D. Reist, J. J. Gibson, J. E. Hobbie, L. M. J. Lévesque, and W. F. Vincent. 2006. Climate change effects on hydroecology of arctic freshwater ecosystems. *Ambio* 35:347–58.

Rautio, M., F. Dufresne, I. Laurion, S. Bonilla, W. F. Vincent, and K. S. Christoffersen. 2011. Shallow Freshwater Ecosystems of the Circumpolar Arctic. *Ecoscience* 18:204–222.

Rawlins, M. a., M. Steele, M. M. Holland, J. C. Adam, J. E. Cherry, J. a. Francis, P. Y. Groisman, L. D. Hinzman, T. G. Huntington, D. L. Kane, J. S. Kimball, R. Kwok, R. B. Lammers, C. M. Lee, D. P. Lettenmaier, K. C. McDonald, E. Podest, J. W. Pundsack, B. Rudels, M. C. Serreze, A. Shiklomanov, Ø. Skagseth, T. J. Troy, C. J. Vörösmarty, M. Wensnahan, E. F. Wood, R. Woodgate, D. Yang, K. Zhang, and T. Zhang. 2010. Analysis of the Arctic System for Freshwater Cycle Intensification: Observations and Expectations. *Journal of Climate* 23:5715–5737.

- Raynolds, M. K., D. a. Walker, H. E. Epstein, J. E. Pinzon, and C. J. Tucker. 2012. A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. *Remote Sensing Letters* 3:403–411.
- Reeburgh, W., and S. Whalen. 1992. High-Latitude Ecosystems as CH₄ Sources. *Ecological Bulletins*:62–70.
- Reyes, F. R., and V. L. Lougheed. (n.d.). Rapid nutrient release from permafrost in Arctic aquatic ecosystems. *Arctic, Antarctic, and Alpine Research*. Accepted Ju.
- Richardson, A. D., B. H. Braswell, D. Y. Hollinger, J. P. Jenkins, and S. V Ollinger. 2009. Near-surface remote sensing of spatial and temporal variation in canopy phenology. *Ecological Applications* 19:1417–28.
- Richardson, A. D., J. P. Jenkins, B. H. Braswell, D. Y. Hollinger, S. V Ollinger, and M.-L. Smith. 2007. Use of digital webcam images to track spring green-up in a deciduous broadleaf forest. *Oecologia* 152:323–34.
- Riordan, B., D. Verbyla, and a. D. McGuire. 2006. Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research* 111:G04002.
- Romanovsky, V. E., S. L. Smith, and H. H. Christiansen. 2010. Permafrost thermal state in the polar Northern Hemisphere during the international polar year 2007-2009: a synthesis. *Permafrost and Periglacial Processes* 21:106–116.
- Sachs, T., M. Giebel, J. Boike, and L. Kutzbach. 2010. Environmental controls on CH₄ emission from polygonal tundra on the microsite scale in the Lena river delta, Siberia. *Global Change Biology*:3096–3110.
- Saitoh, T. M., S. Nagai, N. Saigusa, H. Kobayashi, R. Suzuki, K. N. Nasahara, and H. Muraoka. 2012a. Assessing the use of camera-based indices for characterizing canopy phenology in relation to gross primary production in a deciduous broad-leaved and an evergreen coniferous forest in Japan. *Ecological Informatics* 11:45–54.
- Saitoh, T. M., S. Nagai, N. Saigusa, H. Kobayashi, R. Suzuki, K. N. Nasahara, and H. Muraoka. 2012b. Assessing the use of camera-based indices for characterizing canopy phenology in relation to gross primary production in a deciduous broad-leaved and an evergreen coniferous forest in Japan. *Ecological Informatics* 11:45–54.
- Sannel, a. B. K., and P. Kuhry. 2011. Warming-induced destabilization of peat plateau/thermokarst lake complexes. *Journal of Geophysical Research* 116:G03035.
- Schafer, J. L., and M. C. Mack. 2014. Growth , Biomass , and Allometry of Resprouting Shrubs after Fire in Scrubby Flatwoods Growth , Biomass , and Allometry of Resprouting Shrubs after Fire in Scrubby Flatwoods. *The American Midland Naturalist* 172:266–284.
- Schaphoff, S., U. Heyder, S. Ostberg, D. Gerten, J. Heinke, and W. Lucht. 2013. Contribution of permafrost soils to the global carbon budget. *Environmental Research Letters* 8:014026.

- Schindler, D. W., and J. P. Smol. 2006a. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. *Ambio* 35:160–168.
- Schindler, D. W., and J. P. Smol. 2006b. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. *Ambio* 35:160–8.
- Schuur, E. a. G., B. W. Abbott, W. B. Bowden, V. Brovkin, P. Camill, J. G. Canadell, J. P. Chanton, F. S. Chapin, T. R. Christensen, P. Ciais, B. T. Crosby, C. I. Czimczik, G. Grosse, J. Harden, D. J. Hayes, G. Hugelius, J. D. Jastrow, J. B. Jones, T. Kleinen, C. D. Koven, G. Krinner, P. Kuhry, D. M. Lawrence, a. D. McGuire, S. M. Natali, J. a. O'Donnell, C. L. Ping, W. J. Riley, a. Rinke, V. E. Romanovsky, a. B. K. Sannel, C. Schädel, K. Schaefer, J. Sky, Z. M. Subin, C. Tarnocai, M. R. Turetsky, M. P. Waldrop, K. M. Walter Anthony, K. P. Wickland, C. J. Wilson, and S. a. Zimov. 2013. Expert assessment of vulnerability of permafrost carbon to climate change. *Climatic Change* 119:359–374.
- Schuur, E. a. G., J. Bockheim, J. G. Canadell, E. Euskirchen, C. B. Field, S. V. Goryachkin, S. Hagemann, P. Kuhry, P. M. Lafleur, H. Lee, G. Mazhitova, F. E. Nelson, A. Rinke, V. E. Romanovsky, N. Shiklomanov, C. Tarnocai, S. Venevsky, J. G. Vogel, and S. a. Zimov. 2008. Vulnerability of Permafrost Carbon to Climate Change: Implications for the Global Carbon Cycle. *BioScience* 58:701.
- Segers, R. 1998. Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry* 41:23–51.
- Shaver, G., F. C. Iii, and W. Billings. 1979. Ecotypic differentiation in *Carex aquatilis* on ice-wedge polygons in the Alaskan coastal tundra. *The Journal of Ecology* 67:1025–1045.
- Shaver, G. R., L. C. Johnson, D. H. Cades, G. Murray, J. a. Laundre, E. B. Rastetter, K. J. Nadelhoffer, and a. E. Giblin. 1998. Biomass and Flux in Wet Sedge Tundras: Responses To Nutrients, Temperature, and Light. *Ecological Monographs* 68:75–97.
- Shiklomanov, N. I., D. a. Streletskiy, F. E. Nelson, R. D. Hollister, V. E. Romanovsky, C. E. Tweedie, J. G. Bockheim, and J. Brown. 2010. Decadal variations of active-layer thickness in moisture-controlled landscapes, Barrow, Alaska. *Journal of Geophysical Research* 115:G00I04.
- Sitch, S., a D. McGuire, J. Kimball, N. Gedney, J. Gamon, R. Engstrom, A. Wolf, Q. Zhuang, J. Clein, and K. C. McDonald. 2007. Assessing the carbon balance of circumpolar Arctic tundra using remote sensing and process modeling. *Ecological applications : a publication of the Ecological Society of America* 17:213–34.
- Smith, L. C., Y. Sheng, and G. M. Macdonald. 2007. Short Communication A First Pan-Arctic Assessment of the Influence of Glaciation , Permafrost , Topography and Peatlands on Northern Hemisphere Lake Distribution 208:201–208.
- Smith, L. C., Y. Sheng, G. M. MacDonald, and L. D. Hinzman. 2005. Disappearing Arctic lakes. *Science (New York, N.Y.)* 308:1429.

- Smol, J. P., and M. S. V Douglas. 2007. Crossing the final ecological threshold in high Arctic ponds. *Proceedings of the National Academy of Sciences of the United States of America* 104:12395–7.
- Sonnentag, O., M. Detto, R. Vargas, Y. Ryu, B. R. K. Runkle, M. Kelly, and D. D. Baldocchi. 2011. Tracking the structural and functional development of a perennial pepperweed (*Lepidium latifolium* L.) infestation using a multi-year archive of webcam imagery and eddy covariance measurements. *Agricultural and Forest Meteorology* 151:916–926.
- Sonnentag, O., K. Hufkens, C. Teshera-Sterne, A. M. Young, M. Friedl, B. H. Braswell, T. Milliman, J. O’Keefe, and A. D. Richardson. 2012. Digital repeat photography for phenological research in forest ecosystems. *Agricultural and Forest Meteorology* 152:159–177.
- Soudani, K., G. Hmimina, N. Delpierre, J.-Y. Pontailier, M. Aubinet, D. Bonal, B. Caquet, a. de Grandcourt, B. Burban, C. Flechard, D. Guyon, a. Granier, P. Gross, B. Heinesh, B. Longdoz, D. Loustau, C. Moureaux, J.-M. Ourcival, S. Rambal, L. Saint André, and E. Dufrêne. 2012. Ground-based Network of NDVI measurements for tracking temporal dynamics of canopy structure and vegetation phenology in different biomes. *Remote Sensing of Environment* 123:234–245.
- Stone, R., E. Dutton, J. Harris, and D. Longenecker. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research* 107.
- Stow, D. a, A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, S. Houston, C. Racine, M. Sturm, K. Tape, L. Hinzman, K. Yoshikawa, C. Tweedie, B. Noyle, C. Silapaswan, D. Douglas, B. Griffith, G. Jia, H. Epstein, D. Walker, S. Daeschner, A. Petersen, L. Zhou, and R. Myneni. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment* 89:281–308.
- Streletskiy, D. A., N. I. Shiklomanov, F. E. Nelson, and A. E. Klene. 2007. 13 Years of Observations at Alaskan CALM Sites : Long-term Active Layer and Ground Surface Temperature Trends.
- Stroeve, J., M. M. Holland, W. Meier, T. Scambos, and M. Serreze. 2007. Arctic sea ice decline: Faster than forecast. *Geophysical Research Letters* 34:1–5.
- Ström, L., T. Tagesson, M. Mastepanov, and T. R. Christensen. 2012. Presence of *Eriophorum scheuchzeri* enhances substrate availability and methane emission in an Arctic wetland. *Soil Biology and Biochemistry* 45:61–70.
- Sturm, M., C. Racine, K. Tape, T. W. Cronin, R. L. Caldwell, and J. Marshall. 2001. Increasing shrub abundance in the Arctic. *Nature* 411:2001–2002.
- Sutton-Grier, A. E., and J. P. Megonigal. 2011. Plant species traits regulate methane production in freshwater wetland soils. *Soil Biology and Biochemistry* 43:413–420.
- Swann, A. L., I. Y. Fung, S. Levis, G. B. Bonan, and S. C. Doney. 2010. Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. *Proceedings of the National Academy of Sciences of the United States of America* 107:1295–300.

- Tarnocai, C., J. G. Canadell, E. a. G. Schuur, P. Kuhry, G. Mazhitova, and S. Zimov. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles* 23:n/a–n/a.
- Tieszen, L. 1973. Photosynthesis and respiration in arctic tundra grasses: field light intensity and temperature responses. *Arctic and Alpine Research* 5:239–251.
- Tieszen, L. L. 1972. The seasonal course of aboveground production and chlorophyll distribution in a wet Arctic tundra at Barrow, Alaska. *Arctic and Alpine Research* 4:307–324.
- Torgersen, T., and B. Branco. 2008. Carbon and oxygen fluxes from a small pond to the atmosphere: Temporal variability and the CO₂/O₂ imbalance. *Water Resources Research* 44:n/a–n/a.
- Tweedie, C. T., C. G. Andresen, R. D. Hollister, J. L. May, D. R. Bronson, A. Gaylord, and P. J. Webber. (n.d.). Land cover classification and change detection near Barrow, Alaska using QuickBird satellite imagery.
- Uhlířová, E., H. Šantrůčková, and S. P. Davidov. 2007. Quality and potential biodegradability of soil organic matter preserved in permafrost of Siberian tussock tundra. *Soil Biology and Biochemistry* 39:1978–1989.
- Verbyla, D. 2008. The greening and browning of Alaska based on 1982–2003 satellite data. *Global Ecology and Biogeography* 17:547–555.
- Villarreal, S., R. D. Hollister, D. R. Johnson, M. J. Lara, P. J. Webber, and C. E. Tweedie. 2012. Tundra vegetation change near Barrow, Alaska (1972–2010). *Environmental Research Letters* 7:015508.
- Viña, A., A. a. Gitelson, A. L. Nguy-Robertson, and Y. Peng. 2011. Comparison of different vegetation indices for the remote assessment of green leaf area index of crops. *Remote Sensing of Environment* 115:3468–3478.
- Walker, D. a, H. E. Epstein, M. K. Raynolds, P. Kuss, M. a Kopecky, G. V Frost, F. J. a Daniëls, M. O. Leibman, N. G. Moskalenko, G. V Matyshak, O. V Khitun, a V Khomutov, B. C. Forbes, U. S. Bhatt, a N. Kade, C. M. Vonlanthen, and L. Tichý. 2012a. Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. *Environmental Research Letters* 7:015504.
- Walker, D. a. 2003. Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research* 108:8169.
- Walker, D., U. Bhatt, and H. Epstein. 2012b. Changing Arctic tundra vegetation biomass and Greenness. *Bull. Am. Meteorol. Soc.* 2011–2012.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir, J. a Klein, B. Magnússon, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. a

- Wookey. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103:1342–6.
- Walter Anthony, K. M., P. Anthony, G. Grosse, and J. Chanton. 2012. Geologic methane seeps along boundaries of Arctic permafrost thaw and melting glaciers. *Nature Geoscience* 5:419–426.
- Walther, G., E. Post, P. Convey, and A. Menzel. 2002. Ecological responses to recent climate change. *Nature*:389–395.
- Wang, J., Y. Sheng, K. M. Hinkel, and E. a. Lyons. 2012. Drained thaw lake basin recovery on the western Arctic Coastal Plain of Alaska using high-resolution digital elevation models and remote sensing imagery. *Remote Sensing of Environment* 119:325–336.
- Weintraub, M. N., and J. P. Schimel. 2003. Interactions between Carbon and Nitrogen Mineralization and Soil Organic Matter Chemistry in Arctic Tundra Soils. *Ecosystems* 6:129–143.
- Wendler, G., B. Moore, J. Curtis, and M. Stuefer. 2002. Beaufort sea ice concentration and the climate of the Alaskan North Slope. Pages 202–210 *Ice in the Environment: Proceedings of the 16th IAHR International Symposium on Ice*. Dunedin, New Zealand.
- Wendler, G., M. Shulski, and B. Moore. 2009. Changes in the climate of the Alaskan North Slope and the ice concentration of the adjacent Beaufort Sea. *Theoretical and Applied Climatology* 99:67–74.
- Westergaard-Nielsen, A., M. Lund, B. U. Hansen, and M. P. Tamstorf. 2013. Camera derived vegetation greenness index as proxy for gross primary production in a low Arctic wetland area. *ISPRS Journal of Photogrammetry and Remote Sensing* 86:89–99.
- White, D., L. Hinzman, L. Alessa, J. Cassano, M. Chambers, K. Falkner, J. Francis, W. J. Gutowski, M. Holland, R. M. Holmes, H. Huntington, D. Kane, A. Kliskey, C. Lee, J. McClelland, B. Peterson, T. S. Rupp, F. Straneo, M. Steele, R. Woodgate, D. Yang, K. Yoshikawa, and T. Zhang. 2007. The arctic freshwater system: Changes and impacts. *Journal of Geophysical Research* 112:G04S54.
- Yoshikawa, K., and L. D. Hinzman. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near council, Alaska. *Permafrost and Periglacial Processes* 14:151–160.
- Zeng, H., and G. Jia. 2013. Impacts of snow cover on vegetation phenology in the arctic from satellite data. *Advances in Atmospheric Sciences* 30:1421–1432.
- Zeng, H., G. Jia, and B. Forbes. 2013. Shifts in Arctic phenology in response to climate and anthropogenic factors as detected from multiple satellite time series. *Environmental Research Letters* 8:035036.
- Zona, D., W. C. Oechel, J. Kochendorfer, K. T. Paw U, a. N. Salyuk, P. C. Olivas, S. F. Oberbauer, and D. a. Lipson. 2009. Methane fluxes during the initiation of a large-scale water table manipulation experiment in the Alaskan Arctic tundra. *Global Biogeochemical Cycles* 23:n/a–n/a.

Biographical Sketch

Christian G. Andresen

Environmental Science and Engineering Ph. D.

Christian G. Andresen earned his Bachelor Degree in Environmental Science from UTEP in 2008 with honors. After graduation, he worked as a Research Associate at UTEP where he collaborated in several projects related to wetland characterization and land-cover mapping in the desert southwest and the Arctic tundra using remote sensing. Then, in 2010 he entered the doctoral program in Environmental Science and Engineering at UTEP under the direction of Dr. Vanessa L. Lougheed.

His dissertation entitled “*Monitoring and understanding decadal scale changes in hydrology, productivity and carbon balance in Arctic tundra ponds*” is an interdisciplinary study that investigates decadal scale changes in surface hydrology, plant biomass and methane efflux of Arctic wetlands, important drivers of global climatic feedbacks. During his studies, Dr. Andresen spent over 300 days in the Arctic region of Northern Alaska collecting environmental data and samples for his dissertation work. Results of his research have been published in several peer-reviewed journal articles in different scientific fields including ecology, hydrology and remote sensing. He has given over 30 conference presentations from local to international levels. Dr. Andresen was awarded several prestigious fellowships including the National Science Foundation Graduate Research Fellowship (GRFP) and the Louis M. Stokes Alliance for Minority participation (LSAMP). In addition, Dr. Andresen was awarded the Dr. Diana Natalicio Dissertation Fellowship, a recognition by the president Dr. Natalicio to the most outstanding doctoral candidate at UTEP.

Dr. Andresen research interests focus on the effects of climate change on hydrology, vegetation structure, and ecosystem function in extreme environments such as the Chihuahuan desert and the Arctic tundra. In particular, he is especially interested in assessing long-term changes at different spatial and temporal scales and in the further development of novel remote sensing approaches to monitor and model environmental change.

Permanent address: 697 Pete Payan, El Paso, Texas. 79912. cgandresen@gmail.com

This dissertation was typed by Christian G. Andresen