Diatoms as Indicators of Climate Change on St. Lawrence Island, Alaska

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Abstract

The Alaskan and Bering Sea region has warmed twice as fast as the rest of the United States over the past 60 years. St. Lawrence Island, Alaska, the most northern large island in the Bering Sea, has had some recent monitoring of climate; however, these data are of fairly short duration and thus long-term environmental change is relatively unknown. To develop a more complete assessment of anthropogenic climate change in the region, I applied paleolimnological techniques to assess changes over the past ~150 years in diatom assemblages and primary production estimates for two sites located on St. Lawrence Island. Sediment cores were obtained from Reindeer Pond and Atuk Lake in July of 2012. Examining these two different waterbodies provides the opportunity to assess the ecological variability in the region and compare how a lake and a pond differ in their response to warming. Diatom assemblages in both Atuk Lake and Reindeer Pond showed a response to anthropogenic climate change beginning in the late 19th and early 20th century. Shifts towards more diverse assemblages of benthic diatoms at both sites suggest greater benthic habitat availability, which is most likely due to the increased growing season allowing for the development of greater substrate complexity. The diatom change is accompanied by a corresponding increase in sedimentary chlorophyll-*a*, a change likely driven by a longer-ice free season allowing for increased phytoplankton and periphyton production. Cluster analyses on the diatom assemblages also detected a primary split around the 1970s for the Atuk Lake profile, which is consistent with a known period of marked warming in the Bering Sea region. This study provides important ecological information and a longer-term perspective on recent climate changes for this under-studied region and for the vulnerable subsistence communities that live in the on St. Lawrence Island, Alaska.

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List of Common Abbreviations

1. Dissolved Organic Carbon –DOC
2. Constrained Incremental Sum of Squares – CONISS
3. Principal Components Analysis – PCA
4. Chlorophyll-*a* – Chl-*a*
5. *Paleoecological Environmental Assessment and Research Lab – PEARL*
6. Visible Reflectance Spectrometry -VRS

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Introduction and Literature Review

St. Lawrence Island

St. Lawrence Island is a large (~4600 km^2) volcanic island situated within the Bering Sea, west of mainland Alaska, and just south of the Bering Strait (Figure 1). The Bering Sea is one of the major marine ecosystems in the world and that is already experiencing the effects of anthropogenic climate change, including decreased sea ice stability and shifts in the marine ecosystem (Overland and Stabeno, 2011). However, there still remains variability in the regional climate due to the influence of a number of semi-decadal to decadal scale climatic oscillations such as the Pacific Decadal Oscillation (PDO), the Arctic Oscillation, and El Nino/La Nina events. In the past century, there have been two major shifts in climate (the first in the late 1970s and the second around 2000), which are associated with higher temperatures and an increase in warm winds in the winter (Grebmeier *et al.,* 2006). A shift towards a positive phase in the PDO in the 1970s is believed to be the principal driver behind a marked increase in temperature resulting in a major ecosystem reorganization in the Bering Sea (Hunt *et al*., 2002; NOAA 2014). The inhabitants of St. Lawrence Island corroborated the instrumental data, reporting a shift away from Arctic conditions in the 1970s (Grebmeier *et al.,* 2006).

One of the most striking results of climate change in this region is the changing condition of sea ice in the summer. During the summer, ice persists over the shallow shelf in the Chukchi Sea (northern Alaska); however, recently, the ice has retracted and only persists over deeper waters (Holland *et al.,* 2006). St. Lawrence Island is an important component of the Bering Sea ecosystem due to the formation of a polynya, a cold pool of open water, on the southern, leeward side of the island. The St. Lawrence Island polynya, is an epicenter of sea ice formation, and is an important feeding habitat for marine mammals. The Pacific walrus, for example, use this ice as a platform to rest and feed off of; however, since at least 2007, vast numbers of walrus have been migrating to mainland Alaska due to the lack of stable sea ice in the Bering Strait (Deiviscio *et al.,* 2014). The lack of accessible sea ice is likely to be deleterious to the walrus population and the people who rely on them for a major source of their diet, including the St. Lawrence Yupik people (Deiviscio *et al.,* 2014). Yupik communities on St. Lawrence Island also rely on berries, greens, fish and marine mammals (including bowhead whale and walruses) as the mainstays of their diet, but these resources may be compromised because of the changing climate (Carpenter and Miller, 2011).

Subarctic and Arctic regions are particularly sensitive to environmental changes, and especially to those related to climate warming. It is well established that global warming is especially pronounced in the Arctic through amplified feedbacks (Smol *et al.,* 2005; Overpeck *et al*., 1997) and that the Arctic ecosystems are vulnerable to environmental change (NOAA, 2014). In particular, the Alaskan and Bering Sea region has warmed twice as fast as the rest of the United States over the past 60 years (Chapin *et al*., 2000). Furthermore, the Yupik hunters of St. Lawrence Island have observed an increase in warm winds in winter and the replacement of stable pan and pack ice with brash and thin ice, changes that have affected their ability to hunt and fish (Grebmeier *et al.,* 2006). Although monitoring of the Bering Sea ecosystem and climate is being conducted (NOAA, 2014), long-term data are sparse, and there has been little monitoring conducted on St. Lawrence Island, thus the history of environmental change for this region is relatively unknown.

Paleolimnology

Lakes and ponds are common features across Arctic landscapes and are often remote and largely isolated from most direct human impacts. Consequently, climate is expected to be one of the principal drivers of environmental and biotic change in these freshwater systems, and changes in climate can have both direct and indirect effects on Arctic freshwaters (Smol and Cumming, 2000). Lakes are important sensors and records of environmental change (Battarbee, 2000). Climate can affect a number of important physical and chemical properties of waterbodies by influencing the depth, duration, and intensity of water-column stratification, and changing the timing and duration of the ice-free period, which in turn controls many chemical and biological processes such as pH and primary production. Sediment records contain a wealth of paleoclimate proxy data due to the many indirect and direct linkages between climate and the physical, chemical and biological factors within a lake (Smol and Cumming, 2000). Sediment is generally deposited in a lake in a continuous fashion through time, such that the most recent material (which may be comprised of siliciclastics, diatoms, chironomids, phytoliths, etc.) accumulates at the top of a core, and thereafter the greater the depth, the older the sediment. A continuous record of sediment can be retrieved from most lakes using a variety of coring techniques (e.g. Glew 1989), after which the core can be sectioned into specified intervals (usually 0.25cm or 0.5cm intervals) (Glew, 1988; Smol and Cumming, 2000).

The usefulness of diatoms (siliceous algae) in reconstructing past environmental change has been well documented (Smol, 2008). Diatoms are especially useful paleoenvironmental indicators as they have: 1) siliceous cell walls that are species specific and that preserve in lake sediment; 2) they are ubiquitous in aquatic systems; and 3) they exhibit a variety of life strategies, and have specific ecological preferences (Battarbee, 2000). Diatoms are an indirect indicator of climate change, responding to factors such as the length and strength of thermal stratification (Rühland *et al.*, 2008), the length of the growing season (Smol and Douglas, 2007a), pH (Battarbee, 2000), nutrient inputs (Anderson, 2010), dissolved organic carbon (Pienitz *et al.*, 1999), and habitat availability (Smol and Douglas, 2007a). There are thousands of species of diatoms, whose taxonomy is based on the size, shape, and sculpturing of their siliceous cell walls (Smol, 2008). Furthermore, they have very fast migration rates, which means that they can colonize new habitats very quickly, and their short-lifespan enables them to respond rapidly to environmental change (Rühland *et al.*, 2003). Changes in temperature and wind patterns over a lake can have a significant bearing on water-column turbulence and thermal stratification. These processes can exert a strong influence on the competitive abilities of phytoplankton, by either controlling buoyancy, sinking rates, or indirectly through changing the alkalinity of the lake and nutrient patterns (Battarbee, 2000).

Primary Production

Primary production is the amount of autotrophic biomass produced within a system and is an important variable that can summarize the overall lake trophic status. Climate change may influence ice patterns, which can impact the primary production in a lake, particularly in Arctic regions where production is limited by the short growing season. Climate warming, for example, could increase the length of the growing (ice-free) season and result in an increase primary production (Douglas *et al.*, 1999), leading to a corresponding increase in sedimentary chlorophyll-*a* content, which can be tracked by Visible Reflectance Spectrometry (VRS) (Michelutti *et al.*, 2010). Changes in temperature and wind patterns over a lake can have a significant bearing on water-column turbulence and thermal stratification and these processes can exert a strong influence on the competition of diatoms. Assessing the changes in primary production for Atuk Lake and Reindeer Pond, in conjunction with diatom species changes, will provide additional information on the timing and scope of climate change on St. Lawrence Island.

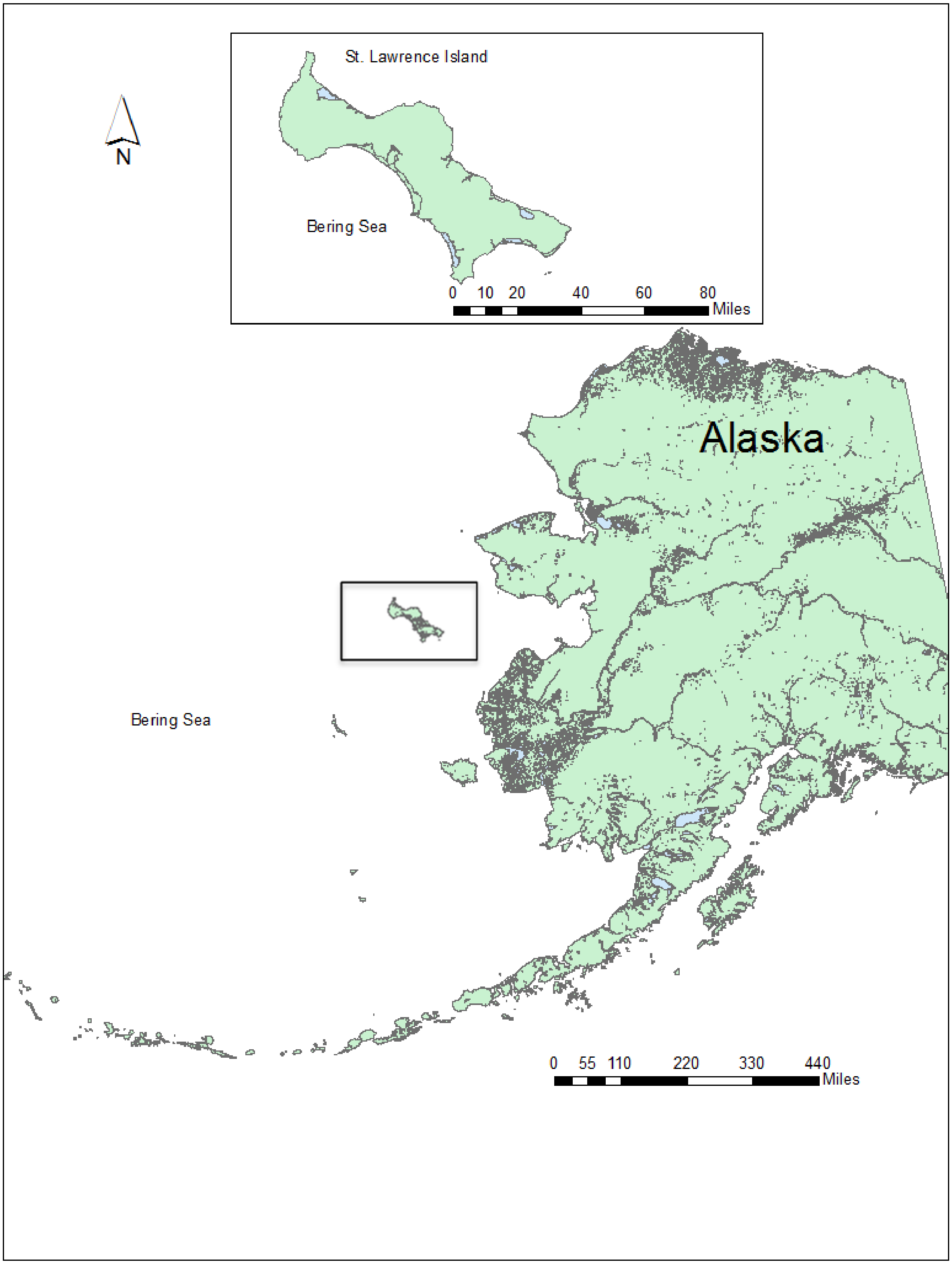


Figure 1: The location of St. Lawrence Island in relation to mainland Alaska and the Bering Sea.

Figure 2: Topographic map of Saint Lawrence Island, Alaska. The black star denotes the study site Atuk Lake and the white star indicates Reindeer Pond (from US geological survey, 1970).

Study Rationale

There have been only a few paleoliminological studies conducted in the Bering Sea region. On mainland Alaska, several studies examined historical salmon populations (Holtham *et al*., 2004; Gregory-Eaves *et al*., 2003), while chironomids have been used to reconstruct past Holocene environments (Kurek and Cwynar, 2009). On St. Lawrence Island, there has only been one published paleoclimate record, a Holocene pollen record by Colinvaux (1967). Recent, unpublished diatom work by Katherine Griffiths (PhD Candidate at PEARL) has also been completed for several lowland ponds on St. Lawrence Island. My work is an important part of this larger study examining climate change on St. Lawrence Island.

Hypotheses

I expect to document changes in the nature and timing of the diatom response in both Reindeer Pond and Atuk Lake. Reindeer Pond freezes completely to the bottom in winter, thaws completely in the summer, and has considerable vegetation in the catchment. Atuk Lake, in contrast, is deeper, has a rocky catchment and the possibility of a planktonic diatom community, as it is deeper and sheltered by the wind in 2 directions. At both lakes I expect to document an increase in diversity of diatoms through time and an increase in primary production, as the length of the growing season likely increased at these sites due to climate warming. In Atuk Lake, it is possible that, with warming, a planktonic diatom community may have developed with decreased ice cover (Rühland *et al*, 2003). In shallow Reindeer Pond, I do not expect any planktonic development but rather I might record a habitat shift with increased diversity and the emergence of epiphytic species, as was reported by Douglas *et al.* (1994) in the Canadian High

Arctic. This is because an increase in the ice-free period can result in the expansion of available diatom habitats, while in deeper systems, the establishment of longer, stronger periods of thermal stratification can favour relatively buoyant, lightly silicified planktonic taxa (Rühland and Smol, 2005, 2010; Smol *et al*. 2007).

Expected Significance

Besides Colinvaux's (1967) early research, there are currently no paleoenvironmental records published from St. Lawrence Island. Furthermore, there are few well-documented floristic studies of diatoms in Alaska (e.g. Potapova, 2014; Bahls, 1982; Patrick and Freese, 1960). However, it is important to understand the climate change that has happened in this region as the native communities that live on the island are largely dependent on the traditional hunting practices. Furthermore, the island is home to abundant wildlife, such as birds, seabirds, walruses, arctic foxes, and seals, all of which are affected by climate change. With a small number of jobs, high cost of living, and rapid social changes, the Yupik people are highly vulnerable to climate change through impacts on their traditional hunting, fishing, and cultural connection to the land and sea.

Materials and Methods

Study Site Descriptions

The study sites are on St. Lawrence Island, Alaska (63°25' N, 170°24' W) in the Bering Sea, just south of the Bering Strait (Figure 2). The remote nature of the sites means they are unlikely to have been subjected to practices that could have disrupted the sediments, allowing the sediment cores to represent an accurate record of past limnological changes in this region.

Atuk Lake

Atuk Lake (63.59712°N, 170.441.97°W; Figure 2) has a maximum depth of 5.1m and lies within a collection of inactive, volcanic cinder cones at a high elevation (480m a.s.l.). Atuk Lake was cored in July 2012 by Katherine Griffiths and Josh Kurek, and the core is ~30cm in length. Physical and chemical parameters for Atuk Lake can be found in Table 1.

Reindeer Pond

Reindeer Pond (63.59690°N, 170.22511°W; Figure 2) is shallow (maximum depth 0.5m), is at a slightly lower elevation (320m a.s.l.) than Atuk Lake, and has a predominantly rocky, volcanic catchment, with emergent grasses at the inlet and outlet. The northern shore is a pebble and boulder beach about 20m wide, and a rocky hill lies to the south. Furthermore, there was a permanent snow bank on the southern shore when the pond was sampled. The pond was cored in July 2012 and the core is ~30cm in length. A summary of physical and chemical variables for Reindeer Pond can be found in Table 1.

Table 1: Limnological variables recorded from Atuk Lake and Reindeer Pond at time of sediment collection.

Parameter	**Atuk Lake**	**Reindeer Pond**
Date of sampling	July 19, 2012	July 22, 2012
Coring Depth (m)	5.1	0.5
Water temperature at surface (°C)	9.1	14
pH	7.6	7.6
DOC (mg/L)	0.6	1.1
TP_u (mg/L)	0.025	0.0108
TN (mg/L)	0.16	0.154

Field Methods

Sample Collection

In July 2012, sediment cores (each approximately 30cm in length) were recovered from the deepest points of Atuk Lake and Reindeer Pond using a Glew (1989) gravity corer. A Glew (1988) extruder was used on site to section the core into 0.25cm intervals and sediment samples were stored in Whirl-pak$^{®}$ bags and then frozen until processing. Water was also collected at each site and analyzed for a suite of chemical parameters (outlined in Smol *et al.,* 1994) at the National Laboratory for Environmental Testing in Burlington, ON, Canada.

Lab Methods

Radioisotope dating

After the cores were collected, extruded, and sectioned, the sediment samples were returned to the Paleoecological Environmental Assessment and Research Laboratory (PEARL). Sediment intervals were freeze-dried and subsequently dated with gamma spectrometry using excess ^{210}Pb activities (Appleby 2001) and ^{137}Cs radioisotopes (Appleby 2001). Lead-210 is a commonly used radioisotope for dating sediments back to ~100 or 150 years, depending on the activity (Appleby and Oldfield, 1978). Core chronologies were developed using the ^{210}Pb activities by applying the Constant Rate of Supply (CRS) model in the ScienTissiME package in MatLab® (Barry's Bay, ON, Canada).

Chlorophyll-a analysis

Sedimentary chlorophyll-*a* concentrations were analyzed for both Atuk Lake and Reindeer Pond using Visible Reflectance Spectroscopy (VRS), a proxy method to assess changes in primary production over time (Michelutti *et al*., 2005). For this procedure, approximately 15 samples were freeze-dried, sieved through a 125-µm mesh and sediment reflectance spectra were acquired using a 6500 series Rapid Content Analyzer (FOSS NIRSystems Inc.). The reflectance spectra were then compared to calibration samples from a range of sedimentary chl-*a* concentrations and, following procedures from Wolfe *et al.* (2004), the area under the absorbance curve between 640 and 700 nm in a plot of wavelength versus percent absorbance was calculated using RStudio v 0.98.501.

Diatom sample preparations and enumerations

The sediment samples were processed in accordance with standard procedural methods outlined by Kathleen Rühland (2010). Approximately 0.2-0.5g of wet sediment was processed for every 0.25cm up until 30cm in each core. The diatom samples for both Atuk Lake and Reindeer Pond were prepared using the following steps. First, 15ml of a 1:1 molar mixture of nitric and sulphuric acids were added to the sediments in glass vials in order to digest away the organic matter. The samples were then placed in a hot water bath (~75°C) for 3 hours to speed up the digestion and stirred occasionally. The sediment slurries were removed from the bath and left overnight to cool and for the diatoms to settle out. After the 24 hours, excess acid was aspirated off the slurries and the sediments were washed with deionized water. The samples continued to be aspirated and rewashed with deionized water until they reached a neutral pH. Diatom slurries of various dilutions were then plated, using an integrated subsample of the whole slurry, and dried onto glass cover slips (using slide warmers to speed up the drying process). Once the cover slips were dry, they were mounted onto slides using Naphrax®.

Diatom samples were counted and identified at 1.0cm intervals from 0-18cm. For each sample, diatoms were identified and enumerated along transects using a Leica® microscope (1000x magnification) with the aim of identifying a minimum of 350 diatoms per interval (typically between 400-500 diatom valves were enumerated per sample). Due to low abundances and high silici-clastic content, however, some samples did not meet the minimum count, as indicated in the results.

Data Analysis

The diatom species counts from the sediment cores were converted to percent relative abundance of each taxa in the diatom assemblage. A constrained incremental sum of squares (CONISS) analysis was performed on the diatom assemblages to determine the significant groupings among all intervals (Grimm 1987). After the CONISS analysis was performed, a broken stick analysis, using the vegan package v 2.0-10 in RStudio v 0.98.50 (Oksanen *et al.* 2013), was used to determine the number of significant zones in the stratigraphy.

To display the data clearly, rare diatoms (those that did not exceed >5% relative abundance in at least two sediment intervals) were not included in the stratigraphy, but were grouped as other taxa. The major patterns of variation in the diatom assemblages in both waterbodies were summarized by applying a principal components analysis (PCA) on square root transformed species data on the paired down dataset (to obtain species scores). The diatoms were ordered in the stratigraphies based on their species scores, such that taxa that had similar trends were grouped together. Diatom analyses were done to 18cm in both cores for both lakes.

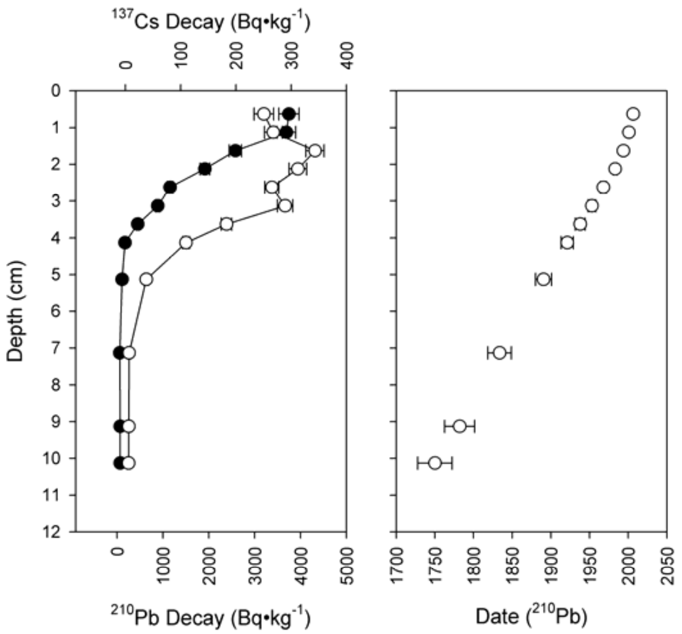
Hill's N2 diversity index, a diversity measure that takes into account both the relative abundances and the number of occurrences of species (Räsänen *et al.,* 2007), was run on both Atuk Lake and Reindeer Pond to estimate the diversity changes in the diatom assemblages (Harper, 1999). Hill's N2 was calculated on rarified data (rarefied to 137 diatoms per interval for Atuk Lake and 116 diatoms per interval for Reindeer Pond) with the vegan package v 2.0-10 in RStudio v 0.98.50. Due to the low rarefication targets the values of Hill's N2 should be interpreted with some caution.

Results

Radiometric dating

Northern sites typically have low levels of ^{210}Pb deposition (Wolfe *et al.*, 2004), often making reliable sediment dating difficult. However, for both Atuk Lake and Reindeer Pond, the ^{210}Pb profiles showed relatively high rates of deposition and a robust decay curve, suggesting no sediment mixing (Figure 3, Appendix 2). The ^{210}Pb was also compared to the ^{137}Cs profile to validate the dates. The ^{137}Cs peaks were not very clear in the Atuk Lake and Reindeer Pond profiles, although they are in general agreement with the ^{210}Pb CRS dates (Figure 3). The ^{210}Pb activity profile for Reindeer Pond and Atuk Lake suggested that the deposition date of ~1850 occurs at a depth of 9cm and 6cm, respectively (Figure 3) suggesting our records extend back well past the period since major human impacts on the climate began (my period of interest).

Atuk



Reindeer

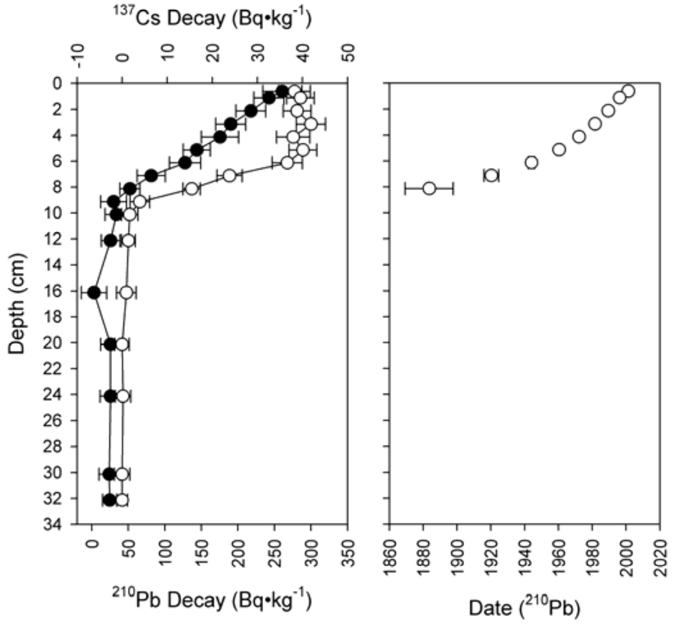


Fig. 3. Age-depth models generated from gamma-ray spectrometric dating using ^{210}Pb activities and the Constant Rate of Supply (CRS) method. The left panel for each site (Atuk Lake (Top) and Reindeer Pond (Bottom), St. Lawrence Island, Alaska) depicts the decay of ^{210}Pb (black circles) and ^{137}Cs (white circles) activities. The right panel depicts the CRS sediment ages with depth.

Atuk Lake

A total of 33 taxa were identified in the Atuk Lake Core (Appendix 2), however only those that achieved at least 5% abundance in any interval will be discussed here. _The dominant diatom species present included: *Achnanthidium kriegeri, Stauroforma exigua, Achnanthdium* spp., *Psammothidium helveticum, Tabellaria flocculosa, Nitzschia palea, Eunotia tenella, Eunotia lunaris, Encyonema gaeumannii, Asterionella raffaii, Navicula variostriata, Brachysira arctoborealis, Pinnularia appendiculata, Frustulia rhomboidis,* and *Aulacoseira alpigena*. A complete list of my raw diatoms counts are presented in Appendix 2.

The CONISS analysis indicates that there are 3 significant zones. The first zone is from the base of the core to ~1880's (6.5cm), followed by zone 2 that extends to the mid 1970's (~2.5cm), and zone 3 extends from the mid 1970's to the present. Zone 1 has no significant change in diatoms. Zone 2 corresponds to incremental increases in *Achanthdium* spp., *Psammothidium helveticum,* and *Tabellaria flocculosa*, with concomitant relative decreases in *Pinnularia appendiculata,* and *Brachysira arctoborealis* (figure 4). Finally, Zone 3 corresponds to increases in *Achanthdium* spp., *Psammothidium helveticum,* and *Tabellaria flocculosa* and decreases in *Aulacoseria alpigena, Brachysira arctoborealis, Psammothidium helveticum,* and *Frustulia rhomboidis* Furthermore, the Hill's N2 diversity index indicates a general increase in diversity in the core, with the most pronounced increase occurring at 4cm (~1920s) to present.

Sedimentary chlorophyll-*a* begins to increase after 6.5cm (~1900's) and markedly increases in the recent sediments of Atuk Lake, starting at ~2.5cm (~1970's).

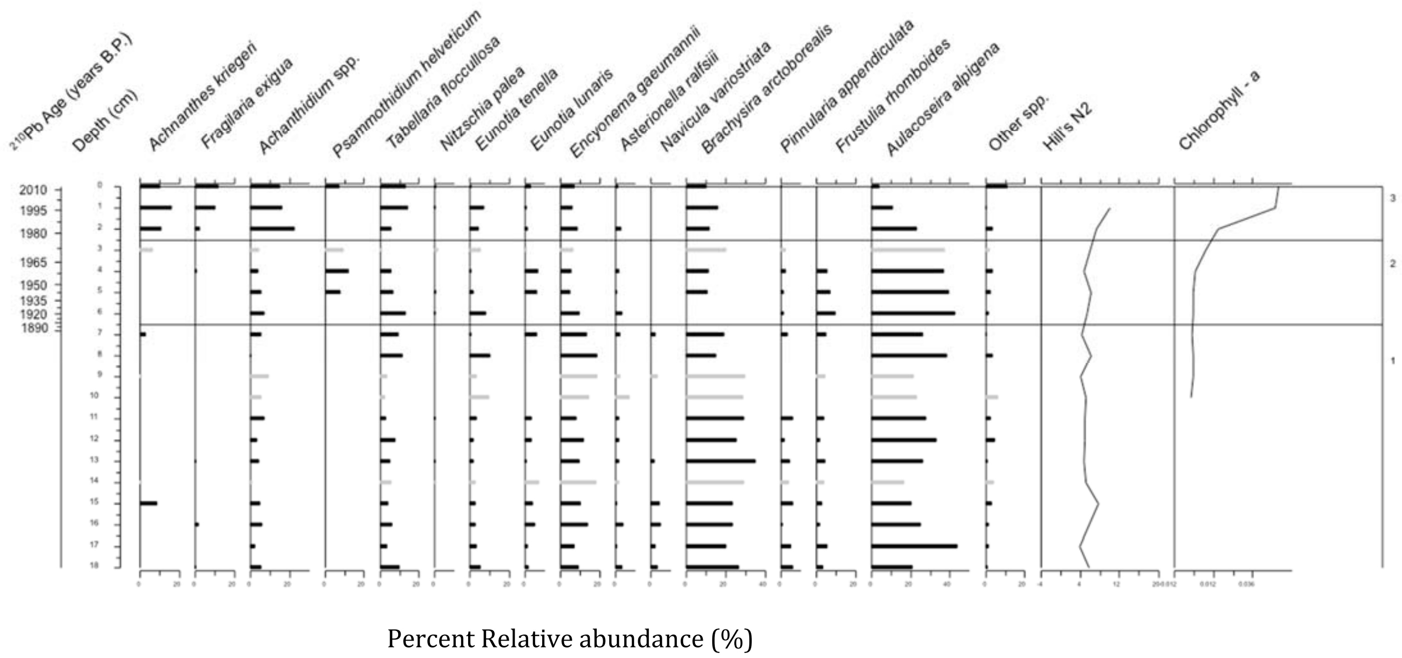


Figure 4. Relative abundance diagram of dominant diatom taxa versus ^{210}Pb ages and sediment core depths from Atuk Lake, St. Lawrence Island, Alaska. Diatom taxa are ordered by principal components analysis species scores. Zonation based on constrained incremental sum of squares (CONISS) cluster analysis is included to identify the major changes in diatom species assemblage. Hill's N2 shows the change in diversity of the diatom assemblage, and sedimentary chlorophyll-*a* reflects the changes in inferred primary production**.** Grey denotes intervals that were under the recommended counts of 350.

Reindeer Pond

A total of 44 taxa were identified in the Atuk Lake Core (Appendix II), however only those that achieved at least 5% abundance in any interval will be discussed here. CONISS analysis of Reindeer Pond indicates that there are no significant zones. There is a muted increase in *Achnanthidium* species, *Nitzschia perminuta, Psammothidium helveticum,* and *Aulacoseira alpigena* and a relative decrease in *Stauroforma exiguiformis* and *Fragilaria capucina* occurring around ~1880 (Figure 5). Furthermore, the Hill's N2 diversity measurement indicates a general increase in diversity in the core since 1965 (4.5cm). Chlorophyll-*a* content increases in recent sediments, starting in the 1880s (8cm), while below that depth, inferred chlorophyll-*a* was very low, well below the detection limit of 0.01mg/g of dry sediment (Figure 5). Chironomids were also enumerated by Katherine Griffiths (Appendix 3).

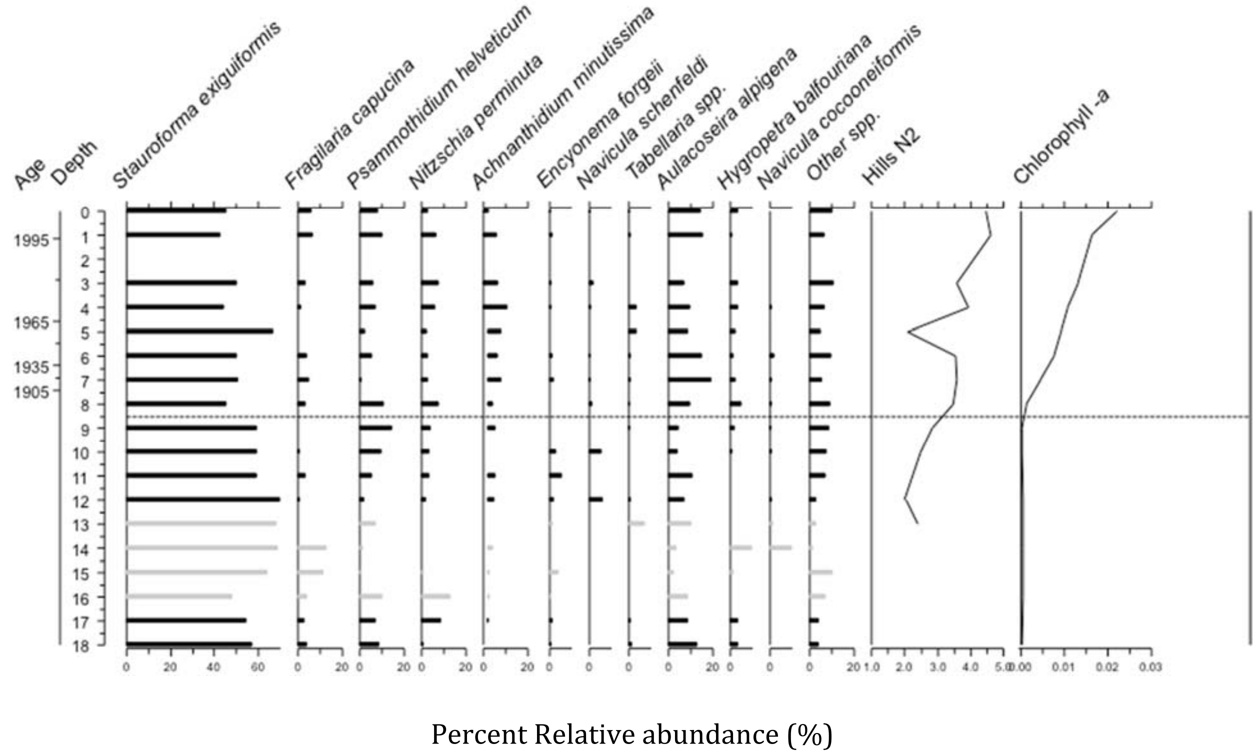


Figure 5. Relative abundance diagram of dominant diatom taxa versus ^{210}Pb ages and sediment core depths from Reindeer Pond, St. Lawrence Island, Alaska. Diatom taxa are ordered by principal components analysis species scores. Zonation based on constrained incremental sum of squares (CONISS) cluster analysis is included to identify the major changes in diatom species assemblage. Hill's N2 shows the change in diversity of the diatom assemblage, the Hill's N2 stops at 13cm as these intervals had counts too low for reasonable rarefaction analyses. The visible reflectance spectroscopy chlorophyll-*a* reflects the changes in inferred primary production. Grey denotes intervals that were under the recommended counts of 350.

Discussion

Atuk Lake

There have been marked changes in the diatom assemblage during the last ~150 years in Atuk Lake. As Atuk Lake is fairly remote on St. Lawrence Island, local disturbance is unlikely and so climate is the most likely dominant driver of the biotic change.

In Atuk Lake, the heavily silicified tychoplanktonic *Aulacoseira alpigena* is one of the dominant taxa below 2.5cm (before ~1970). After about 1970 (core depth of 2.5cm), the relative abundance of *Aulacoseira alpigena* decreases and a diverse assemblage of benthic species, such as *Achnanthidium kriegeri, Stauroforma exigua, Achnanthdium* spp., and *Psammothidium helveticum* become more abundant. In many deep lakes across the Subarctic, a decline in *Aulacoseira* has been recorded and attributed to the development of periodic thermal stratification, which means that with reduced mixing *Aulacoseira* can no longer retains its advantage of being higher in the water column (Rühland *et al*., 2008). The *Aulacoseira* decrease may be a response to reduced wind mixing due to reduced wind speeds, as it has been documented that there has been a steady decrease in wind speed observed across the Bering Sea region (Wendler *et al.,* 2013). Atuk Lake is quite shallow (only 5m), very clear, and dilute, and is almost entirely littoral zone (mosses grow even at the maximum depth, through sparsely). Although thermal stratification is one possible explanation underlying the reduction in *Aulacoseira* in Atuk Lake, the cold temperatures and lack of planktonic species development strongly suggest that another mechanism is underlying the trend. Given that inferred primary production increases markedly in concert with the diatom shift, it is possible that the perceived decline in *Aulacoseira* is rather reflecting an increase in benthic production. In fact, the chlorophyll-*a* concentrations also increase at this time, suggesting overall increases in production. This increase in benthic species may be due to an increasing temperature trend, which results in reduced ice cover and the development of more complex and productive habitats (Douglas *et al.*, 1994). Additionally, if Atuk Lake once retained a permanent ice raft through summer, it is possible that with warmer temperatures, more and more of the central raft and snow and ice melted, exposing additional, deeper open-water habitats for algal and other biological growth (Smol and Douglas, 2007a). It is also possible that water levels have decreased with warming (Smol and Douglas, 2007b), decreasing the competitiveness of planktonic taxa. Furthermore, the most accelerated changes in primary production are consistent with the major ecosystem reorganization that occurred in the 1970s in the Bering Sea, where there was a transition from primarily cold Arctic ecosystems, to subarctic conditions (NOAA, 2014).

In Atuk Lake there is also a notable decrease in the dominant taxa *Brachysira arctoborealis*, which was one of the dominant taxa below 2.5cm and then substantially decreases after the ~1970s. *Brachysira arctoborealis* are commonly part of the attached diatom assemblage in acidic freshwater ponds and lakes (Vouilloud *et al.*, 2014) and may be indicative of low pH environments. For example, it was present in the sediments of Big Moose Lake in the Adirondack Mountains as well as Whirligig Lake near Sudbury (Wolfe and Kling, 2001). Currently Atuk Lake has a circumneutral pH (pH of 7.6); however, the volcanic geology of the catchment likely means that it is poorly buffered, and thus may experience large pH fluctuations. Climate could be affecting the pH by manipulating the in-lake processes, related to dissolved inorganic carbon (DIC) dynamics. If there is a longer duration of ice cover, the ice will trap CO_2 within the lake, leading to a decrease in lake pH (Rühland *et al.,* 2008). Expanding on this idea, ice acts as a barrier to gas exchange in the winter because when there is ice cover the water becomes supersaturated with the CO_2 produced by respiration and decomposition (Koinig *et al.*, 1998a, b). However, if there is a decrease in ice cover, the pH may have slightly increased and leading to a decrease in *Brachysira arctoborealis* in recent years.

Atuk Lake shows three significant zones that have occurred since the 1880s. The most notable change is the transition from zone 2 to zone 3 in the 1970s. This change shows a drastic decrease in *Aulacosiera alpigena, Frustulia rhomboides,* and *Brachysira arctoborealis* and an increase in *Achnathidium* spp.*,* and *Fragilaria exigua.* In the early 1970s, there was a major regime shift in Bering Sea, related to the positive phase of the PDO that resulted in a notable reorganization of species in the Bering Sea (NOAA, 2014). The change in climate due to the positive phase of the PDO and likely amplified by anthropogenic warming, likely led to the increased benthic habitat complexity in Atuk Lake, which was unprecedented in the >200 year diatom record.

Finally, in Atuk Lake, there is an exponential increase in chlorophyll-*a* starting at about 2.5cm corresponding to the increase in the diversity of diatom species and the zone 2 to zone 3 transition. The increase in sedimentary chlorophyll-*a* likely reflects the lengthening of the ice-free period due to warmer temperatures in the Bering Sea region, a trend that is commonly seen throughout the arctic (Michelutti *et al*., 2010).

Reindeer Pond

Reindeer Pond, as compared to Atuk Lake, has a fairly muted diatom assemblage response to climate warming. The principal trends in Reindeer Pond are decreases in the benthic *Stauroforma exiguiformis*, *Gomphonema angustatum*, and *Fragilaria capucina* and relative increases in *Psammothidium helveticum, Nitzschia perminuta, Achnanthidium minutissimum,* and *Aulacoseira alpigena.* The decline in the benthic, acidophilic fragilarioid *Stauroforma* *exiguiformis* (Flower *et al.*, 1996) and *Fragilaria capucina* is fairly consistent with warming trends of other Arctic ponds (Douglas *et al*. 1994; Smol *et al*. 2005), as benthic, non-motile fragilarioid diatom species are replaced by a more complex, motile diatom assemblage including *Achnanthidium* spp. (*sensu lato*) and *Nitzschia* spp., reflecting an increase in habitat complexity and possibly an increase in nutrients from increased weathering and vegetation development in the catchment (Douglas *et al*. 1994). The diatom changes in Reindeer Pond are muted compared to Atuk Lake and other High Arctic sites (e.g. Smol *et al*. 2005). Furthermore, the pre-warming assemblage is diverse, which may suggest that the pre-anthropogenic warming ice-free season was likely long enough to allow a relatively high diversity of diatom habitats.

Sedimentary chlorophyll-*a* indicates primary production likely increased in the late ~1880s in Reindeer Pond. Additionally, Hill's N2 diversity increases in Reindeer Pond are concomitant with the inferred increase in primary production. The more muted diatom change in Reindeer Pond as compared to Atuk Lake may be due to the already high diversity assemblage present in Reindeer Pond before the warming trend (given its shallow nature). Atuk Lake also has a later response than Reindeer Pond, with the most pronounced diversity and production changes happening in concert with the 1970's Bering Sea climate shift. The larger and deeper morphometry of Atuk Lake may be underlying this trend, as the greater thermal inertia of Atuk Lake means it is less susceptible to seasonal variation or to slight changes in climate.

St. Lawrence Island (63°25' N, 170°24' W) lies further south (~10º S) than High Arctic sites (e.g. Resolute Bay, 74.6975ºN, 94.8322ºW) where much of the Arctic diatom work has been focused (e.g. Smol and Douglas, 2007a) and has more subarctic conditions, which are moderated by the Bering Sea. Temperatures on St. Lawrence Island range from 4 to 10ºC in the summer to -22 to -12ºC in the winter (http://aksik.org/village/savoonga). In comparison, at more northern Arctic sites, such as Resolute (Nunavut, Canada), temperatures range from -5 to -32^{o}C during the winter months and from 0 to 4^{o}C during the summer months. This difference in average temperatures between the two locations may be a reason as to why there is more of a muted response in the Reindeer Pond diatom assemblages on St. Lawrence Island, compared to similar ponds in the High Arctic. The ponds in the High Arctic undergo threshold-like responses to warming, reflecting a shift from a very limited growing season and almost exclusively epilithic habitats to a longer growing season and new periphytic habitats (epipelic and epiphytic) developing (Douglas *et al*., 1994).

Finally, Katherine Griffiths conducted a complementary study on the chironomid assemblage changes in Reindeer Pond (unpublished data; see Appendix C). The chironomid profiles supported my diatom inferences, showing a shift from cold-adapted taxa towards a warmer-adapted assemblage in the late 19th century.

Potential Limitations

It is impossible to account for all the factors that may be affecting the diatoms on St. Lawrence Island. Diatoms are affected by climate in multiple, indirect ways and it is possible that I did not account for all the factors that might affect the assemblages, such as increased weathering of volcanic bedrock and changes in winter precipitation and snowmelt. However, the consistency across sites on St. Lawrence Island in the nature of the diatom response (unpublished data) and the consistency of my finding with the other records in the circumpolar arctic (Smol *et al*. 2005) gives me confidence in my interpretation. Although, it may be difficult to identify the multiple stressors in this particular region, this data provides a good baseline of conditions within the area.

Conclusion

This study was conducted to characterize the diatom assemblage of Atuk Lake and Reindeer Pond on St. Lawrence Island. It was observed that diatom diversity and primary production increased in both Atuk Lake and Reindeer Pond in the late 19th and the early 20th century, and then became more pronounced in the 1970s, in response to a known warm shift in the Bering Sea. The diatom assemblages also reflect the opening up of new, diverse habitats with a shorter ice-free season, suggesting the aquatic communities are changing in response to regional anthropogenic warming.

The complex interactions highlight the complexity of interpreting the impacts of climate change on St. Lawrence Island and emphasize the need for multiple proxy analyses of the waterbodies.

Future research should better characterize how climate is affecting the region in all aspects (ecological, economic, political, and social) to help aid in environmental management and help contribute to a more informed collaboration with the Yupik people that live on the island. My assessment of the ecological changes in both Atuk Lake and Reindeer Pond is important for understanding how St. Lawrence Island is being affected by climate change and critical in understanding how this ecosystem might be changing the future.

Summary

1. In Atuk Lake, the diatom assemblages have most likely been impacted by climate change. There has been a marked shift towards a much more diverse benthic diatom assemblage, and a corresponding increase in inferred primary production. This is likely due to the lengthening ice-free period due to climate warming, which is leading to a longer growing season for the diatoms. The diatom changes begin in the early 20th century with the most pronounced shift corresponding to the development of the positive phase of the Pacific Decadal Oscillation in the 1970s, which led to an ecosystem reorganization in the Bering Sea. The diatom changes that correspond to this event are unprecedented in our >200 year record.
2. Reindeer Pond diatom assemblages have had a more muted response to climate warming than Atuk Lake. The diatoms shift from benthic fragilarioid species to a more diverse benthic assemblage. Furthermore, the sedimentary chlorophyll-*a* profile indicates an increase in primary production around 1880, before any production changes in Atuk Lake. The muted diatom response, relative to other Arctic sites, is likely due to the fact that this site is warmer than many other comparable High Arctic ponds where paleolimnological studies had been completed, and the pond was already relatively ice free for long time periods, even before the period of anthropogenic warming.
3. Overall diversity and production have increased in both Atuk Lake and Reindeer Pond beginning in the late 19th and early 20th century, and accelerated in the 1970s likely in response to regional anthropogenic warming intersecting with decadal-scale climate cycles.

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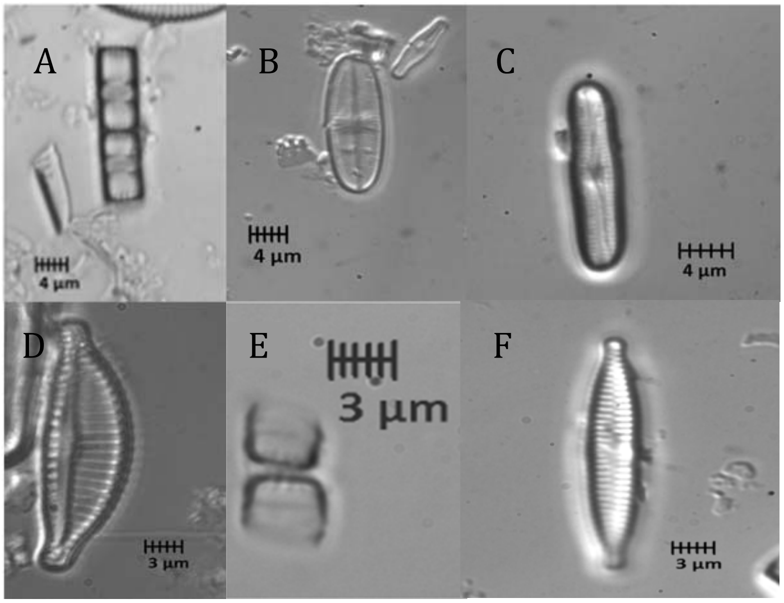
Appendix 1: Microscope pictures of diatoms found through Atuk Lake and Reindeer Pond. Scale bars are indicated for each separate image.



A) *Aulacoseira alpigena* B) *Achnanthidium bioretti* C) *Achnanthidium minutisimma*
D) *Encyonema obscurum* E) *Fragillaria construens* F) *Fragillaria capucina*

Appendix 2:

Table 2.1. Raw data counts for number of Diatom individuals recorded from Atuk Lake

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Achnanthes helvetica	50			20	62	30									
Achnanthes Montana			6	4					4		5				
Achanthdium spp.	100	62	100	10	20	22	20	24	2	20	8	26	12	20	4
Achnanthes CF	68														
Aulacoseira alpigena	28	44	104	80	182	146	120	110	106	46	32	96	116	112	70
Caloneis aerophila	6	2					2								
Cymbella gaeumannii	48	24	40	14	28	20	28	56	52	40	20	28	42	42	74
Cymbella elginense	2														
Cymbella minuta															
Cymbella forgeii	2														
Frustulia rhomboidis					28	28	28	22		10		14	7	20	18
Eunotia arcus	8	28	22	12	4	8	24	4	28	8	14	12	8	10	12
Eunotia paludosa															
Eunotia bilunaris	20	4	8	2	34	24		26				12	12	4	30
Fragilaria construens															
Fragilaria capucina	20														
Fragillaria exigua	80	40	12		4									2	
Gomphonema augur	2														
Gomphonema gracile	20														
Asterionella raffaii	10		14		10	4	10	10		6	10	8	8	8	8
Achnanthes kriegeri	2	62	50	14				14		2					4
Navicula cryptochepla	6										4		2		8
Brachysira arctoborealis	70	62	53	43	58	40		80	42	64	40	100	90	150	120
Navicula schoenfelei					6										
Navicula pseudocurtformis	6		2		10	10						10	14		
Navicula cocooneiformis	4														10
Navicula explanata					2										
Navicula variostriata								12		8				8	
Nitzschia palea	8	2		4		4	2					2		2	4
Pinnularia microstauron	6		8				2		6						
Pinnularia appendiculata	4			6	12	6	4	16				22	8	20	18
Pinnularia CF								2						4	
Tabellaria flocullosa	90	56	26	2	30	26	38	40	32	8	4	12	28	22	25

Table 2.2. Raw data counts for individuals of Diatoms recorded from Reindeer Pond

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	1
Achnanthes bioretti	62	42		24	30	6	26	6	40	48	20	6	4	10	
Achnanthes ventralis	8	2		4	2		6	2	4						
Achnanthes minutissima	20	24		26	44	14	20	36	10	12		4	6		
Achnangehs fragilariodes															
Achnanthes stolida	12	6		10	4	6	4	2	6	8	4				
Achnanthes rossi	4						2	6							
Achnanthes cf	2														
Amphora inariensis		2		4	2	2	4	2			2	2			
Aulacoseira alpigena	110	63		28	40	20	67	114	35	16	9	12	14	14	
Caloneis Bacillum	4						4								
Cymbella clevel-eulera	2				2										
Cymbella elginense				2	2		4		2				2		
Cymbella forgeii	4	6		4	4		8	12			6	6	4	2	
Cymbella minuta	16	2											2		
Cymbella neocistula															
Cymbella tumida	2													2	
Cymmbella obscurum	2			2	2			2	4						
Eunotia steineckei				2							2		2		
Eunotia praerupta										4				2	
Eunotia bilunaris					2					9					
Eunotia arrcus						2									
Fragilaria exigucaa	336	170		198	176	154	224	294	164	191	122	64	130	92	8
Fragilaria capucina	46	26		14	6		18	30	14		2	4	2		1
Gompphonema angustum															
Gomphonema augur											4				
Gomphonema gracile		2					6			2		2			
Gomphonema acuminatum		2													
Meridions circulare	4			4			8	2	4						
Navicula cryptocephala	22	4		2	8	4		2	4	2	6				
Navicula cocooneiformis					4		10	5	4	2	2		2	2	
Nacicula pseudosilicula		2		6			2								
Navicula pseuoscutiofrmis	10	4		2	6	2		6	4		2				
Navicula digitulus	8			4	2		2	4	8		2				
Navicula schenfeldi	3			8	4		2	4	6		12		12		
Navicula forgii									2						
Navicula pupula								8							
Pinularia subcapitata	2				2					4		4			
Pinularia microstaron				4			2			2					
Pinularia balforiana	28	4		14	14	6	6	16	18	6	2				
Staurineis gracilis	2	4													
Nitzchia perminuta	22	26		30	24	6	14	18	28	14	8	4	4		
Tabellaria Flocculosa	1	2			10	6	2	1		2				6	
Tabellaria centricosa	3	2			4	2	2	6	2				2	4	
Surirella linearis					2										

Appendix 3: Relative percent diagram of chironomid taxa from Reindeer Pond enumerated by Katherine Griffiths, PhD candidate.