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Long-Term Records of Climate-Induced Changes in the Zooplankton of West Greenland Lakes

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Abstract

Recent research documents climate-induced changes in the algal communities of West Greenland lakes; however, less is known about the response of zooplankton to climate change effects in this region. Zooplankton are predominantly the top predator in these lakes, and thus may be changing due to direct climate effects on physical lake habitat and chemistry or indirect effects on their food source. Cladoceran remains from two lake sediment cores were collected in the Kangerlussuaq region of southwest Greenland: SS1341, located midway between the Greenland ice sheet and the coast, and SS901, close in proximity to the ice sheet. Modern zooplankton data were analyzed from a suite of 26 lakes across both regions and utilized neo- and paleolimnological methods to characterize shifts in zooplankton communities.

Paleolimnological results suggest a shift to increased dominance of a particular pelagic genus, *Bosmina*, over the benthic genus *Chydorus* in modern times. This trend differs from an established long-term record of zooplankton change from another lake in this region that observed a modern decline in pelagic genera, suggesting variability among systems in zooplankton community response to climate change. Similar variability within paleolimnological records in this region has been observed for small centric diatom species. Modern analysis yielded a correlation of *Bosmina* and *Eubosmina* spp. distribution to increased lake clarity and reduced algal biomass, suggesting the effects of climate change may be mediated by bottom-up food web mechanisms. By pairing modern and paleoecological approaches, we are better able to understand the mechanisms driving long-term shifts in plankton communities in these Arctic lakes.

Introduction

The Arctic represents a unique region of the world in which direct effects of climate change on lakes with little to no direct human impacts can be examined. In general, high-latitude lakes display particular sensitivity to climate change, given that the Arctic is warming at a greater rate than the global average and the ice-free season is lengthening accordingly (Prowse *et al.*, 2006). Additionally, vegetation succession in the Arctic is limited and these lakes tend to contain simpler trophic structures with low biodiversity and low resilience to change (Wrona *et al.*, 2005; Anderson *et al.*, 2008; Presthus Heggen *et al.*, 2010). These characteristics and the absence of historical anthropogenic disturbance lead to the assumption that long-term changes in the biological communities of Arctic lakes result from climate impacts (Wolfe, 2002; Anderson *et al.*, 2008).

A crucial sub-region of the Arctic for paleoenvironmental lake research and climate studies is western Greenland. This region of Greenland is ideal because it contains more than 20,000 lakes that have not experienced cultural disturbance; therefore, shifts in biological communities should be dependent on local catchment differences and climate change (Anderson *et al.*, 1999). Given the remote location and short span of ice-free months, data have been procured infrequently and from a very small number of these abundant lakes in the better part of the last century; little is known about their contemporary ecology (Williams, 1991; Anderson *et al.*, 2001). A synthesis of Arctic paleolimnological data (Smol *et al.*, 2005) documents recent signs of change in biological communities in lakes throughout the region, but did not include records from this part of Greenland. This indicates a gap in recent Arctic research (Perren *et al.*, 2009). In theory, each lake could

yield a paleolimnological record in its sediment that would add to our collective knowledge of community composition changes over time throughout the region.

Across the Arctic, lake sediment records provide some of the few key archives documenting rates of ecosystem change since the last ice age. In particular, striking changes in communities of diatoms have occurred over the last 150 years (Perren *et al.*, 2009; Saros *et al.*, 2013). Diatoms are a type of algae that make up the base of the aquatic food web, respond rapidly to environmental change, and preserve as fossils in lake sediments. Shifts in diatom community structure often occur rapidly in response to ecological perturbations to lakes (Perren *et al.*, 2009; Smol and Stoermer, 2010; Saros *et al.*, 2013; Saros and Anderson, 2015). For example, recent research on climate-mediated change in the lakes of southwest Greenland documented dynamic but variable changes in diatom communities over the last century (Perren *et al.*, 2009).

These lakes typically have small catchment areas with continuous permafrost, and are rarely connected to each other, limiting inflow to spring thaw and outflow to evaporation (Anderson *et al.*, 2009). Limnological variables in lakes within the same region are expected to react synchronously to changes in climate over time (Magnuson *et al.*, 1990). Additional research in Boreal Shield lakes suggested that lakes within and across a region exhibit heterogeneous ecosystem responses to changing climate factors (Arnott *et al.*, 2003). The asynchronous changes in the diatom communities of these lakes are attributed to climate change; additionally, the response of a particular diatom taxon to climate-mediated change is dependent on ecological interactions within individual lake ecosystems (Anderson *et al.*, 2008; Perren *et al.*, 2009; Saros *et al.*, 2012). These recent

studies have focused on the effects of climate change on algae in southwest Greenland; however, much less is known about the next link in the food chain, zooplankton.

Numerous factors potentially influence zooplankton community structure, including in-lake processes like species interactions (competition, grazing), or external elements like climate variability, catchment inputs and other indirect factors (Carpenter *et al.*, 1985; Anderson *et al.*, 2008). Preferences like the relative importance of pelagic or benthic habitat can influence biological structure; these shifts are traceable in the sediment record, but often ignored in larger analyses (Vadeboncoeur *et al.*, 2002). It is notoriously difficult to extract clear climate mechanisms that are independent of factors like predation or habitat shift from sediment records (Battarbee *et al.*, 2000; Jeppesen *et al.*, 2001). A major documented effect of climate on zooplankton biomass and community composition is phenology, or a temporal mismatch between zooplankton emergence and their food source that potentially increases dominance of temperature-cued genera (Winder and Schindler, 2004). Phenology as a dynamic environmental signal is an example of an external factor that influences zooplankton in an indirect way through shifted timing and abundance of their food source.

Climate is influencing eutrophication trends in Danish lakes by increasing chlorophyll a and phytoplankton biomass, resulting in reduced size of cladocerans, zooplankton biomass, and zooplankton: phytoplankton biomass ratio with warming (Jeppesen *et al.*, 2008). Similarly, a review of climate change effects on lakes in the Netherlands concluded a likely increase in phytoplankton carrying capacity that mimics eutrophication, thus affecting higher trophic levels through greater primary productivity (Mooji *et al.*, 2005). However, Magnuson *et al.* (1997) also addresses potential climate

impacts on Laurentian Great Lakes in Wisconsin and discovered a variety of impacts on the ecological properties of the lakes. Significantly, thermocline depth would change, DOC inputs would decline, light penetration would deepen, and dissolved oxygen would drop below the newly formed thermocline, prompting variable responses in the biotic communities in the lake. Like the Netherlands study, Magnuson concludes that primary production may increase, but more complexity in the response of both phytoplankton and zooplankton to the climate-induced physical changes is expected. The complexity of the interactions of biotic communities with altered temperatures, nutrient inputs, amount of light penetration, and other external physical factors is underscored in this study. Overall these studies highlight the dynamic nature of in-lake interactions, which increase in complexity up through the trophic levels. Key interactions documented in these studies are mapped out in Figure 1, which is modelled after a food-web diagram. The bottom level consists of major climate factors, temperature, wind speed, and precipitation, which directly affect physical lake properties like water level, mixing, clarity and catchment

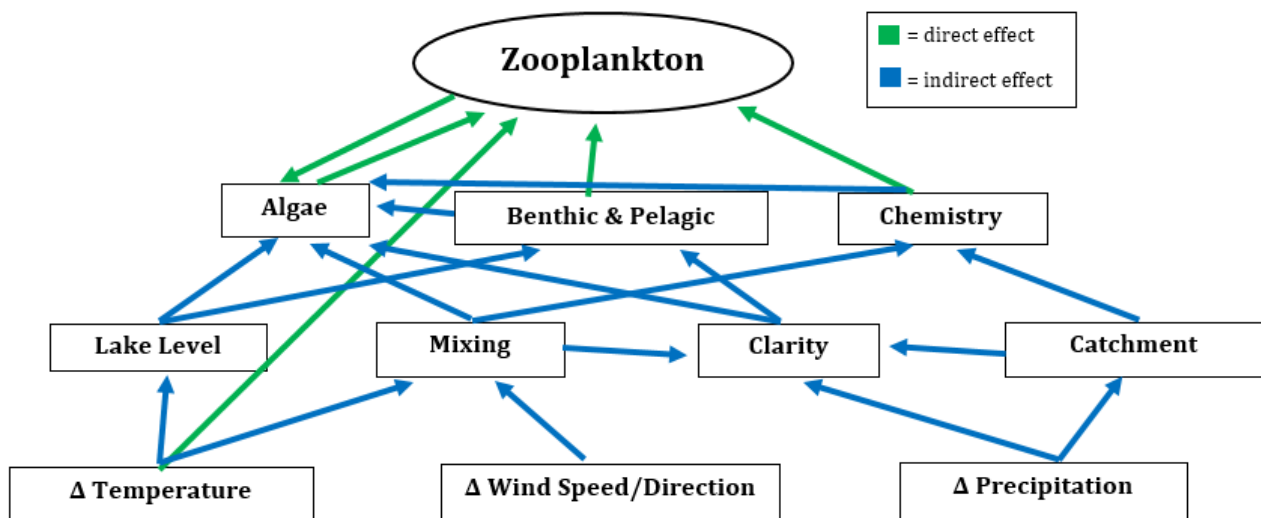


Figure 1: Diagram of factors that directly and indirectly affect zooplankton communities in lakes.

inflow. These properties have a direct relationship with phytoplankton community composition and abundance, benthic or pelagic habit preference, and water chemistry, all of which directly affect zooplankton.

Zooplankton represent the highest trophic level in most of these lakes, and as such, directly impact diatom and other algae populations through in-lake factors such as grazing and competition in a top-down trophic cascade (Carpenter *et al.*, 1985; Anderson *et al.*, 2008). Given that zooplankton consume algae, potential zooplankton community shifts over time would occur either from bottom-up changes in their food source or as a direct result of external climate factors. Here, I address potential impacts of climate change on zooplankton communities, and aim to fill a gap in the research relating to this next level in the food web. To the best of my knowledge, a focused study on the community changes of these organisms in a neo- and paleolimnological context has not been conducted in this region. This work compliments ongoing research aimed at understanding the described changes in diatom community composition.

Understanding the ecology of these ecosystems is key to interpreting lake sediment records in this region (Anderson *et al.*, 2008; Saros *et al.*, 2012). With rapid shifts observed in algal communities, it is increasingly important to document changes in the next level of the food web, zooplankton. Shelled remains of the order Cladocera preserve in sediment cores and can be identified down to species in order to reconstruct biological population and community trends over time. Zooplankton remains in sediment have been used to understand other large-scale disturbances, such as the effects of acid rain throughout the last century (Arseneau *et al.*, 2011), human disturbance (Jeppesen *et al.*, 2001), changes in

food web structure (Jeppesen *et al.*, 1997), and lake chemistry (Jeziorski *et al.*, 2008, Deasley *et al.*, 2012).

There are numerous further examples of recent studies linking sedimentary cladoceran analysis with paleoenvironmental factors, including bottom-up influences and external climatic characteristics. In varying high-latitude locations from Scandinavia to Canada, bottom-up forces (e.g. nutrient concentrations influencing algal productivity) were determined to be significant predictors of zooplankton biomass, species composition, and distribution (Bos and Cumming, 2003; Gyllström *et al.*, 2005). Climate was also found to contribute to the predictions of zooplankton biomass and community composition in European lakes, indicating that climate interacts with food-web dynamics like productivity in a significant way (Gyllström *et al.*, 2005). Cladocera abundance and community composition has been connected with changes in temperature (Rautio, 1988; Duigan and Birks, 2000; Gillooly and Dodson, 2000; Bos and Cumming, 2003), lake depth (Hofmann 1998; Bos and Cumming, 2003; DeSellas *et al.*, 2008), pH (Rautio, 1988; DeSellas *et al.*, 2008), ultraviolet energy (UV) and dissolved organic carbon (DOC) (Williamson *et al.*, 2001, DeSellas *et al.*, 2008), altitude (Rautio 1988), ion concentrations (DeSellas *et al.*, 2008), and trends in acidification and oligotrophication (Duigan and Birks, 2000). More specifically, *Daphnia* abundance was linked to temperature changes in Wisconsin lakes (Gillooly and Dodson, 2000), and Chydoridaen cladocerans were found to be most dominant in a Scandinavian lake survey that found a decrease in cladoceran species number and change in community composition in lakes situated at higher altitudes with lower temperatures and pH (Rautio, 1988). Hofmann (1998) concluded that lake level changes

directly affect the littoral zone and likely influence the planktonic/littoral ratio of cladoceran assemblages, thus potentially influencing relative abundance in the sediment. Furthermore, recent studies document trends of oligotrophication and declining DOC in these lakes (Anderson et al, 2008; Saros et al, 2015; Saros et al, 2016). The role of acidification may also be a factor influencing zooplankton community composition in these lakes. Clearwater, oligotrophic lakes may be less resilient against cladoceran assemblage shifts in response to acidification, although such responses are also varied due to other in-lake mechanisms like changing habitat, predation, metal toxicity, or a decline in pH (Korosi and Smol, 2012a). These studies examine multiple different variables that connect to cladocerans; however, they all emphasize the complexity of in-lake biotic interactions and how they react to external ecological conditions.

Research Questions

The above studies use either neo- or paleoecological techniques to determine how varying environmental conditions will influence zooplankton communities. Here, I use a combined analysis to examine long-term zooplankton records and modern zooplankton and environmental data. In general, I am asking if, how, and why zooplankton communities are changing in the lakes of southwest Greenland. The first part of the question is framed in a paleolimnological context and asks: how have zooplankton communities changed over the last century (or more) in an inland lake and a lake in close proximity to the ice sheet? Relationships among environmental factors vary due to spatial and temporal differences in the climate and ecology of the region between lakes that lie adjacent to the ice-sheet and those located closer to the coast (Anderson *et al.*, 2008). However, sampling from

geographically and climatically different regions aims not only to extract interesting comparisons in the data, but also to mitigate such variability in external factors such as temperature and precipitation patterns as determined by altitude. This question is paired with a modern analysis to ask: how does modern zooplankton species distribution relate to a suite of physical, chemical, and biological lake variables? By pairing these two components, I ask: how can modern ecological relationships inform our understanding of the mechanisms responsible for changes observed in the paleo-record? This study will ultimately provide important tools to decipher the extent to which direct and indirect effects of climate are contributing to rapid ecological change in the Arctic.

Methods

Study Site

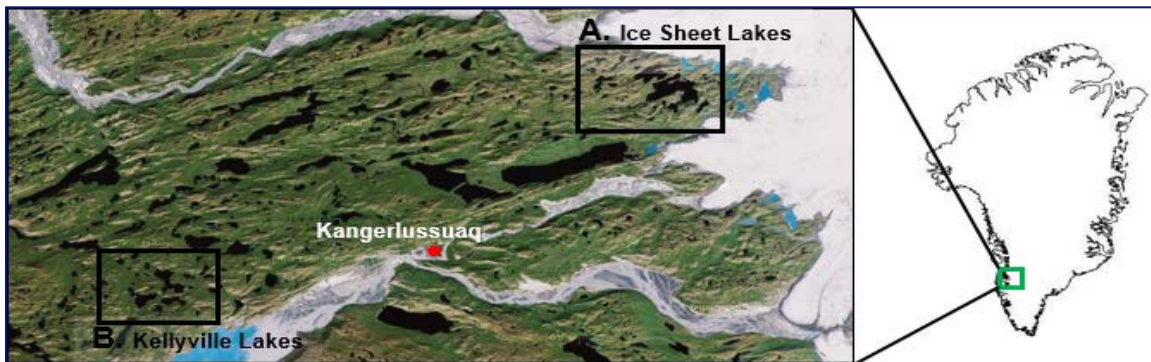


Figure 2: The study region in southwest Greenland. Black boxes indicate the two study regions: A) Ice sheet lakes (six lakes sampled, 1 lake sediment core collected) B) Kellyville lakes (six lakes sampled, 1 lake sediment core collected).

Approximately 20,000 lakes lie in part of the widest ice-free margin of southwest Greenland, in which Kangerlussuaq is located. In general, most of the lakes in the region are classified as chemically dilute and oligotrophic (Anderson et al, 2001; Saros et al, 2013). Kangerlussuaq has a population of approximately 500. This factor reinforces the assertion that these lakes are largely untouched by human activities. It is generally

acknowledged that West Greenland may be one of the few pristine places left in the Arctic to study lake ecosystems without confounding anthropogenic variables (Perren *et al.*, 2009). The Kangerlussuaq and nearby Kellyville region (66.5-67.2°N and 50-53.3°W) experience a continental, low Arctic climate with an average June-August temperature of 10.2°C and precipitation of 150 mm year⁻¹. Comparatively, climate in the ice sheet region (Figure 2A) varies greatly, with drier and windier climate patterns, a mean summer temperature of 8°C, and annual precipitation <150 mm year⁻¹ (Saros *et al.*, 2013). Sediment core collection and lake sampling occurred in two different regions near Kangerlussuaq during a two-week field expedition in June-July 2015: a site adjacent to the ice sheet at a higher elevation with colder temperatures (Figure 2A); and the Kellyville region with lakes at a lower altitude, with warmer temperatures (Figure 2B).

The Intergovernmental Panel on Climate Change's (IPCC) 2014 Synthesis Report, asserts that temperature trends in the Arctic will continue to rise at more than double the global average rate, a phenomenon known as Arctic amplification (Serreze *et al.*, 2009), with precipitation likely to increase in high-latitudes. The magnitude of warming in the Greenland-northeastern Canada segment is nearly twice as large as the whole Arctic mean, as temperatures rise throughout the troposphere and occur in all seasons but with particular prominence in winter (Ding *et al.*, 2014). Figure 3 shows recent and accelerated warming of Greenland temperatures through a time series reconstruction and a temperature anomaly chart of 2003-2013 with 1958-1968 as its reference decade.

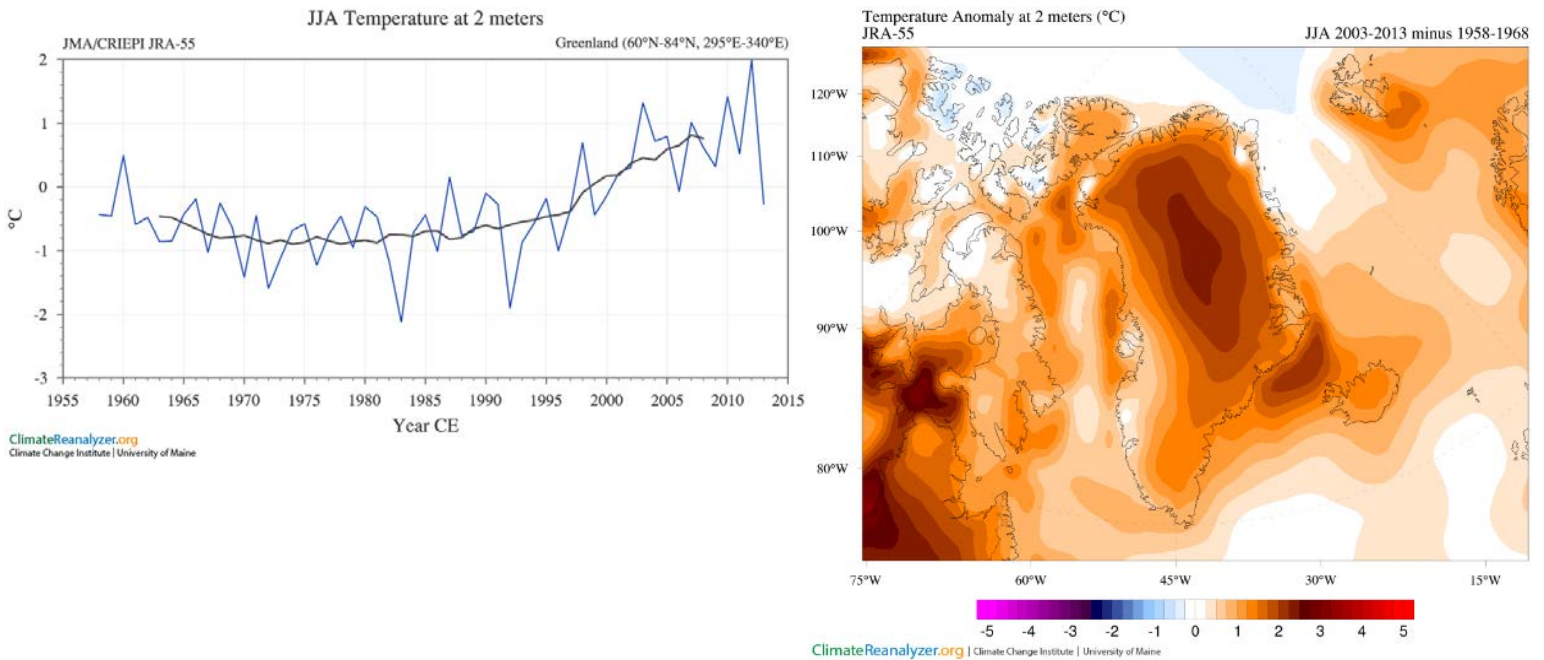


Figure 3. Average surface temperature at 2 meters for June, July, and August from 1958 to 2013 (data from Climate Reanalysis: Kobayashi, S. *et al.* (2015)). Shown as time series on the left and as temperature anomaly (average temperatures from 1958 to 1968 subtracted from average temperatures from 2003 to 2013) on the right. Data and image obtained using Climate Reanalyzer (<http://cci-reanalyzer.org>).

Coring and Sampling

Lake SS1341 (hereafter 1341) is located in the Kellyville region, at an altitude of 350 meters above sea level (m.a.s.l.) and with an area of 7 ha. Lake SS901 (hereafter 901) is located near the ice sheet margin, at a higher altitude. Two cores (A and B) were taken for each lake with a gravity corer from the deepest point in each lake (13.2 m in 1341 and 15 m in 901) to account for sediment focusing, and extruded onshore at 0.5 cm intervals. 1341 yielded a 20 cm core and 901 yielded a 15 cm core. The 901 core contained visibly finer sediment and was darker in color than 1341, with a gray clay-like sediment input near the bottom of the core (12-12.5 cm). The 1341 core contained plant matter throughout and was comparatively coarser and looser than the 901 sediment. Sediment samples were stored in

the dark at 5°C and carefully transported back to the United States and stored until lab processing in August 2016.

Modern zooplankton tows were collected in June-July of 2015 from 12 lakes surveyed in the two-week data collection period. These samples were preserved with isopropyl alcohol and are awaiting analysis. The modern zooplankton data utilized for this study were collected in June-July of 2013 from 26 lakes spanning both of the study regions. Zooplankton were collected with a 80µm mesh vertical tow net, dropped to a determined maximum depth and dragged from the hypolimnion to the epilimnion to account for vertical migration of species and a wide sampling range. The data were collected and shared by Erin Hayes-Pontius and Jasmine Saros at the University of Maine Climate Change Institute. Physical, chemical, and biological variables were measured at the time of zooplankton sample collection and included temperature, epilimnion thickness, pH, conductivity, photosynthetically active radiation (PAR), Secchi depth, lake surface area, maximum depth, elevation, dissolved organic carbon (DOC), total nutrients (total nitrogen (TN) and total phosphorus (TP)), dissolved nutrients (nitrate (NO_3^{1-}), ammonium (NH_4^+), phosphate (PO_4^{3-})), chlorophyll *a*, and ion concentrations (calcium (Ca) and iron (Fe)).

Lab Processing

One of each set of core sediment samples (901A and 1341B) were freeze-dried, processed and deflocculated with 10% KOH and 10% HCl, filtered through a 38µm sieve, transferred to coverslips, stained with safranin-glycerin jelly, and permanently mounted on slides (0.05 mL volume) in August 2016 following methodology developed by Korhola and Rautio (2001) and modified by Chen (2006). Duplicate slides were prepared for each depth in

both cores to maximize density of remains. Cladocera remains were identified to the genus-level at 10x magnification using a Carl Zeiss Axio Scope.A1 oil immersion microscope. Identification to the genus was based on an illustrated guide of cladoceran remains found in the northeastern United States, from which shape and distinguishing features of headshields, postabdominal claws, and carapaces were traceable (Korosi and Smol, 2012b). An average of 50 individuals were identified per segment in the 1341 core and an average of 30 individuals per segment were identified in the 901 core, using the sum of all identifiable appendages (headshield/antennules, carapaces, and postabdominal claws). Metrics used to reconstruct zooplankton community trends in both lakes are relative abundance and density. Relative abundance is the percentage of each number of individuals per taxon from the total sum of individuals for each segment of the core. Density represents the number of individuals per gram dry sediment for each segment of the core. For the modern analysis, linear regressions and t-tests were performed to ensure significant relationships.

Results

Paleolimnological Analysis

Five genera of zooplankton were identified in the 1341 core: *Bosmina* spp., *Alona* spp., *Chydorus* spp., *Eurycercus* spp., and *Pleuroxus* spp. *Pleuroxus* were only found in the bottom 2 cm of the core at low levels (between 0.74 and 4.88 % relative abundance). In general, both *Alona* and *Chydorus* trends decrease towards the present as *Bosmina* increases, with *Chydorus* spp. exhibiting more dynamic abundance trends (Figure 3). In

particular, *Chydorus* abundance ranges from 13.95% to 62.00% with a mean abundance of 45.67% in the top 10 cm as compared to a mean abundance of 34.50% in the bottom 10 cm. *Chydorus* dominates the abundance from 10 to 5 cm, where it peaks, and then declines until 0 cm where it is lowest. The top 5 cm represent the spike in *Bosmina* spp. from minimum abundance at 17% at 5.0-5.5 cm to maximum abundance at 77.91% in the 0-1.0 cm segment, dominating the relative distribution. In the top 10 cm, *Bosmina* spp. represent an average abundance of 35.98% versus 33.76% in the bottom 10 cm. *Alona* spp. range in abundance between 2.33% at 0-1.0 cm and 40.21% at 17.0-17.5 cm. Mean abundance in the top 10 cm of the core is 11.00% and 24.47% in the bottom 10 cm for *Alona* spp.. *Eurycerus* spp. remain relatively constant throughout the core with a relative abundance ranging from 1.32% at 14.0-14.5 cm-15% at 5.0-5.5 cm.

The *Bosmina* trend is the most dynamic throughout this core and the bottom half of the core contains a more proportional species distribution among *Bosmina*, *Chydorus* and *Alona* spp with average bottom-half abundances of 34.50%, 33.76%, and 24.47% respectively. In the top 1 cm, however, the distribution is heavily *Bosmina* skewed, with a relative comparison of 77.91% to 2.32% and 13.95% abundance of *Alona* and *Chydorus* respectively, both of whose relative abundance is lowest at the surface layer.

Remains in 901 indicate fewer dynamic trends and less species richness when compared to the relative abundance results from 1341 (Figure 4). *Bosmina* spp. are extremely dominant throughout the whole core, and this trend shows little fluctuation. Relatively, very few *Alona*, *Chydorus*, and *Eurycerus* remains were found in this core. Specifically, *Eurycerus* remains were found in three segments, and exhibited a small abundance between 1.85% and 3.64%. Similarly, *Chydorus* relative abundance was found

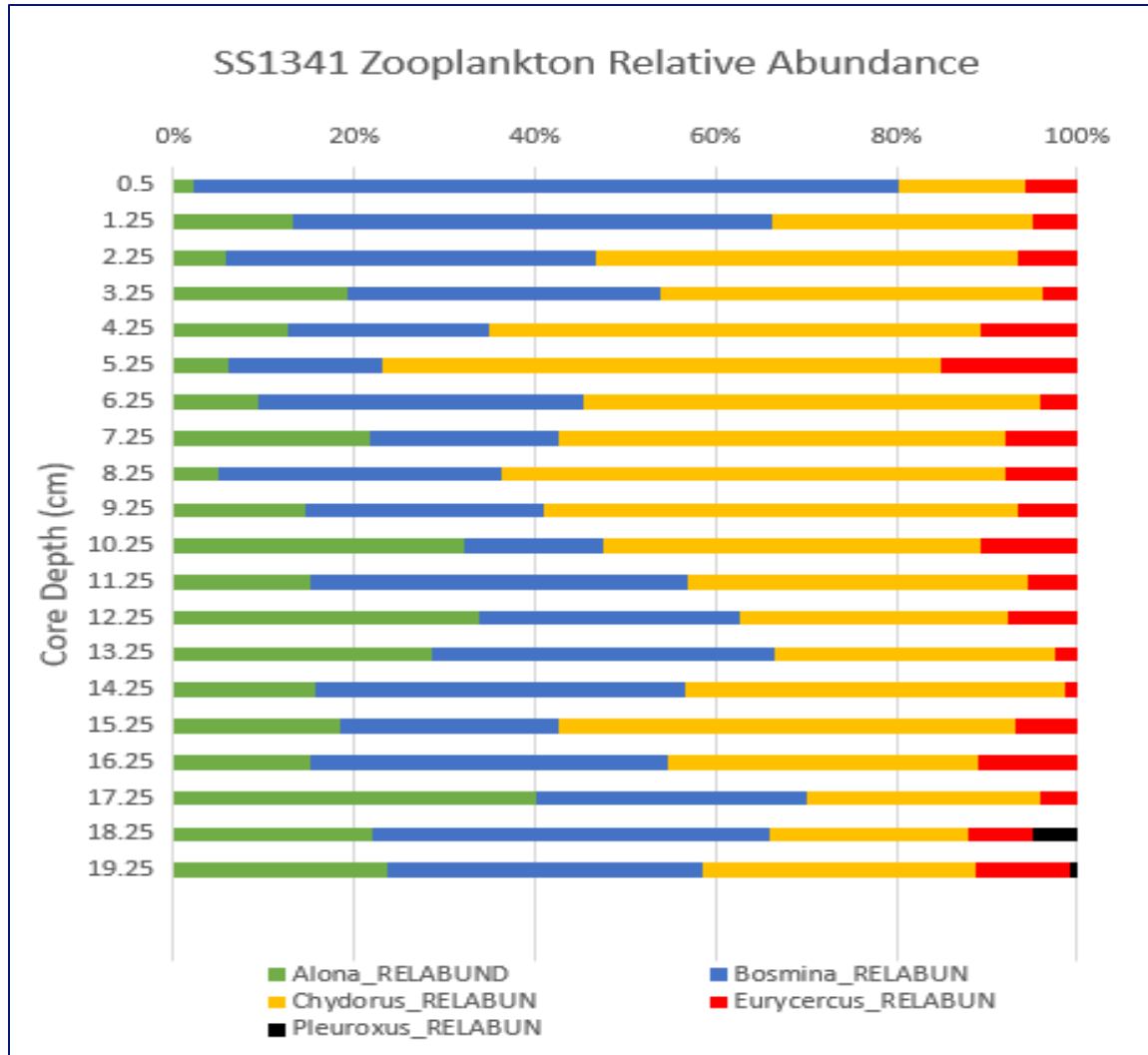


Figure 3: Relative abundance in 1341 depicting varying species distribution throughout the core, with a pronounced increase in *Bosmina* dominance at the top of the core.

within the narrow range of 1.82% and 4.32%. *Alona* abundance ranged from 0.72% to 13.33%. This peak was at 11.0-11.5 cm, where only two *Alona* individuals were identified, skewing the relative abundance distribution. In terms of species distribution, 901 shows full dominance of *Bosmina* spp. The relative abundance of this genus was between 50% and 100%, with a total average of 91.27%. Mean *Bosmina* abundance in the top 7 cm is 96.60% versus 85.18% in the bottom 7 cm. The lowest recorded values for *Bosmina* in 901 were 75% and 50% at 9.0-9.5 cm and 10.0-10.5 cm, where a very few number of total individuals were found (4 and 2, respectively), skewing the results for the relative

abundance metric. For example, at 10.0-10.5 cm, one *Bosmina* individual and one *Eurycercus* individual were found, determining a 50% split in the relative abundance result for this segment, despite clear dominance of *Bosmina* spp. as a whole in terms of species distribution throughout this core.

The second metric used to examine results from both cores is a density calculation. Figure 5 depicts total density based on the total sum of individuals found in each segment of both cores. Density ultimately declines in each core over time into the past, with a noticeable spike at 7.0-7.5 cm in 901. Peak density in 901 is at 7.0-7.5 cm, with 59,040

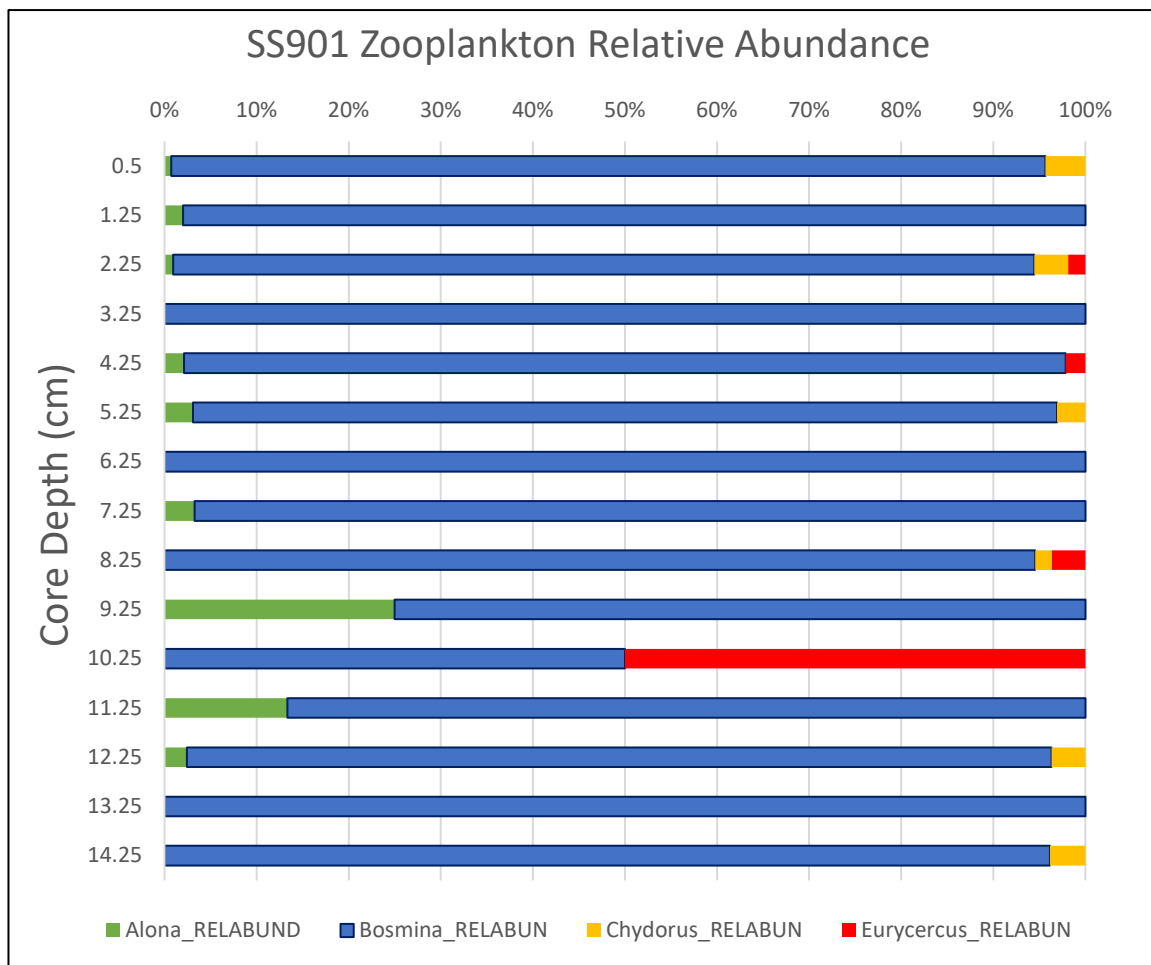


Figure 4: Relative abundance in 901 depicting *Bosmina* species dominance throughout the core.

individuals/g dry sediment (ind/ g dry sed), then drops to 3,990 ind/g dry sed at 6.0-6.5 cm. 901 density increases from 6 cm to the top of the core, peaking a second time at 0 cm with 58,127.27 ind/ g dry sed. Overall, the top half of the core displays an average density of 31,545.91 ind/g dry sed. In the bottom 7 cm of this core, average density is minimal (6,106.75 ind/g dry sed), given only an average of only 15 individuals found per segment below the 7.5 cm mark. The 1341 trend also fluctuates throughout the core with several peaks in the top 7 cm as well. Maximum density is 73,810 ind/g dry sed at 2.0-2.5 cm. There is another peak of 51,510 ind/g dry sed at 7.0-7.5 cm, like in the 901 core, but showing a less steep decline at 6 cm to 48,450 ind/g dry sed. The top 10 cm of 1341 have

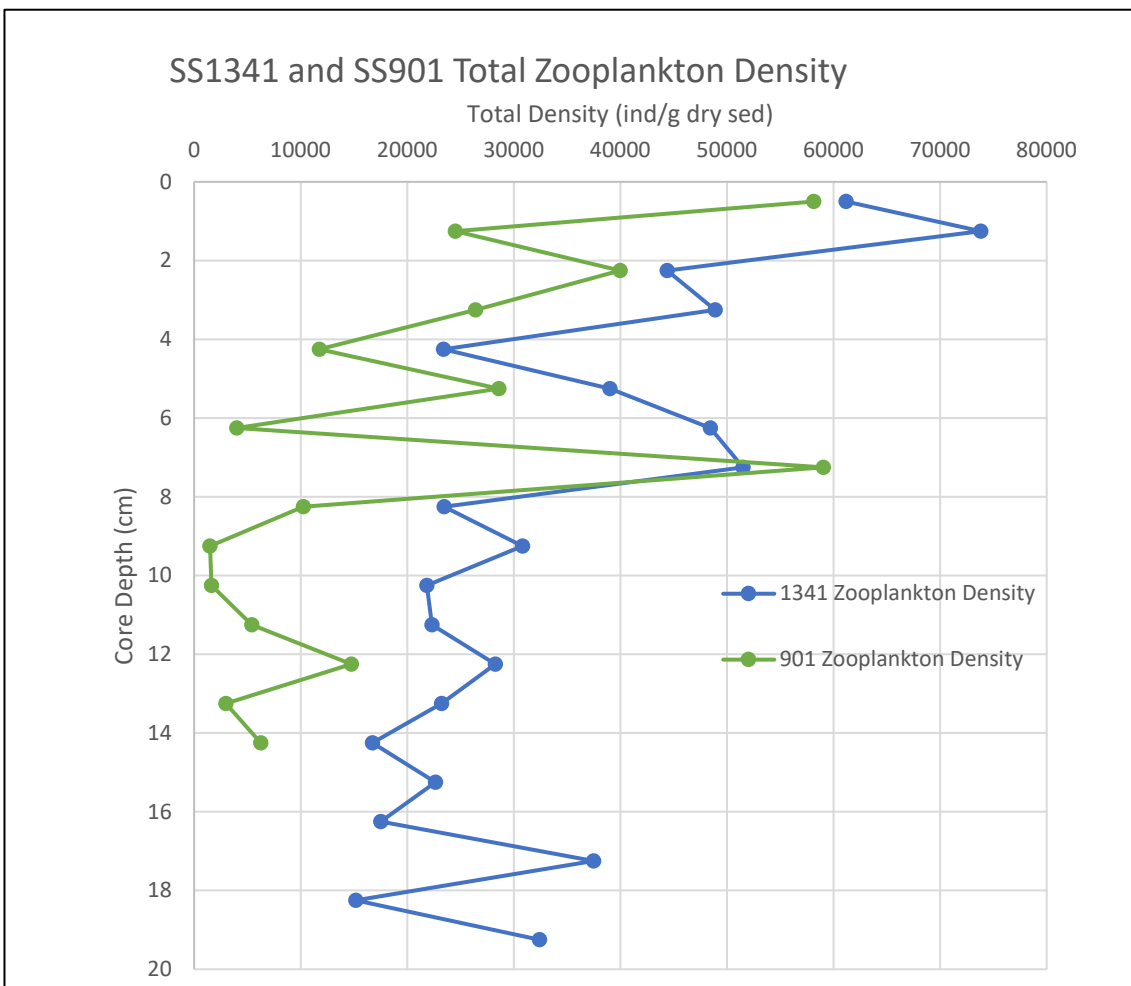


Figure 5: Total density trend comparison between 1341 and 901.

an average density of 42,430.88 ind/g dry sed. Average density is similarly lower in the bottom 10 cm of the core with 23,758.73 ind/g dry sed, but this average is much higher than the findings from the bottom half of the 901 core.

Density trends in each core are also divided by genus in each lake for more in-depth analysis of community shifts (Figure 6). As *Bosmina* spp. increase in density in the top cm of the 1341 core from 39,040 to 47,644.44 ind/g dry sed, *Alona* spp. and *Chydorus* spp. decrease in density from 9,760 to 1,422.22 ind/g dry sed and 21,350 to 8,533.33 ind/g dry sed respectively. *Bosmina* and *Chydorus* show a particularly divergent trend in the top 2 cm with a major change in density in opposing directions. *Eurycercus* spp. density remains relatively constant in 1341 with an average density of 2,317.80 ind/g dry sed. *Bosmina* spp. increase in density in the top 1 cm in 901 from 24,010 to 55,200 ind/g dry sed. *Alona* and *Eurycercus* spp. remain constantly low in density with an average of 401.36 and 165 ind/g dry sed respectively. *Chydorus* spp. exhibit a similarly low trend with an average density of 811.52 ind/g dry sed; however, density increases slightly in the top 1 cm of 901 from 0 to 2,509.09 ind/g dry sed.

No *Daphnia* ephippia were found during the initial identification and counting of zooplankton appendages and a brief re-examination yielded only one found in the top 1 cm of the 1341 core (approximately 4 mL of wet processed sediment). A mid core depth (9.0-9.5 cm) and lower core depth (19.0-19.5) cm from 1341 were analyzed (approximately 2 mL of wet processed sediment each) to represent a potential broad shift through the whole core; no ephippia were found in either segment.

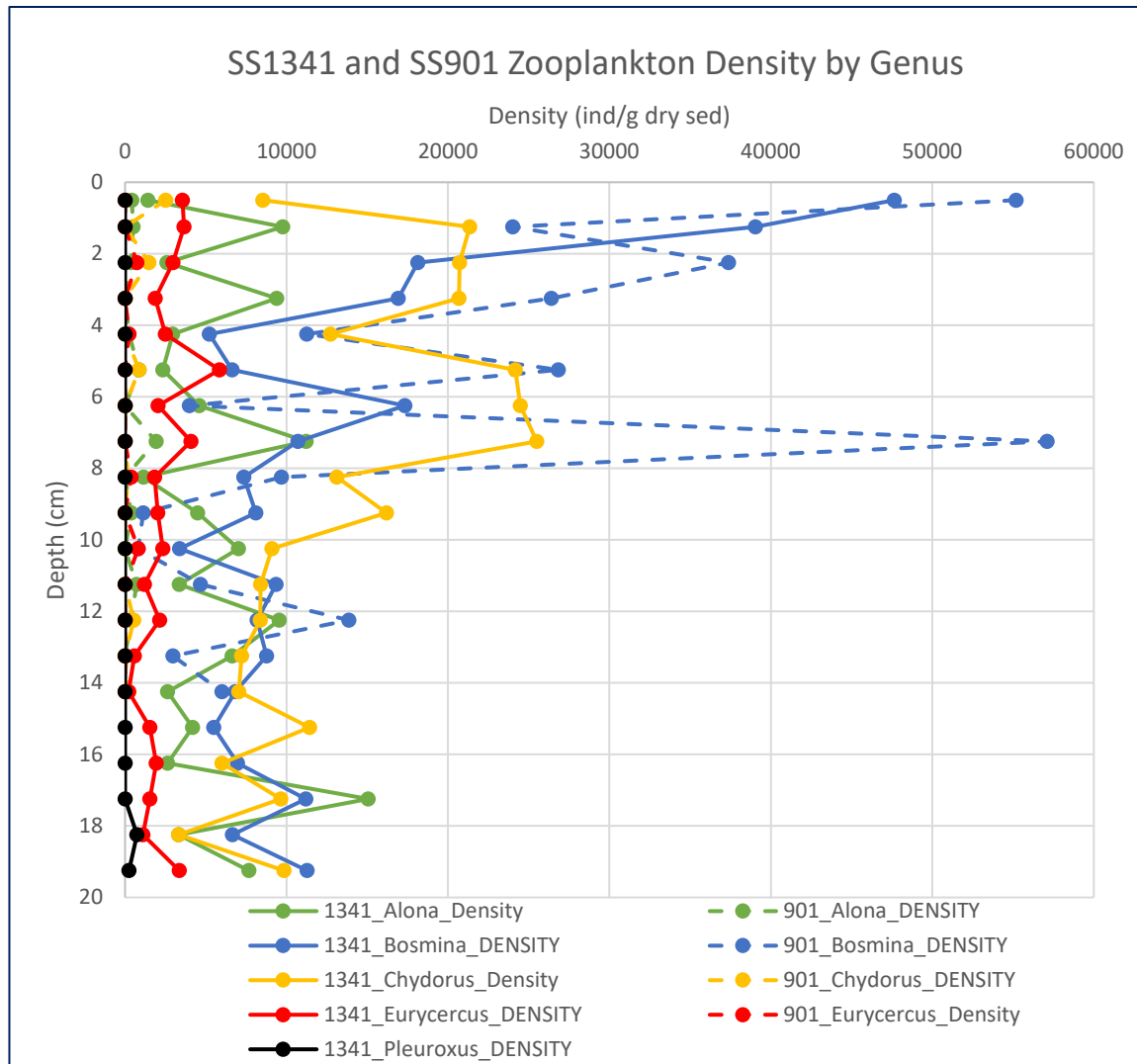


Figure 6: Density comparison by zooplankton genus between 1341 and 901.

Modern Analysis

From the range of modern zooplankton and environmental data collected from a suite of 26 lakes in this region, focus was placed on *Bosmina* spp. and *Eubosmina* spp. abundance to find potential mechanistic relationships that could inform the interpretation of community shifts observed in the sediment record. Of the 26 lakes, half contained *Bosmina* and *Eubosmina* species. *Bosmina* and *Eubosmina* abundance was compared to temperature, epilimnion thickness, pH, conductivity, photosynthetically active radiation

(PAR), Secchi depth, lake surface area, maximum depth, elevation, dissolved organic carbon (DOC), total nutrients (total nitrogen (TN) and total phosphorus (TP)), dissolved nutrients (nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-})), chlorophyll *a*, and ion concentrations (calcium (Ca) and iron (Fe)). The first significant relationship found ($p < 0.05$) was between photosynthetically active radiation (PAR) and abundance of these two related genera (Figure 7). Higher abundance of *Bosmina* and *Eubosmina* spp. is correlated with higher 1% PAR values, which indicates that light was able to penetrate deeper in the water column. The square on the chart represents the mean level of PAR for the 13 lakes that did not contain either of these taxa (10.56 m), which is lower than the 14.19 m average PAR found in the lakes containing these two genera.

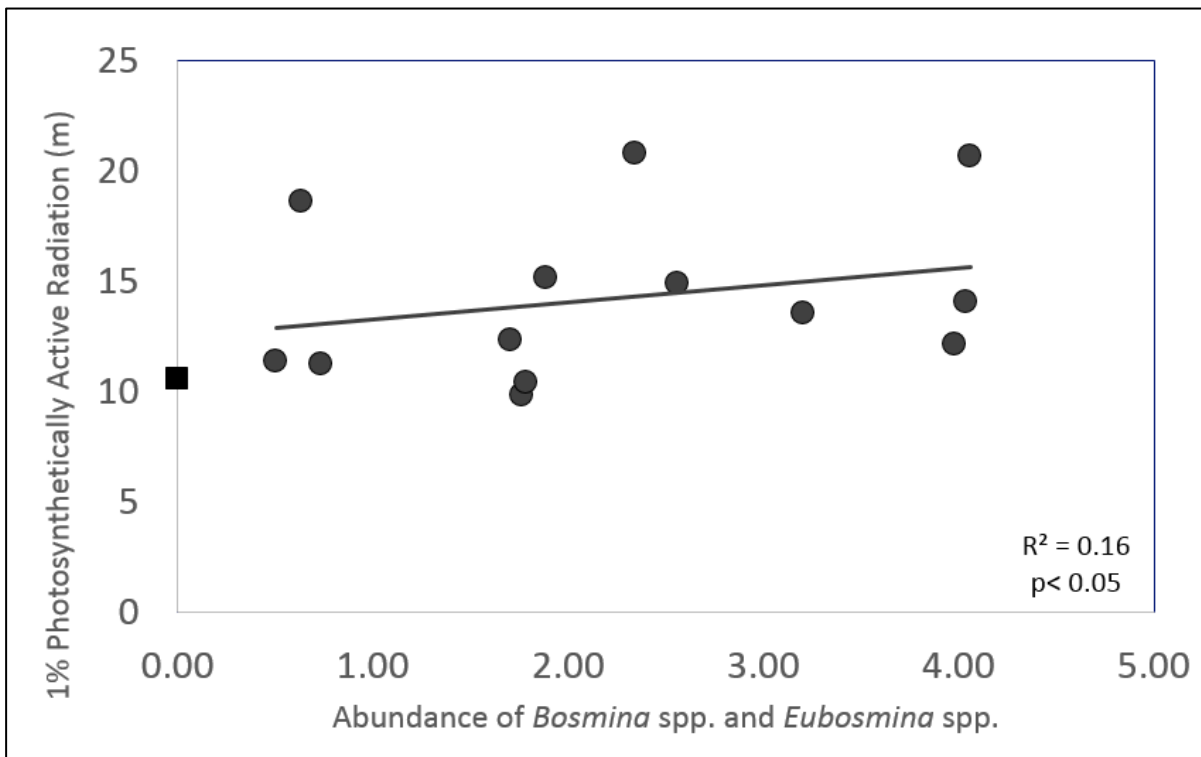


Figure 7: Significant relationship between higher *Bosmina/Eubosmina* abundance and greater PAR depths.

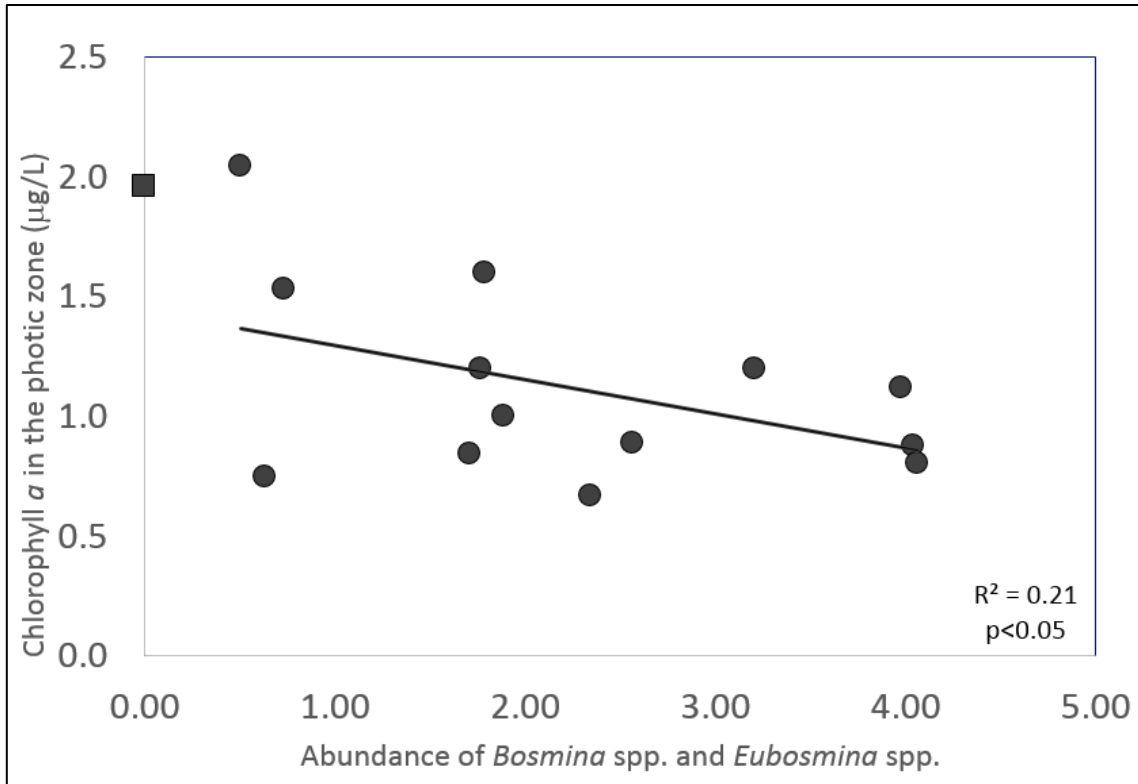


Figure 8: Significant relationship between higher *Bosmina/Eubosmina* abundance and lower concentrations of algal biomass.

A second significant relationship ($p < 0.05$) is between *Bosmina* and *Eubosmina* spp. abundance and concentration of algal biomass (chlorophyll a in the photic zone) (Figure 8). Higher abundance of *Bosmina* and *Eubosmina* spp. is correlated with reduced algal biomass in the 13 lakes with these taxa. Average concentration of these 13 lakes is 1.12 µg/L versus 1.96 µg/L in the lakes without these taxa. These two significant relationships are likely not independent drivers.

Discussion

Variability is demonstrated in the results of these two cored lakes when relating to the questions if and how zooplankton are changing over time. In both cores, the top 4 cm contains a major increase in zooplankton density, driven by *Bosmina* spp. abundance as the most dominant genus present. The most notable change in zooplankton community dynamics is an increase in the relative abundance and density of *Bosmina* spp., which increase in dominance compared to *Alona* and *Chydorus* spp. in the top 4 cm of the 1341 core and dominate the total zooplankton community throughout the record in 901. Genera are approximately evenly distributed in relative abundance in the bottom 10 cm of the 1341 core among *Chydorus* and *Alona* spp.. *Chydorus* spp. dominate the abundance record from 10 to 5 cm until *Bosmina* increase to the top and become the most abundant by a large margin. It can be concluded that *Bosmina* spp. are the most significant taxa observed in both of these records and could be driving community shifts accordingly.

In the 901 core, fewer dynamic trends were discernable. Relative abundance findings suggest dominance of *Bosmina* spp. throughout the whole core, with minimal numbers of *Alona*, *Chydorus*, and *Eurycercus* spp. found overall. Number of remains in general declined sharply in this core in the bottom half. When examining the *Bosmina* trend more closely through the density metric, fluctuations are visible. Despite higher total density in both cores in the top segments, maximum density in *Bosmina* spp. in 901 is at 7 cm. The next cm yields a large decline in *Bosmina* spp. density. This could indicate a disturbance in the lake at this time, and given proximity to the ice-sheet, the input was potentially glacial in nature. However, the change in sediment consistency to a finer, grayer material occurred at 12.0-12.5 cm in the 901 core, so this is unrelated to my field

observations. Although a specific explanation is not traceable using the methods here, it seems likely that the disturbance reset biological communities in the lake back to a much lower level. Density then climbs to another peak in the most modern time.

It should be noted that total remains in the bottom 7 cm of the core are very low and density declines in both lakes, which could be attributed to an issue with fossil preservation. There are a number of factors that affect preservation success, including turbulence, abundance and composition of bacterial communities (Ryves *et al.*, 2001), and specific chemical conditions or presence of certain ions like calcium (Frey, 1960). Also, the rate of particle descent in the water column and sedimentation in the lake can affect preservation success (Leavitt and Carpenter, 1990). Deterioration can also occur when samples are handled or preserved poorly; however, good preservation is considered the exception rather than the rule, as even a dissolved appendage can represent the best-known contemporary data (Ryves *et al.*, 2001). Given that whole, identifiable appendages were found in each segment of both cores, even in very low numbers in certain segments, it is concluded that results do not indicate major preservation issues.

The mechanisms behind the observed shifts are difficult to determine from the paleolimnological record, thus a modern analysis was conducted with the aim to ascertain specific environmental drivers that would leave a trace in the contemporary ecological condition of the lakes. *Bosmina* spp. and *Eubosmina* spp. were focused on in the modern analysis because of their relative importance in both cores and that discerning mechanisms behind shifts in these communities would best inform results from the sediment records. Findings include significant relationships between higher abundance of these two genera and both higher PAR and lower algal biomass. The distribution of *Bosmina* spp. in the

modern lake survey is correlated to increased lake clarity, which is directly connected to concentrations of chlorophyll a in the photic zone. Additionally, cladoceran zooplankton as grazers may influence the relationships with algal biomass and water clarity (Carpenter et al, 1985; Lampert et al, 1986; Gyllström et al, 2005; Ekvall et al, 2014). The observed increase in *Bosmina* spp. in the paleo record could suggest increased water clarity over time. However, determining causation in the relationship between biological and environmental variables with confidence is difficult. Despite this assertion, such a conclusion fits with documented trends of recent oligotrophication in these lakes (Anderson et al, 2008; Saros et al, 2015; Saros et al, 2016). Recent studies document decreasing DOC in these lakes in the last decade, and that DOC is a major factor that influences PAR attenuation (Saros et al, 2015; Saros et al, 2016). Therefore, water clarity in the majority of these lakes have been increasing in the recent past, and findings from this study add zooplankton community shifts as potential drivers of this environmental change.

Bosmina spp. are pelagic organisms, *Alona* spp. inhabit plants and the benthic zone, *Chydorus* spp. are pelagic-benthic, and *Eurycercus* spp. primarily plant-associated (Anderson *et al.* 2008). Habitat preferences like the relative importance of pelagic or benthic can influence biological structure and these shifts are traceable in the sediment record, but often ignored in larger analyses (Vadeboncoeur et al, 2002). Diatom community data are a good indicator of shifts between benthic and pelagic habitat, additionally examining zooplankton microfossils provides a potentially more objective explanation for inferring littoral vs planktonic production (Jeppesen et al, 2001; McGowan et al, 2005). Therefore, the distinct habitat preferences of the reconstructed zooplankton communities

play a significant role in interpreting results from the study. An increase in *Bosmina* spp. may suggest increased availability of pelagic habitat; however, with no significant shift in benthic species it suggests there was no reduction in benthic habitat.

Synchronous responses to climate change are expected across lakes in the same region (Magnuson *et al.*, 1990) with some exceptions (Arnott *et al.*, 2003), and existing data on zooplankton community change in southwest Greenland is limited. However, a study of a Kellyville lake, SS2, suggests results that counter those observed in 1341, also an inland lake in the Kellyville region (Anderson *et al.* 2008). The SS2 study observed reduced algal production and pelagic cladoceran communities over the last 900 years to the present. The abundance of benthic zooplankton increased at the expense of plant-associated cladocerans in the upper 2-3 cm of the sediment record studied by Anderson *et al.* (2008), indicating reduced plant abundance. The decrease in cladoceran taxa in the most modern period was attributed to oligotrophication of lakes in the region (Anderson *et al.*, 2008). The modern lake survey presented here also suggests a relationship between productivity and *Bosmina* spp.; however, the sediment record from 1341 would suggest increasing productivity to accompany an increased density of *Bosmina* spp. in modern times. Again, the divergent recent records of two lakes in the Kellyville region follow the pattern of dynamic but variable changes in the biological communities of lakes in this region, and heterogeneity in the response of these two lakes in the same region is clearly shown (Arnott *et al.*, 2003; Perren *et al.* 2009; Saros and Anderson, 2015).

Paleolimnological results show a dynamic shift within the *Bosmina* community of the lake at the top of the 1341 core, indicating some recent change in this lake like increased productivity or some indirect climate factor. If productivity has been increasing, it would

be indicated by higher concentrations of algal biomass. However, given that my results determined an inverse relationship between *Bosmina* spp. abundance and algal biomass, this driver is not a logical explanation for the observed increase in these pelagic cladocerans. The lakes are also exhibiting declining trends in DOC, not mimicking eutrophication through climate-induced productivity increases (Mooji *et al.*, 2005). The predominant mechanism is also not likely related to phenology changes observed in Winder and Schindler (2004), because if food-source emergence and signals were mismatched, that would be indicated by a decline in *Bosmina* abundance. It is likely that other environmental variables are responsible for total zooplankton density increase, which is not just limited to pelagic forms.

The geographic analysis component between a Kellyville and an ice-sheet lake yielded some interesting comparisons. Both cores increased in density to modern times, with pronounced increases in density in the top half of each core. 1341 zooplankton density peaked at 1 cm and declined slightly to 0 cm whereas 901 peaked at 7 cm and then reached a second peak at 0, indicating total density increase. Both cores contained the same genera except for a slight appearance of *Pleuroxus* spp. in the bottom of 1341. Pelagic *Bosmina* spp. played the most significant role in community composition in both lakes. The 1341 core yielded a dynamic community trend within the genus *Bosmina* at the top of the core, whereas this genus dominated relative abundance throughout the whole 901 core. Both this comparison and the findings of this study in general further support the conclusion that the relationships and mechanisms within lake ecosystems are complex, variable, and difficult to predict and/or isolate (Magnuson *et al.*, 1997; Battarbee 2000; Jeppesen *et al.*, 2001).

Conclusion

To summarize, I use a combined neo- and paleolimnological approach to address the questions if, how, and why zooplankton communities are changing due to direct or indirect effects of climate change in the lakes of southwestern Greenland. An increase in *Bosmina* spp. was observed in recent time in 1341. These changes suggest climate change impacts are not just isolated to the base of the food web but are also influencing upper trophic levels in these lakes. Modern relationships among *Bosmina* and *Eubosmina* genera and lake variables suggest this change may be driven by bottom-up mechanisms that alter lake water clarity and productivity. However, it is not certain if indirect effects of climate change through bottom-up processes or direct effects of external climate forcing are the cause of the observed shifts. Examining the long-term records in both a Kellyville and ice-sheet lake provides a platform for geographic and climatic comparison. Paleo results differed between 1341 and 901, with more dynamic shifts in zooplankton community found in the 1341 core. Variability in the trends suggests similar lake to lake variability observed in diatom community composition in the region (Perren et al, 2009; Saros et al, 2013). These results add to the limited body of research known about west Greenland lake ecosystems, and especially fill in some gaps about zooplankton community composition in the Kangerlussuaq region.

Lakes are significant features of the region; as such, the implications of altered ecology and other environmental characteristics are numerous. As climate change continues to affect this region intensely, as it is predicted to do through increasing temperatures, decreasing precipitation, and melting sea-ice (Post et al, 2009), changes in the biological, chemical, and physical properties of the lakes could impact their ability to

function as drinking water sources for human and wildlife populations. Drinking water is difficult to attain in communities as remote and isolated as Kangerlussuaq and is thus a very precious natural resource. Continued changes in the biotic communities of these lakes have the potential to affect this population significantly. Key fauna like muskox, caribou, Arctic hares, and waterfowl also rely on these lakes as drinking water sources.

This study ultimately relates to humans through our role in causing our current climate situation, which is prompting biotic communities to change and potentially act as signals for change in other lakes. Lakes as sentinels have been well established in the literature (Adrian et al, 2009; Williamson et al, 2009), including examples from the Arctic (Smol and Douglas, 2007; Mueller et al, 2009). Given the unique location of west Greenland and the ability to study isolated impacts of climate change independent of other anthropogenic factors, these lakes could potentially act as sentinels for other high-latitude, alpine or even temperate systems. Zooplankton are the top predators in these lakes, as they have very simple trophic structures. Many other lake systems throughout the world are much more complex and contain other organisms that would also exert top-down predation pressures on zooplankton. Therefore, it is difficult to predict how these lakes could act as models of climate-induced ecological change for other regions of the world. However, any knowledge gained from climate change effects on Arctic lakes could potentially inform future changes and strategies for the management of other lake systems that hold significance for larger human populations, and which also lie under the threat of global climate change.

Recommendations for further research

This study would benefit from a deeper analysis in several aspects. First, ^{210}Pb dating of both sediment cores would provide specific timelines, which could be lined up for more precise comparison of zooplankton trends. Additionally, remains could be identified to the species-level to gain a more in-depth understanding of change and potential drivers. *Bosmina* spp. mucro and antennule lengths and shape (*cornuta*-form) can inform community size structure (Alexander and Hotchkiss, 2010), which would be useful to expand our knowledge of food web dynamics, despite zooplankton having no predators in most of these lakes. Further data could be obtained from an analysis of the diatom community composition in these two lakes, and a loss-on-ignition (LOI) analysis. Long-term physical and chemical data of the lakes would also provide clarity to the question of why the communities shifted. Lastly, a larger sampling size would better inform widespread regional and climate-induced changes in the paleo and modern ecology of these lakes.

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