THE ECOLOGICAL RESPONSE OF LAKES AND LITTORAL BENTHIC MACROINVERTEBRATES TO ALTERATIONS IN FLOOD REGIME IN A CLIMATE-SENSITIVE ARCTIC RIVER DELTA

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A DISSERTATION SUBMITTED TO
THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

GRADUATE PROGRAM IN BIOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO

SEPTEMBER 2021

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Abstract

The Mackenzie River Delta is a major outlet to the Arctic Ocean, an important habitat for freshwater organisms, migratory birds, and mammals, and a critical economic and social resource for the Gwich'in and Inuvialuit people. The Delta is also sensitive to climate change, with an increased likelihood of more variable discharge and rising sea levels, leading to forecasts of increasing isolation of many high-elevation floodplain lakes and increasing connectivity of low-elevation lakes. While extensive and ongoing studies of the biogeochemistry of these lakes exist, lower secondary producers such as macroinvertebrates represent an overlooked element of the Mackenzie Delta ecosystem. The objective of this thesis is to identify the effects of flooding on the limnology and benthic invertebrate ecology of this climate-sensitive Arctic region. This thesis addresses this knowledge gap by examining responses of lake water chemistry (Chapter 1) and littoral benthic invertebrates (Chapter 2) to variation in peak flooding, in addition to examining patterns of metacommunity structure across lakes with differing connectivity to the river (Chapter 3). Using a five-year time series that captured recent extremes in peak flood level, I found that connection time was a dominant factor influencing lake water chemistry because of direct flooding inputs and the effects of spring flooding that carried forward through the growing season. The response of lake chemistry to differing annual peak flood levels differed according to the flooding regime of the lakes. Benthic invertebrate communities sampled over five years in the East Channel were also significantly related to connection time and several of the identified water chemistry variables, indicating that they are sensitive to alterations to flooding hydrology. Analyzing the metacommunity and functional structure of macroinvertebrate communities suggested that the hydrological diversity of lakes contributes to the regional diversity, with aquatic dispersers more limited by dispersal opportunity than aerially dispersing insects. These results suggest the promise of further study of benthic macroinvertebrates in this rapidly changing Arctic delta, the importance of considering habitat diversity for freshwater conservation, and the potential for environmental change in response to climate change in north-flowing northern freshwater systems worldwide.

Acknowledgments

First, I acknowledge that my research was done on the traditional lands of the Gwich'in and Inuvialuit peoples who, through the licensing process, gave permission to sample their lakes.

My supervisors Roberto Quinlan and Sapna Sharma provided invaluable support and guidance throughout the research and writing process. Roberto gave me the opportunity to pursue my PhD in his lab and provided unwavering support through five field seasons and the long process of analysis and writing. When circumstances intervened, Sapna very kindly stepped in as supervisor, and her guidance was indispensable to the final stages of analysis and writing.

I am also indebted to my committee members. Suzanne Tank provided valuable guidance on my study design and the Mackenzie Delta in general and was generous with her time and advice as a committee member and afterwards. Chris Lortie, the only constant member of my committee through the whole process, always provided thought-provoking questions and advice. Bridget Stutchbury, Dawn Bazely, Jennie Korosi, and Bob Bailey formed my defense committee under short notice and offered insightful questions that made my defense a lively conversation.

A number of people contributed to the field and data acquisition for my studies. Xiaowa Wang of Environment Canada and Climate change provided water chemistry data that was integral to this thesis. Andrew Medeiros played a key role in introducing me to the Quinlan lab, and provided field support and valuable advice during my initial years of Arctic field work. Chris Lusczcek, Sara Massod, Frankie Talarico, Cait Carew, and Dmitri Perlov travelled up with me to assist with field sampling, and their support was indispensable.

A number of organizations contributed to this work through field support and/or funding. The Western Arctic Research Centre provided logistical and licensing support, and the advice of Jolie Gareis and William Hurst was particularly valuable. This research was funded by a NSERC Discovery Grant and Northern Supplement to Roberto, grants from the Northern Student Training Program, and Ontario Graduate Student grants that supported me during my research.

I would not be on my current career path without the supervisors from my master's degree at Waterloo, David Barton and Marlene Evans (ECCC), who introduced me to the worlds of aquatic invertebrates and Arctic field research. I am indebted to both of them.

Last but not least, I thank my family and friends for their love and/or support while I was working on this long project, especially my parents Gary and Joan. I would not be here without you. I’d also like to thank my extended family of Jamie, Sam, Eric, Jordan, Deb & Pat for their support. Advice, support, or just needed distraction was provided by many friends, especially Tim, Dmitri, Chris, Jessica, Ryan H., Katherine, and Andrew.

Dr Ryan W Scott
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23 September 2021

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General Introduction

Water is an essential resource for all aspects of life on earth, from physical processes that shape habitats, to cellular biochemical processes, to ecosystem processes that influence biodiversity and carbon and nutrient fluxes, to the global hydrological cycle. The natural state of water resources is under increasing stress due to global climate change (IPCC 2014) and anthropogenic impacts such as flow regulation (Grill et al. 2019). The magnitude of these changes is likely to be greatest in Arctic regions (Box et al. 2019), with increases in precipitation (Bintanja & Andry 2017) and expected changes in the thermal, hydrological, and biological regimes of Arctic freshwater systems (Prowse et al. 2006). Permafrost provides a constraint on hydrological and fluvial processes that is unique to high-latitude regions, and permafrost warming (Biskaborn et al. 2019) or subsidence (Segal et al. 2016) will increasingly impact rates of discharge (Peterson et al. 2002) and transport of dissolved (Tank et al. 2016) and particulate sediment, carbon, and nutrients (Lafrenière & Lamoureux 2019). Widespread alterations to permafrost are likely to alter habitat characteristics and ecological function in aquatic ecosystems in the Arctic (Vonk et al. 2015). Arctic floodplain systems may be particularly susceptible to alterations due to climate change because they are sensitive to changes in upstream discharge and permafrost stability (Lininger & Wohl 2019) and because flooding dynamics are the result of ice-jam processes that are sensitive to increases in air temperature (Lesack et al. 2014). However, despite studies indicating global effects of climate change on population densities (Wagner 2020) and life cycle attributes (Kharouba et al. 2018), there is a lack of knowledge on the responses and trajectories of freshwater organisms and communities in a changing climate (Heino et al. 2009).

Hydrological connectivity is a fundamental structuring factor in freshwater ecosystems. Differences in connectivity among floodplain aquatic habitats leads to differential opportunities for colonization by aquatic organisms and influences habitat heterogeneity (Ward & Tockner 2001), increasing or decreasing the diversity of habitat templates, and therefore regional biodiversity (Ward et al. 1999). Low levels of connectivity may lead to higher environmental heterogeneity but limited opportunities for species dispersal, while high levels of connectivity (such as from flooding) can increase similarity among habitats (Thomaz et al. 2007), potentially decreasing regional diversity. Maintaining optimal levels of connectivity and heterogeneity in floodplain systems is an important requirement for maintaining or enhancing biodiversity and ecosystem sustainability (Ulanowicz et al. 2009).

In this thesis, I examine floodplain lake habitats and their benthic macroinvertebrate communities in the Mackenzie River Delta, Northwest Territories, to shed light on the biological response of lakes to alterations in flood levels related to climate change. Flooding in the Delta is driven by ice jam formation, a process that is sensitive to changes in air temperature (Lesack et al. 2014) and is likely to respond to projected climate change with isolated lakes becoming more isolated and connected lakes becoming more connected (Lesack & Marsh 2007, 2010). Benthic macroinvertebrates have long been used in biomonitoring because of their taxonomic and ecological diversity, ability to disperse so their distributions reflect ecological conditions, and ease of sampling (Cairns & Pratt 1993). Despite the extent of the literature on the ecology of Mackenzie Delta lakes, which will be reviewed throughout the chapters of this thesis, and studies of benthic communities in streams and lakes located in the surrounding uplands (e.g., Scott et al. 2011, Cohen et al. 2020), our knowledge of benthic macroinvertebrate communities within the Delta is lacking, with the only previous study limited to a nearly five-decade old government report (Brunskill et al. 1973). This thesis intends to fill this knowledge gap, and contribute to the literature on the response of Arctic deltaic lakes to climate-related variation in flood levels, the utility of benthic macroinvertebrate communities as indicators of climate-induced alterations to flood regime, and the regional benthic macroinvertebrate metacommunity structure and its potential response to climate-related alterations to the flooding regime.

In the first chapter, I examine changes in dissolved and particulate constituents of lake water in lakes spanning the connectivity gradient over a five-year time span. This study was conducted on a set of lakes located in the East Channel of the Delta near Inuvik. This chapter addresses the following questions: (1) does water quality differ among lakes with contrasting flood regimes and connectivity to the surrounding landscape?; (2) does water quality change over the time period of the study in relation to variation in connection time?; and (3) do lakes with contrasting flood regimes respond similarly to alterations in flood regime over the course of the study? (Scott et al. in review).

In the second chapter, I examine changes in benthic macroinvertebrate communities in the same set of East Channel lakes spanning the connectivity gradient over a five-year time period and the utility of benthic macroinvertebrate communities as biological indicators of changes to flooding ecology. This chapter aims to answer the questions: (1) are there distinct assemblages among lakes or groups of lakes in the Delta?; (2) is benthic assemblage variation related to the observed environmental gradients?; and (3) is the assemblage classification useful in predicting environmental conditions, and so useful for biomonitoring purposes? (Scott et al., 2020).

In the third chapter, I examine metacommunity structure of benthic macroinvertebrate communities, including the relative influence of spatial versus environmental factors and the functional (trait) community structure, using a set of lakes that spanned the longitudinal width of the Delta. For this study, I sampled lakes spanning the connectivity gradient in three regions, corresponding to the East, Middle, and West Channels. This chapter aims to answer the research questions: (1) What is the relative importance of environmental factors and spatial patterns that influence benthic community structure?; (2) How is the metacommunity structured in relation to lake-river connectivity and dispersal mode?; and (3) How does functional community structure vary across the environmental and spatial gradients?

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Chapter 1: The limnological response of Arctic deltaic lakes to alterations in flood regime

Ryan W. Scott, Sapna Sharma, Xiaowa Wang, & Roberto Quinlan

Author's Contributions

RS and RQ conceived of the research ideas, RS, SS, and RQ acquired funding, XW provided chemical analysis of water samples, RS conducted field sampling, analyzed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Inland Waters.

This chapter has been submitted for publication to Inland Waters as Scott, R. W., Sharma, S., Wang, X., & Quinlan, R. In review. The limnological response of Arctic deltaic lakes to alterations in flood regime. *Inland Waters*, submitted 5 July 2021.

Summary

Arctic freshwaters are being rapidly altered by global climate change with consequences to hydrology, biogeochemistry, and ecology, but in many cases the trajectory of these changes is poorly understood. We collected a unique five-year time series of major ion, nutrient, and trace metal data from lakes in the Mackenzie Delta to examine limnological changes during a period of variable flood conditions, including years of recent historic high and low peak river levels. Previous work in the Mackenzie Delta has established that lake water chemistry is strongly related to connection time with the river during the period of spring ice jam flooding or via channel connections through the growing season. We show that differences in peak spring water levels explain differences in lake chemistry in lakes that are isolated from the channel during the summer. Isolated, macrophyte-rich lakes in the Mackenzie Delta have been shown to be CO_2 absorbers during the summertime. We demonstrate a response to alterations in flood regime by variables related to macrophyte productivity in isolated lakes with the greatest connectivity to the river that suggests productivity declines with increasing connection time. The connectivity of low-elevation lakes, which represent a majority of lake number and area in the Delta, has been projected to increase with climate change. Our work suggests that an increase in connection time may decrease the macrophyte productivity of these lakes, with potential consequences to the CO_2 balance of individual lakes and the Delta as a whole.

Introduction

The pan-Arctic river systems of Eurasia and North America are critical components of the global hydrological and carbon cycles. These watersheds deliver ca. 4200 km^3 yr^{-1} of freshwater (Haine et al. 2015), 34 Tg dissolved organic carbon (DOC), and 57 Tg dissolved inorganic carbon (DIC) to the Arctic Ocean, with nearly half of the annual flux originating from the six largest Arctic rivers (Holmes et al. 2012; Tank et al. 2012). Arctic lakes and rivers are important sites of biogeochemical cycling (Cole et al. 2007; Bastviken et al. 2011; Tank et al. 2018), contributing to global fluxes of CO_2 and CH_4 (Emmerton et al. 2016; Jammet et al. 2017). Under current climate conditions, freshwater discharge and dissolved carbon fluxes to the Arctic Ocean have increased over the last several decades (Peterson et al. 2002; Tank et al. 2016; Rood et al. 2017), with consequences to marine ecology and freshwater storage (Carmack and Macdonald 2002; Haine et al. 2015) and implications for global circulation patterns (Brown et al. 2019).

At the same time, the release of aged carbon and increases in terrestrial-aquatic connectivity related to permafrost degradation will lead to increased carbon emissions from northern regions (Abbott et al. 2016). Permafrost thaw has been observed across the Arctic (Wild et al. 2019; Plaza et al. 2019) and at increasing rates in some regions (Segal et al. 2016; Kokelj et al. 2017). Thaw releases permafrost-derived organic matter which may be particularly labile to mineralization (Vonk et al. 2013; Drake et al. 2015), with impacts to the hydrology (Walvoord and Kurylyk 2016), biogeochemistry (Frey and McClelland 2009) and ecology (Vonk et al. 2015) of freshwater systems, and potentially contributing to a positive carbon feedback leading to further warming (Schuur et al. 2015). Considerable uncertainty exists regarding the net carbon balance of Arctic lakes (Abbott et al. 2016), particularly in regard to the importance of terrestrial-aquatic connectivity in determining transport rates and lake responses to releases of permafrost carbon (Tank et al. 2009; Feng et al. 2013; Vonk et al. 2015; Bogard et al. 2019). Since Arctic and boreal regions contain the greatest abundance of lakes and smaller water bodies (Lehner and Döll 2004) and ca. 50% of global soil carbon stores (Tarnocai et al. 2009), it is critical to develop our understanding of the changes occurring in the great Arctic drainages.

A common feature of many pan-Arctic rivers is ice-jam flooding (Prowse and Culp 2003), which occurs when increased discharge during snowmelt induces mechanical breakup of solid river ice in the northern parts of the system (Beltaos et al. 2012). Ice jam floods generate higher river levels than would occur with increased discharge alone (Goulding et al. 2009; Lesack et al. 2013). This process is mediated by climate: higher air temperatures may weaken the ice before discharge rises, resulting in thermal breakup (Beltaos 2013), with reduced peak water levels and earlier ice breakup (Beltaos and Prowse 2009; Lesack et al. 2014; Wang et al. 2017). Combined with multidecadal trends towards earlier onset of spring freshet in tributary basins (Woo and Thorne 2003; Abdul Aziz and Burn 2006), lower spring maximum discharge, and increased winter baseflow (Lesack et al. 2013; Yang et al. 2015), the hydrological regime of ice-jam deltas are potentially susceptible to alterations due to climatic change (Rouse et al. 1997).

Climate-mediated alterations to the hydrological regime of Arctic deltas may likely impact the ecological and biogeochemical functioning of deltaic lakes which depend on the annual influx of water, sediment, nutrients, and organisms (Junk et al. 1989; Tockner et al. 2000). In the Mackenzie River Delta, globally the second-largest Arctic delta, the extent and duration of connections between lakes and the river are determined by variation in the elevation of the sill above the channels (Marsh and Hey 1989). The resulting flooding gradient has profound implications for habitat quality and lake functioning, including impacts on water renewal (Lesack and Marsh 2010), water balance (Marsh and Lesack 1996), sedimentation (Marsh et al. 1999), major ion composition (Lesack et al. 1998), transparency (Squires and Lesack 2003a), and primary productivity (Squires and Lesack 2002; Squires et al. 2002; Squires et al. 2009). Variation in primary productivity, particularly of macrophytes, has been shown to influence the quality (Tank et al. 2011) and biogeochemical processing (Febria et al. 2006; Cunada et al. 2018) of DOC, as well as lake metabolic balance (Squires et al. 2009). In many cases thick macrophyte beds cause the lakes to absorb CO_2 rather than emit it (Tank et al. 2009) as is more typical of Arctic lakes. In contrast, thermokarst – the process of permafrost degradation in ice-rich soils that is generally responsible for lake formation in the Delta (Hill et al. 2001) – causes deepening of lake basins (Emmerton et al. 2007) and release of recalcitrant coloured DOC (Tank et al. 2011). Lakes that are highly affected by thermokarst are typically net CO_2 emitters (Tank et al. 2009). Variation in flooding and thermokarst result in a mosaic of lakes across the Delta in which nearby lakes can differ greatly in characteristics and function.

While the studies cited above have contributed greatly to understanding of lake processes and function in the Delta, considerable uncertainty remains as to the response of lake environments to alterations in the overall flooding regime, particularly in regard to lakes that are less connected to the surrounding landscape (Lesack and Marsh 2010). In this paper we take a step towards addressing this knowledge gap using a unique five-year data set of lake water quality (major ions, nutrients, and trace metals) to examine responses in water quality among lakes spanning a hydrological connectivity gradient to changes in connection time during flooding. Fortuitously, our study spans years that include recent historical highs and lows of peak discharge river height in the East Channel of the Mackenzie River, allowing us to collect observations of lake limnological responses to a range of flood conditions and lake connectivity to the river. We use water quality parameters collected during the summers of 2013 – 2017 in combination with river level data to address the following questions: 1) does water quality differ among lakes with contrasting flood regimes and connectivity to the surrounding landscape?; 2) does water quality change over the time period of the study in relation to variation in connection time?; and 3) do lakes with contrasting flood regimes respond similarly to alterations in flood regime over the course of the study? Finally, we interpret gradients in water quality in light of prior research and understanding of lake function to suggest implications for the carbon balance of Arctic deltaic lakes under conditions of climate-induced alterations to flood regimes.

Methods

Study area

The Mackenzie system is the largest Arctic drainage in North America with a watershed area of 1.8×10^6 km^2 that encompasses a large portion of northwestern Canada (Rosenberg and Barton 1986). The north-flowing Mackenzie River mainstem terminates at Point Separation, where the river divides into anastomosing channels that run through the Mackenzie Delta into the Beaufort Sea. Marine discharge from the delta is rich in nutrients, suspended sediment, and dissolved organic and inorganic compounds (Holmes et al. 2002; Graydon et al. 2009; Emmerton et al. 2008; Tank et al. 2016). Spring flooding with concurrent ice breakup is the major annual hydrological event in the Delta, typically commencing in mid-May and ending in early June (Marsh and Hey 1989). Nearly half of the discharge during this period is temporarily stored on the floodplain where it mixes with lake water before approximately 80% of this stored water is exported eventually to the Beaufort Sea as the flood recedes (Emmerton et al. 2007). The remaining water is stored on the delta floodplain in the form of approximately 45,000 mainly small, shallow lakes (Emmerton et al. 2007). These basins are formed by thermokarst processes in which standing water on top of permafrost causes increases in active layer depth, which leads to thaw subsidence of ice-rich permafrost and the formation of depressions which deepen into lake basins (Hill et al. 2001). The progressive deepening of lake basins from thermokarst activity combined with estimates of maximum ice cover thickness (0.6 – 1.2 m, depending on snow cover) suggest that the vast majority of the lakes are of sufficient depth to retain unfrozen water through the winter (Emmerton et al. 2007).

The physicochemical diversity of lakes in the Mackenzie Delta is primarily a result of differences in the length of connection of the lakes to the distributary channels during the flowing water season that lasts from May to September, and in particular the period of high water levels during ice breakup (Lesack and Marsh 2010). Mackay (1963) classified Delta lakes as No Closure (NC), Low Closure (LC), and High Closure (HL), defined by the frequency and duration of connections between the lake and the river. NC lakes possess connecting channels ranging from several m to km in length that allow flow between the lake and the channel. Flow in the connecting channels is typically into the lake during spring flooding and out of the lake during base flow periods in the summer but may briefly reverse during precipitation-driven increases in discharge (Hill et al. 2001). Over 80% of lakes in the Delta lack connecting channels and are perched to varying degrees above the river (Marsh and Hey 1989), only exchanging water during the spring flood period when river levels are higher than the minimum elevation of the sill of land between the lake and the channel. LC lakes have sill elevations that are lower than average peak river levels, so they are flooded annually during the spring high flow, but high enough to isolate them from the channels during summer base. HC lakes have sill elevations approaching or exceeding average peak flood levels and are inundated only for a period of days during the spring flood, or not at all in years with low peak river levels. HC lakes with the highest sill elevations may have a flood return period of up to 10 years and are subject to evaporative water loss in the absence of water renewal from flooding for consecutive years (Marsh and Lesack 1996). In the upper delta, NC lakes account for approximately 12%, LC for 55%, and HC for 33% of all lakes (Marsh and Hey 1989) and for 23%, 51%, and 25%, respectively, of total lake area (Marsh et al. 1999).

Site selection and sample collection

Study lakes were located in the southeastern portion of the subaerial delta along the East Channel and adjacent Big Lake Channel near the town of Inuvik, NT (Figure 1). Isolated lakes were located close to the main channels and were accessed by boat directly from the channel, while lakes connected to the river by distributary channels (ranging from ~ 0.1 – 2.1 km) were accessed via canoe. The lakes were selected to represent the three closure groups, with 6 HC and 2 LC sampled each year (2013 – 2017). In 2013, three NC lakes were sampled, but access via boat to these lakes was prevented in 2014 by low water levels in the distributary channels, so two more accessible NC lakes were selected for sampling in subsequent years (2015 – 2017). Lake connection time (CT) was determined using water level data from a hydrometric monitoring station (10LC002) operated by Environment and Climate Change Canada (ECCC) (extracted from the ECCC Real-time Hydrometric Data web site (https://wateroffice.ec.gc.ca/mainmenu/real_time_data_index_e.html) on 30 May 2021) and historical lake sill elevation measurements (Marsh and Hey 1988). Water level in the East Channel of the Mackenzie Delta is provided by ECCC for the periods of 1985 – 1990 and 2002 – 2019, which we use to assess ranges in date and water stage at peak flow. CT was calculated as the number of days the river level exceeded the lake sill elevation (Figure 2).

Surface water was collected by hand in the near-shore zone of each lake in duplicate 2 L Nalgene bottles. Temperature, specific conductivity, pH, and dissolved oxygen (DO) were measured in situ using a YSI-600QS multiparameter probe. The samples were transported to the Western Arctic Research Centre, Aurora Research Institute, in Inuvik where they were processed within 12 hours of sampling. All samples were first run through a 200 µm seive to remove filamentous algae or floating debris. A subsample was passed through a pre-ashed 25 mm GF/C filter (pore size 1.2 µm) for analysis of particulate organic carbon (POC), particulate organic nitrogen (PON), and a 47 mm GF/C filter for chlorophyll *a* (Chla). The filtrate was retained for measurement of total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP) and dissolved kjeldahl nitrogen (DKN), and unfiltered subsamples collected for total phosphorus (TP) and total kjeldahl nitrogen (TKN). Subsamples were also collected for analysis of dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC), major ions, ammonia (NH_4), nitrate/nitrite (NO_3/NO_2), and trace metals. Filters were kept frozen and samples were transported under refrigerated conditions to the National Laboratory for Environmental Testing, Burlington, ON, for analysis using standardized protocols (ECCC 2017a,b). Water quality data for the East Channel was obtained from a public monitoring database (NWT-wide Community-based Water Quality Monitoring, Environment and Natural Resources, Government of the Northwest Territories, doi: 10.25976/4der-gd31).

Data analysis

All water chemistry parameters were tested for normality (Shapiro-Wilk, $\alpha = 0.05$; Royston (1995)), and variables transformed as necessary to achieve normal distributions (Table A1). To establish water quality differences among lake closure types, we first examined differences in all water quality variables, separately for ions/nutrients and trace metals, among lake closure types (High, Low, or No Closure) using a permutational multivariate analysis of variance of the Euclidean distances among samples (Anderson 2001) followed by pairwise PERMANOVA among the closure types. To assess differences among closure types in individual water chemistry parameters, we used analysis of variance (ANOVA, $\alpha = 0.05$). Water chemistry parameters with globally significant differences among closure types were further examined using a Tukey pair-wise comparison (Tukey 1949) among closure types as well as the main channel. For all pairwise tests, p values were adjusted for multiple testing using the method of Benjamini and Hochberg (1995).

To assess temporal changes in water quality parameters over the study period, and the relationship of any changes to differences in CT resulting from variation in spring flood levels, we used principal component analysis (PCA) of the nutrient/ion and trace metal variables separately. The relationship of the resulting PCA axes to variation in CT was assessed by a posteriori projection of CT onto the ordination and using permutations of the environmental variables to test for significance using the envfit function of the vegan package in r (Oksanen et al. 2019).

Results

Peak flood levels and lake connectivity during the study period

Over the period of record, peak water levels ranged from 4.43 m above sea level (m.a.s.l) in 2016 to 6.13 m.a.s.l in 2007 (Figure 3). The date of the annual peak occurred within 2.5 weeks in the spring, the earliest peak occurring on 20 May 2016 and the latest on 7 June 1986. The 2013 – 2017 sampling period included years of high peak water level and late date of peak (2013), two years of low peak levels (2014 and 2016), and two years within one standard deviation of the average for level and date of peak (2015 and 2017).

CT differed markedly among the lake types based on differences in sill elevation (Table 1). HC lakes were flooded for up to 11 days but usually for a week or less, and the HC lakes with highest sill elevations were not connected for any period during the years with the lowest peak channel levels. LC lakes were inundated for two weeks to over a month in the spring, and NC lakes were connected for approximately half of the year on average.

Does water quality differ among lakes with contrasting flood regimes and connectivity?

Water chemistry differed significantly among lake closure types. The total composition of ions and nutrients of lake water was significantly different in a PERMANOVA across the three closure types ($R^2 = 0.443$, df = 2, $p < 0.001$), and significant differences ($p < 0.001$) were found in pairwise tests among all three lake closure types. The greatest differences were between the NC lakes and each of the isolated lake groups (NC vs HC: $R^2 = 0.480$; NC vs LC: $R^2 = 0.525$; LC vs HC: $R^2 = 0.183$), indicating that water quality in the isolated (HC and LC) lakes was distinct from the NC lakes. Of the 24 water quality parameters, nine were significantly different among closure type (Figure 4, Table A1). HC lakes were characterized by high pH and nitrogen (primarily as DON) and low Ca^{2+}, Si and specific conductivity, and LC lakes by high DIC. Concentrations of most water quality parameters were similar in the NC lakes and the main channel (Figure 4). Chemical parameters in the channel showed lower variation across years than those in the lakes and differed significantly from the HC lakes but not the LC or NC lakes.

The composition of major ions, represented by fractions of the sum of ionic constituents, varied among the closure types (Figure 5). DIC was the dominant anion in all lake types, with high concentrations of SO_4^{2-} in NC lakes equivalent to ~ half of the SO_4^{2-} in the channel (Table A1). Dominant cations in the lake types were Mg^{2+} in HC lakes and Ca^{2+} in LC and NC lakes. Of the major ions Mg^{2+} had the clearest relationship to connection time, decreasing among the closure types from highest elevation to lowest (Figure 5).

Trace metal composition was significantly different in a multivariate ANOVA across the closure types ($R^2 = 0.615$, $p < 0.001$), with pairwise contrasts significant between HC and the other two groups, and not significant between the LC and NC groups ($p = 0.055$). Only six metals were significantly different among closure groups (Figure 6, Table A2). Fe and Sr were the dominant trace metals in the lakes, comprising 45.1% and 26.6% of total trace metals on average, followed by Ba (13.9%), Al (7.8%), Mn (2.0%) and B (1.8%), with all other elements comprising < 1% of the total ionic concentration (Table A3). While missing variables in the channel data prevented direct comparison of percentages between the lakes and the channel, trace metals in the channel were dominated by Fe and Al. Concentrations of nearly all trace metals for which channel data were available were significantly higher in the channel than the lake (ANOVA, $p < 0.001$; Table A3), the exceptions being Ba and Sr. Elements that were particularly enriched in the channel relative to the lakes were Ti (channel with 55x the mean lake concentration), Al (44x), Cs (38x), Be (31x), V (17x), Ag (17x) and Pb (16x). Averaged across variables, concentrations of trace elements were approximately 13.4x higher in the channel than the lakes regardless of closure type.

Does water quality change over the time period of the study in relation to variation in connection time?

A PCA of nutrient/ion variables across all sites and years (Figure 7a) produced two axes that cumulatively explained 41.9% of the variation among samples (PC1: 22.1%; PC2: 19.8%). These axes were significantly related to variation in connection time (Table 1), both in an *a posteriori* projection onto the ordination ($r^2 = 0.688$, $p < 0.001$) and in individual linear regressions between each of the first two axes and connection time (PC1: $r^2 = 0.287$, $p < 0.001$; PC2: $r^2 = 0.370$, $p < 0.001$). Among lakes, PC2 clearly reflected a sill elevation gradient from a cluster containing the NC lakes to a cluster containing high elevation lake L520, whereas PC1 reflected a gradient among the isolated lakes from lake MD3 (the lowest elevation LC lake) to HC lakes. Among years (Figure 7b), the NC lakes showed little variation, whereas 2013 was distinct from the 2014 – 2017 samples for each of the LC and HC lakes. 2013 was notable in having the highest peak flood level and latest date of breakup during the study period (Figure 3) and the longest connection times in the isolated lakes (Table 1).

The first two axes of a PCA of the trace metals (Figure 8) explained a cumulative 51.1% of the variation across all lakes and years, primarily along the first axis (PC1: 39.4%; PC2: 11.7%). Unlike the analysis of nutrients and ions, trace metals had no significant relationship with either connection time as an *a posteriori* projection ($r^2 = 0.11$, $p = 0.076$) or to the lake closure types. Instead, there was a strong distinction across years, with 2013 having higher concentrations of nearly all trace metals, reflected in the positioning of samples and variables on PC1 (Figure 8). The only exceptions to this trend were Ba, Cd and Li.

Drainage of lake MD4

In the preceding analyses, we excluded an unnamed high closure lake (provisionally called MD4) that partially drained between the sampling seasons of 2013 and 2014. In 2013 the lake was > 1 m deep in the nearshore region, but in subsequent years water levels were reduced to < 0.5 m in the centre of the basin and previously submerged sediment around the edges of the lake were now exposed mud flats (Figure 9a). Historical satellite imagery shows that this lake was full throughout the decade prior to the sampling period, and visibly contracted in 2014 and thereafter, with successional vegetation in the exposed former lake bed occurring from 2015 onwards (Figure 9b). This alteration of the lake had strong effects on observed water chemistry, with highly elevated particulates and trace metals post-alteration (Figure 9c). While the extreme values of water chemistry components dominated variation in statistical analyses of the full lake set and required removal of MD4 as an 'outlier' (to discern inter-lake variation within the rest of the dataset), we include MD4 in subsequent discussion of temporal variation, as it may represent a limnological future of extended lake isolation and subsequent lake level drawdown in a warmer climate.

Temporal changes in water chemistry variables

Temporal changes of the significant parameters from the ANOVA and PCA analyses differed among lake closure types and in some cases individual lakes (Figure 10). NC lakes were similar to the channel for each variable with the exception of SO_4^{2-}, which was considerably higher in the channel than in any lake. Variables with high loadings on PC2 reflected closure type most strongly and were relatively stable over time. SO_4^{2-} was higher on average in the NC lakes than the HC lakes, with lowest concentrations in the thermokarst L520, and declined over the study period in the LC lakes. Mg^{2+} in the HC lakes was quite variable but most concentrated in the highest elevation HC lakes (L520 and L521). TKN was not distinct among closure types in the high flood year 2013 but became increasingly so over time due to increases in the HC lakes.

Of the variables that contributed to PC1, DIC and Ca^{2+} also reflected closure type. HC lakes had lower DIC and Ca^{2+} than the closure types with longer connection times to the main channels. An exception was thermokarst lake L520 with high concentrations of DIC, Ca^{2+} and Si that increased over time. In LC lakes DIC and Ca^{2+} declined over the study period, with higher concentrations and more prominent declines in lake MD3. Si was high in both LC lakes in 2013 but declined in subsequent years, with precipitous drops occurring in 2013 (L280) and 2015 (MD3).

While there was little overall difference in Na^{+} between closure types or years, individual lakes had temporal trends worth noting because they potentially reflect water source. NC lakes had similar Na^{+} to the main channel with isolated (HC and LC) lakes having slightly lower concentrations. Uniquely, Na^{+} increased steadily over the study period in lake MD2, nearly doubling in concentration between 2013 and 2017. Cl^{-} also increased in MD2 over the study period, but most of the increase occurred between 2013 and 2014 and was subsequently stable.

The drained lake MD4 had anomalous values and/or trends for each of these variables other than Ca^{2+}. SO_4^{2-} was lowest in the high-flood year 2013 and increased after the lake drained, stabilizing by 2017 at ~ 20x the 2013 concentration. Dissolved ions (Mg^{2+}, DIC, Na^{+} and Cl^{-}) were extremely low in all years of the study. TKN and Si increased following the drainage event in 2014, similar to the trends in DOC, particulates, and trace metals (Figure 9).

Discussion

In this study we analyzed a unique multi-year data set of surface water chemistry from a set of lakes along a gradient of hydrological connectivity in the Mackenzie River Delta during a period that encompassed extreme conditions in flood regime (as maximum river level height during spring peak discharge). Here we build upon prior work to demonstrate how lake chemistry depends on connection to the river and to the landscape and how autochthonous processes mediate this relationship. We further demonstrate that the response of lakes to alterations in flood regime depends on their position on the connectivity gradient and suggest that these differences in response have implications for the delta under conditions of projected climate change.

Lesack et al. (1998) conducted a major survey of major ions in Mackenzie Delta lakes, identifying three end members of ionic composition: 1) Ca^{2+} + HCO_3^- corresponding to lakes with frequent and sustained connection to the river, 2) Mg^{2+} + HCO_3^- corresponding to lakes that are flooded infrequently for short periods, and 3) Ca^{2+} + SO_4^{2-} corresponding to lakes with sufficiently high sill elevation to prevent inundation during spring flooding for multiple consecutive years. Although our study differs in design and methodology, our results are consistent with the framework they proposed (Figure 5). Dominant cation/anion pairs in HC lakes corresponded to end member 2 (Mg^{2+} + HCO_3^-) and LC and NC lakes to end member 1 (Ca_{2+} + HCO_3^-). Although the fraction of Ca^{2+} in HC lakes was nearly as high as that of the dominant cation Mg^{2+} (Figure 5), the absolute concentration of Ca^{2+} was considerably lower in the HC lakes than the other groups (Figure 4). Evidence for end member 3 (Ca^{2+} + SO_4^{2-}), which comprised a small set of very high elevation lakes in Lesack et al. (1998), is equivocal: thermokarst lake L520 had high Ca^{2+} relative to other HC lakes, and MD4 had high SO_4^{2-} following drainage (Figure 10), but no lake was dominated by the pair of Ca^{2+} + SO_4^{2-}. Overall, our results fit within the interpretive framework of Lesack et al. (1998) and subsequent studies. Using a gradient-based PCA approach we found that variation in limnological condition among lakes and years was concentrated along two interpretable axes which were both significantly associated with connection time (Figure 7).

PC2 in Figure 7a directly represents a gradient of connection time and flood inputs, from connected (NC) lakes to highly isolated thermokarst lakes. Lakes with distributary connections or long spring connection times receive suspended solids (POC and PON) from the river (Marsh et al. 1999), limiting light available for primary productivity (Squires and Lesack 2003a,b). The river is also the likely source of SO_4^{2-} in the more connected lakes (Lesack et al. 1998), especially given the high levels recorded in the main channel during the study period (Figure 10). We suggest that dissolved trace metals in the lakes originate from the river and are introduced by flooding or distributary connections for two reasons. First, riverine trace metals were enriched relative to lake water, often greatly so (Table A3). Work from Siberian thermokarst lakes, reviewed in Colombo et al. (2018), suggests that while thermokarst processes release trace elements during periods of active thaw and subsidence, surface concentrations are primarily a factor of lake ontological development in which concentrations decrease as the lake deepens, and in mature lakes metals are sequestered in the sediments. Second, nearly every metal in all lakes regardless of closure type decreased between the high flood year of 2013 and subsequent years (Figure 8), suggesting trace elements in the water column in late summer reflect flood conditions from the spring of the same year.

Increased loads of Mg^{2+} and F^{+} were associated with lakes that flood infrequently (PC2, Figure 7a). Evaporative concentration is a possible explanation since the annual water balance of closed lakes in the Delta is usually negative in the absence of spring flooding (Marsh and Bigras 1988). However, it would be expected that other conservative solutes such as Na^{+} and Cl^{-} would be similarly enriched in the most isolated lakes, and we found no relation of Na^{+} or Cl^{-} to Mg^{2+} (Figure 7a) or the closure gradient (Figure 5, Figure 10). In lake MD2, evaporative concentration is a likely explanation for the observed increase in Na^{+} and Cl^{-} (Figure 10), but in this case Mg^{2+} had no trend over time. Lesack et al. (1998) provided two other explanations for ionic enrichment in high closure lakes. Post-flood rillflow (water entering the lake indirectly as flood waters recede) is enriched in Mg^{2+}, but this seems likely to affect all lakes equally and the effect should therefore be a function of lake volume, which does not appear to be the case. Ionic concentrations may also increase due to solute exclusion during ice formation and incomplete flushing due to persistent ice cover during spring flooding. However, this also does not explain the discrepancies among the conservative ions. A final possible explanation is release of ions from thermokarst. Slumping of lake margins occurs as ice-rich permafrost soils degrade, exposing surface soils to the overlying water column and allowing release of sequestered ions into overlying water, including Ca^{2+}, Mg^{2+}, SO_4^{2-}, and Si (Reyes and Lougheed 2015). The lake with the most pronounced thermokarst activity, L520, had elevated Mg^{2+} and Si relative to all other study lakes and elevated Ca^{2+} relative to other high closure lakes. Combined with the enrichment of Mg^{2+} in post-flood rillflow (Lesack et al. 1998) it seems likely that the catchment is the source of the elevated Mg^{2+} in high closure lakes, whether it originates in the permafrost or the active layer.

Elevated dissolved organic matter (DOM; DOC and DON) in the HC lakes (particularly L520) is likely also due to thermokarst activity. However, our DOM measurements must be treated with caution because we measured bulk DOM. While DOM generally increases with sill elevation in Mackenzie Delta lakes, this DOM has diverse origins and characteristics (Tank et al. 2011). While most DOM in NC lakes originates from the river, lower turbidity in closed lakes permits high productivity of macrophytes which release colourless, highly labile DOM (Squires et al. 2009; Tank et al. 2011) which is rapidly utilized by bacterial communities (Spears and Lesack 2006; Cunada et al. 2018). In thermokarst lakes, coloured DOM originating in the permafrost and/or from shoreline slumping accumulates since it is relatively recalcitrant to bacterial metabolism (Squires and Lesack 2003b; Tank et al. 2011; Cunada et al. 2018). So while prior knowledge of L520 suggests thermokarst as a source of DOM, much of the variability in DOM in other HC and LC lakes (Figure 9c) is potentially allochthonous DOM originating from macrophytes. We also point to evaporative concentration as a possible cause of elevated DOC in higher elevation lakes.

The PC2 axis therefore represents a gradient of sources of chemical constituents from riverine inputs (POC, PON, SO_4^{2-}) to those derived from the terrestrial landscape including permafrost (Mg^{2+}, DOM). Within lakes, variability among years was related to closure type and spring flood conditions, with 2013 having greater peak flood level (Figure 3) and longer connection times (Table 1) than subsequent years. No systematic variation was observed in the main channel over the study period (e.g. Figure 10), so there was little interannual variation in NC lakes, which are strongly influenced by riverine inputs. Every HC lake shifted on PC2 between 2013 and subsequent years, becoming more distinct from the NC lakes when peak flood levels were at or below historical average. The active thermokarst lake (L520) is notably distinct from the other HC lakes in all years, so it is not clear that the shift along PC2 represented the development or increase (in L520) of thermokarst activity as opposed to shifting to alternate stable states based on flood conditions. In either case, our results demonstrate a limnological response to large changes in flood conditions based on physical and chemical processes.

We also observed evidence of permafrost degradation in individual HC lakes that otherwise lacked signs of advanced thermokarst. Lake L521 is adjacent to L520 (Figure 1) and converges to the L520 trend for each of SO_4^{2-}, Mg^{2+}, and Si over the course of the study (Figure 10). This shift may be an indication of early thermokarst activity in L521, although it could also reflect isolation post-2013. A more dramatic example occurred in lake MD4 (Figure 9), though it is unclear whether erosion of near-surface ground ice beneath the lake or failure of the sill was responsible for the water level decline. Low post-drainage concentrations of Mg^{2+}, Na^{+}, and Cl^{-} suggests after 2014 the lake was replenished by dilute sources such as snowmelt (Lesack et al. 1998), and that the increase in particulates and trace metals was not caused by evaporation, but rather likely caused by wind-driven resuspension in the shallow basin. The rapid drainage and ultimate disappearance of lakes over permafrost has been observed across the Arctic (Smith et al. 2005), though evidence is conflicting as to whether this phenomenon is increasing (Lantz 2017).

A second limnological gradient (PC1 in Figure 7a) operating within the closed lakes (HC and LC) involved a set of variables suggesting this axis represents a gradient of summer macrophyte productivity. Prior work (Squires et al. 2009) has demonstrated turbidity and depth limitation of submerged macrophytes (primarily *Potamogeton* spp.) in Delta lakes, which form dense communities that cover the entire lakebed in clear, shallow closed lakes. In the most isolated lakes (e.g. L520) increased water transparency and sediment fertility allows a shift to dominance by *Chara* and *Ceratophyllum* (Squires and Lesack 2003b). Uptake of HCO^{3-} (represented here as DIC), particularly by *Potamogeton*, raises the pH (Figure 4c, e) causing precipitation of $CaCO_3$. Concentrations of some ions (K^{+}, Si) are also likely limited by macrophyte growth during summer (Lesack et al. 1998). In our PCA analysis this gradient was correlated to connection time, from the lowest elevation closed lake (MD3) to high sill lakes with transparent water and dense *Potamogeton* communities (L275, MD2). Depth and physical factors in L520 favour a macrophyte community distinct from other HC lakes, and the DIC drawdown associated with *Potamogeton*-dominated lakes did not occur.

We observed that LC and HC lakes responded differently to alterations in flood regime, particularly contrasting the high-flood year 2013 to subsequent years. Whereas HC lakes did not vary among years on PC1, each LC lake shifted in the positive direction between 2013 and subsequent years (Figure 7b), indicating greater Potamogeton production in years of low or average connection time. Differences in connection time between 2013 and subsequent years were only ~5 – 10 days for HC lakes (Table 1), presumably not enough for variation to affect production of rooted macrophytes in late summer. LC lakes were flooded for 4 – 7 weeks in 2013, compared to 2 – 3 weeks in subsequent years, with potential mixing with turbid river water occurring into July 2013. The longer turbid period could delay the onset of macrophyte recruitment, leading to lower productivity in late summer. Markers of productivity indicated neither of the LC lakes was as productive as the non-thermokarst HC lakes: Ca^{2+} and DIC were high (Figure 10) and pH was < 9 (Figure 4) throughout the study period. However, Si had dropped markedly in both lakes by 2015 (Figure 10). No such changes occurred in the NC lakes, which mix with turbid river water throughout the growing season and have low macrophyte productivity compared to closed lakes (Squires and Lesack 2003b). Lake metabolism as determined by primary productivity appears to uniquely respond to changes in connection time in those lakes for which flood duration and related turbidity is a limiting factor on macrophyte growth.

Alterations to the primary productivity of Mackenzie Delta lakes may have implications for the carbon budget of the overall delta. (Tank et al. 2009) demonstrated that isolated, non-thermokarst lakes with high macrophyte production were net absorbers of CO_2 over the ice-free season, in contrast to thermokarst and connected lakes which emitted CO_2 on balance on an annual basis. Since LC lakes account for 51% of total lake area in the Mackenzie Delta (Marsh et al. 1999), changes in macrophyte-mediated CO_2 absorption in this lake type would potentially impact the overall CO_2 budget of the delta. However, there is considerable uncertainty in the direction such a change would follow. High elevation lakes in the Mackenzie Delta are becoming less connected to the river as ice-jam flooding declines and the onset of break-up occurs earlier (Lesack et al. 2014), while connection times of low elevation lakes are increasing due to rising baseflow levels and increased storm surges (Lesack and Marsh 2007). The response of LC lakes to climate-mediated changes in hydrology likely depends on their elevation: lakes with sills that remain above the predicted higher river levels could become more productive and therefore stronger CO_2 absorbers, while those that become inundated through more of the ice-free season would have lower macrophyte productivity and become CO_2 emitters. Further research to confirm the emission status of low closure lakes using pCO_2 measurements and to model the effect of climate-mediated hydrological changes on low-sill, isolated lakes would greatly refine our understanding of the CO_2 balance of the Mackenzie Delta and the potential consequences of alterations due to climate change.

Acknowledgments

This research was conducted as a part of Scientific Research Licenses 15272, 15403, 15652, 15811 and 16149 from the Aurora Research Institute and supported by an NSERC Discovery and NSERC Discovery Northern Research Supplement grants to RQ and Northern Scientific Training Program support to RWS. We thank the Western Arctic Research Centre, Aurora Research Institute for technical and logistical support, and to Jolie Gareis, William Hurst and Edwin Amos for their valuable advice and assistance. We are grateful to Suzanne Tank (University of Alberta) for comments on an earlier version of this manuscript. We thank Andrew Medeiros, Christopher Luszczek, Sara Masood, Frankie Talarico, Cait Carew, and Dmitri Perlov from York University for assistance in the field.

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Tables and Figures

Table 1 – Connection time of lakes over the study period. Spring and summer sill elevations were determined by Marsh and Hey (1988) or estimated based on field observations (MD2, MD3 & MD4).

	Spring sill (m)	Summer sill (m)	Connection time (days)				
			2013	2014	2015	2016	2017
High Closure Lakes							
MD4	5.8	5.74	5	0	0	0	0
MD2	5.4	5.22	8	0	2	0	2
L521	5.169	4.92	10	0	4	0	6
L520	4.913	4.587	13	3	6	4	8
L275	4.768	4.398	15	4	7	7	10
L56	4.623	4.21	16	6	8	9	11
Low Closure Lakes							
L280	3.838	3.189	28	19	16	18	18
MD3	3.5	2.75	51	32	23	27	30
No Closure Lakes							
L79A	2.631	1.62	157	116	155	148	120
L80	2.631	1.62	157	116	155	148	120
L85A	2.363	1.272	191	159	187	199	184
L129A	2.363	1.272	191	159	187	199	184
L129	2.363	1.272	191	159	187	199	184

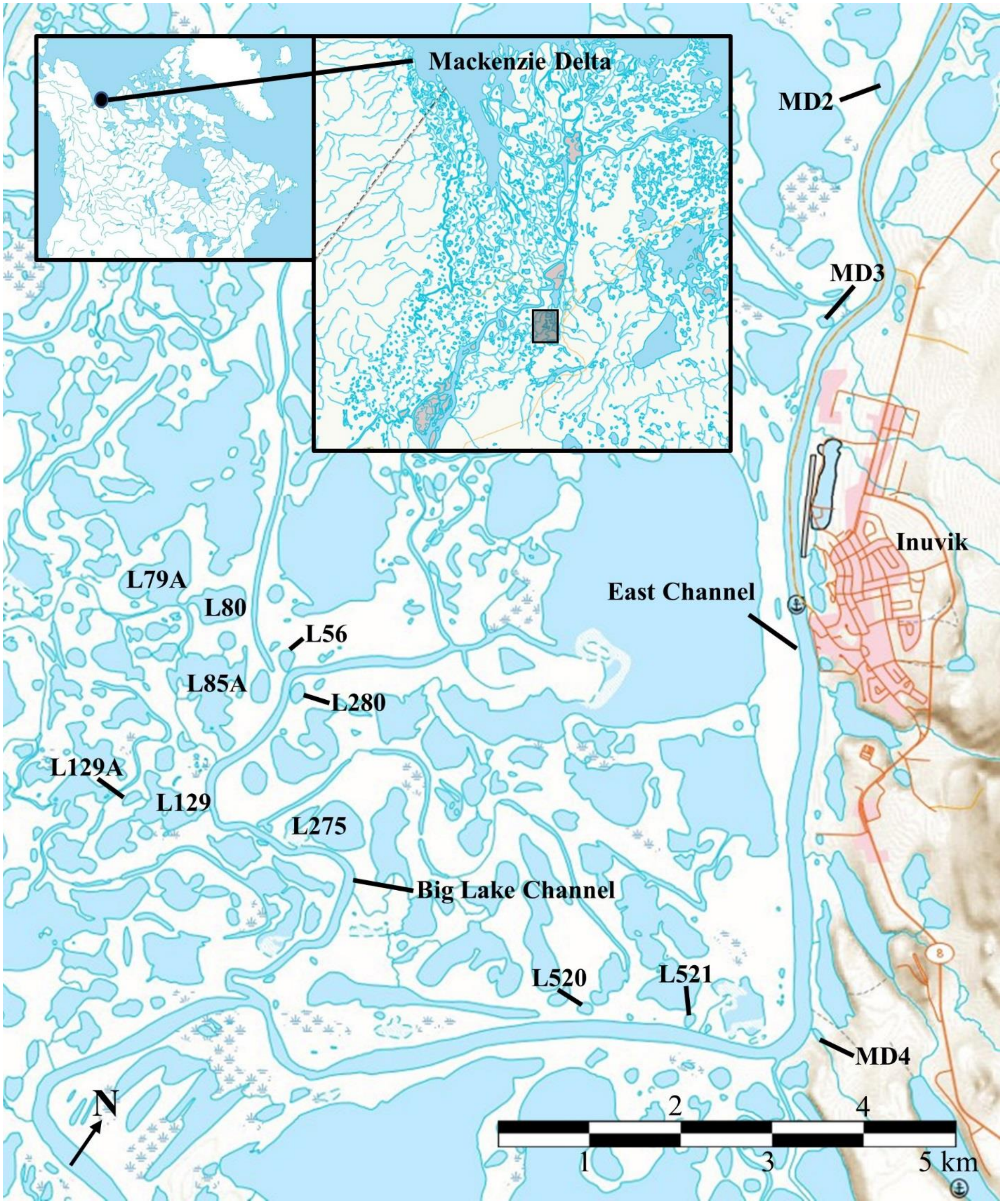

Figure 1 – Map of the study area. Base map data from Natural Resources Canada (https://atlas.gc.ca/toporama/en/index.html). Contains information licensed under the Open Government Licence – Canada.

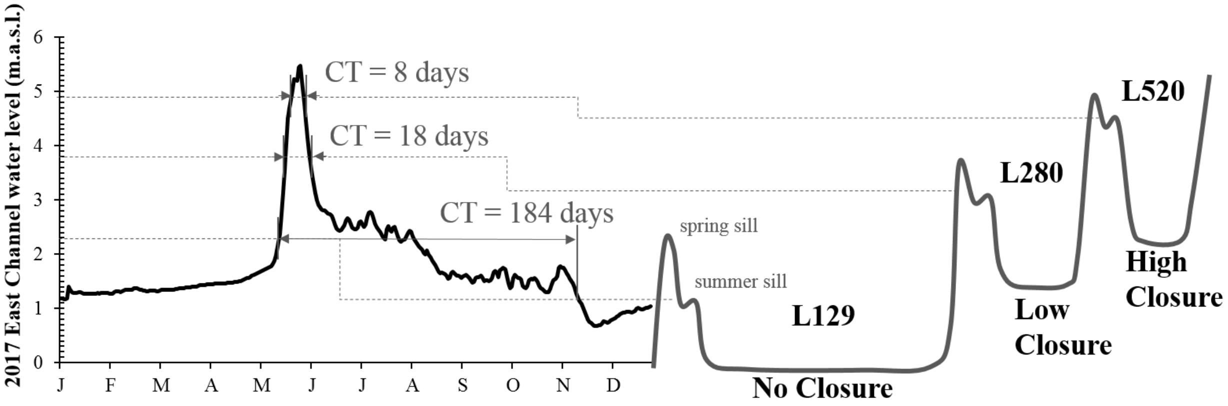

Figure 2 – Lake connection time in representative lakes for the three lake closure types in 2017. The hydrograph depicts daily maximum water level measured by an ECCC hydrometric monitoring station in the East Channel at Inuvik. Lake sill elevations were obtained from Marsh and Hey (1988). Due to snow and ice accumulation over the winter that persists into the spring flooding period, spring sills are higher than summer sills; spring sill elevations are used for CT calculations up until the date of the first post-peak rise in water levels, and summer sill elevations used after this date. Lake basins are drawn to scale based on sill elevations, average depth, and maximum width, but do not portray basin morphometry. Lake 129 is directly connected to the East Channel by a distributary channel, so the summer sill value represents the elevation of the thalweg of the distributary channel rather than the elevation at which overbank flooding occurs.

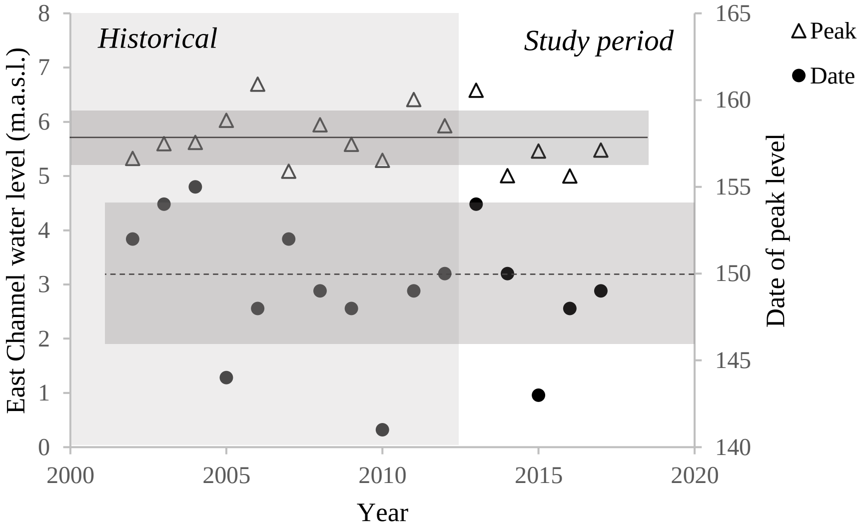

Figure 3 – Peak annual water level and the date it occurred measured in the East Channel of the Mackenzie Delta at Inuvik. The period of the current study is from 2013 – 2017. Lines and shaded bars indicate historical means and standard deviations for peak level (solid line) and date of peak (dashed line). Data from 2002 – 2012 are included for historical comparison, and the means and standard deviations were calculated using additional historical data from the same station (1985 – 1990, 2002 – 2017).

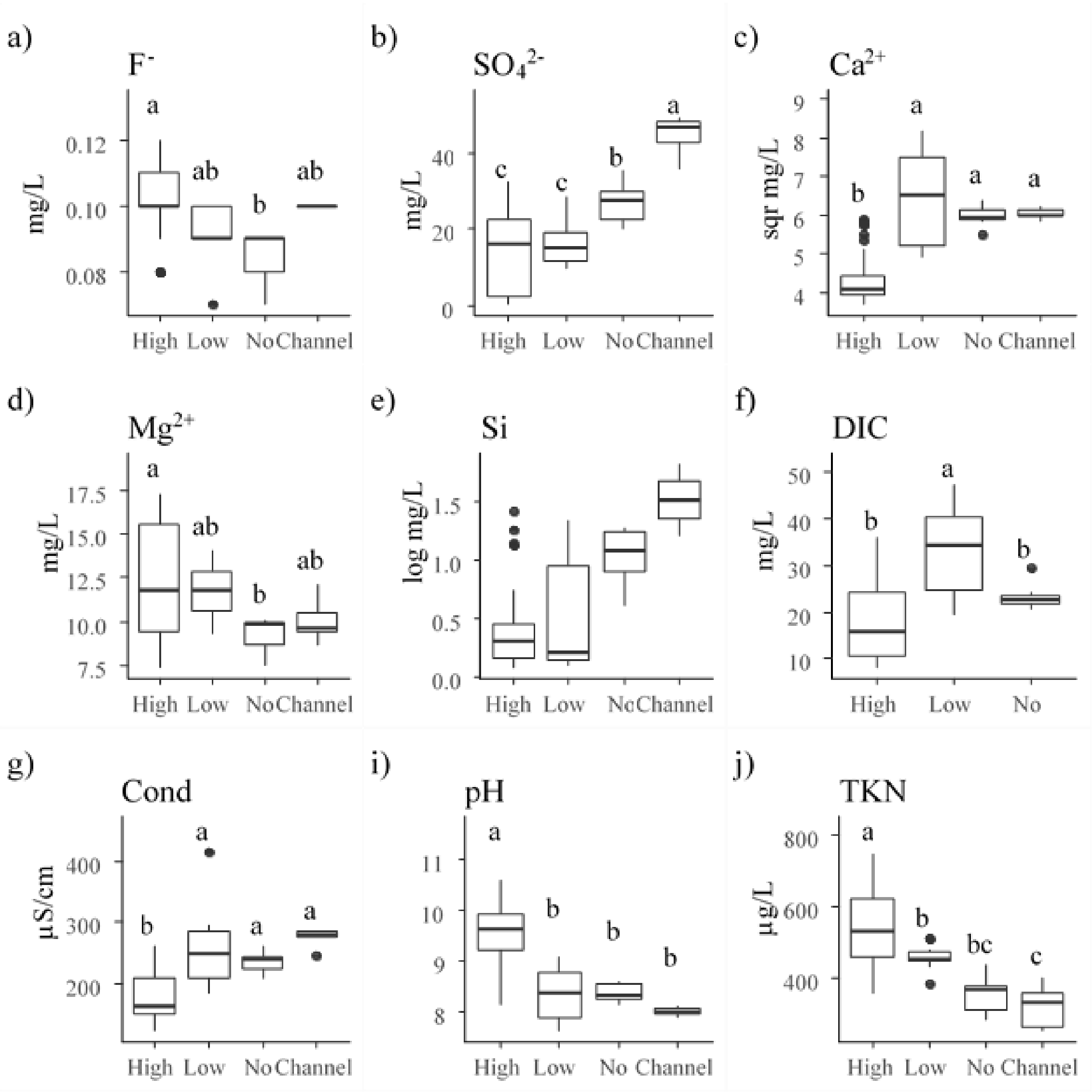

Figure 4 – Boxplots of ions and nutrients with significant differences among closure types and the main channel. Plots display the median (horizontal line), first and third quartiles (lower and upper hinges), smallest and largest values no further than 1.5 x the interquartile range from the lower or upper hinge (whiskers), and outliers (dots). Significantly different pairwise tests are indicated by different letters.

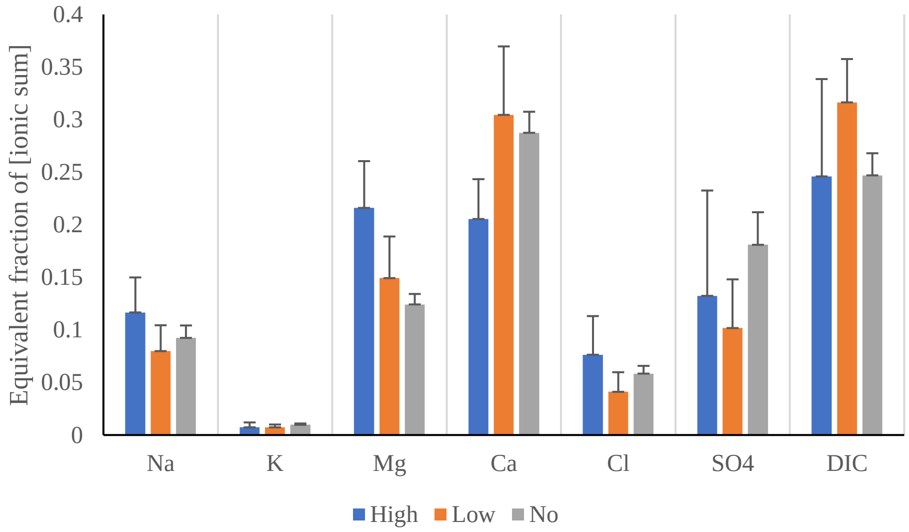

Figure 5 – Major ion composition of lakes by closure type. Mean concentrations of major ions represented as fractions of ionic sum. Error bars are one standard deviation.

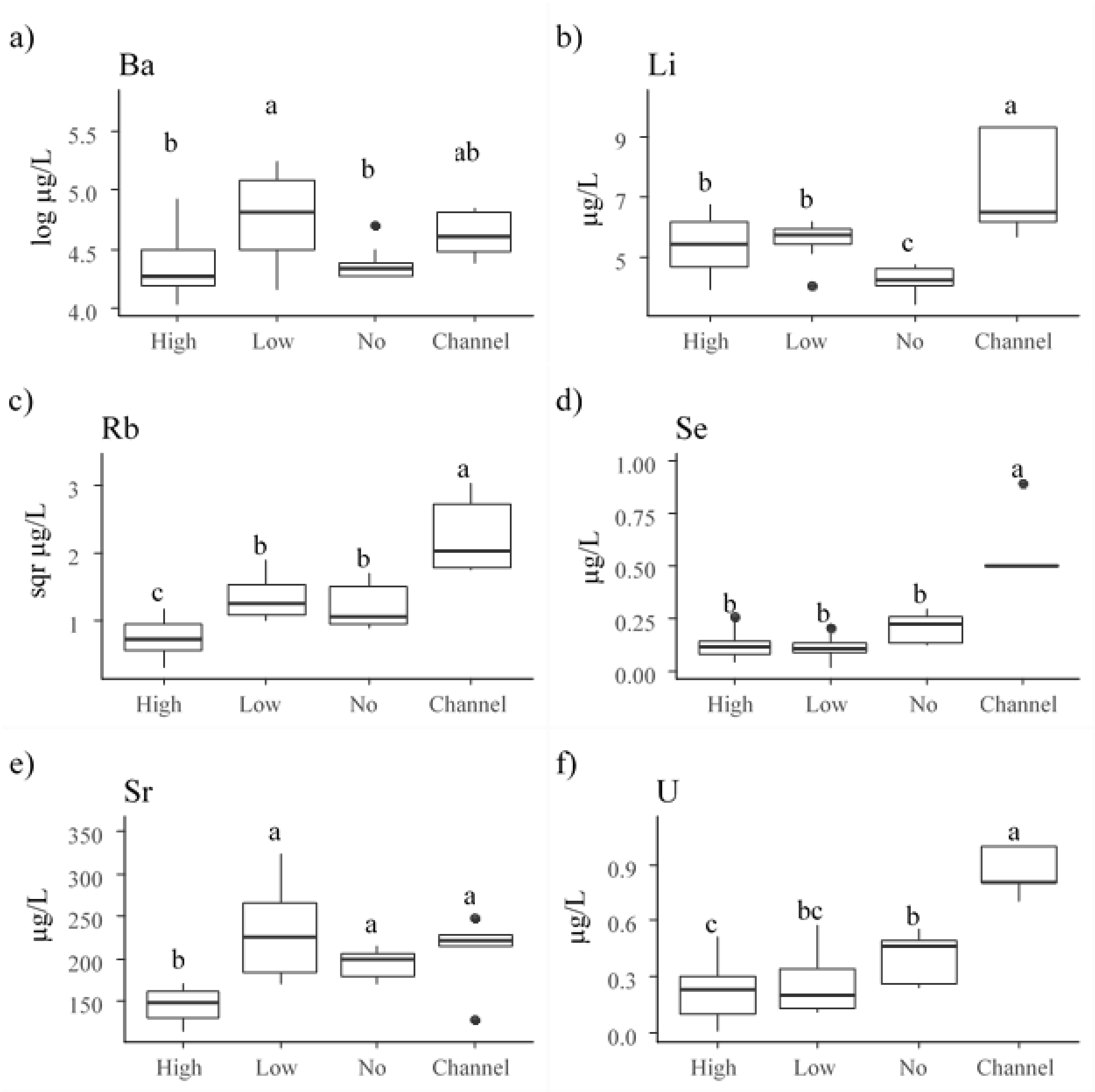

Figure 6 – Boxplots of trace metals with significant differences among closure types and the main channel. Plots display the median (horizontal line), first and third quartiles (lower and upper hinges), smallest and largest values no further than 1.5 x the interquartile range from the lower or upper hinge (whiskers), and outliers (dots). Significantly different pairwise tests are indicated by different letters.

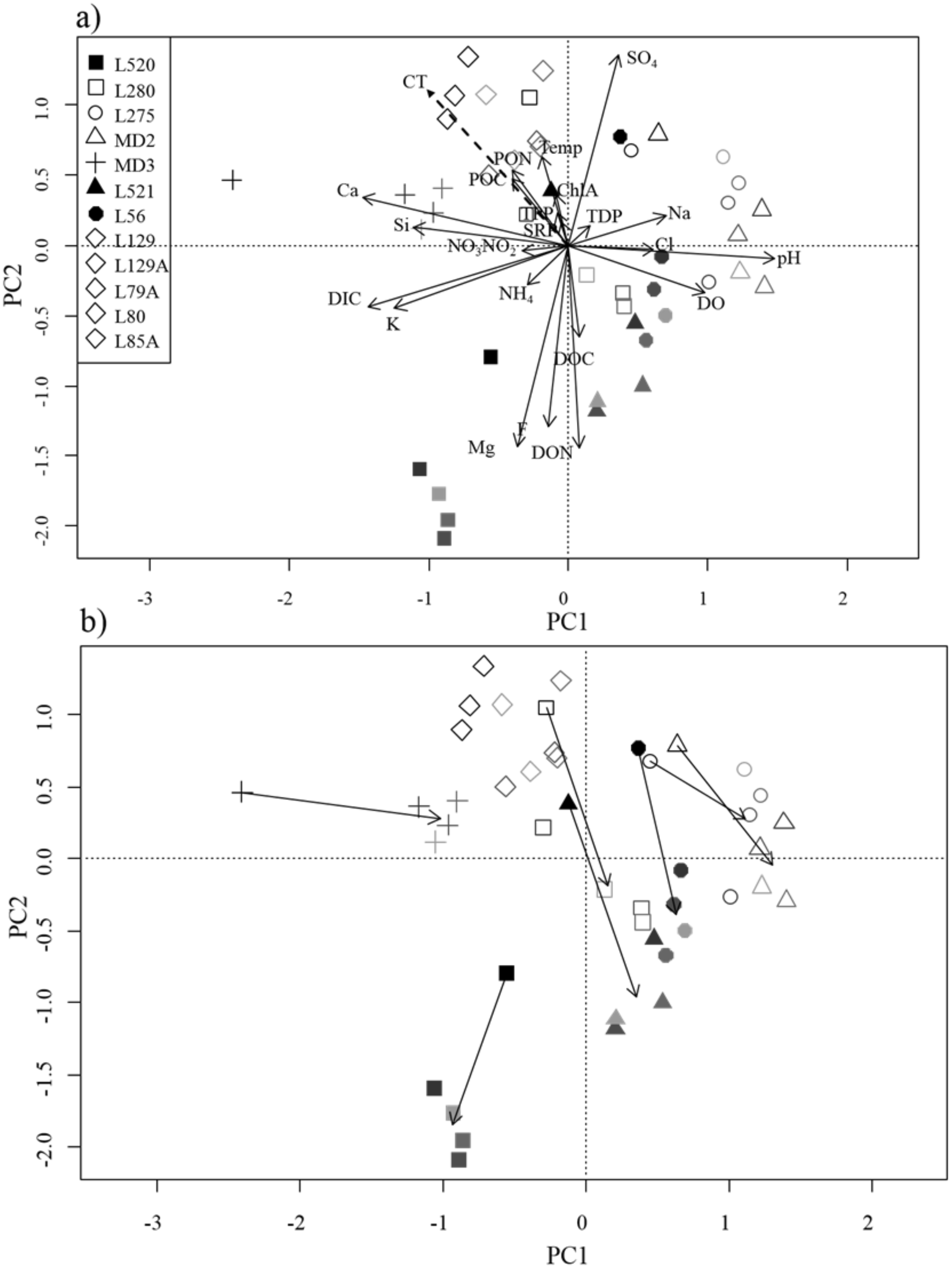

Figure 7 – Principal component analysis of nutrients and major ions of Mackenzie Delta lakes 2013-2017. a) PCA scaling 2 showing relationships of sites to gradients of water chemistry parameters, with connection time (dashed arrow) projected onto the ordination. b) PCA scaling 2

showing contrast between 2013 and later years for each isolated (LC or HC) lake; the arrows are drawn from the 2013 sample to the mean coordinate of the 2014-2017 samples for each lake, and years are indicated by shade of the symbols (darkest for 2013 and lightest for 2017).

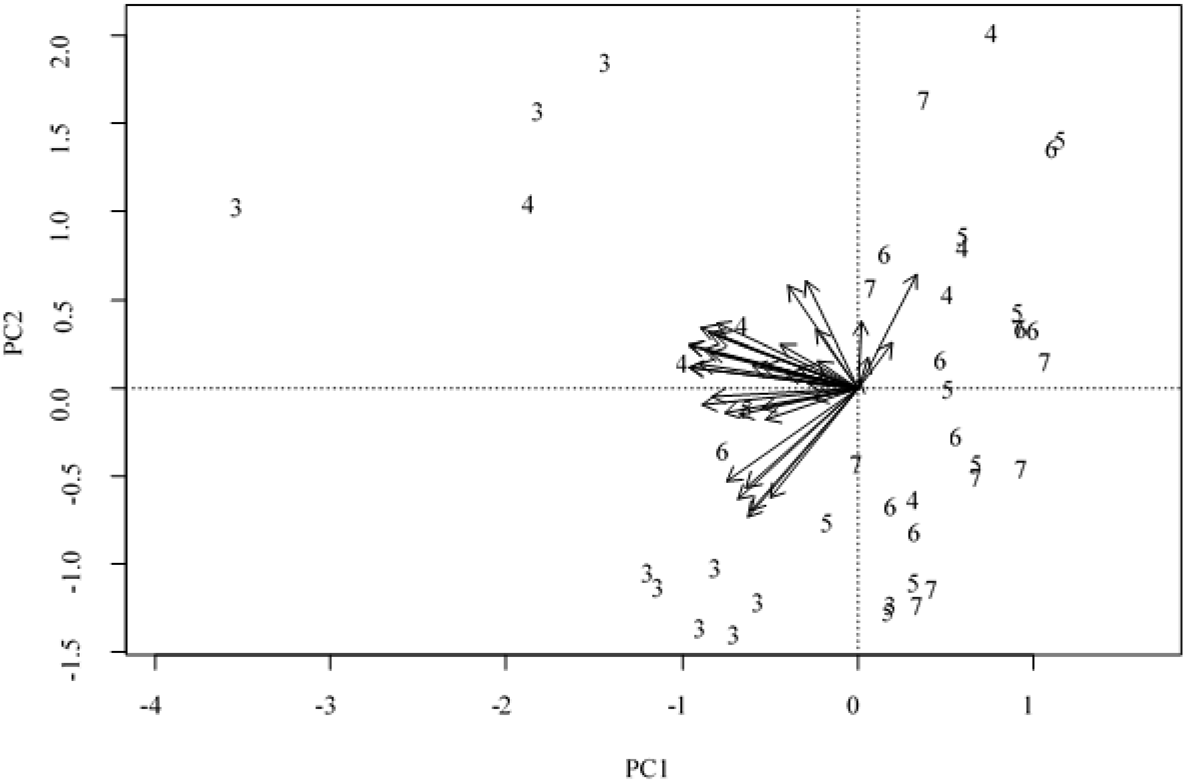

Figure 8 – Principal component analysis (scaling 2) of trace metals in Mackenzie Delta lakes 2013-2017. Variable labels excluded for clarity. Numerals are the last digit of the year the sample was taken (3 = 2013, 4 = 2014, 5 = 2015, 6 = 2016, 7 = 2017).

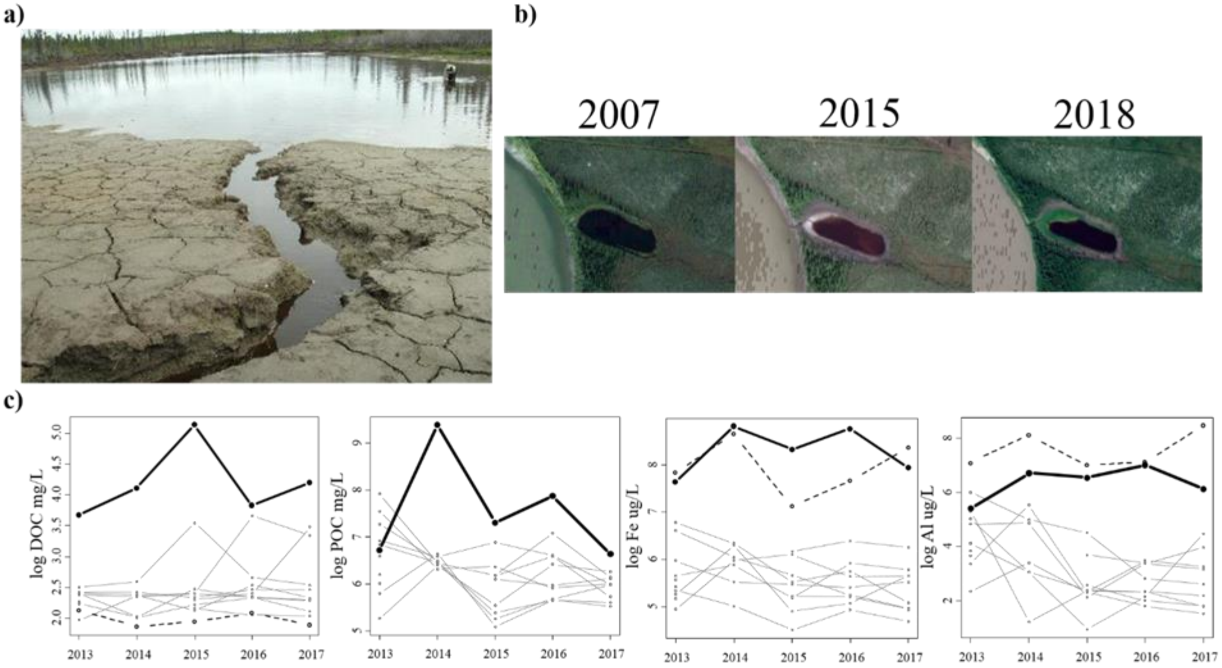

Figure 9 – Physical and chemical changes in lake MD4. a) Bank of MD4 in 2014 (post-drainage) showing previously submerged substrate and small outflow channel. b) Historical satellite images of MD4 (obtained from Google Earth) showing changes to the shoreline and basin. In 2007 the lake basin was full, as it was in 2013 (the first year of the sampling period). After the drainage event that occurred between the 2013 and 2014 sampling seasons water had visibly receded and barren shoreline is visible. By 2018 vegetational succession along lake margins is apparent. c) Elevated levels of DOC, POC and two representative trace metals in MD4 (bold solid line). Channel data is represented by a dashed line when available.

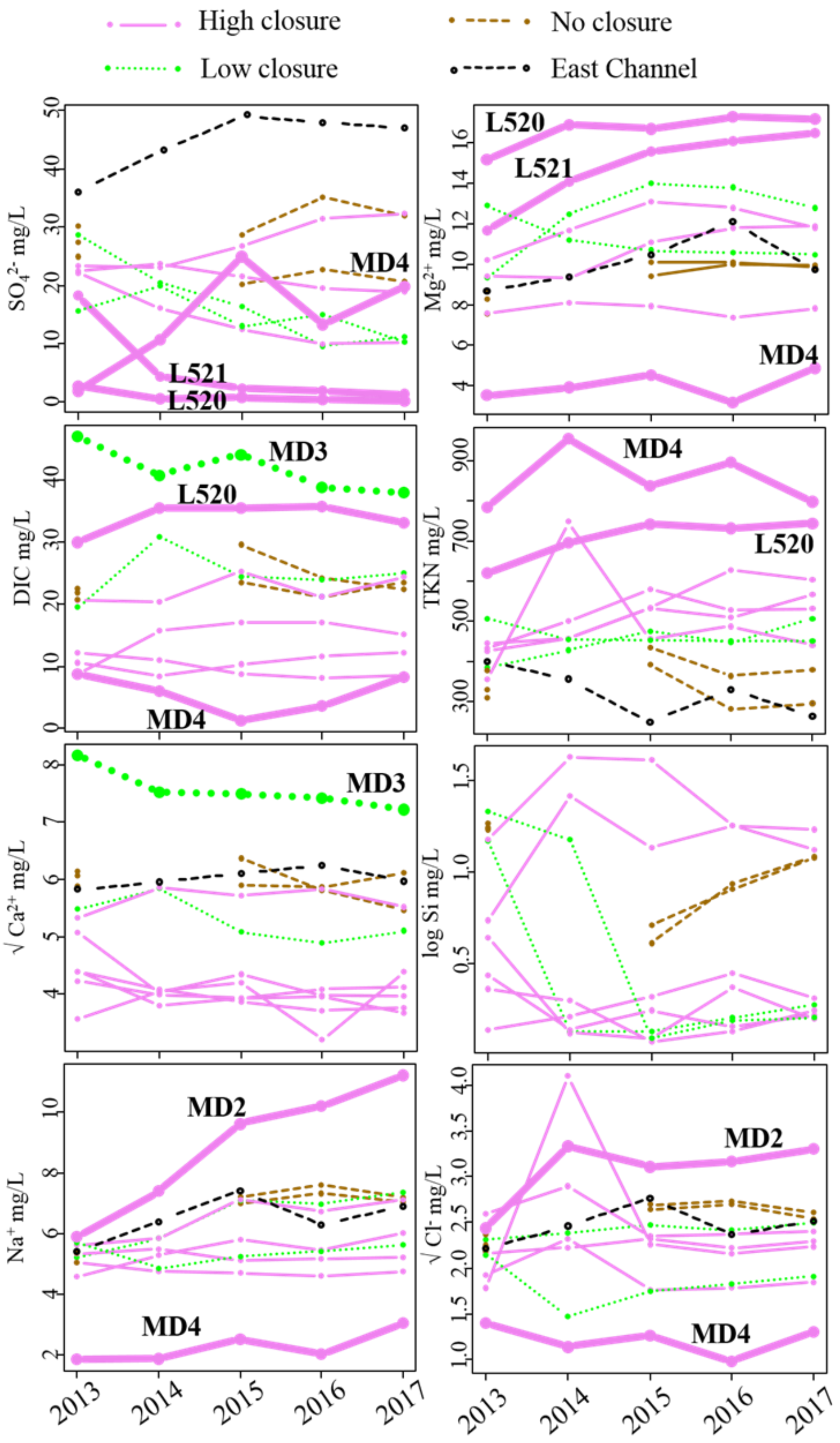

Figure 10 – Water chemistry parameters over the sampling period for eight important variables in each study lake. Channel concentrations are shown by a dotted line when available. Lakes discussed in the text are highlighted and labelled.

Chapter 2: Are different benthos communities in Arctic delta lakes distinguishable along a hydrological connectivity gradient using a rapid bioassessment approach?

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Author's Contributions

RS, RQ, and ST conceived of the research ideas and study design, RS and RQ acquired funding, XW provided chemical analysis of water samples, RS conducted field sampling, analyzed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Arctic Science.

This chapter has been published in Arctic Science as Scott, R. W., Tank, S. E., Wang, X., & Quinlan, R. 2020. Are different benthic communities in Arctic delta lakes distinguishable along a hydrological connectivity gradient using a rapid bioassessment approach? *Arctic Science*, 6, 463–487. https://doi.org/10.1139/as-2019-0024

Summary

Aquatic habitats in the Canadian Arctic are expected to come under increasing stress due to projected effects of climate change. There is a need for community-based biomonitoring programs to observe and understand the effects of these stressors on the environment. Here we present results from a 5-year annual sampling program of benthic invertebrates from lakes in the Mackenzie Delta, Northwest Territories, using a rapid bioassessment protocol. Connectivity between the deltaic lakes and main channels is a major driver of lake function and is expected to be substantially impacted by climate change. Lakes were selected along a gradient of connectivity based on sill elevation above the river. Using multivariate analyses of community structure, we determined that benthic assemblages responded to differences in connection time among lakes. This response was detected using a coarse taxonomic level that could be applied by community groups or volunteers but was stronger when invertebrates were identified to the family and genus levels. A secondary gradient was observed that corresponded to productivity gradients in lakes that are isolated from the river during summer. We show that benthic assemblages have potential use as sensitive indicators of climate-mediated changes to the hydrology of lakes in the Mackenzie Delta.

Introduction

The western Canadian Arctic has experienced increases in mean annual temperature of 2-3 °C and in winter temperature of 3-4 °C over the past six decades, which are projected to rise a further 3-4 °C and 7 °C by the end of the 21st century, respectively (ACIA 2005). Climate change is likely to have effects on the water balance (MacDonald et al. 2017), hydrology (Lafrenière and Lamoureux 2019, Lininger & Wohl 2019, Krogh & Pomeroy 2018), productivity (Kendrick et al. 2018) and community structure (Klobucar et al. 2018, Laske et al. 2016) of aquatic ecosystems, but considerable uncertainty exists in projections of factors such as precipitation, discharge, evapotranspiration rates and ice dynamics, such that the direction and magnitude of ecosystem changes are difficult to predict (ACIA 2005). Prediction of the ecological effects of these physical changes is more difficult still due to the complexity of ecological interactions (Kharouba et al. 2018) and region- or lake-specific differences in trajectories of change (Vonk et al. 2015, Lesack and Marsh 2010, Rouse et al. 1997). Given this uncertainty there is a need for ecosystem monitoring tools that use bioindicators that are integrative (respond to ecological changes along multiple gradients) and capable of responding to environmental change on a suitably rapid time scale.

The composition of biotic communities is widely used to assess the ecological state of a habitat in relation to its environmental characteristics. Bioassessment programs can be used to detect impairments in ecological function and changes to community structure caused by altered environmental gradients, e.g. climate change, altered flow regimes, or anthropogenic pollution. Benthic macroinvertebrate (BMI) communities are widely used in bioassessment programs as indicators of freshwater habitat quality (Rosenberg and Resh 1993). Many programs incorporate rapid bioassessment techniques in which field surveys can be conducted by non-experts (e.g. community or volunteer groups; Thornhill et al. 2019) and can provide benthic community count data with a minimum of processing (Borisko et al. 2007). The Canadian Aquatic Biomonitoring Network (CABIN) protocol for stream bioassessment has been deployed across the Northwest Territories to establish baseline conditions prior to gas pipeline development, as well as by community-based monitoring programs supported by the Cumulative Impacts Monitoring Program of the Government of the Northwest Territories and frequently supported by local indigenous organizations (Government of Northwest Territories 2018). Due to the logistical difficulty and expense of working at remote northern sites most surveys of BMI communities in the Canadian Arctic conducted by southern researchers have been based on single sampling events, which can bias results towards short-term conditions (Huttunen et al. 2018), and efforts to conduct annual sampling are generally limited to areas near towns which can be accessed relatively easily (e.g. Medeiros et al. 2011, the present study). The use of a rapid bioassessment approach (RBA) that can be carried out by non-experts that have better access to sites would therefore be of great use in generating repeated sampling of remote areas.

In recent years there has been increased understanding of the role of hydrological connectivity in shaping the BMI communities in floodplain systems (Funk et al. 2017). Hydrological connection among sites determines many aspects of the physicochemical habitat template including disturbance, water balance and nutrient inputs (Junk et al. 1989). In semi-isolated water bodies, connectivity determines the accessibility of a site to organisms with entirely aquatic life cycles, which limits the occurrences of some BMI (e.g. mollusks and crustaceans) directly (Petsch et al. 2017) as well as the occurrence of fish (Scarabotti et al. 2017, Laske et al. 2016) which may influence BMI composition by top-down control (e.g. Ruetz et al. 2002; González-Bergonzoni et al. 2014). Much of this research has focused on lateral hydrological connectivity gradients within the floodplains of major river corridors in temperate or tropical regions, in which flooding may occur multiple times a year and is driven by increases in upstream discharge (Tockner et al. 2000, Gallardo et al. 2014). To our knowledge, no such studies have examined BMI communities in northern systems with ice jam-driven flood regimes.

The Mackenzie Delta is the largest outlet to the Arctic Ocean in North America and an important habitat for many fish, mammals, and migratory birds. Between the main channels, over 50% of the land area is occupied by ~49,000 small deltaic lakes (Emmerton et al. 2007), which depend on annual spring flooding from the river to maintain water & sediment balances, refresh the lake water, and provide dispersal routes among lakes for aquatic organisms. Spring flooding is the major annual hydrological event, and sedimentation and biogeochemical transformation of the river water during inundation alters the quantity and quality of water and sediments exported to the Beaufort Sea (Emmerton et al. 2008). Lakes are perched over the main channels at varying elevations, which determines the extent to which they flood during peak water levels, which occur once per year in late May-early June (Marsh & Hey 1989). Overbank flooding in the delta is caused by ice jams which form when mechanical breakup precedes thermal melting of the ice (Beltaos 2013), so the extent and duration of hydrological connections are likely to be highly sensitive to changes in air temperature during the spring (Lesack et al. 2013, 2014). Previous surveys of BMI communities in the Mackenzie Delta have been rare and were related to environmental assessment of possible pipeline development in the 1970s (e.g. Rosenberg & Snow 1975, Weins et al. 1975).

The aim of the present paper is to determine the usefulness of BMI communities as rapid bioindicators of lake environments along a gradient of hydrological connectivity. We do this by 1) classifying the sites based on BMI assemblage composition using a non-hierarchical clustering method; 2) identifying environmental gradients that explain community variation; and finally 3) evaluating the fit between BMI-based site classification and the important environmental gradients. Previous work in the Mackenzie Delta has shown the duration of river-lake connection to be a dominant factor determining the chemical composition (Lesack et al. 1998, Tank et al. 2011), primary productivity (Squires et al. 2009), and metabolic balance (Tank et al. 2009a, 2009b) of deltaic lakes in the region, and susceptible to alterations due to climate change (Lesack et al. 2013, 2014) with likely effects on habitat quality and diversity in the Delta (Lesack and Marsh 2010). BMI communities and habitat conditions were sampled in a set of lakes near the town of Inuvik, NT, that spanned the range of lake sill elevations present in the study area. We sampled the lakes each summer over five consecutive years that spanned a range of timing and magnitude of peak flood. Here we evaluate the ability of three taxonomic resolutions (a low resolution appropriate to a rapid bioassessment approach, family, and genus-level) to classify lake communities based on hydrological connectivity and to detect ecological changes within lakes related to changing hydrological conditions.

Methods

Study area

The study area was situated along the East Channel of the Mackenzie Delta near the town of Inuvik (68° 21’ N, 133° 43’ W), approximately 90 km downstream of Point Separation where the Mackenzie River enters the delta (Figure 1). The Mackenzie System drains 1.75 x 10^6 km of northwestern Canada with an average annual discharge of 316 km^3/yr, the largest Arctic drainage in North America and globally among the six largest river systems draining into the Arctic Ocean (Holmes et al. 2012). The subarctic climate is characterized by a growing season that is cool and short (14 °C average July temperature) with ice cover from late October until late May, and with low precipitation (~300 mm/yr, Stewart et al. 1998). Due to the region's high latitude there are extremes in solar radiation with a period of 24-hour darkness from early December to early January and 24-hour daylight from late June to early July. Continuous permafrost is present throughout the region with active layer depth ranging from 0.3 – 1.5 m (Mackay 1995). The study area is located at the eastern edge of the Delta approximately 10 km south of treeline in the nearby uplands (within the Delta treeline extends approximately 75 km northwest of the study area; Palmer et al. 2012) and is densely covered by coniferous forest, predominantly white spruce (*Picea glauca*), alder (*Alnus crispa*) and willows (*Salix* spp.) (Burn and Kokelj 2009).

Within the delta are nearly 45,000 discrete, generally shallow floodplain lakes that cover approximately 25% of the active delta area (Emmerton et al. 2007). The major hydrological event in the Mackenzie Delta is the spring flood, with the increase of the river level and duration of the flood determined by the timing of ice pack breakup in the main channels. Mackay (1963) classified Mackenzie Delta lakes according to their degree of connection to the main channels. While a portion (approx. 12%) of lakes are connected to the main river channels by perennial distributary channels (No Closure lakes), most lakes are isolated from the river during the ice-free season to a degree determined by the elevation of the sill between the lake outlet and the river channel. Most of these lakes (55%) are inundated during spring flooding, remaining connected to the river for two weeks or longer and referred to as Low Closure lakes. The remaining 33% of lakes have high sill elevations such that they are flooded only for a brief period (up to 2 weeks) in the spring and may have return periods of greater than 1 year (2 to 4 years at the high end of the range of sill elevations) (Marsh and Hey 1989). These High Closure lakes may have negative water balances due to low precipitation (Marsh and Lesack 1996), and often have physical signs of thermokarst activity (Tank et al. 2011) such as deepening of basins and slumping banks and trees (Bouchard et al. 2017).

Collection methods

Sampling was conducted annually during the summers of 2013 to 2017 and occurred between 20 July and 10 August of each year to ensure seasonal comparability. The study lakes (Figure 1) were located close to the town of Inuvik where a hydrometric monitoring station operated by Environment & Climate Change Canada (station 10LC002) provides real-time water level data applicable to the main channels in the study area. Lakes were selected to represent the gradient from High Closure to No Closure lakes according to their sill elevation (Figure 2a). Sill elevations of the lakes were obtained from the literature (Marsh and Hey 1988) for all but three of the lakes for which historical data were lacking. For these three lakes (MD2, MD3, MD4) sill elevation was interpolated based on the difference between elevations measured lakeside with a GPS unit and the historical sill elevations for the rest of the lakes. In 2013, three connected (no closure) lakes were sampled (L79A, L80, and L85) but in 2014 and 2015 blockages in the long distributary channel leading to the lakes prevented boat access and these lakes were replaced with two more accessible lakes (L129A and L129B) in 2015 to 2017.

To characterize water quality and aquatic habitat we measured temperature, conductivity, pH and dissolved oxygen with a YSI probe, and collected a 2 L water sample for measurement of dissolved and suspended organics, nutrients, major ions and chlorophyll (see Table 1). Water samples were sent to the National Laboratory for Environmental Testing for analysis using standardized methods (Environment Canada 2017). The variables were chosen to represent established physical and ecological gradients in the Mackenzie Delta (Lesack et al. 1998, Squires et al. 2009, Tank et al. 2011) and include variables that have been found to structure BMI communities in Arctic regions (e.g. Culp et al. 2019) and/or deltaic floodplain lakes (e.g. Gallardo et al. 2008).

BMI samples were taken from the littoral zones of the lakes. Average depth for all lake closure types is quite shallow (1.66 m for No Closure, 1.37 m for Low Closure, and 1.84 m for High Closure; Emmerton et al. 2007) and macrophyte growth occurred throughout the basins of most lakes, so littoral sampling was chosen because (1) it is representative of the majority of BMI habitat in the study area and (2) the method was applicable to every site regardless of maximum depth. At each sampling event three replicate D-net benthic samples were collected at stations dispersed along the littoral zone. For each D-net sample, approximately 1 m^2 of substrate was kicked and suspended while sweeping with a 500 µm mesh D-net for 3 minutes. Samples were taken approximately 1 m from shore unless the depth at 1 m was too great to be wadeable or too shallow for proper functioning of the D-net. Samples were preserved with 95% ethanol and kept cold through transport to the laboratory, where the ethanol was changed immediately. A fixed count of 500 invertebrates per sample was used, and the total and unsorted portions of the sample were weighed to determine subsampling factors. Invertebrates were identified to three taxonomic resolutions: (1) rapid bioassessment level (RBA): a low resolution taxonomic level typical of RBA field protocols (e.g. Ontario Benthos Biomonitoring Network, OBBN), with the exclusion of lotic taxa (e.g. Simuliidae) and the addition of groups that were abundant in the study region but not typically represented in bioassessment programs (Conchostraca and Chaoboridae), (2) Family level, and (3) Genus level, the latter two requiring increasing time for microscopic examination and amount of taxonomic expertise.

Data analysis

Connection time (CT) was estimated annually for each lake as the number of days the water level at 10LC002 (extracted from the Environment and Climate Change Canada Real-time Hydrometric Data web site (https://wateroffice.ec.gc.ca/mainmenu/real_time_data_index_e.html) on 21 October 2019) exceeded the elevation measured at the lake outlet. Environmental variables were assessed for normality (Shapiro-Wilkes tests) and if necessary square root or log transformations were applied (Table 1) to improve normality prior to analysis, and the major environmental gradients were assessed using principal component analysis (PCA).

Analyses of the invertebrate count data were conducted separately on each taxonomic level to compare the percent variation explained by measured environmental gradients at the three different resolution levels. We first used Moran's eigenvector maps (MEM) analysis to assess spatial gradients in the BMI assemblages (Borcard & Legendre 2002). To identify the environmental variables that were important in structuring benthic assemblages we used forward selection to identify the set of variables that maximized the adjusted R^2 in a redundancy analysis (RDA). We employed *k*-means partitioning, a non-hierarchical clustering method, to identify groups of samples with different assemblage types, using the simple structure index (*ssi*) to determine the best number of groups. Statistical significance of the differences (Bray-Curtis distances) among the groups were assessed with a permutational multivariate analysis of variance as well as pairwise tests using Bonferroni-corrected *p* values (Martinez Arbizu 2019), and significant taxonomic differences were determined using similarity percentages (SIMPER) analysis (Clarke 1993). We then assessed the relevance of these groupings at both taxonomic resolution levels to the environmental variables identified by forward selection using linear discriminant analysis (LDA). The success of the environmental variables at predicting *k*-means group membership was determined using LDA with jackknifed cross-validation. Analyses were performed in R using package rrcov (Todorov and Filzmoser 2009) for the LDA and package vegan (Oksanen et al. 2019) for all other analyses.

Results

Over five years of sampling a total of approximately 72,000 macroinvertebrates were identified belonging to 135 genera in 65 families. The RBA identification scheme consisted of 22 taxa, ranging in taxonomic level from family to phylum, that are easily identified and tallied in the field. The dominant invertebrate groups were the non-biting midge family Chironomidae (32% of all specimens collected) and freshwater snails (Gastropoda, 20% of all specimens), followed by amphipods, bivalves (8% each), oligochaete and nematode worms (5% each), damselfly larvae (Zygoptera, 5%), clam shrimp (order Diplostraca, 4%), water mites (3%), water bugs (Hemiptera, 2%) and caddisfly larvae (Trichoptera, 2%). All other insects apart from the chironomids made up 14% of the collected specimens, and in addition to groups already mentioned included dragonfly (Anisoptera), mayfly (Ephemeroptera), biting midge (Diptera: Ceratopogonidae), phantom midge (Diptera: Chaoboridae) and horsefly (Tabanidae) larvae, as well as larvae and adults of aquatic beetles (Coleoptera), each totaling < 2% of specimens collected.

CT ranged from 0 days in the highest elevation lakes during years of lower spring flood levels to just under 200 days in the connected lakes. Flood conditions during the study period fortuitously captured the range for which historical data is available, with 2013 having high water levels, low levels observed in 2014 and 2016, and average values in 2015 and 2017 (Figure 2b). PCA of the environmental variables (Table 1) explained 49.9% of the variation on the first two axes, which represented gradients in particulates and nutrients (PC1, explaining 30.4% of the variation) and pH and major ions Ca and K (PC2, explaining 19.5%), with strong contributions of CT and DIC to both axes. Lake MD4 experienced a sill collapse in the spring of 2014 and subsequent drainage, leading to reduced depth and increased nutrients and particulates in subsequent years. Post-drainage observations at this site were responsible for high maximum values of particulates and phosphorus in Table 1 and were responsible for much of the variation along PC1. When we ran PCA omitting post-drainage observations from MD4 we found the same environmental gradients, however after removing these samples the pH/ion gradient explained more variation (23.8%) than the particulate/nutrient gradient (16.9%).

Spatial analysis using MEM was not significant for any of the taxonomic levels (RBA: $p = 0.899$; Family: $p = 0.642$; Genus: $p = 0.679$). This was likely due to the small (~ 120 km^2) geographic range of the study area relative to the dispersal abilities of many BMI as the most distant pair of lakes were separated by only ~12 km, and to the fact that all of the lakes were hydrologically connected at some point during the study period, particularly in the first year of the study (2013; Figure 2).

We ran k-means partitioning at $k = 2$ to $k = 10$ to determine the optimal number of groups for each taxonomic level (Table 2). The ssi was lowest at $k = 7$ for the RBA level and $k = 6$ for each of the Family and Genus levels. Rather than separating into three lake closure groups, analysis of *ssi* levels suggested that benthic assemblages diverged into multiple clusters: seven groups at the RBA level and six groups at the Family and Genus levels. To clarify gradients related to connection time, the groups were labelled by their rank mean connection time, with Cluster 1 having lowest CT (1st row of Figure 3). At the RBA level there were 5 clusters of unconnected lakes with increasing CT and two groups of lakes with high CT, with Cluster 7 exclusively consisting of connected lakes with high CT (Figure 3a). At the Family level (Figure 3b) there were three clusters of lakes with low CT (Family Clusters 2 – 4) and two clusters with high CT (Family Clusters 5 & 6), with Family Cluster 1 consisting of MD4 after it drained and a few high-sill sites from 2013, the year with the highest peak flood (Figure 2b). Family Cluster 6 consisted only of lakes that were connected throughout the summer. The Genus level k-means clustering was similar to the Family level, with variations in group identity for individual samples in Clusters 3 & 4 (Figure 3c).

While global analyses of variance of assemblage composition at all taxonomic levels were significant, this was less so for the RBA level ($R^2 = 0.100$, $p < 0.002$) than the Family or Genus levels ($R^2 = 0.124$ (Family) and 0.123 (Genus), $p < 0.001$). Pairwise tests showed all groups to be significantly different at the Family and Genus levels (Bonferroni adjusted $p < 0.03$), but this was the case for only about half of the pairs of groups at the RBA level (Table 3). Taxonomic richness was not significantly different between any of the k-means groups at the RBA or Family levels (t-test, $\alpha = 0.05$), but generic richness (Figure 4) was significantly lower in Genus Cluster 1 (containing the lake that experienced drainage) and Genus Cluster 3 (containing lakes experiencing thermokarst activity) than in the other groups of High Closure lakes (Genus Clusters 2 and 4).

SIMPER analysis of pairwise differences among *k*-means groups (Table 4) revealed taxa for which significant differences ($p < 0.001$) in relative abundance contributed to the Bray-Curtis dissimilarities between the groups. As in the global ANOVA (Table 3) there were fewer significant differences in taxa at the RBA level than at the higher resolutions, particularly among low-CT groups. The RBA groups with higher CT (RBA Clusters 5 – 7) had higher proportions of non-insect BMI, although contrasts with the lowest CT groups were not significant (Table 4). At the Family and Genus levels, which had similar *k*-means site classifications, Cluster 1 had a depauperate fauna with higher proportions of dorylaimid nematodes and the chironomid *Tanytarsus* (van der Wulp, 1874) compared to most other clusters. Cluster 3, which had low richness compared to the other low-CT groups also had the greatest number of significant taxa, mainly predatory insects including the tanypode chironomids *Ablabesmyia* (Johannsen, 1905), *Guttipelopia* (Fittkau, 1962) and *Labrundinia* (Fittkau, 1962), the dragonflies *Leuchorrhinia* (Brittinger, 1850) and *Cordulia* (Leach, 1815), and the hemipteran *Notonecta* (Linnaeus, 1758). Cluster 4 also had higher proportions of the dragonfly *Aeshna* (Fabricius, 1775) and the chironomid *Microtendipes* (Kieffer, 1915), while the other low-CT group (Cluster 2) had higher proportions of non-insect grazers including the snails *Physa* (Draparnaud, 1801) and *Fossaria* (Westerlund, 1885) and the water mite *Limnesia* (Koch, 1935). Cluster 5, which contained high-CT lakes that were still usually isolated from the river during the summer, had higher proportions of the chironomids *Chironomus* (Meigen, 1803) and *Einfeldia* (Kieffer, 1924), the water beetle *Ilybius* (Erichson, 1832), and the planorbid snail *Gyraulus* (Agassiz, 1837). A notable observation in this cluster is the occurrence of the orthocladiine chironomid *Propsilocerus* (Kieffer, 1923), which despite being common in the Palearctic and in the Nearctic as sub-fossilized remains has only been observed in one other location in North America in a lake in northern British Columbia (Cranston et al. 2011); here, this genus was observed only in the Low Closure lake MD3. Cluster 6, containing connected lakes, had higher proportions of the amphipod *Hyalella* (Smith, 1874) and large-bodied insects such as *Limnephilus* (Leach, 1815) and water-boatmen (Corixidae).

Forward selection of the environmental variables produced similar sets of variables at each taxonomic level with CT, DIC, pH and POC selected in each model, and as the first four variables at the RBA and Family levels (Table 5). A larger set of variables was selected explaining the Genus level data, with SO_4 and CT the first variables selected followed by a number of major ions (Table 5). RDA of the Hellinger-transformed invertebrate counts against the reduced set of environmental variables produced significant models ($p < 0.001$) at all taxonomic levels (Table 5). Both adjusted R^2 and % explained variance increased across the models with increasing taxonomic resolution (RBA: 43.3%, R^2 =0.388; Family: 47.0%, R^2 = 0.415; Genus: 53.1%, R^2 = 0.436), although only at the genus level did the RDA model explain > 50% of the variation.

There were differences among the taxonomic levels in the relationship between *k*-means groupings and important environmental variables as determined by forward selection (Figure 3). DIC increased in the Family level groups that were not connected to the river during the summer (Family Clusters 1-5) as CT increased, but this pattern was not as apparent at the RBA or Genus levels. SO_4 was very low in Genus Cluster 3, which mainly consisted of two high elevation lakes experiencing various stages of thermokarst activity (Lakes 520 and 521). POC (as well as PON) was notably higher in RBA Cluster 4 and Family/Genus Cluster 1, which contained the lake that drained in 2014 (MD4) and was subsequently more susceptible to wind-driven resuspension of sediments.

When the *k*-means groups were plotted on the RDA ordinations the higher distinctiveness of groups at the Family level was apparent (Figure 5). The samples from MD4 post-drainage grouped apart at the bottom of the ordination while the remainder of Family Cluster 1 groups with other samples from high closure lakes (Figure 5b). Connected lakes (Family Cluster 6 and part of Family Cluster 5) were clearly separated from the unconnected lakes, which fell along a gradient mainly related to DIC, but this separation was less distinct in the RBA and Genus levels. In addition, there was some separation of the low closure lakes from the high closures in the Family RDA ordination. The RBA level ordination (Figure 5a) showed both less separation of *k*-means clusters and greater overlap among *a priori* closure types, while the Genus level ordination had distinct *k*-means clusters but less distinct separation of closure types. Pairwise contrasts among the three *a priori* closure types were significant at the Family level, as were all contrasts between the connected and low- and high-closure lakes at all taxonomic levels (Bonferroni-corrected $p = 0.003$) but contrasts between the low- and high-closure groups were not significant at the RBA level ($p = 0.120$) and only slightly significant at the Genus level ($p = 0.006$).

There were similarities among the taxonomic levels in the species responses to environmental gradients (Figure 6). In each analysis, relative abundance of the clam shrimp *Lynceus brachyurus* (Müller, 1776) was directly associated with CT. Chironomids (Tanytarsini: *Tanytarsus* in the Family & Genus analyses) were negatively associated with CT and *Hyalella* (or Amphipoda) were positively associated with CT at all three levels. A secondary gradient was present in the RBA and Family analyses involving two or more of the variables DIC, pH, Si and POC that was associated with a taxonomic gradient from snails (Family: Planorbiidae) and damselfly larvae (Family: Coenagrionidae) to *Chaoborus* (Lichtenstein, 1800), dorylaimid nematodes, and corixid nymphs.

Prior to linear discriminant analysis the *k*-means groups were tested for multivariate homogeneity of within-group covariance (RBA: $p = 0.015$; Family: $p = 0.36$; Genus: $p = 0.254$) and differences of means using Wilk's λ test (RBA: $\lambda = 0.024$, $p < 0.001$; Family: $\lambda = 0.0049$, $p < 0.001$; Genus: $\lambda = 0.0041$, $p < 0.001$). LDA with jack-knife cross-validation (Table 6) indicated that congruence between groupings based on environmental variables and BMI assemblages increased with increasing taxonomic resolution. The RBA level had the lowest success rate (51% of sites classified correctly) and the greatest number of different errors (non-zero results in the non-diagonal cells of Table 6a). Jack-knifed classification success at the Family level (Table 6b) was considerably higher (76%) and classified most of the sites in each group correctly. The Genus level had the highest success rate in the LDA (84%) and classified some groups (Genus Clusters 2 & 4) with 100% accuracy.

Discussion

Comparison of taxonomic level

The required taxonomic sufficiency of biomonitoring programs is a contentious issue. The increased information afforded by high-resolution identification to genus/species must be balanced by consideration of the higher cost in personnel training and expertise, money and time relative to lower resolution identification (Jones 2008). Many studies have found acceptably congruent results between family-level and genus/species-level identifications in representing assemblage structure (Törnblom et al. 2011, Kallimanis et al. 2012, Landeiro et al. 2012, Carew et al. 2018) and assemblage-environment relationships (Chessman et al. 2007, Schmera & Erős 2011, Vilmi et al. 2016). In many cases the family level is sufficient to establish the overall or most important environmental relationships, but with reduced statistical power (Hawkins et al. 2000, Monk et al. 2012) or loss of ability to detect subtler environmental changes or relationships (Greffard et al. 2011, Forcino et al. 2012, Jiang et al. 2013). Key factors determining the success of broad taxonomic resolutions are the number and ecological diversity of species being aggregated into larger groups (Bennett et al. 2014, dos Santos Ribas and Padial 2015, Lu et al. 2016) and assemblage richness at the broader taxonomic resolution (Hawkins et al. 2000, Milošević et al. 2014).

Jones (2008) identified a number of analytical considerations pertaining to the multivariate statistical methods that we used. First, agglomerating taxa lowers the number of variables available for analysis, in our case from 135 genera to 64 families to 22 RBA taxa. Agglomeration therefore decreases the total variance of the multivariate data (Table 5). Second, as higher levels of agglomeration are used the informative value of presence/absence data declines. More than half of our RBA taxa (compared to approximately 1/6 of our families and only 9% of our genera) were present in every sample (Figure 7a). If we were to agglomerate taxa higher than the RBA level (e.g. to Class), presence-absence data would produce the trivial result of every taxon being present in every sample. Presence-absence RDA at every level produced much lower adjusted R^2 values (RBA: 0.293, Family: 0.332, Genus: 0.292). This is unfortunate from a rapid bioassessment perspective as collection of presence-absence data is more time-efficient than generating count data in a field survey. Third, agglomeration decreases the number of potential distinct sources of information available to elucidate species-environment relationships in the canonical analysis and to make ecological interpretations. Like many freshwater environments, our study lakes were dominated by the family Chironomidae (here considered an RBA taxon, divided into subfamilies/tribes in our Family analysis). Chironomids are a species-rich and ecologically diverse family, so, by agglomerating them into one variable, information is lost compared to the more equitable division of chironomid subfamilies/tribes in the Family analysis (Figure 7b). This is also true of less numerically dominant but taxonomically diverse RBA groups (e.g. Trichoptera, Coleoptera). This loss of information may decrease the ability to detect subtle environmental changes (Jones 2008, Greffard et al. 2011) and may explain why the family and genus levels were able to distinguish between connected and closed lakes (Figure 5) and had higher classification success in the LDA (Table 6).

Relationship to environmental gradients

We expected CT to be an important variable structuring the benthic assemblages, and this was largely confirmed in our analyses. At each taxonomic level, *k*-means classification produced groups that differed significantly in CT (Figure 3), and CT was among the first variables included in the forward selection RDA models (Table 5) and explained large amounts of benthic community variation in ordinations at all taxonomic levels (Figure 5). The observation that CT had the highest loading on the first axis of the RBA-level RDA supports the importance of CT in structuring the benthic assemblages. However, at the RBA resolution there was little apparent relationship between assemblage types defined by *k*-means partitioning and limnological variables or separation among either *a priori* closure types or *k*-means groups in the ordination (Figure 5a). At the Family level the No Closure lakes occupied a distinct ordination space (top left quadrant of Figure 5b), while Clusters 2-5 formed a gradient along RDA 2 with little overlap in the clusters compared to the RBA analysis in which there was a great deal of overlap among the low-CT *k*-means groups. At the Genus level a distinct set of explanatory variables were selected through RDA analysis (Table 5), including SO_4 which explained more variation than CT, and there was more overlap among closure types (Figure 5b) than in the family ordination, although more total variation was explained at the genus level (Table 5). SO_4 has multiple sources in Mackenzie Delta lakes (Lesack et al. 1998), either being introduced by the river via flooding or distributary channels in connected lakes or released from the sediment in very shallow lakes, such as MD4 (Cluster 1) in this study.

Despite the importance of CT as an explanatory variable, much of the variation among low-CT assemblages at the Family level was explained by a secondary gradient that reflected lake productivity. Previous work in the Mackenzie Delta has established a gradient of lake primary productivity between phytoplankton-dominated production in turbid, connected lakes and macrophyte-dominated production – along with associated epiphyton – in relatively clear, unconnected lakes (Squires et al. 2009). In connected lakes, river inputs provide suspended solids that limit the growth of macrophytes and benthic algae, but also nutrients that stimulate the growth of phytoplankton closer to the surface (Squires and Lesack 2002). Lakes with short connection times or that infrequently flood have lower river-derived inorganic turbidity (Squires and Lesack 2003) and nutrients, and primary production is dominated by macrophytes, which derive their nutritional requirements from nutrient-rich sediments and reach very high biomass

(>2000 g m^{-2}) in the lakes with greatest water transparency (Squires et al. 2002). During the summer macrophyte photosynthesis can draw down dissolved inorganic carbon and cause elevated pH levels (Hesslein et al. 1991, Tank et al. 2009a, 2009b) and high macrophyte biomass limits the light available to phytoplankton and epipelic algae via shading, while providing surfaces for growth of epiphyton (Squires et al. 2009). This turbidity-driven productivity gradient was reflected in RDA2 of the Family-level ordination (Figure 5b), with a gradient primarily from high-DIC (low primary productivity) lakes to low DIC (highly productive lakes). Evidence from stable isotopes suggest that at least some primary consumers (zooplankton and molluscs) derive more carbon from phytoplankton in turbid, connected lakes and rely on benthic algae (epipelon and epiphyton) in unconnected lakes with large macrophyte communities (Hecky and Hesslein 1995). Bacteria are likely to be a major food source for many benthic grazers (e.g. most Chironomidae), and previous work has demonstrated bacterial production and activity to vary along the described productivity gradient although the relationship is more complex and less fully understood. Bacterioplankton abundance and production is higher in more isolated lakes than connected lakes (Spears and Lesack 2006), possibly due to greater supplies of autochthonous DOC from macrophytes (Tank et al. 2011), but are limited by alkalinity-related stress when photosynthetic rates are high enough to drive up pH (Tank et al. 2009). Macrophyte-mediated differences in DOC quantity and quality are also important drivers of the activity of methanogenic microbial communities (Cunada et al. 2018), which can also be important food sources for benthic invertebrates (e.g. Yasuno et al. 2013).

Given the above explanation for the major environmental gradients, we interpret the constrained ordination of benthic families and genera as follows: no-closure lakes (Cluster 6) have distinct assemblages, including higher proportions of crustaceans (*Lynceus*, *Hyalella*) and large-bodied insects (Corixidae, *Limnephilus*), from lakes that become disconnected during the summer or flood less than once per year, which have greater proportions of insects, particularly Chironomidae and Odonata (Anisoptera and Zygoptera), capable of aerial dispersal. When the lakes have sills high enough to separate the lake from the river channels, assemblages are structured along a gradient of lake primary productivity, which as described above is strongly related to CT. Among these, the more productive lakes (Cluster 2) have greater proportions of grazers (e.g. *Gyraulus*) that may be supported by abundant epiphyton (Squires et al. 2009) while more turbid water in the lower-sill lakes (Cluster 5) limits macrophyte productivity and dissolved

O_2, leading to a distinct community type dominated by *Chironomus* spp. Lakes that are cut off from the river for > 1 year have distinct communities depending on the ecological trajectory of the lake during the period between inundations (Lesack and Marsh 2010). Shallow lakes subject to evaporative losses lack many taxa present elsewhere in the study area (Cluster 1). Deeper high-sill lakes (Cluster 3) may be disconnected for multiple years and are often subject to thermokarst activity and are distinguished from similarly low-CT lakes in having greater proportions of invertebrate predators.

Implications for biomonitoring and future ecological changes

Based on our comparison of the performance of the different taxonomic levels, we conclude that a biomonitoring effort based on at least the Family level is sufficient to detect changes in lakes in the Mackenzie Delta in response to changes in hydrological connectivity. While CT was an important structuring variable, a minimal RBA approach was less able to differentiate between connected and isolated lakes and is therefore less likely to be useful in detecting subtler effects due to changes in primary productivity or isolation of high closure lakes. Our Family-level results were likely also improved by the separation of subfamilies/tribes of the dominant family Chironomidae. The Family level analysis also showed closer correspondence between *k*-means groups defined by the assemblage and group membership predicted by LDA on the environmental variables (Table 6). Identifying BMI further to the genus level resulted in identical site classification to the Family analysis, and moderate improvements in the RDA model and LDA performance. Conversely, differences in richness were only apparent at the genus level, as were additional ecological details such as increased proportions of predators in high-sill thermokarst lakes and the presence of an extremely uncommon chironomid in a small Low Closure lake. Therefore it seems that detailed ecological or biodiversity studies of BMI communities should identify specimens to the genus or species level, while family identification may be sufficient for routine monitoring.

Our study is the first to examine differences in invertebrate communities in lakes along the connectivity gradient in the Delta. The strong relationship between benthic assemblages and connection time in our study indicates that the former will be a useful indicator of the changes that are expected to occur to the hydrology and ecology of the Delta under climate warming scenarios. Peak water levels in the spring determine the connectivity and degree of flushing of the ~ 45,000 lakes in the Delta (Marsh and Hey 1989, Emmerton et al. 2007) and the peak levels are determined by ice-breakup processes to a far greater degree than increases in discharge (Rood et al. 2017), both of which are associated with climatic changes (Lesack et al. 2013). Mechanical breakup of the ice cover which causes ice-jam flooding is temperature-sensitive (Beltaos 2013), and declines in the date of ice breakup (Marsh et al. 2002) and the lag time between onset of spring discharge and ice breakup (Lesack et al. 2013) have been attributed to increases in local spring air temperature (Lesack et al. 2014, Wang et al. 2017). Declines in ice jam-driven flooding likely will lead to decreased connection times of high elevation lakes (Lesack & Marsh 2007), which may dry up if not flooded for many years (Emmerton et al. 2007). On the other hand, low elevation lakes are likely to experience increased connection times due to rising sea levels in the northern Delta and possibly longer ice-free seasons (Lesack & Marsh 2007, Emmerton et al. 2007). Lesack & Marsh (2010) proposed that a consequence of these changes would be high elevation lakes becoming increasingly ecologically distinct from each other while also declining in abundance, while abundance and ecological similarity of low elevation or connected lakes is expected to increase, with a net result of a loss of ecological diversity (Lesack & Marsh 2010) and a decrease in storage and transformation of flood waters before delivery to the Arctic Ocean (Emmerton et al. 2007, 2008). Since we found that BMI responded to variation in CT, benthic assemblages should be useful as rapid indicators of ecological change due to varying flood levels, as well as long-term indicators of the ecological changes that have been predicted including greater ecological diversity in high elevation lakes (Lesack & Marsh 2010).

Our results indicate that connection time (CT) is of fundamental importance to benthic community structure even when the community is described at a coarse taxonomic level, and that BMI at the family level or lower are useful for monitoring changes to lake ecosystems related to altered flooding hydrology (e.g. gradients in primary productivity in low-closure lakes). Our family-level ordination suggests that with increasing time between floods, BMI communities in high-closure lakes (which are somewhat distinct from low-closure lakes in Figure 5) will become more distinct and occupy unique ordination spaces from lakes that regularly flood, as lack of dispersal routes limit opportunities for colonization and changes to habitat quality alter the food resources and niches available. Increases in CT in the low-closure lakes would increase dispersal opportunities for BMI and increase similarity in limnological characteristics among these lakes, so BMI communities in these lakes may become more homogeneous and similar to the no-closure lakes, which formed a distinct community type in our analysis. The precise effect of the predicted changes in CT on lake ecology is difficult to predict given current knowledge because as lakes become more isolated they may follow unique trajectories based on the relative importance of evaporation and thermokarst, as well as variation in conditions prior to isolation (Lesack & Marsh 2010). Given the environmental complexity of the Mackenzie Delta system, the use of an integrative bioindicator such as BMI communities would be of great use in monitoring the effects of current and future climate change.

Acknowledgments

This work was supported by an NSERC Discovery and NSERC Discovery Northern Research Supplement grants to RQ and Northern Scientific Training Program support to RWS. Logistical and technical support was provided by the Western Arctic Research Centre, Aurora Research Institute, in Inuvik NT, and we express thanks to Jolie Gareis, William Hurst and Edwin Amos for their valuable advice and assistance. for their advice and logistical support. We thank Andrew Medeiros, Christopher Luszczek, Sara Masood, Frankie Talarico, Cait Carew, and Dmitri Perlov from York University for assistance in the field. We are also grateful to Professor Lance Lesack from Simon Fraser University for providing valuable advice on calculating connection times. We also thank two anonymous reviewers for their valuable suggestions on a previous version of this manuscript. This research was conducted as a part of Scientific Research Licenses 15272. 15403, 15652, 15811 and 16149 from the Aurora Research Institute.

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Tables and Figures

Table 1 – Summary of environmental variables collected from all sites, with the transformation applied for analysis and the scores on the first two PCA axes. POC = particulate organic carbon, PON = particulate organic nitrogen, TDN = total dissolved nitrogen, DIC = dissolved inorganic carbon, TP = total phosphorus, TDP = total dissolved phosphorus, SRP = soluble reactive phosphorus, ChlA = chlorophyll *a*. Variables selected in RDA models in at least one BMI taxonomic level are in bold.

	Min	Max	Mean	Transformation	PC1	PC2
CT (days)	0	199	42.3	log	0.793	-0.659
POC (mg/L)	0.161	11.9	0.907	log	0.286	-0.293
PON (mg/L)	0.013	0.595	0.0699	log	0.308	-0.316
F (mg/L)	0.04	0.12	0.0914	n/a	-0.057	0.860
Cl (mg/L)	0.96	16.8	5.5	sqr	-0.423	-0.221
SO_4 (mg S /L)	0.22	35.2	16.7	n/a	-0.135	-1.005
Ca (mg/L)	10.3	66.6	26.9	sqr	1.055	-0.066
K (mg/L)	0.03	1.79	0.814	n/a	0.885	0.362
Mg (mg/L)	3.18	17.3	10.9	n/a	0.086	1.04
Na (mg/L)	1.86	11.2	5.79	n/a	-0.442	-0.254
Si (mg/L)	0.08	4.1	1.17	sqr	0.830	-0.059
TDN (mg N/L)	0.283	0.983	0.533	n/a	-0.026	0.856
DIC (mg C/L)	1.3	47	21	n/a	0.957	0.497
NH_4 (μg/L)	5	67	19	sqr	0.226	0.157
TDP (μg/L)	3.2	35.3	10.0	log	0.096	-0.221
TP (μg/L)	8.1	158	19.3	log	-0.105	-0.201
SRP (μg/L)	0.2	13.1	0.963	log	0.120	-0.249
ChlA (μg/L)	0.1	7.2	1.25	log	0.118	-0.301
Temp (°C)	11.2	22.2	15.9	n/a	0.210	-0.506
Cond (μS/cm)	42	415	196	n/a	0.968	-0.057
DO (mg/L)	4.9	18.2	12.3	n/a	-0.718	0.243
pH	6.77	10.6	8.86	n/a	-1.040	-0.031

Table 2: Evaluation of *k*-means partitioning of the invertebrate samples at different taxonomic resolutions. *SSE* (total error sum of squares) decreases with increasing numbers of clusters, and *ssi* (simple structure index) is maximized at the number of groups (shown in bold) that best fits the data.

k	RBA *SSE*	RBA *ssi*	Family *SSE*	Family *ssi*	Genus *SSE*	Genus *ssi*
2	7.514	0.03	12.071	0.023	15.997	0.019
3	6.221	0.044	10.207	0.025	13.921	0.025
4	5.377	0.052	9.029	0.028	12.487	0.027
5	4.778	0.068	8.064	0.04	11.136	0.027
6	4.345	0.071	**7.281**	**0.061**	**10.204**	**0.046**
7	**3.951**	**0.108**	6.609	0.057	9.315	0.042
8	3.621	0.092	6.061	0.059	8.622	0.044
9	3.312	0.059	5.599	0.054	8.041	0.043
10	3.032	0.057	5.163	0.036	7.488	0.041

Table 3: Pairwise analysis of variance of assemblage composition across *k*-means groups at different taxonomic levels. Bonferroni-corrected *p* values are shown with those with $p \leq 0.03$ in bold.

RBA level						
k	1	2	3	4	5	6
2	0.042					
3	**0.021**	0.042				
4	0.042	**0.021**	**0.021**			
5	0.189	**0.021**	0.042	**0.021**		
6	0.042	0.084	0.147	**0.021**	**0.021**	
7	0.084	0.042	0.042	0.063	**0.021**	0.105
Family level						
k	1	2	3	4	**5**	
2	**0.015**					
3	**0.015**	**0.015**				
4	**0.015**	**0.030**	**0.015**			
5	**0.015**	**0.015**	0.045	0.045		
6	**0.015**	**0.015**	**0.015**	**0.030**	**0.015**	
Genus level						
k	1	2	3	4	5	
2	**0.030**					
3	**0.015**	**0.015**				
4	**0.015**	**0.015**	**0.015**			
5	**0.015**	**0.015**	**0.015**	**0.015**		
6	**0.015**	**0.015**	**0.015**	**0.030**	**0.015**	

Table 4: Taxa identified by similarity percentages (SIMPER) analysis as contributing significantly ($p < 0.001$) to pairwise differences among *k*-means groups at different taxonomic levels. Only the significant taxa for pairs of sites which had significant overall differences in assemblage composition (Table 3) are shown. Reading down the column for each site group gives the taxa that were more abundant for that group in each comparison.

RBA level

		Higher average abundance						
		1	2	3	4	5	6	7
Lower average abundance	1			Nematoda				
	2							
	3							
	4			Nematoda		Gastropoda	Conchostraca	
	5				Chironomidae		Conchostraca	Amphipoda Hemiptera
	6				Chironomidae			
	7					Gastropoda Zygoptera		

Family level

		Higher average abundance					
		1	2	3	4	5	6
Lower average abundance	1			Planorbidae Coenagrionidae Aeshnidae	Mermithidae	Planorbidae	Hyalellidae
	2	Dorylaimidae		Planorbidae Libellulidae	Orthocladiinae Mermithidae		Oligochaeta
	3	Dorylaimidae	Limnesiidae		Mermithidae		Hyalellidae Corixidae Pionidae
	4	Dorylaimidae	Physidae				Hyalellidae Corixidae Pionidae
	5	Tanytarsini Dorylaimidae	Tanytarsini Limnesiidae				Hyalellidae
	6	Tanytarsini Dorylaimidae		Planorbidae Coenagrionidae Hydroptilidae Libellulidae	Orthocladiinae	Planorbidae	

Genus level

		Higher average abundance					
		1	2	3	4	5	6
Lower average abundance	1		*Physa*	*Ablabesmyia* *Leuchorrhinia*	*Aeshna*	*Gyraulus* *Einfeldia* *Ilybius*	*Hyalella*
	2	*Dorylaimus*		*Psectrocladius* *Ablabesmyia* *Paratanytarsus* Libellulidae *Guttipelopia* *Leuchorrhinia* *Cordulia* *Orthocladius* *Notonecta*	*Aeshna*	*Chironomus* *Einfeldia* *Propsilocerus*	*Limnephilus* *Limnophyes* *Piscicola*
	3	*Dorylaimus*	*Physa* *Fossaria* *Limnesia* *Stictochironomus* Phryganeidae		*Microtendipes*	*Propsilocerus* *Ilybius*	*Hyalella* Corixidae *Piona* *Limnephilus* *Limnophyes* *Piscicola*

	4		*Fossaria* *Limnesia*	*Ablabesmyia* *Guttipelopia* *Cordulia* *Labrundinia*		*Chironomus* *Einfeldia* *Propsilocerus* *Ilybius*	*Hyalella* Corixidae *Piona* *Limnephilus* *Piscicola*
	5	*Tanytarsus* *Dorylaimus*	*Limnesia*	*Ablabesmyia* *Guttipelopia* *Leuchorrhinia*	*Microtendipes* *Aeshna*		*Hyalella* Corixidae *Limnephilus*
	6	*Tanytarsus*	*Fossaria* *Limnesia*	Libellulidae *Leuchorrhinia* *Pseudochironomus*	Coenagrionidae *Aeshna*	*Gyraulus* *Chironomus* *Agrypnia* *Einfeldia* *Helisoma* *Propsilocerus*	

Table 5: Redundancy analysis of Hellinger-transformed benthic counts at the RBA, Family and Genus levels against forward-selected environmental variables. Only the significant RDA axes are shown.

	RBA level			Family level			Genus level		
	Variance	*F*	*p*	Variance	*F*	*p*	Variance	*F*	*p*
RDA1	0.038	14.65	0.001	0.051	13.01	0.001	0.070	14.42	0.001
RDA2	0.024	9.07	0.001	0.036	9.17	0.001	0.048	9.93	0.001
RDA3	0.012	4.63	0.01	0.027	6.81	0.001	0.038	7.91	0.001
RDA4	--	--	--	0.014	3.49	0.01	0.019	3.93	0.001
Model	0.194	5.35	0.001	0.304	5.23	0.001	0.401	4.53	0.001
Constrained	0.084			0.143			0.213		
Residual	0.110			0.160			0.182		
Adjusted R^2	0.352			0.381			0.426		
Variables included			CT DIC POC pH SRP Si F			CT DIC pH POC Si Mg F			SO_4 CT Na Ca K Mg Conductivity pH POC F

Table 6: Contingency tables showing classification (%) of sites based on environmental variables compared to *k*-means classification of BMI assemblages at a) RBA, b) Family and c) Genus taxonomic levels. Diagonals in bold are the classification success rates (%) for each *k*-means group.

K means groups	**a) RBA level**							**b) Family level**						**c) Genus level**					
	1	2	3	4	5	6	7	1	2	3	4	5	6	1	2	3	4	5	6
1	**38**	25	0	33	0	0	0	**71**	0	0	0	0	12	**67**	0	0	0	0	12
2	25	**62**	0	11	22	0	0	14	**90**	11	25	0	0	17	**100**	10	0	0	0
3	0	0	**60**	22	0	20	0	14	10	**89**	12	0	0	0	0	**80**	0	0	0
4	25	12	20	**11**	11	0	0	0	0	0	**62**	0	0	0	0	10	**100**	0	0
5	12	0	20	22	**67**	0	0	0	0	0	0	**71**	12	0	0	0	0	**71**	0
6	0	0	0	0	0	**40**	20	0	0	0	0	29	**75**	17	0	0	0	29	**88**
7	0	0	0	0	0	40	**80**	**--**	**--**	**--**	**--**	**--**	**--**	**--**	**--**	**--**	**--**	**--**	**--**

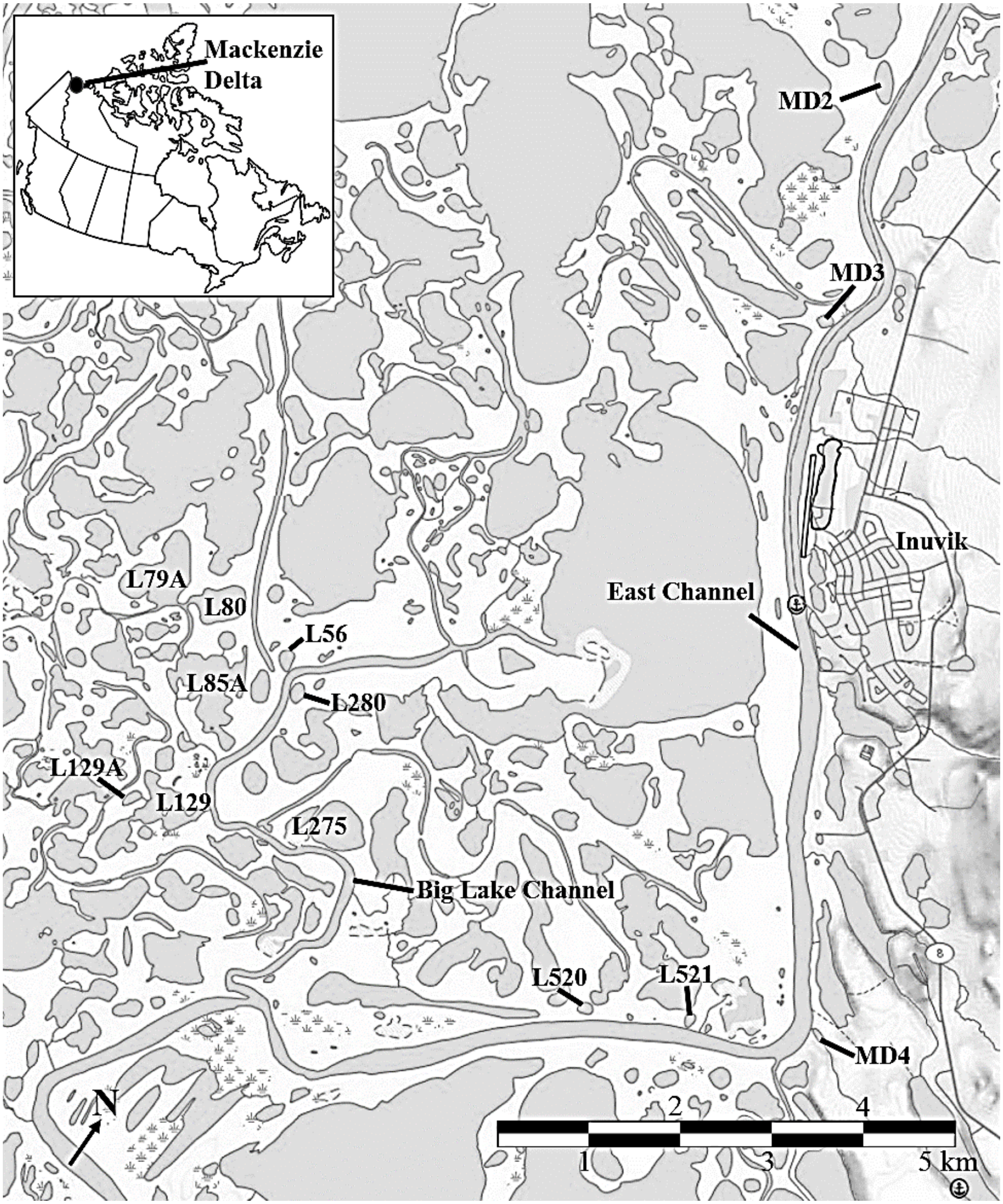

Figure 1: Locations of study sites along the East Channel of the Mackenzie Delta near Inuvik, NT. Base map data from Natural Resources Canada (https://atlas.gc.ca/toporama/en/index.html). Contains information licensed under the Open Government Licence – Canada.

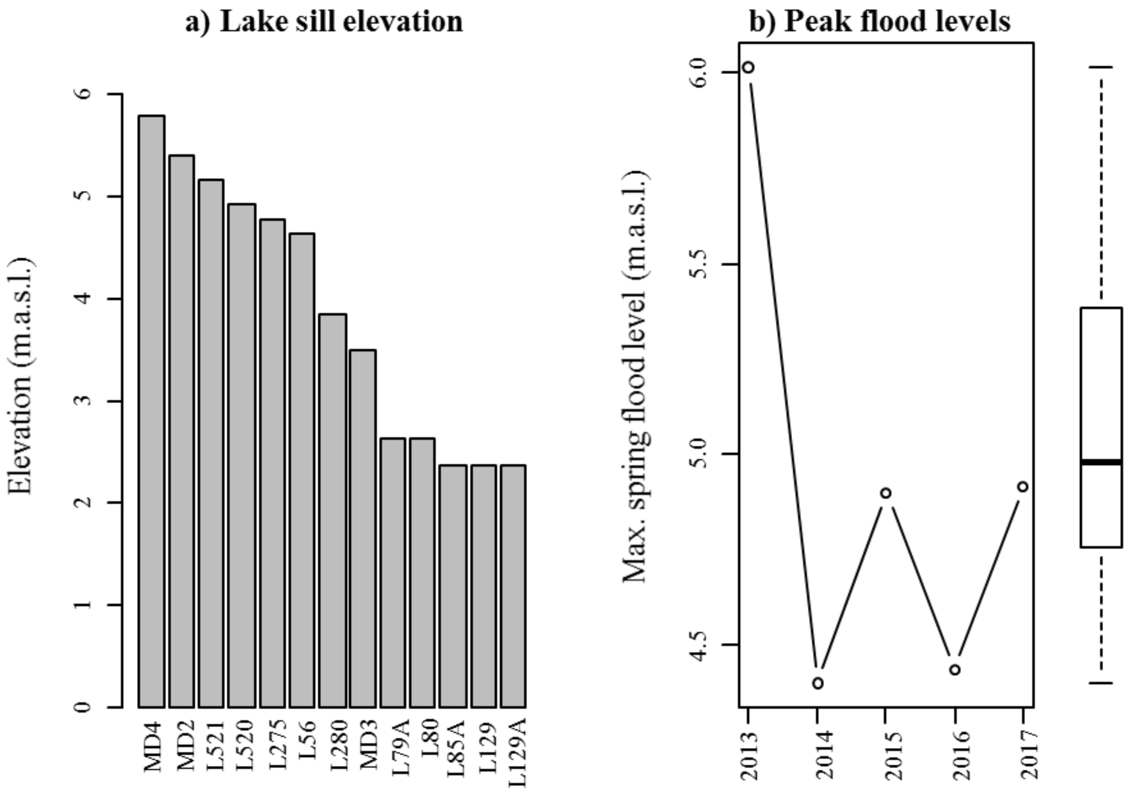

Figure 2: a) Spring sill elevation of the study lakes. b) Peak flood levels at station 10LC002 in the main channel adjacent to the study lakes during the study period. The boxplot shows the distribution of historical flood levels for the station (1985-1990, 2002-2017).

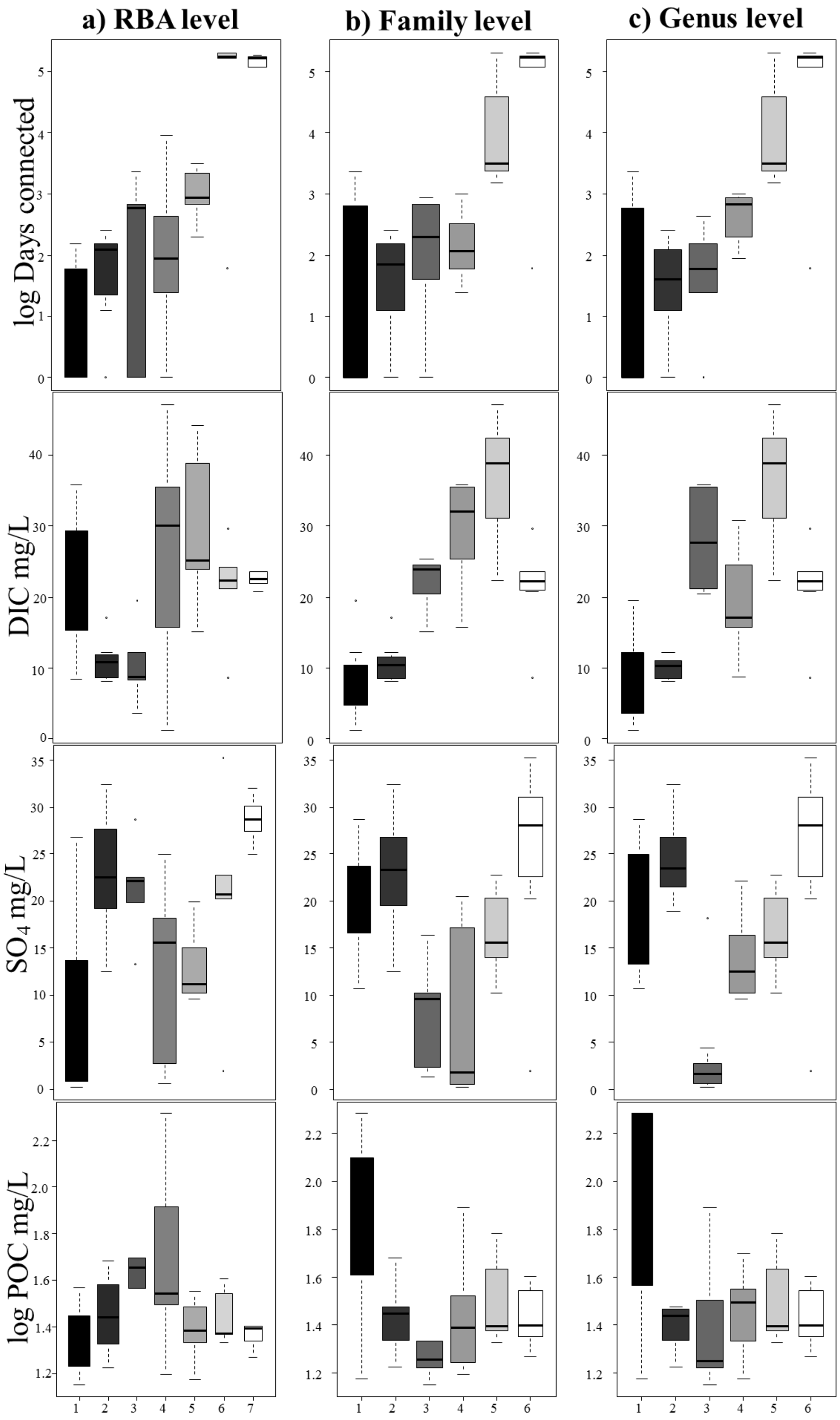

Figure 3: Distribution of important environmental variables within the *k*-means groups at the a) RBA and b) Family and c) Genus taxonomic levels. CT, DIC, SO_4 and POC were identified by forward selection as explaining benthic variation in both in one or more RDA models.

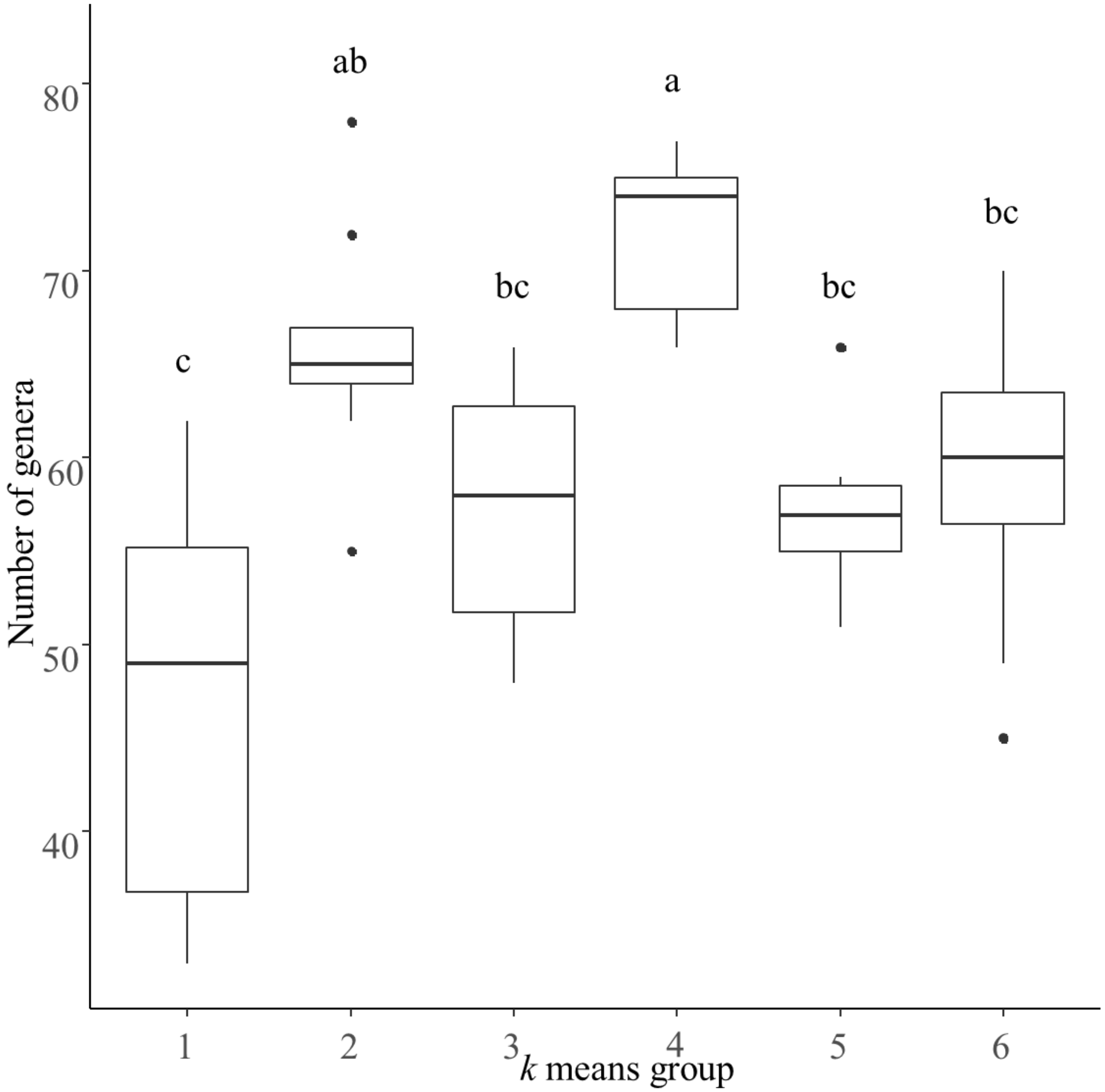

Figure 4: Generic richness among Genus-level *k*-means groups. Significant differences from pairwise *t* tests (α = 0.05) are indicated by letters.

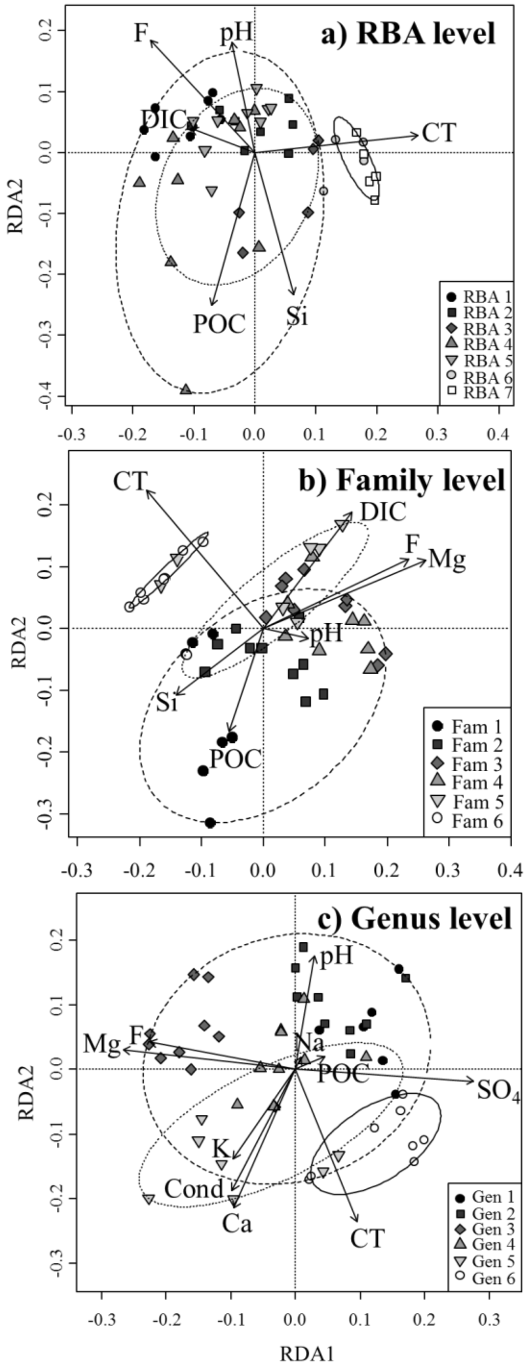

Figure 5: Redundancy analysis biplots (scaling 1) showing sites after forward selection of environmental (explanatory) variables at a) RBA taxonomic level, b) family level and c) genus level. Symbol shape and shading corresponds to the *k*-means partitions for each taxonomic level. The ellipses enclose all members of each of the *a priori* lake closure groups: solid line = High Closure, dashed line = Low Closure, dotted line = No Closure.

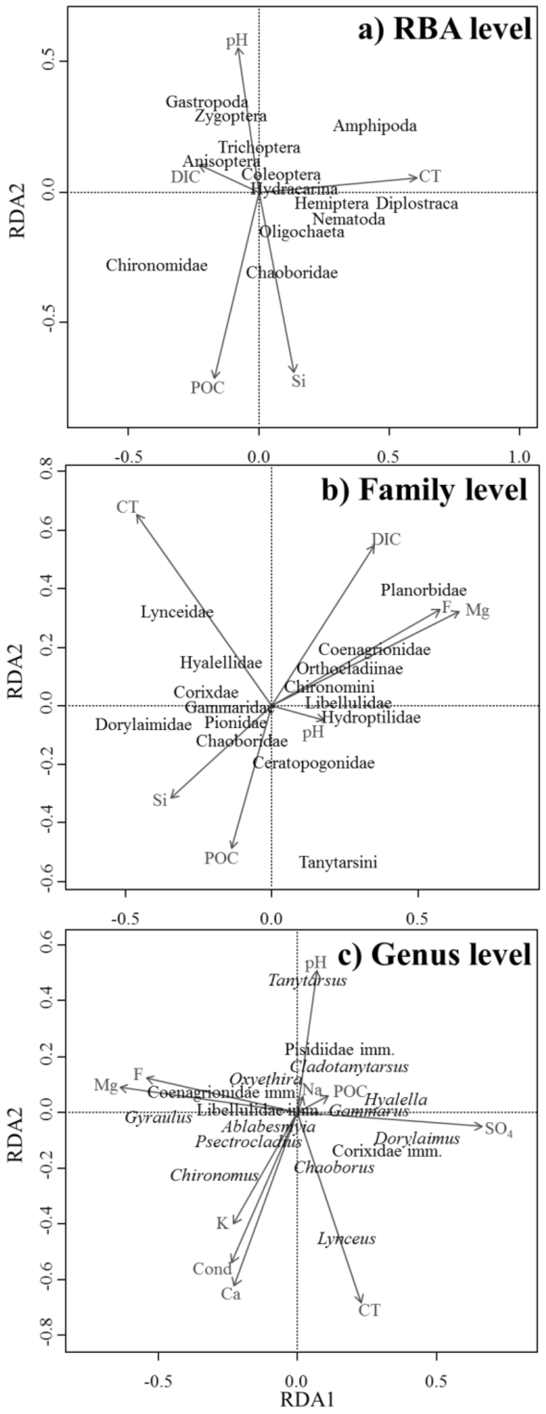

Figure 6: Redundancy analysis biplots (scaling 2) showing responses of a) RBA taxa, b) Families and c) Genera to gradients in forward-selected environmental variables. For clarity only taxa with scores above a threshold on either RDA axis were plotted; these were > 0.05 for the RBA level and > 0.1 for the Family and Genus level ordinations.

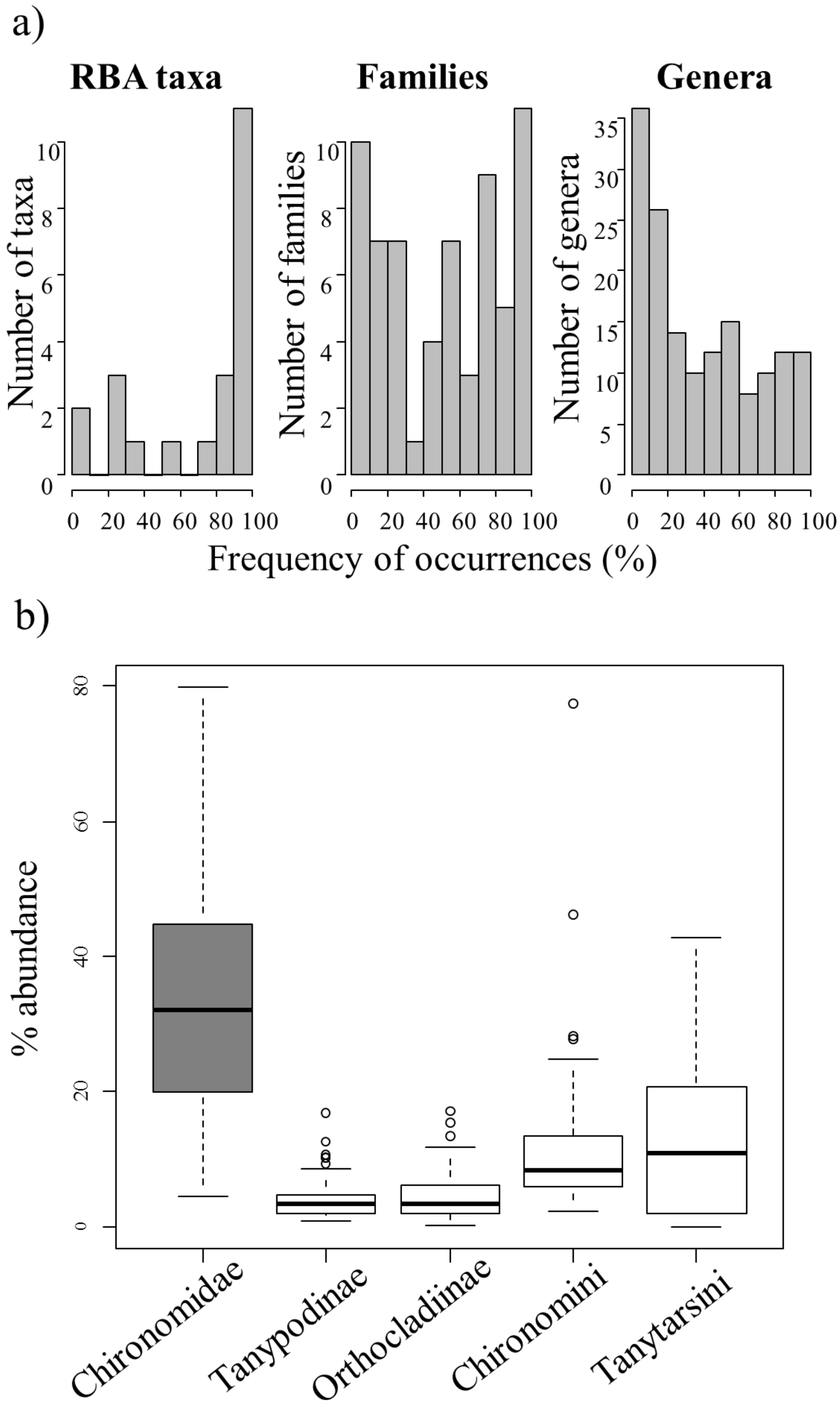

Figure 7: a) Occurrence frequencies of RBA taxa, Families and Genera. b) Relative abundance of Chironomidae (RBA analysis, shaded box) and chironomid subfamilies/tribes (Family analysis, unshaded boxes).

Chapter 3: The importance of hydrological connectivity on the benthic macroinvertebrate metacommunity structure of an Arctic delta floodplain

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Author's Contributions

RS, RQ, and SS conceived of the research ideas and study design, RS, SS, and RQ acquired funding, RS conducted field sampling, analyzed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and will have the opportunity to give final approval for publication in Freshwater Biology.

This chapter has been submitted to Freshwater Biology as Scott, R.W., Sharma, S., Wang, X., & Quinlan, R. The importance of hydrological connectivity on the benthic macroinvertebrate metacommunity structure of an Arctic delta floodplain. *Freshwater Biology*, submitted 30 August 2021.

Summary

1. Understanding the factors that structure ecological communities across landscapes is a fundamental goal of metacommunity ecology. Hydrological connectivity is a particularly important component of aquatic metacommunity structure owing to dispersal limitation of aquatic organisms. The interactions between connectivity and taxonomic or functional metacommunity structure, and their potential responses to altered patterns of connectivity in a changing climate, remain poorly understood.

2. To address this knowledge gap, we examined a littoral benthic invertebrate metacommunity along a gradient of hydrological connectivity in the Mackenzie River Delta, a major Arctic floodplain. We utilized three complementary analytical techniques (ordinations and variation partitioning, elements of metacommunity structure, and fourth corner analysis) to determine the relative influence of environmental versus spatial variation, the structure of metacommunities across dispersal modes, and the functional organization of the metacommunity.

3. Approximately 35,000 macroinvertebrate specimens were collected from the lakes representing 207 distinct taxa. We found environmental factors explained the most variation in metacommunity structure and low importance of spatial factors, attributed to mixing effects of annual flooding and lack of barriers to aerial dispersal.

4. The structure of the overall metacommunity and of aerial dispersers indicated taxa distributions were determined by environmental factors, whereas both dispersal limitation and environmental factors were important in determining aquatic disperser metacommunity structure. The functional structure of the metacommunity was mainly related to dispersal mode and lake isolation. Aerial dispersers were able to selectively colonize suitable habitat with no evidence of spatial dispersal limitation, whereas aquatic dispersers were more limited by dispersal opportunities determined by the degree of lake isolation.

5. Our results indicate that hydrological connectivity and lake isolation is of fundamental importance to metacommunity structure in the Mackenzie Delta, where permanent water bodies are connected for a brief annual period in a flooding process driven by climate-mediated ice jam dynamcs. Loss of habitat heterogeneity and increased connectivity owing to climate change are likely to lead to loss of aquatic invertebrate biodiversity in the Delta.

Introduction

Understanding the factors influencing distributions of species and patterns of assemblage composition in natural communities is a fundamental goal of community ecology. Traditionally community studies have focused on the role played by local environmental factors in determining the presence and abundance of species in local communities. Over the last few decades, metacommunity ecology (Leibold et al. 2004) has expanded this view to include the role of dispersal among communities in shaping species distributions and determining assemblage composition. Species vary in their dispersal abilities and environmental tolerance, so species distributions may be limited by dispersal across various spatial scales (Lansac-Tôha et al. 2020), by filtering due to limiting environmental factors, or by interaction between environmental and spatial factors (Heino et al. 2015). When dispersal abilities and population densities are high, mass effects may occur where species occur in habitats outside their preferred environmental ranges, having dispersed from more suitable source habitats (Mouquet & Loureau 2003). Understanding the patterns of species distribution within a metacommunity and the environmental, spatial, and ecological factors that influence metacommunity dynamics provide important information to develop predictive models of community structure to aid efforts at assessment and conservation of the ecological status of freshwater habitat (Heino 2013b, Siqueira et al. 2013) in this rapidly changing Arctic region.

The inclusion of functional traits in explanatory ecological models provides a link between environmental variation and the ecological gradients that underly taxonomic variation (Poff et al. 2006). In recent years, this approach has been widely applied to a wide array of aquatic organisms including macrophytes (Delatorre et al. 2020), zooplankton (Deosti et al. 2021), fish (Poveda-Cuellar et al. 2021), and benthic macroinvertebrates (Bhowmik & Mandal 2021). Much progress has been made in constructing databases of benthic invertebrate functional traits in North America (Vieira et al. 2006) and Europe (Sarremejane et al. 2020). However, significant challenges remain in developing a globally consistent trait database (Maasri 2019) and addressing the applicability of trait determinations across biogeographical and ecological regions. For example, life history characteristics within a widespread species may vary from temperate to Arctic latitudes (Danks 1992), and even generic feeding group classifications have been found to vary across biogeographic regions (Saigo et al. 2016). Caution must therefore be used when applying all but the most basic traits (e.g. dispersal mode, habit) using trait databases derived from specific geographic regions.

Hydrological connectivity is a fundamental driver of ecological patterns in complex floodplain systems (Junk et al. 1989, Ward et al. 1999, Tockner et al. 2000). In the case of benthic invertebrate metacommunities, variation in connectivity between aquatic habitats provides dispersal routes for entirely aquatic organisms or prevents access to these habitats to all but aerial dispersers. Hydrological connectivity has been linked to variation in benthic invertebrate metacommunity structure in lateral aquatic habitats of river floodplains (Arscott et al. 2005, Bonada et al. 2006, Gallardo et al. 2009, Zilli & Marchese 2011, Blettler et al. 2016, Saigo et al. 2016, Petsch et al. 2017, Dong et al. 2021). Fewer studies have considered the influence of hydrological connectivity on benthic communities in deltaic floodplains (Petsch et al. 2017), and fewer still have taken place in Arctic deltaic environments. Given the high susceptibility of Arctic floodplains to alterations due to climate change in the near future (Rouse et al. 1997), this represents a significant knowledge gap which we attempt to address in this paper.

In this study, we examine a littoral benthic macroinvertebrate metacommunity sampled across spatial and connectivity gradients in the Mackenzie Delta, Northwest Territories, with the aim of addressing the following questions: 1) What is the relative importance of environmental factors and spatial patterns that influence benthic community structure?; 2) How are metacommunities structured in relation to lake-river connectivity and dispersal mode?; and 3) How does functional community structure vary across the environmental and spatial gradients? First, we expect macroinvertebrate dispersal to be high but sufficiently limited to allow species to occupy their preferred niche. Given that previous work on a smaller spatial scale in the Delta has demonstrated that environmental factors related to lake-river connectivity are predictive of macroinvertebrate composition (Scott et al. 2020), we expect factors related to connectivity to structure community structure at a Delta-wide scale. Because of annual mixing that occurs during spring flooding, we expect spatial factors to be relatively low in importance relative to environmental factors. However, we note some possibility for a large-scale longitudinal gradient owing to a potential dispersal route from a distinct biogeographical region in the west of the study area. Second, we expect to observe Clementsian gradients in which species sort into discrete assemblages along environmental gradients, but species lacking an aerial phase are likely to exhibit evidence of dispersal limitation (e.g., low turnover or nestedness). Third, we expect aerial dispersals to be positively related to lake isolation and related factors, and aquatic dispersers the opposite. We further expect predators to be positively related to lake isolation owing to the exclusion of many fish (e.g., Laske et al. 2017), and feeding groups that rely on coarse organic material (collector-gatherers, shredders) to be positively associated with connected lakes due to greater abundance of food sources originating from the river.

Methods

Study area and site selection

The Mackenzie River Delta is located in northwestern Canada at the outlet of the Mackenzie River system to the Beaufort Sea. It is among the largest river deltas draining into the Arctic Ocean and contains an estimated 45,000 floodplain lakes (Emmerton et al. 2007). The region is underlain by continuous permafrost and experiences a short summer with continuous daylight. Despite the Arctic climate, the Mackenzie River basin and the upper Delta represent a northward extension of boreal forest, with dense black spruce and alder present in contrast to the tundra landscape of the lower Delta and surrounding uplands. Water primarily enters the Delta via the mainstem of the Mackenzie River, which drains an area of 1.8 x 106 km^2 of western Canada east of the Rocky Mountains, with a secondary input from the Peel River draining from the Western Cordillera from the west. The hydrological regime is dominated by spring flooding, driven by ice jam floods. This flooding is responsible for forming and replenishing the deltaic lakes (Marsh & Hey 1989), and influences lake sedimentation (Carson et al. 1999, Marsh et al. 1999), water balance, lake carbon balance (Tank et al. 2009), and primary (Squires et al. 2009) and secondary (Scott et al. 2020) producers.

The abundant deltaic lakes are situated at varying elevations above the main channels, and this factor determines the duration and extent of inundation during the spring (Marsh & Lesack 1996). We sampled lakes at representative levels along this elevation gradient in three study areas located along the East, Middle, and West Channels of the Delta (Figure 1). While reliable estimates of connection time were available near the town of Inuvik thanks to an Environment Canada & Climate Change hydrometric station and precise determinations of sill elevation, water levels were unavailable for the Middle Channel area and sill elevation was unavailable for the Middle and West Channel areas. Therefore we sampled three closure types in each of the study areas, corresponding to the classification of Mackay (1963): 1) highly isolated lakes, located at high elevation and flooding for a period of days during spring flooding, occasionally going multiple years without flooding; 2) isolated lakes, separate from the river during the summer but with low elevation such that they are flooded throughout the spring peak water period; and 3) connected lakes, which are connected to the main channels throughout the growing season by distributary channels.

Sampling methods

Lakes were sampled between 28 July and 15 August 2015. At each site, duplicate 2 L surface water samples were collected with a Nalgene bottle. Water temperature, specific conductivity, pH, and dissolved oxygen were measured with a multiparameter sonde (YSI600-QS). Benthic invertebrates were collected approximately 1 m from shore by kicking an area of approximately 1 m^2 and sweeping a 500 µm mesh net through the water column to collected suspended material and invertebrates. Three replicate benthic samples were taken at representative areas along the shoreline of each lake. Benthic samples were preserved with 95% ethanol and transported to the Aurora Research Institute in Inuvik for refrigeration and filtration of water samples. Water samples were analyzed at the National Hydrology Research Centre in Burlington, ON, for major ions (F, Cl, SO_4, Ca, Mg, Na, K, Si), particulate organic carbon (POC), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total nitrogen (TKN), total phosphorus (TP), and chlorophyll *a*. Benthic samples were sorted using a fixed-count method of 500 individuals per sample and averaged before analysis. Lake area was estimated using satellite imagery from Google Earth. The closure types of the East Channel lakes were known from historical measurements and previous studies, while those of the West and Middle Channel lakes were determined using GPS elevation measurements and observations of the lake sill or connecting channels, when present.

Statistical analysis

Continuous environmental variables were transformed to ensure normality based on Shapiro-Wilk tests. Closure type was represented as a categorical scale (connected = 1, isolated = 2, highly isolated = 3). We began by assessing taxa richness and proportion of aerial and aquatic dispersers overall and within the study regions and lake closure types. Differences in richness across the regions and lake types were assessed using analysis of variance (ANOVA, α

= 0.05). We assessed the relationship of richness to the environmental explanatory variables using a linear multiple regression. Rare taxa (those occurring at only one site) were removed prior to further analysis.

Question 1: Environmental and spatial structure

We used a variation partitioning approach (Figure 2a) to assess the influence of environmental and spatial structure on the invertebrate community composition (Peres-Neto et al. 2006). We first modelled the environmental component of community variation using redundancy analysis (RDA) of the Hellinger-transformed abundance constrained by the normalized environmental variables. Environmental variables were chosen using stepwise forward selection (Blanchet et al. 2008) and the significance of the reduced RDA model was evaluated using permutation tests. Forward selection and redundancy analysis were performed using the *ordiR2step* and *rda* functions of the vegan package in R (Oksanen et al. 2020). Spatial vectors were computed based on the Euclidean distance among the geodesic site coordinates using the Moran’s eigenvector maps (MEM) approach (Borcard & Legendre 2002, Dray et al. 2006) using the *pcnm* function in vegan. This method generates a series of eigenvectors expressing distance among sites at declining spatial scales. These spatial vectors were then subjected to forward selection and RDA with the Hellinger-transformed benthic abundance data to identify the spatial factors that were significantly related to community variation. To determine the pure environmental and spatial components of variation in the benthic communities independent of spatial structure in the environmental variables, we used variation partitioning (Borcard et al. 1992, Peres-Neto et al. 2006) using the forward selected environmental and spatial variables followed by permutation tests of the environmental and spatial fractions. Variation partitioning was performed using the *varpart* function of the vegan package.

Question 2: Metacommunity structure

To describe the metacommunity structure of the benthic macroinvertebrate communities we used the elements of metacommunity structure (EMS) approach (Leibold & Mikkelson 2002, Presley et al. 2010). This approach utilizes a species occurrence matrix reordered by site loadings in a correspondence analysis and three sequential tests to identify which of eight idealized patterns (1–8) describe the metacommunity (Figure 2b). The first is coherence, which tests for whether the number of embedded absences in the reordered matrix is similar to the number expected under a random null model. Significantly negative coherence indicates a (1) chequerboard pattern (Diamond 1975) in which species are negatively associated with one another, suggesting patterns of species exclusion generated by interspecific competition, while non-significant coherence indicates a (2) random pattern. Significantly positive coherence indicates that species occurrence is related to an underlying ecological gradient. The second test is for species turnover, which is the tendency for species to replace each other along the gradient of occurrence. Positive turnover implies that communities are different at opposing ends of the underlying gradient. Negative turnover indicates a nested pattern, in which species in the least diverse sites are proper subsets of the species in the most diverse sites. Presley et al. (2010) suggested that where turnover is not significant, the community can be regarded as quasi-structures that are fundamentally similar to either a gradient-based (positive turnover) or nested (negative turnover) structure, but where the strength of the patterns is weaker. The third test is for boundary clumping, which is the tendency for species to occur in distinct assemblages, and applies to both gradient patterns (where distinct assemblages may occur along an underlying gradient) and nested patterns (where species may be lost in groups along an underlying ecological gradient within an overall nested structure). In the case of positive turnover, significant negative clumping indicates (3) evenly spaced, or over-dispersed, structure (Tillman 1982) where species replace one another independently of other species. Significant positive clumping indicates a (4) Clementsian gradient (Clements 1916), in which species replace each other in distinct assemblages, while non-significant clumping indicates a (5) Gleasonian gradient (Gleason 1926), in which species replace each other randomly along an underlying ecological gradient. In the case of negative turnover (nested pattern), the patterns of species loss are equivalent to the three patterns for gradients, but for clarity are termed (6) hyperdispersed species loss for negative clumping, (7) random species loss for non-significant clumping, or (8) clumped species loss for positive clumping (Presley et al. 2010). EMS analysis was performed on presence-absence data using the *metacom* package in R (Dallas 2020). We examined the overall metacommunity pattern as well as the patterns for aerial and aquatic dispersers, on the first and second axes of variation.

To further describe metacommunity structure we extended the EMS approach by testing for species that are likely to exhibit mass effects using the method proposed by Leboucher et al.

(2020). Mass effects occur when the dispersal ability and population density of a species are high enough that they can occupy unsuitable habitats via dispersal from more suitable source habitats (Shmida & Wilson 1985, Mouquet & Loreau 2003). This approach defines species as likely to exhibit mass effects when three conditions hold: (1) low negative co-occurrences with other species, (2) average to low niche breadths, and (3) high correlation to spatial factors. Co-occurrence was analyzed by applying probabilistic models of species co-occurrence (Veech 2013) using the *coccur* package in R (Griffith et al. 2016). Niche breadth was estimated using the tolerance (tol) parameter of the outlying mean index analysis of Dolédec et al. (2000) using the niche function of the *ade4* package in R (Dray et al. 2020). Spatial variables were represented using the species loadings from the first two axes of the RDA of benthic communities against forward selected MEM variables. Species were then analyzed for mass effects using principal component analysis (PCA) with negative co-occurrences, niche breadth (tol) and the MEM vectors as variables. Classification of species was then validated using *k*-means clustering on the PCA species loadings, with number of clusters determined by maximum ssi (simple structure index, an indicator of optimal partitioning), to test that species identified as susceptible to mass effect form a distinct group.

Question 3: Functional structure

Finally, to determine the influence of environmental and spatial factors on invertebrate functional traits we used RLQ analysis (Dolédec et al. 1996) combined with fourth corner analysis (Legendre et al. 1997, Dray & Legendre 2008) using Hellinger-transformed invertebrate abundance, the selected environmental variables, and three basic benthic invertebrate traits (Table 1, Figure 2c). RLQ analysis provides ordination scores linking three tables, in this case environmental variables (table R), species abundance (L) and traits (Q), while the fourth corner method allows hypothesis testing of the relationships between the individual traits and environmental variables. This approach has been shown to produce accurate estimates of trait-environment relationships (Peres-Neto et al. 2017). We used $\alpha = 0.05$ to minimize Type I error (ter Braak et al. 2012), and model type 6, which permutes the data by both species and sites in significance testing (Dray & Legendre 2008). In order to reduce number of tests and required *p*-value corrections, we further reduced the environmental variables by running forward selection with $\alpha = 0.01$. After assessing significant relationships between individual traits and environmental variables, we combined the two analyses following the approach of Dray et al.

(2014) by analyzing trait and environment relationships with the RLQ axes using the fourth corner method to test trait-environment associations against the overall species assemblage structure. RLQ and fourth corner analysis were performed using the *rlq* and *fourthcorner* functions of the *ade4* package in R (Dray et al. 2020).

Results

Approximately 35,000 invertebrate specimens belonging to 207 taxa were identified from the 23 lakes (Table 2). Total taxa richness was similar in the three regions and lake types, where differences were mainly attributable to differences in sample size. Richness was not significantly different across regions ($F = 1.47$, df = 2, $p = 0.254$) or lake closure type ($F = 0.215$, df = 2, $p = 0.808$). Aerial dispersers were a majority of the community composition in all regions and lake types. After removing non-significant variables, richness was significantly higher in lakes with higher surface temperature and lower chlorophyll *a* and SO_4, the latter having the highest coefficient of variation (adjusted $R^2 = 0.494$, $p = 0.002$).

Environmental and spatial structuring of benthic communities

Seven environmental variables of the original 19 significantly explained 50.4% (27.3% adjusted R^2) of the variation in benthic communities in a redundancy analysis ($F = 2.18$, df = 7, $p < 0.001$). These variables included one physical parameter (area), five chemical parameters (SO_4, DIC, specific conductivity, and pH), and chlorophyll *a*, an indicator of primary productivity.

Two spatial vectors produced by MEM analysis were significantly related to benthic composition, in particular a broad spatial scale (MEM1) and a intermediate spatial scale pattern (MEM4). While the spatial variables were significantly related to benthic composition ($F = 1.72$, df = 2, $p = 0.01$), they explained less variation than the environmental variables (14.6% of total inertia of 0.395, adjusted $R^2 = 6.1\%$).

The combined forward selected environmental and spatial variables explained slightly more variation (58.0% of the total inertia of 0.395, adjusted $R^2 = 28.9\%$) than the environmental parameters alone in an RDA of the seven environmental and two spatial variables against the community composition (Figure 3). Variation partitioning showed that pure environmental factors were responsible for most of the explained variation (23%), with most spatial correlation explained by spatial covariation with environmental variables (4%) and little variation explained by pure spatial factors (2%). Permutation testing of the environmental fraction was significant ($F = 1.91$, df = 7, $p > 0.001$) while the spatial fraction was not ($F = 1.17$, df = 2, $p = 0.215$). There was therefore little spatial structuring of benthic communities across the Delta, whereas they were significantly influenced by environmental variables, though much variation (71%) remained unexplained.

Metacommunity structure of Mackenzie Delta benthic communities

The macroinvertebrate metacommunity had significant positive coherence on the first two dominant axes of variation, regardless of dispersal type according to EMS analysis (Table 3). Species turnover and boundary clumping were significantly positive for the total community as well as aerial dispersers, indicating Clementsian gradients with distinct assemblages occurring along the underlying ecological gradient. In contrast, aquatic dispersers had non-significant negative turnover along the first axis of variation, indicating a nested subset quasi-structure, in addition to significantly positive boundary clumping. This pattern suggests non-random patterns of species distributions, similar to a Clementsian structure within the nested subset. Along the second axis of variation aquatic dispersers had non-significant positive turnover and significant positive boundary clumping, indicating a quasi-Clementsian gradient.

Only a small number of taxa were identified as susceptible to mass effect (where species occupy suboptimal sites due to high rates of dispersal). The optimal k-means partitioning consisted of six clusters, and one of these clusters contained taxa having the characteristics of mass effect dynamics: low numbers of negative co-occurrences, average to low niche breadth, and high correlation to spatial variables (Figure 4). Of these taxa, the clam shrimp *Lynceus brachyurus* most clearly exhibited characteristics of mass effect. The amphipod *Hyalella* sp. had low negative cooccurrence and strong relationship to the spatial variables, but also had wide niche breadth, indicated by tolerance (tol) values. The remaining taxa in the cluster included the amphipod *Gammarus lacustris*, the snail *Physa* sp., and dorylaimid nematodes. Each of these taxa was widespread across the Delta and often abundant.

Functional metacommunity structure

The relationship between invertebrate traits and the environmental variables was globally significant in a multivariate test based on the total inertia (0.146) of the RLQ analysis ($p < 0.001$ for permutations by both sites and species). Fourth corner analysis showed nine significant relationships between individual traits and environmental variables (Figure 5a). Aerial dispersal mode was significantly positively associated with closure and negatively with SO_4, while aquatic dispersers had significant associations in the opposite direction with these variables. No significant relationships were found for predators, but collector-gatherers had significant negative relationships to SO_4 and lake area. The overall gradient (Figure 5b) was of aquatic dispersers and swimmers associated with connected lakes with large area and high SO_4 opposed to aerial dispersers and collector-gatherers associated with highly isolated lakes. The only significant relationship with the spatial variables was between shredders and the small-scale spatial variable (MEM4), and inspection of the location of the sites and species in the ordination space suggested this relationship was largely due to high proportions of amphipods, in addition to limnephilid and phryganeid caddisflies in the East Channel connected lakes. Fourth corner tests of the RLQ axes confirmed these results (Figure 6), with most significant traits and all significant environmental and spatial variables related to the dominant axis of variation described in Figure 5b.

Discussion

The relative importance of environmental versus spatial structuring of communities depends to a large degree on the dispersal abilities of the organisms and on the spatial extent of the study (Heino et al. 2015). We hypothesized that environmental factors would be more important in structuring benthic invertebrate community composition than spatial factors due to the mixing of communities that could occur during spring flooding, and the lack of physical barriers to dispersal in the Mackenzie Delta. We found that environmental variables explained 27.3% (50.4% unadjusted) of the variation in benthic invertebrate communities in lakes spanning the Delta. Including spatial variables increased the amount of variation explained by only 1.6%, and variation partitioning showed pure spatial factors to explain only 2% of the variation compared to 23% for environmental factors. Environmental filtering is an important structuring process for most types of biological community (Cottenie 2005), and particularly so for small, actively dispersing organisms like aquatic insects (e.g., Heino et al. 2017, Hill et al. 2017, Tolenen et al. 2018). Landscape attributes such as vegetation and topography influence dispersal of aquatic insects from their water body of origin (Delettre & Morvan 2000, Phillipsen & Lytle 2013), but the flat, relatively homogeneous landscape of the Delta likely provides little barrier to aerial dispersal. The spatial extent of the study also influences the importance of spatial structuring, with environmental factors predominating at finer scales and spatial factors increasing in importance when the study encompasses different watersheds or regions (Heino et al. 2015, Lansac-Tôha et al. 2020). The extent of this study was about 60 km longitudinally and despite the potential for a large-scale spatial pattern due to migration from the Western Cordillera mountain range via the Peel River in the western Delta, at this scale we did not find significant evidence of spatial structuring in benthic invertebrate metacommunities.

Hydrological connectivity had a large role in the environmental structuring of the metacommunities. The variables most strongly correlated with assemblage composition were either directly (SO_4, area) or indirectly (DIC, pH) related to the degree of lake isolation (Scott et al., in review). Connected lakes in the Delta have much greater surface area than isolated lakes and have elevated SO_4 inputs from the main channels (Lesack et al. 1998). DIC in clear, isolated lakes is depleted relative to the more turbid connected lakes due to macrophyte uptake (Squires et al. 2009, Tank et al. 2009), but may be higher in deeper, highly isolated lakes affected by thermokarst. So, while there was little evidence of overall spatial gradients indicating dispersal limitation, the environmental structuring of the metacommunities, and of the lakes themselves, is fundamentally related to connectivity, and therefore potentially to dispersal-related processes.

We found an overall Clementsian gradient in metacommunity structure using EMS analysis, indicating a pattern of species occurrence in which species replace each other in groups over an underlying ecological gradient (Leibold & Mikkelson, 2002). This result concurs with that of Scott et al. (2020) which found significantly different community composition in response to environmental gradients over five years in lakes in the East Channel study area and is consistent with the species sorting metacommunity paradigm (Leibold et al. 2004). However, we found differing patterns in species turnover when the metacommunity was decomposed by dispersal mode, with a Clementsian gradient in aerial dispersers and a nested pattern in aquatic dispersers. A nested pattern is indicative of dispersal limitation in which species do not fully occupy their potential niche space (Leibold & Mikkelson, 2002). There was also strong evidence for environmental structuring in the aquatic disperser metacommunity in addition to dispersal limitation since the test for species turnover was nonsignificant, and the test for species clumping indicated a clumped species loss pattern, equivalent to a Clementsian gradient within an overall nested structure (Presley et al. 2010). These results agree with those of a number of studies of benthic invertebrate metacommunities that found stronger environmental relationships with aerial dispersers (de Bie et al. 2012, Grönroos et al. 2013) and either spatial control (Heino 2013a, Li et al. 2019) or random patterns (Petsch et al. 2017) in aquatic dispersers. Other studies have found predominantly environmental control in metacommunity patterns regardless of dispersal mode (de Mendoza et al. 2018, Tornero et al. 2018, Ptatscheck et al. 2020). These different results may depend on the spatial scale of the study (Tornero et al. 2018) and landscape characteristics including dispersal limitation in stream networks (e.g. Ptatscheck et al. 2020) and the range of environmental variation (Li et al. 2019).

We identified a small group of common and abundant, mainly aquatic dispersing taxa that were susceptible to mass effect based on moderate niche breadth, correlation with spatial factors, and low negative co-occurrence (Leboucher et al. 2020). These included physid snails, amphipods (*Gammarus lacustris* and *Hyalella* sp.), and large branchiopod clam shrimp (Laevicaudata: *Lynceus brachyurus*). Wide niche breadths and greater aquatic dispersal abilities due to small size may increase the spatial influence in small gastropods (Funk et al. 2013). The amphipod *Hyalella* sp. was found to have a very wide niche breadth, indicating a generalist pattern rather than strictly mass effect (Presley et al. 2010), but also has a high likelihood of temporarily establishing populations in unsuitable habitats due to high fecundity and parthenogenetic reproduction (Wellborn & Capps 2013). Mass effects were found to be most likely to occur in *L. brachyurus*. This species is widespread across the Holarctic (Rabet et al. 2005, Gołdyn et al. 2012, Schmidt et al. 2018), but usually associated with widely dispersed ephemeral pools (Patton 2014) rather than the more permanent lakes of the Mackenzie Delta. The species has long been reported from Delta lakes (Wiens et al. 1975) and pools of streams flowing into the main channels (Scott et al. 2011), although not from other Arctic regions. Distributions of large branchiopods, including *Lynceus* sp., have been found to be patchy both among and within habitats (Wang et al. 2018) and associated with hydrological connectivity to a greater degree than other invertebrates (Dube et al. 2019). Further research on the dispersal mechanisms and biogeographical origins of *L. brachyurus* in the Delta could provide fruitful results.

Fourth corner analysis suggested a strong relationship between functional metacommunity structure and hydrological connectivity. We found that traits varied along a primary axis related to lake isolation (closure type, area, SO_4), and significant relationships between traits and environmental variables were mostly along this axis. As we predicted, aerial dispersers were associated with more isolated lakes and aquatic dispersers were associated with more connected lakes. Taxa that actively swim likely have greater dispersal ability among connected habitats compared to passive aquatic dispersers and were significantly associated with more connected lakes in our analysis. However, our hypotheses regarding feeding type were not upheld. Contrary to our expectations and results from other studies (Zilli et al. 2008, Gallardo et al. 2014) we did not find a relationship between invertebrate predators and connectivity. We did not sample for fish, but small fish (e.g. nine-spine stickleback) were observed even in highly isolated lakes so assumptions about the absence of fish in isolated lakes were incorrect (although large sport fish, abundant in connected lakes, were absent in isolated lakes). Collector-gatherers were associated with isolated lakes and predators did not significantly differ among lake closure types or along the primary axis of community variation. The vast majority of collector-gatherers in our data set were aerial dispersers, so dispersal mode was likely to override feeding type as a significant factor regardless of response to food abundance.

Using a combination of approaches (variation partitioning, species occurrence patterns, fourth corner analysis of traits), we found dispersal dynamics related to the hydrological connectivity of lakes and the dispersal abilities of taxa to be the main factor structuring benthic invertebrate metacommunities across the Mackenzie River Delta. These results concur with many other studies of benthic invertebrates in floodplain systems (Gallardo et al. 2008, Obolewski 2011, Zilli & Marchese 2011, Starr et al. 2014, Petsch et al. 2017, Dube et al. 2019) including a comparison of watersheds across different climatic regions from temperate to tropical (Gallardo et al. 2014). Here we demonstrated the importance of lake connectivity and dispersal mode in an Arctic watershed in which permanent water bodies are connected for a brief annual period in a flooding process driven by climate-mediated ice jam dynamics. Aerial dispersers were able to selectively colonize suitable habitat with no evidence of spatial dispersal limitation, whereas aquatic dispersers were more limited by dispersal opportunities determined by the degree of lake isolation. We found very little explicit spatial variation in benthic communities, which may be explained by a high degree of faunal mixing during the flooding period and by aerial dispersal over the summer. Most of the taxa we observed are widespread across northern Canada, and likely colonized quickly following deglaciation. Over geographical time periods these species would have the opportunity to disperse throughout the upper Delta, similar to patterns observed for native fish metacommunities (Sharma et al. 2011). We also limited our observations to lakes within the subarctic vegetation region of the upper Delta; had we sampled lakes in the tundra region, differences among ecoregions would have produced stronger spatial patterns.

The relationship between connectivity and metacommunity structure has important implications for conservation, particularly in a floodplain as sensitive to climatic change as the Mackenzie Delta. Local spring warming has been driving trends towards earlier ice breakup, leading to a shortened period of flooding (Lesack et al. 2014). Combined with expected sea level rise, this climate-driven change may result in decreased connection times in highly isolated lakes and increased connection times in lower elevation lakes (Lesack & Marsh 2007). These changes may result in the disappearance of many highly isolated lakes due to evaporation in the absence of water renewal (Marsh & Lesack 1996) and increased ecological similarity among the connected and low-elevation isolated lakes (Lesack & Marsh 2007, Thomaz et al. 2007). Increased evaporation in northern regions has been attributed to decreases in ice and snow cover, earlier stratification, and increased surface albedo (Woolway et al. 2020), and decreasing peak flood levels is likely to add to these factors in isolated Mackenzie Delta lakes. The desiccation of previously permanent lakes in the High Arctic has been linked to increase evaporation/precipitation ratios over recent periods (Smol & Douglas 2007), representing the extreme possible outcome for lakes in the Delta. The net result of losses in high elevation, highly isolated lakes and increased connectivity in low elevation lakes is likely to be a decrease in habitat heterogeneity (Lesack & Marsh 2010). Our results suggest that the current hydrological diversity of lakes in the Mackenzie Delta is vital in structuring invertebrate metacommunities, and therefore in maintaining current levels of biodiversity in the Delta. Losses of highly isolated lakes, and the heterogeneity they provide (Lesack & Marsh 2010), may result in the loss of suitable habitat for many aerial dispersing aquatic insects. In contrast, increased connectivity among low elevation lakes may increase ecological similarity and biotic homogenization, with the net result of a loss of biodiversity. Monitoring strategies in the Mackenzie Delta and other Arctic deltas affected by climate change should therefore focus on the range of natural hydrological connectivity on a region-wide scale.

Acknowledgments

This work was supported by an NSERC Discovery Grant and Northern Research Supplement to R.Q. and SS, and conducted under Scientific Research License 15652 from the Aurora Research Institute. We thank Suzanne Tank (University of Alberta), Jolie Gareis and William Hurst (Aurora Research Institute), and Andrew Medeiros, Cait Carew, and Francesco Talarico (York University) for advice and field support. We are grateful to Xiaowa Wang and Derek Muir (Canadian Centre for Inland Waters) for water chemistry analysis.

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Tables and Figures

Table 1 – Traits used in fourth corner analysis.

Trait	Modalities
Dispersal Mode (DM)	Aerial dispersers
	Aquatic dispersers
Functional Feeding Group (FFG)	Collector-filterer (Collector-F)
	Collector-gatherer (Collector-G)
	Predator
	Scraper
	Shredder
Habit	Burrower
	Climber
	Sprawler
	Swimmer

Table 2 – Sample size, benthic invertebrate richness, and % aerial dispersers for the three sampling and regions and lake closure types within the upper Mackenzie Delta.

	Upper Delta	**East Channel**	**Central Channel**	**West Channel**
Sites				
All lakes	23	10	5	8
Highly isolated	12	6	3	3
Isolated	6	2	1	3
Connected	5	2	1	2
Richness				
Total	207	162	128	169
Average (SD)	73.6 (14.5)	73.0 (14.3)	64.4 (10.8)	80.3 (14.9)
By lake type: total (% aerial dispersers)				
Highly isolated	166 (69.9%)	137 (69.3%)	103 (65.0%)	126 (68.2%)
Isolated	152 (68.4%)	111 (70.3%)	47 (55.3%)	126 (67.5%)
Connected	153 (67.3%)	106 (64.1%)	64 (56.3%)	114 (63.2%)

Table 3 – Metacommunity structure of Mackenzie Delta macroinvertebrate communities along the first and second axes of variation. Indices for the tests are *z*-scores for coherence (number of embedded absences relative to those expected at random) and turnover (number of species replacements relative to those expected at random), and Morista (1971)'s index (degree of clumping along the ordination axis compared to a null model) for clumping. Significant results ($\alpha = 0.05$) are in bold.

		Total community		**Aerial dispersers**		**Aquatic dispersers**	
		Index	*p*	Index	*p*	Index	*p*
Axis 1	Coherence	**-2.052**	**< 0.001**	**-2.211**	**< 0.001**	**-7.142**	**< 0.001**
	Turnover	**2.526**	**0.011**	**4.596**	**< 0.001**	-0.841	0.400
	Clumping	**1.594**	**< 0.001**	**3.122**	**< 0.001**	**2.154**	**< 0.001**
	Best fit	Clementsian gradient		Clementsian gradient		Nested subset quasi-structure with clumped species loss	
Axis 2	Coherence	**-1.415**	**< 0.001**	**-1.119**	**< 0.001**	**-6.960**	**< 0.001**
	Turnover	**3.453**	**< 0.001**	**3.064**	**0.002**	0.552	0.581
	Clumping	**2.763**	**< 0.001**	**2.341**	**0.001**	**2.462**	**< 0.001**
	Best fit	Clementsian gradient		Clementsian gradient		Quasi-Clementsian gradient	

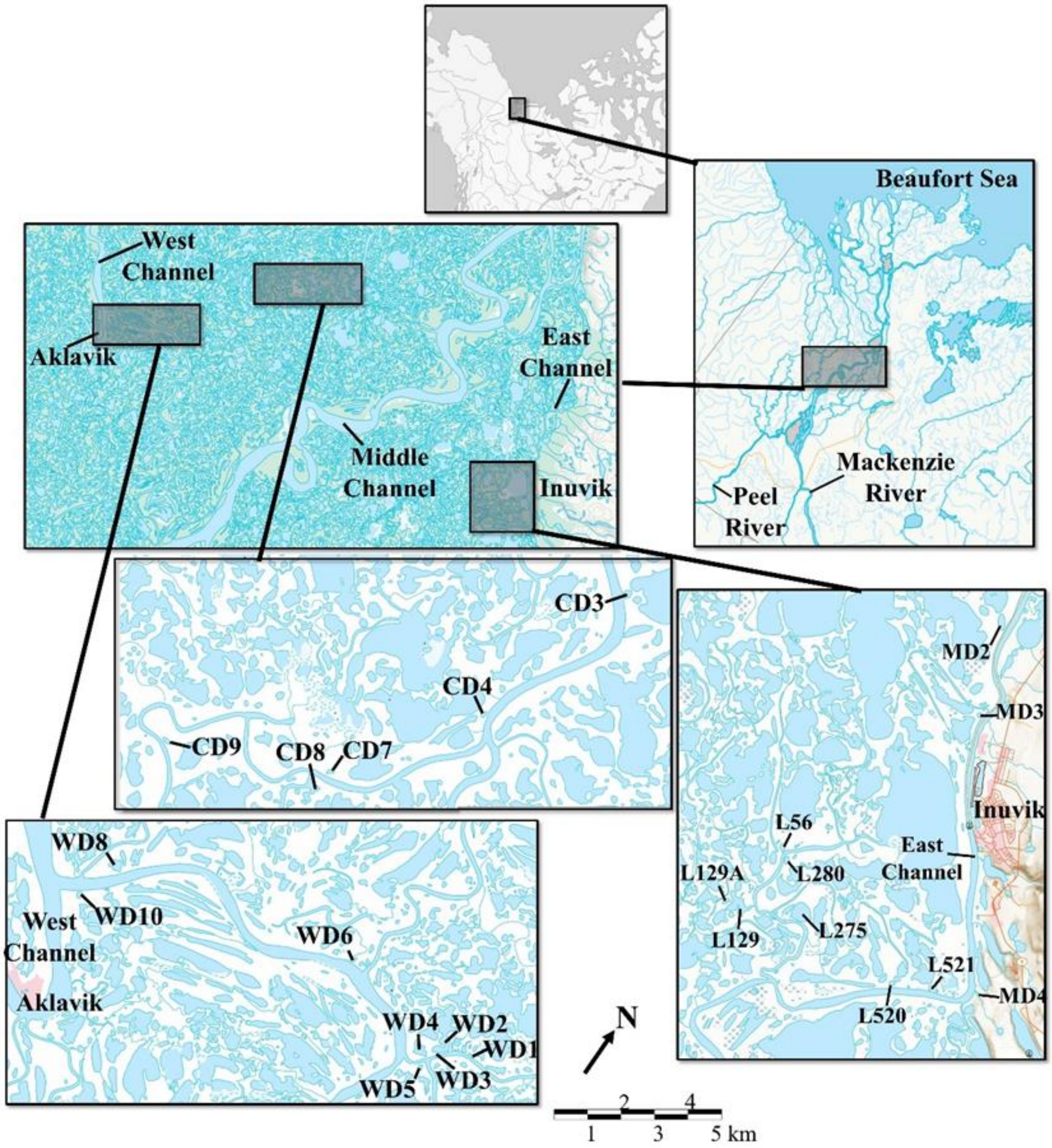


Figure 1 – Map of the Mackenzie Delta showing the East, Middle, and West Channel sampling area and the sites. Scale applies to the study area maps only.

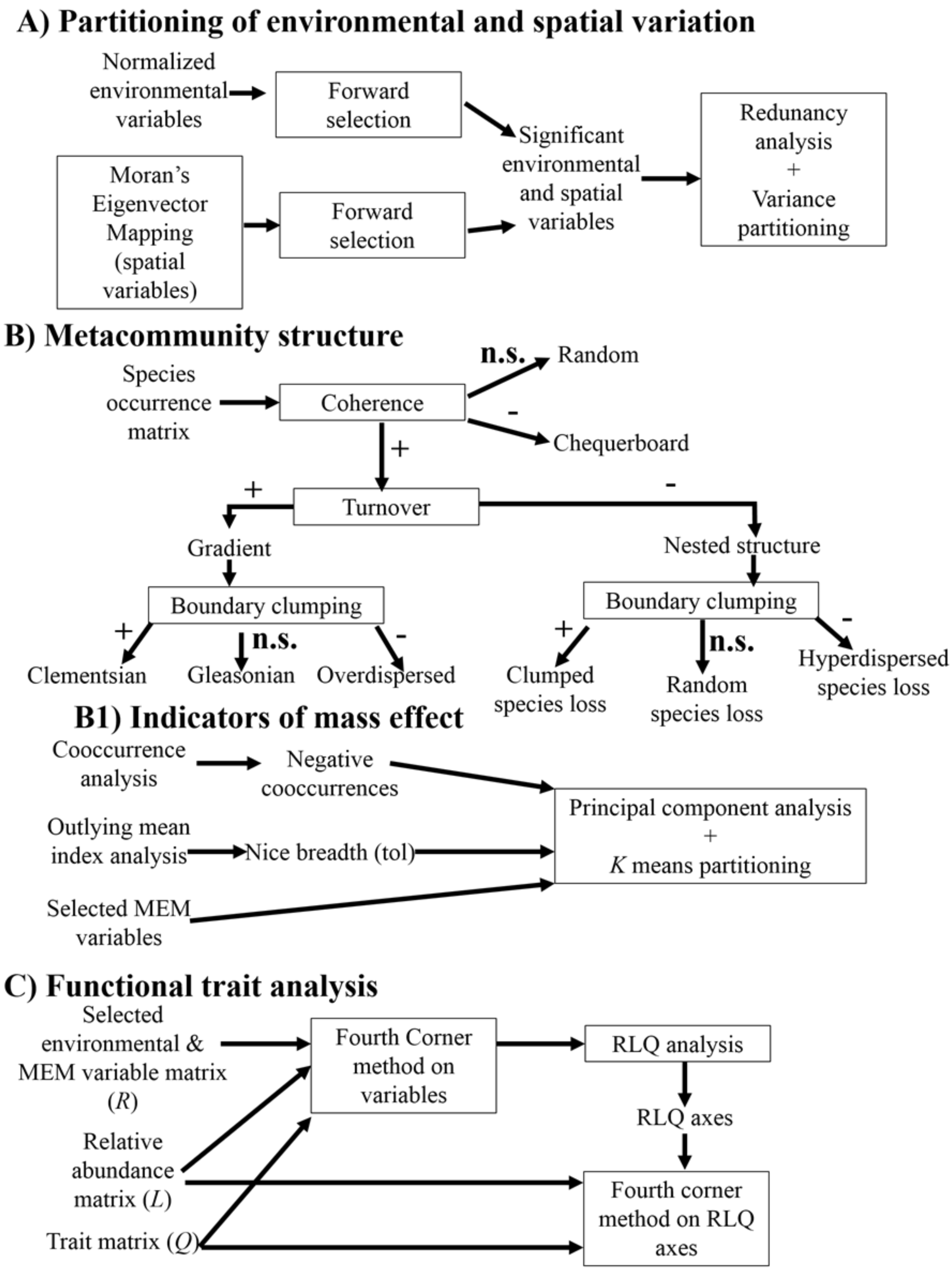


Figure 2 – Flow diagram of statistical analyses. In (1) forward selection, redundancy analysis and variation partition were performed using Hellinger transformed species abundance. Analyses are in rectangles.

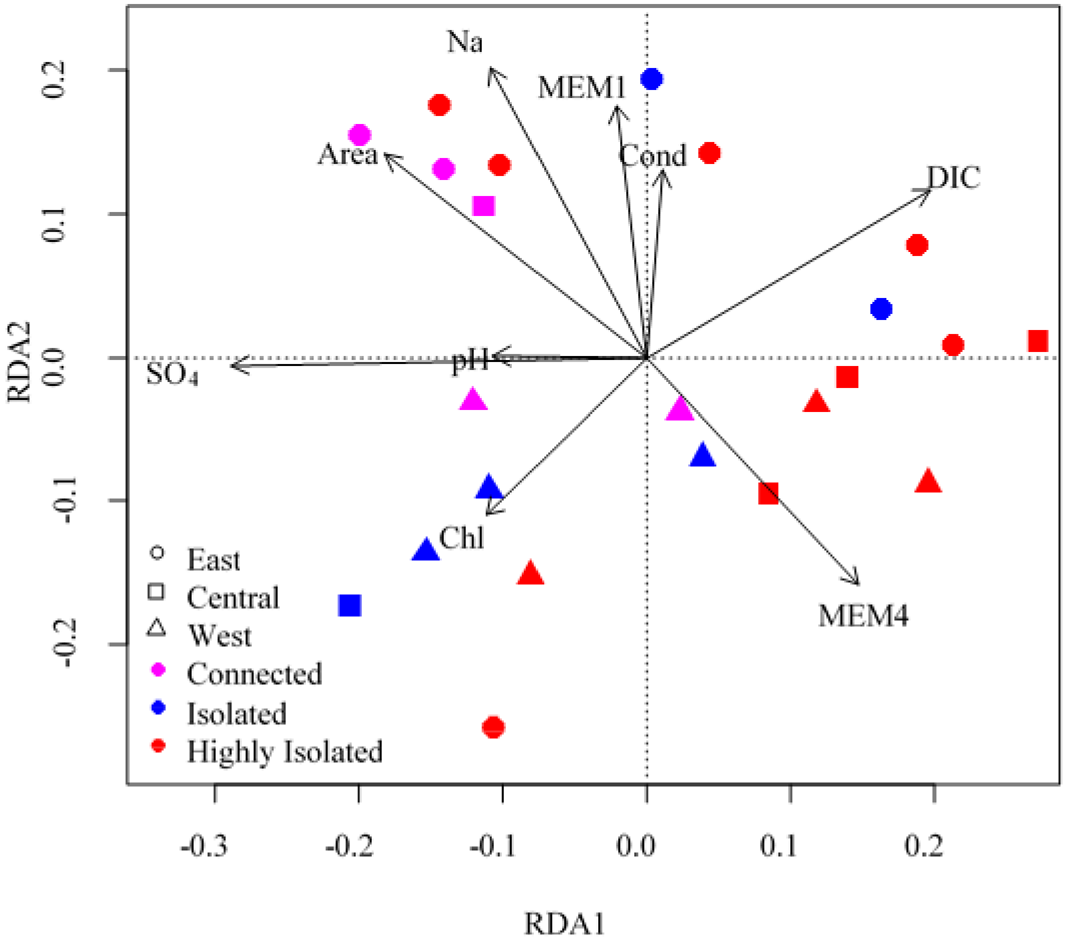


Figure 3 – Redundancy analysis ordination of Hellinger-transformed benthic abundance constrained by forward-selected environmental and spatial (MEM1, MEM4) variables showing sites labelled by region (shapes) and lake closure type (colours). The RDA explained 28.9% (adjusted R^2) of variation. The first axis is associated with environmental variables related to lake closure (SO_4, DIC) while the second axis is related to conductivity, Na, and spatial variables. Variance partitioning indicated that the spatial variables independently explained little (2%) of the variation in assemblage composition, while 23 % of variation was explained the environmental variables.

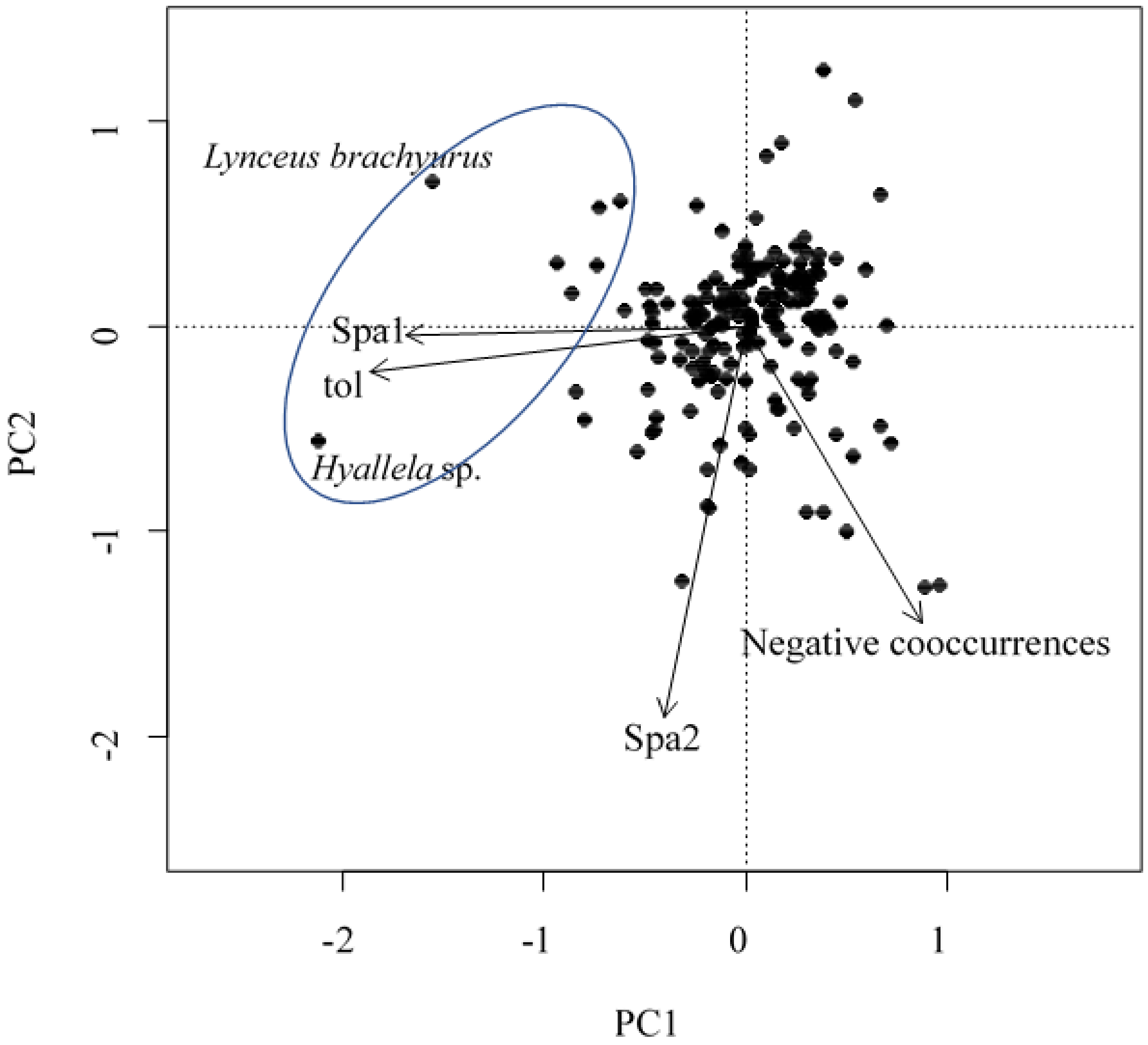
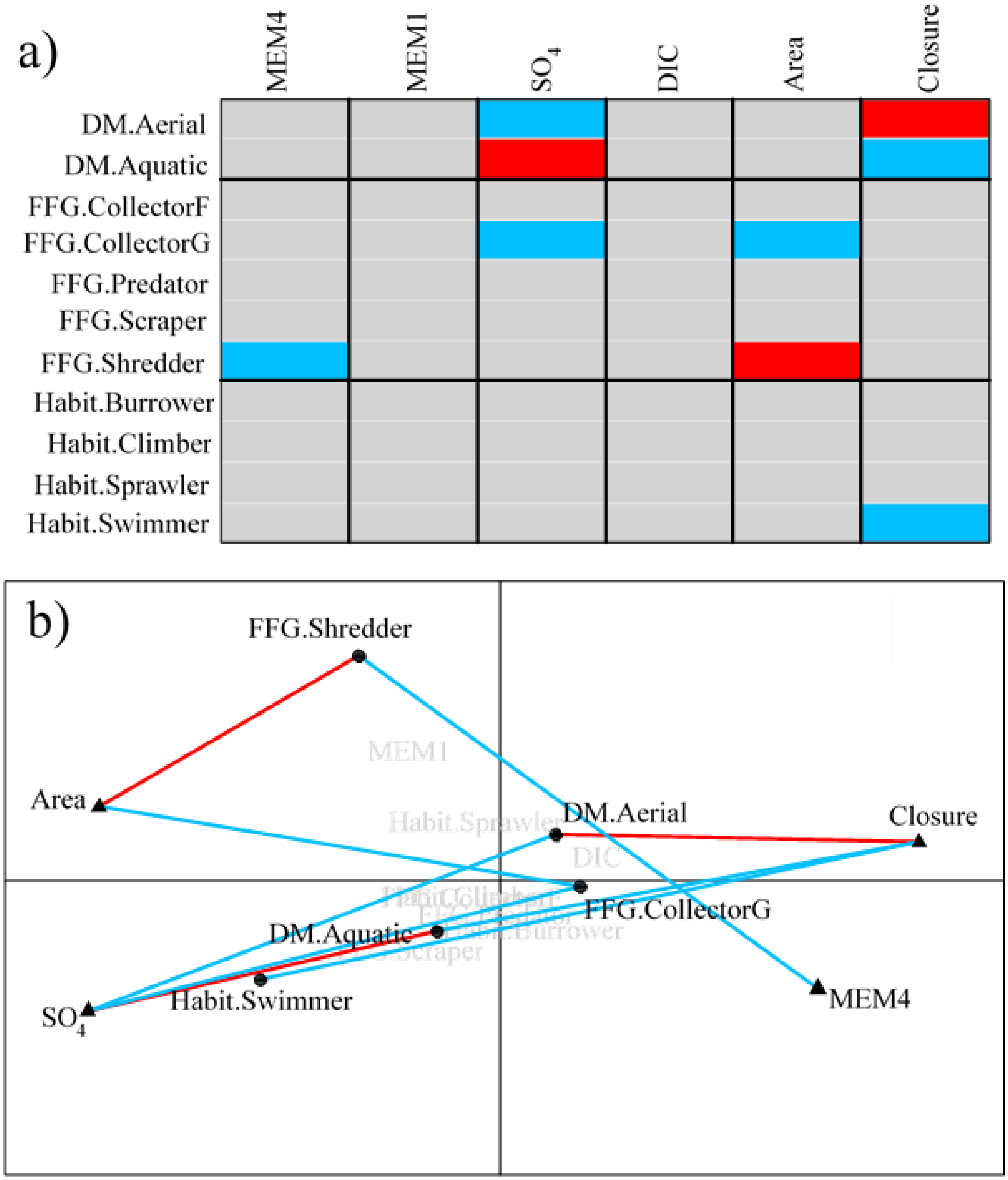


Figure 4 – Principal component analysis of taxa characteristics indicating likely influence of mass effects (where species occupy suboptimal sites due to high dispersal rates). Taxa with low negative cooccurrence, average to low niche breadth (represented by tol values), and high correlation to spatial variables are likely subject to mass effect. Spa1 and Spa2 are the species loadings from an RDA of the forward-selected spatial variables. The ellipse contains taxa grouped together by *k* means clustering and identified as susceptible to mass effect. Only taxa highlighted in the text are labelled.



	MEM4	MEM1	SO_4	DIC	Area	Closure
DM.Aerial			🟦			🟥
DM.Aquatic			🟥			🟦
FFG.CollectorF						
FFG.CollectorG			🟦		🟦	
FFG.Predator						
FFG.Scraper						
FFG.Shredder	🟦				🟥	
Habit.Burrower						
Habit.Climber						
Habit.Sprawler						
Habit.Swimmer						🟦

Figure 5 – Results of Fourth Corner tests (a) and RLQ ordination (b) showing significant relationships between species traits and environmental and spatial (MEM) variables. Significant associations are shown with lines linking a trait to an explanatory variable. Red indicates significant positive associations and blue indicates significant negative associations. The first axis shows aquatic dispersers and swimmers associated with large, connected lakes with high SO_4 and aerial dispersers and collector-gatherers associated with small, isolated lakes.

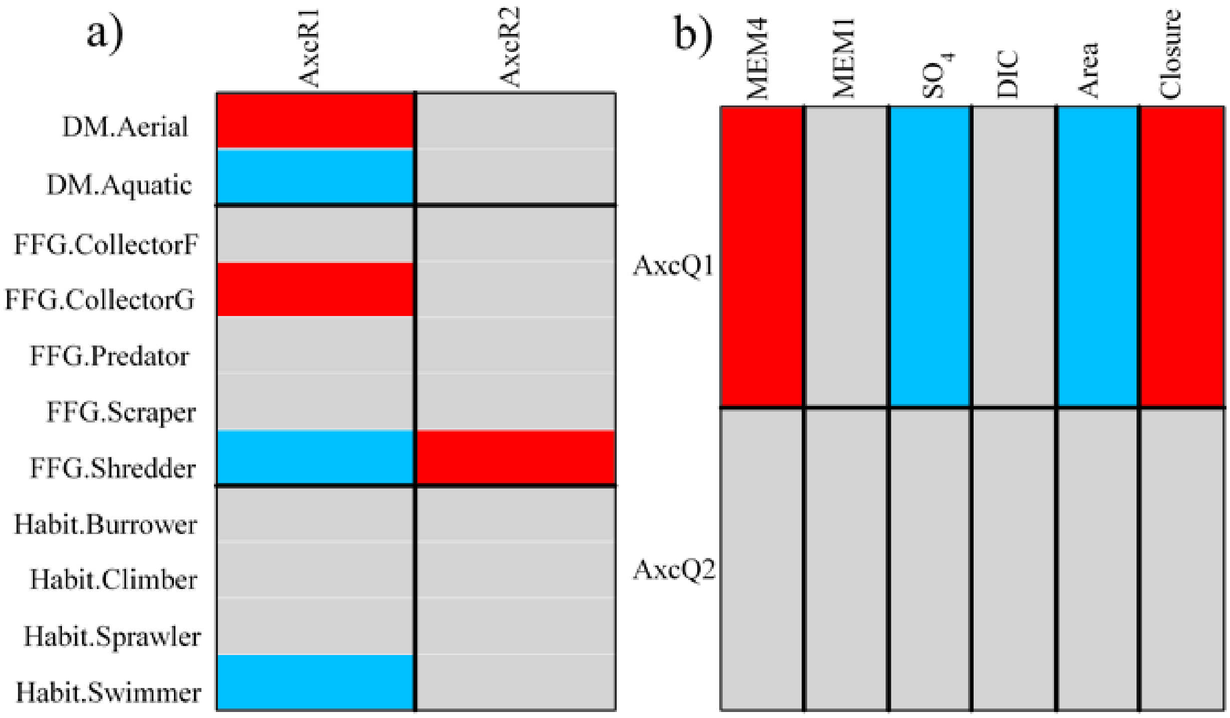


Figure 6 – Combined RLQ and Fourth Corner analyses showing significant relationships of a) traits and b) environmental and spatial variables with the main axes of variation of the RLQ ordination (AxcQ1 and AxcQ2). Red indicates significant positive relationships and blue indicates significant negative relationships.

General Conclusion

Changing flooding hydrology has widespread impacts on the limnology and littoral benthic invertebrate communities of lakes within the Mackenzie River Delta, Northwest Territories. Freshwater in northern regions is increasingly under threat from multiple stressors, including accelerating climate change and permafrost thaw (Reid et al. 2019). However, efforts to consistently monitor freshwater ecosystems in the Arctic regions must be increased and improved in order to understand the magnitude and direction of changes occurring in these systems and to provide scientific guidance to conservation efforts (Heino et al. 2020). This thesis demonstrated differences in lake water chemistry (Chapter 1) and benthic assemblages (Chapter 2) among lakes of varying degrees of isolation, and responses in these variables to variation in peak annual flood level. I suggested that lake connectivity, which is expected to be affected by climate change given more variable discharge and higher spring air temperatures, can be effectively monitored using benthic macroinvertebrates, a heretofore understudied component of the Mackenzie Delta freshwater ecosystem. I further demonstrated how the benthic macroinvertebrate metacommunity structure (Chapter 3) is shaped by the degree of connectivity (or isolation), to a large degree by differences in dispersal mode among species, suggesting the importance of habitat diversity in maintaining regional biodiversity, an important goal for conservation efforts. Taken together, these results show the importance of hydrological connectivity to the structure and function of lake ecosystems in Arctic river delta environments, and suggest how further study of the macroinvertebrate communities in this and other Arctic deltas can aid efforts at monitoring and conservation during the current period of rapid environmental change.

In Chapter 1, I demonstrated differences in lake surface water chemistry in lakes along a connectivity gradient over five years, a time span which fortuitously captured recent extreme highs and lows in peak flood level. Differences among lakes in variables directly attributable to flooding or isolation were apparent according to the degree of isolation of the lake, in similar ways to previous work (Lesack et al. 1998). I further showed that responses to lake variation among years with different peak flood were largely limited to isolated lakes at low elevations above the channels and indicate a negative relationship between the productivity of rooted macrophytes and the duration of connection between the lake and river. This chapter established the importance of connectivity in structuring the habitat template for invertebrates and suggested potential implications for the carbon balance of the Delta under expected climate change trajectories (Scott et al. in review).

In Chapter 2, I showed that littoral benthic macroinvertebrate assemblages were significantly related to the environmental gradients identified in Chapter 1, and so were also influenced by hydrological connectivity. Environmental variables were predictive of taxonomic composition at the family and genus levels, demonstrating the utility of macroinvertebrate-based biomonitoring for assessing ecological change due to climate-induced alterations of the flooding regime. I observed the loss of taxonomic richness following drainage of one isolated lake, suggesting one trajectory of change for these habitats. Family identification was sufficient to establish environment-assemblage relationships, improving the utility of a rapid biomonitoring program in the Delta. However, genus level identification provided additional ecological information and allowed observation of rare taxa, such as the chironomid *Propsilocerus* (Scott et al., 2020).

In Chapter 3, I assessed the metacommunity structure of benthic macroinvertebrates in lakes of varying degrees of isolation located across the longitudinal breadth of the Delta. Environmental relationships were far more important than spatial structuring in determining benthic macroinvertebrate composition, suggesting most variation among lakes is due to environmental filtering rather than spatial structuring. However, analysis of the metacommunity structure of aquatic dispersers suggested a greater degree of dispersal limitation, and an association with more connected lakes, than the metacommunity of aerial dispersing insects. These results suggest efforts at freshwater biodiversity conservation in the Delta should have a goal of conserving a sufficient range of diversity in lake habitats, especially a range of lake isolation.

Future research could expand on the findings of this thesis by expanding the spatial and temporal scale and incorporating additional important factors, including those outlined below. While studies of benthic macroinvertebrate responses to connectivity gradients have been conducted in several temperate and tropical regions, the studies in this thesis are among the few to examine them in Arctic deltaic floodplains. Ice jam flooding is a common feature of north-flowing rivers in northern latitudes, and connectivity is likely to be an important factor shaping community and metacommunity structure in many river floodplains and deltas in the circumpolar

Arctic. The responses found in the five-year time series of water chemistry and invertebrates in this thesis demonstrated the importance of incorporating temporal variation into ecological studies. However, this time scale does not address long-term variation in flooding and connectivity or in benthic communities. Paleolimnological analysis of chironomid subfossil assemblages could shed light on the long-term impacts of altered connectivity and responses to historical changes. Incorporating additional proxies (e.g., diatoms) could also provide links to the gradients in primary productivity and responses in lake function to long-term environmental changes. While some lakes in this thesis are fairly well-studied (e.g., L520), important factors such as permafrost and winter ice cover were lacking. Incorporating these factors into models of benthic composition, for example using remote sensing data on ice cover, could provide additional information on the importance of these environmental factors and community sensitivity to climate change. Finally, establishment of a biomonitoring program is a feasible goal for organizations interested in conserving the ecological health of lakes in the Mackenzie Delta. Such a program could rely on a rapid biomonitoring protocol using family level identification to allow for greater numbers of sites (in particular low-elevation isolated, or no closure, lakes), and could be largely limited to accessible regions of the Delta due to the lack of large-scale spatial structuring. Due to the importance of freshwater processes in the Delta to surrounding regions of the Arctic Ocean, the importance of freshwater habitats and aquatic resources to the Gwich'in and Inuvialuit peoples that inhabit the Delta, and the importance of aquatic production to other important wildlife such as migratory birds, it is vital to monitor current conditions of freshwater ecosystems and their underlying ecological processes in this important and rapidly changing region.

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Appendices

Appendix A – Supplementary information for Chapter 1

Table A1 – Water quality parameter (particulates, nutrients, and major ions) mean values by closure type, with results of ANOVAs between closure types. Asterisks (*) denote variables with significant differences in closure type ($p < 0.05$).

Row	**Units**	**High**	**Low**	**No**	**Channel**	**Transform.**	***F***	***p*(adj)**
POC	µg/L	579	795	492	n/a	log	0.668	0.623
PON	µg/L	49.9	59.8	57.4	n/a	log	0.987	0.510
F^-	mg/L	0.101	0.092	0.0856	0.1		7.33	$6.09x10^{-3}$ *
Cl^-	mg/L	6.33	4.59	6.41	6.09	sqr	2.11	0.216
SO_4^{2-}	mg/L	13.9	16	26.9	44.6		7.09	$6.44x10^{-3}$ *
Ca^{2+}	mg/L	19.7	42.7	35.6	36.3	sqr	27.4	$1.02x10^{-6}$ *
K^+	mg/L	0.706	0.955	1.17	0.82		3.53	0.0787
Mg^{2+}	mg/L	12.4	11.8	9.33	10.1		4.19	0.0494 *
Na^+	mg/L	6.16	5.93	6.58	6.48		0.513	0.638
Si	mg/L	0.684	0.865	1.81	3.77	log	8.30	$3.50x10^{-3}$ *
DOC	mg/L	12.5	9.43	10.8	6.29	log	0.881	0.534
DIC	mg/L	18.3	33.2	23.3	n/a		10.1	$1.25x10^{-3}$ *
NH_4^+	µg/L	19	12.2	21.4	8.13	log	0.498	0.638
SRP	µg/L	0.508	0.41	0.733	n/a	log	2.13	0.216
ChlA	µg/L	1.14	0.92	1.42	1.73	log	0.606	0.629
Temp	deg C	15.7	15.9	17	17.7		1.09	0.488
Cond	uS/cm	179	258	236	275		14.4	$1.09x10^{-4}$ *
DO	mg/L	13.6	12.8	10.4	9.24		5.23	0.0237 *
pH		9.52	8.35	8.38	8.01		19.9	$1.44x10^{-5}$ *
NO_3^-/NO_2^-	µg/L	21.4	17.3	15.1	88.5	log	0.353	0.705
TKN	µg/L	550	456	352	320		17.0	$3.22x10^{-5}$ *
DON	µg/L	481	384	273	253		18.7	$1.82x10^{-5}$ *
TPP	µg/L	8.74	11	8.73	73.1	log	2.44	0.186
TDP	µg/L	15.2	17	13.5	5.52	log	1.11	0.488

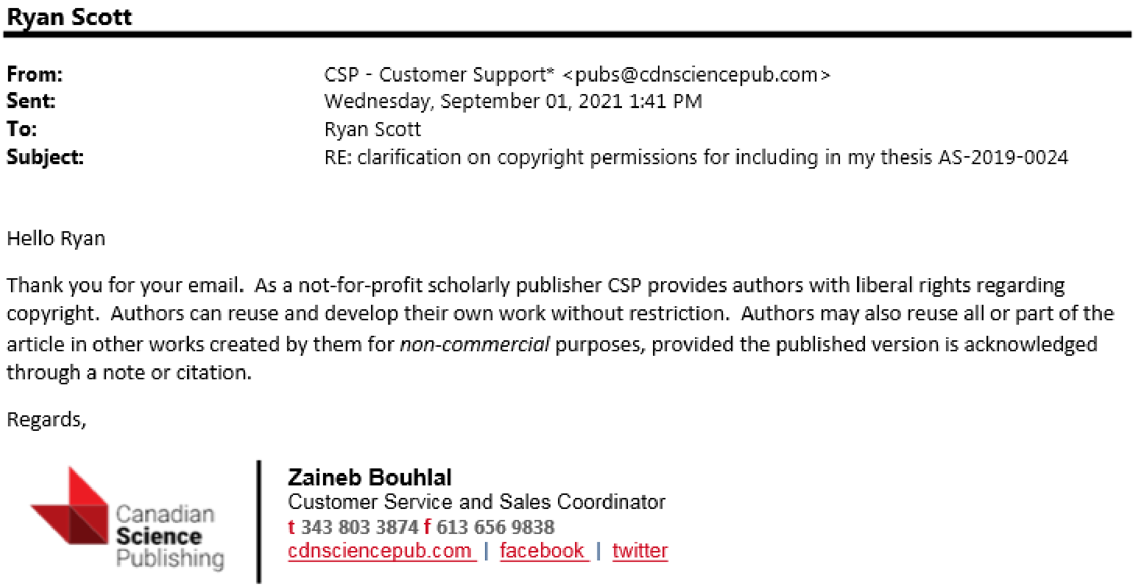
Table A2 – Trace metal mean values by closure type, with results of ANOVAs between closure types. Asterisks (*) denote variables with significant differences among closure types ($p < 0.05$).

Row	**Units**	**High**	**Low**	**No**	**Transform**	***F***	***p*(adj)**
Ag	µg/L	0.0072	0.0067	0.00644	log	0.03	0.97
Al	µg/L	67.2	33	28.8	log	1.17	0.725
As	µg/L	0.975	0.984	1.06	log	0.72	0.733
B	µg/L	10.8	13.7	13.4		4.05	0.121
Ba	µg/L	82	126	79.3	log	7.77	0.0107 *
Be	µg/L	0.00464	0.0036	0.00489	log	0.199	0.862
Bi	µg/L	0.0032	0.0021	0.00389	log	0.651	0.733
Cd	µg/L	0.0316	0.0127	0.0168	log	1.18	0.725
Ce	µg/L	0.0836	0.0511	0.062	log	0.499	0.733
Co	µg/L	0.132	0.0828	0.0732	log	4.57	0.0902
Cr	µg/L	0.286	0.521	0.18	log	0.673	0.733
Cs	µg/L	0.0146	0.0107	0.00889	log	0.467	0.733
Cu	µg/L	1.44	0.968	1.85	sqr	2.6	0.337
Fe	µg/L	299	285	306	log	0.632	0.733
Ga	µg/L	0.0513	0.0415	0.0274	sqr	1.35	0.706
Ge	µg/L	0.0104	0.011	0.01	log	0.541	0.733
In	µg/L	0.004	0.0051	0.00578	log	0.282	0.842
La	µg/L	0.041	0.0265	0.0323	log	0.454	0.733
Li	µg/L	5.42	5.6	4.26		9.83	4.23x10^{-3} *
Mn	µg/L	13.7	13.1	12	log	0.61	0.733
Mo	µg/L	0.935	0.74	1.04		1.12	0.725
Nb	µg/L	0.00336	0.002	0.00256	log	0.719	0.733
Ni	µg/L	0.986	1.41	1.36	sqr	3.47	0.176
Pb	µg/L	0.129	0.0835	0.0923	log	1.48	0.706
Pt	µg/L	0.00516	0.0038	0.00678	sqr	0.632	0.733
Rb	µg/L	0.616	1.86	1.51	sqr	19.6	2.05x10^{-5} *
Sb	µg/L	0.0917	0.0758	0.0981		1.07	0.725
Sc	µg/L	0.026	0.04	0.03	log	0.7	0.733
Se	µg/L	0.125	0.117	0.21		8.46	8.18x10^{-3} *
Sn	µg/L	0.0511	0.054	0.0358	sqr	0.692	0.733
Sr	µg/L	146	230	195		33.3	9.97x10^{-8} *
Ti	µg/L	0.986	0.7	0.489	log	0.53	0.733
Tl	µg/L	0.0022	0.0021	0.00389	sqr	2.17	0.422
U	µg/L	0.218	0.258	0.412		5.85	0.0377 *
V	µg/L	0.433	0.28	0.273		1.4	0.706
W	µg/L	0.00452	0.0025	0.00567	sqr	2.15	0.422
Y	µg/L	0.0523	0.0425	0.056	log	0.195	0.862
Zn	µg/L	3.5	2.56	3.49	log	0.452	0.733
Zr	µg/L	1.11	1.15	1.2	sqr	0.175	0.862

Table A3 – Composition of trace metals in lakes, with comparison with main channel. Asterisks (*) denote variables with significant differences between the lakes and the channel ($p < 0.05$).

Row	**Lakes (μg/L)**	**% of total lake TM**	**Channel (μg/L)**	***p*(adj)**	**Channel:Lake**
Ag	0.00693	0.00105	0.12	$2.99\text{x}10^{-20}$ *	17.3
Al	51.6	7.83	2280	$1.08\text{x}10^{-9}$ *	44.2
As	0.995	0.151	1.55	0.00026 *	1.55
B	12	1.82	n/a	n/a	n/a
Ba	91.4	13.9	103	0.298	1.13
Be	0.00445	0.000677	0.14	$8.69\text{x}10^{-22}$ *	31.4
Bi	0.00308	0.000468	n/a	n/a	n/a
Cd	0.0242	0.00368	0.12	$2.2\text{x}10^{-6}$ *	4.95
Ce	0.0661	0.01	n/a	n/a	n/a
Co	0.109	0.0165	1.33	$1.02\text{x}10^{-16}$ *	12.3
Cr	0.318	0.0482	3.34	$1.87\text{x}10^{-11}$ *	10.5
Cs	0.0126	0.00191	0.48	$4.99\text{x}10^{-21}$ *	38.2
Cu	1.42	0.216	4.07	$3.7\text{x}10^{-6}$ *	2.87
Fe	297	45.1	3190	$5.72\text{x}10^{-12}$ *	10.7
Ga	0.187	0.0284	n/a	n/a	n/a
Ge	0.0104	0.00158	n/a	n/a	n/a
In	0.00458	0.000696	n/a	n/a	n/a
La	0.0345	0.00524	n/a	n/a	n/a
Li	5.22	0.793	7.4	$2.79\text{x}10^{-5}$ *	1.42
Mn	13.2	2.01	55.8	$2.2\text{x}10^{-6}$ *	4.21
Mo	0.911	0.138	1.23	0.134	1.35
Nb	0.00288	0.000437	n/a	n/a	n/a
Ni	1.16	0.176	5.26	$3.12\text{x}10^{-11}$ *	4.54
Pb	0.111	0.0169	1.79	$1.15\text{x}10^{-21}$ *	16.1
Pt	0.0651	0.00988	n/a	n/a	n/a
Rb	1.08	0.165	5.39	$1.86\text{x}10^{-8}$ *	4.98
Sb	0.0894	0.0136	0.2	$1.79\text{x}10^{-8}$ *	2.24
Sc	0.0291	0.00443	n/a	n/a	n/a
Se	0.14	0.0213	0.58	$1.46\text{x}10^{-14}$ *	4.13
Sn	0.207	0.0314	n/a	n/a	n/a
Sr	175	26.6	209	0.134	1.19
Ti	0.819	0.124	44.9	$7.19\text{x}10^{-13}$ *	54.8
Tl	0.00252	0.000383	n/a	n/a	n/a
U	0.267	0.0406	0.86	$7.83\text{x}10^{-10}$ *	3.22
V	0.366	0.0555	6.05	$7.86\text{x}10^{-16}$ *	16.6
W	0.0603	0.00916	n/a	n/a	n/a
Y	0.0484	0.00735	n/a	n/a	n/a
Zn	3.28	0.498	15.6	$1.02\text{x}10^{-6}$ *	4.75
Zr	0.962	0.146	n/a	n/a	n/a

Appendix B – Chapter 2 copyright information from Arctic Science



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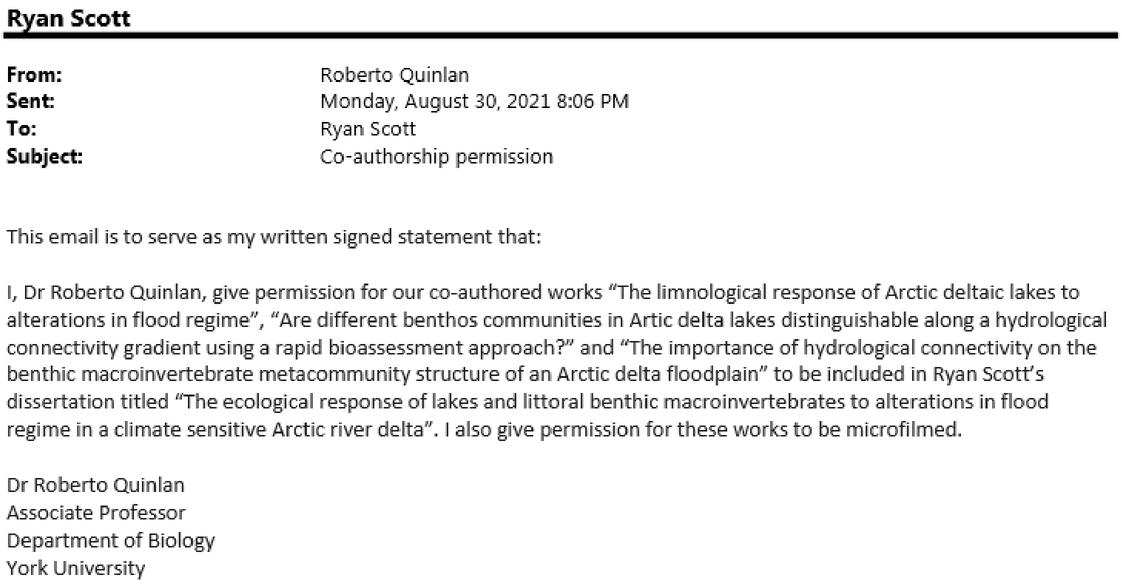

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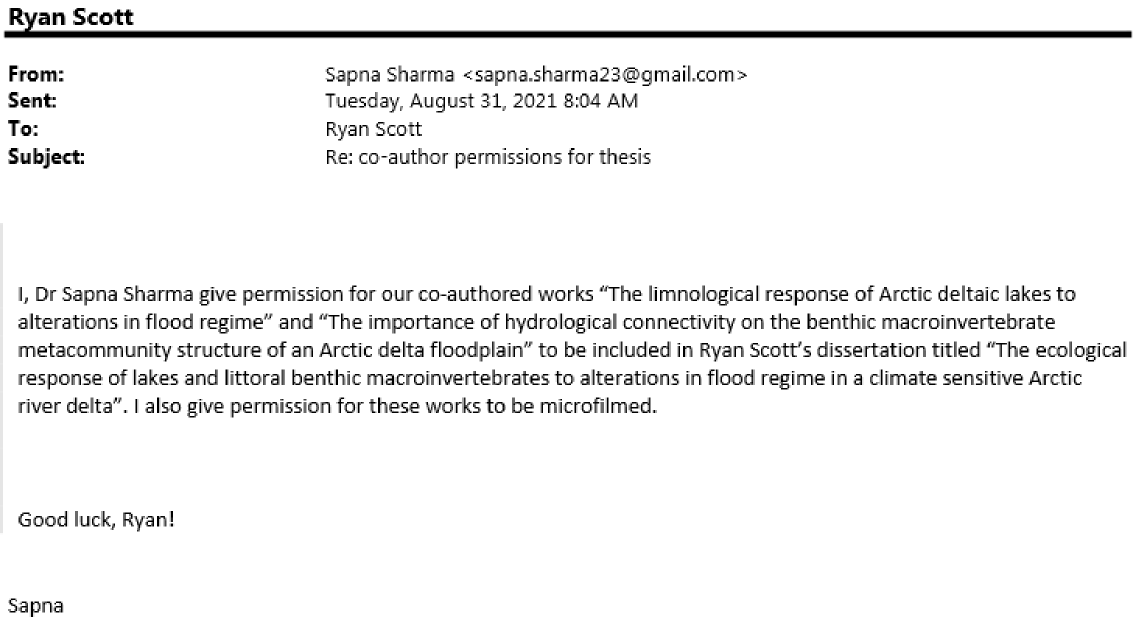
This email is to serve as my written signed statement that:

I, Dr Roberto Quinlan, give permission for our co-authored works "The limnological response of Arctic deltaic lakes to alterations in flood regime", "Are different benthos communities in Artic delta lakes distinguishable along a hydrological connectivity gradient using a rapid bioassessment approach?" and "The importance of hydrological connectivity on the benthic macroinvertebrate metacommunity structure of an Arctic delta floodplain" to be included in Ryan Scott's dissertation titled "The ecological response of lakes and littoral benthic macroinvertebrates to alterations in flood regime in a climate sensitive Arctic river delta". I also give permission for these works to be microfilmed.

Dr Roberto Quinlan
Associate Professor
Department of Biology
York University

Chapters 1 and 3: Dr. Sapna Sharma



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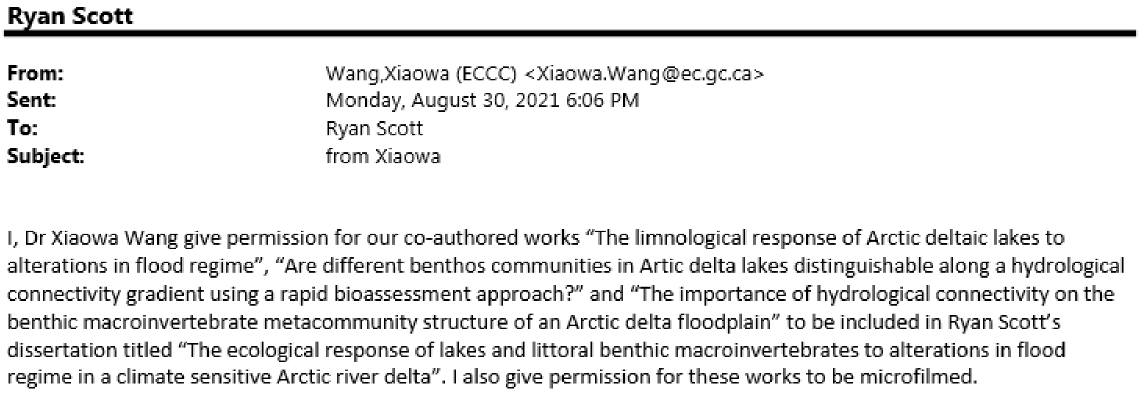
Good luck, Ryan!

Sapna

Chapters 1, 2, and 3: Dr. Xiaowa Wang



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Subject: from Xiaowa

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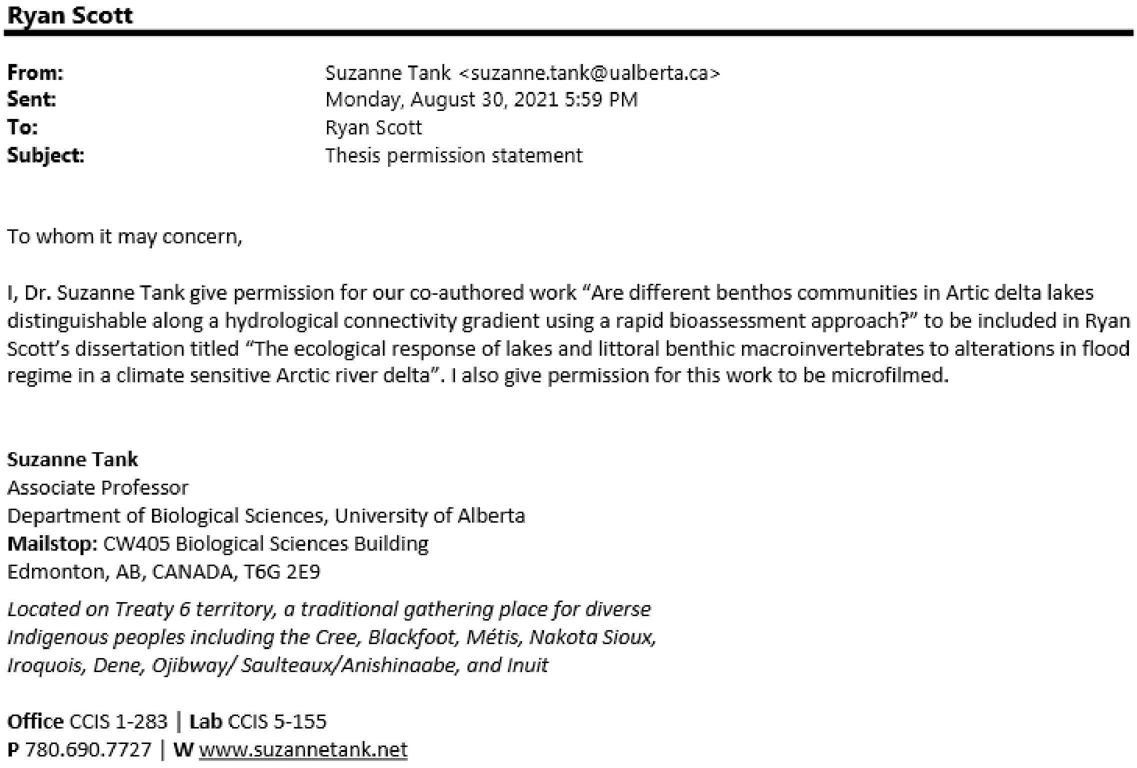

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Subject: Thesis permission statement

To whom it may concern,

I, Dr. Suzanne Tank give permission for our co-authored work "Are different benthos communities in Artic delta lakes distinguishable along a hydrological connectivity gradient using a rapid bioassessment approach?" to be included in Ryan Scott's dissertation titled "The ecological response of lakes and littoral benthic macroinvertebrates to alterations in flood regime in a climate sensitive Arctic river delta". I also give permission for this work to be microfilmed.

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Located on Treaty 6 territory, a traditional gathering place for diverse
Indigenous peoples including the Cree, Blackfoot, Métis, Nakota Sioux,
Iroquois, Dene, Ojibway/ Saulteaux/Anishinaabe, and Inuit

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Appendix C: Candidate's contribution to co-authored work

Statement of Ryan Scott's contribution to co-authored works included in the dissertation titled "The ecological response of lakes and littoral benthic macroinvertebrates to alterations in flood regime in a climate-sensitive Arctic river delta".

Chapter 1: The limnological response of Arctic deltaic lakes to alterations in flood regime

Ryan Scott, Sapna Sharma, Xiaowa Wang, Roberto Quinlan

This chapter has been submitted to Inland Waters as Scott, R. W., Sharma, S., Wang, X., & Quinlan, R. In review. The limnological response of Arctic deltaic lakes to alterations in flood regime. Inland Waters, submitted 5 July 2021.

Candidate's Contribution:

Ryan Scott and Dr. Quinlan conceived of the research ideas, Ryan Scott, Dr. Sharma, and Dr. Quinlan acquired funding, Dr. Wang provided chemical analysis of water samples, Ryan Scott conducted field sampling, analyzed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Inland Waters.

Chapter 2: Are different benthic communities in Arctic delta lakes distinguishable along a hydrological connectivity gradient using a rapid bioassessment approach?

This chapter has been published in Arctic Science as Scott, R. W., Tank, S. E., Wang, X., & Quinlan, R. 2020. Are different benthic communities in Arctic delta lakes distinguishable along a hydrological connectivity gradient using a rapid bioassessment approach? Arctic Science, 6, 463–487. https://doi.org/10.1139/as-2019-0024.

Candidate's Contribution:

Ryan Scott, Dr. Quinlan, and Dr. Tank conceived of the research ideas and study design, Ryan Scott and Dr. Quinlan acquired funding, Dr. Wang provided chemical analysis of water samples, Ryan Scott conducted field sampling, analyzed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Arctic Science.

Chapter 3: The importance of hydrological connectivity on the benthic macroinvertebrate metacommunity structure of an Arctic delta floodplain

This chapter has been submitted to Freshwater Biology as Scott, R.W., Sharma, S., Wang, X., & Quinlan, R. The importance of hydrological connectivity on the benthic macroinvertebrate metacommunity structure of an Arctic delta floodplain. Freshwater Biology, submitted 30 August 2021.

Ryan Scott, Dr. Quinlan, and Dr. Sharma conceived of the research ideas and study design, Ryan Scott, Dr. Sharma, and Dr. Quinlan acquired funding, Dr. Wang provided chemical analysis of water samples, Ryan Scott conducted field sampling, analyzed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and will have the opportunity to give final approval for publication in Freshwater Biology.