EXAMINING THE POTENTIAL EFFECTS OF WATER QUALITY CHANGES ON CHIRONOMIDAE SUBFAMILIES IN SMALL ARCTIC LAKES

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Abstract

Climate change is resulting in permafrost thaw across Canada's Arctic, causing changes in water quality in northern lakes. Chironomids are some of the most abundant macroinvertebrates in northern lakes and represent an important food source for fish. Studies in other regions indicate that chironomids can be affected by water quality variables that are expected to change in response to permafrost thaw, such as calcium, total suspended solids (TSS), and pH. The goal of my study was to examine how chironomid communities in Arctic lakes might respond to water quality changes associated with permafrost thaw. I used samples of chironomid larvae that were collected from 20 lakes in the Gwich'in and Inuvialuit regions of the Northwest Territories and identified the larvae to the subfamily level. I then constructed multiple regression models to determine the environmental characteristics most strongly associated with differences in the abundance of chironomid subfamilies among my lakes. My multiple regression analysis for the four most abundant chironomid subfamilies - Chironominae, Orthocladiinae, Tanypodinae, Diamesinae - explained between 33-69% of the variation in abundance among lakes. Interestingly, the most parsimonious models contained variables expected to be affected by permafrost thaw, including TSS, calcium, turbidity, chlorophyll-a, and total phosphorus. I used data from the literature to determine the potential responses of lake water quality to permafrost thaw, along with my multiple regression models to examine how changes in water quality related to permafrost thaw might influence chironomids. Projections based on my models suggest that Chironominae abundance will significantly decrease while Diamesinae, Orthocladiinae and Tanypodinae will increase in abundance. Further research will be needed to determine if changes in the relative abundance of chironomids may affect food webs in Arctic lakes.

Key words: Chironomidae, permafrost thaw, Mackenzie Delta, lakes, Arctic, climate change

Contents

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Introduction

Changing Northern Environment

The environmental changes occurring in Canada's Arctic are having a profound effect on northern lakes and rivers. The warming climate is leading to the loss of permafrost – ground that is typically frozen year-round. As the permafrost thaws, it results in increased conductivity and total suspended solids (TSS) in the lakes (Houben et al. 2016). In addition to changes caused by permafrost thaw, the development of infrastructure can affect lake water quality. Calcareous road dust from highways can drift in the wind or runoff during rain events, causing increases in conductivity, pH, alkalinity, calcium, and magnesium levels (Houben et al. 2016).

In addition to changes in water quality caused by permafrost thaw and infrastructure development, warming temperatures are likely to significantly alter lake ecosystems. As air temperatures rise, water temperatures are also significantly increasing (Gunter 2017). As lake and air temperatures increase, lakes lose seasonal ice cover, resulting in earlier warming of the lake in the spring and later freezing in the fall because of less reflectivity from the snow (Comiso et al. 2008). The changing temperatures can also affect thermal habitat in lakes, as warming temperatures can result in stronger temperature stratification in lakes (Blais et al. 2017). In most temperate zone lakes, warmer, less dense water layer called the epilimnion floats over a colder denser water mass called the hypolimnion during the summer. A warmer epilimnion is lighter which results in less mixing of the bottom and top water. This can cause nutrient depletion in the epilimnion as nutrients lost to the hypolimnion cannot be mixed back into the surface waters (Charlton 1980). On the other hand, the hypolimnion can become starved of oxygen as organic matter decomposes in the hypolimnion consumes oxygen that cannot be recharged due to the lack of mixing.

The changes in water quality in northern lakes may cause significant changes in the organisms inhabiting them, including the macroinvertebrates. The composition of macroinvertebrates in the lakes can be affected by water quality and physical parameters such as type of substrate. Gastropoda, Odonata and Trichoptera are most abundant in lakes with high macrophyte biomass (Weatherhead and James 2001). Oligochaeta, Chironomidae and Gastropoda are most abundant in lakes with fine substrate (Weatherhead and James 2001). In eutrophic lakes, abundance of organisms often increases overall (Hayden et al. 2017). Using taxon-environment relationships, a study by Cohen et al. (2020) predicted that macroinvertebrate abundance would decline in response to permafrost thaw and road development, but that taxon diversity would increase (Cohen et al. 2020). Unfortunately, the taxonomic resolution of the work by Cohen et al. (2020) was limited to the class and family level, limiting their ability to predict how changes might occur at lower taxonomic levels. For example, chironomids often exhibit variation in responses to environmental characteristics below the family level (Cortelezzin et al. 2020).

Chironomidae

Chironomids are one of the most abundant types of macroinvertebrate in northern ecosystems. Chironomids are commonly called midges, and they are mosquito-like insects that are found in almost every region of the world. In many aquatic ecosystems, midges represent up to 50% of the total macroinvertebrate species recorded (Armitage et al. 1995).

Adult midges can be pollinators and are an important food source for birds, bats and other insect eating organisms (Monckton 2020). They are members of the order Diptera and their suborder is Nematocera, meaning they undergo complete metamorphosis. They have four life stages: egg, larvae, pupa, and adult. Most midges have four larval instars before becoming a pupa (Salmenlin et al. 2015). To reproduce, midge lay a ribbon jelly mass of eggs in lakes and ponds (Allaby 2014). After hatching, midges remain in the larval form for approximately one year and emerge as adults for 1-2 weeks to mate and lay eggs (Monckton 2020). The larvae range from approximately 2-10 mm in length and are often encapsulated in a silken case made of the substrate, such as dirt, pebbles, or sand. The larvae can be olive, red, taupe, brown, or beige. The red larvae are better suited for living in anoxic environments due to the hemoglobin analog found in their tissues (Allaby 2014). The larvae have no true legs but have prolegs and anchor-like tails. Since the larvae are benthic after the first instar, the tail is used to anchor the midge to the substrate, especially in turbulent waters. The head capsule of the larvae is hard and armoured (Figure 1).

Figure 1: Orthocladiinae in ethanol solution. The head capsule and prolegs are visible in this image. The image was taken during identification through a compound microscope at 100x.

Chironomids are notoriously hard to identify in any life stage (Jones 2008). Using morphological features, midge larvae can be identified to the subfamily level, but for higher taxonomic resolution, DNA sequencing is often required (Armitage 1995). Most of the identifying features are on the head capsule, such as the paralabial plate (Figure 2). This plate is near the mouth of the larvae and can have striations, the presence of which indicates the subfamily Chironominae. The paralabial plate can be reduced which indicates subfamily Orthocladiinae or it can be not visible or absent, indicating one of the other three subfamilies that are most common in northern Canada. Tanypodinae have a retractile antenna used for catching prey. The antenna is visible looking through their head capsule. Diamesinae have dark posterior hooks on their parapods. Tanytarsini have long antenna and lauterborn organs that add extra length to their antenna. To make chironomids more difficult to identify, they are prone to deformities in the head capsule due to sediment toxicity (Salmenlin 2015). The mentum, a structure behind the mouthparts, is the most common area for deformities (Salmenlin 2015) (Figure 2).

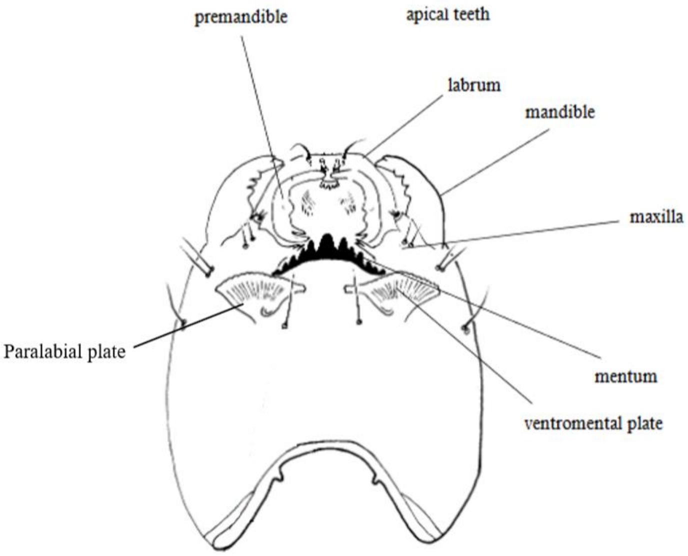


Figure 2: Chironomidae larval head capsule of a Dicrotendipes from the Carolinas, USA. (Epler, 2001) This image is very similar to the appearance of Chironominae – the most common larvae found in this study.

The composition of midges found in particular lakes or streams varies depending on a variety of factors, including climate, latitude, and substrate type. July air temperature is an important determinant of the distribution of chironomids, and Chironomidae abundance can be used to examine the history of temperatures in a lake (Francis 2004; Larocque, Hall 2003).

A study in the Northwest Territories found that the relative abundance of midges increased the further north the lake was located, and eventually monopolized macroinvertebrate communities. At northern latitudes in one study, the most common subfamilies were Orthocladiinae and Chironomini (Scott 2010). According to his analysis, Scott

(2010) found that substrate, flow during winter (water body freeze), and latitudinal gradient were environmental characteristics that had influence on their abundance. Substrate type is often found to have the most impact on the composition of midge taxa (Scott 2010).

Purpose and Objectives

For my thesis, I examined factors that affect chironomid subfamily abundance in twenty Arctic lakes in the Northwest Territories. I had two main objectives: 1) To determine water quality characteristics and environmental factors that influence the abundance of Chironomidae subfamilies in Canadian Arctic lakes; and 2) To predict changes in abundance of Chironomidae subfamilies in a scenario where there is significant permafrost degradation. How will chironomid taxa in Arctic lakes change as a result of to water quality changes caused by permafrost thaw?

I developed multiple regression models to explain variation in chironomid subfamily abundance across lakes using physical and environmental information about the lakes they were collected from. I also used redundancy analysis to predict the relative abundance of the five subfamilies based on environmental differences among the lakes. The insights gained from these analyses allowed me to discuss how permafrost thaw might alter chironomid communities in Arctic lakes. If permafrost thaw or development alters the composition of chironomid communities, then it may affect the rest of the aquatic food web, as they are important prey items for fish. This might have implications for fishes valued by northern residents.

Methods

Study Site

To examine how midge taxa might change in response to water quality and climate change, we collected invertebrate samples from 20 lakes located near Inuvik (68°21’42”N 133°43’50”W) in the Gwich’in Settlement Area (GSA) of the Northwest Territories. The lakes we sampled are within the Mackenzie Delta region, an area of interconnecting lakes and rivers through which the Mackenzie River flows and empties into the Arctic Ocean. The area is north of the Arctic Circle and therefore has short, cool summers and harsh winters. The area is bordered by the Richardson Mountains to the west and the Caribou Hills along the east. The village of Tuktoyaktuk is in the tundra ecosystem while Inuvik and Fort McPherson are in the transition zones between boreal forest and tundra ecosystems. Tuktoyaktuk is beyond the northern limit of trees while Inuvik is very close to the limit and Fort McPherson is below the threshold. The vegetation near Tuktoyaktuk consists mostly of shrubs, grasses, and mosses. Vegetation around Inuvik consists mostly of coniferous forests as well as shrubs, grasses, and mosses. Vegetation surrounding Fort McPherson consists of coniferous and deciduous conifers as well as some deciduous trees, shrubs, grasses, and mosses (Canadian Encyclopedia).

In August 2018, 20 lakes were sampled along the unpaved Dempster Highway and Inuvik-Tuktoyaktuk Highways by the Gray Lab, Wilfrid Laurier (Figure 3). The Dempster Highway runs between Fort McPherson and Inuvik and was completed in the 1960s. The Inuvik-Tuktoyaktuk Highway runs between Inuvik and Tuktoyaktuk and was completed in the late 2010s.

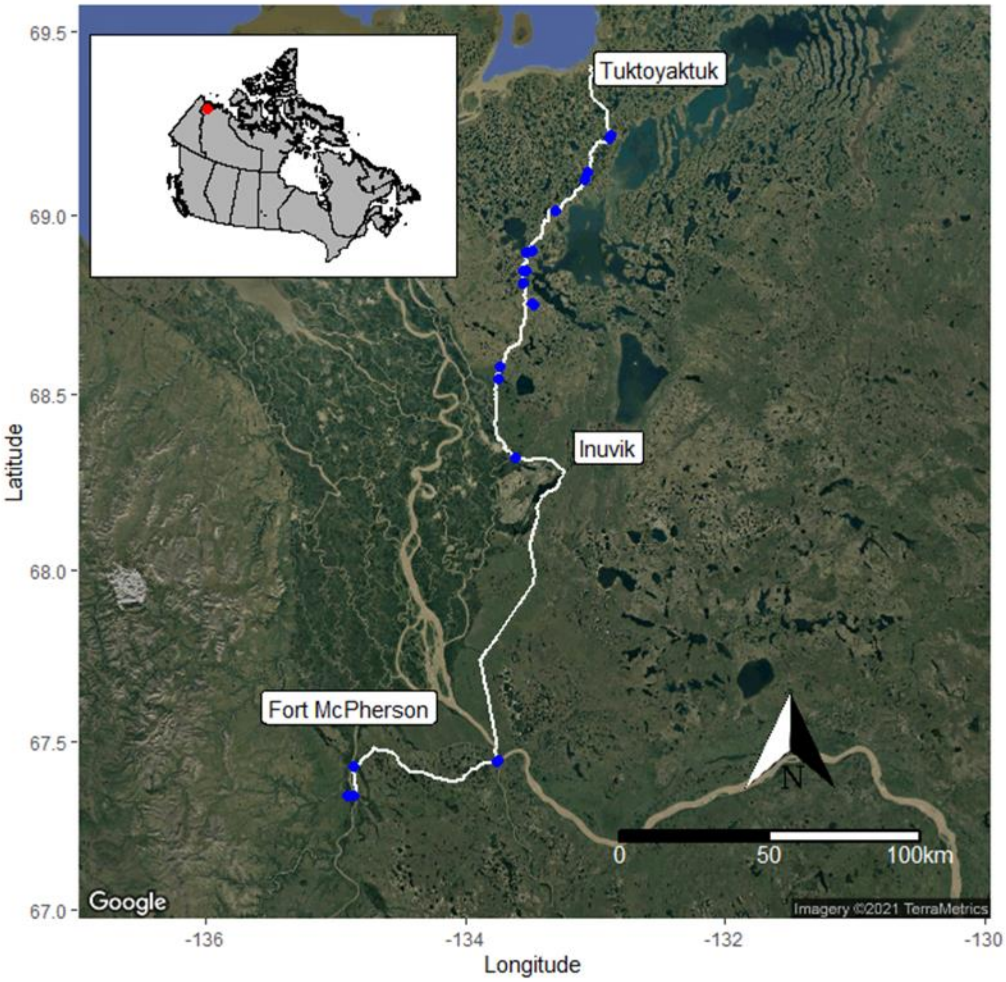


Figure 3: Map of sampling area, Northwest Territories, Canada. Blue dots indicate the location of the 20 sampled lakes for this study, while the white line represent the Dempster and Inuvik-Tuktoyaktuk highways.

Invertebrate collection and identification

We collected invertebrates using a modified version of the protocol developed by the Ontario Benthic Biomonitoring Network (OBBN) (Jones et al. 2007). The protocol uses a traveling kick and sweep collection method, where the substate is kicked enthusiastically at approximately 5 cm of depth and the technician sweeps the net vertically and horizontally in the water to catch the invertebrates before they return to the bottom. We collected three replicate samples from each lake using three-minute travelling kick trials and the sweeps were done with a 500 µm D-frame net. Parallel transects from the shore to 1 m of depth were used to take replicate samples. Two changes were made to the standard OBBN protocol: time spent kicking and selection of locations for replicates. The OBBN protocol suggests 10 minutes of kicking, but we used three-minutes of kicking because of the high organic matter that quickly clogged the D-net. The OBBN protocol also suggested selecting random locations along the shore for invertebrate collection. However, not all parts of the shoreline were accessible, limiting our ability to randomly select locations. Instead, we choose locations based on substrate and horizontal spacing. We observed three types of substrate in the studied lakes: mats of sphagnum moss, sphagnum moss with floating and emergent vegetation, and mixed gravel/cobble. When sampling the lakes, if the habitats along the shore were homogeneous, collections were sampled at least 10 m away from each other. If there were visible differences along the shore, at least one sample per habitat type was collected. Samples were placed in whirl-pak bags and preserved in 95% ethanol for shipment to the laboratory.

In the laboratory, we sorted macroinvertebrates to the order and family level according to the OBBN tally sheet (Jones et al. 2007). We used subsampling to estimate the abundance of invertebrates in each sample rather than counting entire samples which sometimes contained thousands of specimens. We weighed the full sample and then examined 10% of the sample for invertebrates. If we recovered fewer than 100 individuals in a subsample, then we examined additional quantities of sediment until we had identified 100 organisms. We then examined two more subsamples from each sample, resulting in the identification of at least 300 organisms per sample. If the entire sample had less than 300 organisms, the entire sample was processed.

We sorted the midge specimens for the current study into vials separate from the rest of the invertebrate community. We then identified midges to the subfamily level using a key by Jones and Sinclair (2011). During identification, we examined specimens under Leica dissecting microscopes. To see smaller features, we also created wet-mount slides for examination under compound microscopes at 100x magnification. Specimens that were dried up or were unrecognizable were not identified and were not added to the total count for each lake (0-10 individuals/sample).

We collected water quality data from the littoral zone of each lake using a Eureka Manta multiparameter probe (Eureka Water Probes). The probe measured pH, conductivity, temperature, and turbidity. We also measured water clarity by lowering a Secchi disk over the shady side of a boat in the deepest part of the lake. A Humminbird® Helix 5 chart plotter (Johnson Outdoors Marine Electronics, Inc.) and Reefmaster bathymetry software (Reefmaster Ltd.) were used to determine mean depth and surface area by constructing bathymetric map of each lake. We used 2 m resolution digital elevation maps (Porter et al. 2018) and the watershed tool in ArcMap version 10.5 (Esri Inc.) to estimate catchment area for each lake. We collected nearshore water samples to measure total suspended solids (TSS), chlorophyll-*a*, total phosphorus, total nitrogen, dissolved organic carbon, and calcium. We measured by following the procedures laid out in method 2540 D in the standard method guide (Rice et al. 2017). We measured chlorophyll-*a* by filtering 250 mL of a water sample through Fisherbrand G4 glass fiber filters, extracting the chlorophyll with methanol, and then measuring the concentration dissolved in the methanol using a fluorometer (Turner TD700) (Symons et al. 2012). We used a Shimadzu TOC-LCPH carbon and nitrogen analyzer (Shimadzu Corp.) to measure dissolved organic carbon and total nitrogen and a Perkin Elmer Optima 8000 Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) to measure calcium concentrations. We followed EPA method 365.1 to measure total phosphorus, which involved digesting a portion of the water sample in an autoclave using ammonium persulfate and sulfuric acid. Following digestion, we measured total phosphorus colorimetrically using a SEAL Continuous Segmented Flow Analyzer (SEAL Analytic Inc.).

Due to the importance of substrate for determining the composition of macroinvertebrate communities (De Sousa et al. 2008; Namayandeh and Quinlan 2011), we collected sediment samples at the site of macroinvertebrate collections before we sampled invertebrates. We collected sediment using a 250 mL plastic scoop. In the laboratory, we dried sediment samples at 105 °C for eight hours then placed them into a sieve shaker for ten minutes to separate particle sizes. We used sieves with mesh sizes of 4 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, and 63 µm. We also measured the percent organic matter and percent $CaCO_3$ in the sediment by taking 5 g of sediment <2 mm in diameter and using the sample to examine loss on ignition (Santisteban et al. 2004). We performed all analyses at the Center for Cold Regions and Water Sciences at Wilfrid Laurier University.

We collected fish community data using a modified Ontario Broadscale Monitoring (BsM) protocol (Sandstrom et al. 2013). We deployed gillnets for an average of 11 hours in medium to small lakes (<500 ha) and for 37 hours in larger lakes (>500 ha). The standard BsM protocol requires overnight gill net set, but we checked our nets every 45-60 minutes and released live fish. This protocol was used to address community concerns about the standard overnight nets that are more lethal. Using this method, we were able to ascertain the presence/absence of fish species in our studied lakes. The common fish that were captured included whitefish (*Coregonus clupeaformis* or *Coregonus nasus*), northern pike (*Esox lucius*) and cisco (*Coregonus sardinella*). Animal use authorization was approved by the Laurier Animal Use and Care Committee.

Statistical analysis

The goal of my analysis was to determine which water quality and habitat characteristics could explain variation in the abundance of chironomid subfamilies among my 20 study lakes. The response variables for my analyses were the abundance of the five chironomid subfamilies in each lake. The predictor variables included water quality and habitat characteristics: temperature, pH, conductivity, dissolved oxygen, turbidity, latitude, total suspended solids (TSS), chlorophyll-a, dissolved organic carbon (DOC), total nitrogen (TN), calcium, total phosphorus (TP), surface area, mean depth, Secchi depth, catchment area, percent substrate <2 mm, percent silts/clays, percent $CaCO_3$, whitefish presence, pike presence, and cisco presence. My response variables (chironomid subfamily abundances) were evaluated for normality by examining histograms. The abundance data for all five subfamilies were not normally distributed, so they were log-transformed to achieve a normal distribution.

To examine which predictor variables explained variation in chironomid subfamily abundances among lakes, I completed three analyses: 1) Spearman correlations to examine if there were significant linear relationships; 2) Multiple linear regression analysis to build models aimed at predicting the abundance of individual chironomid subfamilies; and 3) A redundancy analysis (RDA) to examine the relationships between predictors and the relative abundances of chironomid subfamilies.

I conducted Spearman correlations to examine relationships among all my environmental predictors and my response variables. Spearman was selected instead of typical Pearson correlations since my examination of histograms showed that some of the predictor variables were not normal. Prior to the analysis I also examined x-y scatterplots for each set of variables to ensure relationships were linear. None of the relationships were obviously non-linear. My correlations allowed me to determine the direction and strength of the relationship between abundance of each subfamily and the environmental characteristics. The cor.mtest function from library corrplot for R was used to determine the correlation using a matrix that contained data on the abundance of subfamilies and the environmental characteristics.

Multiple regression was used to link variation in the abundance of chironomid subfamilies to differences in water quality characteristics (pH, dissolved oxygen, temperature, conductivity, and turbidity) and morphometric factors (lake surface area, and mean depth) among my studied lakes. I used glmulti library in R to perform the regression analysis. This package performs automatic model building using the Akaike Information Criterion to select the most parsimonious model. Assumptions of the selected multiple regression models were tested using the gvlma function in the gvlma package and the vif function in the car library. The gvlma function checked for violations of linear model assumptions, while the vif function tested for collinearity among predictor variables in my models.

Redundancy analysis (RDA) was used to determine which variables are associated with differences in the relative abundance of subfamilies among lakes. This analysis used the abundance of subfamilies in each lake and water quality and physical characteristics for each lake. Prior to analysis the predictors in the data set were standardized with a mean of 0 and a standard deviation of 1 using the decostand function in the vegan library. The RDA model was built using the ordistep function in R, which performs forward selection to construct the most parsimonious model. A permutation test was used to determine the significance of the final RDA using the permutest function. The final RDA was plotted using libraries ggplot and viridis. To test if collinearity existed in the model, I ran a variance inflation factor test using the vif function.

To forecast potential changes in chironomid communities due to permafrost thaw, I collected values from the literature showing how permafrost thaw can affect lake water quality (Table 1). The high impact scenario represents the effects of retrogressive thaw slumps on lakes, while the low and medium values are points in between the current conditions and the high impact scenario. The current values are the means for the 20 lakes in our dataset. Chlorophyll-a, turbidity, total organic carbon, and total nitrogen are all expected to decrease. While the other five variables are expected to increase. I used my multiple regression models and inputted the predicted values for water quality from Table 1 to predict how water quality changes could affect the abundance of the chironomid subfamilies in the future.

Table 1: Scenario table used to project future change in Chironomidae subfamilies. High values are averages taken from the cited studies while current values are averages from the 20 study lakes included in our dataset. Low and medium values are set in between the current and high values.

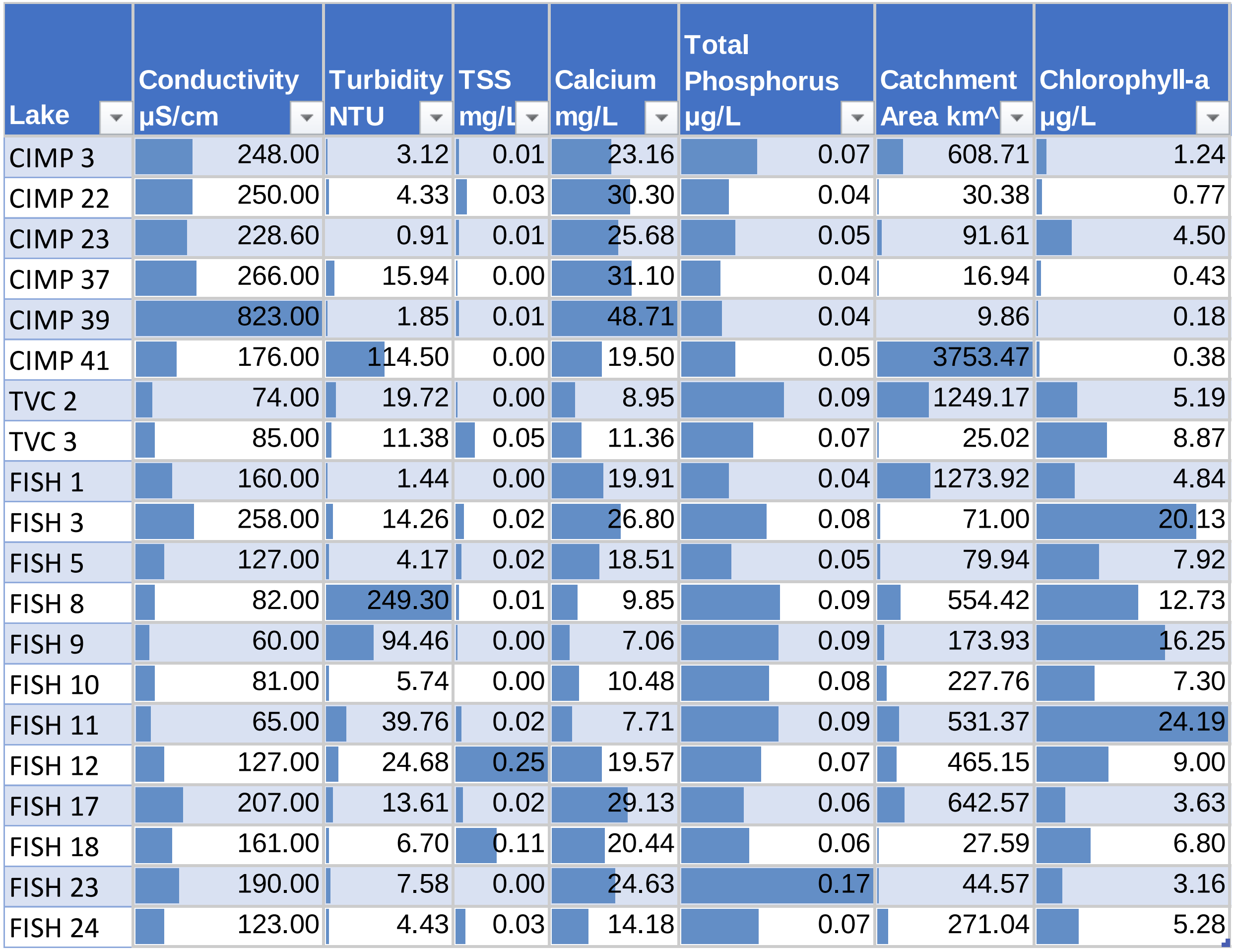
Variable	Current	Low	Medium	High	Slope	References
Secchi depth (m)	1.76	1.80	1.84	1.88	Positive	Houben et al., 2016
Conductivity (µS/cm)	189.58	326.99	464.40	601.80	Positive	Houben et al., 2016 Kokelj et al.,2005 Moquin et al., 2014 Thienpoint et al., 2013
pH	8.18	8.20	8.21	8.23	Positive	Houben et al., 2016
Chlorophyll-a (µg/L)	7.14	5.62	4.10	2.58	Negative	Houben et al., 2016
Turbidity (NTU)	31.89	30.93	29.97	29.01	Negative	Kokelj et al., 2005 Moquin et al., 2014 Thienpoint et al., 2013
Total Organic Carbon (mg/L)	15.31	12.35	9.39	6.43	Negative	Houben et al., 2016
Total Nitrogen (µg/L)	468.18	435.18	402.19	369.19	Negative	Houben et al., 2016
Calcium (mg/L)	20.35	28.39	36.42	44.45	Positive	Houben et al., 2016 Kokelj et al., 2005 Moquin et al., 2014 Thienpoint et al., 2013
Total Phosphorus (µg/L)	69.24	42.48	15.71	4.24	Negative	Houben et al., 2016

Results

Water quality and physical variation among lakes

The 20 lakes included in my dataset showed significant variation in water quality and physical variables important for macroinvertebrates (Table 2). Conductivity was very varied from 60 µS/cm to 823 µS/cm. Calcium varied widely from 7.06 mg/L to 48.71 mg/L. Total phosphorous also varied from 0.04 µg/L to 0.17 µg/L. Turbidity varied from 0.91 NTU to 249.30 NTU. Catchment area varied widely from 9.89 km^2 to 3753.47 km^2. Total suspended solid varied between 0 mg/L and 0.25 mg/L. Chlorophyll-a varied from 0.18 µg/L to 24.19 µg/L.

Table 2: A selection of water quality variables and physical characteristics for the 20 study lakes included in my dataset.



Lake	Conductivity µS/cm	Turbidity NTU	TSS mg/L	Calcium mg/L	Total Phosphorus µg/L	Catchment Area km^	Chlorophyll-a µg/L
CIMP 3	248.00	3.12	0.01	23.16	0.07	608.71	1.24
CIMP 22	250.00	4.33	0.03	30.30	0.04	30.38	0.77
CIMP 23	228.60	0.91	0.01	25.68	0.05	91.61	4.50
CIMP 37	266.00	15.94	0.00	31.10	0.04	16.94	0.43
CIMP 39	823.00	1.85	0.01	48.71	0.04	9.86	0.18
CIMP 41	176.00	114.50	0.00	19.50	0.05	3753.47	0.38
TVC 2	74.00	19.72	0.00	8.95	0.09	1249.17	5.19
TVC 3	85.00	11.38	0.05	11.36	0.07	25.02	8.87
FISH 1	160.00	1.44	0.00	19.91	0.04	1273.92	4.84
FISH 3	258.00	14.26	0.02	26.80	0.08	71.00	20.13
FISH 5	127.00	4.17	0.02	18.51	0.05	79.94	7.92
FISH 8	82.00	249.30	0.01	9.85	0.09	554.42	12.73
FISH 9	60.00	94.46	0.00	7.06	0.09	173.93	16.25
FISH 10	81.00	5.74	0.00	10.48	0.08	227.76	7.30
FISH 11	65.00	39.76	0.02	7.71	0.09	531.37	24.19
FISH 12	127.00	24.68	0.25	19.57	0.07	465.15	9.00
FISH 17	207.00	13.61	0.02	29.13	0.06	642.57	3.63
FISH 18	161.00	6.70	0.11	20.44	0.06	27.59	6.80
FISH 23	190.00	7.58	0.00	24.63	0.17	44.57	3.16
FISH 24	123.00	4.43	0.03	14.18	0.07	271.04	5.28

Association of chironomids with variation in water quality

I identified five different subfamilies of chironomids from the 20 study lakes: Chironominae, Orthocladiinae, Tanypodinae, Diamesinae and Tenytersini. Only two lakes had Tenytersini, so that subfamily was excluded from further analysis. The average abundance of chironomids in the 20 sample lakes was 50.9 chironomids per lake (Figure 4). Chironominae had the highest average abundance at 38.4 followed by Diamesinae at 7.25. The lowest subfamily abundances were Orthocladiinae, Tanypodinae and Tenytersini at 4.15, 0.85 and 0.25 respectively.

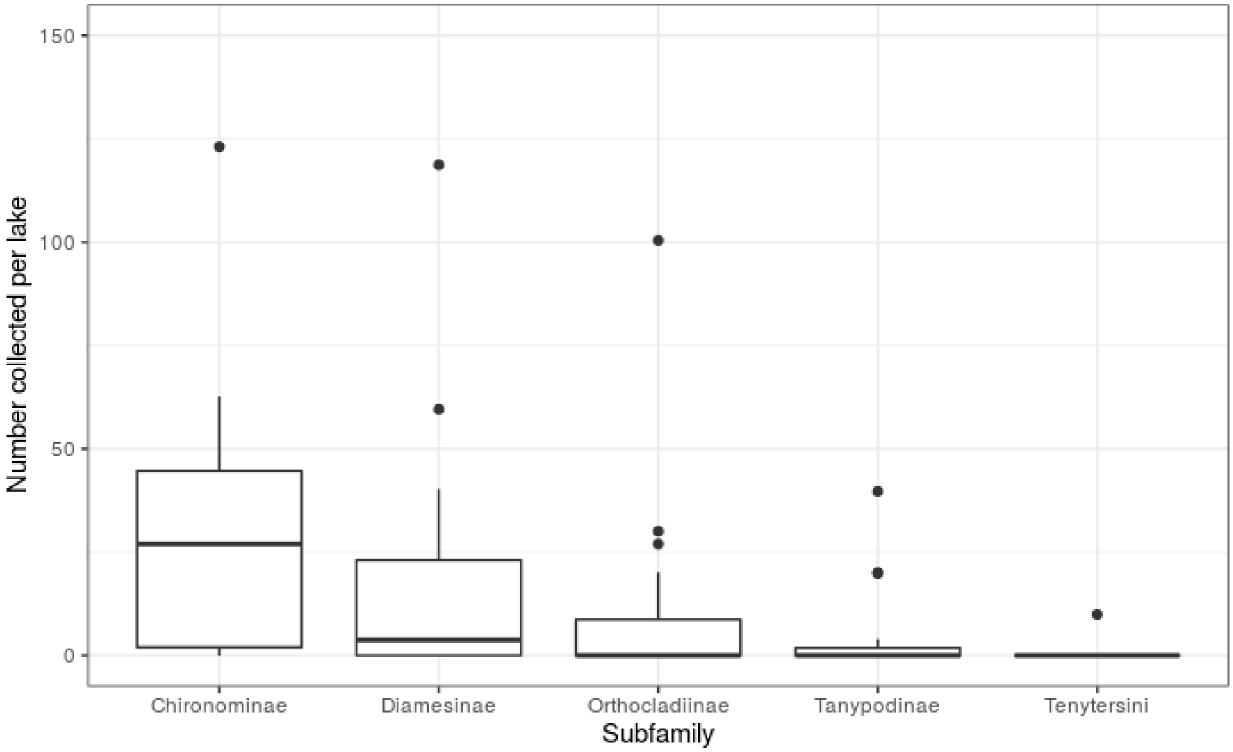


Figure 4: Average abundance of subfamilies found in 20 Canadian Arctic lakes

My Spearman correlations are shown in Figure 5. Chironominae was negatively correlated with fish species cisco and total suspended solids. Diamesinae was positively correlated with chlorophyll-a. Tanypodinae was negatively correlated with mean depth, and fish species cisco. Orthocladiinae was positively correlated with turbidity and Chironomidae. The subfamilies Chironominae, Orthocladiinae and Tanypodinae were positively correlated with one another.

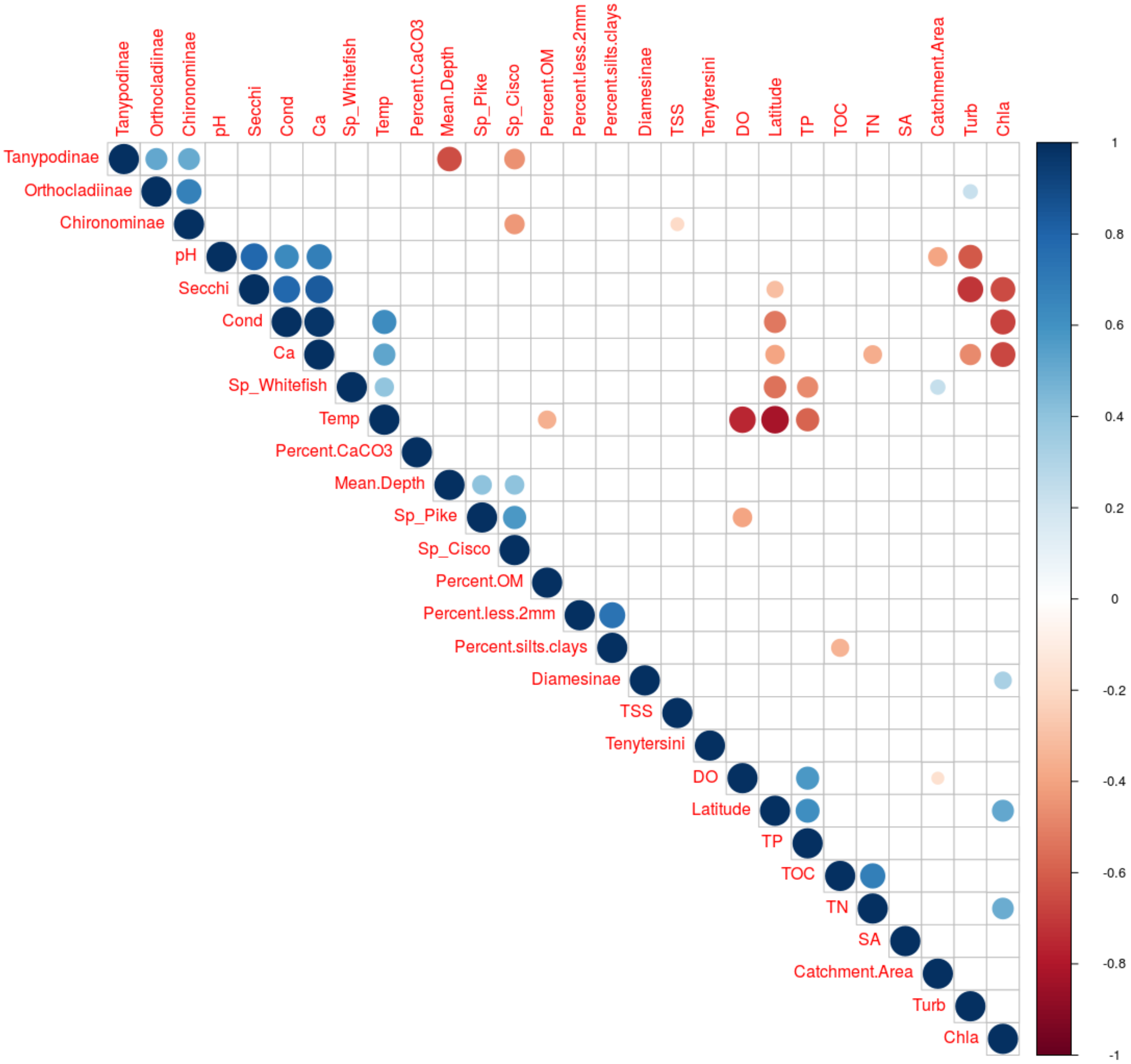


Figure 5: Correlation matrix that shows the correlation between each variable and subfamily analysed.

Multiple Regression

The most parsimonious models produced by my multiple regression analysis showed that (Table 3): Chironominae was most related to total suspended solids and calcium (R^2 = 32.8%), Tanypodinae was most related to turbidity, total suspended solids, mean depth, and catchment area (R^2 = 69.0%), Diamesinae was most related to chlorophyll-a (R^2 = 26.1%), and Orthocladiinae was most related to dissolved oxygen, turbidity, and total phosphorus (R^2 = 60.0%). In the model for Chironominae, calcium was marginally significant but since this was the most parsimonious model, calcium was still included. The variance inflation factor for variables in each multiple regression model did not exceed 5, suggesting no collinearity among predictors in the final models.

Table 3: Results of multiple regression analyses for the four chironomid subfamilies from my 20 study lakes.

Response	Variable	Estimate	SE	t-value	p-value
Chironominae **Model R^2=0.33,** **Adjusted R^2=0.25,** **p=0.034**	(Intercept)	2.54	0.46	5.51	3.82E-05
	Total suspended solids	-7.61	3.52	-2.12	0.05
	Calcium	-0.03	0.02	-1.96	0.07
Diamesinae **Model R^2=0.26,** **Adjusted R^2=0.22,** **p=0.021**	(Intercept)	0.21	0.12	1.76	0.096
	Chlorophyll-a	0.03	0.013	2.53	0.021

Orthocladiinae **Model R^2=0.60,** **Adjusted R^2=0.52,** **p=1.73E-3**	(Intercept)	-4.23	1.45	-2.92	0.01
	Dissolved oxygen	0.48	0.15	3.28	4.76E-03
	Turbidity	8.10E-03	1.85E-03	4.39	4.60E-04
	Total phosphorus	-9.15E-03	4.05E-03	-2.26	0.038
Tanypodinae **Model R^2=0.69,** **Adjusted R^2=0.61,** **p=9.36E-4**	(Intercept)	1.14	2.65E-01	4.29	6.39E-04
	Turbidity	5.43E-03	1.35E-03	4.03	1.09E-03
	Total suspended solid	-3.03	1.34	-2.26	3.90E-02
	Mean depth	-4.90E-01	1.47E-01	-3.34	4.45E-03
	Catchment area	-1.90E-04	9.41E-05	-2.02	6.11E-02

The final redundancy analysis (RDA) included total suspended solids, latitude, mean depth, and percent silts and clays (Figure 6). The RDA explained 69.2% of variation among lakes. This analysis revealed that lakes with lower total suspended solids had a higher Chironominae abundance and lakes with higher total suspended solids had a higher Diamesinae abundance. Shallow lakes at lower latitudes with less silts and clays were found to have a higher Tanypodinae and Orthocladiinae abundance.

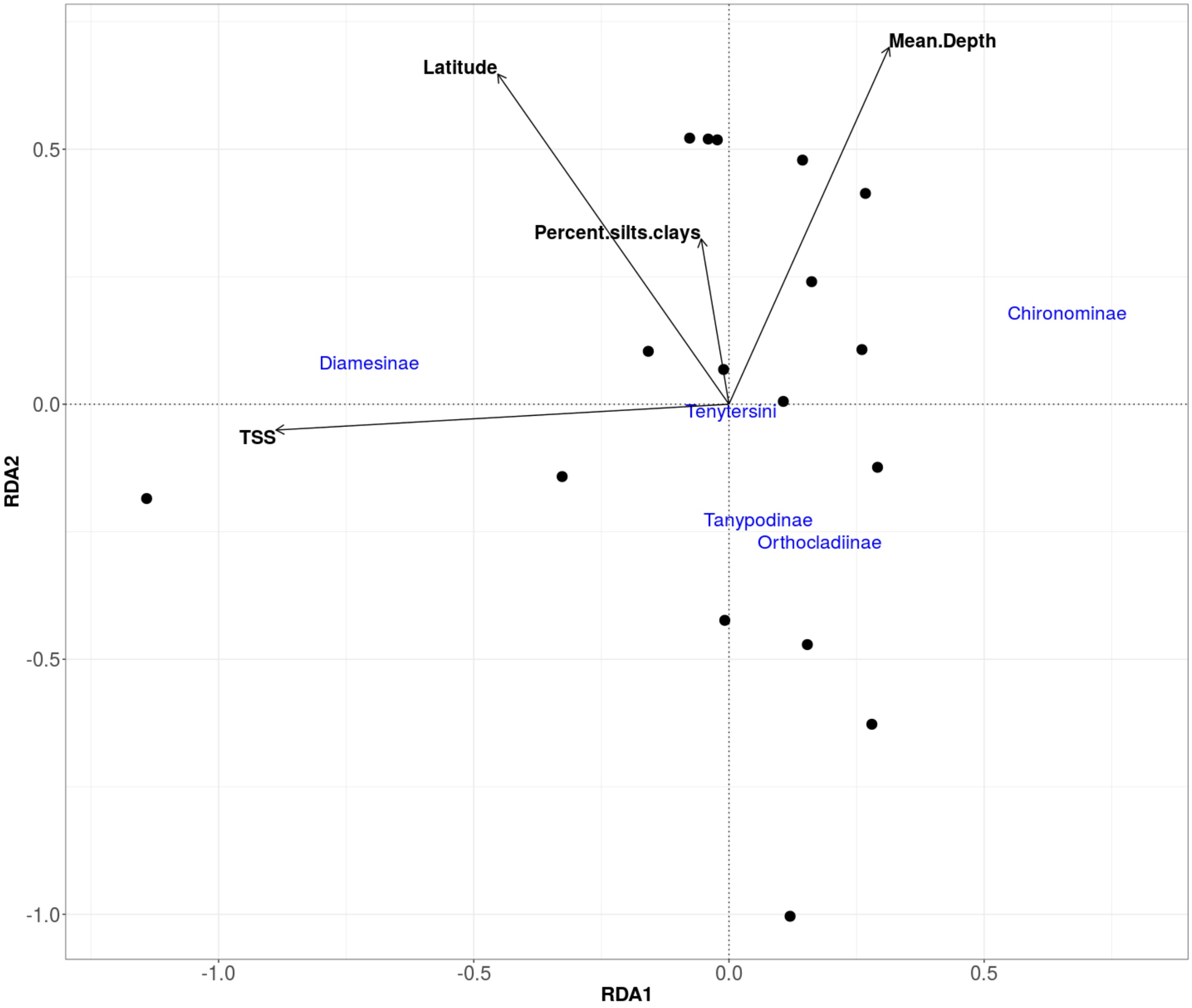


Figure 6: RDA plot showing associations between water quality and physical data with Chironomidae subfamily abundance.

Predicted changes in chironomid communities

My models predicted that Chironominae abundance will significantly decrease, while Diamesinae, Orthocladiinae and Tanypodinae will increase in abundance due to predicted environmental changes associated with permafrost thaw (Figure 7). Looking at these predictions for chironomid abundance, it shows a substantial decrease of the most abundant subfamily (Chironominae), while the other subfamilies may exhibit minor increases.

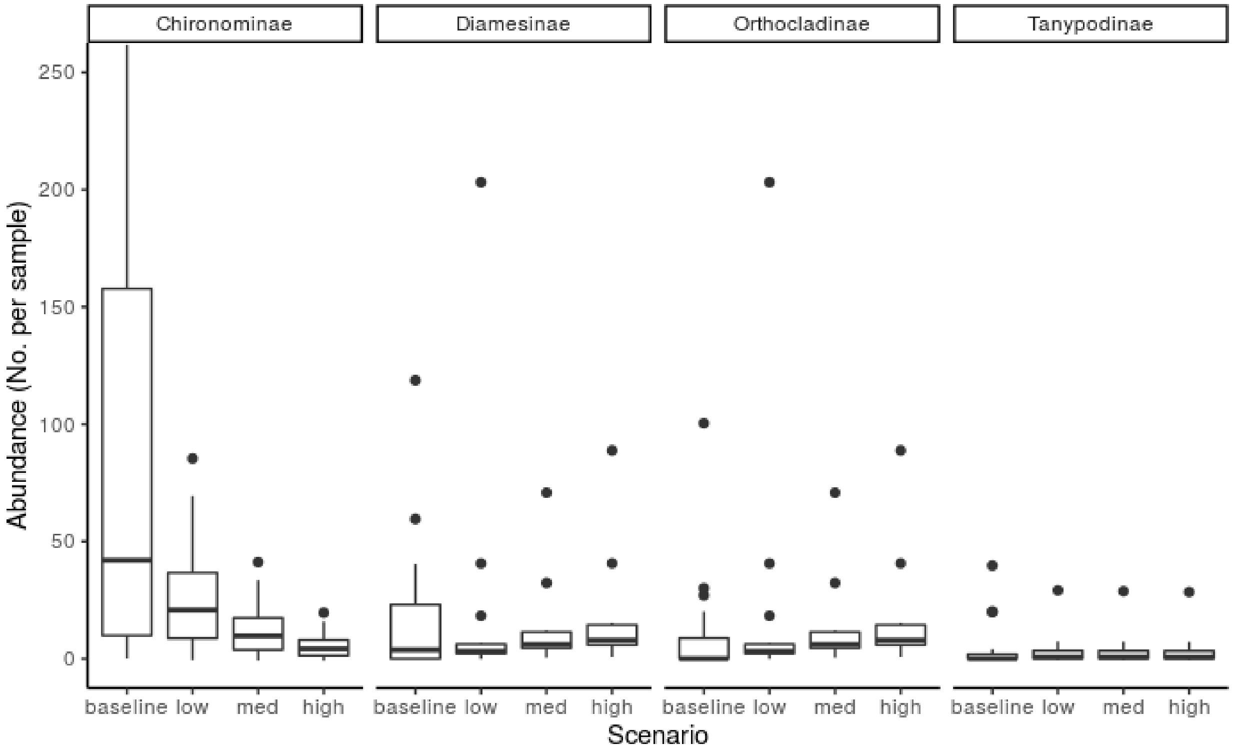


Figure 7: Boxplot of predicted abundance for four Chironomidae subfamilies with current (baseline), low, medium, and high scenarios involving water quality variables from Table 1. Projections are based on my multiple regression models.

Discussion

In this study, I found that water quality variables expected to change due to permafrost thaw were correlated with the abundances of chironomid subfamilies in Arctic lakes. My multiple regression models showed that variables such as total suspended solids, calcium, and mean depth showed negative correlations with abundance for Chironominae and Tanypodinae subfamilies. In addition, my redundancy analysis showed that the relative abundance of subfamilies was influenced by total suspended solids, which can be affected by road development and permafrost thaw. Taken together, these results suggest that climate change may cause significant shift in chironomid communities in Arctic lakes.

Associations between water quality and physical variables and chironomids

My multiple regression models showed Chironominae were less abundant in lakes with high calcium and high total suspended solids, which was also shown in the RDA and correlation matrix. There are several reasons why high total suspended solids levels could be detrimental for this subfamily. First, this subfamily is classified as collector-filtering larvae (Ferrington and Pehofer 1996), and high levels of total suspended solids may make it difficult to gather food. Second, higher total suspended solids could reduce respiration through the cuticle either by clogging the pores or burying the Chironomidae when the solids settle to the bottom of the lake or river (Cooper et al. 2009). High levels of total suspended solids can also smother benthic habitat, leaving fewer places for the larvae to attach to the substrate. The reasons for the negative effects of calcium on Chironominae are less clear. I could not find any past studies that identified a direct association between high calcium levels and Chironominae abundance. I speculate that this relationship might reflect the fact that lakes closer to the road receive more road dust, increasing calcium levels (Gunter 2017). Therefore, this subfamily could be responding to something related to road dust contamination or road proximity, rather than calcium levels directly. In general, species found within the Chironominae tend to respond to a variety of environmental variables, so it can be difficult to generalize how all species in this subfamily will respond to differences in environmental conditions among lakes (Cortelezzi et al. 2020).

My multiple regression model for subfamily Diamesinae showed that abundance was higher in lakes with high levels of chlorophyll-a, this was also shown in the correlation matrix. In addition, the RDA showed that Diamesinae were more abundant than other subfamilies in lakes with higher total suspended solids. These results are consistent with previous studies that have found Diamesinae tend to dominate in harsh conditions, including at colder temperatures (Niedrist et al. 2018, Ólafsson et al. 2000), and at higher total suspended solids levels (Füreder and Nierdrist, 2020). Previous studies in subarctic lakes also suggest that many chironomid species are more abundant in more productive lakes (higher chlorophyll-a; Moore. 1980) which may explain the positive association of this subfamily with chlorophyll-a in my multiple regression model. Since members of this subfamily are opportunistic omnivores that change their feeding behaviour based on their conditions (Füreder and Nierdrist, 2020), they may be making use of extra algal resources in more productive lakes.

My multiple regression model showed that Tanypodinae were most affected by turbidity, total suspended solids, mean depth and catchment area, this was also shown in the correlation matrix. Turbidity was the only variable in the model that had a positive influence on this subfamily. The RDA showed that they were less abundant in deeper lakes at high latitudes with more silts and clays in the substrate. Unfortunately, there is little published information about the environmental preferences for this particular subfamily. However, an experimental study showed that levels of deposited sediments could negatively affect this subfamily (Wagenhoff et al. 2012), likely explaining the negative association with total suspended solids. This subfamily mostly contains carnivores that can vary their diet based on availability of resources but exhibit the best growth patterns when consuming animal food (Baker, McLachlan. 1979). I speculate that variables such as mean depth and catchment area might influence the diversity of prey items available to Tanypodinae, as well as the input of energy resources for their prey in the lake, explaining the importance of those variables in my models. More research is needed to determine how and why this subfamily responds to the environmental gradients found in our study lakes.

The multiple regression indicated Orthocladiinae was most related to dissolved oxygen, turbidity, and total phosphorus, this was also shown in the correlation matrix. The RDA showed that shallow lakes at a lower latitude with less silts and clays were found to have a higher Orthocladiinae abundance. These results are supported by a previous study that examined this subfamily in streams (Cortelezzi et al. 2020). Orthocladiinae are usually abundant in low nutrient environments (Cortelezzi et al. 2020). In general, this subfamily is heavily influenced by the type of substrate, and they tend to be found in areas with higher dissolved oxygen concentrations (Bazzanti et al. 1996). Some species of Orthocladiinae are found in rapids for the highest flow rate and most dissolved oxygen (Cortelezzi et al. 2020). For Chironomidae, the subfamily Orthocladiinae is the lowest taxonomic level needed for bioindication of water quality (Cortelezzi et al. 2020), meaning the subfamily is similar in its reactions to water quality characteristics.

Predicted changes in chironomid communities

I used my multiple regression models, along with data from the literature on expected changes in water quality due to permafrost thaw, to make predictions about how the abundance of chironomid subfamilies might change in the future. My results suggested that Chironominae, the most abundant subfamily, is going to decrease substantially. This result stems from the negative relationship between abundance and calcium and total suspended solids levels. Both calcium and total suspended solids are expected to increase due to permafrost thaw (Houben et al., 2016; Kokelj et al., 2005; Thienpoint et al., 2013). I could not find estimates of change for total suspended solids in lakes from the literature, but if included in the scenario with increasing total suspended solids, the predicted abundance of Chironominae would decrease even more.

My model for Diamesinae suggests that this subfamily will increase in response to changes caused by permafrost thaw. If major thaw slumps were to occur, Diamesinae would increase but would be hindered by the lower chlorophyll-a levels (Houben et al., 2016). Diamesinae was more abundant with lakes that had higher total suspended solids levels. These levels would increase with the slump and would therefore also increase this subfamily abundance. If the chlorophyll-a levels were artificially increased, Diamesinae might compensate for the reduction in the abundance of Chironominae in a thaw slump scenario.

The predicted scenario involving a thaw slump shows a very slight increase in Tanypodinae. The multiple regression linked high turbidity, low total suspended solids, and small catchment area to higher abundance of Tanypodinae (Kokelj et al., 2005; Moquin et al., 2014; Thienpoint et al., 2013). This could be important if stormwater ponds are created in the Arctic because this subfamily could potentially thrive there.

The predicted thaw slump scenario shows the largest increase in abundance for Orthocladiinae out of the four subfamilies that were examined. The multiple regression linked low phosphorus, high dissolved oxygen, and high turbidity to a higher abundance of Orthocladiinae (Kokelj et al., 2005; Moquin et al., 2014; Thienpoint et al., 2013; Houben et al., 2016).

Shortcomings of my research

I was unable to find values for how total suspended solids would change with respect to thaw slumps. This information would be useful because total suspended solids have a strong negative relationship with Chironominae, the most abundant subfamily, as well as Tanypodinae. Having total suspended solids data for thaw slumps would improve the predictions on how Chironomidae subfamilies would react in a thaw slump scenario. In addition, during this study, altitude was not considered. The higher a lake is relative to sea level the longer the ice cover usually lasts. This reduces sunlight penetration and therefore reduces photosynthesis. Lakes of high altitude have significant shifts in productivity come early summer as the ice melts, solar irradiance increases and the temperature rises quickly (Pastorino and

Prearo 2020). This causes a fast shift from very little productivity to ideal living conditions for many organisms (Pastorino and Prearo 2020).

The taxonomic level needed to examine the response of Chironomidae to environmental gradients is different for each subfamily. Members of the Chironominae vary widely and are not consistent with their reactions to environmental factors. Cortelezzi et al. (2020) found that Chironominae need to be identified to a lower taxonomic level - at least the genius level for consistent use as bioindicators. However, Cortelezzi et al. (2020) found that members of some other subfamilies, such as Orthocladiinae and Tanypodinae, respond predictably to the environmental gradients, making the subfamily level a good taxonomic level for generalization of bioindication reactions (Cortelezzi et al. 2020).

To increase the significance of this study, more lakes should be considered as well as more samples from each lake. If more lakes were analysed for Chironomidae, Tenytersini abundance might have been high enough to add to the analysis. Increasing the number of lakes analysed could have also indicated more accurately which environmental factors and lake qualities were influencing the subfamily abundances.

Overall, to further this study, Chironominae should be identified to a lower taxonomic level to have better indication, total suspended solids levels in response to thaw slump should be considered for more accurate predictions of the subfamily abundance, altitude should have been considered in the analysis and a larger data set used in the analysis.

Conclusion

My results suggest that there could be significant changes in the abundance and composition of midge taxa in Arctic lakes as a result of permafrost thaw. Changes in Chironomidae communities may impact the food web since they are usually the most abundant macroinvertebrate in Arctic lakes and streams. They also make up a large portion of fish diet, so an overall decline of midges would be expected to reduce energy available for fish. This study can help with planning and resource management involved in community fishing plans in the Arctic. Indigenous communities have developed community fishing plans for lakes in the area to try and reduce the affects of overfishing. Since the highway from Inuvik to Tuktoyaktuk has been constructed, more lakes are easily accessible by more anglers. Arctic lakes and rivers take a long time to recover from overfishing because of the short growing season. A reduction in Chironomidae could also have negative impacts similar to overfishing. Therefore, informing the communities and management agencies of these potential issues could help with planning and mitigation efforts aimed at softening the impacts of climate change on northern Indigenous communities.

Although my study used statistical models to try to predict future scenarios for chironomid communities in Arctic lakes, long-term monitoring will be required to inform any real policy or management changes (Smol and Douglas 2007). Unfortunately, long-term data in the Arctic are often unavailable. Therefore, the changes happening in the Arctic – which is usually a more sensitive ecosystem - are not being reflected when considering the design and implementation of policies. While continued efforts to collected long-term data proceed, predictive analyses such as those I presented in my thesis may assist with designing future management plans for Arctic lakes.

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