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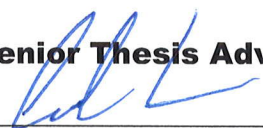
**Title** Arctic zoobenthos of thermokarst and floodplain lakes  
in northeastern Yakutia, Russia

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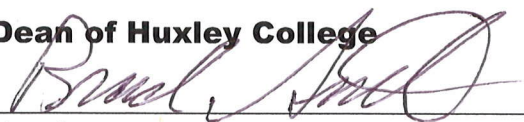
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**SENIOR THESIS**

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## Table of Contents

Abstract .....	1
Introduction .....	3
Methods .....	7
Site Description .....	7
Sampling .....	8
Isotope Analysis .....	9
Results .....	12
Discussion .....	14
Acknowledgements .....	19
Literature Cited .....	20
Tables .....	24
Figures .....	27

## List of Tables

Table 1: Physical and chemical lake parameters .....	24
Table 2: Taxa present in feeding strategy groups .....	25
Table 3: P-values from t-tests comparing lake $\delta^{13}\text{C}$ .....	26
Table 4: P-values comparing feeding strategy methanogenic C .....	26

## List Figures

Figure 1: Map of study site northeastern Yakutia, Russia. ....	27
Figure 2: Zoobenthos diversity .....	28
Figure 3: Mean density by class in lake habitats. ....	29
Figure 4: Comparison of lake $\delta^{13}\text{C}$ .....	30
Figure 5: Comparison of feeding strategy methanogenic C .....	31

## **Abstract**

Freshwater lakes are abundant in northeastern Siberia and a common characteristic of the Arctic. There is limited literature on arctic invertebrates and their roles in these freshwater systems, whereas invertebrates are regularly used to assess lake and stream health in temperate regions. With a snapshot study of benthic macroinvertebrates in Northeast Russia during July 2009, we document diversity and biomass, compare the differences in organism distribution between lake habitats, assess baseline chemistry data and use  $\delta^{13}\text{C}$  isotope analysis to determine their source of energy. All of our lakes are located in the Kolyma River basin, the largest river in the world with the entire basin underlain by continuous permafrost. We sample benthic macroinvertebrates, referred to as zoobenthos, from one floodplain and three thermokarst (thaw) lakes quantitatively by sample area and qualitatively from other lakes and ponds to get a broader look at diversity. Pelagic water samples are taken to assess temperature, dissolved oxygen, dissolved organic carbon (DOC), specific conductivity and pH. We analyze all taxa for carbon isotopes. Despite physical variation, chemical parameters of the thermokarst and floodplain lakes are generally analogous, except for specific conductivity. Density of zoobenthos is higher in the floodplain lake, likely correlated to a greater surface area. The disturbance regime in thermokarst lakes may also inhibit high density of zoobenthos as these lakes display a faster succession than floodplain lakes. The two habitats of thermokarst lakes has similar densities, but the eroding side of thermokarst lakes has a more even richness. Isotopic analysis shows littoral  $\delta^{13}\text{C}$  of the floodplain lake is different from the active thermokarst lakes is likely correlated to methane production and suggests uptake of methanogenic carbon. An endmember  $\delta^{13}\text{C}$  analysis between terrestrial and methanogenic/pelagic carbon supply shows a difference in mean methanogenic carbon supply between feeding strategies. The group of pelagic invertebrates (zooplankton) is

different from the benthic groups as expressed in previous literature. The grazers (snails) mean pelagic/methanogenic carbon supply are greater than the predators and the detritivores (segmented worms), pointing to a difference in methanogenic carbon between living plant matter the snails are eating and the dead matter that the oligochaetes are eating, as these taxa both live in the littoral zone.

## Introduction

Benthic invertebrates are important to nutrient cycling processes in streams and lakes. As primary and secondary consumers, they play an important role in trophic cascades (Covich 1999). The role of nutrient cycling makes zoobenthos responsible for many ecosystem functions such as accelerating detrital decomposition, processing 20-73% of the riparian leaf litter, releasing bound nutrients into solution, accelerating microbial and plant growth, predator control, food for vertebrates, translocating materials, and accelerating nutrient transfer to open water (Wallace & Webster 1996; Covich 1999). Diversity of benthic macroinvertebrates is important due to the many specific niches filled by different taxa, separated by functional feeding strategies, illustrated in streams, estuaries, wetlands, ponds, intertidal and coastal zones (Covich 2004). Benthic invertebrates fit into two of the three traits of biota that have profound effects on their environment since they modify the availability and use of nutrients and they affect the feeding relationships or trophic structure within a community (Chapin & Walker 1997).

The diversity, production, and function of macroinvertebrates from Arctic lakes are poorly understood compared with temperate ecosystems. Thermokarst lakes are well studied for methane emissions and are thought to be of importance to the global carbon cycle (Zimov *et al.* 1997; Walter *et al.* 2006), but basic ecological questions about biota remain unanswered. Investigations from polar lakes in general indicate that even in a cold, low light environment, aquatic invertebrate communities can be stable and abundant (Hershey *et al.* 1995; O'Brien *et al.* 2004). Many Arctic lakes are fish-free and zooplankton and benthic invertebrates are often the highest trophic level in the aquatic food web (Hansson *et al.* 1993). In shallow water bodies where microbial mats increase habitat complexity and food availability, abundance can be as

high as in temperate regions, but the biodiversity of benthic invertebrates decreases towards high latitudes (Hebert and Hann 1986; Gibson and Bayly 2007). Geographic isolation and glaciation history characterize species diversity and abundance of a region (Vincent & Laybourn-Parry 2008). Northeastern Siberia was not covered by a continental-scale ice sheet in the last ice-age (Gauliteri *et al.* 2003), so diversity here may be higher than in other high latitude regions. However, abiotic features usually determine local diversity and abundance because densities are not high enough for competitive exclusion (Strathdee and Bale 1998). *Chironomidae* are the most numerous group of benthic invertebrates in arctic ecosystems and are well adapted to live in these areas (Vincent & Laybourn-Parry 2008). Larval chironomids from soft sediments are found to be the greatest secondary production from arctic lakes (Northington *et al.* 2010).

Northington *et al.* (2010) hypothesizes that something other than autochthonous production must be important in controlling benthic secondary production in arctic lakes. Thus the source of production (e.g. algal, microbial, or terrestrial detrital), in arctic lakes is likely an important factor shaping biotic communities based on food availability. Offshore benthic invertebrates in arctic lakes (mainly chironomids and oligochaetes) show a dependence on carbon derived from biogenic methane (Hershey *et al.* 2006).

The watershed of the Kolyma River in the Yakutia region of Northeast Siberia is the largest in the world that is underlain completely by continuous permafrost. The landscape is dotted with upland thermokarst lakes as well as floodplain lakes located along the river margins.

Thermokarst (thaw) lakes develop in depressions resulting from thawing permafrost, initially triggered by the degradation of ice wedges and followed by surface subsidence and formation of

ponds and taliks, unfrozen portions of permafrost (Vincent & Laybourn-Parry 2008).

Thermokarst lakes comprise approximately 90% of the lakes in the Russian permafrost zone (Walter *et al.*, 2006). Based on residual depressions and cross-cutting relationships, it is thought that thaw lakes are relatively short-lived and are sensitive to underlying bedrock and climate conditions (Hinkel *et al.* 2005). Permafrost has a strong influence on lake hydrological processes and geochemical interactions (Lamoureux and Gilbert 2004). Recent increased global temperatures are causing the permafrost of the region to begin to thaw, representing a vast pool of old organic carbon that is now becoming biologically available (Walter *et al.* 2006). Biogenic methane has a much more depleted  $\delta^{13}\text{C}$  value than organic detritus (Bunn and Boon 1993). The  $\delta^{13}\text{C}$  values of methane from a variety of freshwater environments range from -52 to -80‰ with a mean of -62‰. Methanotrophic bacteria, which readily oxidizes methane in the water column (Ehhalt 1976) incorporate at least 50% and up to 95% of the methane into cellular biomass. Values  $\delta^{13}\text{C}$  can be specific to regions, systems and species, values in this system may be less depleted in  $\delta^{13}\text{C}$  than other systems because they are rich in dissolved carbon. The role of biota in processing this newly available carbon remains poorly understood. Invertebrates are potentially important in these areas of continuous permafrost because of their roles as carbon processors and possible mediators of carbon cycling processes including methanogenesis. Very few studies however have evaluated the diversity, abundance, and source of carbon contributing to invertebrate production (for an exception see Hershey *et al.* 2006).

The broader objectives of our study are to understand the ecology of the invertebrate community in this remote region of the Arctic. Our specific objectives are fourfold: 1) to document zoobenthos diversity and density in lake habitats of the lower Kolyma watershed, 2) to compare

the differences in organism distribution between floodplain and thermokarst lakes, and 3) to compare the differences in organism distribution within the eroding and non- eroding sides of active thermokarst lakes, and 4) to determine the source of energy (algal or methanogenic) supporting different taxa of zoobenthos.



## Methods

*Site Description*-The study site is located north of the Arctic Circle in the Kolyma River Basin. Monthly average temperatures in this area range from -30° C in the January and 12° C in July. Average monthly rainfall is highest in August at 2.46 cm and lowest in April at 0.63 cm. Our research was based out of the Northeast Science Station (69° N, 161°E) located 150 km south of the Arctic Ocean. Our site is located at near the forest-tundra ecotone on the lower reaches of the Kolyma River. The region is underlain by ice-rich continuous permafrost known as Yedoma with an active layer depth of approximately 10 cm in mid-summer. The soils are carbon rich containing 2-5% C (Zimov *et al.* 2006). There is little topographic relief. The forest vegetation is comprised of Dahurian larch (*Larix gmelinii*) with extensive dwarf birch understories. In both areas Labrador tea (*Ledum spp.*), willows (*Salix spp.*), moss and lichens are common. The landscape is comprised of many small, shallow lakes located in the floodplain and in the upland which are increasingly thought to be major sources of methane to the atmosphere (Zimov *et al.* 1997; Walter *et al.* 2006).

Shuchi, Tube Dispenser and Horse Jaw are upland thermokarst lakes, while Fire Lake is located within the floodplain of the Kolyma River. Shuchi and Tube Dispenser are of a similar size and depth (Table 1), but Tube Dispenser has more active erosion. With more active erosion, Tube Dispenser is surrounded by a greater abundance of grasses and willow (*Salix spp.*). The translation of Shuchi means “pike” so it is assumed this lake was once full of fish, but there are none today. Pike (*Esox lucius*) is still found abundantly in Tube Dispenser Lake. The area around Fire Lake was eroded by the Kolyma River approximately 6,000- 8,000 years ago. Vegetation around Fire Lake is dominated by sedges, willow (*Salix spp.*), birch (*Betula spp.*),

and blueberries (*Vaccinium spp.*). This lake is flooded approximately once each year, depending on the size of the spring flood. Fire Lake is expected to have a variety of fish that are found in the Kolyma River and its tributaries.

*Sampling-* We conducted a snapshot study of benthic macroinvertebrates in July 2009. This time period was typical in terms of the long-term climatology of the area with a mean daily temperature of 10.4°C (NOAA NCDC, 2010). Lake areas were found by digitized a polygon around each feature using a 30 m resolution Landsat image to identify position of each lake.

With that layer, a tool in Idrisi (GIS program) was used to find the area of each polygon. Water quality information (temperature, pH, dissolved oxygen, and specific conductivity) was collected from the deepest point in the lake using a YSI 85 sensor and Van Dorn sampler along a longitudinal profile from surface to depth. Zooplankton samples were collected via a vertical haul from depth to surface using a 25-cm-diameter 100 µm plankton net and stored in formalin until identification. We sampled one floodplain and three thermokarst lakes quantitatively for macroinvertebrate density and also sampled qualitatively from other lakes and ponds to get a broader look at diversity in the area (Table 1, Figure 1).

Benthic macroinvertebrates were collected from littoral sediment samples from floodplain and thermokarst lakes. Thermokarst lakes were sampled on both the eroding and non-eroding sides. Two replicate sediment samples at each site were collected by hand using a 12 cm aluminum pipe, with plugs being taken from the surface to approximately 5 cm deep. Sediment and water were transported in sealed bags and then immediately sifted through (200 µm mesh) and hand-picked for all invertebrates. In some lakes, qualitative analysis was attracting invertebrates from

the littoral zone over a period of 24 hours by tying together willow (*Salix* spp.) branches in small bouquets and securing them to the sediment. Invertebrates were identified to the lowest taxonomic resolution possible (e.g. family, genus) using Thorp & Covich (1991) and Merritt & Cummins (1984). North American keys were used in the absence of an available English language key from the region. All insects were identified to the family level. Zoobenthos and zooplankton samples were dried, weighed for biomass and prepared for isotopic analysis at the Aquatic Ecosystem Analysis Laboratory at the University of Nevada, Reno.

*Isotope analysis-* Isotopic  $\delta^{13}\text{C}$  was used to determine the flow of organic matter through food webs (Gu *et al.* 1994; Kling 1994; Vander Zanden *et al.* 1999). The minimal enrichment ( $\pm 4.7$  ‰) from lower to high trophic levels allowed for the differentiation of methanogenic/pelagic and littoral primary production sources (Hecky and Hesslein 1995; Vander Zanden and Rasmussen 2001; Hershey *et al.* 2006). In order to determine the energy sources utilized by zoobenthos, we processed invertebrate samples for stable carbon isotope analysis. Invertebrate samples were dried at 60°C for at least 24 hours then ground into a fine powder by mortar and pestle. The samples were packed into tin capsules (8 x 5 mm) and analyzed for carbon using continuous flow isotope ratio mass spectrometry (IRMS) (20-20 mass spectrometer, PDZEuropa Scientific, Sandbach, United Kingdom). Sample combustion to CO<sub>2</sub> occurred at 1000 °C in an inline elemental analyzer (PDZEuropa Scientific, ANCA-GSL). The gases were separated on a Carbosieve G column (Supelco, Bellefonte, PA, USA) before introduction to the IRMS. These gases were compared to a standard gas (Pee Dee Belemnite) injected directly into the IRMS before and after the sample peaks. Carbon isotopic ratio was expressed as a per mil (‰) deviation defined by the following equation:  $\delta^{13}\text{C} = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}} / ({}^{13}\text{C}/{}^{12}\text{C})_{\text{standard}} - 1] * 1000$ .

Thus, more positive  $\delta^{13}\text{C}$  was more isotopically enriched, or contained proportionally higher concentrations of heavier  $^{13}\text{C}$  isotope. After approximately twenty samples, a replicate and a standard were added to the analysis. Replicate variation was less than 3% and machine analytical error is within 0.2 ‰.

To aid in interpretation, the energetic dependency of zoobenthos were quantified using a two end member mixing model of the  $\delta^{13}\text{C}$  data (Vander Zanden and Vadeboncoeur 2002). Percent methanogenic reliance was estimated as follows:

$$\%_{\text{pelagic|methanogenic}} = \frac{\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{littoral benthic}}}{\delta^{13}\text{C}_{\text{littoral benthic}} - \delta^{13}\text{C}_{\text{pelagic|methanogenic}}} \times 100$$

Where  $\delta^{13}\text{C}_{\text{consumer}}$  was the individual  $\delta^{13}\text{C}$  value for a particulate invertebrate taxa. The littoral benthic autochthonous (most positive  $\delta^{13}\text{C}$  value of zoobenthos within each lake) represented the benthic primary production signal. The methanogenic endpoint (mean  $\delta^{13}\text{C}$  for all *Chaoborus* and *Daphnia* samples within a lake) represented the methanogenic signal. The genus *Chaoborus* was used as the methanogenic endmember because they live in the profundal zone that is typically influenced by anoxia when the lakes stratify and by the thaw bulb. In the absence of an Ekman dredge, *Chaoborus* can be caught with a zooplankton net because they move from the benthos to the water column (Merritt & Cummins, 1984). The genus *Daphnia* was used because they also migrate to the area where methanogenesis is occurring. Of the 60 thermokarst lakes studied by Walter *et al.* (2006) in the same region, half had modest thermokarst erosion with methane hotspots along a 15-m-wide belt along thaw margins. The other half of the lakes studied had more intense thermokarst erosion and a >30-m-wide belt of hotspot erosion. The fluxes from these bands accounted for a majority (79-90%) of the methane emissions from

thermocarst lakes. This methane escaping via ebullition is not available to lake production, but it is assumed to correlate to areas of high dissolved methane, methane trapped in the sediment and bacteria which incorporate methanogenic carbon into their cells. There was only *Chaoborus* and *Daphnia* samples from the three thermocarst lakes, so in order to compare all four lakes the zooplankton were taken out and only the littoral  $\delta^{13}\text{C}$  was used. Taxa of varying specificity were categorized into feeding strategy groups based on their most probable functional feeding group classification with information from Thorp & Covich (1991) and Merritt & Cummins (1984). In this categorization the ‘collector’ group contains a broad spectrum of feeding strategies that did not fit into other categories including: collectors, gatherers, filter feeders, scavengers, shredders and piercers. The category became the catch all due the fact that it is broad in nature and contains generalist species such as the family *Chironomidae*.

## Results

Temperature was slightly higher in Shuchi Lake (Table 1). Fire Lake, the only floodplain lake, had the greatest surface area and shallowest max depth. Tube Dispenser and Shuchi had the greatest maximum depth of the four lakes sampled. The two lake types had similar water chemistry in terms of temperature, dissolved oxygen and pH. Specific conductivity was noticeably higher in the two deeper lakes Shuchi and Tube Dispenser, although sample size was too small to show statistical difference.

The dominant taxa, with qualitative analysis included, were the order *Insecta* and the sub class *Oligochaeta* (worms) from the class *Clitellata* (Figure 2). Other types of animals commonly found included the classes *Malacostraca* (mainly amphipods), *Gastropoda*, and *Bivalvia*. The order *Diptera* made up almost 80 % of all insect families. We found the family *Chironomidae* to have the greatest density of the insects collected. Based on one standard error, the density of zoobenthos was greater in the floodplain lake than in the non-eroding side of thermokarst lakes, and neither were different from the eroding side of thermokarst lakes (Figure 3). Within the thermokarst lakes, the samples showed no difference in density between eroding and non-eroding sides. In the eroding sides of the thermokarst lakes, density of taxa other than *Clitellata* and *Insecta* was a majority of the density found, unlike in the non-eroding thermokarst edges and the floodplain lake (Figure 3).

When comparing all four lakes, only the littoral  $\delta^{13}\text{C}$  values were used in order to separate methanogenic and pelagic signals in  $\delta^{13}\text{C}$  depletion. The floodplain lake was different than the two active thermokarst lakes, Tube Dispenser and Shuchi and not different than the other

thermocarst lake, Horse Jaw (Figure 4, Table 3). The three thermocarst lakes' mean  $\delta^{13}\text{C}$  was not different. Mean pelagic/methanogenic carbon supply was greater in the pelagic group than all the other feeding strategy groups (Figure 5, Table 4). The grazers (snails) mean pelagic/methanogenic carbon supply was greater than the predators and the detritivores (segmented worms), but not significantly different from the collectors (insects, clams and amphipods) (Figure 5, Table 4).

## Discussion

The patterns of density and diversity of zoobenthos in this region are comparable to temperate regions and diversity was greater than expected in arctic lakes. Density was greater in the floodplain lake, suggesting a difference in the habitability of this type of lake compared to thermokarst lakes, either due to a greater surface area or a less frequent disturbance regime. Zoobenthos are important in carbon processing (Wallace & Webster 1996; Covich 1999), but further investigation is necessary to better understand their role in methane-producing thermokarst lakes. A difference in mean littoral  $\delta^{13}\text{C}$  between floodplain and thermokarst lakes shows the difference in methane production through primary and secondary consumer uptake of methanogenic carbon. We found a clear difference in pelagic and benthic consumers' carbon isotope ratio supporting Hershey's (2006) hypothesis that the linkage between pelagic and primary production and benthic secondary production is small. A difference was found between benthic consumer feeding strategy groups, specifically grazers and detritivores suggesting a possible difference in methanogenic carbon at different trophic levels within the benthos. Increased erosion and methane ebullition on the active side might increase zoobenthos richness in thermokarst lakes although our data set is too small to state this with any real certainty.

The overall diversity of benthic macroinvertebrates in the Kolyma Basin was comparable to what might be found in a temperate climate even though biodiversity of benthic invertebrates often decreases towards high latitudes (Hebert and Hann 1986; Gibson and Bayly 2007). This may be because this region was not covered by an ice sheet in the last glaciation (Gauliteri *et al.* 2003) or because area is sparsely populated and littoral and wetland regions are entirely intact. Zoobenthos community structure is more diverse when a lake ecosystem includes an extensive



littoral and wetland region (Wetzel 2001). Compared to arctic lakes however these lakes show relatively high diversity (Figure 2). All zoobenthos taxa (amphipods, mollusks, turbellarians, and oligochaetes) listed by Vincent & Laybourn-Parry (2008) were found in our study. The most dominant taxa found, the order *Clitellata* are known to contribute to high-latitude benthic invertebrate community but the number of species present is often limited (Vincent & Laybourn-Parry 2008). The diversity of oligochaetes in our study remains unfortunately unknown due to the technicality involved in the identification of this subclass. The second most abundant taxa, non-biting midges, *Chironomidae*, are the most numerous benthic invertebrate group and one of the best adapted and most successful insect groups in the arctic. (Vincent & Laybourn-Parry 2008). They can form up to 95% of benthic community species composition (Oliver 1964). Other taxa of the class *Insecta* were present although found in limited abundance.

Density in the floodplain lake was higher than the non-eroding side of thermokarst lakes and not different from the eroding side of thermokarst lakes. This may be due to the higher lake area found in our floodplain lake as mentioned by Heino (2008) as one of the important environmental variables shaping variation in abundance of littoral macroinvertebrates. It is also possible that the difference in organism density between floodplain and thermokarst lakes is due to their respective disturbance regimes. The annual flooding of lakes located along the Kolyma lowlands provides an infrequent, high magnitude disturbance and supports a more abundant macroinvertebrate community while thermokarst lakes are undergoing continuous erosion during the warm season.

The eroding side of thermokarst lakes appeared to have less dominance by the classes *Insecta* and *Clitellata* than in the non-eroding side and floodplain lakes (Figure 3). For some reason the constant disturbance or higher levels of methane are providing a suitable habitat for genus *Gammarus* (scavengers) and class *Gastropoda* (detritivores) to grow in abundance. The density that we found zoobenthos in arctic lakes of this region is comparable to other arctic lakes as well as lakes found in temperate environments (Figure 3) in concurrence with previous literature (Hebert and Hann 1986; Gibson and Bayly 2007). The eroding and non-eroding sides of the thermokarst lakes studied showed no difference in density (Figure 3), so the difference of increased erosion and methane ebullition increase zoobenthos richness and make no noticeable difference in density.

The fact that the littoral  $\delta^{13}\text{C}$  floodplain lake is different from the active thermokarst lakes and not the partially drained less active thermokarst lake, Horse Jaw, leads us to believe that this difference is due to methane production and zoobenthos uptake of methanogenic carbon. The group of pelagic invertebrates (zooplankton) is expected to have more depleted values of  $\delta^{13}\text{C}$  than littoral consumers (France, 1995). An uncoupling of carbon flows between benthic and planktonic food webs may be a characteristic worldwide. The grazers (snails) mean pelagic/methanogenic carbon supply being greater than the predators and the detritivores (segmented worms) points to a difference in methanogenic carbon between living plant matter the snails are eating and the dead matter that the oligochaetes are eating as these taxa both live in the littoral zone. The grazers not being significantly different from the collectors (insects, clams and amphipods) is expected due to the variety in feeding strategies of the collector group (Figure 5, Table 4).

It is difficult to tell if  $^{13}\text{C}$  depletion is due to methanogenic carbon content or if it is signal of pelagic autotrophs due to similar signals. Methanogenic carbon is likely incorporated in biota along both pelagic and benthic trophic flows because these lakes have a large amount of methane production (Walter *et al.* 2006) and although variable arctic lakes in general have lower autotrophic production. The relatively small depletion in  $^{13}\text{C}$  compared to values in other systems may be due to the fact these systems are already abundant in dissolved organic carbon. In this study, the comparison of littoral  $\delta^{13}\text{C}$  between lakes gives some signal to this depletion being correlated methanogenic carbon. More specific identification and increased sampling to include off-shore zoobenthos would likely show higher  $^{13}\text{C}$  depletion related to methanogenic carbon (Hershey 2006). The tribe *Chironomini* constructs tubes (Walshe 1951) that has higher methane oxidation rates and higher densities of methanotrophic bacteria than surrounding surficial sediments (Kajan and Frenzel 1999). Members of the subfamily *Chironiminae* were found, but were not identified to tribe. The  $^{13}\text{C}$  of *Chironiminae* from our study were no more depleted than the mean depletion throughout the lakes studied.

Future work on this topic should include an increased number of study lakes and longer term sampling to compare spring and summer conditions as well as changing conditions over time. A more specific examination of the relationship between macroinvertebrates and their surrounding water and sediment chemistry should be explored, especially because conditions are expected to change dramatically over time. Macrophyte cover, total phosphorus, and water hardness should be assessed and compared to macroinvertebrate communities. They were found to be the environmental variables that most affected the variability in the abundances, diversity and

community structure of functional groups in a similar study (Heino 2008). Analysis of  $^{13}\text{C}$  isotopes could be compared to lake specific methane budgets and should include both offshore and onshore zoobenthos as done by Hershey *et al.* (2006) to better demonstrate incorporation of methanogenic carbon.

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## Tables

Table 1. Pelagic physical and chemical lake parameters for the four focus lakes in northeastern Yakutia, Russia. The temperature, DO, specific conductivity and pH are for the top meter of the water column in each lake, assumed to be equivalent to littoral water.

Lake Parameter	Shuchi	Tube Dispenser	Horse Jaw	Fire Lake
Location	68.74N 161.39E	68.76N 161.40E	68.63N 159.04E	68.73N 161.45E
Lake Type	Thermokarst			Floodplain
Temperature (°C)	17.5	13.85	12.3	14.6
DO (mg/L)	9.16	9.24	9.63	10.55
Specific Conductivity	52.5	60.95	35.6	32.6
pH	7.57	7.8	7.36	7.55
Surface area (m <sup>2</sup> )	49,500	92,700	173,700	63,900
Max depth (m)	~18	~18	4.5	2.5
Secchi depth (m)	3.75	2.95	3.95	2.28
δ13C Range	-43.5 to -28.0	-42.6 to -28.8	-42.7 to -26.3	-37.8 to -26.6

Table 2. Feeding strategy groups of taxa for  $\delta^{13}\text{C}$  methanogenic endmember analysis in three thermokarst lakes in northeastern Yakutia, Russia. Different levels of taxa were put in groups based on most probable feeding strategies. E.g., after Merritt and Cummins (1984). All groups are benthic except the 'Pelagic' feeding strategy.

<b>Pelagic</b>	<b>Predator</b>	<b>Collector</b>	<b>Detritivore</b>	<b>Grazer</b>
Chaoborus n=5 Copepoda n=6 Daphnia n=6 Cyclopoida n=1	Ceratopogonidae n=4 Glossiphoniidae n=4 Hirudinidae n=4 Hirudinea n=1 Coenagrionidae n=1 Piscicolidae n=1	Chironominae n=5 Sphaeriidae n=2 Chironomidae n=8 Gammarus n=3 Caenidae n=1 Sphaerium n=1 Chrysomelidae n=1 Corixidae n=2	Oligochaeta n=6 Turbellaria n=2	Gyalus n=4 Planorbidae n=4 Lymnaeidae n=3

Table 3. P-values from t-tests to test whether the means of each littoral  $\delta^{13}\text{C}$  values (VPDB) of a lake is different than the other three lakes in northeastern Yakutia, Russia.

	Fire	Horse.Jaw	Shuchi
Horse.Jaw	0.077	-	-
Shuchi	0.033	0.653	-
Tube.Dispenser	0.01	0.578	0.975

Table 4. P-values from t-tests to test whether the means of each feeding strategy is different than the other feeding strategy in three thermokarst lakes in northeastern Yakutia, Russia.

	Collector	Detritivores	Grazers	Pelagic
Detritivores	0.2392	-	-	-
Grazers	0.2891	0.0627	-	-
Pelagic	2.80E-07	1.00E-06	0.0005	-
Predators	0.1677	0.9554	0.0349	1.30E-08

## Figures

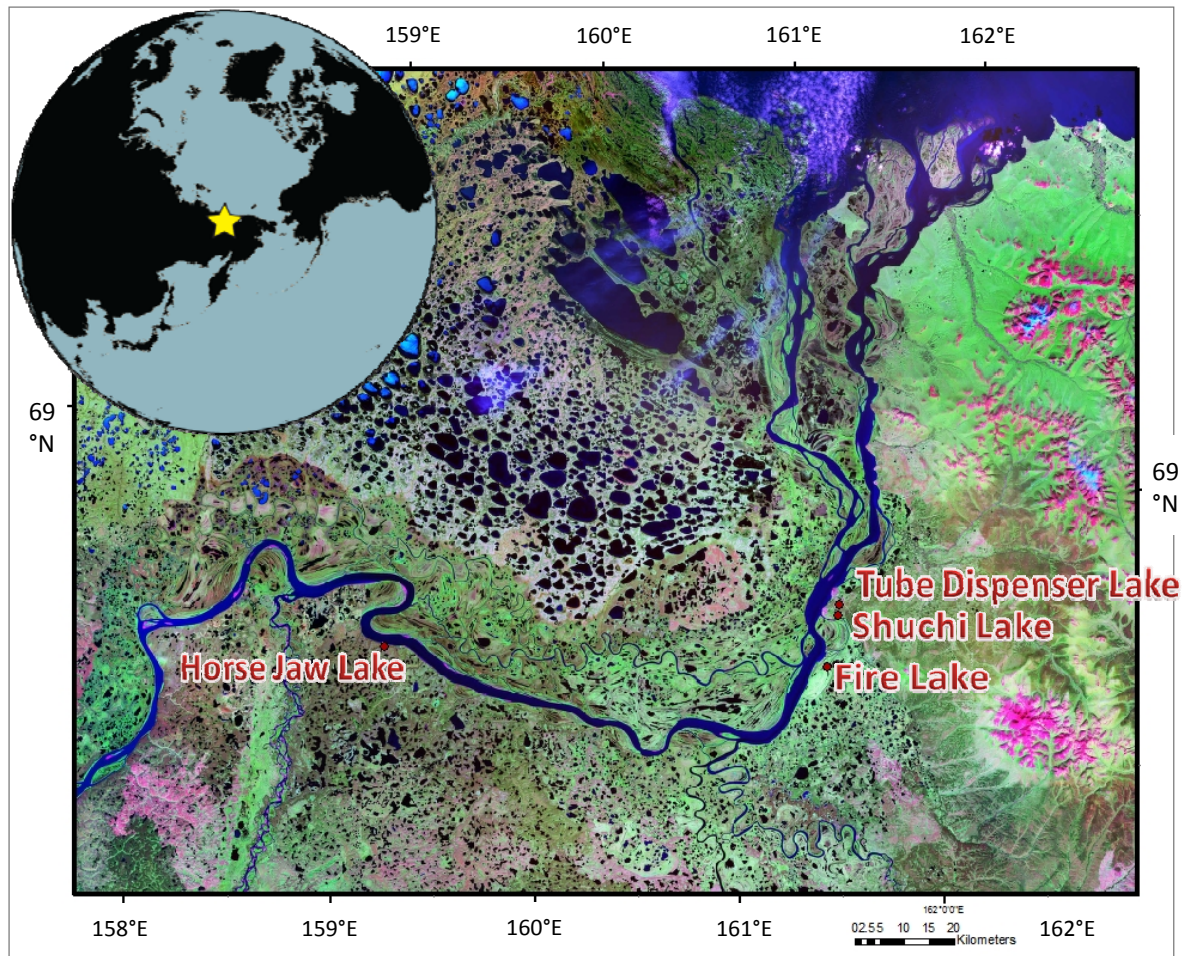


Figure 1. The Kolyma River is the largest arctic river underlain by continuous permafrost. The main study sites are the four lakes marked above found on the margin of the Kolyma River, each of which was sampled for water chemistry and benthic macroinvertebrate communities in the summer of 2009, Landsat 7, USGS.

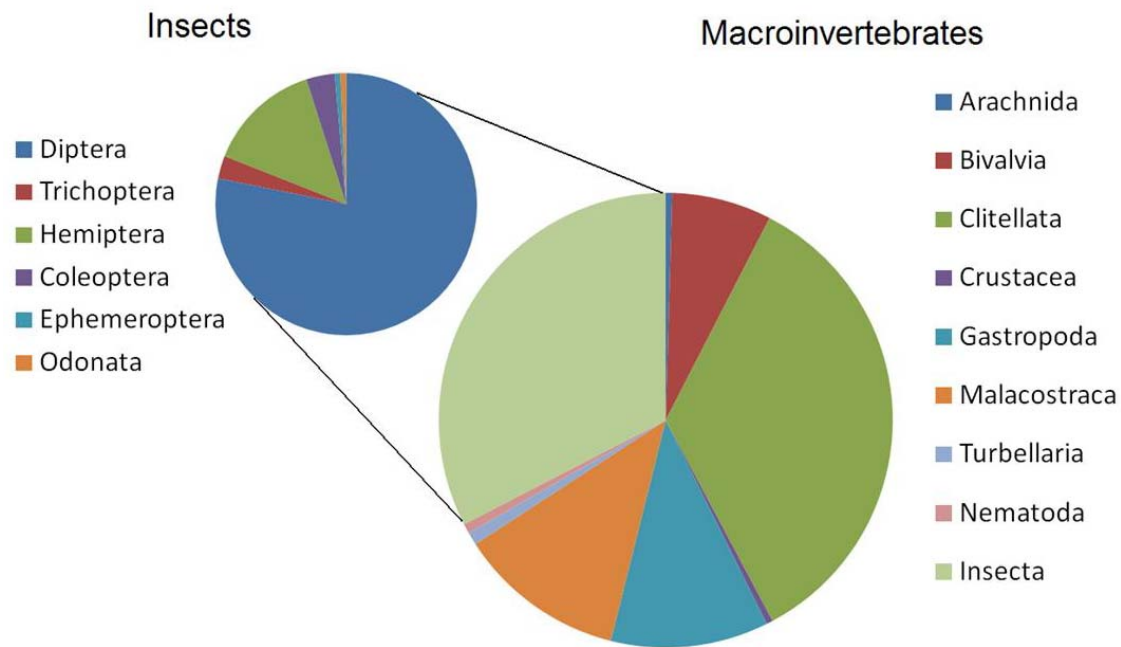


Figure 2. Macroinvertebrate diversity of all samples collected from northeastern Yakutia, Russia divided by order, except nematoda, which was only identifiable to phylum. Insects are further classified to family due to the great taxonomic variation.

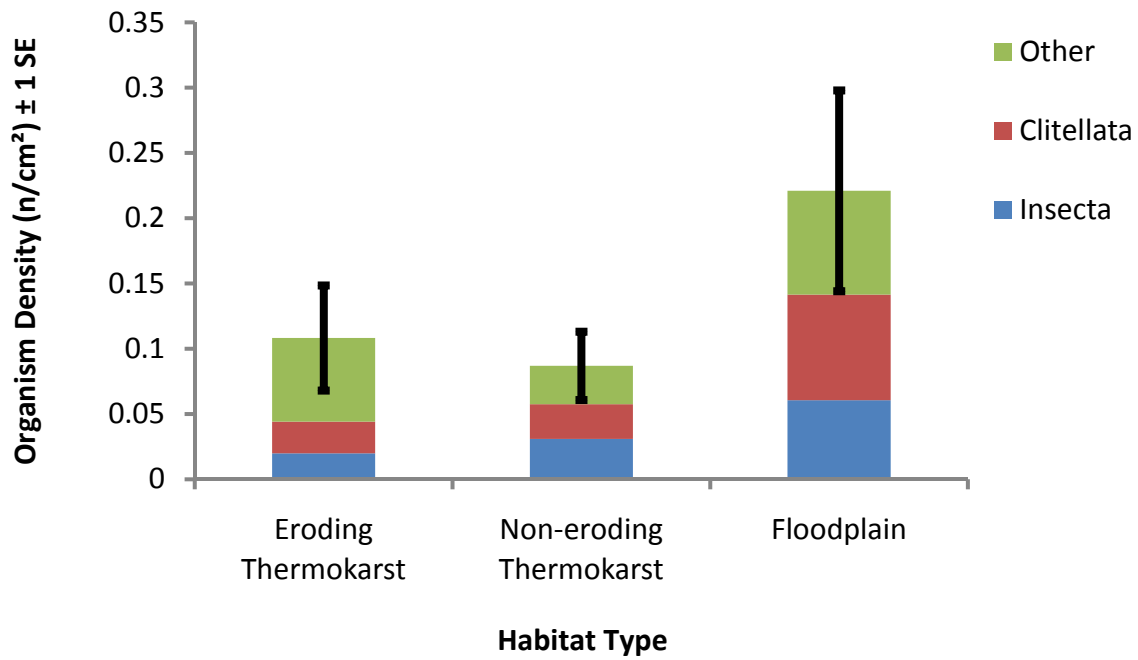


Figure 3. Mean macroinvertebrate density by dominant classes, clitellata (sub-class: (oligochaeta) and insect compared between three arctic lake habitats in northeastern Yakutia, Russia. Error bars are  $\pm 1$  SE of mean density across taxa.

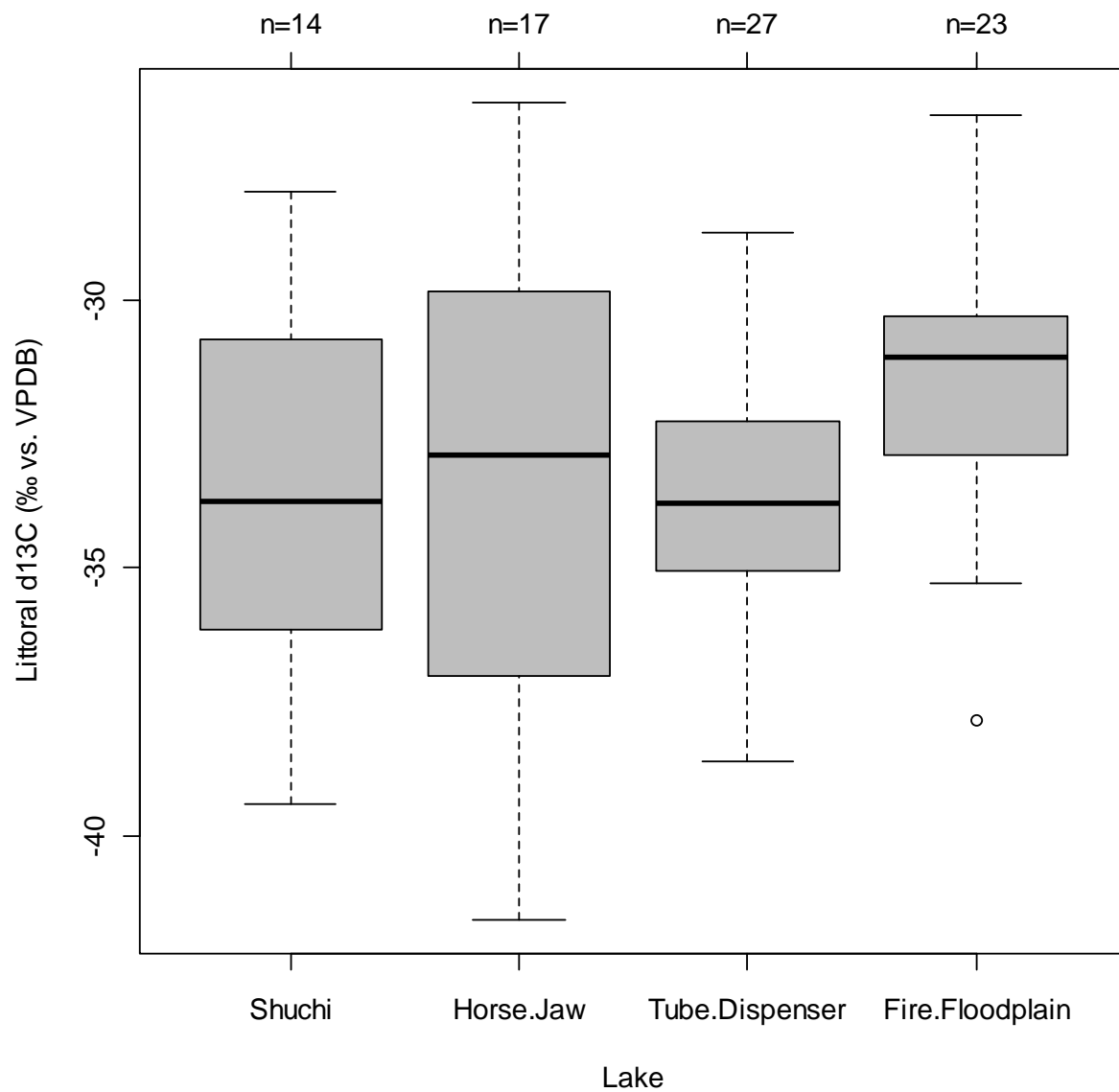


Figure 4. Littoral  $\delta^{13}\text{C}$  values (VPDB) of three thermokarst and one floodplain lakes in northeastern Yakutia, Russia. Within the lakes, the floodplain lake, Fire, is different than the thermokarst lakes, Shuchi and Tube Dispenser, but not Horse Jaw. None of the thermokarst lakes are different (Table 3;  $p > 0.05$ ).



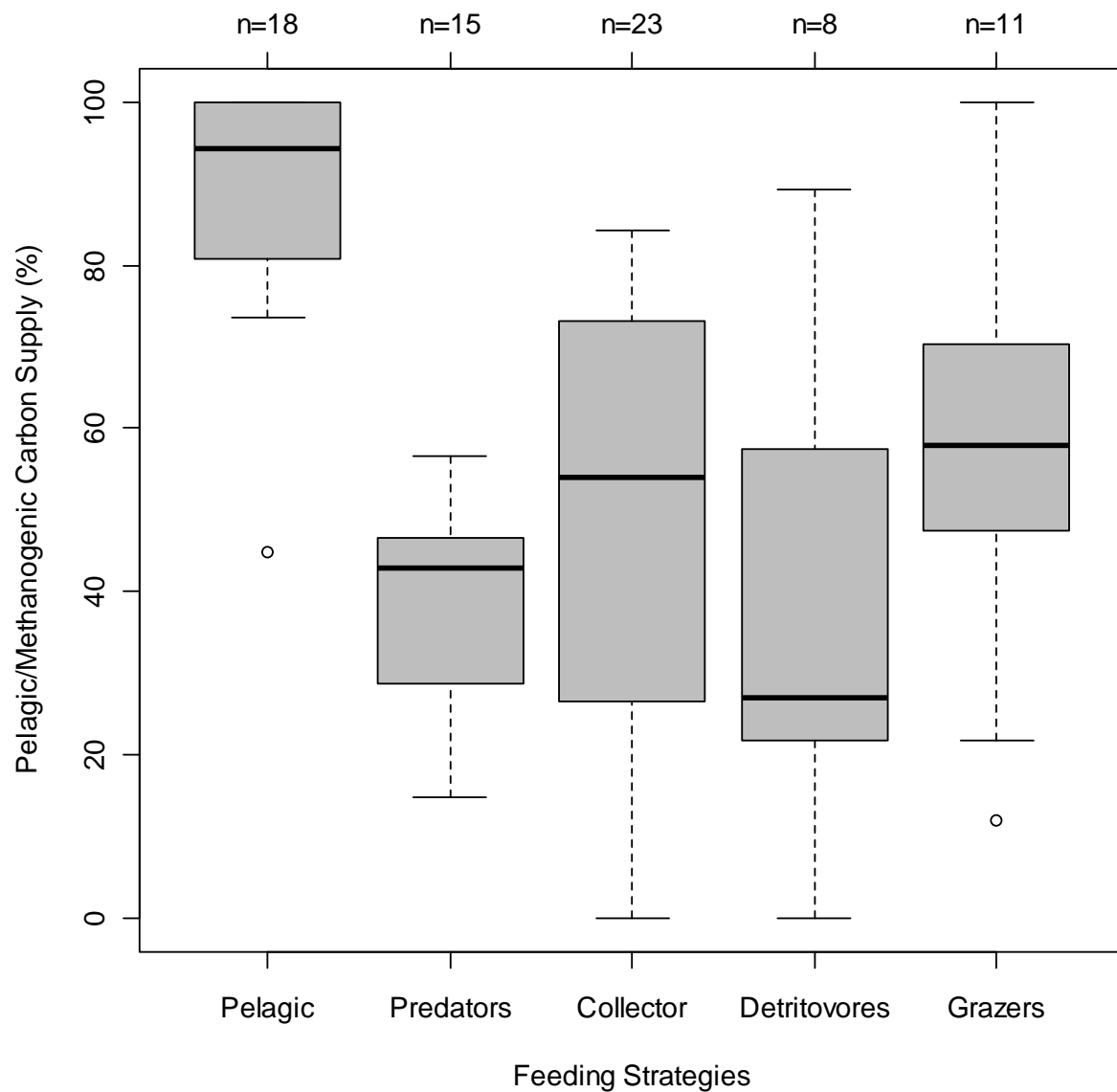


Figure 4. Methanogenic carbon supply as determined from  $\delta^{13}\text{C}$  endmember mixing model for five feeding strategies from three thermokarst lakes in northeastern Yakutia, Russia (compare with Table 2). All groups are benthic except the ‘Pelagic’ feeding strategy. Pelagic feeders differ significantly from the benthic groups. Within the benthic groups, the grazers are different than the predators and the detritivores, but not the collectors (Table 5;  $p>0.05$ ).