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DIFFERENCES IN DRIFTING INVERTEBRATE COMMUNITIES ACROSS ARCTIC ECOZONES AND THE INFLUENCE ON POTENTIAL GROWTH OF GRAYLING (Thymallus arcticus)

Charles Chanyi
chan7050@mylaurier.ca

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DIFFERENCES IN DRIFTING INVERTEBRATE COMMUNITIES ACROSS ARCTIC ECOZONES AND THE INFLUENCE ON POTENTIAL GROWTH OF GRAYLING (*Thymallus arcticus*)

by

Charles-Matthew Chanyi

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Abstract:

Invertebrate drift is a key process that potentially affects multiple levels of food web organization within stream environments. However, our understanding of the mechanistic drivers of drift in high latitude streams and subsequent bottom-up control that drift may have on fish predators in these environments remains understudied. This project aimed to gain the baseline knowledge of how drift functions across two major high latitude ecozones, the boreal forest and tundra, and how those possible differences in drifting community characteristics may impact drift-feeding Arctic grayling (*Thymallus arcticus*). These objectives were accomplished by characterizing stream environments across both ecozones, sampling the benthic macroinvertebrate (BMI) community and drifting components of macroinvertebrate communities, and utilizing drift data in a drift feeding bioenergetics (DFBM) model to calculate potential tissue growth of Arctic grayling. Both benthic and drift compositions differed significantly based on ecozone. Abundances of BMI were 10 times greater in tundra streams. Nevertheless, drift densities between the two ecozones remained equal, suggesting drivers within boreal streams promoted active drift. Potential drivers of drift in boreal streams were higher benthic predator presence, and resource limitations due to significantly lower TDP and increased shading. Body size of drifting invertebrates did not differ between ecozones and, in combination with equal drift densities, produced no difference in potential growth of grayling. Potential growth of grayling differed by age-group, with grayling fry having higher growth potential than juveniles, suggesting the habitat of these smaller tributaries is not suitable for juveniles at this time of year (August 2021). Growth potential also differed significantly based on food resources. Benthic prey items provided the most growth potential across both ecozones. Potential growth derived from terrestrial and upstream lentic sources was significantly higher in boreal and tundra streams respectively, suggesting potential dietary differences between the grayling in boreal and tundra streams.

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List of Abbreviations:

Abbreviation	Meaning
ANOVA	Analysis of the Variance
BCDM	Bray-Curtis Dissimilarity Matrix
BMI	Benthic Macroinvertebrate
CABIN	Canadian Aquatic Biomonitoring Network
DFBM	Drift Feeding Bioenergetics Model
DFS	Drift Feeding Salmonid
DOC	Dissolved Organic Carbon
EMD	Eastern Mackenzie Delta
EPT	Ephemeroptera, Plecoptera, and Trichoptera
GEE	Google Earth Engine
ITH	Inuvik-Tuktoyaktuk Highway
NDVI	Normalized Difference Vegetation Index
NEI	Net Energy Intake
NMDS	Nonmetric Multidimensional Scaling
PERMANOVA	Permutational Analysis of the Variance
SBS	Southeastern Beaufort Sea
SIMPER	Similarity Percentages
TDN	Total Dissolved Nitrogen
TDP	Total Dissolved Phosphorus
TSS	Total Suspended Solids
UD	Upper Dempster Highway
YoY	Young-of-the-Year

CHAPTER 1: INTRODUCTION

1.1 – Invertebrate Drift:

Invertebrate drift is the downstream transport of terrestrial and aquatic invertebrates in fluvial environments and is a key process in stream ecosystem health at multiple levels of organization. For example, drifting is a mechanism of patch selection for individual benthic macroinvertebrates (BMIs), where they balance predator avoidance with resource acquisition (Kohler & McPeek, 1989). Within the benthic population, drift influences spatial structure of BMIs through density-independent dispersal and emigration, or with density-dependent self thinning of the populations (Mackay, 1992; Townsend & Hildrew, 1976). Finally, at the ecosystem scale, drift contributes to a vital pathway within freshwater food-webs, linking basal trophic resources to top trophic drift feeding predators, most notably the salmonids (e.g., trout, salmon, grayling) (Grossman, 2014; Piccolo et al., 2014).

Due to the importance of drift as a mechanism within stream environments, it has been the subject of fluvial ecological research for decades (for reviews of drift see Brittain & Eikeland, 1988; Naman et al., 2016). Despite many research projects focusing on invertebrate drift, the majority of research conducted pertains to temperate regions, with functionality of drift in high latitude streams remaining understudied considering the relevance of drift to stream functionality. Therefore, there is a need to understand drift in high Arctic environments, and more specifically how the functionality and drivers of drift may change across two major Arctic and sub-Arctic ecozones, the boreal forest and tundra.

Drift can be expected to diverge greatly between these two ecozones because of the numerous differences in biotic and abiotic conditions of boreal and tundra stream environments. For example, the denser riparian vegetation surrounding boreal streams may alter drift densities, with denser riparian vegetation and vegetative overhang having been observed to increase allochthonous inputs of terrestrial invertebrates into the drift (Baxter et al., 2005; Nakano & Murakami, 2001). Furthermore, differences in benthic composition could impact drift as well. Scott et al., (2011) found that within Canada's Western Arctic, a decrease in the richness of Ephemeropteran and Plecopteran species, along with an increase in Dipteran and Trichopteran richness is to be expected as you move northward from boreal into tundra streams. Based on this, along with other established ecological trends in temperate regions, boreal streams would be expected to contain a higher diversity of drift prone Ephemeropteran and Plecopteran species (Rader, 1997) due to these taxa groups being cold intolerant, versus tundra environments where Dipterans and other stenothermic taxa hold a greater dominance over the benthic composition (Culp et al., 2019; Scott et al., 2011).With the abiotic and biotic conditions of the steams expected to differ between the ecozones, drift is expected to vary as well, but it is unknown what may drive these differences and, if present, how differences in drift may cascade up the food-web and impact an apex drift feeding predator.

1.2 – Arctic Grayling Ecology:

A common drift-feeding predator present within boreal and tundra streams in Canada's Western Arctic is the Arctic grayling (Figure 1.1; *Thymallus arcticus;* Pallas, 1776). Arctic grayling are a drift feeding salmonid (DFS) from the sub-family *Thymallinae* and have a Holarctic distribution across North America and Asia (Craig & Poulin, 1975; Northcote, 1995). The size and lifespan of grayling differ greatly based on population; however, the life cycle is regarded as ubiquitous, with grayling occupying deep lakes and rivers as overwintering habitat before moving into smaller tributaries during the spring snow melt to spawn. Adults will return to their overwintering areas post-spawn, with juveniles and young-of-the-year (YoY) grayling inhabiting the smaller tributaries throughout the summer, where both life-stages occupy a top trophic position in the food-web (Craig & Poulin, 1975; Hughes & Dill, 1990; Jones et al., 2003).

Arctic grayling are critically understudied in the Arctic. Notably, as a species with Holarctic distribution, it is still relatively unknown how prey availability (drift densities), prey quality (size of drifting invertebrates; mm) and source of prey changes across their distribution. Prey availability and quality are directly related to growth of a salmonid species, with growth being tied to population survival (Piccolo et al., 2014; Rader, 1997). Therefore, to better understand how food quality and quantity for stream fish may change between the boreal and tundra ecozones, there is a need to determine how the drift component of stream macroinvertebrate communities changes across these regions, what are the major drivers of drift differentiating boreal and tundra regions, and how those differences influence potential growth of grayling.

Figure 1.1: Preserved YoY *Thymallus arcticus* (Pallas, 1776) collected in Alaska USA by Fish Collection (Vouchers) (NEON-FISC-V) (licensed under: https://creativecommons.org/publicdomain/zero/1.0/)

1.3 – Drift Feeding Bioenergetics Model:

Potential growth calculations derived from drifting community characteristics contribute to an estimation of habitat suitability for salmonids and can be estimated by a drift feeding bioenergetics model (DFBM). DFBMs use a combination of a stream's physical characteristics (depth, width, velocity), prey characteristics (drift densities, prey size), and the physiological characteristics of a drift feeding fish species to estimate the amount of net energy intake (NEI, J/hr) a stream system can provide, with the end goal of using NEI to calculate potential tissue growth (g/day) (Hughes, 1998; Hughes & Dill, 1990). With both prey availability and size as variables that may determine differences in habitat suitability, the use of a DFBM is ideal to understand how potential differences in drifting communities may have bottom-up control on Arctic grayling within the two ecozones. Larocque et al., (2014) developed a DFBM specifically for northern populations of Arctic grayling, and this model will be applied in this project and to my knowledge is the first instance model use (Table 1.1).

Table 1.1: Summary of equations used in DFBM for Arctic grayling to estimate habitat suitability.

Variable	Equation	Source
Net Energy Intake (J/hr) (NEI)	$Net\ Energy\ Intake = GEI - SC$	Hughes and Dill (1990)
Swimming Cost (J/hr) (SC)	$SC = 10^{(C+M\cdot V)} \cdot 19 \cdot \frac{FW}{1000}$	Hughes and Dill (1990)
Gross Energy Intake (J/hr) (GEI)	$GEI = E \cdot UE$	Hughes and Dill (1990)
Utilization Energy (UE)	$UE = 1 - \frac{SDA + F + U}{100}$	Hughes and Dill (1990)
Energy Intake (J/hr) (E)	$E = CR \cdot PE$	
Consumption Rate (g/hr) (CR)	$CR = \frac{ER}{1 + ER \cdot H} \cdot PM \cdot 60 \cdot 60$	Hughes (1998)
Encounter Rate (#ind./s) (ER)	$ER = CA \cdot V \cdot PD \cdot 10^{-6}$	Hughes and Dill (1990)
Handling Time (s) (H)	$H = \frac{RD}{Vmax}$	Hughes (1998)
Capture Area (cm^2) (CA)	$If\ stream\ depth\ \geq 2 \cdot MCD, then$ $CA = \pi(MCD)^2$ $If\ stream\ depth\ \leq 2 \cdot MCD, then$ $CA = 2\{0.5 \cdot SD[\sqrt{MCD^2 - (0.5 \cdot SD)^2}] + MCD^2 \cdot \sin^{-1}\left(\frac{0.5 \cdot SD}{MCD}\right)\}$	Adapted from Hughes (1998) and Jenkins and Keeley (2010)
Maximum Capture Distance (cm) (MCD)	$MCD = \sqrt{\left[(RD)^2 - \left(V \cdot \frac{RD}{Vmax}\right)^2\right]}$	Hughes and Dill (1990)
Reactive Distance (cm) (RD)	$RD = 12 \cdot PL[1 - e^{-0.2 \cdot FL}]$	Hughes and Dill (1990)
Prey Mass (g) (PM)	$PM = 0.0064 \cdot PL^{2.788} \cdot 10^{-3}$	Benke et al. (1999)
Fish Weight (g) (FW)	$FW = 0.0224 \cdot Fish\ Length^{2.8379}$	Adapted from Bishop (1967)
Maximum Sustainable Swimming Speed (cm/s) (Vmax)	$Vmax = 36.23 \cdot FL^{0.19}$	Jones et al. (1974)

1.4 – Objectives and Hypotheses:

The goals of this thesis are to: **1)** characterize invertebrate drifting communities in streams across boreal and tundra ecozones to better understand this biotic component change across Arctic environments as well as exploring abiotic and biotic drivers of drift,, and **2)** utilize both drift densities (#ind./m^3) and prey size (mm) in a DFBM to determine how potential differences in drift densities and compositions impact an apex drift feeding predator in streams across boreal and tundra ecozones. Chapter 2 addresses the first goal by sampling and examining benthic and drift community compositions across 4 streams in each the boreal and tundra ecozones (n = 8), while Chapter 3 addresses the second goal through the implementation of a DFBM for Arctic grayling calculated across 7 streams (1 boreal stream omitted from drift sampling due to low flow) in both boreal and tundra ecozones. In Chapter 2 I develop hypotheses stating that:

(i) Both benthic and drift compositions would differ significantly based on ecozone.
(ii) Terrestrial drift inputs would be significantly higher in boreal streams.
(iii) EPT drift densities and relative abundance in benthic compositions would be significantly higher in boreal streams.
(iv) Richness and diversity of both benthic and drifting communities would be significantly higher in boreal streams.

In Chapter 3 I develop hypotheses stating that:

(i) Grayling growth potential will be significantly higher in boreal streams.
(ii) Grayling growth potential derived from terrestrial sources will be significantly higher in boreal streams.

(iii) Grayling growth potential derived from upstream lentic sources will be significantly higher in tundra streams.

(iv) Prey size will be significantly larger in boreal streams.

1.5 – Study Area and Study Design:

The Eastern Mackenzie Delta (EMD) and Southeastern Beaufort Sea (SBS) watersheds in Canada’s Northwest Territories are the two major watersheds that this project takes place in (Figure 1.2). The EMD is located within the boreal ecozone and is the more southern of the two watersheds, being near the town of Inuvik. This watershed consists of a mosaic of lakes, marshes, and sinuous tributaries of the Mackenzie River. Continuous permafrost is ubiquitous across the delta, with the sampled portion of the watershed being forested with open spruce woodlands scattered along peat plateaus. In contrast, the more northerly SBS is a tundra dominated landscape above the latitudinal treeline, which is an interconnected network of lakes and tributaries of the Husky Lakes situated near Tuktoyaktuk. Four streams from each region (n = 8) were selected for this project, where a series of environmental sampling included stream morphology, hydrology, water chemistry, along with kick-net sampling of the benthic communities and drift-net sampling of the drifting communities.

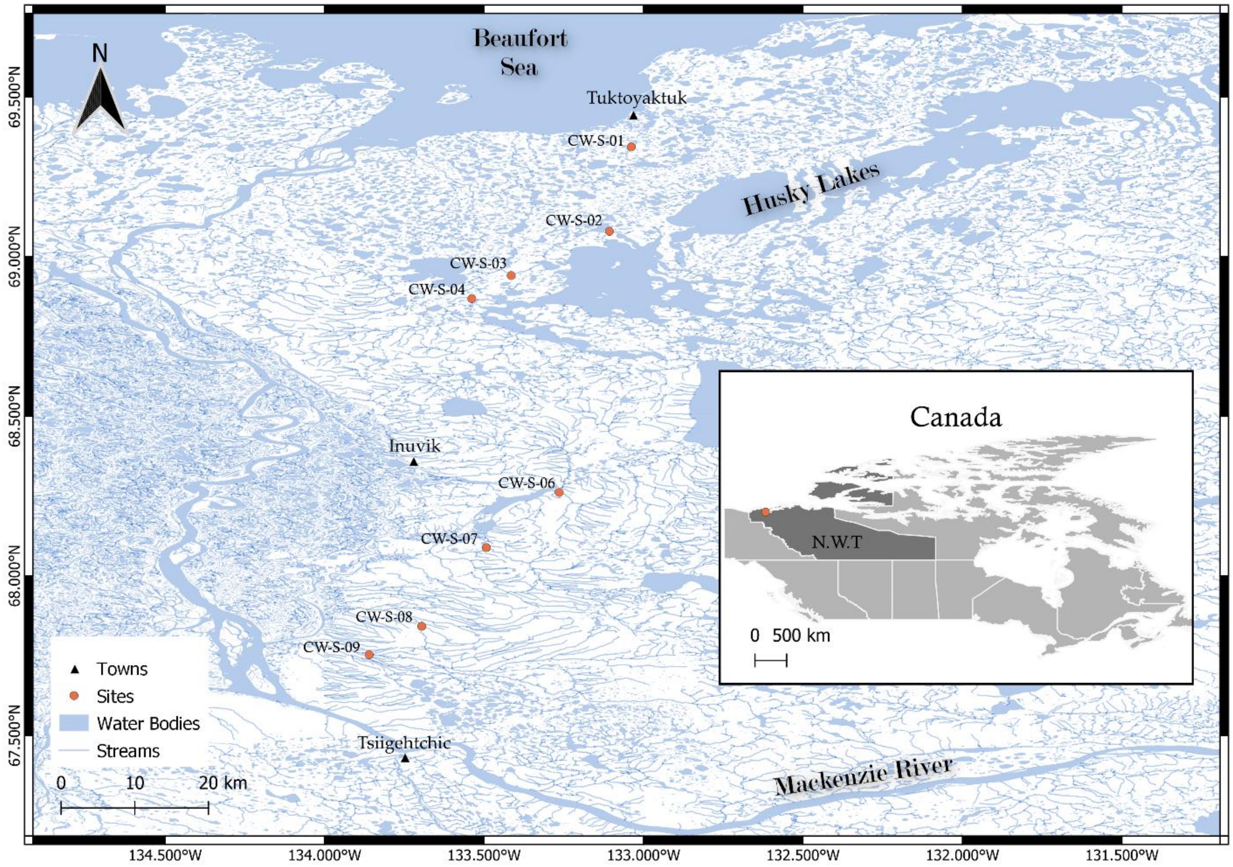

Figure 1.2: Map of the Mackenzie Delta and Southeastern Beaufort Sea watersheds, located Northwest in Northwest Territories, Canada. Towns in the area are represented by black triangles, and streams sampled in 2021 are represented by orange circles (CW-S-N). Blue lines show streams and larger water bodies are represented by blue bodies.

CHAPTER 2: CHARACTERIZING DRIFTING COMMUNITIES ACROSS BOREAL AND TUNDRA ECOZONES TO DETERMINE DRIVERS OF DRIFT

2.1 – Abstract:

Invertebrate drift is an important and well studied process within stream environments that consists of the downstream transport of invertebrates in stream environments. However, the various mechanisms and drivers of drift in high latitude streams are relatively unknown. The objectives of this study were to characterize the benthic and drift components of invertebrate communities, along with the site characteristics of streams in boreal and tundra ecozones to better understand what drivers within the benthic and surrounding environments are associated with patterns of drift densities in high latitude streams. Total dissolved phosphorus concentrations were significantly higher in tundra streams, while the riparian Normalized Difference Vegetation Index measurements and stream water conductivity were significantly higher in boreal streams. There was no significant difference in the base ecological metrics of richness, diversity, and drift density across ecozones. Benthic community abundances of BMI in boreal streams were on average 10% of tundra streams, suggesting drivers within boreal streams likely promoted active drift. Differences in benthic composition, such as significantly higher predator presence, may drive active drift in boreal streams. Significantly higher presence of gatherer mayflies and net-spinning caddisflies present in boreal compositions may increase competition for space and resources, further driving drift. In contrast, tundra drift may largely be passive, with significantly higher benthic abundances, and benthic compositions showing significantly higher relative abundance of passive drifting collector-filters (i.e., dipterans,

brachycentrid caddisflies). Additional analysis into primary production limitations is needed to further substantiate differences in drift functionality across boreal and tundra ecozones.

2.2 – Introduction:

Invertebrate drift is the downstream transport of invertebrates in running water and is important process in maintaining the ecological health of stream ecosystems at multiple levels of organization. At the individual level, drift is a mechanism related to selection of habitat patches within a stream, as invertebrates use the drift process to balance resource acquisition with predator avoidance (Kohler & McPeek, 1989). Within the aquatic invertebrate community, drift contributes to population spatial structure, where populations emigrate to resource rich areas, or disperse due to resource and spatial competition (Mackay, 1992; Townsend & Hildrew, 1976). At the community scale, drift contributes to key trophic pathways, transferring basal resources to top drift feeding predators such as salmonids (Piccolo et al., 2014; Rader, 1997).

Many drivers of drift have been identified and are broadly categorized as active or passive drift. Passive drift refers to invertebrates accidentally being dislodging from the substrate, either due to hydraulic stress or sediment scouring (Gibbins et al., 2007), with larger BMI at more risk of dislodgement (Rader, 1997). Active drift is deliberate behaviour by BMI, whereby drift is a mechanism used to avoid benthic predators (Huhta et al., 2000; Kratz, 1996), escape unfavourable abiotic conditions (Gibbins et al., 2007; James et al., 2009; Larsen & Ormerod, 2010), or move to downstream patches in response to resource limitation and competition (Corkum, 1978; Hildrew & Townsend, 1980; Kohler, 1992). Drift densities and the composition of drift, as a result, are a complex process of abiotic and biotic drivers interacting with each other, and many researchers have attempted to identify the key drivers of drift abundance and composition within specific stream systems (Naman et al., 2016).

Most drift research has occurred in temperate regions, with many gaps in knowledge evident for high latitude environments. Specifically, these gaps have included how drift processes may differ between two prominent Arctic and sub-Arctic ecozones, the boreal forest and tundra. Drift would be expected to diverge between these ecozones as a result of differences in abiotic and biotic conditions of streams environments with boreal and tundra systems. For example, the denser riparian vegetation present in boreal streams would add higher allochthonous inputs of terrestrial invertebrates to the drift (Baxter et al., 2005; Nakano & Murakami, 2001; Ryan & Kelly-Quinn, 2015). Additional inputs of plant detritus from the surrounding vegetation has the potential to increase resource availability for detritivores (Cross et al., 2006; Leach et al., 2012), which could lead to reduced food resource competition and the reduced shredders in the drift (Firmino et al., 2022; Presa Abós et al., 2006). In contrast, the interconnectivity of lakes and streams present in the tundra would allow for the addition of upstream lentic sources of drift (i.e., zooplankton and amphipods) (Jones et al., 2003).

Differences in benthic composition between the two ecozones may also influence drift. While BMI communities in the tundra and boreal streams of the western Canadian Arctic are poorly understood, ecological trends established in temperate streams suggest that boreal streams would support a greater diversity and higher abundances of the active drifting EPT (Ephemeroptera, Plecoptera, and Trichoptera) species (Rader, 1997) due to EPT species being cold-sensitive taxa (Scott et al., 2011; Vinson & Hawkins, 2003). Recent evidence indicates that benthic communities of more northerly stream ecosystems are dominated by dipterans (Culp et al., 2019) that are passive drifters. Previously, Kennedy et al. (2014) found that in Colorado systems, higher benthic abundances are often associated with higher drift rates due to passive drifters (e.g., dipterans) (Kennedy et al., 2014).With many differences between boreal and tundra streams in both biotic and abiotic environmental conditions present, and the lack of baseline knowledge on drift and benthic communities in high latitude streams, there is a need to examine drifting communities across multiple stream environments to better understand the mechanistic drivers of drift in high latitude streams.

This study aimed to assess drift and benthic invertebrate compositions across boreal and tundra environments to help understand the environmental drivers influencing drift in high latitude streams. Through this investigation, I hypothesized that: (i) drift composition would differ significantly between ecozones; (ii) terrestrial drift densities would be significantly higher in boreal streams; (iii) EPT drift densities would be higher in boreal streams; and (iv) richness and diversity of drifting communities would be higher in boreal streams. These hypotheses were tested by sampling both drift and benthic communities of 4 streams in each of the boreal and tundra ecoregions.

2.3 – Methods:

2.3.1 – Study Area

This project spans two major watersheds in Canada's Northwest Territories, namely the Eastern Mackenzie Delta (EMD) and Southeastern Beaufort Sea (SBS) watersheds (Figure 1.2). The EMD located southeast of Inuvik is a part of the Mackenzie River Basin, which is the largest Arctic delta in North America, with an area of 13,000 km^2. This large area is comprised of a mosaic of lakes, marshes, and sinuous tributaries of the Mackenzie River. Continuous permafrost is ubiquitous across the delta and its water features are ice covered or frozen between October and May (Burn, 2017). The southern portion of the EMD watershed is forested with open spruce woodlands scattered along peat plateaus, with riparian vegetation consisting of a variety of grasses and sedges (*Cyperaceae, Gramineae, Carex sp., Eriophorum sp.*), shrubs (alder; *Alnus viridis*), and both coniferous (spruce; *Picea glauca*) and deciduous (white birch; *Betula papyrifera,* and poplars; *Populus balsamifera*) trees (Burn & Kokelj, 2009; Wright et al. 2003).

The EMD has a mean annual temperature of -7.3°C with approximately 310 mm of total precipitation annually (Burn, 2017).

The more northernly SBS contains an interconnected network of lakes and tributaries of the brackish Husky Lakes (Imaryuk) and is located around the town of Tuktoyaktuk. This area is north of the latitudinal treeline and is a tundra-dominated landscape with grasses and sparse shrubs growing in drier uplands, while riparian areas contain a dense barrier of willow (*Salix sp.*) and ground birch typically less than 75 cm in height (Burn & Kokelj, 2009; Wright et al. 2003). The mean annual temperature and total precipitation of the SBS are -9.8°C and 151 mm, respectively. Peak flows for the EMD and SBS occur in May and June and are driven by spring snowmelt (Burn, 2017).

2.3.2 – Sample Design

In 2021, four boreal streams and four tundra streams were selected for macroinvertebrate sampling and comparative analysis based on their location being adjacent to either the Inuvik-Tuktoyaktuk (ITH) or Upper Dempster (UD) highways, as these road systems pass through both the EMD and SBS watersheds. During August 2021, these eight streams were chosen to be sampled for both macroinvertebrate kick and drift net samples. This is the seasonal period with the warmest average temperature as well as high macroinvertebrate diversity and standing crop. Additionally, environmental variables including stream chemistry, hydrological flow, streambed characteristics, nutrients, and physical characteristics such as depth and width were collected to characterize the abiotic conditions.

2.3.3 – Field Methods

2.3.3a – Macroinvertebrate Kick-net Sampling

Sampling of the benthic macroinvertebrate community was performed following a modified Canadian Aquatic Biomonitoring Network (CABIN) protocol for kick-net sampling (Environment and Climate Change Canada, 2012). A 400-µm kick-net was placed in the water facing upstream and a kicking motion was performed in front of the net as the sampler proceeded upstream in a serpentine pattern over 3 minutes of standardized effort. This sampling method aims to collect macroinvertebrates from the dominant habitat consisting of runs and pools, and riffles. The contents of the net were transferred to a 1 L widemouthed Nalgene bottle with contents preserved in 95% ethanol.

2.3.3b – Macroinvertebrate Drift Sampling

Macroinvertebrate drift sampling was done by placing drift nets (15 cm × 15 cm opening: 400 µm mesh) in the stream for a minimum of 24h. One stream was omitted from sampling due to low flow (velocity = 0.002 m/s). Nets were mounted on rebar poles secured with cable ties, with three spatial replicates per stream. All replicates were placed slightly downstream of a riffle, due to drift entry and transport being highest near riffles (Grossman, 2014; Grubaugh et al., 1997; Scullion et al., 1982). The first replicate was located on the left side of the stream, with each subsequent replicate placed approximately 5 – 10 m downstream and to the right of the upstream net to ensure that upstream samples did not affect downstream nets. The bottom of each net was placed a minimum of 4 cm above the stream bed to prevent organisms from crawling into the net, while the top of each net was located above the water surface to capture floating invertebrates, including those from terrestrial origin. Submerged net area (cm^2), water velocity (m/s) at the net opening, and time of day (24:00) were recorded at deployment and retrieval for drift density (#ind./m^3) calculations. Contents of the drift nets were transferred to a 1 L widemouthed Nalgene bottle and preserved using 95% ethanol.

2.3.3c – Environmental Variable Sampling

Bankfull and wetted widths (m) of the stream were determined with a surveyor measuring tape, with depth (cm) and velocity (m/s) being measured across six transects (3-4 if the stream was too shallow. Water velocity was measured using a SonTek FlowTracker1 at approximately 60% of the depth at each transect. Reach characteristics including canopy cover, riparian vegetation, periphyton, and macrophyte coverage were estimated according to CABIN protocol estimating over 6 times the bankfull width at the point of the transect measurement (Environment and Climate Change Canada, 2012). Stream substrate characteristics were determined using the Wolman pebble count method (D_{50}; Wolman, 1954), where 100 random substrate particles were sampled within the reach and their b-axis measured (Sutherland et al., 2010).

During August 2021 water temperature was measured continuously (1 hr intervals) with submerged data loggers (HOBO U20-001-01). In addition, water samples were collected from the centre of the stream in a well-mixed portion of the channel downstream of a riffle, with the sampling bottles being fully submerged in the stream. Water chemistry measurements included major ions (e.g., pH, alkalinity, conductivity), nutrients (e.g., dissolved inorganic/organic carbon, total dissolved nitrogen (TDN), total dissolved phosphorous (TDP)), trace metals (e.g., aluminium, iron, zinc), and total suspended solids (TSS), and were analyzed at the Institut National de la Recherch Scientifique (INRS) following standard operating procedures and QA/QC protocols for each variable measured.

2.3.3d – Catchment Characteristics

The catchment characteristics of catchment area (km^2), and distance from upstream lake (m) were measured using Google Earth Engine (GEE) code editor. Normalized Difference Vegetation Index (NDVI) along the riparian areas of the streams (within one bankfull-width) was calculated in GEE with the Sentinel2 MultiSpectral Instrument (MSI; Frantz et al., 2018) using the percentage of near infrared (NIR) and red-light wave lengths reflected back to the atmosphere.

$$NDVI = \frac{NIR - Red}{NIR + Red}$$

NDVI values range from -1.0 - 1.0, with values closer to 1.0 being denser vegetation. 10 measurements (5 x 5 m) of the NDVI on each side of the stream (20 measurements total per stream) were calculated and used to determine the density of riparian vegetation of every stream in this study. Imaging for the NDVI calculations were obtained over the period May 1st to August 30th, 2020 because NDVI could not be calculated consistently in 2021 across all streams due to excessive cloud cover.

2.3.3 – Lab Methods

Benthic macroinvertebrates from kick-net samples were sorted and identified to the lowest possible taxonomic level by Cordillera Consulting following CABIN sorting protocol, where a Marchant box was used to subsample to a minimum of 300 organisms. If 300 organisms had not been reached by the 50th cell of the Marchant box, then the entire sample was sorted.

QA/QC were completed by checking 10% of randomly chosen samples for a sorting efficiency of >95% in accordance with CABIN protocol (Environment and Climate Change Canada, 2012).

In the laboratory, large debris was removed from drift samples by passing the collected material through a 5-mm sieve with sample material retained on a 250-µm sieve. Material on the 250-µm sieve was placed in a gridded petri dish and examined with a dissecting scope (5× magnification) with all invertebrates removed, sorted to order, and identified down to family level following CABIN protocol (Environment and Climate Change Canada, 2012). Invertebrates were categorized for further analysis by benthic (drift subsidies from the stream bed), terrestrial (drift subsidies that fell into the stream), and lentic (drift subsidies from upstream still-water environments, i.e., zooplankton and amphipods) drifting groups. QA/QC were completed by resorting 20% of the samples (n=4) to confirm that the average sorting efficiency is >95%. Samples with high zooplankton abundance (i.e., average > 50 zooplankton within a grid) were subsampled using a Folsom plankton splitter (McEwen et al., 1954), where samples were divided down to a more manageable level (i.e., average < 20 zooplankton within a grid), zooplankton were counted, then abundances were estimated by using the appropriate multiplier (i.e., multiply by 2 for a ½ sample, multiply by 4 for a ¼ sample etc.).

2.3.5 – Statistical Analysis

All statistical analyses were performed in R Studio statistical software (*version 4.1.3,* R Core Team, 2022), with a significance level set at $p < 0.05$. Boxplots were created for base ecological metrics of benthic and drift samples, such as observed richness, diversity, abundance, and drift density. Each of these metrics was plotted based on ecozone (i.e., tundra or boreal).

Two-sample t-tests and Man-Whitney u-tests were performed for normal and non-normally distributed data sets respectively. Diversity was calculated using the Shannon-Weiner Diversity index (Peet, 1974).

$$H' = -\sum_{i=1}^{s} p_i ln p_i$$

Where p_i is the proportion of species i found in population, and S is the total number of species. Drift density (#ind./m^3) was calculated using the measured values of individuals in the drift sample after 24h (#ind.), and volume of water that passed through the net over 24h (m^3).

$$Drift\ Density\ \left(\frac{\#ind.}{m^3}\right) = \frac{\#individuals\ captured\ in\ 24h}{Volume\ of\ water\ through\ net\ in\ 24h}$$

The relative abundances (% of the population) of the four major benthic invertebrate orders (i.e., Ephemeroptera, Plecoptera, Trichoptera, Diptera) were calculated and arcsine transformed for both benthic and drift samples and compared using standard error bar-plots by ecozone. Relative abundance of functional feeding groups (i.e., Filterers, Collectors, Predators, Shredders, Scrapers) for the benthic samples, and the drifting groups (i.e., benthic subsidies, lentic subsidies, terrestrial subsidies) were also calculated, arcsine transformed, and plotted onto standard error bar-plots for comparisons between ecozones. Relative abundance was further analyzed based on ecozone using two-sample t-tests and Mann-Whitney u-tests for normal and non-normally distributed data (normality tested with Shapiro-Wilk tests), respectively, to examine if significant differences between the two ecozones exist.

Bray-Curtis dissimilarity matrixes (BCDM, Vegan R Package *Version* 2.5-7, Jari et al., 2020) were generated, and permutational multivariate analysis of variance (PERMANOVA) tests (permutations = 999) were conducted to see if compositional differences of the total drift subsidies, benthic drift subsidies, and benthic populations differed significantly based on ecozone. Nonmetric Multidimensional Scaling (NMDS) was performed and biplots were created for total drift, benthic drift, and benthic populations to aid in visualization of potential groupings of compositions based on ecozone. Dimensions (k) were chosen based on stress values generated from NMDS, where if the stress value did not fall <0.1, dimensions would be added until the stress value reached that requirement. Stress values near 0.1 are considered fair fits, with stress values closer to 0.05 being considered good fits. Similarity percentages (SIMPER) analyses were conducted for both the benthic and drifting communities across all sites to evaluate the differences in frequency of occurrence for taxa, and to rank order the cumulative percentages of taxa that account for the most dissimilarity across sites.

2.4 – Results:

2.4.1 – Site Characteristics

There were no differences in the physical characteristics (e.g., depth, widths, D_{50}, slope), velocity, or trace metals in streams across the two ecozones. Conductivity was significantly higher in the boreal streams ($p = 0.005$), where conductivity ranged from 123 – 208 µs/cm, while tundra streams ranged from 68 – 154 µs/cm. The nutrient, TDP, was significantly higher in tundra streams ($p = 0.01$), with values ranging from 0.007 – 0.02 mg TDP/L, while in the Boreal streams it ranged from 0.002 (lowest detection limit) – 0.009 mg TDP/L. NDVI calculations indicated boreal streams had significantly higher riparian vegetation density ($p < 0.0001$), with NDVI values ranging from 0.63 – 0.85 (mean = 0.77), while tundra streams only ranged from 0.58 – 0.62 (mean = 0.6). Distance from upstream lake is notably higher in boreal streams (median = 10,604.4 m) over tundra streams (median = 726.25 m), however Man-Whitney U-tests showed no significance (p = 0.057).

Table 2.1: Site characteristics measured in streams across Arctic ecozones including physical chemical, and hydrological characteristics. “*” indicates significance between ecozones.

Site	**CWS01**	**CWS02**	**CWS03**	**CWS04**	**CWS06**	**CWS07**	**CWS08**	**CWS09**	**$p < 0.05$**
Region	Tundra	Tundra	Tundra	Tundra	Boreal	Boreal	Boreal	Boreal	
Latitude	69.34385	69.07939	68.94159	68.86955	68.26209	68.08900	67.84265	67.75410	
Median Substrate Size (D_{50}; cm)	2.75	3.2	3.15	2.3	3.6	4.15	6.9	6.55	
Bankful Width (m)	3.83	5.97	9.2	11.47	7.61	11.9	3.1	12	
Canopy Coverage (%)	0	0	0	0	80	10	30	0	
Riparian NDVI	0.583	0.579	0.625	0.613	0.848	0.765	0.631	0.841	<0.0001*
Slope (º)	1.4	1.4	0.5	0.5	0.2	1.3	0.4	0.4	
pH	7.26	7.47	6.97	7.22	7.08	6.83	7.09	7.33	
Total Suspended Solids (TSS)	7.2	1.1	3.2	1.5	2.2	2.8	0.8	0.2	
Total Dissolved Nitrogen (mg/L, TDN)	0.516	0.463	0.566	0.412	0.363	0.553	0.701	0.373	
Total Dissolved Phosphorous (mg/L, TDP)	0.015	0.013	0.02	0.007	0.002	0.002	0.009	0.002	0.01*
Dissolved Organic Carbon (mg/L, DOC)	9.8	8.1	7.6	5.73	7.8	6.1	22	8.3	
Dissolved Inorganic Carbon (mg/L, DIC)	14.9	10.8	6.02	18.9	18.9	4.5	15.1	15.1	
Conductivity (μs/cm)	136	102	68	154	206	194	123	208	0.005*

Depth (m)	0.177	0.314	0.45	0.134	0.241	0.177	0.247	0.209	
Velocity (m/s)	0.34	0.11	0.34	0.07	0.006	0.28	0.002	0.23	
Temperature (Cº)	12.1	12.1	11.9	9.4	9.2	12.2	10.4	13.7	
Dist. Upstream Lake (m)	450.3	572	5279.5	880.5	15100.3	18903.2	1195.1	6108.5	
Catchment Area (km2)	49.91	140.27	410.6	313.82	115.16	515.75	78.32	1246.84	

2.4.2 – Benthic Macroinvertebrate Communities

BMI were sorted and identified from kick-net samples across 8 streams in the Arctic (4 boreal streams and 4 tundra streams). Boxplots revealed similar richness and diversity across these ecozones (Figure 2.1). Abundance of benthic communities were significantly higher in tundra streams (Figure 2.1) (Mann-Whitney U-test, $p = 0.029$). Standard error (SE) bar-plots revealed that the relative abundance of all four dominant BMI orders (Diptera, Ephemeroptera, Plecoptera, Trichoptera) overlapped among ecozones. Two-sample t-tests showed higher percentage of Predators (boreal mean = 31.04 +/- 4.94%, tundra mean = 11.84 +/- 2.84%, $p = 0.041$) and Collector-Gatherers (boreal mean = 46.27 +/- 4.12%, tundra mean = 25.72 +/- 8.58%, $p = 0.034$) in boreal steams, while tundra streams have higher Collector-Filterers (boreal mean = 6.3 +/- 1.55%, tundra mean = 34.69 +/- 12.15%, $p = 0.03$) (Figure 2.2), however after Bonferroni correction, $\alpha = 0.008$, thus cannot be considered significant.

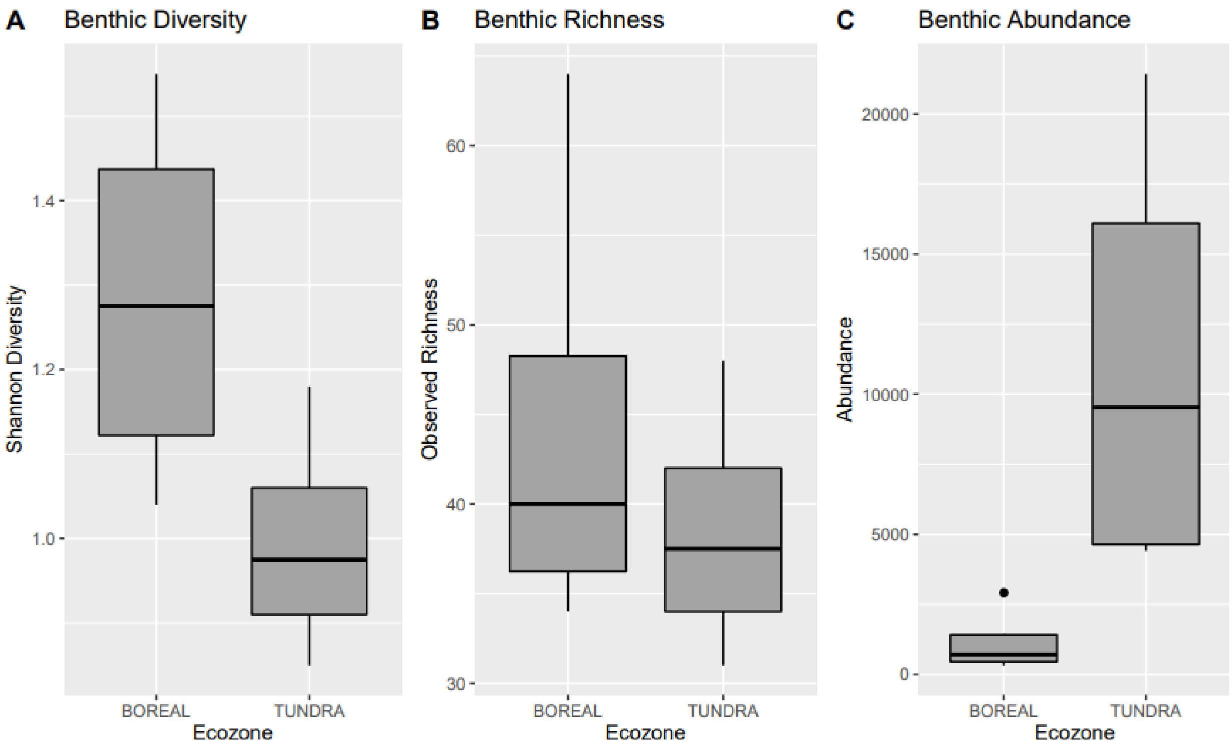

Figure 2.1: Standard error box plots of the of Shannon diversity (boreal mean = 1.285 +/- 0.12, tundra mean = 1.0 +/- 0.07) (**A**), species richness (boreal mean = 44.5 +/- 6.76, tundra mean = 38.5 +/- 3.66) (**B**), and sample abundance (boreal mean = 1165.25 +/- 597.21, tundra mean = 11223.75 +/- 4107.41) (**C**) for benthic populations across boreal and tundra ecozones (n=4 per zone). The left box on Figure 2.8 A, B and C show boreal forest populations, while the right box in these figures indicates tundra populations.

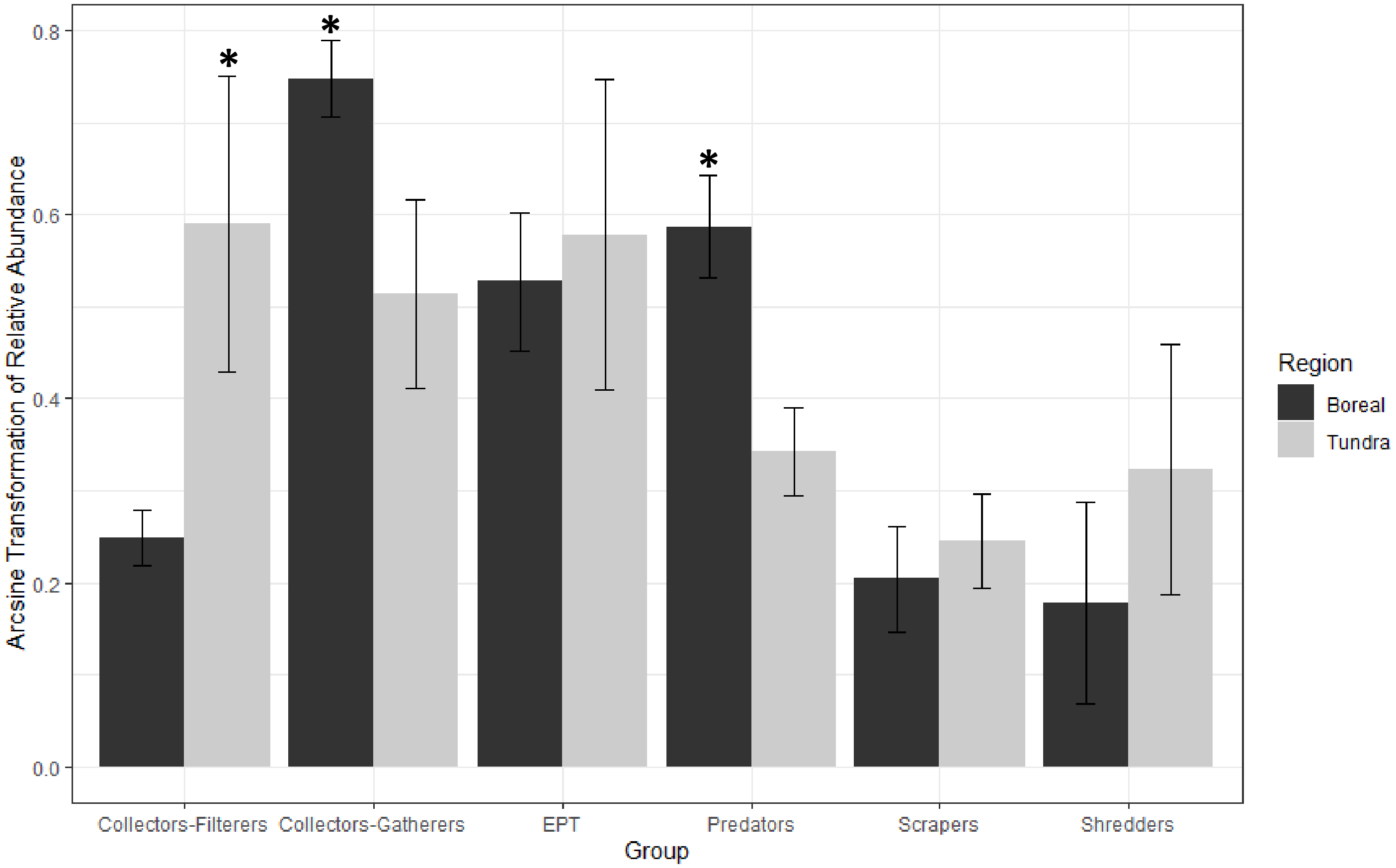

Figure 2.2: Standard error bar plot for the arcsine transformed relative abundance of functional feeding groups (Collector-Filterers (boreal mean = 0.25 +/- 0.03, tundra mean = 0.59 +/- 0.16), Collector-Gatherers (boreal mean = 0.75 +/- 0.04, tundra mean = 0.51 +/- 0.1), Predators (boreal mean = 0.57 +/- 0.06, tundra mean = 0.34 +/- 0.05), Scrapers (boreal mean = 0.2 +/- 0.06, tundra mean = 0.24 +/- 0.05), and Shredders (boreal mean = 0.18 +/- 0.11, tundra mean = 0.32 +/- 0.14)), and %EPT (boreal mean = 0.53 +/- 0.07, tundra mean = 0.58 +/- 0.17) species in the benthic populations across Arctic ecozones. Dark bars show boreal populations while light bars represent tundra populations. “*” indicates significance.

PERMANOVA of the BCDM from the BMI communities showed significant differences in benthic composition based on ecozone (permutations = 999, p = 0.03). An NMDS (NMDS; k = 2, stress = 0.02) biplot (Figure 2.3) was created from the BCDM of the BMI community data to visualize any distinct groupings of communities based on ecozone. The NMDS biplot showed clear groupings in benthic composition based on ecozone.

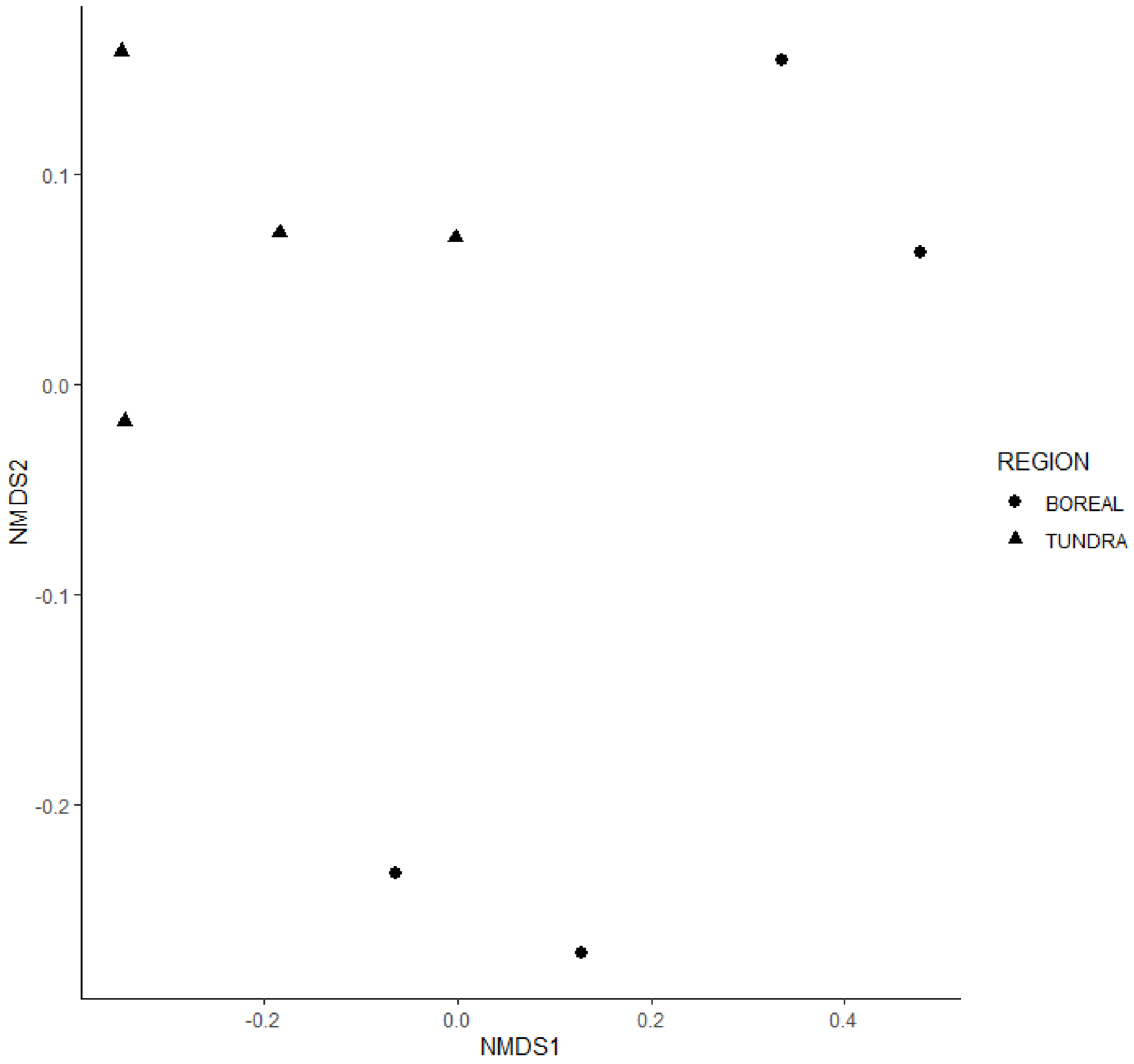

Figure 2.3: Non-parametric multidimensional scaling (NMDS; k = 2, stress = 0.02) biplot of the BMI community samples. Points represent sites. Sites that are more similar to another are ordinated closer together. Circular points show boreal sites and triangular points show tundra sites.

Finally, SIMPER analysis of the BMI communities revealed that the taxa groups of midges (Chironomidae), stoneflies (Nemouridae), mayflies (Ephemerellidae), and water mites (Sperchontidae) accounted for approximately 50.55% of the dissimilarity between ecozones (Table 2.2).

Table 2.2: Similarity percentages (SIMPER) for the differences in frequency of occurrence of taxa between tundra and boreal benthic samples. For each taxa group found the columns respectively show the average dissimilarity, contribution % to dissimilarity, cumulative contribution to dissimilarity, mean relative abundance of tundra samples, mean relative abundance of boreal samples, and the p-value calculated to see if the relative abundances are significantly different. There was no significance.

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Rel.% Tundra	Mean Rel.% Boreal
Chironomidae	12.28	24.07	24.07	52.8	49.6
Nemouridae	7.27	14.26	38.33	13.7	6.23
Ephemerellidae	3.39	6.64	44.97	0.46	6.86
Sperchontidae	2.85	5.58	50.55	0.66	5.69
Brachycentridae	2.70	5.29	55.84	6.28	1.04
Simuliidae	2.56	5.02	60.86	5.19	1.44
Lebertiidae	2.44	4.78	65.64	1.14	5.8
Heptageniidae	2.42	4.75	70.39	2.63	4.48
Baetidae	2.41	4.72	75.1	5.47	0.94
Empididae	1.40	2.75	77.85	0.51	2.87
Hygrobatidae	1.12	2.19	80.04	1.18	2.23
Valvatidae	0.97	1.89	81.93	1.93	0.07
Pisidiidae	0.94	1.84	83.78	1.88	0.0
Hydropsychidae	0.85	1.66	85.43	0	1.69
Ceratopogonidae	0.80	1.57	87.01	0	1.60
Perlodidae	0.70	1.36	88.37	0.10	1.39
Leptophlebiidae	0.62	1.22	89.59	0	1.25
Tipulidae	0.62	1.21	90.8	0.44	1.19
Naididae	0.56	1.10	91.9	0.86	0.99
Glossosomatidae	0.56	1.09	92.99	1.25	0.31

2.4.3 – Drifting Communities

Of the 13,902 drifting invertebrates collected in 3 replicates in 7 streams over 24 hours, 4,132 consisted of drifting benthos (e.g., drift subsidies from the stream bed), 2297 were of terrestrial origin (e.g., invertebrates that fell into the stream) and 7,473 consisted of lentic drift subsidies (e.g., zooplankton and amphipods from upstream still-water environments). Base ecological metrics, including observed richness ($p = 0.547$), diversity ($p = 0.747$) EPT% ($p = 0.554$) and both total ($p = 0.559$) and benthic drift density (#ind./m^3; $p = 0.629$), were not significantly different between ecozones (Figure 2.4).

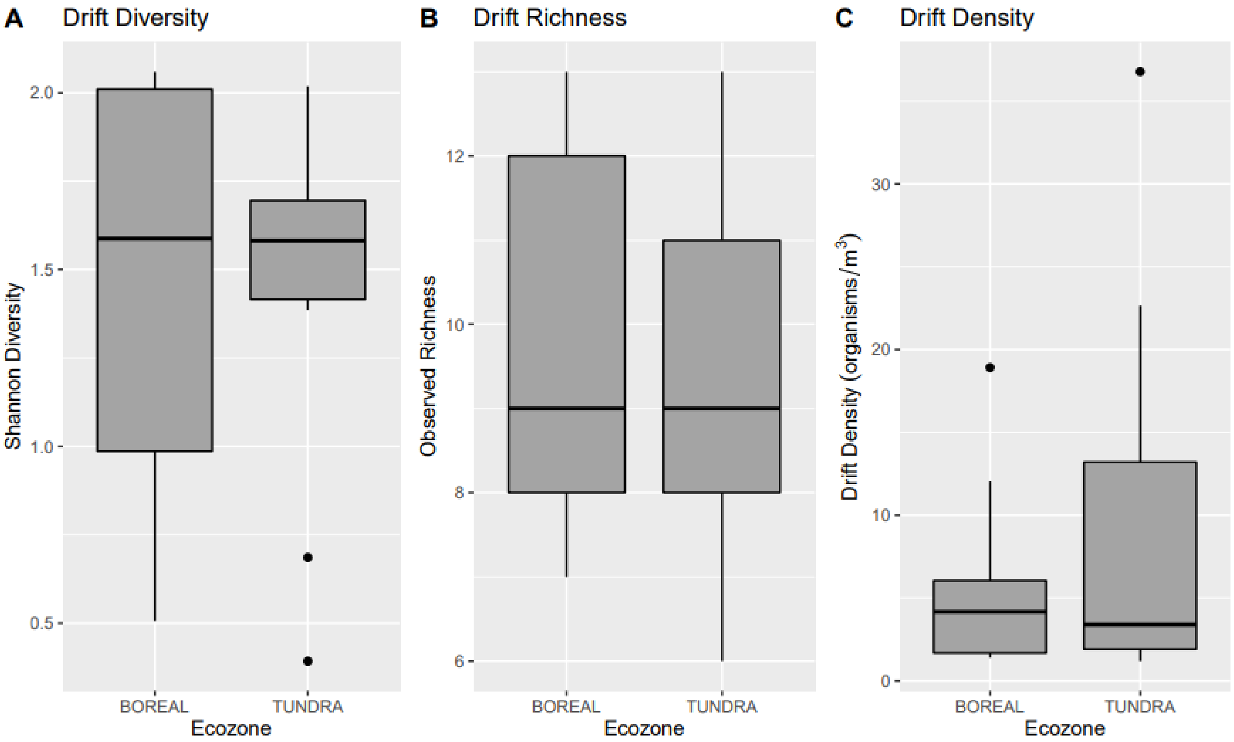

Figure 2.4: Standard error box plots of the of Shannon diversity (boreal mean = 1.52 +/- 0.19, tundra mean = 1.44 +/- 0.14) (**A**), family richness (boreal mean = 9.78 +/- 0.7, tundra mean = 9.27 +/- 0.66) (**B**), and drift density (#ind./m^3) (boreal mean = 5.95 +/- 1.98, tundra mean = 9.73 +/- 3.41) (**C**) for drift populations across Arctic ecozones. The left box on Figure 2.7 A, B and C show boreal forest populations, while the right box in these figures indicates tundra populations.

Within the drifting benthos, the relative abundance of Ephemeropterans was significantly higher in the boreal ecozone (Bonferroni α = 0.0125, p = 0.008). Boreal streams also had significantly higher terrestrial inputs (p = 0.001), and while lentic drift subsides (zooplankton and amphipods) were markedly higher in tundra streams, the majority of these subsides were from a single stream (CW-S-02, n = 2369.67 +/- 1323.3) and therefore were not significant based on ecozone (Figure 2.6).

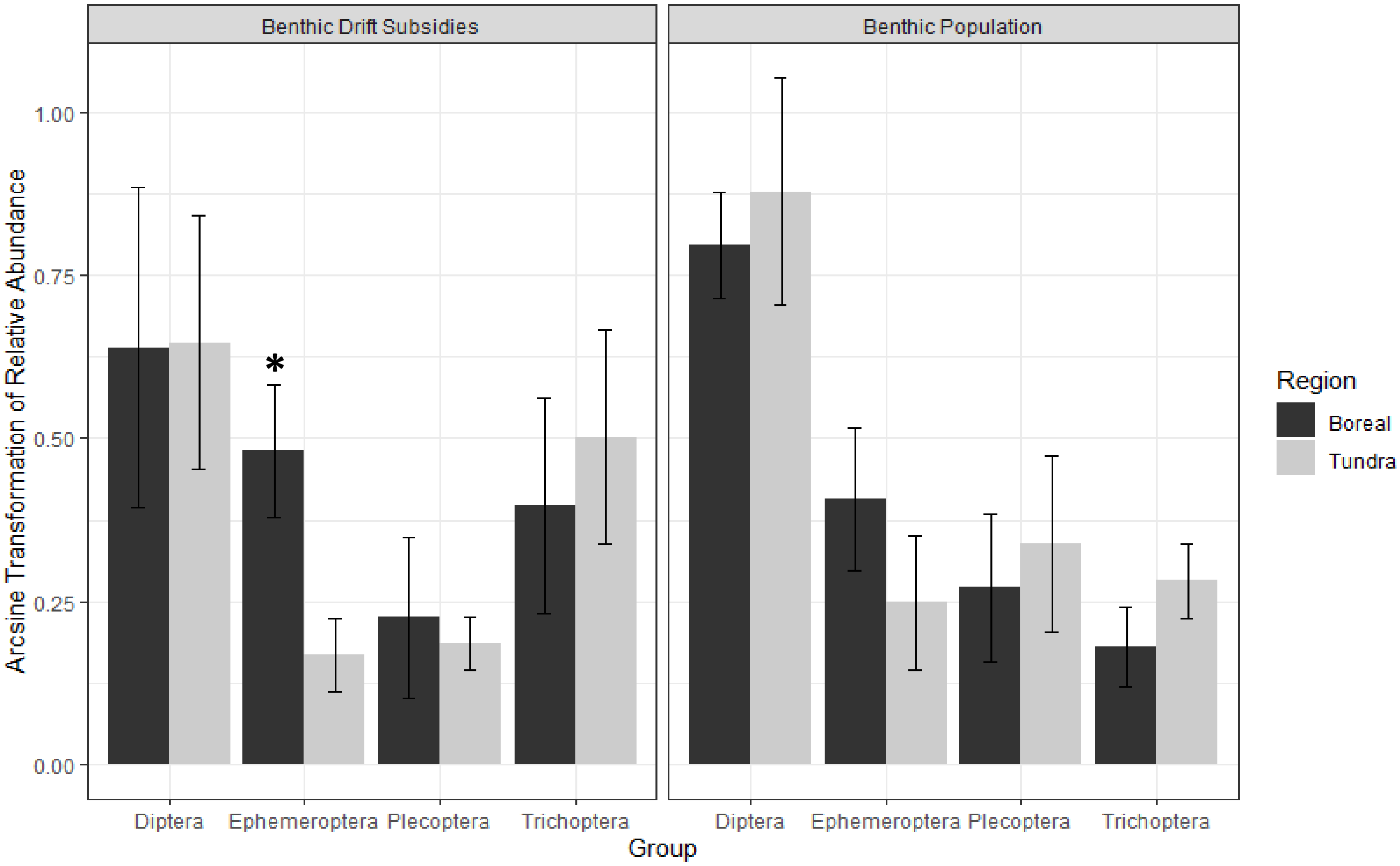

Figure 2.5: Standard error bar plot for the arcsine transformed relative abundance (%) of Diptera (True Flies), Ephemeroptera (Mayflies), Plecoptera (Stoneflies), and Trichoptera (Caddisflies) in both the benthic drift subsidies and total benthic populations across Arctic ecozones. “*” indicates significance.

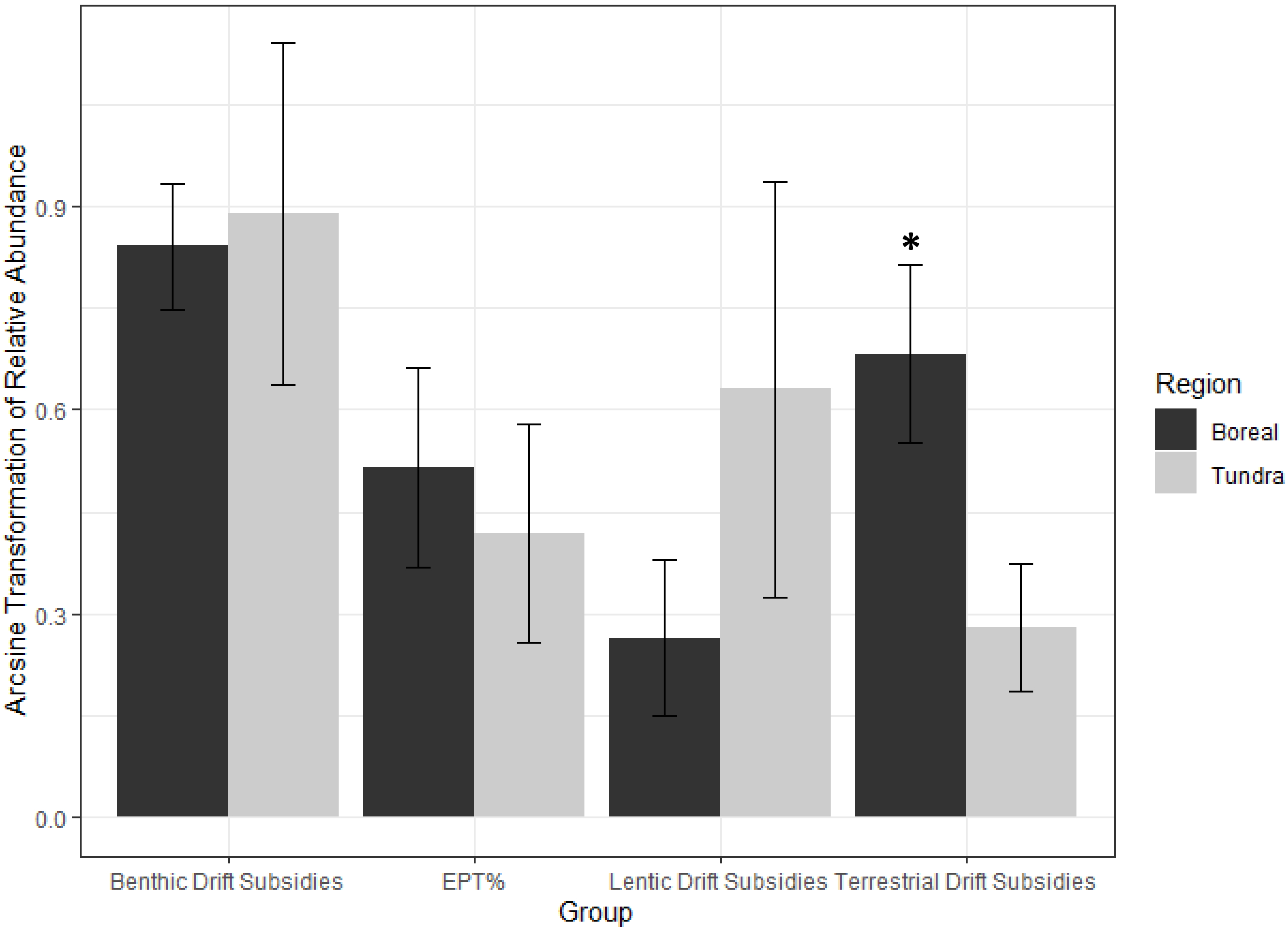

Figure 2.6: Standard error bar plot for the arcsine transformed relative abundance (%) of benthic (boreal mean = 0.84 +/- 0.09, tundra mean = 0.89 +/- 0.25), EPT (boreal mean = 0.51 +/- 0.15, tundra mean = 0.42 +/- 0.16), lentic (zooplankton & amphipods) (boreal mean = 0.26 +/- 0.12, tundra mean = 0.63 +/- 0.31), and terrestrial (boreal mean = 0.68 +/- 0.13, tundra mean = 0.28 +/- 0.09) drift subsidies across Arctic ecozones. Dark bars show boreal populations while light bars represent tundra populations. "*" indicates significance.

PERMANOVA of the BCDM for the total drift subsidies showed no significant difference in composition between ecozones (permutations = 999, p = 0.5). An NMDS biplot (k = 2, stress = 0.03) was generated from the total drift subsidies to visualize any groupings of drift compositions based on ecozone (Figure 2.7). The NMDS of the total drift communities showed some groupings based on ecozone. In addition, SIMPER analysis revealed that within the drift subsidies the taxa groups of zooplankton, Chironomid dipterans, and terrestrial drift subsidies accounted for 71.35% of the dissimilarity between ecozones (Table 2.3).

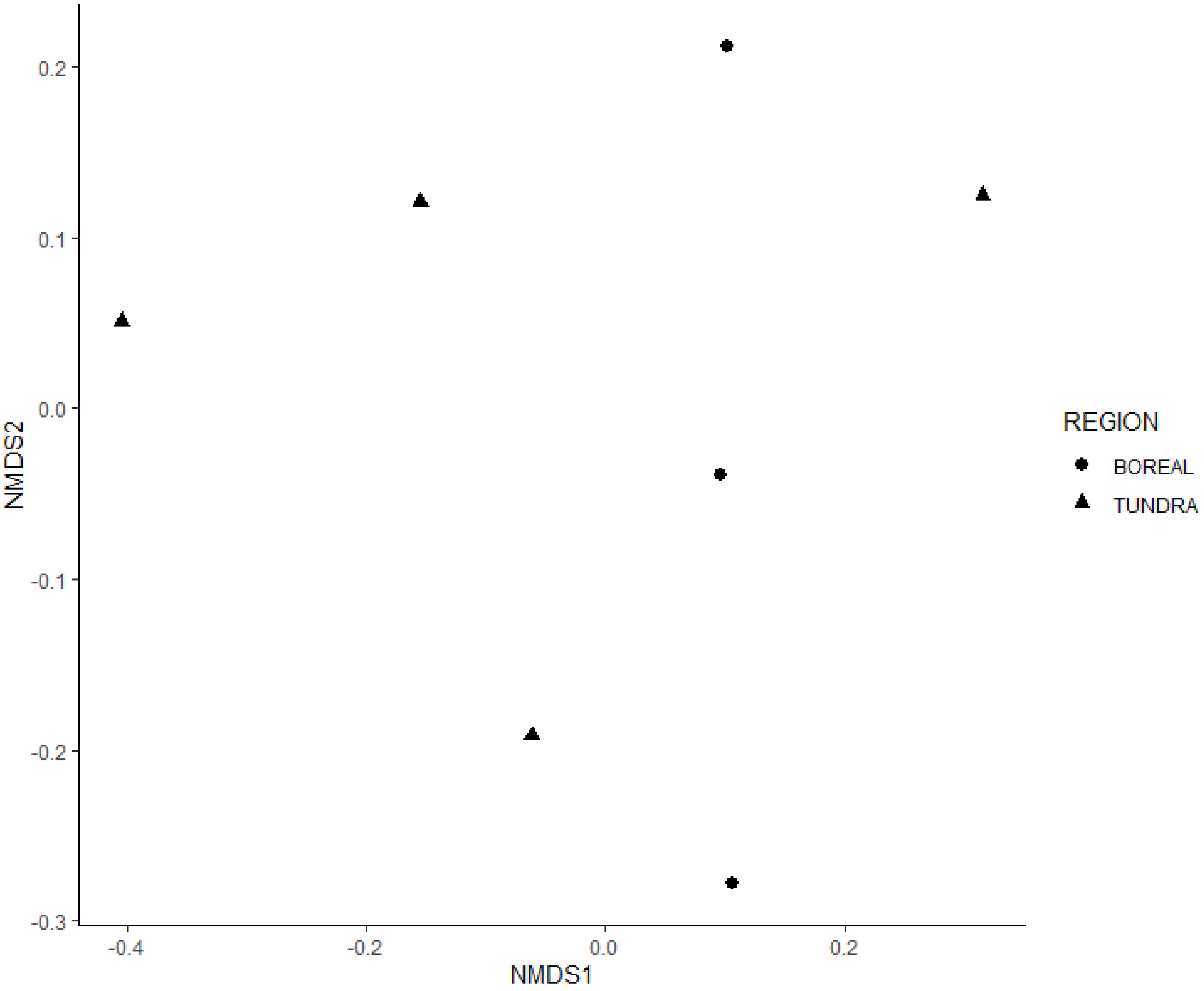

Figure 2.7: Non-parametric multidimensional scaling (NMDS; k = 2, stress = 0.03) biplot of the total drifting community samples. Points represent sites. Sites that are more similar to another are ordinated closer together. Circular points show boreal sites and triangular points show tundra sites.

PERMANOVA of the BCDM for the drifting benthos showed no significant difference in composition between ecozones (permutations = 999, p = 0.42). An NMDS biplot (k = 3, stress = 0.04) was generated from the total drift subsidies to visualize any groupings of drift compositions based on ecozone (Figure 2.8). No groupings were identified in the benthic drift NMDS biplot.

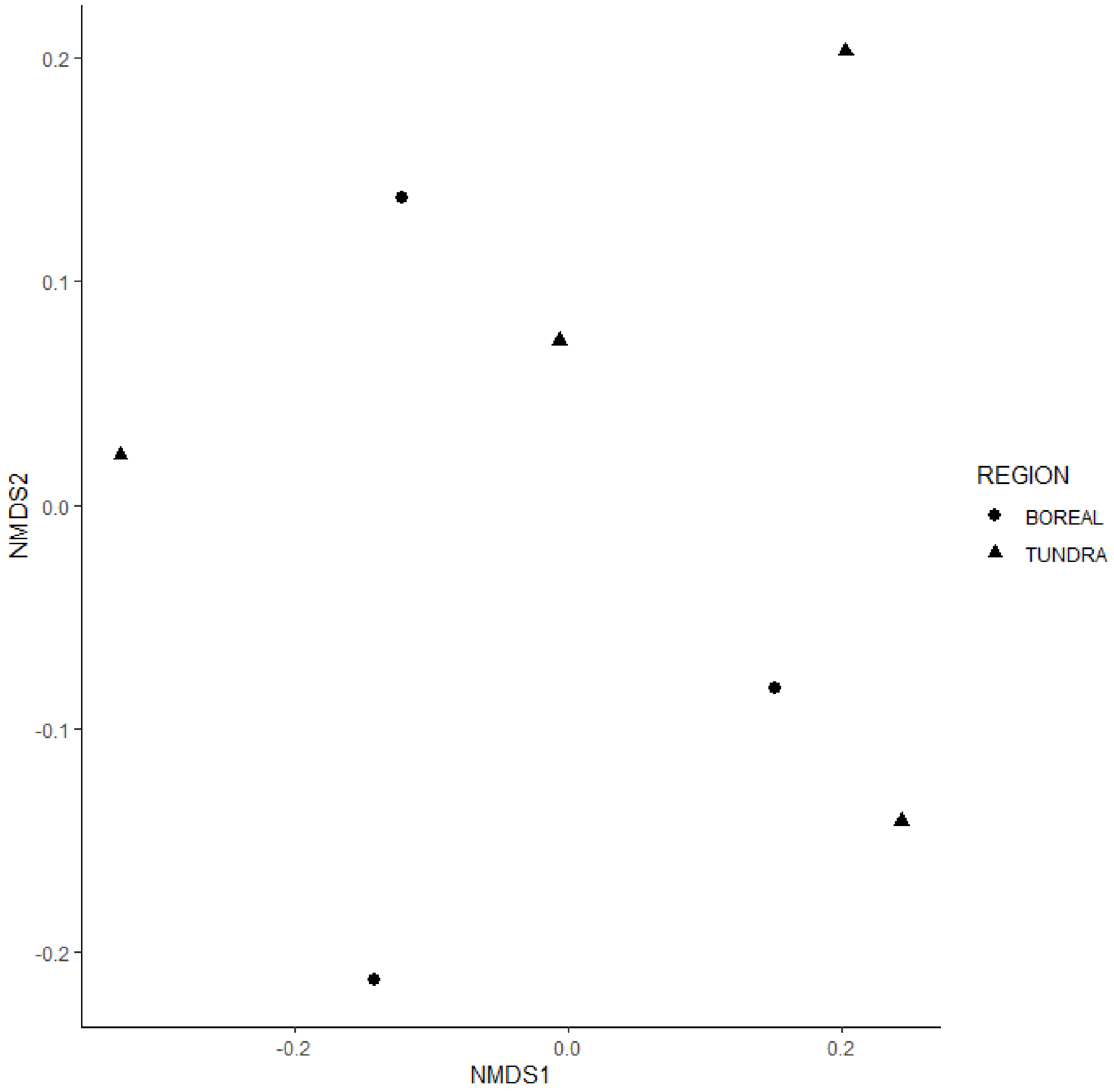

Figure 2.8: Non-parametric multidimensional scaling (NMDS; k = 3, stress = 0.04) biplot of the benthic drifting community samples. Points represent sites. Sites that are more similar to another are ordinated closer together. Circular points show boreal sites and triangular points show tundra sites.

Table 2.3: Similarity percentages (SIMPER) for the differences in frequency of occurrence of taxa between tundra and boreal drift samples. For each taxa group found the columns respectively show the average dissimilarity, contribution % to dissimilarity, cumulative contribution to dissimilarity, mean relative abundance of tundra samples, mean relative abundance of boreal samples, and the p-value calculated to see if the relative abundances are significantly different. "*" indicates significance.

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Rel.% Tundra	Mean Rel.% Boreal
Zooplankton	25.45	32.36	32.36	35.2	4.06
Chironomidae	15.51	19.72	52.08	18.4	17.8
Terrestrial	15.16	19.27	71.35	10.7	40.50
Hydrachnidia	4.68	5.95	77.3	9.68	4.98
Brachycentridae	4.48	5.69	82.99	7.7	0.95
Glossosomatidae	4.43	5.63	88.62	8.29	0.95
Baetidae	1.48	1.83	90.51	2.52	7.50
Limnephilidae	1.41	1.79	92.29	0.34	2.89
Nemouridae	1.36	1.72	94.02	2.02	5.24
Simuliidae	1.31	1.67	95.69	2.69	1.37
Ephemerelidae	0.69	0.87	96.56	0.25	3.03
Hydroptilidae	0.68	0.85	97.41	0.18	2.03
Saldidae	0.51	0.65	98.06	1.03	2.26

2.5 – Discussion:

Macroinvertebrate drift is a major food pathway for fish in riverine food webs, yet our knowledge of factors affecting drift in high latitude streams is very limited. This study predicted that drift would vary greatly across two major ecozones in the Arctic, with significant differences in drift composition between these ecozones, more terrestrial drift subsidies, and higher taxonomic richness and diversity of species in boreal streams. While there was no significant difference in the base ecological metrics of richness, diversity, and drift density across ecozones (Figures 2.1; 2.4), benthic abundance of BMI was significantly higher in tundra streams (Figure 2.1). Furthermore, benthic compositions of boreal and tundra streams were significantly different based on ecozone (Figures 2.3). Differences in benthic composition were further explained by a significantly higher relative abundance of predators and collector-gatherers in boreal streams, while tundra composition showed significantly higher collector-filterers (Figure 2.2). Within the drift, the relative abundance of ephemeropterans and terrestrial drift subsidies were significantly higher in boreal streams (Figures 2.5; 2.6).

2.5.1 – Benthic Abundance and Drift Densities

This study indicates that the abundance of BMI communities in tundra streams was higher than in boreal (Figures 2.1). Trophic dynamics and overall BMI abundance can be affected by many environmental drivers in stream ecosystems. For example, nutrient enrichment can lead to increased primary production at the base of the food web, thus increasing the carrying capacity of BMI (Cross et al., 2006; Mesquita et al., 2010; Peterson, 1993). Nutrient enrichment may be occurring in tundra streams, as despite the relatively equivalent concentrations of TDN, TDP concentrations in tundra streams were significantly higher compared to concentrations in boreal streams. Peterson et al., (1993) showed that enriching tundra streams with P can stimulate the production of algal biomass, and the eventual bottom-up increase on fish production, however further investigations are required to confirm the hypothesized higher primary production in these tundra streams.

Differences in the density of surrounding riparian vegetation in tundra and boreal streams may potentially influence primary producer standing crop in these two ecozones. The removal of shade around boreal streams has been shown to increase primary production (Betts & Jones, 2009; Fuchs et al., 2003), indicating shading from boreal riparian vegetation may limit instream primary production, with limitations of primary production in streams due to shading having long been observed before (Hill et al., 1995). NDVI measurements indicated significantly higher riparian densities for boreal streams (Table 2.1), and in combination with the presence of boreal canopy cover, could further increase differences in primary production between boreal and tundra streams. While denser streamside vegetation would be expected to provide additional food resources to boreal benthic communities through the input of detritus, shredding invertebrates did not differ in relative abundance between ecozones (Figure 2.2), suggesting benthic reliance on the detrital food pathway may not be significantly more important in boreal streams. Instead, primary production may be the primary basal resource in both ecozones. Further examination into the potential limitations of primary production in boreal steams (i.e., shading, low TDP) compared to tundra streams is needed to make a conclusive statement that BMI abundances differences between the two ecozones is the result of basal productivity.

Drift densities may be related to abundance (i.e., if it is passive drift) where, under similar environmental conditions, streams with higher abundances would be expected to have higher drift rates (Kennedy et al., 2014; Naman et al., 2016). The benthic abundances of tundra streams are on average approximately 10 times greater than boreal streams (11 223.75 compared to 1165.25) (Figure 2.1), however both the total and benthic drift densities (#ind./m^3) between the regions were statistically similar (Figure 2.4). Due to drift densities remaining equal among ecozones despite the divergence in benthic abundance, it suggests additional drivers that promote active drift in boreal streams. I hypothesize the denser riparian vegetation, higher benthic predator presence, and lower nutrient concentrations present in boreal streams likely drive drift as a response to these environmental factors.

2.5.2 – Environmental Drivers of Drift

The differences in riparian vegetation density appear to be a primary factor affecting drift abundance and composition in Arctic streams. Firstly, increases in riparian vegetation density and vegetative overhang has been observed to increase the terrestrial component of drift in temperate regions (Baxter et al., 2005; Ryan & Kelly-Quinn, 2015). This pattern was also observed in this study, with the number of terrestrial invertebrates in drift being significantly higher in boreal streams (Figure 2.6). Furthermore, the increase in shade from riparian vegetation (Johnson & Almlöf, 2016; Wilzbach & Hall, 1985) could trigger the onset of diel drift, where certain groups of BMIs will drift under lower light conditions. While the sun did not set during the sampling period, the taller riparian vegetation may allow the light levels in streams to pass below the threshold of 30 lux to initiate diel drift (Haney et al., 1983). Mayfly groups are considered the most prominent diel drifters (Rader, 1997), which make up a significantly larger portion of the drift in boreal streams, thus diel periodicity may be more prominent in boreal streams, however, further analysis into light availability in these Arctic streams is needed to test this hypothesis. Finally, the lower level of primary production in boreal streams resulting from low TDP concentration and riparian shading, could also lead to increased drift rates. Past studies have shown drift rates increase with food resource limitation (Dimond, 1967; Hammock &

Wetzel, 2013; Richardson, 1991), particularly in mayflies grazers (Hildebrand, 1974; Bohle, 1978), which may partially explain the increased drift rates of mayflies in boreal steams.

Differences in benthic composition of predators, collector-gatherers and filter feeders may contribute additional influence on drift rates of the boreal and tundra ecozones. For example, the benthic composition in boreal steams have significantly higher benthic predator presence (Figure 2.2). Higher benthic predator presence can lead to increased drift rates, as BMI will engage in active drift as a benthic predator avoidance strategy (Huhta et al., 2000; Kratz, 1996; Peckarsky, 1980). Although much of the predator presence in boreal streams is driven by Sperchontidae (water mites), which may be too small to exert drifting behaviour, boreal compositions also saw higher presence of larger stonefly (Perlodidae) and caddisfly (Hydropsychidae) families (Table 2.2). Compositions that promote inter/intraspecific competition would also increase drift rates, as BMI are known to drift more when competition for resources (Dimond, 1967; Hammock & Wetzel, 2013; Richardson, 1991) or space (Corkum, 1978; Hildrew & Townsend, 1980; Kohler, 1992) increases. In boreal streams, the collector-gatherers trait group comprise a greater proportion of BMI abundance relative to the tundra, with this difference mostly driven by the presence of four mayfly groups: Baetidae, Ephemerellidae, Heptagenidae, and Leptophlebiidae (Figures 2.2; 2.3; Table 2.2). The concentration of this collector-gatherer feeding group could increase competition that may result in these mayflies drifting to new locations to forage for new resources. However, density-dependent drift is difficult to quantify, so further analysis is required to test this hypothesis. Finally, the high number of net-spinning caddisflies (i.e., Hydropsychidae and Limnephilidae) drifting in boreal streams may be related to benthic competition (Table 2.3). Specifically, because net-spinning caddisflies often compete for space in both an inter/intraspecific manner, whether that space is foraging territory or their cases, the losers of such territorial disputes often enter the drift to relocate downstream (Hildrew & Townsend, 1980; Matczak & Mackay, 1990; Tszydel & Błońska, 2022).

Drift within the boreal streams appears to be driven by an active response to a stressor within the environment, whether that be resource limitation, predator presence, or the promotion of competition within the benthic composition. While most of the drift is comprised of the passively drifting Chironomidae for both tundra and boreal streams, additional BMI found to predominate the drift in tundra streams, such as Brachycentridae and Glossossomatidae, are also considered passive drifters (Rader, 1997), in comparison to the prominent benthic drifters in boreal streams which are known to actively drift (i.e., mayflies and net-spinning caddisflies). Thus, I hypothesize that drift densities between the ecozones remain similar despite the differences in benthic abundance due to boreal drift being a result of an active drifting benthic community.

2.5.3 – Conclusions and Future Research

This project aimed to characterize drift in streams across the tundra and boreal forest ecozones to better understand the potential drivers of this process in high latitude streams. Boreal streams have significantly less benthic abundance, on average approximately 10% of the abundance of tundra streams. Despite this divergence in population abundance, drift densities between the two ecozones were statistically equivalent, suggesting there are additional drivers present in boreal streams that influence active drift. With nutrient concentrations lower in boreal streams, denser riparian vegetation and associated canopy coverage, yet an equal relative abundance of shredders compared to tundra streams, I hypothesized resource limitations are likely, which would drive drift as BMI move to find new resource rich areas. Benthic predator presence is significantly higher in boreal streams, with higher presence of large benthic predators such as Perlodidae and Hydropsychidae, potentially driving drift rates from predator avoidance. Finally, the BMI composition within boreal streams may promote competition for both resources and space which may contribute to drift subsidies. Tundra drift may predominately be passive, where the high abundance of BMI within the streams likely drives drift as there would be little influence from other biotic and abiotic drivers. This is partly shown in that most of the tundra’s benthic drift subsidies are comprised of known passive drifters (i.e., Dipterans, Brachycentrids, and Glossossomatids) (Rader, 1997). In summary, the focus of future research into this subject would benefit from examination of the relative differences in primary production, food resource competition, and light availability of streams between the ecozones to test the hypotheses generated from these results on the potential differences in the drivers of drift between these two high latitude regions.

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CHAPTER 3: IMPLEMENTATION OF A DRIFT FEEDING BIOENERGETICS MODEL TO ASSESS POTENTIAL GROWTH AND HABITAT SUITABILITY FOR ARCTIC GRAYLING (*Thymallus arcticus*)

3.1 – Abstract:

Drift feeding bioenergetics models (DFBM) are useful tools for quantifying habitat suitability to break down sources of potential energy intake, yet they are rarely applied to high latitude streams. This study aimed to use a DFBM for Arctic grayling (*Thymallus arcticus*) across boreal and tundra ecozones to better understand how prey availability (#ind./m^3), prey size (mm), and prominent food sources may differ between these two Arctic ecozones. Body size of drifting mayflies was significantly larger in tundra streams, whereas boreal drift had significantly larger drifting stoneflies, and an increased frequency of drifting invertebrates sized 2-3 mm. However, the overall mean prey size and prey availability did not differ between ecozones, thus growth potential (g/day) of both young-of-the-year (YoY) and juvenile (≥ 1 year old) Arctic grayling did not differ between ecozones. There were, however, significant differences in growth potential based on age group, with mean growth potential for juvenile grayling being negative, while all streams had positive growth potential for YoY grayling. Benthic sources of energy available to grayling were the most prominent in both ecozones, with boreal streams having significantly higher available energy from terrestrial sources, while tundra streams had significantly higher available energy from upstream lentic sources. AICc model selection showed benthic abundance as the best predictor of growth but did not have more predicting power compared to the null model. I recommend further analysis into trophic food-

web structure using isotopic analysis and gut content analysis of Arctic grayling between the two regions.

3.2 – Introduction:

Drift feeding is an energy optimization strategy implemented by many fishes in stream environments where the individual fish hold position facing upstream, allowing the stream current to deliver macroinvertebrate prey items to their location. This allows the fish to optimize net-energy intake (NEI) whilst minimizing energy expenditure. Drift feeding is a common feeding strategy, with many stream dwelling fish species observed to drift feed at least part of the time (Grossman, 2014). While other means of predation exist within these environments, including benthic foraging, the most extensively studied method for stream fishes is drift feeding, with the salmonids (e.g., trout, salmon, grayling) most associated with the process (Larocque et al., 2014; Leung et al., 2009; Piccolo et al., 2014). Drift feeding bioenergetics models (DFBM) have become useful tools for assessing the suitability and growth potential of the environment for salmonids (Hughes, 1998; Piccolo et al., 2014). DFBM use environmental stream conditions, prey availability/size, and the physiology of the salmonid species to objectively quantify habitat suitability for a fish species based on NEI, and the eventual calculation of potential tissue growth (g/day) (Larocque et al., 2014).

DFBM have been implemented across many temperate regions as a means to assess habitat quality and source of growth for salmonid species, however Arctic streams remain a region with limited knowledge on habitat suitability of these stream environments for salmonids. One salmonid of importance to Arctic stream environments, Arctic grayling (*Thymallus arcticus),* has a Holarctic distribution, occupying many stream and lake environments within the Western Arctic of Canada (Craig & Poulin, 1975; Northcote, 1995). During the spring snow melt adult grayling migrate from overwintering habitats (deep rivers and lakes) into smaller tributaries to spawn. Over the course of the summer, newly hatched young-of-the-year (YoY) and juvenile

(≥ 1 year old) grayling inhabit these smaller tributaries, occupying top trophic roles as apex drift feeding predators (Craig & Poulin, 1975; Golden & Deegan, 1998; Larocque et al., 2014). Grayling populations are reliant on the survivability of these two age groups over the course of the summer, with growth rates directly related to the survivability of salmonid populations (Jones et al., 2003; Kratt & Smith, 1979; Piccolo et al., 2014). Thus, a DFBM pertaining to grayling physiology can be implemented across multiple Arctic stream environments to identify important food sources for growth potential and to indicate trophic factors that may drive habitat suitability for YoY and juvenile grayling populations. More specifically, application of this model can illustrate how growth potential may differ between the boreal forest and tundra ecozones, and what differences in prey source and quantity (drift density, #ind/m^3), and prey quality (i.e., prey size) may affect grayling in these two biomes.

High densities of riparian vegetation and vegetative overhang surrounding boreal streams allows for higher population densities of terrestrial invertebrates, and the potential for drifting invertebrates to originate from terrestrial sources as compared to tundra streams that have minimal riparian vegetation (see Section 2.4.3; Kawaguchi et al., 2003; Kawaguchi & Nakano, 2001; Ryan & Kelly-Quinn, 2015). Additionally, the interconnectivity of lakes found in tundra streams often provides smaller lake outlet streams with dense lentic drift subsidies comprised mostly of zooplankton (see Section 2.4.3; Hughes & Dill, 1990; Jones et al., 2003; Kaya, 1989). Quality of prey relates to the prey size, as larger prey items are identified by drift feeding fishes quicker, and also provide greater energetic intake for tissue growth (Hughes, 1998; Hughes & Dill, 1990). Given that terrestrial invertebrates are often much larger than zooplankton, and it is unknown if BMI differ significantly in size between the two ecozones, it is unclear how the quality of prey within drift subsidies differs by ecozone, and if that difference in prey quality significantly impacts the growth potential of these two grayling populations.

The objectives of this study are to calculate prey availability and measure size of prey items to implement a DFBM across boreal and tundra environments to better understand what drives growth potential for grayling across high latitude stream environments. I predict that: (i) grayling growth potential will be higher in boreal streams; (ii) grayling growth potential derived from terrestrial invertebrate subsidies will be significantly higher in boreal streams; (iii) grayling growth potential derived from upstream lentic sources will be significantly higher in tundra streams; and (iv) prey size will be significantly larger in boreal streams. These hypotheses were tested by sampling invertebrate drift, measuring the length of drifting invertebrates, and calculating growth potential for grayling in seven streams across both boreal and tundra ecozones.

3.3 – Methods:

Macroinvertebrate drift sampling was done by placing three spatial replicates of drift nets (15 cm × 15 cm opening: 400 µm mesh) in 7 streams across boreal and tundra ecozones for a minimum of 24h. Given that many BMI and zooplankton captured were <1 mm, the mesh size was deemed suitable. Nets were attached to rebar poles and secured with cable ties to ensure stability during sampling period. For further details into drift sampling procedure and drift density calculations, refer to Section *2.3.3b.*

3.3.1 – Invertebrate Measurements:

In the laboratory, a Motic X3 microscope camera paired with a Leica dissecting scope was used to identify family-level or group (terrestrial, zooplankton, amphipods) of invertebrates from each drift replicate. Sorted invertebrates were placed into separate gridded sorting trays (6 × 6) and pictures of each grid were captured using the Motic X3 at random by rolling dice (ex., if dice A rolled a 3 and dice B rolled a 4, then a picture of the 3rd over and 4th down grid would be imaged). Pictures would be taken until a minimum of 50 individuals from each family or group had been captured on camera; pictures of grids were never repeated. If there were less than 50 individuals of a particular family, then all individuals of that family within the sample were captured on camera. Damaged individuals were not counted. An additional photo of a calibration slide (7.5mm) was taken and saved. Camera images were then transferred to the software ImageJ, where the calibration slide was measured using the line tool 5 times. The average number of pixels of those 5 measurements were calibrated to 7.5mm. Every individual captured on camera would then be measured in pixels and converted to length. Prey mass was estimated using the length to mass conversion equation for macroinvertebrates that was developed by Benke et al. (1999).

$$PM = 0.0064 \bullet PL^{2.788} \bullet 10^{-3}$$

Where *PM* is prey mass (g), and *PL* is prey length (mm).

3.3.2 – Drift Feeding Bioenergetics Model:

The DFBM used for this project was created by Larocque et al. (2014) and can be modified for application to juvenile and YoY Arctic grayling. The basic DFBM equation is:

$$NEI = GEI - SC$$

Where *NEI* is net energy intake (J/h), *GEI* is gross energy intake (J/h) and *SC* is swimming cost (J/h) (Hughes & Dill, 1990; Rosenfeld & Boss, 2001). Arctic grayling are DFS and swim continuously to maintain their position within the current. Thus, it is assumed that the standard metabolic cost is the energetic cost of swimming which can be calculated through:

$$SC = 10^{(C+M \bullet V)} \bullet 19 \bullet \left(\frac{FW}{1000}\right)$$

$$FW = 0.0224 \bullet FL^{2.8379}$$

Where *C* = 2.07-0.37(logFL) and *M* = 0.410-0.0196(logFL) incorporated into the model as dimensionless scalers, *V* is stream velocity (cm/s), *FW* is fish weight (g), and *FL* is fish length (cm) (Hughes and Dill 1990). *FL* was standardized at 15 cm for juvenile Arctic grayling, and 5 cm for YoY with *FW* being calculated from the length-to-weight index for grayling. *GEI* can be characterized as the energy intake multiplied by the utilization efficiency:

$$GEI = E \bullet UE$$

Where *E* (J/h) is the energy intake and *UE* is the utilization efficiency, which is a proportion of the energetic intake. *UE* encompasses all energetic costs with digestion, and faeces and excretion. Digestion is approximately 14% of the energetic intake, with faeces and excretion making up 15% and 10% respectively and it is assumed that the *UE* for Arctic grayling is 0.61 (Jones et al., 2003; Tucker & Rasmussen, 1999):

$$UE = 1 - \left(\frac{14 + 15 + 10}{100}\right) = 0.61$$

The energetic gains for this model come from the grayling consuming food in the drift. Energy intake is the energy gained from consumption of prey items within a given time frame, and can be characterized as:

$$\mathrm{E} = \mathrm{CR} \bullet \mathrm{PE}$$

Where *CR* is the consumption rate (g/h) and *PE* is prey energy (J/g). *PE* is assumed to be 22164 J/g for all life stages of benthic macroinvertebrates (Cummins & Wuycheck, 1971). *CR* is dependent on prey abundance as well as the searching and handling time incurred when capturing prey. Grayling exhibit a Type II functional response as prey increases, where feeding will increase until a point of plateau (John O'brien et al., 2001), which is due to the increases time spent handling and consuming prey items. Thus, *CR* is calculated with a Type II functional response with searching time and handling time (Hughes, 1998):

$$CR = \left(\frac{ER}{1 + ER \bullet H}\right) \bullet PM \bullet 60 \bullet 60$$

Where *ER* is encounter rate (#prey/s) and *H* is handling time (s), with 60•60 converting seconds into hours. *ER* can be estimated by the prey density that falls within the grayling search window over time. *ER* can be calculated through:

$$ER = CA \bullet V \bullet PD \bullet 10^{-6}$$

Where *CA* is capture area (cm^2), *PD* is prey density (#prey/m^3), and 10^{-6} converts m^3 to cm^3. Handling time is the time spent by grayling consuming the prey item they captured and is used to account for when prey densities reach a level where the success of capture in the drift is lower than 100%, with the assumption that capture rate at lower densities is 100%. It can be calculated as:

$$H = RD/Vmax$$

Where *RD* is reactive distance (cm), and *Vmax* is the maximum sustainable swimming speed an Arctic grayling can maintain (Hughes 1998).

Water velocity (cm/s) and depth (cm), and *PD* (prey density/drift density, #ind./m^3) are needed to calculate this *NEI* model. Water velocity is important as it impacts prey encounter rate and swimming costs of maintaining position within the current. Water depth influences search area size available for prey capture. Finally, *PD* directly influences prey availability. Velocity and depth were measured at sampling location and calculated as the average along the transects whereas *PD* is estimated as drift density. After *NEI* is calculated, an estimate of grayling growth (g/day) can be calculated:

$$Growth = \frac{NEI}{ED \bullet 24}$$

Where *ED* is energy density (J/g) and 24 is the number of hours in a day. *ED* for this model was adapted from Hayes et al., 2000 who estimated *ED* for brown trout (*Salmo trutta*), which is a comparable DFS:

$$ED = 3148 \bullet e^{0.332 \bullet \left(100 \bullet \left(\frac{FW}{FL^3}\right)\right)} \bullet FW^{0.072}$$

This model helps determine the quality and quantity of food available for DFS in each stream location. Drift net replicates that were thought to have unacceptable sampling error (e.g., debris or algal buildup blocking the net) were removed from analysis. Additionally, a replicate within CW-S-02 was removed from analysis due an extremely high outlier value. This replicate contained an estimated 4984 zooplankton which produced a growth potential estimate of 2.1 g/day, approximately 42 times larger than the second highest growth potential estimate (0.049 g/day), and thus was considered an error in the model.

3.3.3 – Statistical Analysis:

All statistical tests were performed in R-Studio statistical software (*version 4.1.3*, R Core Team, 2022) with a 95% confidence interval ($\alpha = 0.05$). Body lengths of drifting invertebrates (mm) were plotted onto a SE bar plot and divided based on ecozone with two-sample t-tests used to determine what invertebrate groups are larger between the regions. Invertebrates were placed into size classes (e.g., < 3 mm individuals ranged from 2-3 mm) and plotted onto a frequency of occurrence (%) bar plot to determine which size range occurred most frequently in the drift, along with the frequency of occurrence of size classes based on ecozone to determine how frequency of each size class differed between boreal and tundra ecozones.

Growth potential (g/day) of both YoY and juvenile grayling were calculated and plotted onto a boxplot. Growth potential was divided into four food source categories: benthic, lentic, terrestrial, and total food sources. Growth potential based on food source was plotted onto a SE bar plot to determine where most of the potential growth comes from at each site. Two-sample t-tests and a three-factor analysis of the variance (ANOVA) was conducted to determine if there are significant factors or relationships between factors in potential growth based on region, food source and age-group of graylings. Multiple linear regression models for explaining the observed variation in potential growth of grayling were calculated and ranked using the corrected Akaike Information Criterion for small sample sizes (AICc). The explanatory variables chosen for the candidate model were: (i) prey length (mm), (ii) TDP, and (iii) benthic abundance. The model with the lowest AICc value is considered the “best” model. Models within 7 ΔAICc are considered plausible (Anderson, 2008). All AICc analyses and rankings were conducted using the “AICcmodavg” package in R (Mazerolle, 2019).

3.4 – Results:

3.4.1 – Prey Size

Across tundra streams the most common size class of drifting invertebrates was < 2 mm, where in boreal streams the most common size class is <3 mm, which made up a significantly higher proportion of the population compared to tundra streams (tundra mean = 11.58 +/- 2.36 %, boreal mean = 32.22 +/- 2.61 % (+/- 1 SE), p <0.0001) (Figure 3.1). Overall mean length of invertebrates did not differ significantly based on ecozone (tundra mean = 1.84 +/- 0.16 mm, boreal mean = 2.05 +/- 0.07 mm (+/- 1 SE), p = 0.22). Within specific orders of BMI, drifting ephemeropterans on average were larger in tundra streams (tundra mean = 4.37 +/- 0.09 mm, boreal mean = 2.74 +/- 0.1 mm (+/- 1 SE), p <0.0001) and drifting plecopterans on average were larger in boreal streams (tundra mean = 1.35 +/- 0.03 mm, boreal mean = 1.68 +/- 0.17 mm (+/- 1 SE), p <0.0001) (Figure 3.2).

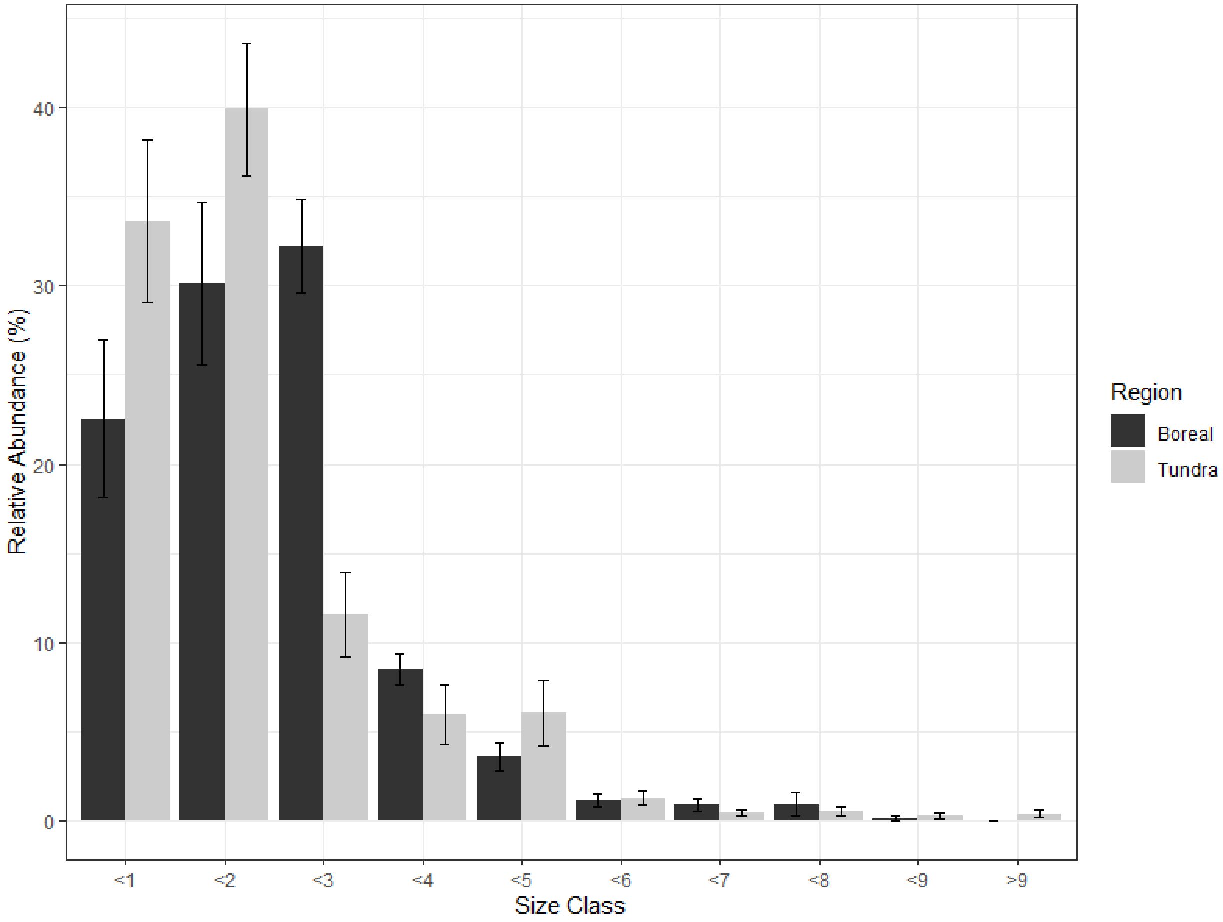

Figure 3.1 – Standard error bar plot of the relative abundance (+/- 1 SE) of size classes of drifting invertebrates based on ecozone. Dark bars represent boreal populations, while light bars represent tundra populations.

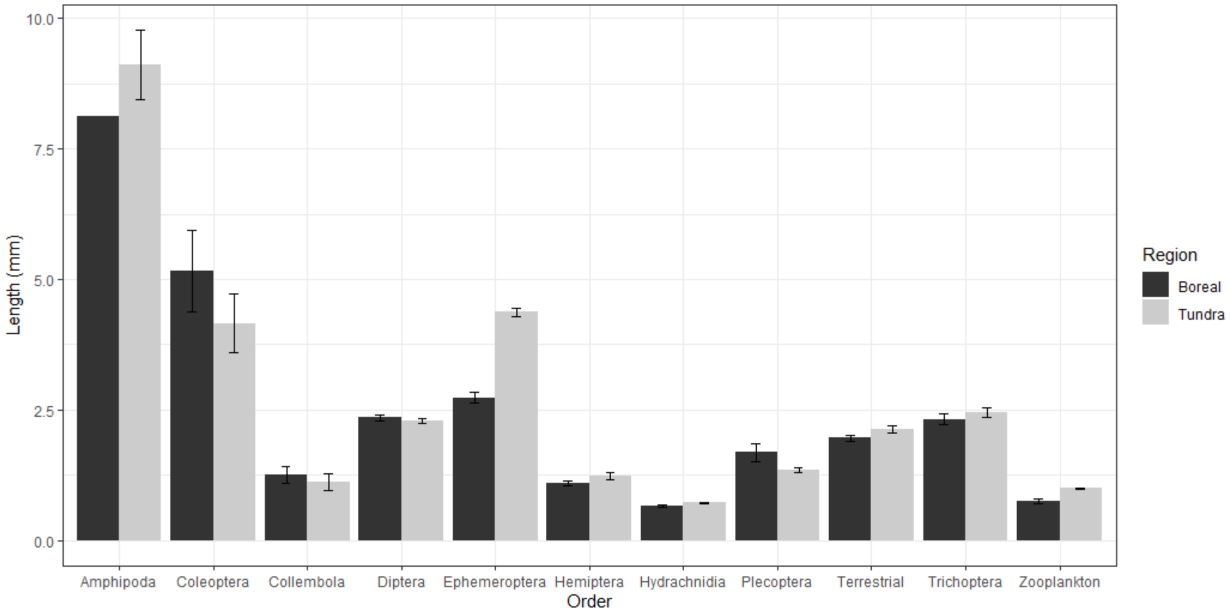

Figure 3.2 – Standard error bar plot of the mean lengths (mm; +/- 1 SE) of drifting invertebrate orders (including terrestrial and zooplankton) across both ecozones. Dark bars represent mean lengths from boreal drift samples, and light bars represent mean lengths from tundra drift samples.

3.4.2 – Growth Potential of Grayling

Growth potential for all drift replicates was calculated for both YoY and juvenile age-groups of grayling (Figure 3.3). Total average growth potential of both age-groups did not differ based on ecozone (tundra mean = 0.005 +/- 0.0052 g/day, boreal mean = 0.00005 +/- 0.0032 g/day, +/- 1 SE), however t-tests showed significant differences in growth based on age-group ($p < 0.0001$), and food source ($p < 0.0001$). The highest % of available energy for grayling (J/hr) in both ecozones was derived from benthic sources (tundra = 61.24 %, boreal = 63.1 %), with boreal streams having significantly higher available energy from terrestrial sources (tundra = 14.76 +/- 5.5 %, boreal = 33.8 +/- 7.7 % (+/- 1 SE), $p < 0.0001$) and tundra streams having significantly higher available energy from upstream lentic sources (tundra = 24 +/- 9 %, boreal = 3.11 +/- 1.7 % (+/- 1 SE), p <0.0001) (Figure 3.4). Growth potential for YoY grayling depending on benthic, lentic, terrestrial, or total food sources was also calculated across all streams (Figure 3.5).

AICc rankings estimated benthic abundance to be the best model for estimating growth potential of grayling, however all 7 other models calculated were within 7 AICc of the best model, including the null model, thus there is no clear predictor of grayling growth potential. A three-factor ANOVA test revealed that food source (benthic, lentic and terrestrial), and age-group (YoY and juvenile) were significant factors in potential growth of grayling, and that the interaction between the factors of ecozone (boreal and tundra) and food source was also significant.

Table 3.1 – Corrected Akaike Information Criterion (AICc) model selection results for predicting growth potential of Arctic grayling growth potential (g/day) against benthic abundance, total dissolved phosphorus (TDP), and prey length (mm). ΔAIC shows the difference in AICc from the best predictor model. AICc Weight is the weighted importance of the model. Models within 7 ΔAIC are considered plausible.

Predictor	**K**	**AICc**	**ΔAICc**	**AICc Weight**
Benthic Abundance	3	86.89	0.00	0.32
TDP	3	87.81	0.92	0.2
null	2	88.51	1.62	0.14
Prey Length + Benthic Abundance	4	89.29	2.39	0.1
Prey Length	3	89.47	2.57	0.09
TDP + Prey Length	4	89.87	2.98	0.07
TDP + Benthic Abundance	4	90.05	3.15	0.07

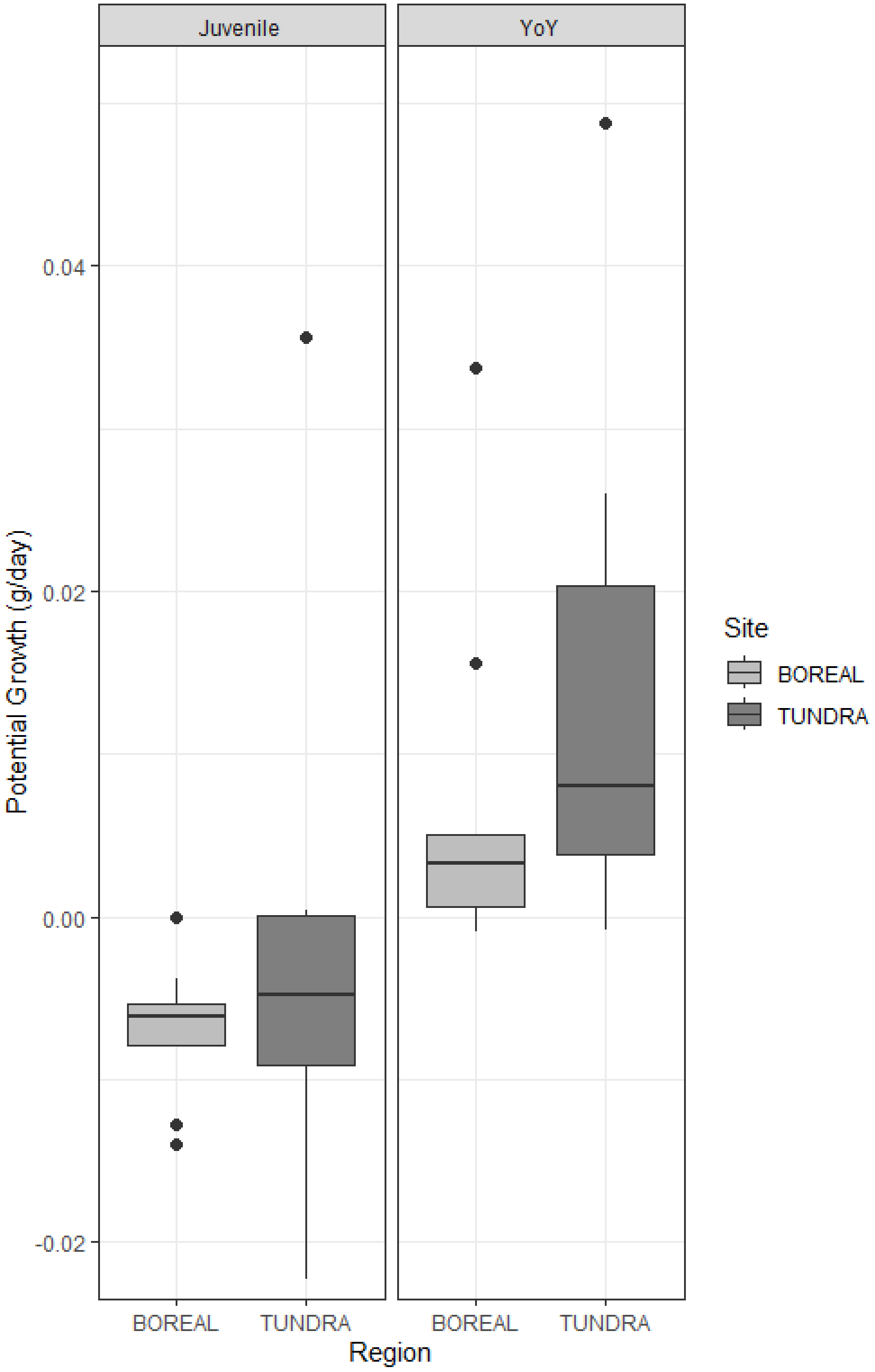

Figure 3.3 – Box plots of the average growth potential (g/day) of juvenile and YoY Arctic grayling across boreal and tundra streams. Light boxes show growth potential of grayling in boreal streams, dark boxes show growth potential of graying in tundra streams.

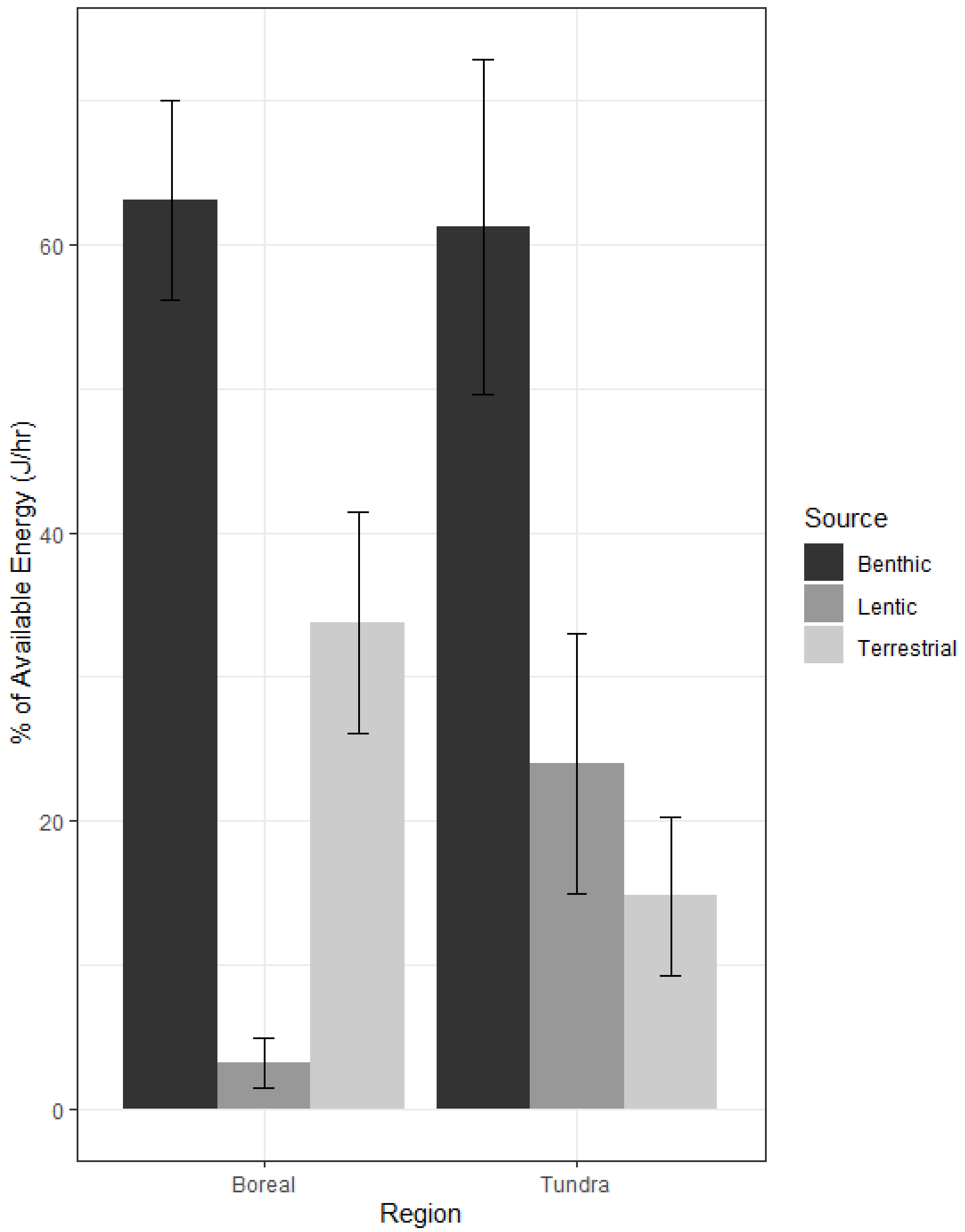

Figure 3.4 – Bar plot showing mean (+/- 1 SE) for the proportion of available energy (J/hr) based on food source (in order from left to right: benthic, lentic, terrestrial) across boreal and tundra ecozones. The 3 left most bars represent boreal streams, and the 3 right most bars represent tundra streams. Benthic sources provide the most available energy across both ecozones ($p < 0.0001$), terrestrial sources of energy are proportionally higher in boreal streams ($p < 0.0001$) and lentic sources are proportionally higher in tundra streams ($p < 0.0001$).

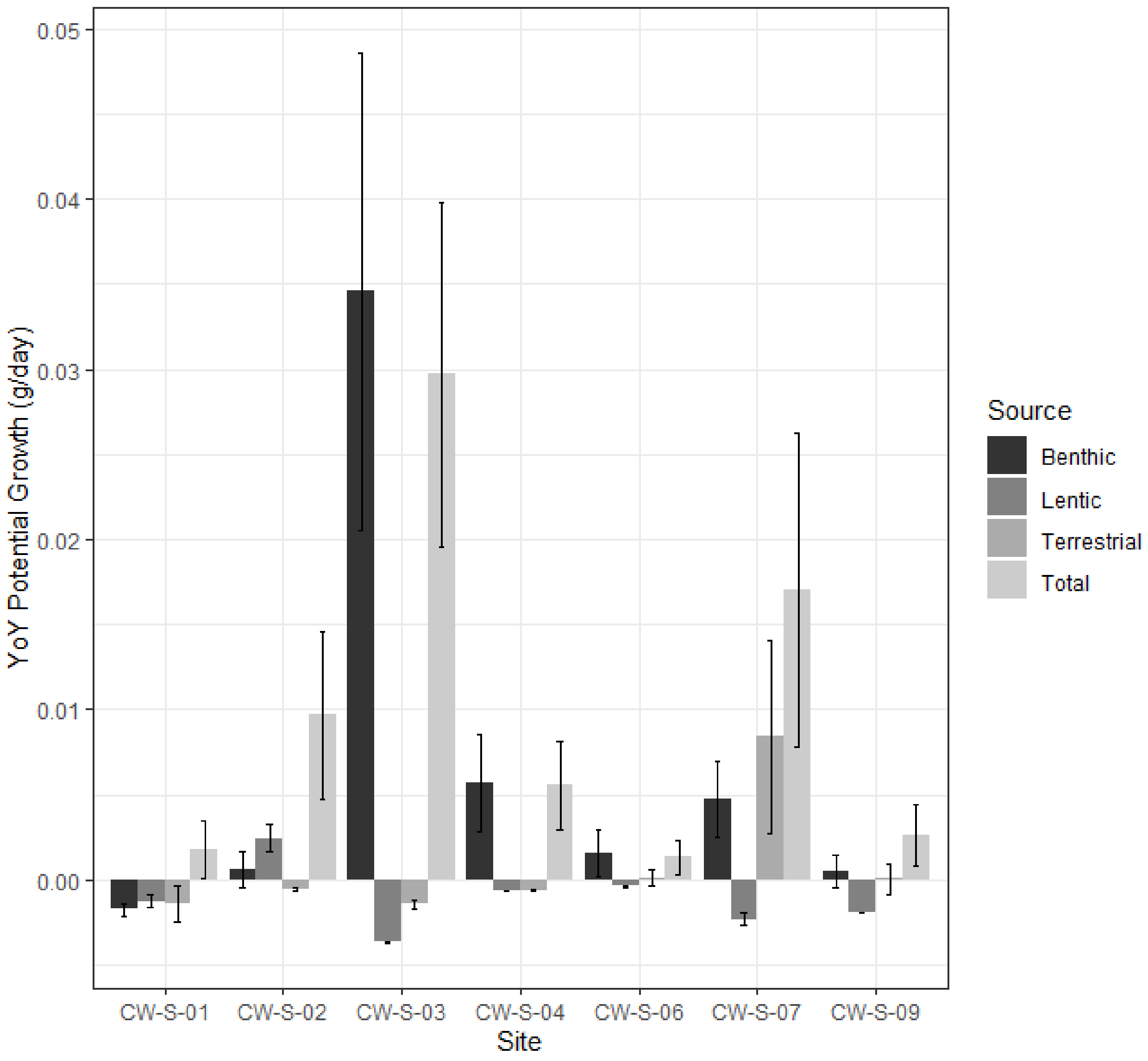

Figure 3.5 – Standard error bar plot of the growth potential (g/day) (+/- 1 SE) for YoY Arctic grayling based on food source (from left to right: benthic, lentic, terrestrial, total) across all streams sampled. Negative growth potential shows not enough of that individual food source to sustain a population.

Table 3.2 – Three-factor ANOVA of growth potential (g/day) testing significance of growth potential between (i) Ecozone (boreal and tundra), (ii) Age Group (juvenile and YoY), and (iii) Food Source (benthic, lentic, and terrestrial). "*****" indicates a statistically significant factor in potential growth of grayling ($p < 0.05$).

Factor	**Df**	**Sum Sq**	**Mean Sq**	**F Value**	**p**
Ecozone	1	6.1e-05	6.1e-05	0.508	0.48
Food Source	2	0.002	0.001	8.262	0.0004*****
Age Group	1	0.0043	0.0043	35.892	3.16e-08*****
Ecozone + Food Source	2	0.0011	0.001	4.58	0.012*****
Ecozone + Age Group	1	3.0e-06	3.0e-06	0.021	0.89
Food Source + Age Group	2	5.6e-05	2.8e-05	0.233	0.79
Ecozone + Food Source + Age Group	2	3.2e-05	1.6e-05	0.131	0.88
Residuals	102	0.012	1.21e-04		

3.5 – Discussion:

The purpose of this study was to assess both prey quality and quantity for Arctic grayling across boreal and tundra ecozones and calculate potential growth as a means of determining how growth potential differs for grayling based on ecozone. Growth potential of YoY and juvenile Arctic grayling in the boreal and tundra ecozones was similar (Figure 3.3), as were the density (prey availability; Figure 2.4) and prey size (prey quality; Figure 3.1) of drifting insects, both of which are key components in the drift-feeding bioenergetics model applied in this study. There were, however, significant differences in potential growth based on grayling age class and food source. Surprisingly, model estimates for all streams, apart from one replicate in CW-S-03, showed negative growth potential for juvenile grayling (Figure 3.3), suggesting these streams are not well suited to juvenile grayling at this time of year (i.e., energy costs exceed inputs). However, growth potential of YoY grayling was positive across all streams (Figure 3.3). Differences in the source of available energy were apparent as terrestrial food sources showed significantly higher amounts of energy available in boreal streams associated with higher drift densities of terrestrial invertebrates. In contrast, lentic food sources in tundra streams were significantly higher due to zooplankton abundance in tundra drift. In both ecoregions benthic food sources were the predominant available energy source (Figure 3.4). The importance of differing food source between ecozones was further substantiated by the three-factor ANOVA, showing a relationship between ecozone and food-source as factors influencing potential growth (Table 3.2). Although benthic abundance was the best predictor for the growth model, the importance of this predictor was low, and similar to null model predictions (Table 3.1).

3.5.1 – Growth Potential of YoY vs Juvenile Grayling

The DFBM produced unsuitable growth potential results for juvenile grayling estimated for these small tributaries in late summer (Figure 3.3). This result aligns with established seasonal movement patterns of grayling. While these complex migratory movements differ among stream ecosystems in response to local conditions (Craig & Poulin, 1975; Northcote, 1995), the migratory patterns of grayling residing within the Mackenzie Delta and surrounding area are expected to be similar to populations in Alaska streams, as these geographic areas display similar seasonal hydrological and ice regimes (Craig & Poulin, 1975; Northcote, 1995). Most adults will return to overwintering habitat after spawning in July, with juvenile populations remaining until late August (during our sampling period), and YoY grayling migrating during the month of September (Craig & Poulin, 1975).

The earlier return of juveniles to overwintering habitat compared to YoY may be associated with reduced drift densities during the lower flows observed near the end of summer in August. Previously, such seasonal drift patterns have been observed to coincide with lower flow in both high-altitude and temperate streams (Hieber et al., 2003; Kownacki et al., 1997; Rashidabadi et al., 2022). A decrease in prey availability would reduce habitat suitability for juveniles but model estimates suggest prey abundance would be sufficient to sustain YoY populations until September (Figures 3.3; 3.5). Migratory patterns of grayling populations are likely stream-dependent and may differ between Arctic ecozones (Stewart et al., 2007). Further analysis into the seasonality of both grayling movement and invertebrate drift throughout the summer within the Mackenzie Delta and Husky Lake tributaries is needed. Based on the current understanding of seasonal movement patterns, grayling migration in late summer should be closely linked to freeze-up times, with grayling in the colder tundra region likely departing for overwintering habitat sooner than in boreal streams.

3.5.2 – Sources of Growth Between Ecozones

In both the boreal and tundra ecozones, benthic food resources were the most important source of potential growth, however, additional sources of available energy differed between ecozones (Figure 3.4). For example, the amount of energy available from terrestrial sources was significantly higher in boreal streams due to the higher amounts of terrestrial drift sources (Table 2.3). Denser streamside vegetation and vegetative overhang have been observed to increase terrestrial drift densities and salmonid consumption of terrestrial invertebrates (Nakano & Murakami, 2001; Ryan & Kelly-Quinn, 2015), and with boreal streams having higher riparian density (Table 2.1), this observation suggests potential differences in diet of grayling between the boreal and tundra ecozones.

Allochthonous prey inputs may play an important role for sustaining healthy Arctic grayling populations residing in Arctic boreal streams during the late summer. For example, terrestrial prey contribution to salmonid diets can make up 50-86% of total energy intake during the summer months (Garman, 1991; Nakano et al., 1999; Wipfli, 1997), and up to 50% of their entire energy intake through the year (Kawaguchi & Nakano, 2001; Nakano & Murakami, 2001). Moreover, salmonid species appear to have a preference and in some cases a dependence on terrestrial inputs in their diet, as Kawaguchi et al., (2003) observed a 50% reduction in the biomass of Dolly Varden (*Salvelinus malma*) when terrestrial inputs were removed from an experimental stream.

Lentic sources of energy may be important for grayling in tundra streams, particularly in lake outlet streams. Model estimates for CW-S-01 indicated that dependence on any one of the benthic, lentic or terrestrial prey sources would result in negative growth potential for YoY grayling, while a combination of these sources could provide positive growth potential (Figure 3.5). Therefore, a varied diet consisting of drifting benthic, lentic, and terrestrial food sources may be necessary sustain YoY grayling occupying this stream. In contrast, CW-S-02 showed lentic sources provided the greatest amount of growth potential for YoY, due to the proportion of drift consisting of zooplankton ranging from 88 – 95 % of the drift (Figure 3.5). This suggests the need for fish to consume lentic sources to provide sustained growth within this stream. Haugen & Rygg, 1996 showed that zooplankton dominated the diet of young European grayling (*Thymallus thymallus*) in lakes and inlet streams in Norway. Thus, it may be plausible similar diets exist for some populations of tundra Arctic grayling under similar environmental conditions. While young Arctic grayling sometimes avoid lentic sources of food (Jones et al., 2003), my research indicates that lentic sources may be important to tundra food-web structure and grayling health. Clearly, further assessment of lake-stream connectivity in tundra regions is needed to improve understanding of grayling diet in tundra regions. Additionally, gut content analysis and isotopic evaluations of diet are also needed to better understand food-web dynamics and potential dietary differences of grayling between the two Arctic ecozones.

3.5.3 – Conclusions and Future Research

While growth potential was similar for Arctic grayling across boreal and tundra streams, differences in growth potential among benthic, terrestrial, and lentic food resources as well as group of Arctic grayling age class were evident between ecozones. Average growth potential of juvenile grayling across was negative in both regions, while estimates of positive growth potential were found for YoY at all sites. This late summer pattern suggests these stream habitats are unsuitable for juvenile grayling but suitable for YoY grayling, a trend that aligns with known migration patterns of Arctic grayling. Across both ecozones, benthic prey items provided the highest growth potential, however, terrestrial sources of energy were higher in boreal streams, and upstream lentic sources of energy were higher in tundra streams, particularly in lake outlet streams. Finally, further analysis into seasonal patterns of drift across both Arctic ecozones would improve understanding of food availability for juvenile grayling and determine if seasonal trends in prey availability are likely an important driver of established migration patterns and habitat occupation during summer months. Such seasonal assessments should include examination of grayling gut content and isotopic evaluations of trophic structures between ecozones to test the hypothesis that ecozone differences in habitat suitability are a major driver of grayling migratory patterns between ecozones.

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CHAPTER 4: SUMMARY AND SYNTHESIS

4.1 – Summary and Synthesis of Results:

Invertebrate drift has been an extensively studied process within fluvial environments for decades, yet the understanding of the potential differences in drift function across high latitude streams, and the subsequent impact for food-webs, has remained a knowledge gap. This thesis aimed to bridge that gap by **1)** determining the potential drivers and differences in drift across two Arctic ecozones, and **2)** calculating how those differences in drift may impact the habitat suitability of an apex drift feeding predator. Chapter 2 addressed the first goal by characterizing the benthic and drifting components of invertebrate communities across boreal and tundra ecozones, along with the physical and chemical characteristics of the streams to determine potential drivers of drift. Chapter 3 utilized the drift data to calculate potential growth food resources for growth for juvenile and YoY Arctic grayling with a drift feeding bioenergetics model, and to analyze how differences in drift subsidies may cascade up the food-web across the two ecozones. This chapter summarizes and synthesizes the findings of Chapter 2 and 3, states the significance of the research, proposes future research based on the findings, and discusses the integrative nature of this thesis.

4.1.1 – Chapter 2 Overview

There were no significant differences in the base ecological metrics of richness, and diversity in both benthic and drifting communities across boreal and tundra ecozones. There were, however, significant differences in both benthic and drift community compositions. These differences were best explained by significantly higher relative abundances of benthic predators and collector-gathers in boreal streams, higher relative abundance of collector-filterers in tundra streams, and higher relative abundance of ephemeropterans and terrestrial invertebrate inputs in boreal drift subsidies. Additionally, benthic abundance was on average 10 times greater in tundra streams, however, despite the discrepancies in abundance between the two ecozones, drift densities remained similar.

Due to boreal and tundra streams having similar drift densities despite differences in abundance, additional drivers within boreal stream systems appeared to drive active drift in response to an environmental driver. Potential drivers of drift in boreal streams, which were absent in tundra streams, were identified including higher predator presence and resource limitations. With boreal streams having significantly higher proportion of benthic-predators occupying the benthic composition, this may have led to invertebrates drifting as a defensive mechanism for predator avoidance (Huhta et al., 2000; Kratz, 1996; Peckarsky, 1980). Due to significantly lower TDP concentrations in boreal streams, and NDVI calculations inferring significantly denser riparian vegetation, primary production in boreal streams appeared to be limited by a combination of nutrients and shading (Cross et al., 2006; Hill et al., 1995). Thus, invertebrates can use drift relocation as a strategy for finding new food resource-rich areas (Dimond, 1967; Hammock & Wetzel, 2013; Richardson, 1991). Such drivers of drift, along with darkness during the night, were absent from tundra streams with drift in boreal streams consisting primarily of active drifters (i.e., mayflies, net-spinning caddisflies). In tundra streams passive drifters (i.e., Brachycentrids, Glossossomatids) predominated drift composition.

4.1.2 – Chapter 3 Overview

The size of drifting invertebrates did not differ between boreal and tundra streams, and thus, in combinations with equal drift densities, the potential growth of grayling calculated through a DFBM did not differ between ecozones. There were, however, significant site differences in potential grayling growth based on food source, and age-group of Arctic grayling.

YoY grayling had positive growth potential across all sites, while positive growth potential for juvenile grayling was limited to one replicate, suggesting the tributaries sampled at this time of year are unsuitable to juvenile grayling. This trend matches established migratory patterns of grayling in Alaskan streams, where juveniles will migrate from smaller tributaries for their overwintering habitat in late summer while YoY will remain until September (Craig & Poulin, 1975; Northcote, 1995) a trend that is hypothesized to be due to a drop in prey availability (Hieber et al., 2003; Kownacki et al., 1997; Rashidabadi et al., 2022).

While benthic sources of food remained the most energetically available across both ecozones, there was significantly higher growth potential linked to terrestrial sources in boreal streams, and significantly higher amounts of growth potential associated with upstream lentic food resources in tundra streams, particularly in lake outlet streams. Salmonid species can rely on and show preference for terrestrial food sources, thus grayling within boreal streams may display similar dietary preferences (Garman, 1991; Nakano et al., 1999; Wipfli, 1997). Arctic grayling have been observed to avoid zooplankton and lake subsidies when feeding benthic sources are highly abundant (Jones et al., 2003), however, the DFBM results showed that within lake outlet streams in my study region, a varied diet consisting of benthic, lentic, and terrestrial food sources is required to sustain growth.

4.2 – Significance of Research:

Drift has been the subject of ecological research for decades, and despite this, might still be considered a developing field in aquatic ecology (Naman et al., 2016). Despite drift being well-studied in temperate regions, the functionality of drift in high latitude streams remains understudied. The drift data obtained in this project provided baseline knowledge into the functionality of drift across Arctic environments, and subsequently aided in understanding the greater role BMIs play within Arctic food-web structures. Results garnered from the DFBM gave insight into energy availability, habitat suitability, and potential dietary differences for Arctic grayling within the Western Arctic. Ultimately, my findings will contribute to the ever-expanding research being conducted in Arctic environments, and the hypotheses proposed will aid in the development of future research projects to further the understanding of high latitude stream environments.

4.3 – Future Research:

4.3.1 – Invertebrate Drift

Diel drift was expected to be absent in Arctic regions during sampling due to 24h of sunlight during the Arctic summer months except in areas with dense riparian shading where light levels may fall below the threshold of 30 lux where BMI initiate diel drift (Haney et al., 1983; Johnson & Almlöf, 2016; Wilzbach & Hall, 1985). Future research into this subject should measure differences in light availability in streams between boreal and tundra ecozones over a 24h period and conduct temporally structured drift sampling sessions to gain estimates of how drift densities change throughout the day. Thus, if diel periodicity is present in boreal regions, yet absent in tundra regions, it could partially explain why drift densities remain equal between the ecozones.

Additional research into the nutrient limitations between the ecozones may help explain the discrepancies in benthic abundance and drift densities. I hypothesized that these Arctic streams are phosphorus limited, and that because TDP concentrations were significantly higher in tundra streams it would increase basal production and the standing crop of BMI. If these streams are phosphorus limited, it would explain the significantly larger benthic populations in tundra streams. Additionally, if boreal streams are resource limited, it would help explain the increased drift rates from BMI (Dimond, 1967; Hammock & Wetzel, 2013; Richardson, 1991).

The seasonality of drift in Arctic regions is also an important gap in drift literature that should be addressed. Past studies have shown that in temperate, and high-altitude stream environments, drift densities peak in the summer and fall off as the season progresses into autumn (Hieber et al., 2003; Kownacki et al., 1997; Rashidabadi et al., 2022). Drift sampling across multiple stream environments should be conducted periodically throughout the summer into autumn to establish whether or not Arctic stream environments across multiple ecozones also follow this established pattern, or if the functionality of seasonal drift patterns is different in high latitude streams.

4.3.2 – Arctic Grayling Ecology

Grayling are a culturally important, and top trophic predator species of fish in the northern hemisphere (Jones et al., 2003; Larocque et al., 2014), so understanding their diet across multiple ecozones would aid in understanding trophic food-web structure in the Arctic. Firstly, future research should conduct gut content analysis to understand the dietary differences that may persist in grayling between the two ecozones. I hypothesize that due to **1)** boreal regions having significantly higher amounts of energy available from terrestrial sources, and **2)** that salmonids residing in forested environments have been observed to favour terrestrial prey items (Garman, 1991; Kawaguchi et al., 2003; Nakano & Murakami, 2001), that analysis into their diet would reveal significant differences in sources of prey items consumed. Additionally, stable isotope analysis into food-web structure would be useful in understanding the structural composition of the food-webs, the interconnectivity of Arctic streams to their adjacent environments, and aid in future conservation endeavours of the region.

Finally, the need to validate the DFBM created by Larocque et al., (2014) for Arctic grayling populations in northern Canada is important to allow the tool to be used confidently in conservation practices as a means to evaluate grayling habitat quantifiably. Research should include multiple sessions of drift sampling throughout the year, measuring the conditions of the stream at the time (velocity, depth), and calculating the model to obtain growth estimations. Grayling of multiple age-groups should also be caught and have their growth tracked to confirm how well the model estimates growth. Additional variables in the model should also be added to better evaluate habitat quality such as: rate of adfluvial foraging and benthic foraging and integrating stream temperatures impact on grayling metabolism.

4.4 – The Integrative Biology of this Thesis:

Ecological research is a highly integrative field of biology, with this project being impossible to accomplish without the integration of multiple disciplines. The drift research conducted in Chapter 2 uses hydrology to calculate drift densities, the application of light physics to estimate riparian vegetation density using the NDVI index, and the integration of geography and chemistry to describe the physical differences among sites sampled. With the DFBM used in Chapter 3, physiological data of Arctic grayling is incorporated, and the geomorphological characteristics of the stream structure are used to estimate growth potential of grayling. Without knowledge of these fields, this project could not be conducted.

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