Evaluating Spatial Variation in Food Web Connectivity and Energetics within the Lake Superior Fish Community

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Abstract

Habitat coupling integrates energy between habitats, a process known to contribute to food web stability, and has been observed in Lake Superior. The degree of coupling differs among species, but the extent to which it may vary across Lake Superior is unknown. A change in the degree of coupling may alter regional trophic transfer efficiency (TTE), which is the amount of energy that is available to be passed on to a successive trophic level. Spatial differences in habitat coupling and TTE in Lake Superior were evaluated using common fish species and their prey, collected from four geographically distinct regions and along a depth gradient. For each species, habitat coupling was assessed using stable isotope analysis, and bioenergetics models were created to estimate conversion efficiency (as a proxy measure of TTE). Species that exhibit diel vertical migration (lake trout, smelt, herring and bloater) showed more variability in resource partitioning with depth, especially in the deeper regions. Overall, there was a large pelagic reliance, but some benthic specialization was observed in the medium and deep depth strata. Lake whitefish and sculpin spp. showed a common use of pelagic resources across all depth strata within a region. Bioenergetic estimates exhibited opposite trends in lake whitefish and smelt across sampled regions, but lake trout bioenergetics were generally well conserved. Conversion efficiency showed a positive relationship with percent benthic reliance in lake whitefish populations and a negative association with percent benthic reliance in the smelt populations, suggesting species are better able to utilize energy from which they are most commonly associated. This study contributes to a better understanding of how food webs large lakes are structured, and the inherent variation in ecosystem function that should be considered in whole-lake modelling or regional management. Because Lake Superior is a relatively undisturbed ecosystem, these features can be compared with other large lakes and used as an example to identify common properties of healthy systems to protect or re-establish the functionality of disturbed systems.

Lay Summary

Lake Superior, being the largest freshwater lake by area in the world, is an important resource as both a commercial and recreational fishery. It has a food web that has been the least affected by invasive species and pollution out of all the Laurentian Great Lakes. In order to continue to best manage this resource, it is important to understand how the fish communities are structured. This thesis focuses on what resources the fish communities in Lake Superior rely on, how well they are able to transform their resources into growth, and how this varies across the lake. The data I present here suggests the resources that a fish species uses will vary across regions. As well, fish are best able to convert the energy they obtain into growth when consuming their more preferred prey item. This thesis contributes to a better understanding of how variable a large lake such as Superior can be. These results can be compared to other large lakes to identify common features of healthy large lake populations. Understanding how resource use and energy allocation varies spatially will help us to manage this resource better and continue to protect it for future generations.

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Chapter 1: General Introduction

Variation in the pathways of energy flow has been observed across many aquatic ecosystems(Hoffman et al. 2008; Gamble et al. 2011b; Tunney et al. 2018), but few studies have quantified the amount of variation in energy flow pathways that occur within a single system, particularly in large ecosystems where spatial variability is likely to alter these flow paths. If a study chooses a large scale approach to classify ecosystems, it may overlook important details due to a homogenized view of the environment. Integrating energy flow with spatial variability may be one way to provide a more complete understanding of both the rates and pathways of energy flow within an ecosystem. The ways in which different food web components are interconnected across habitats and how those connections might differ from one region to the next can help to indicate differences in trophic position, pathways of energy flow, and distributions of biomass among ecosystems that seem otherwise similar in structure.

Food web analysis aims to evaluate which species coexist together; it also explains how these species interact at various trophic levels to analyze the ecological community broadly. An early paper that summarized the vital aspects of trophic dynamics in ecology was by Raymond Lindeman in 1942. When this paper was published, some important ecological concepts on food webs and trophic structure were just emerging. Ecosystem dynamics was a contemporary concept, and biologists had just begun considering the ecological community as an interconnected system. This paper was one of the first to discuss the idea of distinct trophic levels, each relying on the successive level as a source of energy (Lindeman 1942). There are relationships of productivity and biomass between subsequent trophic levels. For example, higher trophic levels usually have a smaller overall biomass, but the individuals within the trophic level are larger. Lindeman (1942) also noted how consumers at progressively higher trophic levels are increasingly more efficient in energy use; this is because increased or more efficient foraging provides a better chance of finding prey. Energy is lost as it is transferred between trophic levels; Lindeman made one of the first attempts to try and quantify this loss of energy from each successive trophic level to the next; and the proportion of energy lost between successive levels is still a prevalent topic in ecology today. Bioenergetics models used in contemporary studies use the same concept of calculating energetic losses, but the focus is on individual organisms as opposed to ecosystems. Individual conversion efficiency can be estimated; that is, the proportion of energy consumed that is used to contribute to the growth of an individual fish. Higher conversion efficiencies reflect more efficient foraging, a focus on higher quality prey and/or a more abundant prey base in a given habitat.

Historically, there has been a major focus on pelagic ecosystems within lake ecosystems (Vadeboncoeur et al. 2002), but within the past 20 years there has been a shift in understanding to recognize how benthic and littoral habitats can make significant contributions to the whole-lake ecosystem (Vander Zanden et al. 2011; Sierszen et al. 2012; Turschak et al. 2014). Connections between near shore and offshore habitats allow for energy to be transferred, and in some cases this interaction is necessary to sustain the ecosystem (e.g. Schindler and Scheuerell 2002; Gamble et al., 2011a; Sierszen et al., 2014; Stockwell et al., 2014). The littoral benthic energy supply has been shown to provide an important energy source for the entire food web in large lake systems (Vadeboncoeur and Steinman 2002) and these types of connections between food webs can result in healthier and more resilient food webs in both aquatic and terrestrial ecosystems (McCann et al. 2005; Rooney et al. 2006; Haddad et al. 2011).

Benthic energy pathways are typically characterized as channels of slow energy transfer relative to pelagic pathways (Rooney and McCann 2012). This is due to the higher biodiversity and weaker interaction strengths that are often observed in benthic habitats. When there is reliance on resources from an adjacent energy source, this can increase productivity; if this interaction is somehow disturbed, there could be energetic constraints on the overall carrying capacity of the aquatic ecosystem (Cloern 2007). Ecosystems that are most stable or resilient will be characterized by a combination of both strong and fast benthic and pelagic energy pathways (Rooney et al. 2006; Rooney and McCann 2012).

How spatial heterogeneity influences energy flow and food web function is not well understood, and there may be many influential contributing factors. When dealing with large lakes, often studies are conducted in one region to make lake-wide inferences, which may miss fine scale differences in biological interactions or resource use. Few studies have been conducted to evaluate the importance of spatial variability and heterogeneity within habitats. The food webs of large lakes are often considered as single homogeneous habitats (e.g., Gamble et al. 2011a, 2011b), even though there is major variation in habitat complexity, bathymetry, environmental conditions and species composition at different spatial resolutions across large lakes. This variability strongly suggests this generalization is an oversimplification of the ecosystem. Instead of looking at large lake populations as homogeneous, a more comprehensive understanding how lakes are organized and the variation that exists within the food web may be revealed at a smaller spatial resolution. For instance, differences exist in the consumption, abundance and biomass of zooplankton and fish communities between three defined ecosites within the western arm of Lake Superior (Johnson et al. 2004). These biological differences clearly show that spatial heterogeneity exists in Lake Superior food webs. However, the degree to which this variation affects which resources are relied upon and rates of energy transfer within large lakes remains unknown.

Across smaller lakes, the degree of benthic-pelagic coupling of mobile predators may depend on habitat complexity (e.g. lake shape; Dolson et al. 2009). Generally, more circular lakes had steeper depth gradients, whereas in more reticulate lakes there is a shallower depth gradient contributing to a larger littoral area. The steeper depth gradients in circular lakes allow cold water species to move quickly between the pelagic and littoral zone and forage outside of their preferred temperature range. In more reticulate lakes this littoral forage is not accessible due to its further distance from the preferred cold water habitat (Dolson et al. 2009). Other cross-sectional studies have suggested that the amount of coupling could be due to variation in littoral productivity (Schindler and Scheuerell 2002) or lake size (Post et al. 2000b). Overall, these studies exemplify the importance of both depth and spatial heterogeneity when considering food web dynamics.

The size of the area being studied likely also affects the amount of connectivity and flow observed between habitats due to the higher possibility of interactions among food webs in smaller ecosystems. Habitat coupling does exist in large, deep lakes but may be stronger in shallow lakes due to high perimeter: area ratios (Schindler and Scheuerell 2002). Due to the highly varied shoreline of large lakes, it would also be expected that the amount of coupling would vary between the more shallow reticulate bays and the deeper, more open lake regions (Schindler and Scheuerell 2002; Dolson et al. 2009). It may also be beneficial to consider large lake fish populations separately at large spatial scales as dispersal over such great distances would be improbable for most fish species (Kapuscinski et al. 2005; Hayden et al. 2014). Considering large lakes as spatially variable ecosystems with many interacting components may provide greater insights into how resource use differs, rather than considering it to be homogenous across the entire lake. Few papers have quantified spatial differences in energy movement across large ecosystems, but within-lake variance in large lakes has been observed in the literature. For instance, within-lake differences in bioenergetics (consumption, activity and conversion efficiency) of lake whitefish have been observed in lakes Superior, Michigan and Huron (Rennie et al. 2012).

Lake Superior is an important freshwater resource, being the largest freshwater lake by area in the world, with a food web considered to be the least disturbed among the Laurentian Great Lakes (Schmidt et al. 2009; Zimmerman and Krueger 2009). There has been less of an effect of over-harvesting, and invasive species in Lake Superior (such as dreissenid mussels and sea lamprey) compared to the lower great lakes (Kitchell et al. 2000; Rennie et al. 2009). By understanding the trophic structure and energetic processes in Lake Superior, these features can be compared with other large lakes and used as an example to identify common properties of healthy large lake systems as guidelines to protect or re-establish the functionality of disturbed systems.

The Lake Superior food web, like in many large deep lakes, is separated by depth gradients (Schindler and Scheuerell 2002) with the near shore food web in Lake Superior being generally more complex than the offshore food web (Gamble et al. 2011b). The near shore food web appears to rely mostly on benthic primary production (mainly via the amphipod *Diporeia* spp.), whereas the offshore fish community diet seems to be more dominated by pelagic production via the freshwater shrimp *Mysis diluviana* (Yoshii 1999; Gamble et al. 2011b; Sierszen et al. 2014). This is likely a consequence of higher densities of *Diporeia* near shore than offshore (Gamble et al. 2011b). The main species of fish inhabiting the near shore areas are the lean morph of lake trout (*Salvelinus namaycush*), lake herring (*Coregonus artedi*), lake whitefish (*Coregonus clupeaformis*), rainbow smelt (*Osmerus mordax*), sucker spp. (*Catostomus catostomus* and *Catostomus commersonii*), and slimy sculpin (*Cottus cognatus*) (Sierszen et al. 2006; Gamble et al. 2011b). The offshore region is typified by species such as the "siscowet" morph of lake trout, bloater (*Coregonus hoyi*), kiyi (*Coregonus kiyi*), and deep-water sculpin (*Myoxocephalus thompsonii*). There also exists some overlap between regions with species like the slimy sculpin, lake herring, and rainbow smelt (Sierszen et al. 2006; Gamble et al. 2011b). However, the degree to which this overlap permits energetic coupling between near shore and offshore ecosystems remains poorly understood.

Habitats in lake ecosystems, that might otherwise seem discrete, can be linked by the movement of energy through a number of processes. For instance, sedimentation of planktonic material from the pelagic zone into the benthic zone links these habitats (Schindler and Scheuerell 2002). *Diporeia*, a benthic feeder is a good example of a benthic–pelagic coupler in Lake Superior utilizing pelagic energy deposited via sedimentation. *Diporeia* in Lake Superior is most abundant in depths ~40-70m but can be found in depths that range from 5 to over 100 m in the benthic zone of the lake (Sierszen et al. 2006). *Diporeia* gain a large proportion of energy by feeding on settled pelagic algae (Flint 1986), which allows them to be more abundant in the regions further offshore, and remain an important prey species, not only in Lake Superior, but in all of the Laurentian Great Lakes (Auer et al. 2013). Fish movement may also facilitate habitat coupling, through offshore predators using the near shore area as an energy source, or vice versa (Schindler and Scheuerell 2002). This process is observed in Lake Superior lean lake trout, which is able to move horizontally in the water column to predate upon planktivorous ciscoes and rainbow smelt (Gorman et al. 2012; Sierszen et al. 2014). As well, fish migration during spawning can cause a movement of energy across boundaries in Lake Superior; longnose suckers move from the lake to streams to spawn, providing lake-derived energy to streams (Jones and Mackereth 2016). Lastly, offshore cisco species act as a benthic-pelagic coupler as they deposit their eggs near shore in the fall, supplying near shore lake whitefish with a necessary pelagic-derived energy source during the winter months (Stockwell et al. 2014).

Diel vertical migration (DVM) of macroinvertebrates may also be important to consider in habitat coupling (Lindén and Kuosa 2004, Patwa et al. 2007). This is the process where species will migrate within the water column, moving shallower during the night and migrating deeper during the day on a 24 hour cylce. *Mysis* DVM occurs due to the changes in light intensity at depth, migrating up as far as the thermocline at night and back to deep waters during the day (Gal et al. 2004). Fish have been hypothesized to undergo DVM based on both foraging benefits, following prey (Brett 1971), and by bioenergetic theories that predict fishes are maximizing growth rate by seeking out optimal water temperature (Bevelhimer and Adams 1993). In Lake Superior, deep-water biota such as kiyi and siscowet use DVM to forage on *Mysis* in the pelagic zone

(Ahrenstorff et al. 2011). This movement provides deep-water fishes a high energy pelagic foraging opportunity in a that otherwise would only offer few benthic food resources, and also should lead to integration between profundal and pelagic habitats (Sierszen et al. 2014).

Carbon and nitrogen are the most commonly used isotopes in ecologic studies, being used both separately and in unison. The stable nitrogen ratio ($\delta^{15}N$) is used to deduce trophic positions of an individual relative to the base of the food web. A consumer is enriched by 3-4‰ relative to its prey, which gives evidence towards the trophic relationships (DeNiro & Epstein 1981, Minagawa & Wada 1984, Peterson & Fry 1987). In comparison, the ratio of stable carbon isotopes ($\delta^{13}C$), changes very little as it moves through the food web. On average ^{13}C differs less than 1 ‰ as it moves through the food web, meaning the isotopic composition of the food web base will be reflected in all of the consumers it supports (DeNiro & Epstein 1978, Hecky & Hesslein 1995). In aquatic ecosystems this may discriminate between offshore/pelagic and the nearshore/benthic production which tends to be more enriched in ^{13}C relatively (France 1995). Examples include terrestrial versus aquatic (Carpenter et al. 2005), nearshore versus offshore (Rennie et al. 2013) or littoral versus profundal or pelagic sources (France 1998; Vander Zanden and Rasmussen 1999). This method of examining resource use has been favoured over gut content analysis as it provides an integrated isotopic signature over a larger time frame allowing for a temporally integrated picture of feeding ecology compared to point-in-time diet analysis. White muscle is often chosen for stable isotope analysis in fish as the rate at which the isotopic signature reflects that of its diet (turnover rate) is slower relative to other tissues (e.g. liver, mucus, blood), representing a longer feeding period (Hesslein et al. 1993; MacAvoy et al. 2001; Vander Zanden et al. 2015). Another reason white muscle is usually the tissue of choice when analysing stable isotopes is due to the low lipid content. Lipids tend to have highly negative $\delta^{13}C$ relative to protein and carbohydrates (Hoffman et al. 2015); a low lipid content is important as to provide the most accurate carbon signature without being influenced by lipids which can be synthesized by the organism, and provide misleading results when compared to baselines. However high limit content can be estimated using C:N ratios and mathematically corrected using known relationships.

Energy transfer in food webs is commonly characterized using bioenergetics models to estimate conversion efficiency (as a proxy for trophic transfer efficiency) in aquatic ecological studies. Expressed as a ratio of the energy consumed to the energy converted into growth, conversion efficiency can vary between near shore and offshore habitats as well as habitat quality (Sherwood et al. 2000; Trudel et al. 2010). Using conversion efficiency it is possible to calculate how much energy would be required to sustain one individual at a certain trophic level, and how that would relate to the number of individuals at the next lower trophic level. As such, this concept is similar to the larger scale concept of trophic transfer efficiency. Trophic transfer efficiency estimates the amount of lower trophic level production that is necessary to sustain the successive trophic level under consideration (Pauly and Christensen 1995). Conversion efficiency uses the growth and consumption rates of a single individual, whereas trophic transfer efficiency assesses the amount of prey biomass needed to sustain the entire successive trophic level. Consumption estimates from an individual-based bioenergetics model can be combined with known biomass and prey production values within a region to determine the trophic transfer efficiency. As such, conversion efficiency (which reflects efficiency of conversion of consumed mass into growth, and therefore related to production and biomass) can be used as a proxy measure of trophic transfer efficiency. Estimates of consumption from bioenergetic models can provide actual estimates of transfer efficiency in regions by using known regional population estimates and consumption rates.

Carbon and nitrogen stable isotopes of common Lake Superior fish and their prey were used to understand the reliance of benthic and pelagic energy pathways across four geographically distinct regions in the lake. Four geographically distinct study regions were chosen, two shallower embayments that are more protected from the main effects of the lake, and regions with a steeper depth gradient which are relatively more exposed to the wind and wave action of the main lake. In addition, a combination of a mercury mass-balance model (MMBM) and bioenergetics model was used to understand variation in bioenergetics across regions to estimate consumption, activity rate, and conversion efficiency. Ultimately, these two approaches were combined to gain a better understanding of how energy transfer relates to habitat coupling among key fish species in Lake Superior. The objective of is study was to assess the spatial variability of habitat coupling within Lake Superior and how it relates to trophic transfer efficiency, this will contribute to our understanding of the properties of a healthy large lake system. I expect that there will be within species variability in resource use due to the regional bathymetry and morphometrics (Dolson et al. 2009; Johnson et al. 2004; Post et al.), and that species ability to move within the water column will increase the mixed use of resources. As well, I predict that a species ability to convert energy into growth will be related to the amount of pelagic resources that are utilized (Rooney et al. 2006; Rooney and McCann 2012).

Chapter 2: Regional Variability of Resource Use and Habitat Coupling Within Lake Superior

Abstract

As one of the largest freshwater lakes in the world, size and scale present challenges when conducting research on Lake Superior. Many studies are only able to analyze a specific region and make general inferences about the lake as a whole, even though it is reasonable to expect that community structure and energetic pathways are spatially variable. Though instances of habitat coupling on Lake Superior have been documented, the degree to which coupling and resource specialization varies spatially, particularly within taxonomic guilds, remains unknown. Stable isotopes of common fish species and their prey were analyzed to understand the variability of resource use and energy flow through the lake and compared along a depth gradient across four geographically and limnologically distinct regions. Species that undergo diel vertical migration (lake trout, rainbow smelt, herring and bloater) showed more resource specialization than the species that did not. This pattern was especially present in the deeper more exposed regions. Typical benthivorous species (lake whitefish and sculpin spp.) did not show the same amount of depth specific specialization, but instead showed a high amount of pelagic resource use at all depths. The specialization of resource use within the deeper regions allowed for a more balanced use of both the benthic and pelagic energy pathways. This is especially true for lake trout and smelt, which seem to follow a pattern with the morphometric properties of the lake.

This study demonstrated significant variation in resource use within fish species across habitats and depth strata in Lake Superior. Overall, this study reinforces the need to

consider large lake systems on a regional basis over simpler approaches which may overgeneralize patterns of energy flow across entire lakes of this scale.

2.1. Introduction

Habitat coupling is defined as the utilization and integration of nutrients and energy across more than one discrete energy pathway. This is a common occurrence in large lake systems and can occur through processes such as foraging (Dolson et al. 2009), migration (Jones and Mackereth 2016), and sedimentation (Schindler and Scheuerell 2002) among other physical, chemical and biological processes. These types of connections between food webs can result in healthier and more resilient food webs in both aquatic and terrestrial ecosystems (McCann et al. 2005; Rooney et al. 2006; Haddad et al. 2011). Greater overall production can also occur due to the transport of excess nutrients between habitats (Cloern 2007). Additionally, habitat coupling can be essential to support a species through seasonal changes in food availability (Stockwell et al. 2014) and are important to understanding ecosystem processes in large lakes (e.g. Schindler and Scheuerell 2002; Gamble et al. 2011; Sierszen et al. 2014).

It is now well accepted that the littoral-benthic energy pathway provide an important energy subsidy for lake ecosystems (Hecky and Hesslein 1995), as the nearshore littoral region receives more light and has more primary productivity than the offshore benthic region (Vadeboncoeur et al. 2002). However, several abiotic factors may alter the degree of importance of littoral-benthic pathways in lakes. For instance, lakes with more shoreline and shallower depth gradients restrict the ability of some mobile predators to facilitate energy movement due to being limited by a lack of thermal refugia (Dolson et al. 2009). Other studies have suggested that the degree of coupling depends on variation in littoral productivity (Schindler and Scheuerell 2002) or lake size (Post et al. 2000b). Depth of occurrence also influences near shore-offshore coupling (Vander Zanden and Rasmussen 1999; Sierszen et al. 2006). Previous work has shown organisms at the base of the food web (*Diporeia* spp.) rely heavily on near shore benthic algae (Sierszen et al. 2006). As depth increases, the reliance on benthic algae decreases and in regions deeper than 40 m almost all resource use is from profundal sedimented phytoplankton (Sierszen et al. 2006). Similar patterns in the variation in depth observed in these invertebrates can also be expected at higher trophic levels (e.g. fishes) due to the basal signature being preserved up the food web, to reveal lake-wide depth specific organization in the aquatic ecosystem (Sierszen et al. 2014). Although depth is known to modulate the degree of benthic-pelagic coupling in Lake Superior (Sierszen et al. 2014), little is known about how this relationship with depth varies spatially around the lake or within a species in a single region.

Degrees of benthic-pelagic or near shore-offshore coupling are observed in large lakes, including one of the world’s largest, Lake Superior (Gamble et al. 2011a, 2011b; Sierszen et al. 2014; Stockwell et al. 2014). The nearshore and offshore food webs are defined by unique species composition, different sets of species interactions and differences in overall complexity. By quantifying the biological linkages between near shore and offshore communities it is possible to gain a better understanding of the importance of these energetic pathways (Gamble et al. 2011a, 2011b), and understand how these connections may change with depth (Sierszen et al. 2014).

Community composition is known to vary spatially in large lakes. A study comparing the fish and zooplankton composition proposed three ecozones within the western arm of Lake Superior based on depth (Sierszen et al. 2006), and other bathymetric and limnological properties (Johnson et al. 2004). Differences were found in the abundance, size and species composition of zooplankton and fish species associated with depth between these regions. Similar variation in community composition may also vary, either reflecting or facilitating differences in near shore-offshore coupling around the entire lake.

One frequently used method to understand energy transfer throughout an ecosystem (and therefore estimate degrees of benthic-pelagic coupling) is stable isotope analysis, which traditionally has focused on using variation in carbon and nitrogen stable isotopes. Carbon stable isotopes are frequently used to characterize the production pathways exploited by consumer species as there is negligible fractionation of the heavier isotope between prey and predator (DeNiro and Epstein 1978; France 1995; Vander Zanden and Rasmussen 2001). Examples include terrestrial versus aquatic (Carpenter et al. 2005), nearshore versus offshore (Rennie et al. 2013) or littoral versus profundal or pelagic sources (France 1998; Vander Zanden and Rasmussen 1999). This resource use information is supplemented by nitrogen isotopic information, which can also differentiate between habitats of varying depths, but also characterizes trophic levels of a food web where it tends to fractionate by approximately 3.4‰ between trophic levels (Vander Zanden and Rasmussen 2001; Post 2002).

Lake Superior is a large oligotrophic water body, which has a complex web of biotic interactions separated by depth gradients (Schindler and Scheuerell 2002). A great deal of research has been conducted to try and better understand the food web of Lake Superior and the biological interactions it supports; such as the distinction between the near shore and offshore food webs (Gamble et al. 2011a, 2011b), and linkages between them (Dolson et al. 2009; Gorman et al. 2012; Rennie et al. 2013; Stockwell et al. 2014). Understanding the structure of the food web is important to fully grasp the importance of feeding pathways and better manage aquatic resources. For example, the near shore food web relies mostly on benthic primary production (via the amphipod *Diporeia* spp.); whereas the offshore fish community diet is more dominated by pelagic production via the filter feeder *Mysis diluviana* (Yoshii 1999; Gamble et al. 2011a; Sierszen et al. 2014). Benthic energy pathways are an important component for many species in the lake (Vadeboncoeur and Steinman 2002; Vadeboncoeur et al. 2002), and can influence the overall understanding of the function and stability of large lakes (Rooney and McCann 2012).

The three main objectives of this study were to (1) analyze the Lake Superior food web across four geographically and limnologically distinct regions to quantify variability in resource use lake wide, (2) compare how resource use varies with depth among these regions, and (3) provide a better understanding of within-species variability in habitat coupling lake-wide. Based on the regional bathymetry of the study sites, I predict that the deeper more exposed regions will show more mixed use of benthic and pelagic resources (habitat coupling) due to less thermal limitations on movement (Dolson et al. 2009). As well, the deeper regions are relatively larger than the shallower bays, and a larger size can contribute to a more complex habitat (Post et al. 2000b) and more opportunity for mixed resource use within species. Based on the study species, I predict that the species able to undergo diel vertical will have a more mixed use of the benthic and pelagic energy resources due to their increased ability to move within the water column compared to the species that do not vertically migrate. In this study the species that exhibit diel vertical migration are lake trout (Gorman et al. 2012), the coregonines (herring and bloater: Hrabik et al. 2006), and smelt (Appenzeller and Leggett 1995).

Lake Superior is a large, oligotrophic freshwater lake in the Laurentian Great Lakes chain. It is the largest freshwater lake by area in the world (82,000 km^2), and averages 147 m in depth (Sierszen et al. 2014). I chose Lake Superior as a study site because there are (a) well established publications regarding a generalized food web for the lake (Gamble et al. 2011a, 2011b), as well as clearly-described variation in benthic-pelagic coupling with depth for various species (Sierszen et al. 2014), and (b) is the least impacted of the Laurentian Great Lakes due to environmental contamination and invasive species (Gorman et al. 2010). However, the results of this study should be broadly representative of other temperate great lakes.

2.2. Methods

2.2.1 Study Site

This study was conducted in four study regions spread across the lake; Nipigon Bay, Whitefish bay, the western side of the Keweenaw Peninsula, and the western arm of Lake Superior. These sites are geographically separate, located at essentially the cardinal directions of the compass rose around the lake, and represent common major ecotypes within Lake Superior. Nipigon Bay and Whitefish bay represent regions with shallow bathymetry and are relatively closed off embayments, somewhat protected from the strong wind and wave action of the open lake. The western arm and Keweenaw Peninsula regions are deep regions with steep depth gradients, and are open to wind and wave action of the main lake (Figure 2.1).

Within each region, fish, invertebrate and zooplankton samples were collected based on a near shore-offshore gradient ranging from 5 to 100+ metres in depth. The gradient covered three main depth strata, 5-30m (shallow), 30-100 m (medium) and over 100 m (deep). In previous studies, the near shore zone of Lake Superior has been defined to extend from depths of 80 meters (Gorman et al. 2012; Stockwell et al. 2014) to as far as 100m (Sierszen et al. 2014). The depth gradients chosen for this study follow a recommended stratification by Sierszen et al. (2006) in an effort to capture ecologically relevant characteristics of large lakes. The shallow littoral zone receives significant light penetration; the medium depth zone is suggested to be the site of significant benthic-pelagic coupling; and the deepest profundal zone is characterized by the inability of light to penetrate effectively (Sierszen et al. 2006).

2.2.2 Sample Collection

During the 2016 and 2017 field seasons, samples of ten common fish species across all sites and depths were targeted for collection: lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), herring (*Coregonus artedi*), bloater (*Coregonus hoyi*), kiyi (*Coregonus kiyi*), rainbow smelt (*Osmerus mordax*), longnose sucker (*Catostomus catostomus*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*Cottus ricei*) and deepwater sculpin (*Myoxocephalus thompsonii*). These species are abundant in all four regions that were selected and are representative of most of the feeding guilds and energy pathways amongst Lake Superior fishes (Table 2.1). Samples were collected from June-September in 2016 and 2017 by multiple government agencies with the majority of the samples being collected during the 2016 Cooperative Sampling and Monitoring Initiative (CSMI) sampling year for Lake Superior. Sample collection was possible through multi-agency collaborations lake-wide; these agencies included the Ontario Ministry of Natural Resources and Forestry (OMNRF), the United States Environmental Protection Agency (US-EPA), the United States Geological Survey (USGS), United States Fish and Wildlife Service (USFWS), Bay Mills Indian Community (BMIC), Great Lakes Indian Fish and Wildlife Commission (GLIFWC), Wisconsin Department of Natural Resources (WiDNR) and the Minnesota Department of Natural Resources (MiDNR). Agencies used a combination of trawl nets and gill nets for the collection of fish samples, individuals were selectively chosen in an effort to obtain a wide range of sizes where possible.

Prey species were also collected from sampling regions along the same depth gradient. Benthic invertebrates were collected with Ekman or Ponar dredges at each depth strata and sieved to remove sediment using a 500 micron wash bucket or metal sieve. Zooplankton samples were collected with triplicate vertical night-time net tows (153 micron) between sunset and sunrise to account for diel vertical migration. All invertebrate and fish samples were immediately frozen upon collection to be transported to Lakehead University. Age structures, lengths and weights of the fish samples were taken upon arriving at Lakehead University, and then kept in the freezer for storage. Supplementary length and weight data from previous years was also used to help create the growth curves for lake trout and lake whitefish from MNRF (Nipigon Bay, Whitefish Bay), Environment Canada (Whitefish Bay) and GLIFWC (Keweenaw).

2.2.3 Stable Isotope Analysis

In total, 1,186 fish and 64 invertebrate samples were analyzed for $\delta\ ^{15}$N and $\delta\ ^{13}$C (Table 2.2). For fish, a small portion of white muscle was extracted (<1 gram) from the dorsal portion of the fish above the lateral line. White muscle was chosen due to its low lipid content. For fish smaller than 5 grams, a whole body homogenate of an individual was used instead of white muscle tissue. For zooplankton and invertebrates, whole body composites by taxonomic group were used. Samples were dried at 60ºC over a 48 hour period, or until weight was constant, to remove water content. Dried samples were then homogenized with a mortar and pestle. All samples were then weighed into 8mm x 5mm tin capsules on a microbalance at specified amounts (0.4-0.6mg for fish, 0.6-0.8mg for invertebrates). Stable isotopes of all tissues were analysed by the Great Lakes Institute for Environmental Research (GLIER) at the University of Windsor using an Elemental Analyzer – Isotope Ratio Mass Spectrometer (EA-IRMS). Nitrogen (^{15}N/^{14}N) and carbon (^{13}C/^{12}C) stable isotope composition were reported in standard delta notation (δ). Precision, assessed by the standard deviation of replicate analyses of four standards (NIST1577c, internal lab standard (tilapia muscle), USGS 40 and Urea (n=15 for all), measured ≤0.15‰ for δ^{15}N and ≤0.14‰ for δ^{13}C for all the standards. The accuracy, based on the certified values of USGS 40 (n=15 for $\delta\ ^{13}$C and $\delta\ ^{15}$N) analysed throughout runs and not used to normalise samples showed a difference of -0.20‰ for δ^{15}N and -0.06‰ for δ^{13}C from the certified value. Instrumentation accuracy checked throughout the period of time that these samples were analysed was based on NIST standards 8573, 8547 and 8574 for δ15N and 8542, 8573, 8574 for δ^{13}C (n=20 for all except n=9 for NIST 8574). The mean difference from the certified values were -0.04,-0.07,-0.05‰ for δ^{15}N and -0.23,-0.10 and -0.07‰ for δ^{13}C respectively.

2.2.4 Lipid correction

Lipids were not extracted prior to analysis due to evidence that many extraction methods alter δ ^{15}N values (Logan et al. 2008). Instead the carbon to nitrogen ratio (C:N), determined during stable isotope analysis, was used to evaluate if lipid content was high in the samples. Samples with a C:N ratio >3.4 were considered to have high lipid content (Post 2002). Fish samples with high lipid content were corrected using a generalized model for tissue specific analysis across a range of aquatic species (Logan et al. 2008):

(Eqn 2.1) $$\delta^{13}C' - \delta^{13}C = \frac{a*C{:}N+b}{C{:}N+c}$$

Where a = 7.415, b = -22.732, c = 0.746 (from Logan et al. 2008), δ^{13}C is the lipid corrected carbon value, δ^{13}C is the original carbon value, and C:N is the carbon to nitrogen ratio of the sample. This equation represents a variety of fish species, since no species specific relationships were available for all species in this study. Just over 70% (839/1,186) of samples had C:N ratios above 3.4 and were lipid corrected using this formula.

Invertebrate samples were mathematically corrected using a model specifically designed for freshwater invertebrates, as ground whole invertebrates typically have a higher carbon content than fish muscle (Smyntek et al. 2007):

(Eqn 2.2) $$\delta^{13}C_{ex} = \delta^{13}C_{bulk} + 6.3\,(\frac{C{:}N_{bulk}-4.2}{C{:}N_{bulk}})$$

Where $\delta^{13}C_{ex}$= lipid extracted carbon, $\delta^{13}C_{bulk}$= non-lipid extracted carbon, and $C{:}N_{bulk}$= non-lipid extracted carbon to nitrogen ratio.

2.2.5 Isotopic baseline evaluation and mixing model selection

Benthic and pelagic habitats often have distinct isotopic signatures; algae in the near shore-benthic region generally exhibits less carbon fractionation than algae in the pelagic zone (Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999), and in the profundal zone $\delta^{13}C$ is more negative than both the near shore-benthic and pelagic regions. This extremely negative signature is thought to be due to a large amount of respired CO_2 that is found in the deeper regions of freshwater lakes (Rau 1980). Because of this, the benthic near shore, benthic profundal and pelagic regions all have distinct carbon signatures. The stable isotope of nitrogen (^{15}N) also tends to have distinct differences between regions in freshwater lakes, increasing with depth (Vander Zanden and Rasmussen 1999; Sierszen et al. 2006). This is likely due to the lighter nitrogen isotope being preferentially released as detrital plankton settles through the water column; in turn a positive relationship is formed with $\delta^{15}N$ and depth (Ostrom et al. 1998). Benthic invertebrate and zooplankton samples were first analysed to determine if these same patterns were observed in our dataset to use as benthic-near shore, pelagic and benthic-profundal baselines. Boxplots were created to see if consistent systematic differences existed for both carbon and nitrogen with depth across regions.

Commonly with stable isotope analysis, both carbon-13 and nitrogen-15 signatures are used to create three source mixing models, which are able to tease apart the variation in the benthic, pelagic and profundal energy pathways. This is only possible if there are consistent depth specific patterns across all sample sites. For most baseline species in this study, carbon-13 was the least negative in the shallow depth strata, followed by the deep depth strata, with the medium depth strata having the most negative carbon signature (Figure 2.2). This pattern was generally consistent among all four regions. No consistent pattern of nitrogen with depth was observed in the baseline samples (Figure 2.3). Because all variation in the isotopic signatures with depth was associated carbon-13, a two-source mixing model was chosen to explain resource use along depth gradients and across regions of Lake Superior. To account for both regional and depth-specific variation in mixing models, benthic and pelagic baselines were estimated as the average value across all baseline organisms within regions and depth strata.

2.2.6 Two-Source Mixing Model

A two-source mixing model was used to estimate the proportion of benthic versus pelagic resources used by each consumer. Depth-specific benthic reliance was calculated using lipid corrected carbon values from each region and depth strata. To increase sample size of the benthic energy pathway baseline in near shore environments, longnose sucker samples were used in addition to benthic invertebrates. This was possible because longnose sucker rely on a diet of invertebrates, aquatic plants and settled algae in the sediment (Edwards 1982), and since carbon does not fractionate up the food web (DeNiro and Epstein 1978; Hecky and Hesslein 1995) this carbon signature should be indicative of the near shore benthic energy pathway. The benthic energy pathway was characterized using an average of all benthic invertebrate and longnose sucker samples from each depth strata, and an average of *Mysis* and zooplankton samples were used to characterize the pelagic energy pathway (Table 2.2). The two-source mixing model requires differences between the benthic and pelagic baselines to differentiate sources. Therefore any depths/regions where benthic and pelagic end-members differed by less than 1‰, percent benthic reliance was not calculated. The percent benthic contribution was estimated as:

(Eqn 4) $\%\text{benthic contribution} = [(\delta^{13}C_c - \delta^{13}C_p)/(\delta^{13}C_b - \delta^{13}C_p)] * 100$

Where $\delta^{13}C_c$ = consumer carbon, $\delta^{13}C_p$= pelagic prey, $\delta^{13}C_b$= benthic prey (Vander Zanden and Vadeboncoeur 2002)**.**

This model assumed there was no trophic enrichment (fractionation) in $\delta^{13}C$, as studies have found that carbon fractionation is usually <1‰ between trophic levels (Vander Zanden and Vadeboncoeur 2002). If the benthic reliance of the consumer was estimated to be greater than 100% or less than 0% (occurred in 52% of cases, 36% were less than 0 and 17% were greater than 1), values were set to 100% or 0% respectively indicating all resource use was either benthic or pelagic.

2.2.7 Statistical Analysis

All analyses were conducted in R (R Core Team 2018). Linear regressions were used to assess relationships between fish size (total length; TLEN) and $\delta^{13}C$. Due to missing values in the data and an unbalanced design, non-parametric tests were conducted to evaluate depth specific patterns while ignoring depth across regions. As well, region specific patterns were evaluated ignoring depth specific effects. This was done in an attempt to better understand how both location and depth independently affect resource use, when a 2-factor design was not possible due to missing values and non-normally distributed residuals. Even though data appeared to be somewhat non-normal, visual analysis of the residuals showed mostly normal distribution, as well as homogeneous variance in all species. Regardless, a conservative analytical approach was adopted, using either Kruskal-Wallis tests or Mann-Whitney tests the main effects (region and depth) independently to determine any trends or patterns within the data. The critical *P*-value was adjusted to account for the number of tests that were being analyzed within a species by dividing $\boldsymbol{\alpha}$ (0.05) by the number of tests conducted within each species (number of tests/comparisons = 5-7). For the Kruskal-Wallis tests, Dunn's test was chosen for post-hoc analysis as it has been shown to be appropriate for groups with unequal numbers of observations (Zar 2010). Kiyi was not included for the rest of the analysis, as the sample size was too small to be informative.

2.3. Results

Size vs. Carbon

Almost all species showed a significant relationship between size (total length in millimeters) and $\delta\ ^{13}C$ (in per mille) except kiyi (Table 2.4), but does not seem to consistently increase or decrease in all species. A significant negative relationship was observed between lake trout size and $\delta^{13}C$ in Keweenaw ($F_{1,17}$ =12.502, p=0.0025, R^2=0.42), western arm ($F_{1,83}$=42.125 , p=<0.0001, R^2=0.40) and Nipigon Bay ($F_{1,65}$=4.694, p=0.029), but not in Whitefish Bay (p>0.05). Herring only showed a relationship with depth in the western arm ($F_{1,79}$=12.539, p=0.001, R^2=0.14), where carbon and size were negatively related. Bloater showed a significant positive relationship between size and $\delta^{13}C$ in Nipigon Bay ($F_{1,25}$= 7.79, p=0.0099, R^2=0.24) and Whitefish Bay ($F_{1,37}$= 6.432, p=0.0156, R^2=0.15) but not western arm or Keweenaw.

Rainbow smelt showed a positive relationship between size and $\delta^{13}C$ in all regions (KW: $F_{1,37}$ =22.629, p=<0.0001, R^2=0.38, WA: $F_{1,60}$=27.088 , p=<0.0001, R^2=0.31, NB: $F_{1,52}$= 73.731, p=<0.0001, R^2=0.59, WF: $F_{1,79}$= 43.63, p=<0.0001, R^2=0.36). Lake whitefish had a significant negative relationship between size and $\delta^{13}C$ in the western arm ($F_{1,34}$= 28.363, p=<0.0001, R^2=0.45) and Whitefish Bay ($F_{1,41}$= 3.996, p= 0.0523, R^2=0.09). The combined sculpin spp. only showed linearity in the western arm site ($F_{1,38}$= 6.817, p=0.0129, R^2=0.15), and it was a slightly positive relationship. Given the influence of body size on isotopic signatures of the fishes of interest, the degree to which patterns in fish body size reflected observed patterns in resource use was evaluated (below).

Depth patterns

For all species except lake trout, percent benthic reliance was significantly different across all regions for fish in the shallow depth strata (smelt: p_{crit}=0.008, X^2(3,n=107) =28.262, p=<0.0001, herring: p_{crit}=0.007, X^2(3,n=94) =19.702, p=0.0002, bloater: p_{crit}=0.007, X^2(3,n=55) =22.16, p=<0.0001, whitefish: p_{crit}=0.01, X^2(3,n=102) =12.211, p=0.0067, sculpin: p_{crit}=0.007, X^2(3,n=74) =40.989, p=<0.0001). The benthic reliance in the shallow depth strata follows a consistent pattern across smelt, cisco, bloater and lake whitefish (Figure 2.5); with the highest benthic reliance in Nipigon Bay, followed by Keweenaw, western arm and Whitefish Bay in descending order. There was less variation in the medium depth strata, as only smelt (p_{crit}=0.008, X^2(2,n=81) =22.028, p=<0.0001) and bloater (p_{crit}=0.008, X^2(2,n=48 =22.028, p=<0.0001) had significant differences in benthic reliance across regions. Lake trout (p_{crit}=0.008, X^2(2,n=53) =7.129, p=0.0283) and herring (p_{crit}=0.007, X^2(2,n=34) =9.6122, p=0.008) in the medium depth strata were close to being significant, but due to the adjusted p-value it was not. In the deep strata there was no significant differences shown across regions for any of the species, but the analysis in the deep depth strata was only able to be conducted on bloater and sculpin spp. due to small sample size (i.e. only one observation for lake whitefish in Whitefish Bay)

In all of the species where there were significant differences across regions in the shallow depth strata, body size was also significantly different (smelt: $X^2(3,n=107) = 41.105$, $p=<0.0001$, herring: $X^2(3,n=94) = 19.218$, $p=<0.0001$, bloater: $X^2(3,n=55) = 39.075$, $p=<0.0001$, whitefish: $X^2(3,n=102) = 46.785$, $p=<0.0001$, sculpin: $X^2(3,n=74) = 41.105$, $p=<0.0001$). The only species that showed a similar pattern in body size to what was observed in percent benthic reliance was lake whitefish, which displayed an inverse pattern with body size to what was observed in the isotopes. Across regions in the medium depth strata, significant differences were observed (smelt: $X^2(2, n=81) = 32.302$, $p=<0.0001$), bloater: $X^2(2, n=48) = 39.789$, $p=<0.0001$), but patterns were not consistent with percent benthic reliance across regions within the medium depth strata (Figure A1).

Regional Patterns

The benthic reliance among depths within regions was most variable across depth in the western arm, being significantly different across depth in 4 of 6 of the study species (Smelt: $W_{75}=14.923$, $p=0.0001$, Herring: $W_{41}=111.5$, $p=0.0048$, whitefish: $W_{34}=260$, $p=<0.0001$, sculpin: $W_{20}=10$, $p=0.0004$). The region that showed the least amount of depth related differences within a species was Nipigon Bay, only having significant differences in 1 of 4 of the species analyzed (Herring: $W_{30}=136$, $p=0.0007$). Both Whitefish Bay and Keweenaw showed depth related differences within a species in

2/6 species analysed; for Whitefish Bay smelt (p_{crit}= 0.007, X^2(3,n=80) =28.754, p= <0.0001) and whitefish (p_{crit}= 0.01, X^2(3,n=42) =10.4, p= 0.0055) varied with depth, and for Keweenaw, smelt (p_{crit}=0.008, W_{38}=60.5, p=0.0001) and herring (p_{crit}=0.007, W_{20}=14, p=0.0048) varied with depth. Lake trout was the only species examined that did not show any significant differences in benthic reliance with depth in any region.

Understanding the proportion of resource use and benthic-pelagic coupling was further explored by considering regional variability of percent benthic reliance within a species across depth. Mean percent benthic reliance for each depth strata was determined within each region, and those values were averaged to give an overall regional value for percent benthic reliance (Figure 2.6). The range of resource use could vary from 0%, meaning there was no use of the benthic energy pathway and the pelagic pathway was being completely relied upon, to 100% where only the benthic energy pathway was being utilized. It was expected that species which display diel vertical migration would have some sort of mixed reliance on both energy pathways. There was a trend in a decrease of regional benthic reliance for lake trout, whitefish and somewhat in herring from the deepest Keweenaw site to the shallowest Whitefish Bay site. However, no statistically significant differences existed between regions for the averaged percent benthic reliance within any of the species, most likely due to the small sample size (n=3, across three depth strata).

The regional percent benthic reliance varied within species (averaging across depths), but was predominantly characterized by a consistent pelagic energy signature (Figure 2.5). Keweenaw and Nipigon Bay had the highest occurrences of species that shared the benthic and pelagic energy pathways almost equally (e.g. proportions closest to 50%), due to the high specialization at depth. In Keweenaw, smelt, whitefish, lake trout and herring all showed an almost even amount of benthic and pelagic resource use when looking at the regional average across all depths. The region with the next highest occurances of equal resource use was in Nipigon Bay, with herring and bloater also exhibiting an almost even use of both the benthic and pelagic resources. All other species and regions relied more heavily on the pelagic energy pathway, even common benthivorous species such as sculpin.

Percent benthic reliance of all species within each region was averaged to observe the overall resource partitioning within the entire community. Proportions of percent benthic reliance were converted into percent values and reported here. The pelagic energy pathway still dominated over the benthic energy pathway. Keweenaw Peninsula was observed to have 41.2 percent average benthic reliance across all 6 species, which was relatively high compared to the other 4 sites. Nipigon Bay closely followed with a percent benthic reliance across all species of 40.6 percent. These regions show almost even resource use (i.e., close to 50%), similar to what was observed within species. Western arm and Whitefish Bay showed a greater reliance on the pelagic energy pathway when averaged across all species (western arm: 27.9% benthic reliance, Whitefish Bay: 14.3% benthic reliance).

When considering regional patterns, it was important to understand if the effects of body size were affecting percent benthic reliance within regions across the three depth strata (Figure A2). Some species showed a relationship between body size and $\delta^{13}C$. Rainbow smelt in the Keweenaw Peninsula, and sculpin in the western arm showed a positive relationship with size; where $\delta^{13}C$ signature becomes more positive with an increase in body size. Whitefish and herring in the western showed the opposite pattern and a negative relationship with size was observed; where $\delta^{13}C$ signature becomes more negative with an increase in body size.

2.4. Discussion

This study established clear trends in how different species use energy pathways both on a depth-specific and regional scale within Lake Superior. The difference in percent benthic reliance between depth strata was highly dependent on the region. Resource use varied the greatest between depths within Keweenaw lake trout populations with a difference of 77.3 percent benthic reliance between the shallow (22.7%) and medium depth strata (100%), but as little as 6.3 percent in Nipigon Bay between the shallow (28.2%) and deep (21.9%) depth strata. Sculpin populations commonly show the least amount of variation across all regions and species analyzed, varying on average between shallow and medium depths by 30.7% across all sites where shallow and medium samples were available. Herring varied 35.4% on average between the shallow and medium depth strata. Bloater varied 31.2% on average between the shallow and medium depth strata. And lastly lake whitefish populations varied 37.6% on average between the shallow and medium depth strata.

Species that have been observed to undergo diel vertical migration showed the greatest variance in resource use across depth. Lake trout, smelt, herring and bloater, are highly dependent pelagic resources in the shallow depth strata and more dependent on benthic resources in the medium depth strata. This disparity of resource use at depth does not exist in the more shallow enclosed study sites. The deeper more exposed study regions may be showing patterns similar to those observed in large lakes, where dietary specialization increases with lake size due to increased habitat heterogeneity and prey refugia (Post et al. 2000b). This increased habitat heterogeneity allows fish within the same species to specialize on different resources, more dietary specialization would lead to a reduction in trophic omnivory.

Lake trout showed resource use specialization with depth as well, which was expected due as lake trout have very plastic feeding habits and will change their prey based on what is available (Martin 1966). Lake trout in the two more exposed regions show a greater benthic reliance in the medium depth strata and in the shallow depth strata show a greater pelagic reliance, this could be due to which resources are most available at each depth. In the shallow regions where there is a lot of primary productivity, lake trout may shift to consume more of a planktivorous diet if it is more available (Martin 1966). In the medium depth strata there may not be the high volume of pelagic primary production, and lake trout could be consuming either benthic invertebrates or fish with a highly benthic reliance.

A variety of lake trout morphotypes are known to exist within Lake Superior, but individuals were chosen in an effort to only analyse the ‘lean’ lake trout in this study. Even though lake trout at depth are utilizing different resources it is unlikely that the differences observed are due to different morphotypes, but instead differences in feeding patterns. Lake trout, along with other salmonids, can adapt to a high degree of intraspecific competition where there is a switch to a new resource resulting in morphological divergence (Chavarie et al. 2013); this is most common when there is high environmental heterogeneity (Post et al. 2000a). Previous literature noted that among multiple generalist morphs in a large lake system there is variation in the amount of omnivory, which could not be explained through stable isotope analysis (Chavarie et al. 2016). The depth-specific sampling that was conducted here suggests some sort of depth-specific resource partitioning and therefore some influence of depth specialization in the resource use of Lake Superior lake trout. Previous work in Great Bear Lake indicated some isotopic differences observed among different lake trout morphotypes occupying different depths (Chavarie et al. 2018), but without baseline data it was not possible to determine whether these isotopic differences are due to variation in resource partitioning between benthic and pelagic resources. Previous studies have also provided evidence for resource partitioning by depth in Lake Superior; neutral genetic partitioning and increasing morphological variation was observed along a depth gradient (Baillie et al. 2016). This suggests that even though there are genetic differences between species it is not specifically affecting fitness. Therefore lake trout are able to adaptively feed on any resources available with depth within Lake Superior.

Across all species, the shallow depth strata commonly shows a greater amount of pelagic specialization, and the deep strata shows a much greater benthic specialization, especially in the species that exhibit diel vertical migration again. The medium depth strata is the only region where the benthic energy source dominates; this could be due to an increase of the benthic amphipod *Diporeia*. *Diporeia* is an important resource for nearshore populations in lake superior (Gamble et al. 2011a, 2011b). Recently it has been observed that *Diporeia* have an increase in abundance between the depths of 30-125m in Lake Superior (Auer et al. 2013), which closely mirrors the medium depth strata in this study. The higher amount of *Diporeia* available, combined with the fact that the medium depth strata is commonly characterized by high benthic-pelagic coupling (Sierszen et al. 2006), provides good evidence to an increase in benthic resource use between 30 and 100m. If the increase in benthic energy was large enough it could be reflected in all higher trophic levels up the food web, through increased foraging on the benthic pathway and the basal resource signature being preserved up the food web.

The coregonines and rainbow smelt showed a consistent pattern across study sites when considering the shallow depth strata. Significant differences existsed between regions, but did not follow the more exposed versus more protected grouping that was expected. Thus, site factors influencing energy use may be more complex than the physical characteristics considered here. This shallow pattern observed in smelt, herring, bloater and lake whitefish showed that Nipigon Bay had the highest percent benthic reliance, followed by Keweenaw, and then western arm and Whitefish Bay had the lowest percent benthic reliance. It is possible that Nipigon Bay exhibits the highest amount of benthic reliance due to an alternate benthic energy subsidy via the Nipigon River, which is the largest inflow into Lake Superior. The Keweenaw study site also has a potential benthic energy subsidy, as there is a current that could transport energy from the highly productive Apostle Islands habitat to the Keweenaw Peninsula.

Since there are no data available for the deepest depth strata in the two more open deep regions (Keweenaw and western arm), it is hard to speculate what the resource use would look like based on the two more shallow, sheltered regions that I do have data for. There does not seem to be any trends that follow the other depth strata consistently, so to gain a better understanding of resource use in the deep strata more samples would have to be collected.

The typical benthivores sculpin spp. and lake whitefish, which have a life history and morphology traditionally adapted to the bottom of a lake, displayed just as much reliance on a pelagic source as their pelagic counterparts in some cases. Studies have suggested that generally there is a high amount of benthic energy use in near shore populations across Lake Superior (Gamble et al. 2011b; Sierszen et al. 2014), which was somewhat observed within this study, but generally there was a much higher dependence on the pelagic energy pathway. It is possible that these species have such a high amount of benthic reliance as mysis is a known food source to both. Since *Mysis* is a major prey species within Lake Superior, it would be expected that there would be a higher pelagic signature, and since *Mysis* undergo diel vertical migration (Bowers 1988; Jensen et al. 2006), this would allow benthivorous species access to this more pelagic prey. Even though both are typically benthivorous, whitefish (Rennie et al. 2012) and sculpin (Gamble et al. 2011b) have been observed consuming a large portion of sculpin in their diet throughout the year.

Previous literature has suggested that there is use of the littoral and profundal energy pathways regardless of the depth of their habitat (Sierszen et al. 2014), which was observed here, but the amount that each resource was relied upon varied greatly both along a depth gradient and regionally. As well, because Lake Superior is such a deep oligotrophic lake, most of the lake is composed of pelagic habitat; so it would be expected to dominate the main energy source that is reflected within most species. But due to the great depths that Lake Superior gets to, the deepest water columns would not have a lot of offshore pelagic productivity, but instead benthic resources may be more productive. There was a strong reliance on pelagic energy pathways within all species and regions, with most of the percent benthic reliance not rising above 50%.

As aquatic species are highly mobile, the average percent benthic reliance across all depths was calculated to obtain a single value for regional resource use within a species. Considering resource use as an average across all depth showed that the coregonines show a similar regional pattern of resource use that was observed in the shallow regions for the same species. More reticulate regions (like Nipigon Bay) have a larger area available for benthic-littoral production which could increase the overall amount of benthic energy available (Schindler and Scheuerell 2002). As well, there may be more access to benthic prey resources relative to regions with reduced shoreline contouring (Dolson et al. 2009). Nipigon Bay is a shallow embayment that rarely gets deeper than 100m, so there is a possibility that this higher amount of benthic habitat is why they utilize the benthic energy pathway to a greater degree.

The lake trout and smelt show a different trend when considering the regional average of resource use. These species display more benthic reliance in the deeper more exposed regions, and more pelagic specialization in the shallower more protected regions. This pattern was evaluated statistically, but since values were averaged across the three depth strata within each region the sample size was very small (n=3), no statistically significant differences were found but trends are still apparent. not show Lake trout and smelt do not show the spike in benthic reliance in Nipigon Bay, which may be due to a more abundant benthic energy source. This could be due to the extremely plastic feeding habits.

Even though there was relatively higher benthic energy usage for coregonines in Nipigon Bay, the regional average of percent benthic reliance typically does not exceed 50%. This indicates that pelagic energy dominates the primary energy obtained by fishes even in a region where benthic specialization might be expected on the basis of regional morphology (i.e., relatively shallow mean depth). However, it may also speak to the overwhelming influence of connectivity to the massive volume that is Lake Superior and the importance of water exchange with the main lake, or the nearshore region having a high amount of pelagic primary production. The extremely high pelagic reliance in the sculpin species conflicts with what was expected, but as this study is novel in examining resource partitioning with depth, it provides a comparison for future investigations.

Where there were significant differences in percent benthic reliance, the same regions/depths were analyzed to evaluate if differences being observed were solely based on a function of fish size. This study also suggests differences in feeding with size, based on significant linear regressions between $\delta^{13}C$ and body size (Figure 2.4). Some variability (<1‰: Vander Zanden and Vadeboncoeur 2002) was expected, but much larger differences are observed. The smallest rainbow smelt in Nipigon Bay (42mm) had a predicted $\delta^{13}C$ value of -29.90‰, and the largest smelt in the same region (220mm) had a predicted $\delta^{13}C$ value of -22.29‰, which was a 7.61‰ difference between the largest and smallest fish. Lake trout also showed variance in $\delta^{13}C$ with body size, ranging from -24.79‰ at 193mm to -30.26‰ at 763mm for an overall difference of 5.48‰. Rainbow smelt, bloater and sculpin all show an increase $\delta^{13}C$ with body size, while lake trout, lake whitefish and herring showed a decrease in $\delta^{13}C$ with body size. This was not an effect of sampling gear as no consistent size-at-depth relationships were observed. A larger body size allows for an increase in the range of movement (McMeans et al. 2016), which could be the reason for this variation. These data suggest that as lake trout, lake whitefish and herring grow, their resource use shifts towards a benthic energy source. Conversely, bloater, rainbow smelt and sculpin are shifting towards a higher reliance on a pelagic energy source. Although body size may have some effect on the amount of percent benthic reliance exhibited within a species, it does not account for all of the variability observed in this study. Most likely all three variables (depth, location and body size) contribute to the proportion of benthic or pelagic resources used as aquatic ecosystems are highly complex.

Looking solely at similarities between the percent benthic reliance across regions in the shallow depth strata and comparing to body size across the same depth strata, most were not consistent between the two variables. There was a positive relationship between rainbow smelt in Keweenaw and sculpin in the western arm. This means that in those regions a smaller body size is most likely what’s driving the shift to a more negative carbon signature. Also whitefish and herring in the western arm show a negative relationship with depth; it is most likely that in those cases size is driving the change in $\delta^{13}C$, not region or depth. There seemed to be a relationship between bloater size and site within the shallow depth strata, as smaller individuals were observed in the two deeper regions, and larger individuals were observed in the two shallower regions. The size pattern did not relate to the observed patterns in percent benthic reliance. Even though there were significant differences in all species for body size regionally within the shallow depth strata, only lake whitefish populations displayed a pattern which could be related to percent benthic reliance. If this pattern with body size does relate to percent benthic reliance it suggests that larger fish have a lesser percent benthic reliance than the smaller fish. This could be due to larger fish being more mobile and able to forage within a greater area.

When considering regional patterns, it was important to understand if body size was correlated with benthic resource exploitation within regions across the three depth strata (Figure A2). Significant differences in size at depth were observed in rainbow smelt within the Keweenaw and Whitefish Bay locations, which did relate to the percent benthic reliance.

Where we see these body size relationships with $\delta^{13}C$, it is possible that species are inhabiting different depths, which could be explain why they are consuming different resources. If the difference in resource use observed was solely due to body size, there would be significant differences in body size in the same instances that percent benthic reliance values were significantly different. Since this is not the case, all three factors (size, depth, region) most likely have an effect on resource use in Lake Superior.

Based on the methods employed, it is likely that pelagic resource use reported here may be underestimated in the shallow. Nearshore benthic end-members reported here are somewhat more depleted in $\delta^{13}C$ than what would be expected, particularly at depth. Previous studies have shown that most of the carbon-13 variation in benthic invertebrates occurs within the first 15 metres (Sierszen et al. 2006). Since the near shore zone in this study extended to 30 meters, it is possible that benthic invertebrates included between 15-30 m may reflect some mixing effects with the open-lake pelagic region. This would mean that the higher amount of benthic reliance observed in the medium depth strata may actually have a more pelagic reliance than what was shown in this study. If pelagic resource use was underestimated in this study it would not change the overall trend in the data, nor my overall conclusions, but instead, it would cause a shift towards a lower percent benthic reliance across all species.

This study illustrated clear depth specific variation of resource use within common Lake Superior species, which has not previously been reported. Not only does this variation occur along a depth gradient, but it was also affected by regional lake morphometry and body size. Previous more generalized studies which did not consider depth have shown the importance of the benthic pathway in near shore species such as lake trout and lake whitefish (Sierszen et al. 2014), but depending on the depth that is being considered, offshore species such as smelt, herring and bloater may utilize the benthic energy pathway to similar or greater extents. As well, even though there are lake-wide similarities in how the near shore and offshore fish communities are structured (Gamble et al. 2011b), there are regional differences that must be considered when conducting a whole lake study. More studies must be conducted to understand how size of an individual affects the resource use at depth within a species in Lake Superior. This study showed that body size is related to the level of percent benthic reliance, but not consistently in the same ways as depth and region. Understanding the complexities of ecosystem function may allow us to relate how variable Lake Superior is to understand other large lake systems; more studies must be conducted to evaluate other variables that may be able to predict benthic reliance variability. Comparing these results to both healthy large lake systems and disturbed systems can advance our understanding of how stressors affect the function of large aquatic ecosystems, and specifically the fish communities. Future research might focus on collecting more extensive baseline data to create a three source mixing model at depth to potentially create a more detailed resource mixing landscape.

Though there was an overall large sample size for many of the species and regions, there were still gaps in sample collection that were not able to be filled. Specifically the lack of samples, and distinct baselines in the medium and deep regions, leave many questions unanswered about the resource use within these strata. Collecting a robust sample size from across a large lake such as Superior requires a large amount of time and effort, and may be challenging, if not impossible to conduct, so as to capture both temporal consistency as well as the spatial heterogeneity required to better characterize baselines in the ecosystem.

This study showed that species able to undergo diel vertical migration, are able to rely on mixed resources with depth facilitating habitat coupling where possible. This is especially prominent in the deeper, more exposed regions. These results support my hypotheses of deeper regions exhibiting more habitat coupling, or a more mixed use of resources, and species moving vertically within the water column are more able to integrate the benthic and pelagic resources. The traditionally more benthic species show more resource specialization, not having much depth specific variability in resource use.

Tables

Table 2.1. Species sampled, organized by feeding group. Depth ranges are averages taken from Scott & Crossman 1973. Shorthand for regions is as follows: KW = Keweenaw Peninsula, WA= western arm, NB = Nipigon Bay, WF= Whitefish Bay.

Group	**Species**	**Depth range (m)**	**Length range (mm)**			
			KW	**WA**	**NB**	**WF**
Piscivore	Lake trout		80-653	232-763	193-785	355-604
Benthivore	Lake whitefish	5-60	111-441	183-488	186-957	176-560
	Slimy sculpin	5-80	30-80	31-83	54-85	41-90
	Spoonhead Sculpin	20-115	34-60	40-56	36-109	50
	Deepwater Sculpin	45-180	59-104	21-114	--	--
Planktivore	Herring	13-53	92-417	118-394	170-425	183-410
	Bloater	40-120	81-241	86-261	156-300	89-310
	Kiyi	50-180	89-237	174-232	178-261	--
	Rainbow smelt	18-35	51-163	35-167	42-220	45-200

Table 2.2. Average values of zooplankton and *mysis* samples for the pelagic baseline, and average values of benthic invertebrates and longnose sucker samples for the benthic baseline. Baselines were created to represent the pelagic, benthic-littoral (S) and benthic-profundal (M & D) regions.

Location	**Depth**	**Pelagic $\delta^{13}C$**	**Benthic $\delta^{13}C$**	**$\Delta\ \delta^{13}C$**
Keweenaw	S	-27.8	-24.6	3.19
	M	-28.1	-26.8	1.25
	D	-27.1	--	N/A*
Western Arm	S	-26.7	-22.2	4.55
	M	-27.9	-25.0	2.99
	D	-27.4	-27.3	0.149*
Nipigon Bay	S	-27.1	-23.8	3.26
	M	-28.5	-28.4	0.146*
	D	-28.1	-24.9	3.17
Whitefish Bay	S	-25.2	-17.7	7.52
	M	-27.2	-20.0	7.15
	D	-26.2	-24.7	1.48

* Not used due to less than one per mille difference between benthic and pelagic baselines

Table 2.3 Samples collected and analyzed for carbon (δ13C) and nitrogen (δ15N) stable isotopes, dashed lines denote no samples collected at that depth strata. LT = lake trout, WF = lake whitefish, HR = herring (cisco), BL = bloater, KY=kiyi, RS = rainbow smelt, LS = longnose sucker, SS = slimy sculpin, SP= spoonhead sculpin, and DS= deepwater sculpin. Shallow (S) = 0-30m, medium (M) = 30-100m, deep (D) = 100+ m.

Region	**Depth**	**Total**	**LT**	**WF**	**HR**	**BL**	**KY**	**RS**	**LS**	**SS**	**SP**	**DS**
Keweenaw	S	127	16	26	15	21	--	16	7	22	4	--
	M	31	1	--	7	--	1	20	--	2	--	--
	D	50		--	--	1	34	1	--	1	--	13
Western Arm	S	167	26	25	22	26	--	32	28	5	2	1
	M	113	29	9	13	21	--	16	15	5	--	5
	D	119	8	--	27	18	39	9	--	3	1	14
Nipigon Bay	S	166	18	29	31	2	--	33	23	10	20	--
	M	100	25	24	20	7	--	--	24	--	--	--
	D	81	18	13	16	10	7	15	--	1	1	--
Whitefish Bay	S	84	1	20	20	2	--	16	23	2	--	--
	M	113	9	21	10	21	--	35	11	5	1	--
	D	35	--	1	--	10	--	19	--	5	--	--
Total		1186	151	168	181	139	81	212	131	60	29	33

Table 2.4. Range of predicted $\delta^{13}C$ (‰) along with the corresponding total length (mm), where a significant linear relationship was observed KW = Keweenaw, WA = western arm, NB = Nipigon Bay, WF = Whitefish Bay, NS means no significant relationship existed in the dataset

Species	**Value**	**Range of values (min, max)**			
		KW	**WA**	**NB**	**WF**
Lake trout	length	80, 653	232, 763	193, 785	355, 604
	$\delta^{13}C$	-23.38, -28.37	-24.78, -30.26	-26.42, -29.51	NS
Lake whitefish	length	111, 441	183, 488	186, 957	176, 560
	$\delta^{13}C$	NS	-24.05, -28.79	NS	-22.93, -27.01
Sculpin Spp.	length	30-104	21-114	36-109	41-90
	$\delta^{13}C$	NS	-28.77, -26.37	NS	NS
Herring	length	92-417	118-394	170-425	183-410
	$\delta^{13}C$	NS	-26.02, -28.14	NS	NS
Bloater	length	81-241	86-261	156-300	89-310
	$\delta^{13}C$	NS	NS	-26.21, -24.21	-30.11, -27.51
Rainbow smelt	length	51-163	35-167	42-220	45-200
	$\delta^{13}C$	-29.20, -24.42	-28.28, -25.14	-29.90, -22.29	-26.91, -24.03

Figures

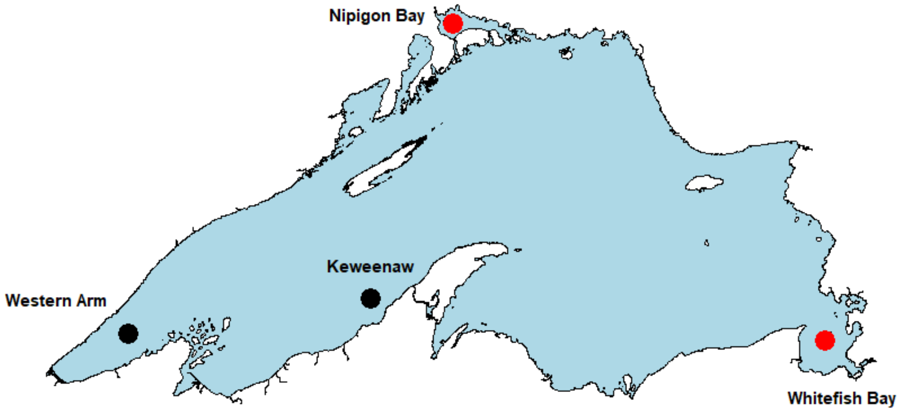

Figure 2.1. Map of Lake Superior, labelled with the four study regions. Black dots denote the sites with a steeper depth gradient, and red dots denote the more shallow closed off embayments in the study.

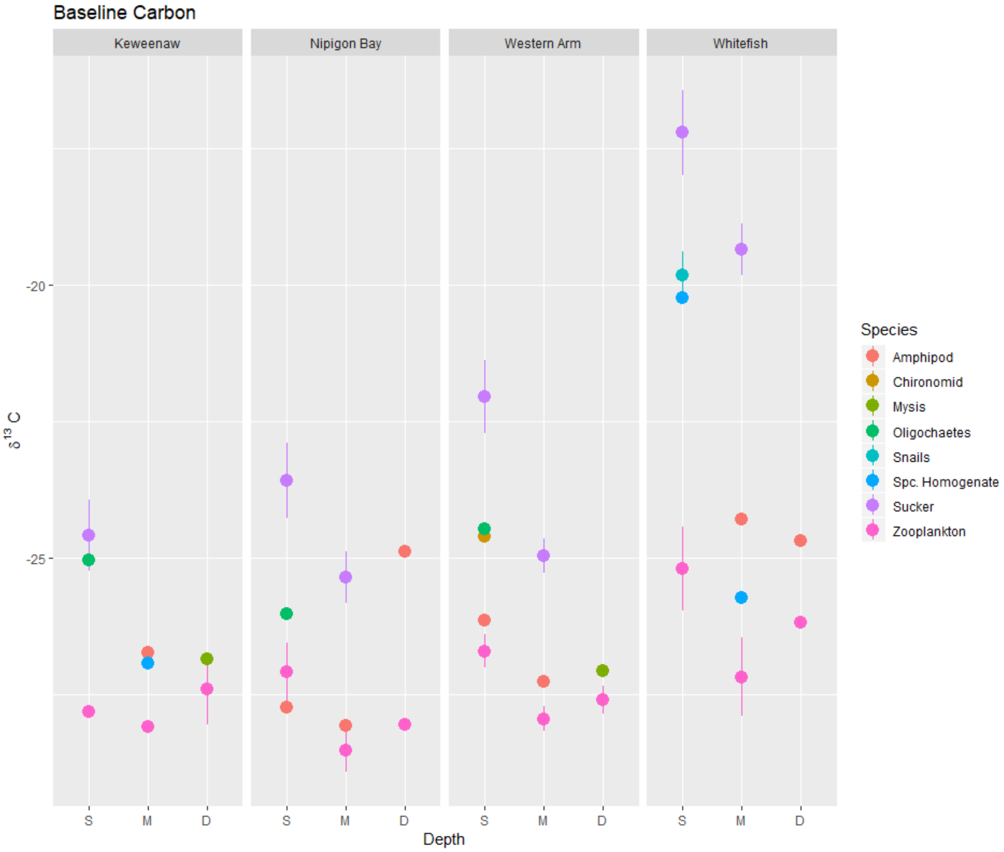

Figure 2.2. $\delta^{13}C$ values of all baseline species organized by region and by depth strata, values have been mathematically lipid corrected. Shallow (S) = 0-30m, medium (M) = 30-100m, deep (D) = 100+ m. Error bars are ± standard error.

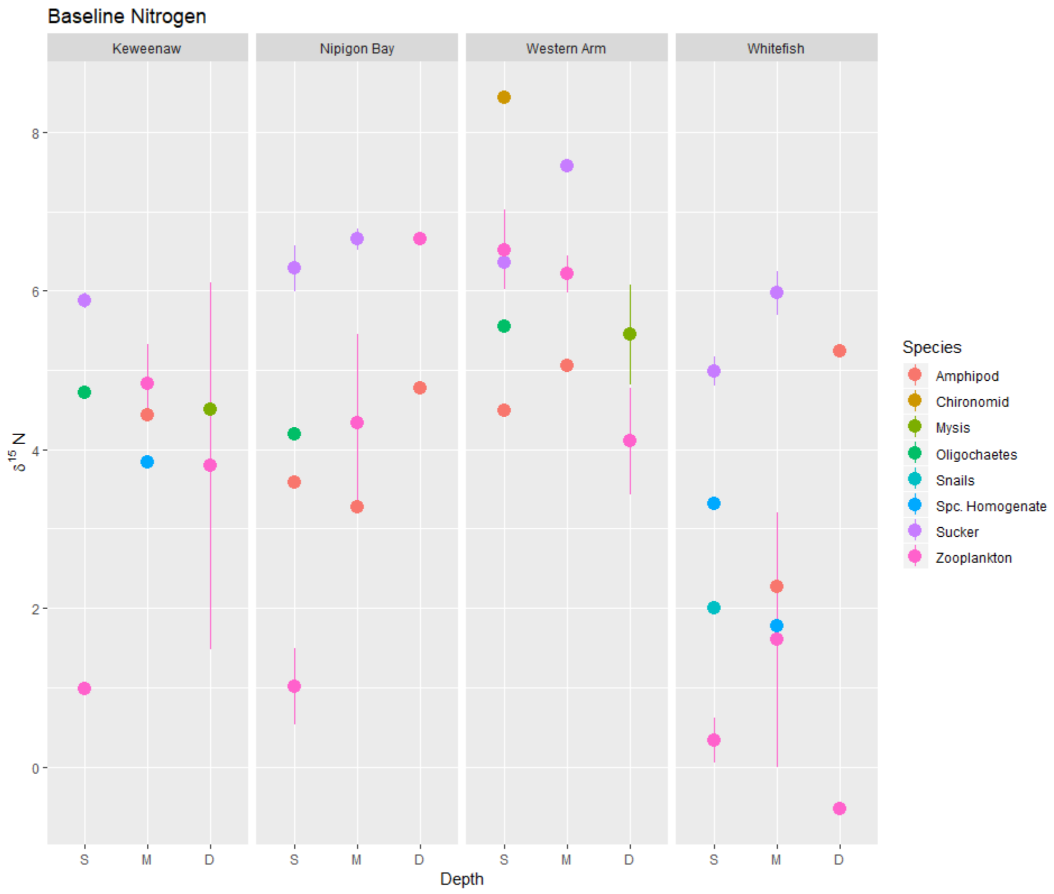

Figure 2.3. δ^{15}N values of all baseline species organized by region and by depth strata. Shallow (S) = 0-30m, medium (M) = 30-100m, deep (D) = 100+ m. Error bars are ± standard error.

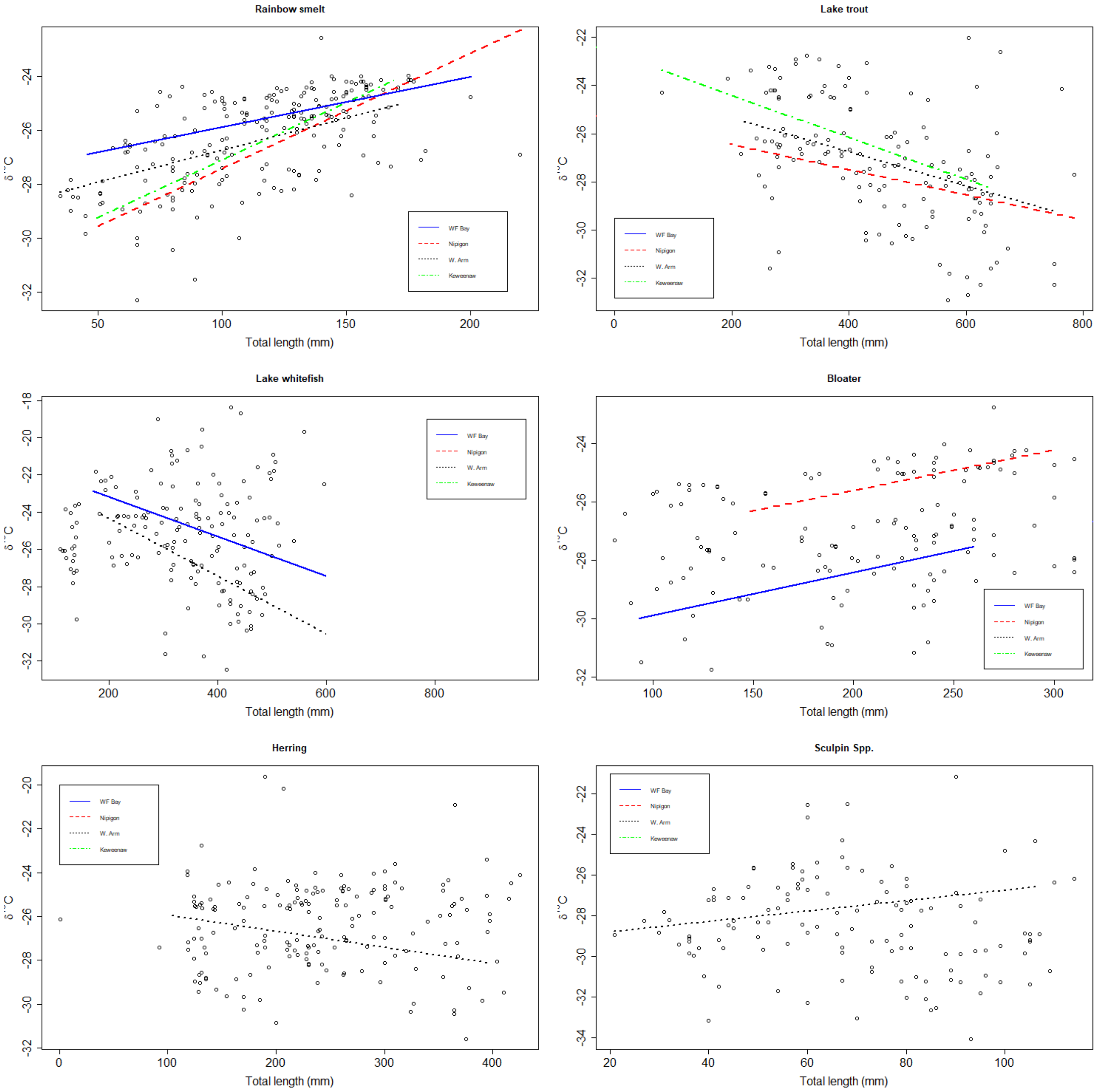

Figure 2.4. Linear regressions between the lipid-corrected carbon signature ($\delta^{13}C$ in per mille) and total length of common Lake Superior species. Data points are for all regions, and regression lines are specific for individual regions.

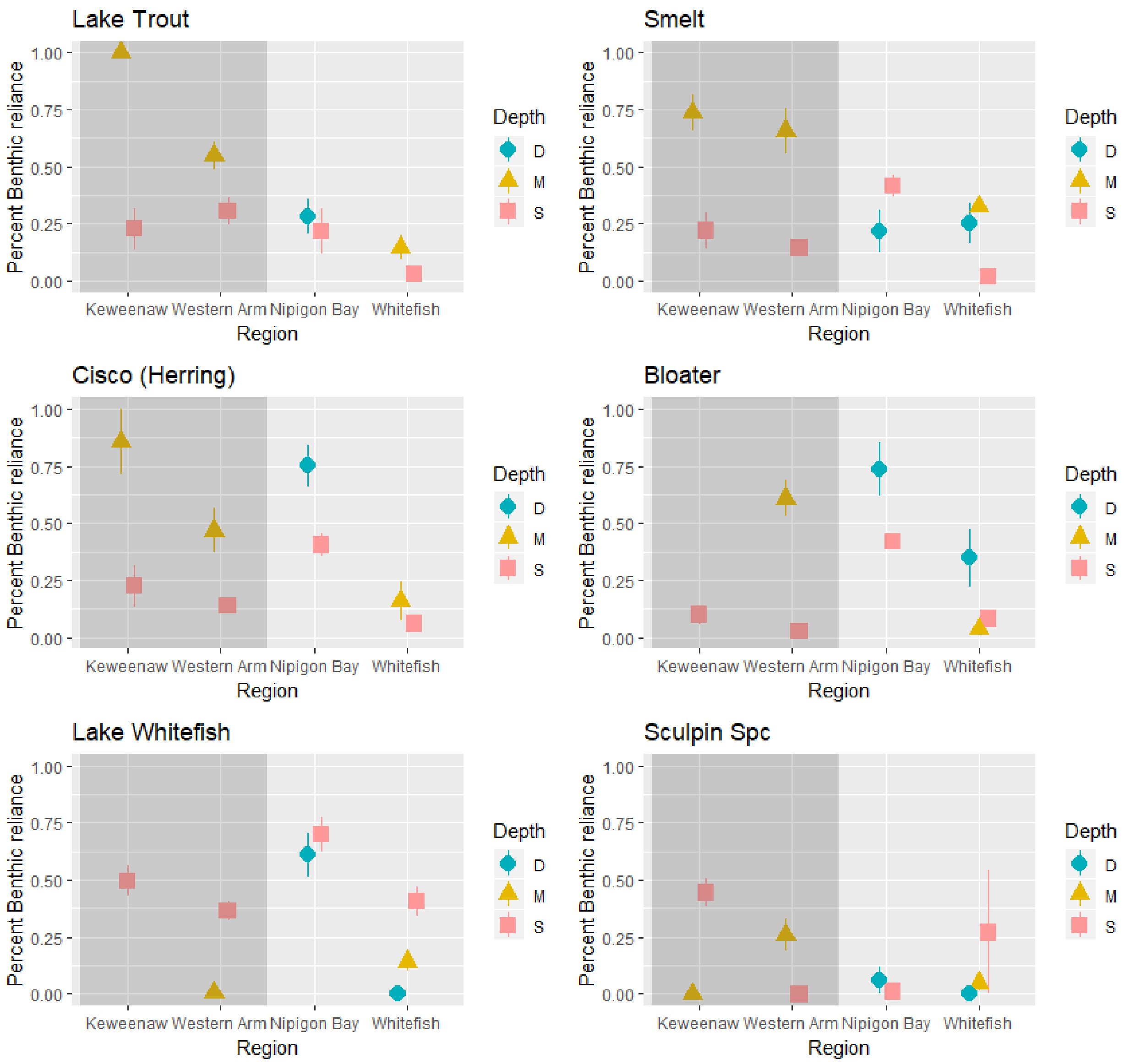

Figure 2.5. Percent benthic reliance plots, showing the proportion of pelagic resource use to the proportion of benthic-littoral (S) or benthic-profundal (M & D). Regions are organized from deepest to shallowest with the two deeper sites being highlighted in grey, error bars are ± standard error.

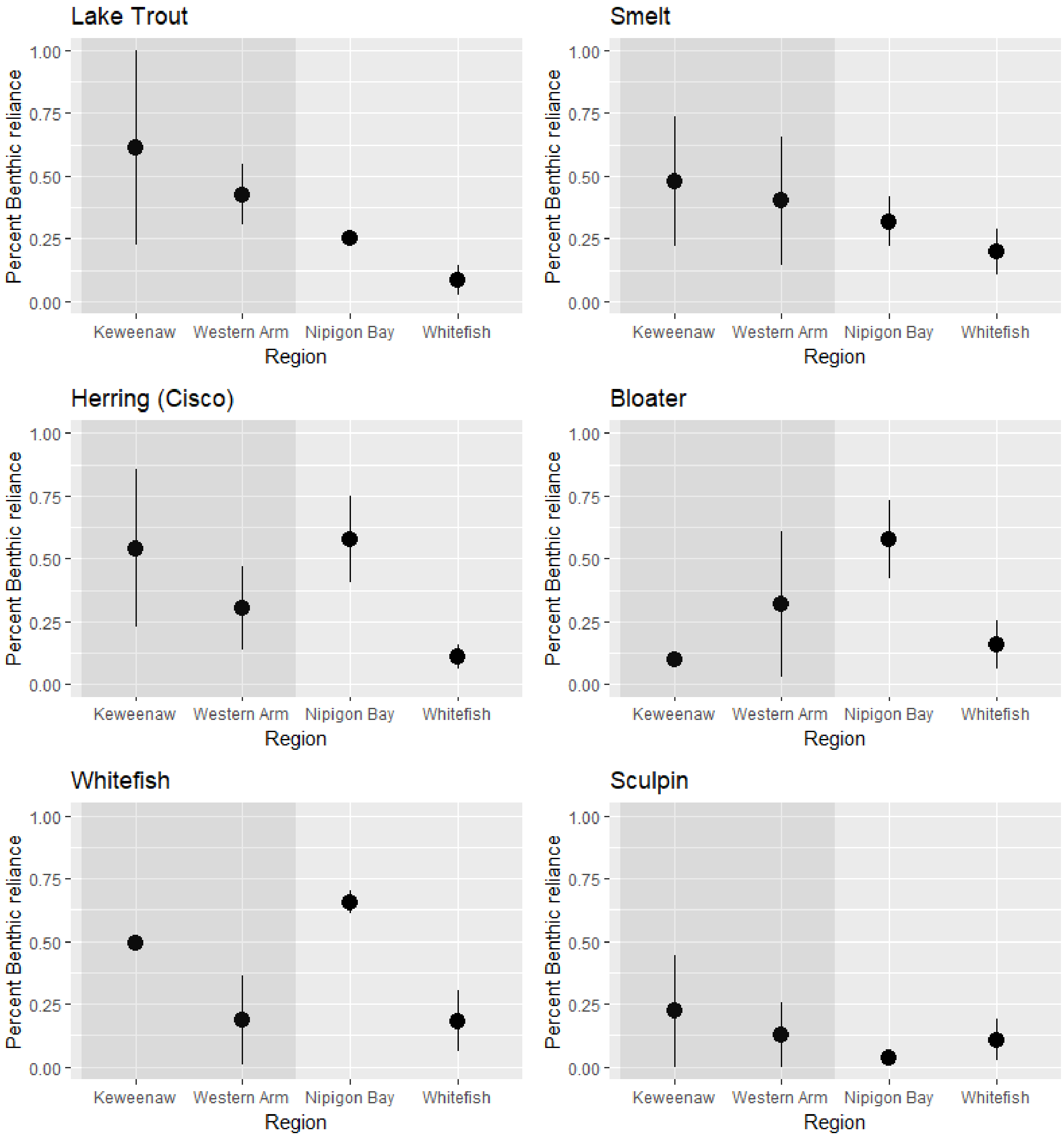

Figure 2.6. Percent benthic reliance across regions, depth specific values from Figure 2.5 were averaged to gain a better understanding of overall regional differences in resource use. Regions are organized from deepest to shallowest, the two deeper more exposed sites arestan highlighted in grey, error bars are ± standard error.

Chapter 3: Spatial bioenergetics variation among Lake Superior fishes and association with resource use

Abstract

Lake Superior's fish community is unique in the Laurentian Great Lakes in retaining healthy stocks of primarily native fish species. How energy and nutrients flow through large lake habitats is still relatively unknown, and the variability of within species bioenergetics has not been quantified previously. Knowing more about how well species are able to utilize different resources regionally may help managers make informed decisions to protect the natural biota both in Lake Superior and in other North American large lakes. A combined contaminant mass balance and bioenergetics modeling approach was used on three common Lake Superior fish species (lake trout, lake whitefish, and rainbow smelt) from four geographically distinct regions to evaluate spatial variation in growth, activity, consumption, metabolic costs and energy transfer. Further, model estimates of conversion efficiency were compared to estimates of regional habitat coupling to determine how coupling influences energy conversion in these key species. Overall, the benthic lake whitefish showed opposite patterns to that of the planktivorous smelt; conversion efficiency by lake whitefish was highest in the deeper regions, whereas conversion efficiency in rainbow smelt populations was highest in the shallow regions. Lake trout bioenergetics only varied within activity rates; the deeper regions had significantly higher activity than the shallow regions. No other bioenergetics estimates varied regionally, suggesting lake trout are able to assimilate energy equally among all regions. Within Lake Superior, the feeding group that a species belongs to appears to affect conversion efficiency. Lake trout, as a piscivorous top predator, was able to convert food at the same rate in any region. Overall, this study indicates that large

within-species variation in bioenergetics exists across Lake Superior, and lake-wide studies modelling bioenergetics estimates may be missing this within species regional variability.

3.1. Introduction

Ecosystem health and stability is dependent on having distinct energy pathways and mobile consumers that are able to transfer energy between them (Rooney et al. 2006), but these dynamics are difficult to quantify. Food web ecology and how the ecosystem is organized has been a prominent topic in aquatic ecology (e.g. Hairston and Hairston 1997, Kitchell et al. 2000,McMeans et al. 2016). Within biological systems there is a flow of nutrients from the base of the food web that producers and consumers successively rely upon as a source of energy (Lindeman 1942). Understanding the food web and how different species utilize energy pathways can sometimes be difficult to measure due to the complex biotic and abiotic natural processes that occur. Grouping species into interconnected webs based on their resource use allows us to evaluate these patterns across different trophic levels, identify alternative pathways of energy flow, and link these processes to the observed distribution of biomass and productivity.

Understanding how energy moves through an aquatic food web and is transferred between habitats can help us understand other factors such as resource availability, ecosystem productivity and the energetic demands of fishes. At the individual level, resource availability dictates the amount of surplus energy available for growth and reproduction (Brown et al. 1993; Barneche and Allen 2018). Individual growth rates and reproductive output directly influence population size, productivity, and ultimately resource availability for organisms occupying the next trophic level (Savage et al. 2004;

Andersen et al. 2009; Irigoien et al. 2014). Therefore, understanding the energetic connections at the individual level can inform population level dynamics and ecosystem function.

Bioenergetic modelling is a common approach used by researchers to assess the effects on fish communities of resource limitation, changes in climatic conditions, mortality and a variety of other factors (e.g. Lantry and Stewart 1993; Negus et al. 2008; Ferriss and Essington 2014). These models provide estimates of parameters useful in understanding production and energy transfer such as consumption, activity rate, and conversion efficiency. Gross conversion efficiency is a measure of how well an animal is able to convert ingested food into new tissue (i.e., ratio of energy consumed that is converted into mass accumulation or growth). The conversion efficiency of a fish depends on the quantity and quality of food available and the prevailing environmental conditions of the habitat (Lantry and Stewart 1993). Conversion efficiency can vary greatly in aquatic habitats (Sherwood et al. 2000; Trudel et al. 2010) and it would be expected to change between near shore and offshore habitats due to the difference in productivity in the two environments. Using conversion efficiency it is possible to calculate how much energy would be required to sustain one individual of a certain trophic level, and how many individuals of the lower trophic level that would relate to. This concept is similar to the larger scale concept of trophic transfer efficiency; trophic transfer efficiency estimates how much production from the lower trophic level is necessary to sustain the successive trophic level under consideration (Pauly and Christensen 1995). Instead of looking at a single individual, trophic transfer efficiency looks at how much of an entire trophic level would be needed to sustain the entire successive trophic level (i.e., a ratio of production estimates, as opposed to a ratio of consumption and growth rates). However, as an individual measure that scales effectively to production, examining conversion efficiency can be used as a proxy to understand trophic transfer efficiency.

Recently there have been many studies focused on understanding energy flow rates and pathways between benthic-pelagic ecosystems. Connections have been found linking near shore and offshore habitats, and in turn, the transfer of energy between them. In some cases, this interaction between two distinct energy pathways is necessary to sustain the ecosystem (e.g. Schindler and Scheuerell 2002; Sierszen et al. 2014; Stockwell et al. 2014). The littoral benthic energy supply has been shown to provide an important energy source for the entire food web in large lake systems (Hobson and Welch 1995; Vadeboncoeur and Steinman 2002; Vadeboncoeur et al. 2002). The ability to utilize more than one energetic pathway is an example of habitat coupling, the process by which two mostly unconnected aquatic communities are connected through transfer of energy and nutrients due to fish movement, water currents, and many other biotic and abiotic processes (E.g. Sierszen et al. 2014; Stockwell et al. 2014; Jones and Mackereth 2016). Several studies have demonstrated this connection between the benthic and pelagic food webs, as well as the use of different carbon sources and healthy and resilient food webs in both aquatic and terrestrial ecosystems (McCann et al. 2005; Rooney et al. 2006; Haddad et al. 2011). This can result in greater overall production due to the possible movement of prey species into food-limited habitats (Cloern 2007).

Resilience and stability of food webs has been a concept of interest in many areas of ecology, and aquatic ecology is no exception. Aquatic ecosystems where species are able to use more than one resource pathway can promote greater production (Cloern 2007) and greater overall ecosystem stability due to greater complexity and increased links between habitats (MacArthur 1955). Much of this comes from having resources accessible from more than one distinct energy pathway. Benthic energy pathways in aquatic ecosystems have been characterized as slow energy pathways whereas pelagic pathways are considered fast energy pathways. This slow designation refers to a less efficient energy transfer, due to a higher diversity and weaker interactions among trophic levels and habitats compared to the pelagic pathway (Rooney et al. 2006; Rooney and McCann 2012). Pelagic energy pathways have been the focus of many ecosystem studies when considering productivity in aquatic systems (Vadeboncoeur and Steinman 2002); but the benthic energy pathway may also play a significant role in the diversity and productivity in large lakes (Vadeboncoeur et al. 2002; Vander Zanden et al. 2011; Chapter 2).

Within benthic and pelagic energy pathways, differences have been observed in the conversion efficiency and energetic processes of fish. Benthic lake whitefish are able to consume more food, grow to a larger size and mature later than its pelagic dwarf whitefish counterpart (Trudel et al. 2001). This was thought to be due to the dwarf form contributing more energy to metabolic processes and having a higher overall standard metabolic rate within the species. Both resource use and how well a species is inherently able to utilize the energy it obtains will factor into the complete energetic understanding of an ecosystem.

Lake Superior is the largest freshwater lake by area in the world and uniquely in the Laurentian Great Lakes, its food web is dominated by native species and in many other respects considered to be the least disturbed of all the other lakes in the chain (Schmidt et al. 2009; Zimmerman and Krueger 2009). Understanding how rates of energy flow vary spatially within species, and integrating this information with rates of benthic-pelagic coupling, may assist in understanding distributions in biomass, overall ecosystem health and potential resilience of populations to disturbance (Rooney and McCann 2012). Resource use varies regionally within Lake Superior, depending on the limnological characteristics of the region (Chapter 2). In deeper, more open regions, fish utilize multiple energy pathways resulting in increased benthic-pelagic coupling compared to shallow, closed off embayments which show higher reliance on pelagic resources.

The objectives of this study were to (1) better understand spatial variation in growth and condition, as well as generate bioenergetic estimates of consumption, activity and conversion efficiency within a large lake system, and (2) determine associations between these variables with the degree of habitat coupling. Across four diverse regions around the lake, the bioenergetics of a pelagic planktivore (smelt, *Osmerus mordax*), a cold-water benthivore (lake whitefish, *Coregonus clupeaformis*) and a top predator (lean lake trout, *Salvelinus namaycush*) were evaluated. Resource use varies regionally within these and other species depending on the morphometric characteristics of the region (Table 3.1; results from Chapter 2). I predict that species that are more relient on the pelagic energy pathway would have a greater conversion efficiency, due to the pelagic energy channel being characterized by faster rates of energy transfer (Rooney et al. 2006). As well, I predict that tradbenthic energy pathitionally ways are characterized by slower rates of energy transfer (Rooney and McCann 2012); therefore common benthivorous species such as the lake whitefish, are more likely to have a lower conversion efficiency compared to a pelagic specialists such as lake trout and smelt.

3.2. Methods

3.2.1 Study Site

Lake Superior is a large, highly oligotrophic freshwater lake in the Laurentian Great Lakes chain. It is the largest freshwater lake by area in the world (82,000 km^2), and averages 147 meters in depth and has a maximum depth of 406 meters (Sierszen et al. 2014). This study was conducted in four prominent regions spread across the lake; Nipigon Bay, Whitefish bay, the western side of the Keweenaw Peninsula, and the western arm of the lake. These sites differ in bathymetric, limnological and biological patterns, as well as being geographically spread across the lake; Nipigon Bay and Whitefish bay represent regions with a shallow bathymetry and are relatively closed off embayments, whereas the western arm and Keweenaw Peninsula regions are exposed to the open lake, and have a steeper depth gradients. Fish species were sampled along a depth gradient within each region to ensure proper representation, trying to capture variability associated with depth and other related factors.

3.2.2 Sample Collection

Fish samples were collected between May and September 2016 and 2017 by a variety of government agencies lake-wide. This includes the United States Geological Survey (USGS), United States Fish and Wildlife Service (USFWS), Great Lakes Indian Fish and Wildlife Commission (GLIFWC), Wisconsin Department of Natural Resources (WiDNR), Minnesota Department of Natural Resources (MiDNR), the Environmental

Protection Agency (EPA), and Environment Canada. Three species that are common across Lake Superior were collected: lake trout, lake whitefish, and the non-native rainbow smelt. These species also represent different trophic and feeding pathways; a piscivorous top predator (lake trout), a benthivorous secondary consumer (lake whitefish) and a planktivorous secondary consumer (rainbow smelt). Samples were collected through multi-agency collaborations using a combination of trawl net and gill net sampling, and individuals were selected in an effort to obtain a range of sizes. Prey species were also collected from the sampling regions along the same depth gradient for estimates of prey methylmercury to inform contaminant-bioenergetic models (see below). Benthic invertebrates were collected with Ekman or PONAR dredges at each depth strata and sieved to remove sediment. Zooplankton were collected with triplicate vertical net tows between sunset and sunrise to account for diel vertical migration. All invertebrate and fish samples were immediately frozen upon collection to be transported to Lakehead University. Age structures (otoliths), lengths (in millimetres), and weights (in grams) of the fish were taken upon arriving at Lakehead University, and then kept in the freezer for storage.

3.2.3 Growth rates

Size-at-age data for each of the three species were collected from different agencies. Otoliths were extracted from all whole fish samples for aging. These structures were prepared for ageing by the MNRF Upper Great Lakes Management Unit. Supplementary age data for lake trout and lake whitefish was used from the Upper Great Lakes management Unit’s ongoing Fish Community Index netting program (2011-2016), which encompasses the Nipigon Bay and Whitefish Bay regions, as well as from GLIFWC and Environment Canada (2015-2016).

Length-at-age models were created for each species and within each region using a von Bertalanffy growth equation:

(Eqn 2.1) $$L_t = L_\infty * (1 - e^{-k*(t-t_0)})$$

Where L_t is the length (mm) at age t (yrs), L_∞ is the asymptotic length (mm), k is the Brody growth coefficient (year^{-1}), and t_0 is the age intercept (year) which was assumed to be zero (Beauchamp 2002; Table 3.2). Differences in asymptotic length and growth rate were analysed using bootstrapping (Table 3.3, further discussed in section 3.2.8 below). Once cohort lengths were determined, length-weight regressions were created for each species and each region to find weight at age using the region specific data (Table 3.4). Estimated cohort weights were then input into the bioenergetics models. von Bertalanffy growth curve fits for each species were also compared among regions to help interpret differences in growth (Figures 3.1-3.3).

3.2.4 Direct Mercury Analysis

Total mercury was analysed for a minimum of 10 fish (but as many as 22) from across the broadest size range available for each region and species using a Milestone DMA-80 direct mercury analyzer according to the United States Environmental Protection Agency (US-EPA) method 7473 (SW-846). I assumed that total mercury concentrations reflected methylmercury concentrations in the fish analyzed (Bloom 1992). Dried whole fish homogenate was analyzed and the final mercury value (mg/kg) was converted into wet weight using the dry:wet weight ratio of each sample. A minimum of 5 certified reference material (CRM) samples (TORT-3, lobster hepatopancreas) were analyzed on each run of the DMA to ensure ongoing accuracy and precision. Mean estimate of TORT-3 across 10 runs was 0.283 μg·g-1 (± 0.007 $\mu g \cdot g^{-1}$ standard deviation), which is well within the 95% confidence limit of the reported CRM (0.292±0.022mg/kg total mercury).

Mercury inputs for each cohort were estimated by creating a predictive model of total mercury with fish wet weight. Linear regressions were created for each species and within each region, no data transformations were needed (Table 3.5). For Keweenaw and Whitefish Bay fish (lake trout and whitefish), supplementary mercury data from GLIFWC and Environment Canada was combined with samples run on the DMA to increase sample size. Diagnostic plots were used to visually ensure normality of the data and homogeneity of variance.

3.2.5 Methylmercury Analysis

Benthic invertebrate and zooplankton samples were analyzed for methylmercury at the Lakehead University Environmental Laboratory (LUEL) using both a BROOKS-RAND and MERX MeHg System following EPA method 1630 (U.S. EPA. 2001). Eight zooplankton samples and 13 benthic invertebrate samples were analyzed based on available tissue and regional coverage. The MeHg System accuracy was determined to be 91.3%, with 5% system precision, calculated using DORM-3 (Environment Canada; certified value = 0.355±0.056μg/g) as the certified reference material. Values for benthic invertebrate methylmercury can be found in table 3.6.

3.2.6 Bioenergetics model

Consumption and energy expenditure in fish were estimated using a mass-balance contaminant tracer model combined with a bioenergetics model (Trudel and Rasmussen

1997, 2001; Trudel et al. 2000). Consumption was estimated using mercury as the contaminant tracer, along with water temperature, average initial and final fish weight, average initial and final fish methylmercury concentrations, and prey MeHg concentrations (Eqn 3.2). All mercury in fishes was assumed to be methylated (Bloom 1989, 1992; Hall et al. 1998) and I assumed fishes in uncontaminated waters accumulate all MeHg through diet (Hall et al. 1997; Mason and Lawson 1998; Leaner and Mason 2002). Linear relationships were created with THg (g/kg) and body size (g) to estimate the mercury concentration at W_0 and W_t. Diet MeHg concentrations were estimated within each of the four Lake Superior regions to account for spatial variability (Table 3.5), and combined across species to obtain a single diet estimate for each region as described in section 3.2.6.1 below.

Methylmercury accumulation in fish was represented as:

(Eqn 3.2)

$$\frac{dHg}{dt} = (\alpha * C_d * C) - (E * G * K)Hg$$

Where *Hg* is the average amount of MeHg (µg Hg g $^{-1}$ wet weight), α is the assimilation efficiency of MeHg from food, C_d is the prey MeHg (µg Hg g $^{-1}$ wet weight), *C* is the consumption rate (g/day) over the time period, *E* is the elimination rate of MeHg (g/day), *G* is the growth rate (g/day), and K is the amount of losses due to spawning. If modelling is conducted over a short time span the differences between these parameters will be small and can be considered constant over a one day increment (Rennie 2003). Treating Hg, G, E, and K as constants allows for (Eqn 3.2) to be integrated and solved for consumption (C):

(Eqn 3.3)

$$C = \frac{[Hg_t - Hg_0 * e^{-(E+G+K)t}]}{[\alpha * C_d * (1 - e^{-(E+G+K)t})]} * (E + G + K_s)$$

Where Hg_0 and Hg_t are the MeHg concentration in the fish at time 0 and t respectively.

The Mercury Mass Balance Model (MMBM) output provided *C*, for use in the Wisconsin Bioenergetics Model (Hanson et al. 1997), which is expressed as

(Eqn 3.4) $$W_t = W_0 + \left[C * ED_{Prey} - (F + U + R_T)\right]/ED_{Fish}$$

Where W_t is fish final weight, W_0 is initial fish weight, ED_{Prey} is energy density of prey, F is losses due to egestion, U is losses due to excretion, R_T is losses due to metabolism, and ED_{Fish} is the energy density of fish.

Energy density of fish samples was estimated directly using either calorimetry or using dry-mass relationships. Rainbow smelt energy densities were determined solely with calorimetry; 11 samples of a range of sizes were analyzed from each region. There was a significant interaction between region and body size (ANOVA, $F_{3,36}$=4.3806, p=0.01), so there was no consistent lake-wide mass specific relationship present. Linear dependency was still checked for individual regions, and two of the four locations had a linear dependency. Nipigon Bay energy density decreased with body size ($F_{1,9}$ =17.692, p=0.0023) and energy density in Keweenaw smelt increased with body size ($F_{1,9}$ =6.6193, p=0.003). Since no consistent increases with body size were able to be modelled, a constant value was used for smelt energy density within all cohorts (Table 3.7).

Lake Whitefish fish energy density was estimated using a mass specific relationship created for the Great Lakes (Rennie and Verdon 2008).

(Eqn 3.5) $$ED = 0.5650 * W + 5233.70$$

Where ED is energy density in J/g wet weight and W is the round weight of the whitefish.

Since no Lake Superior specific relationship existed between energy density and mass for lake trout, energy density was estimated from the percent dry weight using empirically derived constants (Hartman and Brandt 1995):

(Eqn 3.6) $$\frac{J}{g}\, wet\ weight = a + b * DW$$

Where *a* and *b* are empirically derived constants (Lake Trout: a = -3,809, b=397.9), and DW is the average percent dry weight.

3.2.6.1 Prey model inputs

Prey items were assigned *ED* and methylmercury values from a combination of analysed prey items and literature values (Tables 3.6, 3.7). As a pelagic planktivorous specialist, smelt diet energy density was estimated to reflect the MeHg and ED from composite zooplankton hauls specific to each region. Diet proportions for lake trout were estimated using Lake Superior specific diet information reported in Gamble (2010). Studies quantifying the diet of lake trout show that it is mainly piscivorous, with majority reliance on coregonines in the summer and smelt in the fall (Gamble 2010). Since the majority of samples were collected in the summer coregonines were assumed to make up 75% of the diet and the proportion of smelt was assumed to be 25%. Smelt MeHg values were analyzed for each region, and combined with literature values of coregonines. Energy density values for smelt and coregonines were averaged using the same proportions, to obtain a single input value for each region (Table 3.8).

Lake whitefish are known to eat a variety of benthic prey items (Rennie et al. 2012), so the benthic invertebrates collected and analyzed from each region were used as the prey inputs averaged under the assumption species collected were representative of the available prey in the region. All benthic prey species that were analyzed for MeHg within a region were averaged to estimate the prey MeHg for lake whitefish. Literature values for prey energy density were averaged based on the same invertebrate species used for the regional MeHg. No energy density values for lake whitefish prey species were regionally available, so literature values of the same species used for prey MeHg were averaged and used as a single prey ED value for each region.

Total metabolism (R_T) was expressed as:

(Eqn 3.7) $$R_T = ACT * R_S + R_d$$

Where R_d is specific dynamic action, R_S is the losses due to standard metabolism, and ACT is the losses to active metabolism. ACT can be isolated from this equation to obtain the activity multiplier.

Last, gross conversion efficiency (V) was derived from the mass specific rates of C and G (Kerr 1971):

(Eqn 3.8) $$V = G/C$$

In this study, gross conversion efficiency was used as a proxy for trophic transfer efficiency. At the scale of individual based modelling, gross conversion efficiency represents the proportion of energy consumed that is converted into growth. This can be related to trophic transfer efficiency as both represent amounts of energy that are required to permit growth and production at the next trophic level, but at different scales (conversion efficiency at the individual level, trophic transfer efficiency at the population or trophic level). Because production relies on both individual growth rates and reproductive output/recruitment, both of which are individual processes directly linked to conversion efficiency, these two quantities (conversion efficiency and trophic transfer efficiency) are very likely correlated.

Bioenergetics models were parameterized using daily surface temperature. In Nipigon Bay, a temperature logger (HOBO Pendant ® Waterproof Temperature Data Logger, Hoskin Scientific) measured surface water temperatures from June- October 2016. Hourly temperatures were averaged to obtain a daily mean. For all other regions, daily average temperature data was collected by NOAA buoys (KEW_PCLM4, STN45028_WA, DULM5, PTIM4). Most of the temperature data regionally only existed during the time of ice off, so for the winter months daily average lake-wide values were used. It was assumed that fish will opportunistically move within the water column away from sub-optimal temperature, so the temperatures within each model were capped at the fishes optimum temperature; lake trout optimum temperature was capped at 10ºC, and lake whitefish was capped at its thermal optimum of 16.8ºC (Jobling 1981; Edsall 1999). For smelt species this optimum temperature changed between juveniles (14 ºC) and adults (10ºC). Daily temperatures were used to parameterize bioenergetics models for basal metabolism and theoretical maximum consumption.

Fish samples were collected from a variety of sources, many of which did not have any reliable sex data associated with each fish or fish were too degraded from being frozen to determine sex once they were dissected. All species and regions were modelled as male which may introduce some bias as energy allocation to reproduction differs between males and females. Consistently modelling males across all species and regions will allow us to make comparisons across bioenergetic estimates, as the patterns should not drastically change since there is no major body size sexual dimorphism in lake trout (Esteve et al. 2008) or lake whitefish (Scott and Crossman 1973) which would skew our data due to an unbalanced sex ratio. There is sexual dimorphism in body size of rainbow smelt, but in freshwater systems the sex ratio of males to females is about even, except during spawning there is a higher number of males (Warfel et al. 1943). However, because sampling of smelt occurred within the lake and outside of spawning,. All populations were modelled as male consistently across all regions, therefore estimates should be comparable as I did not expect biased sex ratios in our samples.

3.2.8 Statistical Analysis

The bioenergetics model was run through Microsoft excel, using a spreadsheet based approach to solve for the unknown variables. All statistical analyses were carried out using R statistical analysis program (R Core Team 2018). For all tests, residuals were checked for normality using visual inspection of residuals in R. Residuals followed a mostly normal pattern, and were distributed homogeneously with no major outliers; since there was a balanced design and ANOVAs are robust to minor violations (Quinn and Keough 2002), data were interpreted with caution. Issues with violations in the assumptions arose within rainbow smelt activity estimates and consumption, as well as whitefish growth; because of small sample sizes (smelt: n=5, lake trout and lake whitefish: n=10) transformations were unsuccessful at normalizing the data. Diagnostic residual plots for data with minor violations are available to be evaluated by the reader (appendix A: Figure A3-A5). The mass-specific bioenergetics outputs from the model were compared across the four regions using ANOVA. More specifically, the estimates of interest were consumption (C, g food per g consumer day^{-1}), activity multipliers (ACT, unitless), conversion efficiency (V, g consumed per g of growth day^{-1}) and growth (G, g growth *g fish^{-1}day^{-1}). ANOVAs were conducted for each of the four energetic variables to look for significant differences among regions. The critical P-value was adjusted to account for each of the bioenergetic outputs evaluated within a species by dividing $\boldsymbol{\alpha}$ (0.05) by 4 (p_{crit}=0.0125). Tukey's honestly significant difference (HSD) test was used as a posthoc analysis to evaluate differences among regions.

To evaluate differences in growth rates among regions further, the von Bertalanffy growth curves for each age were bootstrapped (2000 iterations to ensure normality) to obtain 95% confidence intervals around the maximum body size and growth rate estimates for each species and in each region.Non-overlapping confidence intervals were considered to represent significant differences among the von Bertalanffy growth curves.

Relationships between mercury concentrations and body mass for model inputs were created using linear models and checked for significance using ANOVA. For all of the species and regions there was a significant relationship present between size (weight) and mercury concentration (mg/kg) except for lake whitefish from the Keweenaw Peninsula region, which used a total length (mm) and mercury relationship instead (Table 3.4). No transformations to the data were necessary.

3.3. Results

3.3.1 Modelling length-at-age

Growth curves were created for all three species within each study region. Specific growth parameters used to create the Von Bertalanffy growth curves were reported in Table 3.2 with sample size. Lake whitefish and lake trout in the Keweenaw Peninsula region seem to be able to grow to a much larger size than in the other three regions (Figures 3.1 and 3.2). Lake trout in the Keweenaw Peninsula region grew to a significantly larger asymptotic length (non-overlapping 95% CI's, Table 3.3) compared with the other three regions. However, there were no differences in the Brody growth coefficient (Table 3.3). Lake whitefish populations in Keweenaw had a significantly larger Brody growth coefficient (rate of approach to L_∞) than the other three regions. Lake whitefish from Whitefish Bay had a significantly smaller L_∞ than those in Nipigon Bay (Table 3.2). Significant differences existed between the Brody growth coefficients of lake whitefish in the four study regions. Lake whitefish in Whitefish Bay had a significantly larger Brody growth coefficient and grew faster than Keweenaw and Nipigon Bay populations (not significantly different from western arm). There were no significant differences observed in lake trout growth coefficients based on non-overlapping 95% confidence intervals (Table 3.3). Growth conditions were not analysed in the smelt populations due to small sample size. But the much larger maximum body size for Keweenaw that can be observed in lake trout (Figure 3.1) and lake whitefish (Figure 3.2), is not obvious in the growth curves of rainbow smelt in any of the study regions (Figure 3.3).

3.3.2 Bioenergetics

Bioenergetics parameters estimated from spatially distinct Lake Superior regions were significantly different across regions for rainbow smelt and lake whitefish. Rainbow smelt activity and consumption increased with between the shallower and deeper sites, whereas the conversion efficiency decreased (Figure 3.4). Activity rates and conversion efficiency were significantly different among regions (ANOVA, V, $F_{3,\,16}$=5.105, p=0.01; ACT, $F_{3,\,16}$=33.27, $p < 0.0001$). Only the Whitefish Bay (most shallow) and Keweeaw Peninsula (deepest) regions were significantly different for conversion efficiency (p=0.0069); for activity rates Keweenaw was significantly different from all regions (WA: p=0.0007, NB: p=<0.0001, WF: p=<0.0001) and Whitefish Bay was also significantly different than western arm (p=0.0001) and Nipigon Bay (p=0.0039). Nipigon Bay and western arm were not significantly different from each other. Even though there was no statistical difference between the energetic estimates for growth or consumption among regions, visual inspection suggests that growth seems to decrease with regional average depth and consumption seems to increase moving from the more shallow enclosed regions to the more open deeper sites (Figure 3.4).

Lake whitefish populations showed the exact opposite trends that were found in rainbow smelt (Figure 3.5); activity and consumption decreased across regions, and conversion efficiency increased from the more shallow embayments to the deeper more open regions. There were significant differences observed in consumption ($F_{3,\,36}$=9.679, p=<0.0001), conversion efficiency ($F_{3,\,36}$=6.567, p=0.0012), and activity ($F_{3,\,36}$=25.13, p=<0.0001) but not growth. Across all regions where a difference was observed Keweenaw, the deepest site was always significantly different than Whitefish Bay, the most shallow site (C: p=<0.0001, K: p=<0.0001, A: p=<0.0001). There were no significant differences in growth, but visual interpretation suggests that grow decreased as the depth of the region decreased.

Less distinct patterns were shown across lake trout regional populations, which did not seem to follow a pattern with depth (Figure 3.6). There was a significant difference in lake trout activity rates among sites ($F_{3,36}$= 49.32, p=<0.0001), which demonstrated a pattern with across the sites, with lower activity rates in the shallow closed off regions and higher in the deeper more exposed regions. Activity rates in Keweenaw and western arm were statistically different than in Nipigon Bay and Whitefish Bay (KW-NB: p=<0.0001, KW-WF: p=<0.0001, WA-NB: p=<0.0001, WA-WF: p=<0.0001).

Study species within a region were compared to gain a better understanding of how bioenergetics estimates compare across species. Conversion efficiency in lake whitefish populations was consistently lower than the other two species in all four study regions. The species that exhibited the highest conversion efficiency was most often smelt, with the highest values in the western arm, Nipigon Bay and Whitefish Bay, but within Keweenaw lake trout had a marginally higher conversion efficiency (smelt: 0.115 $g \cdot g^{-1 \cdot} day^{-1,}$, lake trout: 0.136 $g \cdot g^{-1 \cdot} day^{-1}$).

To see if there was a relationship between bioenergetics parameters and habitat coupling, each bioenergetics estimate was plotted against percent benthic reliance. There seemed to be a strong negative relationship between conversion efficiency and percent benthic reliance in smelt populations, a positive relationship between conversion efficiency and percent benthic reliance in lake whitefish populations and no significant pattern in lake trout populations (Figure 3.7).

No other bioenergetics parameters showed clear relationships to the degree of benthic reliance (Appendix figures A6-A8).

3.4. Discussion

Clear spatial differences among growth and bioenergetics were demonstrated among three species of fish representing distinct functional groups within Lake Superior. Opposite pattern for bioenergetics estimates were observed between the pelagic rainbow smelt and the benthivorous lake whitefish across regions. Consumption and activity increased in lake whitefish populations from the deepest most open region (Keweenaw), to the most shallow region (Whitefish Bay); conversion efficiency decreased as consumption and activity increased. Growth did not show any significant differences between regions. The pelagic-specialist smelt, showed the opposite pattern; consumption and activity rates were highest in the deep open regions (Keweenaw and western arm) and lower in the more shallow regions (Nipigon Bay and Whitefish Bay); growth and conversion efficiency estimates of smelt were lowest in the deeper regions and increased in the shallow regions. The only trend observed in the lake trout populations regionally was that the deeper regions were estimated to have significantly higher activity than the shallow regions. No trends were observed in the consumption, growth or conversion efficiency of lake trout.

It was expected that smelt would have the highest conversion efficiency estimates within Keweenaw, as it is a high energy pelagic channel characterized by ‘faster’ rates of energy transfer (Rooney and McCann 2012, Chapter 2), but smelt showed the highest conversion efficiency in Whitefish Bay; mean conversion efficiency for Keweenaw smelt populations was 0.115 $g \cdot g^{-1} \cdot day^{-1}$ compared to the Whitefish Bay smelt population which showed the highest conversion efficiency of 0.140 g· g$^{-1\cdot}$day^{-}. Energetic changes were not due to variation in prey energy densities; a constant prey energy density value for smelt was used across all regions in energetic models used in this study. For smelt, the pattern observed in the model was most likely due to the amount of prey MeHg that was input for each region, as regionally explicit values for prey MeHg was available, whereas a constant lake-wide value from the literature was only available for energy. Keweenaw had the lowest prey MeHg, which means for the model to reach the next age cohort, there had to be a higher amount of consumption within that region to account for a lower value of prey MeHg being modelled than the other regions.

Smelt conversion efficiency may have been highest in Whitefish Bay populations compared to smelt in the other three regions due to the increased habitat complexity. The highly reticulate shoreline is indicative of a more heterogeneous habitat and higher amounts of prey refugia (Dolson et al. 2009). The heterogeneity of the habitat may increase the amount of habitat coupling that is observed regionally and in turn facilitate the higher conversion efficiency estimates. Bioenergetic estimates for smelt in Keweenaw and western arm (the deeper more open regions) show higher activity rates and higher consumption rates compared to Nipigon Bay and Whitefish Bay (the more shallow regions), without the same differences being observed in growth rate (Figure 3.4). Activity and consumption are often correlated in actively foraging fish (Kerr 1982) and this is observed in both the lake whitefish and rainbow smelt populations. It is possible that since fish are consuming more without showing a significant increase in conversion efficiency or growth rate that there may be poor food availability in these deeper regions (Rennie et al. 2012). If there is less food available then more energy must be put into foraging for food, and less can be allocated to growth; or if the resource is less energetically rich more time would have to be spent foraging to collect more prey and overall end up with the same amount of energetic gains as a region with a more energetically rich prey species.

When comparing conversion efficiency estimates across species, my hypothesis suggested that the smelt would have a greater conversion efficiency as they belong to the faster pelagic energy pathway (Rooney and McCann 2012), and that was what was observed through this study. Out of the three species, conversion efficiency in each region was always the lowest in whitefish populations, and smelt had the highest conversion efficiency in all of the regions except Keweenaw where lake trout dominated. Trudel et al. (2001) suggested that lake whitefish generally had a higher conversion efficiency estimate than the pelagic-specialized counterparts within the same ecosystem, due to the larger body size and slower growth. These data support the fast and slow energy pathway theory (Rooney et al. 2006; Rooney and McCann 2012), in which benthic species are less efficient at converting resources into growth than pelagic species using the faster energy channel. Though there are highly variable ecosystems that exist across Lake Superior, the pelagic species consistently had higher conversion efficiency estimates.

Lake trout populations showed no clear regional patterns for most of the bioenergetics estimates that were modelled. Growth, consumption ad conversion efficiency values stayed near constant across all Lake Superior sites, suggesting lake morphometrics do not affect lake trout in the same way it affects the other two study species. The activity rates were the only bioenergetics estimate that grouped together based on regional bathymetry and exposure; with the highest activity rates in the deep open regions, and lower activity rates in the more shallow enclosed regions. Since lake trout are an extremely mobile predator and are able to follow their food, they may be less sensitive to regional differences in the proportion of available benthic or pelagic energy. Lake trout can follow their food both through diel vertical migration (Gorman et al. 2012) and through diel bank migration (Stockwell et al. 2010; Ahrenstorff et al. 2011). It is unlikely that the lack of variation observed in lake trout energetics was due to integration of energy across regions as they have been observed travelling up to 42 km in Lake Superior (Kapuscinski et al. 2005), and the regions of interest in this study are greater than 100 km apart. But because they are capable of moving such great distances this would provide more opportunity for resource acquisition within a region and overall integration of energy across a range of habitats.

Through comparing bioenergetics rates within the three study species across regions, it appears that bioenergetics rates are linked to the ecological niche that a species belongs to. Whitefish, representing the traditional benthivores, had a high conversion efficiency and growth with more benthic feeding, whereas smelt shows the opposite trend with a greater conversion efficiency. Where the planktivorous niche was thriving (higher conversion efficiency and growth) the other exhibits signs of poor food availability or an inability to convert the energy into growth. With this information it can be expected that fishes within a similar ecological niche would exhibit similar bioenergetics patterns. In the context of my study it can be inferred that benthivorous species thrive in the deeper more open regions, and pelagic open water species best thrive in the more shallow enclosed regions.

Conversion efficiency in the fish species considered here generally reflected adaptation of these species to particular environments. The most obvious relationship that was observed when comparing conversion efficiency to habitat coupling was a negative relationship between conversion efficiency and percent benthic reliance in rainbow smelt. Rainbow smelt showed the lowest benthic reliance and the highest conversion efficiency estimate in Whitefish Bay, to the highest amount of percent benthic reliance but the lowest conversion efficiency in Keweenaw. This suggests that smelt is best able to convert food into energy when able to forage on highly pelagic resources. Smelt is still able to exist in regions where it is using a higher amount of benthic energy, but it needs to consume more and Lake whitefish exhibit the opposite trend to smelt when comparing percent benthic reliance and conversion efficiency, suggesting that lake whitefish are most able to convert resource into energy when using more benthic resources. It is possible that lake whitefish are able to show a high percent benthic reliance in these deep open sites as they have a higher abundance of *Diporeia* (Auer et al. 2013). *Diporeia* abundance peaks within the 50-150m depth strata, and this is more characteristic of our deep sites than our shallow embayments. Lake whitefish are able to exhibit better resource use (conversion efficiency) within the deeper regions where there are higher densities of one of their more preferred prey species (Rennie et al. 2012).

Lake trout populations do not show any obvious trends when comparing percent benthic reliance to conversion efficiency. This suggests that in any region, regardless of the predominant morphology, lake trout display similar resource utilization. This lack of trend could be due to lake trout being opportunistic predators with highly plastic feeding habits (Vander Zanden et al. 2000). Theoretical models of fish growth suggest that foraging costs increase when the size of a predator increases relative to its prey, since it must find and consume more prey to satisfy its energy demands (i.e., decreased growth efficiency, Kerr 1971). A shift in larger prey species would also increase the growth rate of fish (Werner and Gilliam 1984). Lake trout grow to a much larger size in Keweenaw than in any other Lake Superior region, so one assumption would be that the prey species within Keweenaw also grow larger. Growth curves for smelt and herring, which are common lake trout prey species, did not grow to a significantly larger size in Keweenaw compared to the other three regions. In this dataset it does not seem as though the size of prey (smelt and herring) is different among regions, it is possible that there is a greater abundance of prey species, or an alternative prey species available in Keweenaw allowing trout to grow larger. A more comprehensive study on regional differences of lake trout prey would help to examine this question. Knowing the mechanisms and influences that dictate how capable a species is of converting energy into new growth provides more insight into the energetic capacity of the species to thrive in the current environmental conditions.

Overall, the bioenergetics modeling results presented here fit within the ranges of previously created models for smelt (Lantry and Stewart 1993), lake whitefish (Rennie et al. 2012) and for lake trout populations (Stewart et al. 1983) within the Laurentian Great Lakes. The conversion efficiency estimates for lake trout populations within this study were about half of what was estimated for lake trout within Lake Michigan (Stewart et al. 1983), which is most likely due to bathymetric and community composition differences across the Great Lakes. No other values seemed to deviate from what was considered to be normal within previous studies and the results make sense from a biological standpoint. This study provides regionally-explicit estimates of consumption rates for important components of the Lake Superior fish community. These rates can now be combined with regional population estimates derived from lake-wide hydroacoustic survey such as those conducted by the USGS to explicitly determine trophic transfer efficiency estimates for populations. This will allow us to confirm that our estimates of conversion efficiency can provide a reasonable proxy of these measures.

In conclusion, this study quantified the bioenergetics of three common Lake Superior fish species encompassing three different feeding guilds, and showed there is a relationship between conversion efficiency and percent benthic reliance. Within species bioenergetics variation consistently and follows a morphometric pattern and it is assumed that species belonging to the same trophic guild would follow the same pattern based on resource use. Smelt and whitefish show an opposite pattern between the deeper regions and the more shallow regions, which is opposite to what was expected when compared to the amount of habitat coupling in a region. Energetics of Lake Superior fish species seem to be related to their functional/feeding group (benthivore/planktivore/piscivore) as well as the morphometric characteristics of a region. Planktivorous species may be better suited to the more shallow enclosed regions whereas the benthivorous species may be best suited to the deeper open regions. These results show that there are regional differences within Lake Superior and lake wide studies observing bioenergetics estimates are missing a great deal of spatial variation. Future studies would benefit from calculating actual energy density and diet items from each species analyzed to get a more clear representation of the processes that are occurring. As well, if population estimates for each region are known then actual regional estimates of trophic transfer efficiency can be derived to compare to results with conversion efficiency reported in this study. With population level data it would be possible to estimate the carrying capacity and gain an understanding of its spatial variation in Lake Superior.

Tables

Table 3.1. Percent benthic reliance averaged within each of the four study regions for all study species. 0% would indicate full reliance on the pelagic energy pathway, and 100% would indicate all resource use from the benthic energy pathway, with values in between being a combination of benthic and pelagic

Species	Morphometry	Region	Benthic reliance (%)
Rainbow smelt	Deep, exposed region	Keweenaw	50.34
		Western arm	31.52
	Shallow embayment	Nipigon Bay	35.41
		Whitefish Bay	24.03
Lake whitefish	Deep, exposed region	Keweenaw	61.36
		Western arm	42.60
	Shallow embayment	Nipigon Bay	25.04
		Whitefish Bay	8.69
Lake trout	Deep, exposed region	Keweenaw	49.40
		Western arm	18.56
	Shallow embayment	Nipigon Bay	65.43
		Whitefish Bay	18.34

Table 3.2. The von Bertalanffy growth equation parameters for each fish species, where L∞ = asymptotic length (mm), k = Brody growth coefficient (per year), and sample sizes (n), t_0 was assumed to be zero for all curves.

SPC	Location	Size range (mm)	n	L ∞	k	p
LT	Keweenaw	486-897	33	721.05	0.2573169	< 0.0001
	Western Arm	216-631	23	507.78	0.2351502	< 0.0001
	Nipigon Bay	184-836	1001	551.87	0.2929751	< 0.0001
	Whitefish Bay	263-745	37	563.04	0.243958	< 0.0001
WF	Keweenaw	111-701	33	592.42	0.2514266	< 0.0001
	Western Arm	206-488	20	424.81	0.3816562	< 0.0001
	Nipigon Bay	180-721	3370	467.30	0.2966474	< 0.0001
	Whitefish Bay	188-588	425	413.70	0.5340421	< 0.0001
RS	Keweenaw	51-163	11	143.90	0.834704	< 0.0001
	Western Arm	35-159	16	162.23	0.5064	< 0.0001
	Nipigon Bay	40-136	24	117.11	1.034173	< 0.0001
	Whitefish Bay	45-118	8	138.78	0.5307102	0.0259

LT= lake trout, WF = lake whitefish, RS = rainbow smelt

Table 3.3. Bootstrapping results (95% confidence intervals, 2000 iterations) from the growth curves for each species for asymptotic length (L∞) and the Brody growth coefficient (K). Small sample size in rainbow smelt would not allow an equation to be fit for 3 of the locations. Significant differences (Sig. diff.) represent non-overlapping 95% confidence intervals.

SPC	**Region**	**L∞**	**Lower CI**	**Upper CI**	**Sig. diff.**	**K**	**Lower CI**	**Upper CI**	**Sig. diff.**
RS	Keweenaw	---	---	---		---	---	---	
	Western Arm	163.42	137.42	192.24		0.51679	0.32709	0.73098	
	Nipigon	---	---	---		---	---	---	
	Whitefish Bay	---	---	---		---	---	---	
LT	Keweenaw	744.70	675.69	852.42	**a**	0.22991	0.14987	0.32514	**a**
	Western Arm	505.56	373.51	557.83	**b**	0.26247	0.15037	0.31128	**a**
	Nipigon	552.15	541.09	563.76	**b**	0.29273	0.27142	0.31565	**a**
	Whitefish Bay	566.38	516.18	634.33	**b**	0.25267	0.15065	0.38288	**a**
WF	Keweenaw	597.17	545.13	685.57	**a**	0.25118	0.17696	0.31032	**a**
	Western Arm	428.32	372.72	482.54	**bc**	0.38432	0.26761	0.53751	**ab**
	Nipigon	467.32	464.76	469.95	**b**	0.29668	0.28907	0.30442	**a**
	Whitefish Bay	413.76	395.42	432.62	**c**	0.53605	0.47806	0.60436	**b**

Table 3.4. Length-weight regressions for each species in each region; TLEN is the total length in millimetres, RWT is the round weight of fish in grams. Age represents the span of ages used to create the growth curve YOY represents young of year fish.

Species	Age	Region	Equation	p
Rainbow smelt	YOY-7	Keweenaw	$\log_{10}RWT = \log_{10}(TLEN) * 3.70245 - 6.75473$	<0.0001
	YOY-5	Western Arm	$\log_{10}RWT = \log_{10}(TLEN) * 2.9741 - 5.2685$	<0.0001
	YOY-4	Nipigon Bay	$\log_{10}RWT = \log_{10}(TLEN) * 3.15723 - 5.72576$	<0.0001
	1-4	Whitefish Bay	$\log_{10}RWT = \log_{10}(TLEN) * 3.48159 - 6.40125$	<0.0001
Lake trout	5-17	Keweenaw	$\log_{10}RWT = \log_{10}(TLEN)*3.1548-5.5059$	0.0025
	3-19	Western Arm	$\log_{10}RWT = \log_{10}(TLEN)*3.2052-5.6568$	<0.0001
	2-36	Nipigon Bay	$\log_{10}RWT = \log_{10}(TLEN)*3.26167-5.76191$	0.0293
	4-30	Whitefish Bay	$\log_{10}RWT = \log_{10}(TLEN)*3.1618-5.4061$	0.1596
Lake whitefish	YOY-15	Keweenaw	$\log_{10}RWT = \log_{10}(TLEN)*3.26292-5.76869$	0.1544
	1-18	Western Arm	$\log_{10}RWT = \log_{10}(TLEN)*3.30771-5.86180$	<0.0001
	1-41	Nipigon Bay	$\log_{10}RWT = \log_{10}(TLEN)*3.371839-6.038867$	0.5132
	YOY-21	Whitefish Bay	$\log_{10}RWT = \log_{10}(TLEN)*3.24623-5.76170$	0.0523

Table 3.5. Slope and intercept parameter estimates and associated R^2 values for the linear models used to relate wet weight (g) to mercury (mg/kg) for each species in each of the four regions. Whitefish from the Keweenaw Peninsula (highlighted row) modelled length (in millimetres) and mercury instead of weight.

SPC	Location	M (slope)	B (intercept)	df	F	p	R^2
RS	Keweenaw	0.008075	0.085715	1,10	13.6	0.004	0.576
	Western Arm	0.009540	0.063673	1,16	20.86	0.0003	0.566
	Nipigon	0.009460	0.086114	1,28	18.84	0.0001	0.402
	Whitefish Bay	0.007770	0.17553	1,15	4.36	0.05	0.225
LT	Keweenaw	4.096e-05	8.632e-03	1,29	6.675	0.0151	0.187
	Western Arm	7.866e-05	8.274e-02	1,15	22.7	0.00025	0.602
	Nipigon	1.872e-05	1.176e-01	1,6	5.9	0.05	0.496
	Whitefish Bay	4.965e-05	3.652e-02	1,7	7.707	0.027	0.524
WF	Keweenaw	0.00008034	0.01471	1,27	13.26	0.001	0.329
	Western Arm	0.00002340	0.02161	1,8	8.133	0.025	0.537
	Nipigon	0.0001894	-0.002312	1,5	12.58	0.016	0.716
	Whitefish Bay	0.00005738	0.02760	1,13	6.165	0.027	0.322

Table 3.6. Methylmercury of bulk zooplankton hauls and benthic invertebrates collected from the four study regions within Lake Superior. Number of individuals analyzed is n, where n >1 the value presented is the mean of both values.

Region	Species (Group)	MeHg Average (mg/kg)	n
Keweenaw	Bulk zooplankton	0.00115	2
	Amphipod	0.002	1
	Mysis	0.0093	2
	Oligochaetes	0.0066	1
Western Arm	Bulk zooplankton	0.0018	2
	Amphipod	0.0005	1
	Mysis	0.00305	2
Nipigon Bay	Bulk zooplankton	0.0016	2
	Amphipod	0.0015	1
	Oligochaetes	0.0137	1
Whitefish Bay	Bulk zooplankton	0.0035	2
	Amphipod	0.0026	1
	Mysis	0.00025	2
	Oligochaetes	0.0035	1

Table 3.7. Energy densities (J/g wet weight) of predator and prey species used in bioenergetics models

Predator-Prey Species	Energy Density (J/g)	Source
Rainbow smelt		This study
▪ Keweenaw	▪ 5,204.81	
▪ Western Arm	▪ 4,839.61	
▪ Nipigon Bay	▪ 5,383.44	
▪ Whitefish Bay	▪ 4,973.14	
Lake Trout	$ED = a + b * DW$	Hartman and Brandt 1995
▪ Keweenaw	▪ 13,069	
▪ Western Arm	▪ 12,435	
▪ Nipigon Bay	▪ 14,279	
▪ Whitefish Bay	▪ 13,351	
Lake Whitefish	$ED = 0.565 * W + 5233.7$	Rennie and Verdon 2008
Zooplankton	2,170	Fernandez et al. 2009
Coregonines	Average: 8,565	
▪ Cisco	▪ 6,500	▪ Pangle et al. 2004
▪ Bloater	▪ 9,879	▪ Rottiers and Tucker 1982
▪ Lake whitefish	▪ 9,317	▪ Madenjian et al. 2006
Diporeia spp.	4,386	Gardner et al 1985
Mysis diluviana	3,537	Gardner et al 1985
Oligochaeta	3,347	Eggleton and Schramm 2004

Table 3.8 Regional diet input parameters (energy density and methylmercury) for each species, using a combination of analyzed values where available and literature values. Methylmercury (MeHg) is in mg/kg and energy density (ED) is in J/g. Diet proportions were based on Gamble 2010 and Rennie et al. 2012

Species	Region	Prey inputs	Diet Proportions
Rainbow smelt	Keweenaw	Prey ED: 2170 Prey MeHg: 0.00115	100% bulk zooplankton
	Western Arm	Prey ED: 2170 Prey MeHg: 0.0018	
	Nipigon Bay	Prey ED: 2170 Prey MeHg: 0.0016	
	Whitefish Bay	Prey ED: 2170 Prey MeHg: 0.0035	
Lake trout	Keweenaw	Prey ED: 6885 Prey MeHg: 0.0418	50% rainbow smelt 50% coregonines
	Western Arm	Prey ED: 6702 Prey MeHg: 0.0410	
	Nipigon Bay	Prey ED: 6974 Prey MeHg: 0.0436	
	Whitefish Bay	Prey ED: 6769 Prey MeHg: 0.0409	
Lake whitefish	Keweenaw	Prey ED: 3685 Prey MeHg: 0.00597	33% Amphipod 33% *Mysis* 33% Oligochaetes
	Western Arm	Prey ED: 3962 Prey MeHg: 0.0022	50% Amphipod 50% Mysis
	Nipigon Bay	Prey ED: 3760 Prey MeHg: 0.0076	50% Amphipod 50% Oligochaetes
	Whitefish Bay	Prey ED: 3685 Prey MeHg: 0.00212	33% Amphipod 33% *Mysis* 33% Oligochaetes

Figures

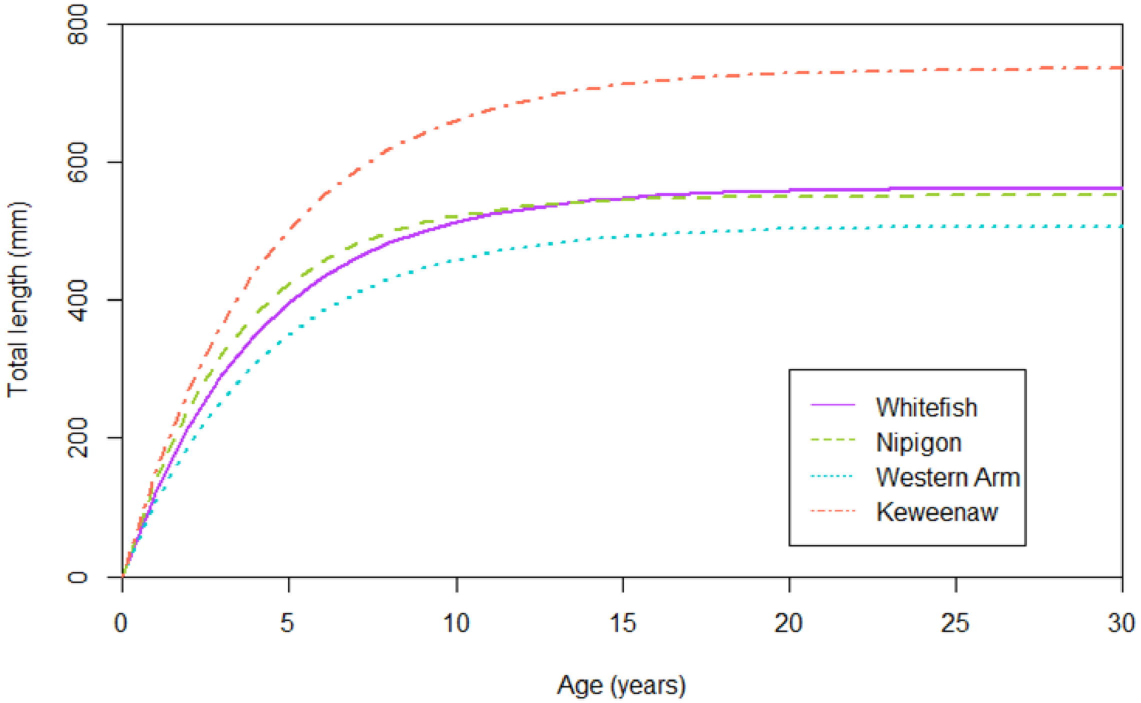

Figure 3.1. Von Bertalanffy growth curves of lake trout from the four regions of Lake Superior

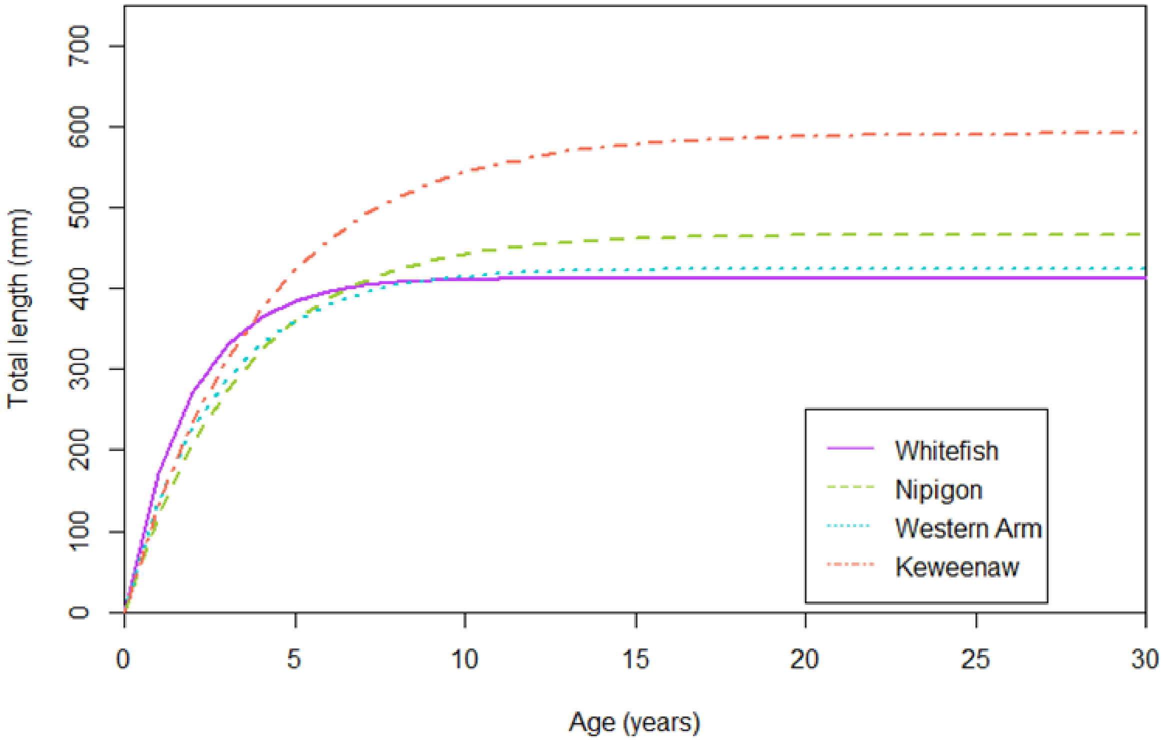

Figure 3.2. Von Bertalanffy growth curves of lake whitefish from the four regions of Lake Superior

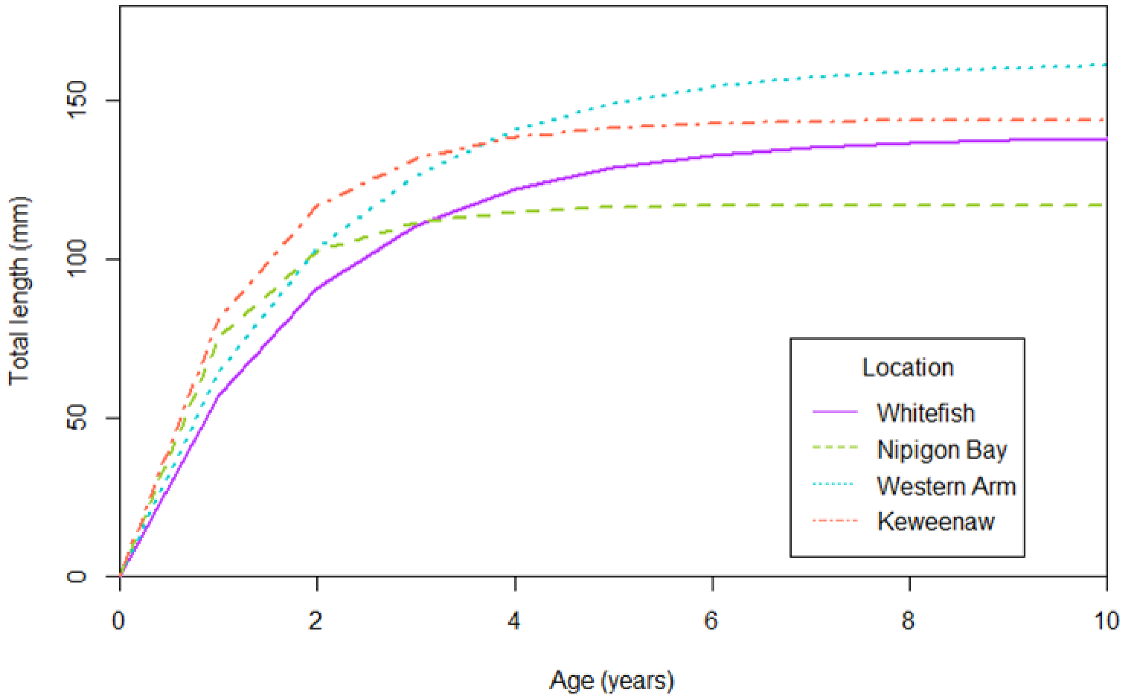

Figure 3.3. Vonbertalanffy growth curves of rainbow smelt from the four regions of Lake Superior

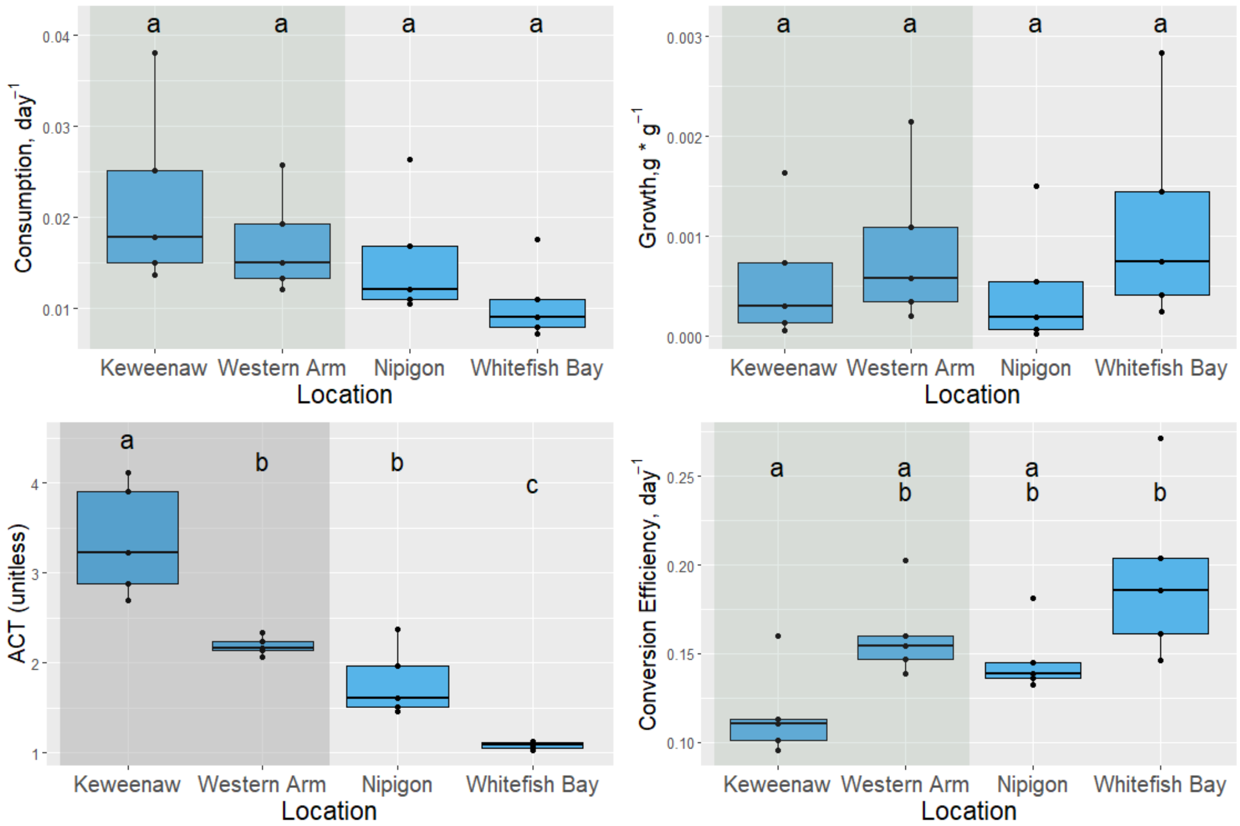

Figure 3.4. Boxplots show energetic output from modelling age 1-5 smelt from four different regions, moving from the most deep (shaded) to most shallow regions. Different letters above each box indicate statistically significant differences among sites (Tukey's honestly significant difference (HSD) test).

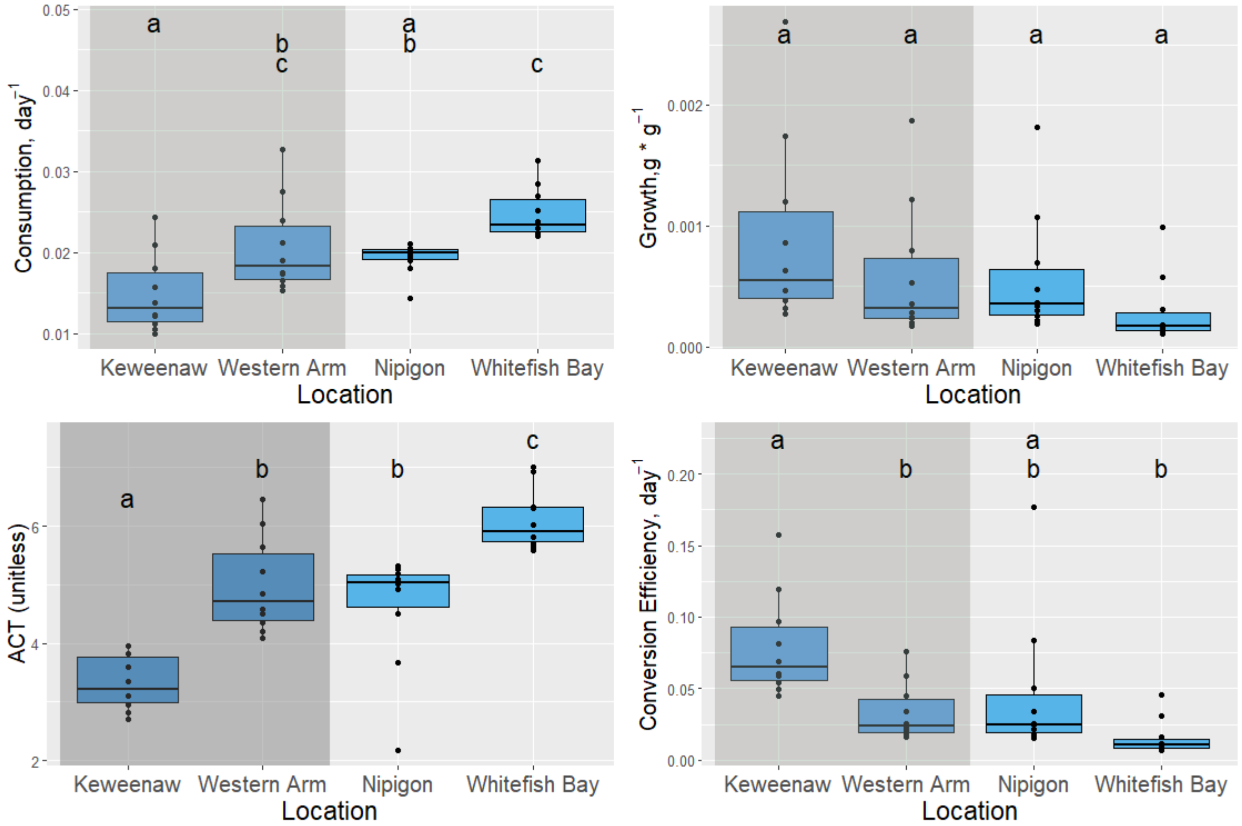

Figure 3.5. Boxplots showing lake whitefish energetics from 10 cohorts and from four geographically distinct regions; moving from most deep (shaded) to most shallow. Different letters above each box indicate statistically significant differences among sites (Tukey's honestly significant difference (HSD) test).

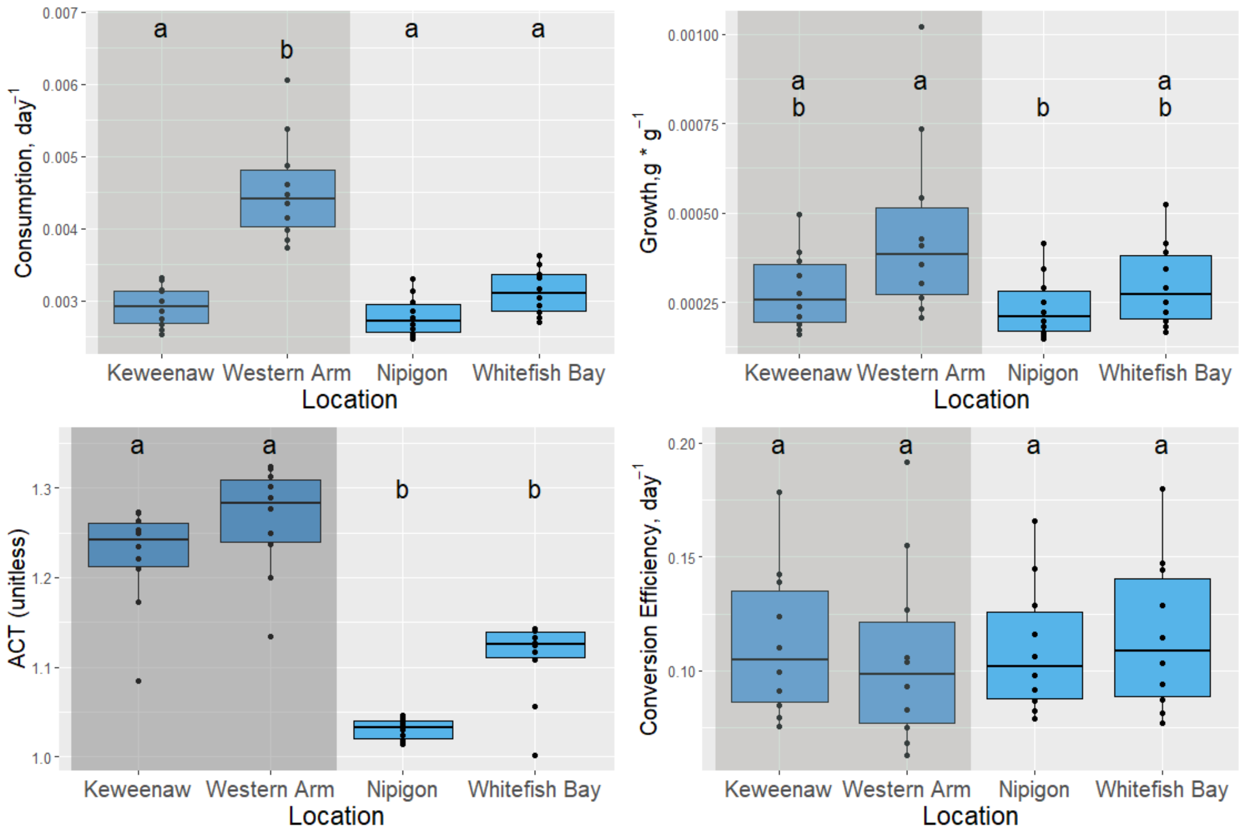

Figure 3.6. Boxplots show lake trout energetics from 10 age cohorts and from four geographically distinct regions; moving from most deep (shaded) to most shallow. Different letters above each box indicate statistically significant differences among sites (Tukey’s honestly significant difference (HSD) test).

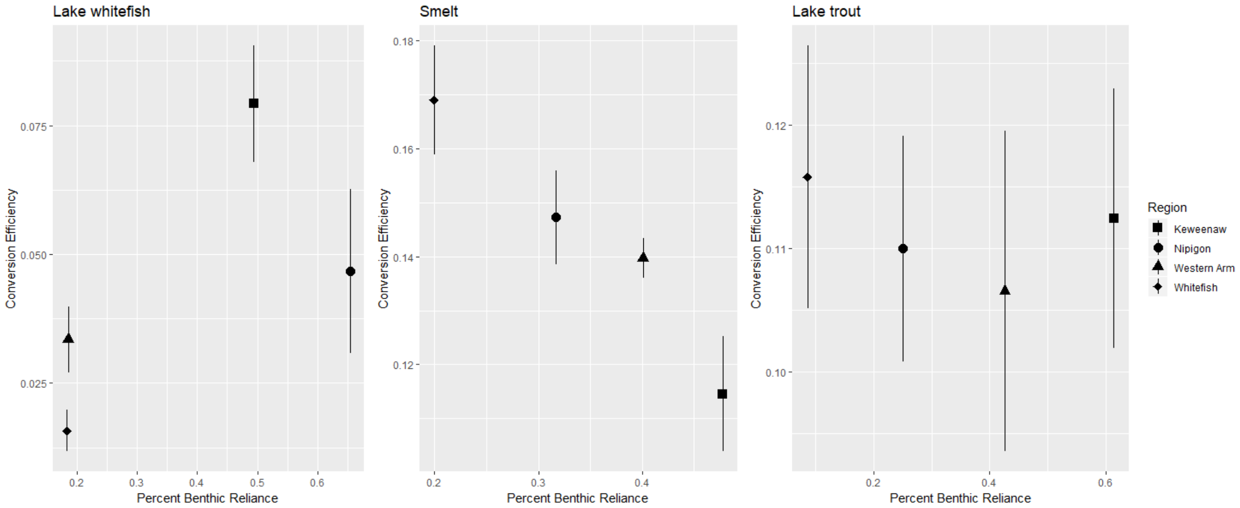

Figure 3.7. Mean conversion efficiency and standard error plotted against the regional average for percent benthic reliance to observe any correlations between the variables.

Chapter 4: Synthesis

In summary, this study calls attention to the spatial variability within large lake systems by examining resource use, habitat coupling, and how the degree of coupling observed in a region relates to the bioenergetics of fish. This was achieved by using stable isotopes analysis to determine the amount of benthic versus pelagic resources that were being used within a species both along a depth gradient and across four distinct regions, as well as using a combination of a mercury mass-balance model (MMBM) to estimate consumption rates and bioenergetics modelling. Lake Superior was chosen as a study site as it is of great economic importance being the largest freshwater lake by area in the world; as well, it is the least impacted of all the Laurentian Great Lakes due to environmental contamination and harmful invasive species. The results of this study should broadly represent how healthy temperate large lake systems are structured.

Chapter two focused on how resource use varied spatially across depth and between geographically distinct regions. When examining within region differences of percent benthic reliance, there was variation within all species. Mobile species like lake trout, smelt, and herring showed the most among region variation in the deeper regions, and the variation was less within the shallower regions. Traditional benthic specialists, lake whitefish and sculpin spp., exhibited the same amount of variation with depth across all regions. When looking at the depth specific analysis, the shallow strata usually had a stronger pelagic reliance in general. The medium depth strata showed the highest amount of benthic reliance, and this is thought to be due to the benthic pelagic coupling occurring within that strata. Patterns within the deep depth strata were hard to decipher due to little to no sample size. Overall there is a large amount of pelagic reliance in Lake Superior as a whole and within all studied Lake Superior species.

Previous studies have often focused on the whole lake instead of considering specific regions or depths. These studies have suggested that the importance of the benthic pathway is highest in near shore species such as lake trout and lake whitefish (Sierszen et al. 2014). Based on the stable isotope analysis conducted on common Lake Superior fish, traditional offshore planktivores may utilize the benthic energy pathway just as much as the typical nearshore species. As well, even though there are lake-wide similarities in how the nearshore and offshore fish communities are structured (Gamble et al. 2011b), there are regional differences that must be considered when conducting a whole lake study.

Chapter three focused on modelling energetics of three common Lake Superior fish species from different trophic guilds to observe spatial differences across the lake. A contaminant mass balance model was combined with a bioenergetics model to obtain estimates for consumption, growth, activity and conversion efficiency. Lake whitefish and rainbow smelt had opposite patterns among regions. Lake trout did not show any consistent patterns across the study regions. Within species bioenergetics variation is consistent follows a morphometric pattern and it is assumed that species belonging to the same trophic guild would follow the same pattern based on resource use. This study shows that accounting for spatial variation when conducting studies on fish bioenergetics in large lake systems is important for more specialized species; but if the study species is an extremely mobile generalist feeder regional variation will not account for much of the variability observed.

This study was able to show that overall Lake Superior is characterized by ecosystems that have a majority reliance on the pelagic energy pathway, but some specialization is present regionally. Habitat heterogeneity and the ability to use multiple energy pathways is what encourages ecosystem health and stability (Rooney and McCann 2012), and as lake size increases there will be more specialization due to an increase in habitat heterogeneity and prey refugia which allows individuals within a population to use a separate resource and reduce trophic omnivory (Post et al. 2000b). The high amount of resource specialization that was observed within Chapter Two agrees with this previous literature, showing that in the deeper regions there is a higher degree of specialization. Based on that alone it would be suggested that the deeper regions be more stable due to a mixed use of resources across species which would facilitate a more stable and resilient fish populations than the shallower regions.

Chapter Three also found that the benthivorous whitefish were better suited to living in the more open deeper regions of Lake Superior, whereas rainbow smelt were more suited to living in the shallower more enclosed regions. This seemed counterintuitive as the shallower regions would have a relatively larger and more productive littoral area which may contribute to higher primary production and overall benthic energy throughout the food web. When comparing the bioenergetics in Chapter Three to the percent benthic reliance in Chapter Two the data suggests that lake whitefish have a higher benthic reliance in Keweenaw and Nipigon Bay. This is most likely due to alternate benthic inputs from wind and wave action in Keweenaw, as well as inputs from the Nipigon River. Also, because Lake Superior is extremely large and deep even the ‘shallow’ regions (0-30m depth) aren’t shallow relative to most of the lakes in the world, and different ecological patterns may exist. Lake whitefish may exhibit a higher benthic reliance in the deeper/more exposed regions due to a larger prey population. Another, less likely explanation is that there is a more complex prey community structure for lake whitefish in the deeper more exposed regions. This is unlikely as deeper regions generally have less complex community structures, More cross-basin studies need to be conducted to understand this phenomenon better.

Although the main focus of this study was spatial variability, body size also had an impact on the resource use within fish species. There are a variety of reasons that resource use could vary with fish size. Firstly, there could be a shift towards a larger prey size with growth based solely on gape limitations. Lake trout are able to consume both invertebrates and fish (Gamble et al. 2011b), some of the variation in prey species may be due to the difference between juveniles and adults, where adults are not gape limited and have a mainly piscivorous diet. It has also been observed that nonpiscivorous lake trout do not grow as large as piscivorous lake trout (Pazzia et al. 2002), so regional resource availability may restrict the overall growth of fish. As well, a larger body size allows for an increase in the distance moved (McMeans et al. 2016). Species able to move a greater distance may be able to opportunistically forage on a more energy rich prey, find a more prey rich community to forage upon, or move to an area where there is less competition for resources therefore have to use less energy,.

Regions that are healthier and more resilient would be expected to have fish populations that are better able to convert resources into energy, which I measured using conversion efficiency (Chapter 3). With that assumption only, conversion efficiency would be expected to be the highest in Keweenaw and western arm, but that does not take into account the biological differences within species and trophic guilds. Lake trout, lake whitefish and rainbow smelt all use different resources, so resource availability within a region would have a large effect on the bioenergetics of each species regionally. More benthic resources in a region would be positive for the lake whitefish, but may not have the same effect for the rainbow smelt or lake trout. This idea was tested when comparing the results of the percent benthic reliance within a species (Chapter 2) to the conversion efficiency estimates (Chapter 3).

This study will help contribute to the overall understanding and protection of the Lake Superior fish community by providing regionally explicit data that has not been available previously. In this study, gross conversion efficiency was used as a proxy for trophic transfer efficiency. At the scale of individual based modelling, gross conversion efficiency represents the proportion of energy consumed that is converted into growth. This can be related to trophic transfer efficiency as both represent amounts of energy that are required to permit growth and production at the next trophic level, but at different scales (conversion efficiency at the individual level and trophic transfer efficiency at the population or trophic level). Though using conversion efficiency as a proxy for trophic transfer efficiency is theoretically sound, using these data along with regional population estimates it will be possible to confirm the relationship. Not only will this study then be able to fill in a knowledge gap within our understanding of energy pathways within large lake systems, but this study will be providing the first step in a greater understanding of lake-wide resource use and potentially help to create an easier method to estimate trophic transfer efficiency.

This study observed large size differences in the lake trout within the four study regions, but there were no obvious bioenergetics trends to explain this (Figure 3.1). The bioenergetics model output would suggest that lake trout in the deeper regions should be smaller as they have a higher activity rate, but since they are also consuming more in the same regions this is not necessarily the case (Figure 3.6). The length at age data does not suggest that rainbow smelt or coregonines grow significantly larger in any of the study regions, which might provide an increased energy input, as theoretical models of fish growth suggest that foraging costs increase when the size of a predator increases relative to its prey, because it must find and consume more prey to satisfy its energy demands (i.e., decreased growth efficiency, Kerr 1971). Previous studies have observed that fish are able to grow to a larger size in larger lakes due to a more complex prey fish population (Shuter et al. 2015). A similar effect could be occurring in the Keweenaw Peninsula region, being a much larger area than the other three regions, and experiencing a constant influx of energy due to the extensive wave and current action that the area receives, creating a region with a high amount of pelagic prey biomass.

Future studies can build off of the other knowledge gaps in energy and nutrient flow as described in Ives et al. (2018). Overall this study calls attention to the lack of understanding in large lake food webs. In order to better protect the health and sustainability of our resources we need to have a more complete understanding of the importance of energy pathways and resources to whole ecosystem function.

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Appendix A

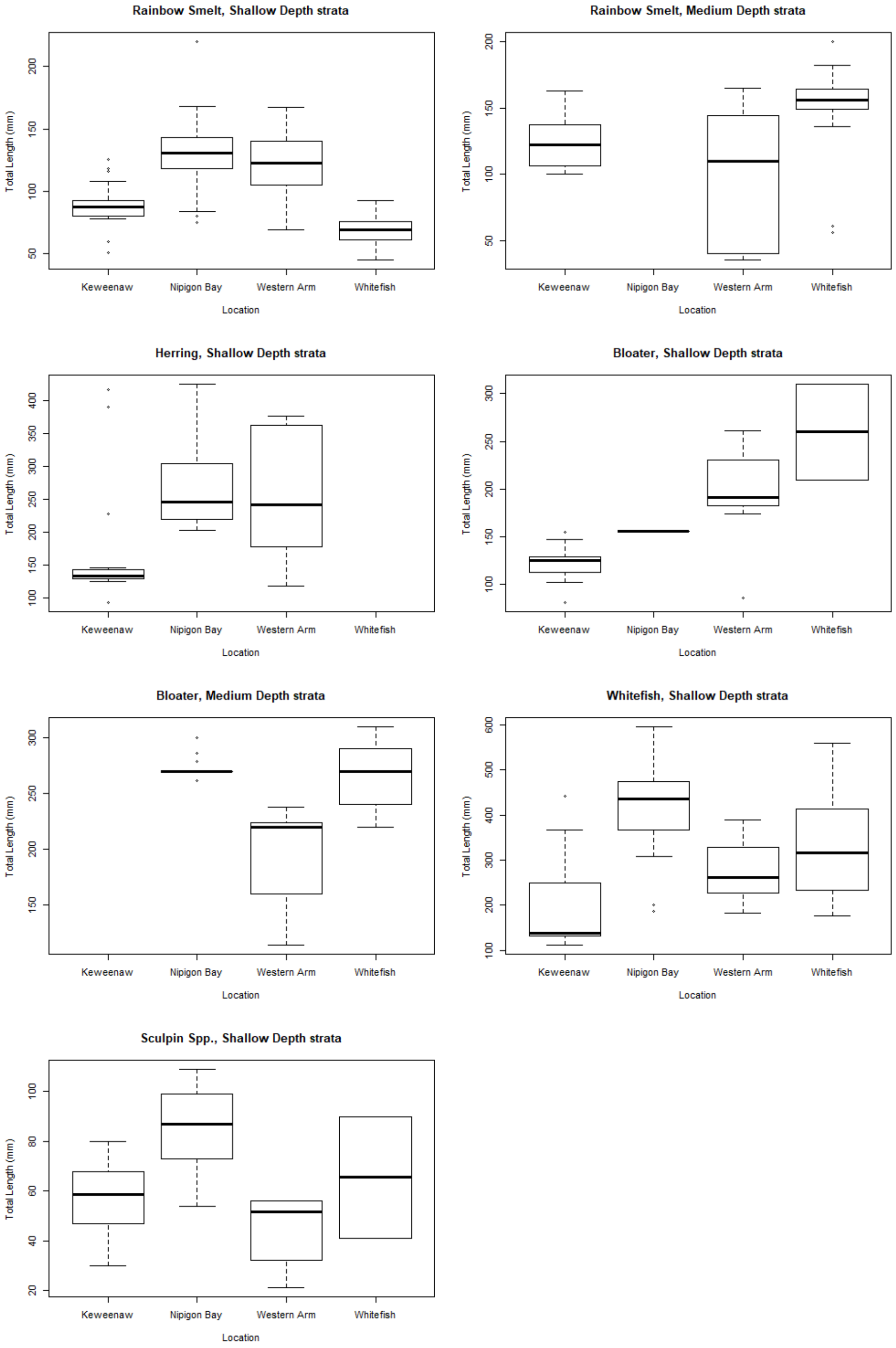

Figure A1. Relationship between fish size and location, within each depth strata where a significant relationship with δ^{13}C was observed

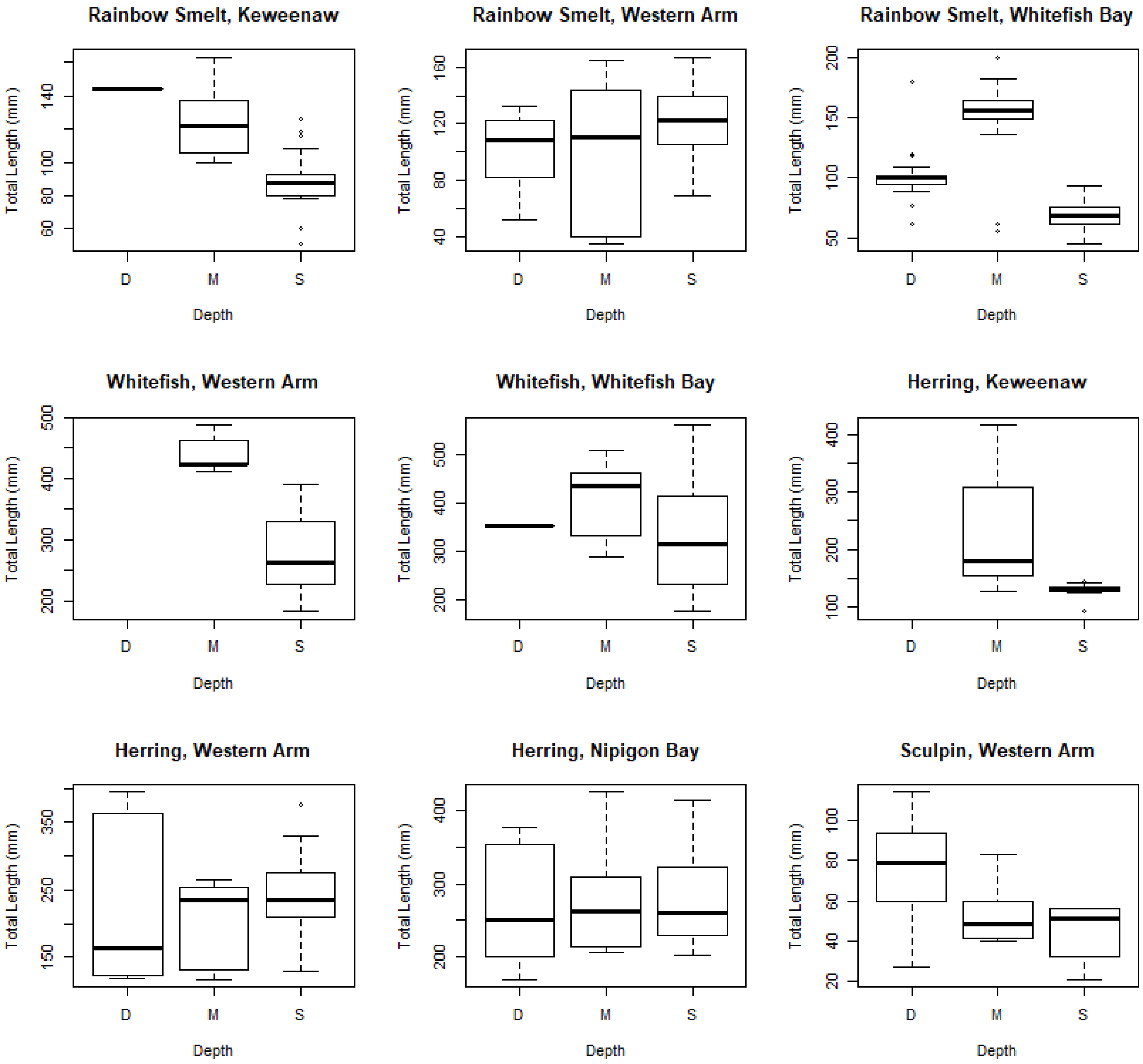

Figure A2. Relationship between fish size and depth, within each region where a significant relationship with $\delta^{13}C$ was observed

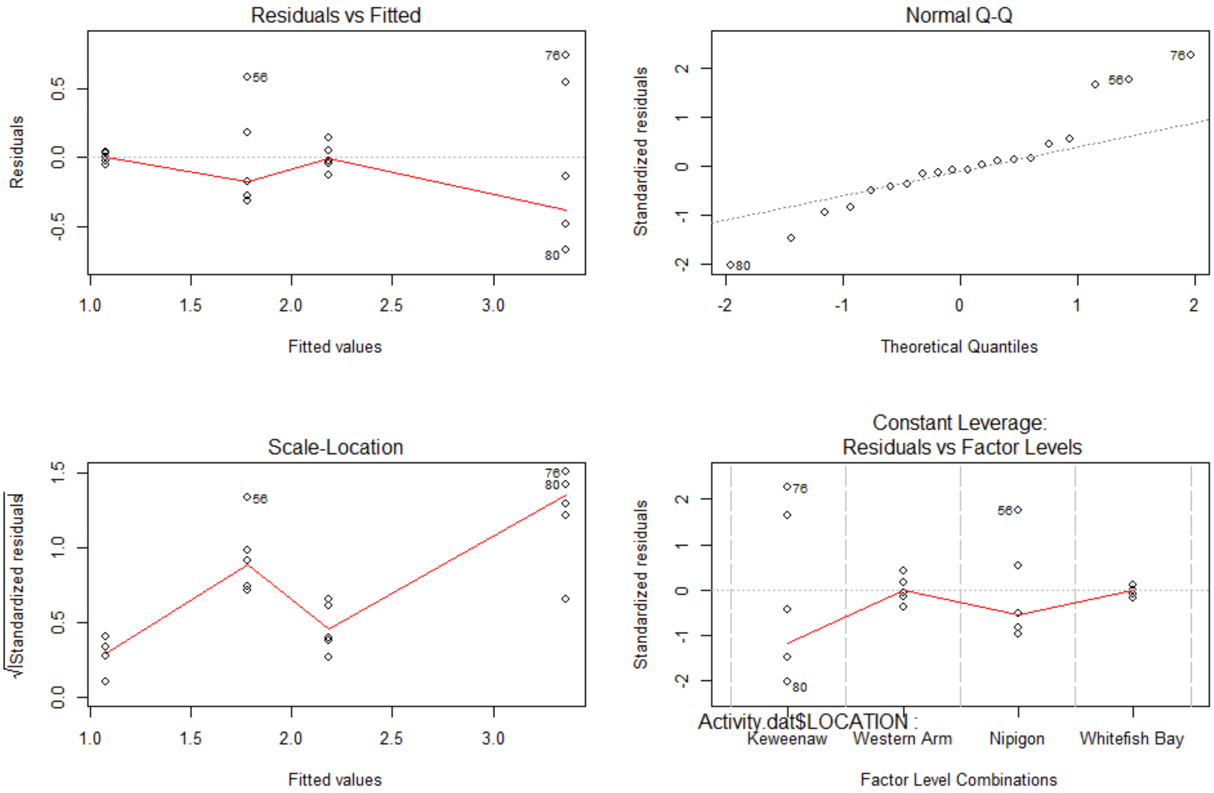

Figure A3. Diagnostic residual plots for the activity rates within rainbow smelt populations across Lake Superior; plots show some deviation from normality and homogeneity

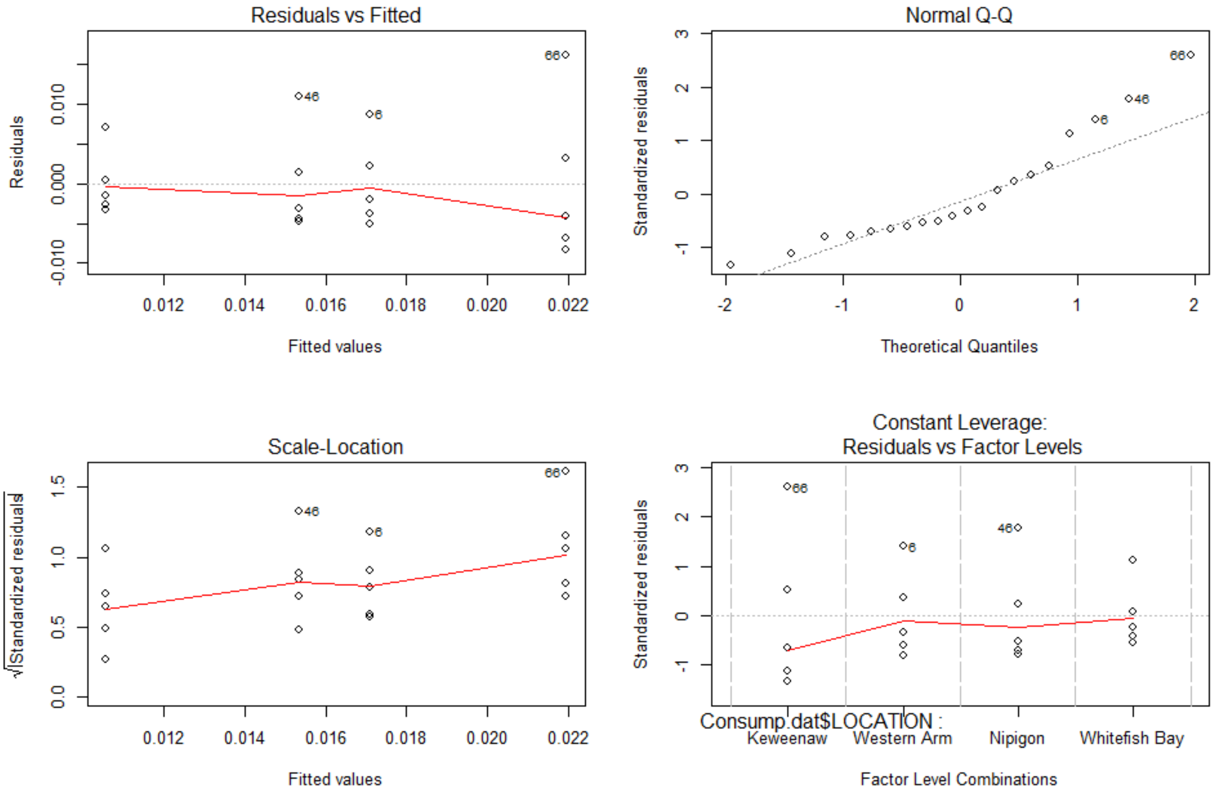

Figure A4. Diagnostic residual plots for the consumption rates within rainbow smelt populations across Lake Superior; plots show some deviation from normality and homogeneity

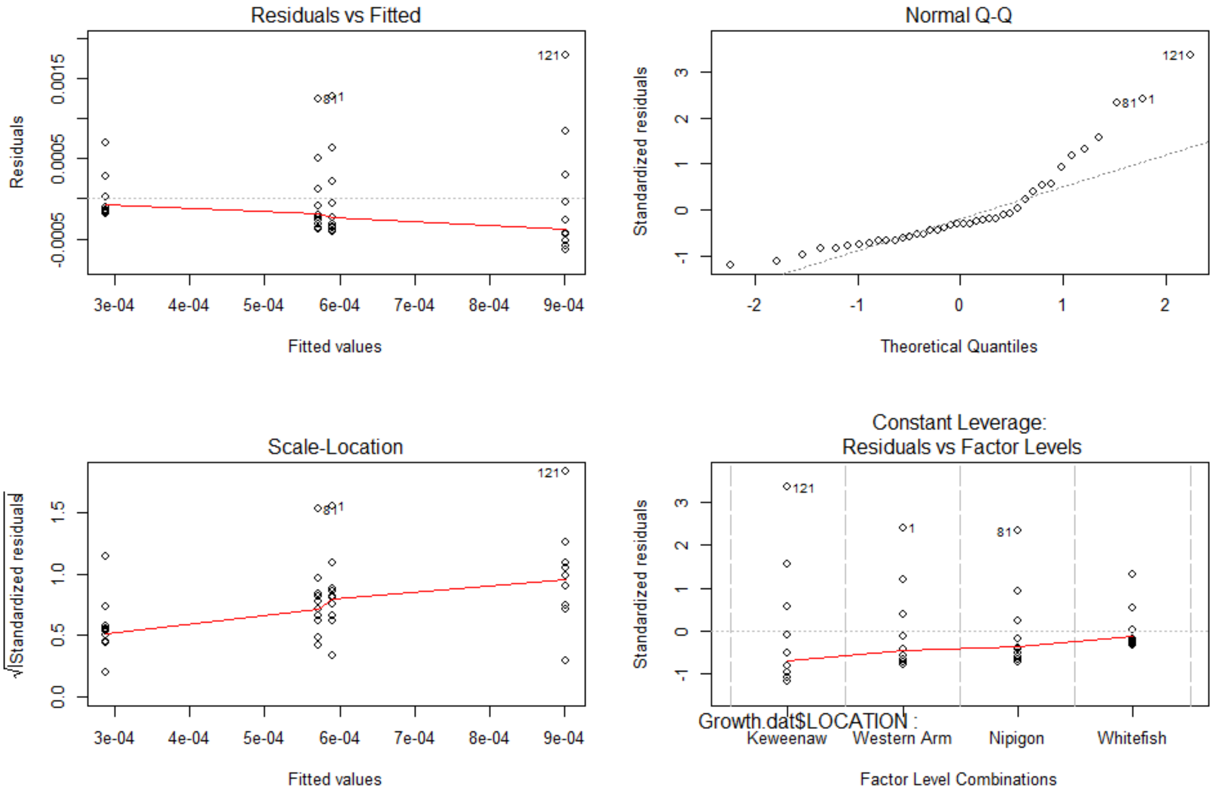

Figure A5. Diagnostic residual plots for the growth rates within lake whitefish populations across Lake Superior; plots show some deviation from normality and homogeneity

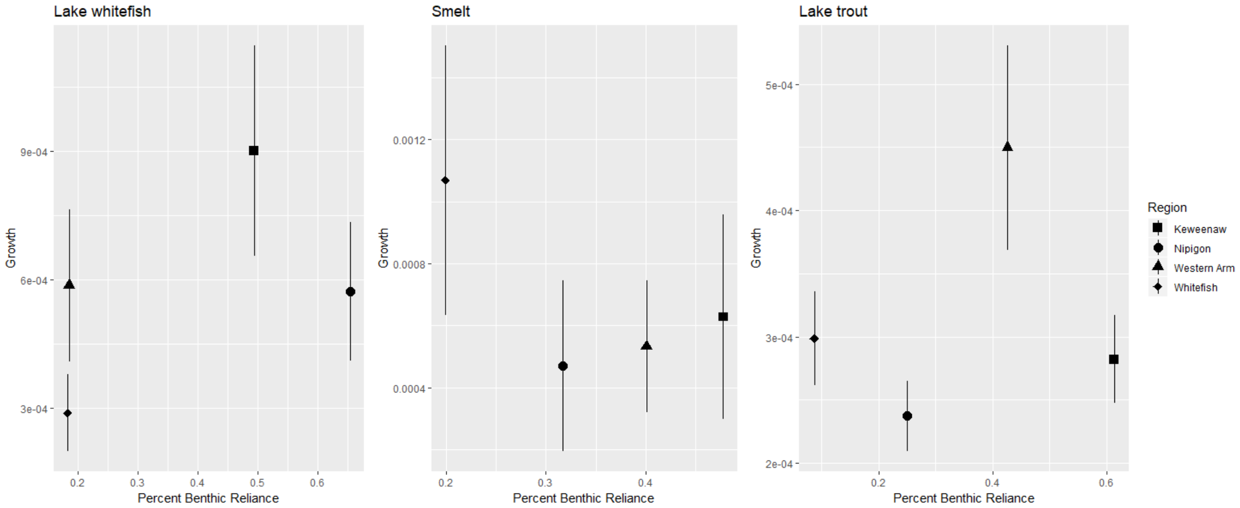

Figure A4. Comparisons of growth (with standard error) and mean percent benthic reliance within four Lake Superior regions.

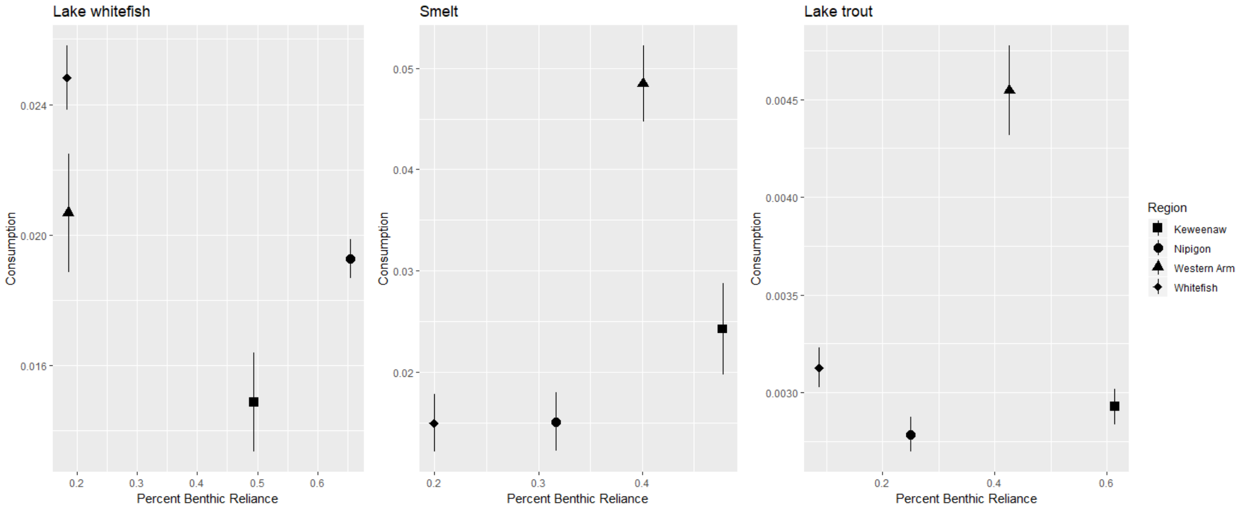

Figure A5. Comparisons of consumption (with standard error) and mean percent benthic reliance within four Lake Superior regions.

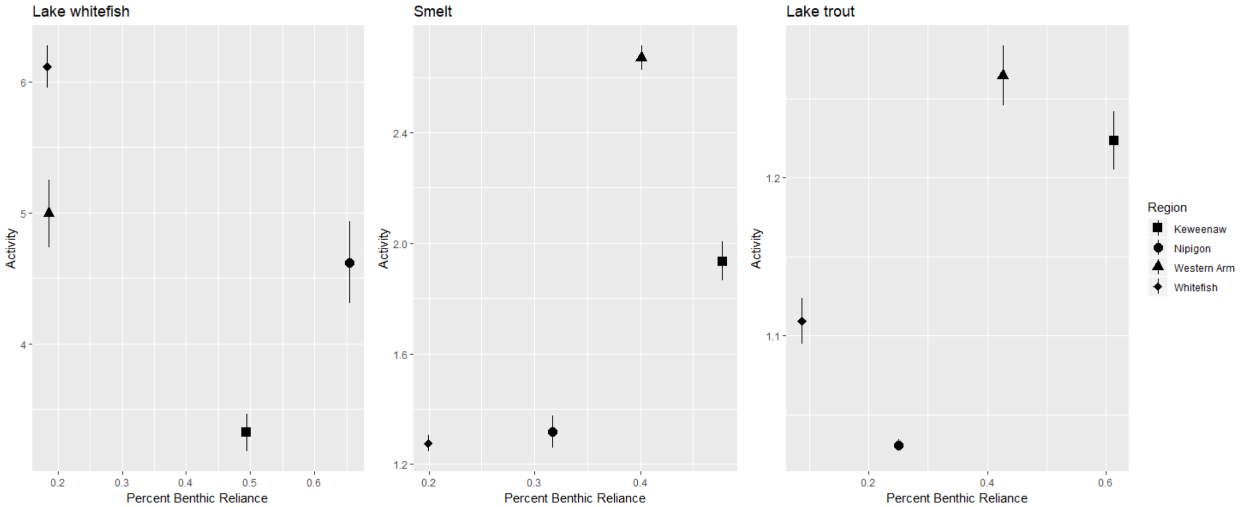

Figure A6. Comparisons of activity (with standard error) and mean percent benthic reliance within four Lake Superior regions.

Table A9. Bioenergetic inputs for age cohorts of rainbow smelt (RS), lake trout (LT), and lake whitefish (WF) for each region. Average prey MeHg and prey ED were averaged for each region by using a combination of analyzed samples and literature values (see Chapter 3, Methods)

SPC	Location	Age	Sex	Maturity	W_0	W_t	Hg_0	Hg_t	$MeHg_{Prey}$	ED_{Prey}
RS	Keweenaw	1	1	1	2.0902	7.9397	0.0240	0.0335	0.00115	2170
		2	1	1	7.9397	12.539	0.0335	0.0409	0.00115	2170
		3	1	2	12.539	15.042	0.0409	0.0449	0.00115	2170
		4	1	2	15.042	16.234	0.0449	0.0468	0.00115	2170
		5	1	2	16.234	16.772	0.0468	0.0477	0.00115	2170
	Western Arm	1	1	1	1.2958	5.2694	0.0193	0.0258	0.0018	2170
		2	1	1	5.2694	9.6739	0.0258	0.0330	0.0018	2170
		3	1	2	9.6739	13.242	0.0330	0.0389	0.0018	2170
		4	1	2	13.242	15.765	0.0389	0.0430	0.0018	2170
		5	1	2	15.765	17.429	0.0430	0.0457	0.0018	2170
	Nipigon Bay	1	1	1	1.5956	4.1689	0.0261	0.0309	0.0018	2170
		2	1	1	4.1689	5.5241	0.0397	0.0341	0.0016	2170
		3	1	2	5.5241	6.0704	0.0341	0.0354	0.0016	2170
		4	1	2	6.0704	6.2732	0.0354	0.0358	0.0016	2170
		5	1	2	6.2732	6.3464	0.0358	0.0360	0.0016	2170
	Whitefish Bay	1	1	1	0.5200	2.6028	0.0135	0.0201	$0.0028^{\dagger}$	2170
		2	1	1	2.6028	5.1692	0.0201	0.0283	0.0035	2170
		3	1	2	5.1692	7.3228	0.0283	0.0351	0.0035	2170
		4	1	2	7.3228	8.8523	0.0351	0.0400	0.0035	2170
		5	1	2	8.8523	9.8513	0.0400	0.0432	0.0035	2170
LT	Keweenaw	6	1	1	1518.0	1833.1	0.071	0.084	0.041806	6885
		7	1	1	1833.1	2105.3	0.084	0.095	0.041806	6885
		8	1	2	2105.3	2333.7	0.095	0.104	0.041806	6885
		9	1	2	2333.7	2521.6	0.104	0.112	0.041806	6885
		10	1	2	2521.6	2673.6	0.112	0.118	0.041806	6885
		11	1	2	2673.6	2795.4	0.118	0.123	0.041806	6885
		12	1	2	2795.4	2892.2	0.123	0.127	0.041806	6885
		13	1	2	2892.2	2968.5	0.127	0.130	0.041806	6885
		14	1	2	2968.5	3028.4	0.130	0.133	0.041806	6885
		15	1	2	3028.4	3075.4	0.133	0.135	0.041806	6885
	Western Arm	4	1	1	212.1	317.5	0.099	0.108	0.040997	6702
		5	1	1	317.5	422.9	0.108	0.116	0.040997	6702
		6	1	1	422.9	521.5	0.116	0.124	0.040997	6702
		7	1	1	521.5	609.9	0.124	0.131	0.040997	6702
		8	1	2	609.9	686.7	0.131	0.137	0.040997	6702
		9	1	2	686.7	751.8	0.137	0.142	0.040997	6702
		10	1	2	751.8	806.3	0.142	0.146	0.040997	6702
		11	1	2	806.3	851.2	0.146	0.150	0.040997	6702
		12	1	2	851.2	887.9	0.150	0.153	0.040997	6702
		13	1	2	887.9	917.7	0.153	0.155	0.040997	6702
	Nipigon Bay	8	1	2	1202.8	1344.5	0.100	0.107	0.04359	6974
		9	1	2	1344.5	1463.1	0.107	0.113	0.04359	6974
		10	1	2	1463.1	1561.0	0.113	0.117	0.04359	6974
		11	1	2	1561.0	1640.7	0.117	0.121	0.04359	6974
		12	1	2	1640.7	1705.0	0.121	0.124	0.043595	6974
		13	1	2	1705.0	1756.6	0.124	0.127	0.043595	6974

		14	1	2	1756.6	1797.8	0.127	0.129	0.043595	6974
		15	1	2	1797.8	1830.5	0.129	0.130	0.043595	6974
		16	1	2	1830.5	1856.5	0.130	0.132	0.043595	6974
		17	1	2	1856.5	1876.9	0.132	0.133	0.043595	6974
	Whitefish Bay	6	1	1	849.6	1037.3	0.083	0.092	0.040928	6769
		7	1	1	1037.3	1202.8	0.092	0.100	0.040928	6769
		8	1	2	1202.8	1344.5	0.100	0.107	0.040928	6769
		9	1	2	1344.5	1463.1	0.107	0.113	0.040928	6769
		10	1	2	1463.1	1561.0	0.113	0.117	0.040928	6769
		11	1	2	1561.0	1640.7	0.117	0.121	0.040928	6769
		12	1	2	1640.7	1705.0	0.121	0.124	0.040928	6769
		13	1	2	1705.0	1756.6	0.124	0.127	0.040928	6769
		14	1	2	1756.6	1797.8	0.127	0.129	0.040928	6769
		15	1	2	1797.8	1830.5	0.129	0.130	0.040928	6769
WF	Keweenaw	1	1	1	14.0	91.8	0.0253	0.0335	0.00597	3685
		2	1	1	91.8	238.5	0.0335	0.0399	0.00597	3685
		3	1	1	238.5	429.4	0.0399	0.0449	0.00597	3685
		4	1	1	429.4	636.6	0.0449	0.0488	0.00597	3685
		5	1	1	636.6	839.2	0.0488	0.0518	0.00597	3685
		6	1	1	839.2	1024.8	0.0518	0.0541	0.00597	3685
		7	1	2	1024.8	1187.5	0.0541	0.0559	0.00597	3685
		8	1	2	1187.5	1325.8	0.0559	0.0574	0.00597	3685
		9	1	2	1325.8	1440.8	0.0574	0.0585	0.00597	3685
		10	1	2	1440.8	1534.8	0.0585	0.0593	0.00597	3685
	Western Arm	1	1	1	15.2	85.1	0.0220	0.0236	0.0022	3961.5
		2	1	1	85.1	191.1	0.0236	0.0261	0.0022	3961.5
		3	1	1	191.1	301.7	0.0261	0.0287	0.0022	3961.5
		4	1	1	301.7	398.9	0.0287	0.0309	0.0022	3961.5
		5	1	1	398.9	476.6	0.0309	0.0328	0.0022	3961.5
		6	1	1	476.6	535.3	0.0328	0.0341	0.0022	3961.5
		7	1	2	535.3	578.2	0.0341	0.0351	0.0022	3961.5
		8	1	2	578.2	608.8	0.0351	0.0359	0.0022	3961.5
		9	1	2	608.8	630.3	0.0359	0.0364	0.0022	3961.5
		10	1	2	630.3	645.3	0.0364	0.0367	0.0022	3961.5
	Nipigon Bay	2	1	1	61.0	154.3	0.0092	0.0269	0.0076	3760
		3	1	1	154.3	268.7	0.0269	0.0486	0.0076	3760
		4	1	1	268.7	385.2	0.0486	0.0707	0.0076	3760
		5	1	1	385.2	492.2	0.0707	0.0909	0.0076	3760
		6	1	1	492.2	584.0	0.0909	0.1083	0.0076	3760
		7	1	2	584.0	659.7	0.1083	0.1226	0.0076	3760
		8	1	2	659.7	720.3	0.1226	0.1341	0.0076	3760
		9	1	2	720.3	767.7	0.1341	0.1431	0.0076	3760
		10	1	2	767.7	804.4	0.1431	0.1500	0.0076	3760
		11	1	2	804.4	832.4	0.1500	0.1553	0.0076	3760
	Whitefish Bay	2	1	1	137.7	260.3	0.0355	0.0425	0.00280	3685
		3	1	1	260.3	359.3	0.0425	0.0482	0.00280	3685
		4	1	1	359.3	428.1	0.0482	0.0522	0.00212	3685
		5	1	1	428.1	472.3	0.0522	0.0547	0.00212	3685
		6	1	1	472.3	499.7	0.0547	0.0563	0.00212	3685
		7	1	2	499.7	516.2	0.0563	0.0572	0.00212	3685
		8	1	2	516.2	526.1	0.0572	0.0578	0.00212	3685
		9	1	2	526.1	532.0	0.0578	0.0581	0.00212	3685
		10	1	2	532.0	535.4	0.0581	0.0583	0.00212	3685

		11	1	2	535.4	537.4	0.0583	0.0584	0.00212	3685

[†] In one instance model did not converge and prey MeHg was adjusted from 0.0035 to 0.0028