Trophic disruption effects on the diet and condition of Lake Whitefish

by

Kelly-Anne M. Fagan

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Master of Science
in
Biology

Waterloo, Ontario, Canada, 2010

AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any

required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Recently, the growth and condition of Lake Whitefish (*Coregonus clupeaformis*), an important commercial fishery commodity, has declined in some areas of the Great Lakes. As Lake Whitefish are benthic feeders, historically the bulk of their diet was made up of the energy rich *Diporeia hoyi*, an amphipod whose abundances declined concurrently with reductions in Lake Whitefish growth and condition. Lake Whitefish populations from lakes Michigan, Erie and Superior have been used to determine whether there is a plausible link between the declines in Lake Whitefish condition and *Diporeia* abundance as indicated by stable isotope analysis, dietary and condition indices for Lake Whitefish.

The first study was Lake Michigan specific and tested the hypothesis that condition, in terms of relative weight, percent lipid and docosahexaenoic acid (DHA), improved as the proportion of high quality prey (e.g., *Diporeia*) in the diet increased. Samples of spawning whitefish from four regions (northwest, Naubinway, Elk Rapids and southeast) around Lake Michigan had distinct mean carbon and nitrogen isotope signatures. The signatures indicated Lake Whitefish may be using a variety of prey items, especially the Naubinway population where fish occupy the largest isotopic niche space. However, trophic niche width inferred from $\delta^{13}C$ stable isotope measures did not vary among regions. Relative weight was significantly higher in the southeast and lower for all northern regions. The mean measured lipid from Lake Whitefish dorsal skinless muscle biopsies was highest for northwest region fish. DHA was significantly different among studied regions, with higher mean values in Elk Rapids and the northwest. No linear relationships between stable isotope measures and condition metrics were found. These results suggest that Lake Whitefish are coping with declining *Diporeia* abundances by feeding on alternate prey. Results do not substantiate the hypothesis of a relationship between condition and prey use, although Lake Whitefish from Elk Rapids and the northwest had high quality prey and good condition.

The second study incorporated eight spawning populations around lakes Michigan, Erie and Superior to determine if there were differences in energy available to female Lake Whitefish. The hypotheses tested were three fold: (1) observed differences in growth and reproduction among populations were driven by energy availability, (2) populations with low energy reserves exhibit reproductive trade-offs and (3) high energy reserves are related to *Diporeia* consumption. Lake Whitefish from lakes Erie and Superior both displayed high growth and no trade-offs between egg size and number. Populations from Lake Michigan all had low investment in growth, significantly lower gonadosomatic index (GSI) and four of these populations displayed significant trade-offs between egg size and number. Growth and GSI tended to increase with mean total lipid stored in muscle and populations displaying reproductive trade-offs had significantly lower muscle lipid, however, these trends were not evident when using DHA as a measure of good nutrition. No relationship was evident between *Diporeia* consumption and populations with high muscle lipid stores. Overall, my results suggest that while changes in the availability of prey resources has had an effect on Lake Whitefish populations, the impact of declining abundances of *Diporeia* alone cannot explain the systemic changes in Lake Whitefish condition across the Great Lakes basin.

Acknowledgements

Many people contributed to the successful completion of this thesis through knowledge sharing, technical support, encouragement, friendship and helpful comments. This thesis would not have been possible without my supervisors: Drs Michael Power and Marten Koops. Thank you for your guidance, our insightful brainstorming sessions and for providing me with opportunities to network and share my project with others at conferences. I appreciate your confidence in my abilities during my graduate work.

Thank you to my committee members, Drs Trent Sutton and Bill Taylor, for insightful comments during the proposal stages of this project and this polished thesis.

Dr. Michael Arts shared lipid and fatty acid data and Dr. Trent Sutton and Andrew Muir shared aging and stomach content data on the Lake Whitefish samples. For that I am very grateful as all of the data played an important role in analyses. Thanks to Jocelyn Gerlofsma, Ashley Bedford and Lisa Ann Neville for their assistance and support in collecting prey organisms in the field and being patient during our adventures to find dry ice.

I would like to thank the University of Waterloo Stable Isotope Laboratory for running my samples. I would like to extend a special thank you to Lois Graham for always brightening my day with a smile and a kind word, even when I added 100 samples to an already high pile. Thanks to William Mark for being patient with my numerous "test" samples.

I will always remember and appreciate the ongoing support, knowledge and friendship of my lab mates. Thanks for being there for me and always providing encouragement and even a slight kick in

Table of Contents

List of Figures

List of Tables

Chapter 1

Background Information

1.1 Lake Whitefish: Ecology and Importance

The Lake Whitefish (*Coregonus clupeaformis*, Mitchell) is a cold-water coregonid species with a distribution extending across North America. Typically found in large rivers and cold freshwater lakes, the southernmost portion of the distribution includes the Laurentian Great Lakes (Scott & Crossman 1973). Lake Whitefish are known to migrate vertically with seasonal temperature changes, moving to deeper colder waters as shallow waters warm in the summer, and back to shallower waters as they cool in the fall (Hardy 1994; Cook et al. 2005). Depth preferences range from 15 to 50 m (Ihssen et al. 1981). Spawning occurs over stoney or sandy substrates in shallow waters of less than 5 m between November and December (Hart 1930; Taylor & Freeberg 1984). Adult Lake Whitefish tend to be benthic feeders, with diets composed of insect larvae, clams, snails, small fishes, fish eggs and zooplankton (Scott & Crossman 1973). Historically, diets of adult Lake Whitefish in the Laurentian Great Lakes have been largely composed of the deep-water amphipod *Diporeia hoyi* (Hardy 1994). Both species are native to the Great Lakes and the trophic connection between Lake Whitefish and *Diporeia* represent an important pathway in the benthic food web linking primary production to harvestable fish for human consumption (Nalepa et al. 2005).

Development of the Lake Whitefish fishery began in the 1700s by European settlers, and by the 1800s Lake Whitefish made up a substantial portion of the recreational and commercial Great Lakes fishery (Ebener 1997; Madenjian et al. 2002). Habitat loss and exploitation pressures decreased the abundance of Lake Whitefish in the early 1900s. Lake Whitefish populations were further suppressed from the 1930s to the 1940s by pollution, over-fishing, invasive species (e.g., Sea Lamprey *Petromyzon marinus*), and competition with Alewife (*Alosa pseudoharengus*), Rainbow

1

Smelt (*Osmerus mordax*) and White Perch (*Morone Americana*) (Ebener 1997). The recovery of

Lake Whitefish populations in the Great Lakes was noted in 1959 (Ebener 1997). By the 1980-90s,

above average harvests were reported in both Lake Michigan and Lake Huron (Nalepa et al. 2005).

The recovery was attributed to strong year classes, Sea Lamprey control and restrictions on

commercial harvest (Ebener 1997). Since 1985, the commercial harvest has increased every year,

exceeding 3 million kilograms per year in recent years (Ebener 1997; Madenjian et al. 2002). In

1995, the greatest commercial catch was reported at approximately 9 million kilograms, with most of

the harvest coming from lakes Huron and Michigan using gill nets and trap nets (Ebener 1997).

1.2 Study Region: the Laurentian Great Lakes

The Laurentian Great Lakes were formed by glacial retreat about 14,000 years BP, and hold one-fifth

of the world's fresh water (Fuller et al. 1995). The Great Lakes basin is heavily populated and

industrialized. The basin is also affected by key resource harvest activities, including forestry,

mining, agriculture, and commercial and recreational fishing. This thesis will focus on Lake

Whitefish populations in three of the Great Lakes: Erie, Michigan and Superior.

Lake Erie has always been the warmest and most productive lake as a result of the shallow

depths (19 m average) that dominate the lake (Fuller et al. 1995). The basin is mainly occupied by

agriculture and industry, and fed by watersheds draining fertile soils that provide the lake with

additional nutrients. The physical characteristics of Lake Erie, combined with increased nutrient

loading from anthropogenic sources, have made the lake very susceptible to eutrophication.

Lake Michigan is the second largest Great Lake with three key bathymetric features: southern

and northern basins and a shallow mid-lake sill (< 100 m) that separates them (Eadie & Robbins

2005). The southern basin of Lake Michigan has the greatest density of municipal and industrial

activities and the largest river input (Fuller et al. 1995). The northern basin is colder, sparsely

populated and less developed. The exception is the Fox River Valley that drains Green Bay and hosts the world's largest concentration of pulp and paper mills (Fuller et al. 1995).

Lake Superior is by far the largest of the Great Lakes, with the greatest surface area (82,100 m^2) and average depth (147 m) and the coldest temperatures (Fuller et al. 1995). Lake Superior also has the least developed, most forested and least populated watershed of the Great Lakes (Fuller et al. 1995). As a consequence, Lake Superior suffers least from anthropogenic impacts.

1.3 Ecosystem Changes

The Great Lakes are large and dynamic water bodies that host a variety of flora and fauna. First introduced in the late 1980s, Zebra (*Dreissena polymorpha*) and Quagga (*Dreissena bugensis*) Mussels have recently invaded and established themselves throughout the Great Lakes basin (Griffiths et al. 1991). Zebra and Quagga Mussels thrive on different substrates, including hard structures, soft silts, sand and mud (Dermott and Munawar 1993). Dreissenids are known to intercept organic matter before it can settle and be consumed by fauna in the deep-water habitats (Nalepa et al. 1998). The result is a shift of energy pathways, with organic matter being moved from the pelagic to the littoral zones of the food webs in the Great Lakes. A conceptual model of the phenomenon, the nearshore shunt, sought to explain the consequent implications of the dreissenid redirection of nutrient and energy flows for the longer-term development of the nearshore benthic community and lake ecosystem (Hecky et al. 2004). The impact of dreissenids on benthic assemblages has been found to vary by species (Dermott and Kerec 1997). Depending on feeding mode and habitat, dreissenids may have a negative impact on a species via competitive exclusion, a positive impact, as a result of the creation of complex habitat structure and increased detrital food sources (pseudofeces and feces), or no impact whatsoever (Dermott and Kerec 1997).

Recently, an important prey item in the Great Lakes food web, *Diporeia*, has declined in abundance (Nalepa et al. 1998; 2000). *Diporeia* are glacial marine relicts and prefer cold temperatures in deep-water lake habitats below the thermocline (Dadswell 1974). *Diporeia* have high lipid content and a high concentration of essential fatty acids that make them a richer energy source than most other prey (Gardner et al. 1985). Historically, a large portion of Lake Whitefish diets in the Great Lakes have been composed of *Diporeia* (Hardy 1994). For example, a population in Lake Michigan had a diet composed of 70% *Diporeia* before documented *Diporeia* abundance declines (Pothoven et al. 2001). Studies have suggested that the declines in *Diporeia* abundances that began in 1993 in Lake Michigan resulted from nutrient competition with zebra mussels (Nalepa et al. 1998; 2000). Similar abundance declines in *Diporeia* also occurred in Lake Erie after the establishment of dreissenids. While an overall inverse relationship between *Diporeia* and dreissenid numbers was observed in lakes Erie and Michigan (Dermott and Kerec 1997; Nalepa et al. 2009), the exact nature of the linkage between dreissenids and *Diporeia* is not known (Madenjian et al. 2002).

Although *Diporeia* were present throughout the eastern basin of Lake Erie in 1979, by 1993 the amphipod was detected at only two sites at low densities (Dermott & Kerec 1997). In Lake Michigan, *Diporeia* density declined from 5,365 m^{-2} in 1994/95 to 329 m^{-2} in 2005 (Nalepa et al. 2009). In contrast, densities of *Diporeia* in Lake Superior appear to be at historic levels (Scharold et al. 2004). Given the variation in relative *Diporeia* densities among the study lakes and the previously documented importance of *Diporeia* as a dietary item for Lake Whitefish (Hardy 1994), the contemporary diets of Lake Whitefish and other demersal feeding fishes in each of the study lakes might be expected to differ. Furthermore, the loss of *Diporeia* as a prey may be expected to have resulted in co-occurring fluctuations in Lake Whitefish population ecology, particularly as studies by Healey (1980), Mills et al. (1998) and Kratzer et al. (2007) have established that Lake Whitefish growth is dependent upon the amount of food available to each fish.

Lake Whitefish abundance has varied depending on location. Lake Whitefish density increases were reported in Lake Michigan between 1980-90 and 1996-2005 (Schneeberger et al. 2005; Kratzer et al. 2007; DeBruyne et al. 2008). In contrast, Lake Whitefish density at Whitefish Point, Lake Superior, declined from 1986-87 to 2003-05 (Kratzer et al. 2007). Nevertheless, Lake Whitefish densities in Lake Superior have fluctuated less over the past century than in the other Great Lakes (Nalepa et al. 2005).

1.4 Status of Lake Whitefish

The ability of Lake Whitefish to cope with ecosystem changes may vary by lake. The literature has reported declines in growth and condition of Lake Whitefish in Lake Michigan (Pothoven et al. 2001; Madenjian et al. 2002; Schneeberger et al. 2005; Pothoven and Nalepa 2006; Pothoven et al. 2006), but not for lakes Erie and Superior (Cook et al. 2005; Kratzer et al. 2007). Condition can be defined using length-based indices or lipid measurements, but in general, condition attempts to describe the surplus energy available to a fish. In Lake Michigan, between 1992-93 and 1998-99, the body condition of Lake Whitefish declined by approximately 27% and length and weight at age were significantly smaller (Pothoven et al. 2001; Madenjian et al. 2002).

Researchers have suggested that declines in the availability of energy rich *Diporeia* have resulted in reduced foraging efficiencies and a switch to lower quality prey (Pothoven et al. 2001; Pothoven et al. 2006; Pothoven and Nalepa 2006). For example, Pothoven et al. (2001) attributed observed declines in Lake Whitefish condition to the reduced consumption of high lipid content *Diporeia* and increased consumption of lower caloric value zebra mussels and sphaeriids. Dreissenid mussels now dominate in many Great Lakes food webs (Nalepa et al. 2005). The higher metabolic costs associated with ingesting mussels instead of *Diporeia* has reduced the capacity of the food web to support consumers at the upper trophic levels (Pothoven and Madenjian 2008). Undigested shell

material from mollusc ingestion does not increase, and may restrict, the energy budget available to an individual, but does fill the digestive tract. Ihssen et al. (1981) noted that Lake Whitefish populations eating smaller and lower energy content prey (e.g., zooplankton and small mollusks) exhibited slower growth than those feeding on larger bodied *Diporeia* and *Mysis*. Average energy content of *Diporeia*, 4,429 J/g, is more than twice that of zooplankton, 1,987 J/g (Lantry and Stewart 1993). Thus, the consequent effect of changes in prey use may include reduced body condition and growth rates in many Lake Whitefish.

1.5 Goal of study

Given the above, the goal of this thesis is to determine if declines of Lake Whitefish condition are related to decreases in the abundance of *Diporeia* by comparing the status of Lake Whitefish populations within and between lakes with varied *Diporeia* densities. The thesis is composed of two data chapters. Chapter two provides a regional comparison of Lake Whitefish within Lake Michigan to determine whether prey choices and proximity to *Diporeia* are reflected in fish condition. The main hypothesis is that Lake Whitefish would exhibit poorer condition in regions of low *Diporeia* abundance compared to regions where *Diporeia* were in high abundance. The third chapter looks at growth, reproduction, energy and diet in Lake Whitefish as a means of determining whether differences in food consumption limit population success in lakes Michigan, Erie and Superior. The hypothesis is that differences in growth and reproduction among populations are driven by energy and that high energy is related to *Diporeia* consumption as hypothesized in the literature (Hoyle et al. 1999; Pothoven et al. 2001; Mohr & Ebener 2005).

Chapter 2

Lake Whitefish feeding habits in a disrupted system

2.1 Introduction

Lake Whitefish (*Coregonus clupeaformis*) has a significant position in the Great Lakes fishery as both fillets and roe are prized for recreational and commercial harvest. An evolutionarily young species, Lake Whitefish in the Great Lakes have experienced fluctuations in population abundance due to pollution, over-fishing, predation by Sea Lamprey (*Petromyzon marinus*), and interspecific competition with Alewife (*Alosa pseudoharengus*), Rainbow Smelt (*Osmerus mordax*) and White Perch (*Morone Americana*) (Ebener 1997). More recently, and despite increasing overall abundance, localized declines in the growth and condition of Lake Whitefish have been reported and such changes pose potentially serious implications for local fisheries (Pothoven et al. 2001; Schneeberger et al. 2005; Pothoven and Nalepa 2006; Pothoven et al. 2006). One suggested cause of localized declines has been the simultaneous decline in the abundance of the amphipod *Diporeia hoyi* (Dermott and Kerec 1997; Nalepa et al. 1998; Nalepa et al. 2000; Nalepa et al. 2009).

Diporeia is a glacial marine-relict amphipod and, similar to Lake Whitefish, prefers cold temperatures in deep-water lake habitats below the thermocline (Dadswell 1974). *Diporeia* has high concentrations of docosahexaenoic acid (DHA; 22:6n-3); a fatty acid that occurs in high concentrations in membrane phospholipids and is known to have positive effects on teleost egg, neural and eye development (Bell and Dick 1993; Dalsgaard et al. 2003). DHA is one of the major components of ocular phospholipids in Herring (*Clupea harengus*) (Bell and Dick 1993), therefore low DHA concentrations in the diet of Lake Whitefish may reduce foraging success as a result of reduced visual acuity. However, this is speculation and must be verified with specific threshold

7

testing under controlled laboratory conditions. In regions of observed *Diporeia* declines, Lake Whitefish foraging efficiency appears to fall as fish switch to lower quality prey (with respect to DHA concentrations), primarily *Dreissena polymorpha*, *Dreissena bugensis*, *Bythotrephes longimanus* and benthic invertebrates (Pothoven et al. 2001; Pothoven et al. 2006; Pothoven and Nalepa 2006; Pothoven and Madenjian 2008). Other prey sources rich in DHA and high in caloric value, such as *Mysis relicta*, exist in Lake Michigan. Low relative abundance, patchy distributions and vertical migration cycles seem to preclude their wide use as a forage resource by Lake Whitefish (Bowers 1988; Levy 1991; Cavaletto and Gardner 1998; Pothoven et al. 2004).

To date, suggested links between observed changes in prey choices and Lake Whitefish growth and condition have not been investigated explicitly. Accordingly, the objectives of this study were to determine whether: [1] Lake Whitefish have different food habits among regions of Lake Michigan, and, [2] Lake Whitefish prey choices are reflected in measures of fish condition. My central hypothesis was that, within areas of Lake Michigan where *Diporeia* were in low abundance or absent, Lake Whitefish would exhibit poorer condition compared to areas where *Diporeia* were in high abundance.

2.2 Materials and Methods

Adult Lake Whitefish were sampled at six sites around Lake Michigan including Saugatuck, Ludington, Elk Rapids, Naubinway, Big Bay de Noc, and Bailey's Harbor (Fig. 2.1). All sites were known to have varying densities of *Diporeia* (Nalepa et al. 2009). Surveys in 2005 indicated the absence of *Diporeia* in the immediate vicinity of Naubinway and Big Bay de Noc, whereas in the Bailey's Harbor area *Diporeia* abundances were high, i.e., 1,340 m^{-2} mean density at a depth of 90 m (Nalepa et al. 2009). Elk Rapids, Ludington and Saugatuck sites also had *Diporeia* present (Nalepa et al. 2009). Fish were collected between October and December in 2004 and 2005 using either

8

commercial trap nets with 40 cm stretch mesh with a pot comprised of 11.4 cm stretch mesh or gill nets with varying mesh grading ranging from 4 to 15 cm. At each site, up to 30 pre-ovulatory females and 30 ripe males were collected. Each fish was measured for total weight (g) and total length (mm). Stomach content analysis was completed on a total of 630 Lake Whitefish. Stomachs were removed, separated, dried and weighed to determine the proportional contribution by dry weight of each prey item in all non-empty stomachs. Skinless dorsal muscle plugs were collected from each fish and stored frozen (-85°C) for stable isotope and lipid analyses.

Potential prey sources were collected between mid-June and early-July of 2005 and included Dreissenid mussels, zooplankton, *Mysis relicta* and *Diporeia*. Particulate organic matter (POM) and various benthic invertebrates were collected late-June 2007 to supplement the 2005 sampling. Benthic invertebrates were collected from rocky littoral zones, separated and held alive in filtered water overnight for gut clearance (Hamilton et al. 1992) prior to freezing (10°C). Benthos were identified to order or family under a dissecting microscope in the lab and separated into replicates for stable isotope analysis (SIA).

Tagging studies during 2003-2004 noted movement of Lake Whitefish away from areas of low *Diporeia* abundance. For example, individuals from the Big Bay de Noc site migrate south to the east side of the Door Peninsula, Wisconsin, between spawning seasons (Jones et al. 2008). Such regional migratory movements suggest foraging can occur over wide areas. Accordingly, for analysis Big Bay de Noc and Bailey's Harbor, data were grouped as a single northwest region. Similarly, due to geographical proximity, Ludington and Saugatuck were grouped as the southeast region. Of the Lake Whitefish tagged in the Naubinway management unit, 87% were recaptured in the same management unit, suggesting that the Naubinway population is sedentary (Jones et al. 2008). Therefore, Naubinway and Elk Rapids were kept as separate feeding populations.

2.2.1 Stable Isotope Analysis

Fish skinless dorsal muscle tissue and whole prey bodies were dried at 50°C for 48 h, pulverized to homogenate with a Retsch MM 301 ball mill grinder or by hand, and approximately 0.3 mg of homogenate was weighed out for SIA. Weighed material was inserted into combustible tin cups (SerCon 5 x 3.5 mm). Stable isotope values for carbon (δ^{13}C) and nitrogen (δ^{15}N) were determined using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer coupled to a Carlo Erba Elemental Analyzer at the Environmental Isotope Laboratory, University of Waterloo, Ontario. Resulting measurements are expressed using standard delta notation (δ) as parts per thousand differences with respect to the international reference standards, which were carbonate rock from the Peedee Belemnite formation δ^{13}C (Craig 1957) and nitrogen gas in the atmosphere for δ^{15}N (Mariotti 1983). Machine analytical precision, respectively, for δ^{13}C and δ^{15}N was 0.2 ‰ and 0.3 ‰ and was determined by repeat analysis (n = 25) of laboratory working standards cross-calibrated to International Atomic Energy Agency standards CH6 for δ^{13}C and N1 and N2 for δ^{15}N.

To compare among regions and account for possible anthropogenic variation in the stable isotope signatures at the base of regional food webs (e.g., Post 2002), nitrogen isotopic signatures were baseline corrected. With appropriate estimates of base δ^{15}N it is possible to determine if observed variation in an organism's isotopic signature occurs because of differences in food web structure and carbon flow or because of variation at the base of the food web (Vander Zanden and Rasmussen 1999; Post 2002). Here, baseline correction was accomplished by subtracting the average POM δ^{15}N signature for each region from all fish and prey δ^{15}N signatures in the respective region. The resulting corrected δ^{15}N measure, therefore, functions to scale fish and prey in terms of trophic distance from the base of the food web and facilitates region to region comparisons.

2.2.2 Lipid and DHA Analysis

Total lipid and DHA concentrations of individual adult Lake Whitefish samples were analyzed at The National Water Research Institute laboratories of Environment Canada, Burlington, Ontario. Skinless dorsal muscle samples were freeze-dried in preparation for total lipid and DHA analyses. Analysis involved three steps: gravimetric extraction, derivitization, and quantification on a HP6890 gas chromatograph following the methods described in Zellmer et al. (2004). Samples were extracted three times by grinding freeze-dried materials in a 2:1 chloroform:methanol solution (Bligh and Dyer, 1959). After centrifugation at 4,000 rpm to remove the majority of non-lipid material, the supernatant was transferred to acid-washed, 15-ml centrifuge tubes and rinsed with chloroform:methanol. This procedure was followed by a salt wash (0.9% aqueous NaCl solution) to remove lipophilic proteins before samples were evaporated to 2 ml. From this volume, 200 μL of sample extract was weighed on a Sartorious ME-5 microbalance to provide an accurate measure of total lipid content. DHA was identified and quantified with a reference to Supelco's 37 component FAME mix (#47885-U). An internal standard (5 α-cholestane; Sigma-Aldrich; #C8003) was added to the tissue before extraction to estimate percent recovery during the extraction procedure. The DHA concentrations are reported as μg FAME/mg dry mass of tissue.

2.2.3 Data Analysis

Polygons encompassing fish and prey item stable isotope signatures in $\delta^{13}C$ - $\delta^{15}N$ space were defined following Layman et al. (2007) and Cornwell et al. (2006). For Lake Whitefish, the resulting enclosed area measures the total amount of dietary niche space occupied by a given population in a given region. For prey items, the polygon represents the total amount of dietary niche space occupied by the regional forage base upon which the fish rely and, therefore, is a suitable proxy for the extent of trophic diversity within each regional forage base (Layman et al. 2007). Studies have shown that

11

convex hull polygons, as defined here, provide useful quantitative measures of ecological trait space suitable for use in testing for the effect of trait filtering, e.g., choice of dietary resources (Cornwell et al. 2006). To avoid biasing estimates of niche central tendency as a result of individual outliers using the geometric center, the mean of all signatures was used to characterize the centre of polygon defined niche space. The variance in $\delta^{13}C$ and baseline corrected $\delta^{15}N$ signatures were used as a second measure of niche width, with greater variation reflecting wider use of available prey resources (Bearhop et al. 2004). Bartlett's test for variance homogeneity (Bartlett 1937a; 1937b) was applied to determine whether there were significant differences in Lake Whitefish $\delta^{13}C$ and $\delta^{15}N$ variances among Lake Michigan study regions.

To estimate possible proportions of Lake Whitefish diets accounted for by each sampled prey type, we used ISOSOURCE, a computer program that uses information on prey and consumer stable isotope signatures to determine all possible combinations of varying prey source contributions (0 – 100%) that sum to the observed isotopic signature of the consumer (Phillips and Gregg 2001; Phillips and Gregg 2003). Total energy density of the suggested diet was then calculated as a weighted average using energy densities for each prey source and dietary proportions as determined by ISOSOURCE. A similar calculation was performed for comparative purposes using dietary proportions determined from stomach content analysis. Energy density values for each prey source were obtained from a compilation of sources (i.e., Cummins and Wuycheck 1971; Driver et al. 1974; Lantry and Stewart 1993; Eggleton and Schramm 2004; Storch 2005; Johnson et al. 2006; Madenjian et al. 2006) as reported in Rennie et al. (2009). When multiple energy density estimates were found, the average was used.

Stomach content data were used to compute the dietary niche overlap index proposed by Horn (1966) as a means of assessing short-term differences in feeding patterns among studied regions as follows:

$$(1) \qquad R_o = \frac{\sum_{i=1}^{n}(p_{ij} + p_{ik})\log(p_{ij} + p_{ik}) - \sum_{i=1}^{n} p_{ij}\log p_{ij} - \sum_{i=1}^{n} p_{ik}\log p_{ik}}{2\log 2},$$

where R_O is the index of dietary overlap between Lake Whitefish captured in regions j and k, p_{ij} is the proportion of prey resource i in the total of prey resources used by Lake Whitefish in region j, p_{ik} is the proportion of prey resource i in the total of prey resources used by Lake Whitefish in region k, and n is the total number of prey resource categories. The index varies between 0 and 1, indicating no dietary overlap and complete overlap, respectively. The index has been found in simulation studies to minimize bias even under conditions of a changing number of prey resource categories, sample size and resource evenness (Ricklefs and Lau 1980; Smith and Zaret 1982). Results were further compared to dietary data reported in the literature (Madenjian et al. 2006) for fish captured in the southeast region in the autumns of 1998-2001.

Relative weight (W_r), the ratio of observed individual fish weight (W) to the length specific standardized weight (W_s), was used as the quantitative measure of condition calculated using Rennie and Verdon's (2008) regression length percentile W_s equations estimated for mature male and female Lake Whitefish from 385 populations in North America. Specifically,

$$(2) \qquad W_r = \frac{weight}{W_s} \times 100 ,$$

where,

$$\text{Female: } \log W_s = 3.19\log L - 5.47$$

$$\text{Male: } \log W_s = 3.13\log L - 5.33$$

Statistical analyses were performed using JMP, Version 7 (SAS Institute Inc., Cary, NC). Maximal type I error rates were set at $\alpha = 0.05$. Normality and homogeneity of variance assumptions were checked using plots of regression residuals or with appropriate F-tests. Significant analysis of

13

variance (ANOVA) results for stable isotope signatures, mean total lipids, DHA and W_r were followed by multiple comparison of means using the conservative Tukey-Kramer post-hoc HSD test (Zar 1999) to determine if there were significant differences in Lake Whitefish condition metrics among study regions.

2.3 Results

Lake Whitefish carbon and baseline corrected nitrogen stable isotope signatures varied among regions in Lake Michigan (δ^{13}C ANOVA, $F_{3, 608} = 277.64$, $P < 0.001$; δ^{15}N ANOVA, $F_{3, 608} = 260.48$, $P < 0.001$). Individuals from Naubinway had the highest δ^{13}C signature (Tukey-Kramer post-hoc HSD test, $P < 0.05$; Table 2.1). Individuals from the southeast had the lowest δ^{13}C and δ^{15}N (Tukey-Kramer post hoc HSD test, $P < 0.05$). Elk Rapids had the highest δ^{15}N signatures (Tukey-Kramer post-hoc HSD test, $P < 0.05$). Proximity to the prey resource base also varied among regions; Lake Whitefish in the southeast were more closely associated with putative prey than Lake Whitefish from the other regions (Fig. 2.2). Available stable isotope signatures for randomly sampled mature male and female fish indicated the most restricted niche space in the southeast and the widest niche space for the Naubinway population. There was no significant difference in δ^{15}N variation among regions (Bartlett's test, $\chi^2 = 0.24$, df = 3, $P = 0.867$) indicating no variability in trophic niche width within the lake. Regional δ^{13}C variances were heterogeneous (Bartlett's test, $\chi^2 = 50.45$, df = 3, $P < 0.001$).

Stomach content analyses indicated that prior to spawning, Lake Whitefish in Lake Michigan fed differently depending on location (Table 2.2). Large proportions of the diet in the northwest consisted of dreissenid mussels and Isopoda, Naubinway Lake Whitefish fed mainly on Ephemeroptera and Gastropoda, while individuals from Elk Rapids ate high proportions of *Bythotrephes*. Lake Whitefish in the southeast had mainly dreissenid mussels and *Bythotrephes* in their stomachs. Dietary overlap between regions varied in the autumn, with high overlap (0.776)

14

between the southeast and northwest, minimum overlap (0.266) occurring between Elk Rapids and

Naubinway and between Elk Rapids and the northwest region of the lake (Table 2.3). Comparison of

literature reported autumn diets (Madenjian et al. 2006) with diets reported in this study indicated

moderately high overlap for the northwest and southeast, but poor overlap with Elk Rapids and

Naubinway.

In contrast to the short-term feeding comparison allowable with stomach content data,

ISOSOURCE analysis suggested a different feeding regime (Table 2.3) marked by high overlap

(0.902) between Naubinway and the northwest regions and low overlap between all other

combinations of regions. ISOSOURCE determined proportional contributions to diet suggest that

Diporeia are the main dietary item for individuals from Elk Rapids (Table 2.4). Both Naubinway and

the northwest region heavily relied on *Mysis relicta* and Chironomidae contributing to the observed

high diet overlap value predicted by ISOSOURCE. Diets in the southeast rely almost exclusively on

Isopoda.

Conversion of ISOSOURCE diets to caloric content (J/g) indicated that Lake Whitefish from

Naubinway have the highest apparent caloric intake (370,000 J/g), followed by fish from Elk Rapids

(365,000 J/g), fish from the northwest (342,000 J/g) and fish from the southeast (282,000 J/g). A

similar pattern was observed when stomach content data were converted to caloric content, with

values for Naubinway (246,000 J/g), followed by the northwest (213,000 J/g), then Elk Rapids

(206,000 J/g), all exceeding those of the southeast region (186,000 J/g). Comparatively, the caloric

content of the diet calculated for Lake Whitefish in the southeast region during 1998-2001

(Madenjian et al. 2006) was approximately 302,000 J/g, a net decline in the southeast region of

116,000 J/g from 1998-2001 to 2004-2005.

Concentrations of DHA in Lake Whitefish dorsal muscle tissues varied significantly among

regions (ANOVA, $F_{3, 614} = 8.41$, $P < 0.001$), ranging from a high of 11.5 µg FAME/mg dry weight of

tissue for Lake Whitefish in Elk Rapids to a low of 10.2 μg FAME/mg dry weight of tissue for individuals in Naubinway (Fig. 2.3). Percent total dorsal lipid and W_r varied significantly among regions (dorsal lipid % ANOVA, $F_{3, 614} = 14.62$, $P < 0.001$; W_r ANOVA, $F_{3, 613} = 33.49$, $P < 0.001$). Percent total dorsal muscle lipid was significantly higher (Tukey-Kramer post-hoc HSD test, $P < 0.05$) in the northwest (12.3%) than in other regions. W_r was significantly higher in the southeast (Tukey-Kramer post-hoc HSD test, $P < 0.05$) and at a minimum for individuals in Naubinway. Although there were some significant linear relationships between $\delta^{13}C$ or $\delta^{15}N$ and measured condition metrics (e.g. W_r, % lipid, and DHA) by region and when regions were grouped, the r^2 were very poor ranging from 0 to 0.06 (Table 2.5).

2.4 Discussion

Distinct mean $\delta^{13}C$ and baseline corrected $\delta^{15}N$ signatures, the variable proximity of Lake Whitefish signatures to the prey resource base, and differences in niche space by region in Lake Michigan suggest that Lake Whitefish have different feeding habits among regions. However, trophic niche width did not vary by region. With the exception of Elk Rapids, regional dietary overlap was moderately high in the autumn, suggesting short-term seasonal convergence in regional Lake Whitefish diets. Dietary overlap based on long-term stable isotope signatures as inferred by ISOSOURCE was low when comparing northern regions to the southern one. Thus, over the longer term, distinct evidence of regional dietary differences exists. Differences in prey choices, however, did not correlate with measures of fish condition, as indicated by weak relationships between stable isotope signatures and the various condition measures. There was no consistent evidence for the hypothesis that Lake Whitefish exhibited poor condition in areas of low *Diporeia* abundance.

Lake Whitefish in the northwest region, comprised of Bailey's Harbor and Big Bay de Noc, were predicted to have a high caloric intake using diet analysis and the isotope mixing model

approach. The main sources of food as determined by ISOSOURCE were *Mysis* and Chironomids, both having high energy densities, but these possess different concentrations of DHA (Dalsgaard et al. 2003; Sushchik et al. 2006). Fish in the northwest also had significantly higher lipid and DHA concentration, suggesting high individual condition and use of high quality food sources. However, relative weight metrics for the northwest did not reflect lipid and DHA trends. All northern regions, including Naubinway, Elk Rapids and the northwest region, had significantly lower relative weights, a trend also evident in DeBruyne et al. (2008) who reported Lake Whitefish in the north region consistently had the lowest length-at-age. Relative weight metrics do not differentiate between whether high water or lipid content contributes to total fish weight, a fact that can be problematic given the inverse relationship between the two (Love 1980). Rennie and Verdon (2008) suggested relative weight as the best indicator of Lake Whitefish condition, however different trends among relative weight, % lipid and DHA suggest that the metric does not accurately describe fish condition for these populations. Lake Whitefish from the northwest have *Mysis* and *Diporeia* available to them as prey, the latter being present in high densities (1340 m^{-2}) in the Bailey's Harbor area (Nalepa et al. 2009). *Diporeia* densities have historically been higher on the western side of Lake Michigan as a result of the prevalence of coldwater upwelling events and higher productivity (Mortimer 1975). Tagging studies have shown that Lake Whitefish from Big Bay de Noc migrate from poorer prey resource areas towards more resource rich areas like Bailey's Harbor (Jones et al. 2008). Spatial feeding patterns and relative lengths of time spent in high and low density *Diporeia* areas, however, are essentially unknown. Thus, increased foraging range may serve to break direct linkages between prey density and fish condition.

Although the southeast region had the highest relative weight metric, diet energy density, percent lipid content, and DHA concentration measures were all low compared to the northwest region. The generally lower condition of Lake Whitefish in the southeast compared to the northwest

may be related to the reported declines in the abundance of *Diporeia* at the southeast location. Mean *Diporeia* densities in 2005 were 454 m^{-2} at a depth of 91 - 98 m in the southeast region, a drop of approximately 4,000 m^{-2} since 1994-95 and 3,000 m^{-2} since 2000 (Nalepa et al. 2000; Nalepa et al. 2009). Decreasing densities of *Diporeia* since 2000 have had an apparent impact on Lake Whitefish condition, probably as a result of increased foraging costs and the consumption of lower quality food as noted in this study. The Lake Whitefish populations in the southeast region had the smallest niche space in Lake Michigan, and a very distinct diet consisting mainly of isopods as determined by ISOSOURCE. Autumn feeding data for this population included mainly Dreissenid mussels and *Bythotrephes*, prey with low energy densities (1,703 and 2,027 J/g respectively). Caloric intake in the southeast region has declined by approximately 116,000 J/g since Madenjian et al. (2006) as *Diporeia* densities have declined (Nalepa et al. 2009). Lake Whitefish abundances in southern Lake Michigan have been simultaneously increasing (Kratzer et al. 2007; DeBruyne et al. 2008), possibly creating greater intraspecific competition for a less abundant, energy rich prey source. Therefore, Lake Whitefish may be required to forage over greater distances for lower quality prey. For example, Ihssen et al. (1981) found that Lake Whitefish populations eating zooplankton and small molluscs, prey sources with low energy content, exhibited slower growth than those feeding on larger bodied *Diporeia* and *Mysis*. After declines in *Diporeia* abundances off Muskegon (1998 to 2000), a site within the southeast region, the contribution of *Diporeia* to Lake Whitefish diets by weight fell from 61% to 18% (Pothoven et al. 2001). Pothoven et al. (2001) attributed observed declines in Lake Whitefish condition to reduced use of *Diporeia* and increased use of lower caloric zebra mussels and sphaeriids.

Elk Rapids Lake Whitefish had a mid-range isotopic niche space, the highest δ^{15}N signature and, as predicted by isotopic analysis, a large portion of the diet consisted of *Diporeia*. However, in the autumn, this population of Lake Whitefish fed heavily on *Bythotrephes*, a small and relatively

18

energy poor zooplankton. The Elk Rapids population had the highest concentration of DHA but mid-level condition in terms of % lipids, relative weight and energy density. The accessibility of *Diporeia* to the Elk Rapids population (Nalepa et al. 2009) and the predicted high reliance of this population on *Diporeia* may explain their significantly higher measured DHA concentration.

The relatively large niche space of Naubinway Lake Whitefish in comparison to other regions and the variety of prey items eaten in the autumn suggest that this population was feeding on a variety of prey items from multiple trophic levels. It was apparent from the ISOSOURCE analysis that there were two main prey sources, Chironomids and *Mysis*, the same main diet scenarios as the northwest region, with a small contribution from isopods. However, in contrast to the northwest, Naubinway Lake Whitefish appear to depend more on Chironomids than *Mysis*. These findings are evidence that the population has adjusted to using other food sources as an alternative to energy rich *Diporeia*. The high energy density calculated for the Naubinway populations was, therefore, related to the high proportions of Chironomids, Ephemeroptera and *Mysis* in the diet, which have a high energy density of 3,730, 3,791 and 3,783 J/g, respectively (Cummins and Wuycheck 1971; Driver et al. 1974; Eggleton and Schramm 2004; Madenjian et al. 2006).

Lake Whitefish in the northern regions of Lake Michigan do not appear to be regulated by stock density (DeBruyne et al. 2008) which suggests that food web changes are influencing observed stock levels. Optimal foraging theory, which assumes that caloric intake is maximized per unit time, predicts that Lake Whitefish will feed on prey possessing the greatest amount of energy acquired with the least amount of foraging and handling time (Stephens and Krebs 1986). Although Chironomids and Ephemeroptera have high energy densities, they are small bodied and lack the high concentration of DHA, which is a good indicator of condition and highly conserved through aquatic food webs (Dalsgaard et al. 2003). Ephemeroptera have high eicosapentaenoic acid (EPA; 20:5n-3) levels, however, the biosynthetic capability of Lake Whitefish to chain elongate and desaturate EPA to DHA

19

is not known. Reliance on these prey items may explain the observed low DHA concentrations and low percent lipid and relative weights in Naubinway, with high energy intake per prey item consumed being offset by high search costs because of target prey size.

The proportional contribution of each prey source to the diet of Lake Whitefish was not the same for the stomach content data and the SIA mixing model analysis. Differences may be attributed to the time scale represented by each analysis. Stomach content analysis is a snapshot of recent feeding, whereas isotope signatures represent the product of diet assimilation over months. Differences may, therefore, indicate seasonal variability in feeding patterns which will not be evident in other measures developed from feeding over long periods of time such as lipids, DHA and/or relative weight. Combining both short- and long-term measures of feeding patterns may, therefore, provide the best insights into condition metric dynamics. Specifically, a snapshot at spawning would not be a good representation of isotopic signatures since the fish are nearshore in shallower waters preparing to spawn. This suggests seasonal variation in food sources due to migration to the spawning grounds.

Although mixing models facilitate inferences about the importance of prey resources to a predator, predictions depend critically on knowledge of the actual prey resources used. A prey resource not considered in the feasible set of consumption items cannot contribute to the calculations used to construct possible diet scenarios on the basis of actual stable isotope signatures. Conversely, a prey resource mistakenly included in the feasible set will contribute to the model calculations. Both scenarios will result in poor predictions and mixing-model results should be ground-truthed against detailed gut content analysis. Thus, while data here suggest significant differences in short- and long-term prey resource use, and differences among regions, results may be an artefact of the prey resources used in the study.

Density-dependent factors may be having a greater impact on Lake Whitefish condition than the availability of high quality food (Kratzer et al. 2007; DeBruyne et al. 2008). There is some evidence that Lake Whitefish in some regions of Lake Michigan, such as Naubinway and the southeast, are coping with declining *Diporeia* abundances by feeding on alternate energy rich food sources lacking in high concentrations of DHA such as Chironomidae and Ephemeroptera. Such Lake Whitefish tend to have a lower condition as measured by percent lipid and DHA. Thus, while there is evidence that Lake Whitefish feed differently throughout Lake Michigan, there is no consistent link between prey choices and the measures of condition used to infer individual or population status.

2.5 Figures and Tables

Figure 2.1 Lake Whitefish and prey source sampling sites in Lake Michigan. Fish were collected between October and December of 2004 and 2005. Potential prey sources were collected June 2005 and 2007.
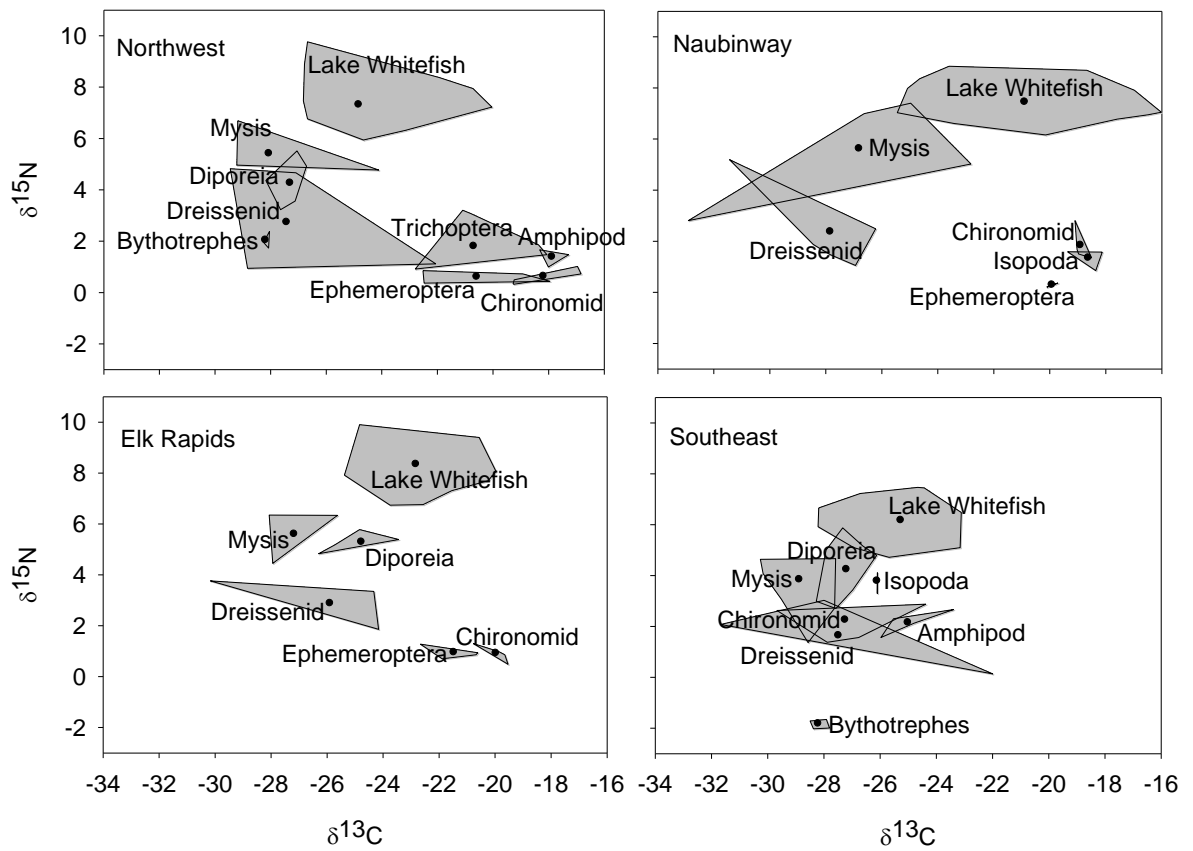
Figure 2.2 Isotopic niche space polygons Lake Whitefish and associated prey resource base are shown for Lake Michigan study regions. All polygons are baseline adjusted. Dots plot the mean of all signatures for each taxon-specific polygon.
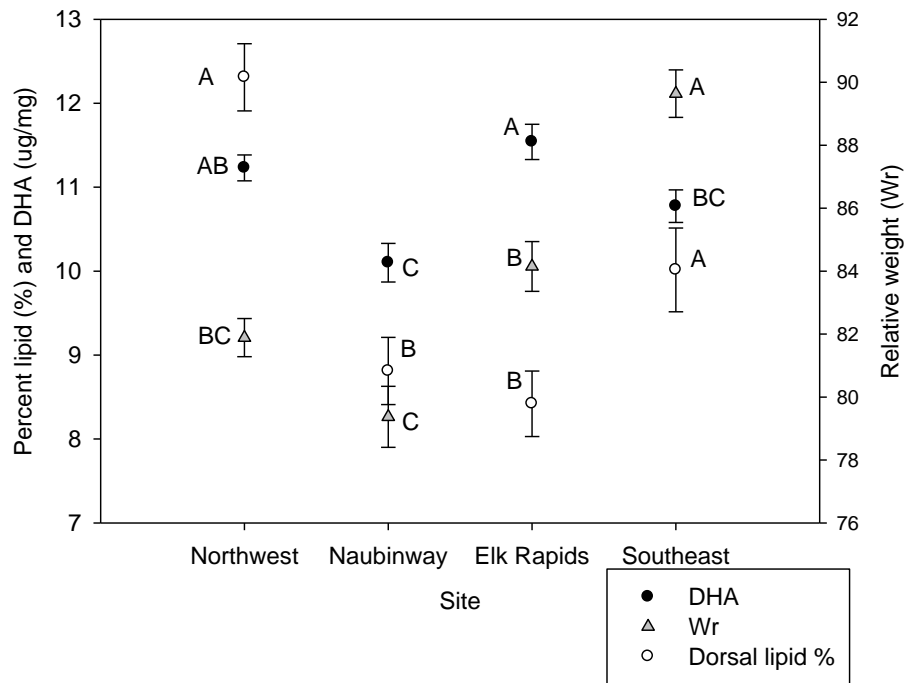
Figure 2.3 Mean ± standard error of measured Lake Whitefish condition metrics by region. DHA defined as concentration of docosahexaenoic acid (µg/mg), W_r defines the relative weight metric and dorsal lipid defines percent of total lipids in dorsal muscle tissue. Letters (e.g., A, B, C) represent homogenous groupings as determined using the Tukey-Kramer post-hoc HSD test.

Table 2.1 Number of Lake Whitefish, their δ^{13}C signatures, POM corrected δ^{15}N signatures and isotopic niche space by region. Superscript letters (e.g., A, B, C) describe Tukey-Kramer post-hoc HSD groups of similarity defined using a significant difference standard of $P < 0.05$.

Region	n	δ^{13}C (‰) Mean	δ^{13}C (‰) Std Dev.	δ^{15}N (‰) Mean	δ^{15}N (‰) Std Dev.	δ^{13}C and δ^{15}N Polygon Area (‰^{2})
Northwest	229	-24.82^C	1.10	7.31^B	0.55	15.23
Naubinway	119	-20.89^A	2.35	7.44^B	0.56	17.64
Elk Rapids	117	-22.82^B	1.06	8.34^A	0.52	12.21
Southeast	148	-25.26^D	1.04	6.16^C	0.56	10.53

Table 2.2 Stomach content percent contribution, by dry weight, of sampled Lake Whitefish in each region from the Fall of 2004 and 2005. For comparison purposes, values reported by Madenjian et al. (2006) for Fall 1998-2001 captured at Muskegon, in the southeast region, are given. Trace refers to items that make up less than 0.1% by weight of the diet.

Diet item and number of stomachs examined	Northwest	Naubinway	Elk Rapids	Southeast	Muskegon 1998-2001 (Madenjian et al. 2006)
Diet Item					
Amphipoda	0.3	-	-	trace	32 (*Diporeia*)
Mysis	-	-	-	-	23
Bythotrephes	9.3	16.5	97.6	34.9	3
Chironomidae	trace	0.8	-	-	9
Dreissenidae	42.9	11.7	0.8	60.7	32
Isopoda	36.7	trace	0.2	4.2	-
Ephemeroptera	-	37.0	-	-	-
Gastropoda	10.8	29.9	-	0.2	-
Unionidae	trace	3.9	-	trace	-
Alewives (age-0)	-	-	-	-	1
Johnny Darter	-	-	1.4	-	-
Stomachs examined					
Nonempty stomachs	19	89	66	52	46
Empty stomachs	212	31	54	106	38

Table 2.3 Summary of Horn (1966) dietary overlap indices for pre-spawning Lake Whitefish by region compared to literature reported values and indices implied by ISOSOURCE percent dietary contributions based on measured stable isotope values. A value of 0 indicates no dietary overlap, whereas 1 infers complete overlap.

	Naubinway	Elk Rapids	Southeast	Madenjian et al. (2006)
Northwest				
Stomachs	0.505	0.266	0.776	0.430
ISOSOURCE	0.902	0.378	0.123	
Naubinway				
Stomachs		0.364	0.478	0.264
ISOSOURCE		0.398	0.247	
Elk Rapids				
Stomachs			0.588	0.124
ISOSOURCE			0.146	
Southeast				
Stomachs				0.507

Table 2.4 ISOSOURCE mean percentage ± standard deviation of feasible diet scenarios. The 1st and 99th percentile values are given in parenthesis below mean entries.

	Northwest	Naubinway	Elk Rapids	Southeast
Diporeia	1.6 ± 1.9 (0-5)	-	73.3 ± 1.3 (70-76)	2.2 ± 2.2 (0-9)
Mysis	65.5 ± 1.5 (59-68)	36 ± 0.6 (35-37)	0.9 ± 1.1 (0-4)	0.7 ± 0.9 (0-4)
Bythotrephes	0.2 ± 0.5 (0-2)	-	-	1.2 ± 1.3 (0-5)
Chironomidae	31.1 ± 1.1 (28-33)	58.2 ± 5.5 (45-65)	23.8 ± 1.7 (19-26)	2.5 ± 2.4 (0-10)
Dreissenidae	0.4 ± 0.7 (0-2)	0.1 ± 0.3 (0-1)	0.3 ± 0.6 (0-2)	2.0 ± 2.0 (0-8)
Ephemeroptera	1.1 ± 1.3 (0-5)	0.6 ± 0.8 (0-3)	1.7 ± 1.8 (0-7)	-
Isopoda	-	5.2 ± 5.3 (0-18)	-	91.3 ± 2.3 (87-97)

Table 2.5 Linear regressions of $\delta^{13}C$ and baseline corrected $\delta^{15}N$ on measured condition parameters: DHA, W_r and mean total dorsal lipid. DHA defines the essential fatty acid docosahexaenoic acid, W_r defines relative weight and dorsal lipid gives the percent of total lipids in dorsal muscle tissue. Statistical significance ($P < 0.05$) is denoted with * and relationships with no significance are denoted with [ns].

	$\delta^{13}C$				$\delta^{15}N$			
	Intercept	Slope	r^2	F Ratio	Intercept	Slope	r^2	F Ratio
Pooled data (df = 1, 611)								
DHA	-22.70	-0.10	0.01	7.15*	6.72	0.05	0.01	8.54*
Wr	-19.51	-0.05	0.05	33.79*	8.41	-0.01	0.02	11.46*
Dorsal lipid (%)	-23.13	-0.06	0.03	21.11*	7.42	-0.02	0.01	6.82*
Northwest (df = 1, 227)								
DHA	-24.92	0.01	0.00	0.09[ns]	6.86	0.04	0.03	7.04*
Wr	-24.42	0.00	0.00	0.39[ns]	7.28	0.00	0.00	0.01[ns]
Dorsal lipid (%)	-24.70	-0.01	0.00	1.13[ns]	7.41	-0.01	0.01	3.28*
Naubinway (df = 1, 118)								
DHA	-19.90	-0.10	0.01	1.26[ns]	10.02	0.01	0.00	0.38[ns]
Wr	-18.56	-0.03	0.02	2.12[ns]	10.38	-0.00	0.00	0.36[ns]
Dorsal lipid (%)	-20.70	-0.02	0.00	0.18[ns]	10.18	-0.00	0.00	0.10[ns]
Elk Rapids (df = 1, 115)								
DHA	-23.18	0.03	0.00	0.52[ns]	11.94	-0.02	0.01	0.76[ns]
Wr	-23.75	0.01	0.01	0.88[ns]	11.31	0.00	0.01	0.72[ns]
Dorsal lipid (%)	-22.70	-0.01	0.00	0.42[ns]	11.78	-0.01	0.00	0.30[ns]
Southeast (df = 1, 147)								
DHA	-24.12	-0.11	0.05	7.12*	6.56	-0.04	0.02	2.94[ns]
Wr	-22.28	-0.03	0.06	9.13*	5.75	0.00	0.00	0.56[ns]
Dorsal lipid (%)	-24.81	-0.04	0.05	7.59*	6.30	-0.01	0.02	2.34[ns]

Chapter 3

Lake Whitefish energy partitioning in Lakes Michigan, Erie and Superior

3.1 Introduction

Lake Whitefish (*Coregonus clupeaformis*) make up an important portion of the Great Lakes commercial and recreational fishery. Commercial Lake Whitefish harvest has increased every year since 1985, and by 1995, Lake Whitefish catch out of lakes Huron and Michigan reached 9 million kilograms (Ebener 1997; Madenjian et al. 2002). As benthic feeders, adult Lake Whitefish primarily feed on energy rich *Diporeia hoyi* in the Great Lakes (Hardy 1994). The two native species play an important role in the benthic food web, connecting primary productivity to harvestable fish for human consumption (Nalepa et al. 2005).

Recently, growth and condition of Lake Michigan Lake Whitefish has been declining, creating a concern for the fishery (Pothoven et al. 2001; Madenjian et al. 2002; Schneeberger et al. 2005; Pothoven and Nalepa 2006; Pothoven et al. 2006). A concurrent decrease in the abundance of *Diporeia* in Lake Michigan has spurred investigations into possible links between the two events (e.g., Pothoven et al. 2001; Madenjian et al. 2002; Kratzer et al. 2007; Fagan et al. *in review*). However, the Great Lakes are dynamic systems and many factors, including Lake Whitefish density increases and food availability, may have played a role in Lake Whitefish condition decline. Kratzer et al. (2007) reported that Lake Whitefish density increases, in combination with declining abundances of *Diporeia*, were affecting Lake Whitefish condition in Lake Michigan (also noted in Schneeberger et al. 2005) through changes in ration, because increased fish density tended to promote additional intra-specific competition for prey resources. Similarly, a regional analysis of Lake

Whitefish condition in Lake Michigan has suggested declines in *Diporeia* abundances per se are not the only factor influencing the declining condition because of use of less energetic alternative prey (Fagan et al. *in review*). However, in productive lakes, such as Lake Erie, changes in Lake Whitefish abundance (Lumb et al. 2007) or the extirpation of *Diporeia* (Cook et al. 2005) have had no impact on Lake Whitefish condition because ration was not limited.

The contrasting findings from lakes Michigan and Erie suggest that effects of ecosystem changes on Lake Whitefish are lake specific (Lumb et al. 2007), possibly driven by primary productivity (Barbiero and Tuchman 2001). Changes at the base of the food web may accumulate at successive trophic levels to affect the overall prey availability and carrying capacity for consumers at the upper trophic levels (Downing et al. 1990) which could lead to the observed differences in energy consumption (Fagan et al. *in review*).

The differences in ration (energy consumption) among lakes are important to Lake Whitefish growth and condition, and may feedback to affect population dynamics. As a rule, energy consumed is partitioned into growth, reproduction, and/or maintenance, which includes foraging costs, metabolism and excretion (Elliot 1994). Surplus energy available, after maintenance costs are met, is treated as an investment in somatic growth and/or gonadal development (Roff 1992) and will vary in response to food availability. For example, the basic energy balance equation predicts that a loss in energy consumed leads directly to decreased surplus energy, under the assumption that maintenance costs remain constant (e.g., Elliott 1994). Thus, food availability, foraging costs and intra-specific competition are linked through food consumption in ways that suggest a complex mosaic of possible trade-offs to maintain either condition or reproductive investment in the face of declining energy intake.

Although it is known that primary productivity, and thus food availability, varies by lake (Downing et al. 1990; Barbiero and Tuchman 2001), research to date has not unveiled the differences

in energy available to Lake Whitefish and the partitioning of energy consumed by Lake Whitefish among lakes and populations. In this study, I examine Lake Whitefish growth, reproductive investment, physiological condition and diet as a means of determining whether differences in food consumption are correlated with measures of population success. Specifically, the following hypotheses are tested using data on female Lake Whitefish from eight different populations sampled from lakes Michigan, Erie and Superior: [1] observed differences in growth and reproduction among populations are driven by energy availability; [2] populations with low energy reserves exhibit trade-offs between egg size and fecundity as a means of maintaining reproductive output; and, [3] high energy reserves are related to *Diporeia* consumption (e.g., Hoyle et al. 1999; Pothoven et al. 2001; Mohr and Ebener 2005).

3.2 Materials and Methods

Adult female Lake Whitefish were sampled at six sites around Lake Michigan including: Saugatuck, Ludington, Elk Rapids, Naubinway, Big Bay de Noc, and Bailey's Harbor, and one site in each of lakes Superior (Whitefish Point) and Erie (Point Pelee) (Fig. 3.1). Fish were collected between October and December of 2004 and 2005 using either commercial trap nets with 40 cm stretch mesh, with a pot comprised of 11.4 cm stretch mesh, or gill nets with mesh sizes ranging from 4 to 15 cm. At each site up to 30 pre-ovulatory females were collected. Each fish was measured for total weight (g), gonad weight (g), and total length (mm). Egg diameter (mm) was measured for 30 eggs selected from each of the anterior, middle, and posterior sections of the ovary and data were used to compute an average egg diameter for each fish. Up to 200 eggs were weighed (g) from each section of the ovary to determine average wet weight per egg and the average of all three sections, mean wet weight per egg (g), was used to calculate fecundity. All fish were aged using scales as defined and identified

by Muir et al. (2008). Skinless dorsal muscle plugs were collected from each fish and stored frozen (-85°C) for stable isotope (SIA) and lipid analyses.

Diporeia were collected at Bailey's Harbor, Elk Rapids, Ludington, Saugatuck and Whitefish Point at depths of 30 to 95 m. Littoral zone water was filtered through 2.2 µm pore size quartz fibre filters (Whatman grade QMA) to obtain representative particulate organic matter (POM) samples for use in stable isotope baseline estimation (e.g., Post 2002). Prior to vacuum filtration, all large particles were removed from water samples using a 20 µm sieve. Filters were immediately frozen for SIA.

3.2.1 Stable Isotope Analysis

Lake Whitefish skinless dorsal muscle tissue, whole *Diporeia* bodies and POM filters were dried at 50°C for 48 h. Fish muscle tissue and *Diporeia* were pulverized to an homogenate with a Retsch MM 301 ball mill grinder or by hand, and approximately 0.3 mg of homogenate was weighed and inserted into combustible tin cups (SerCon 5 x 3.5 mm) for SIA. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values were determined using a Delta Plus continuous flow stable isotope ratio mass spectrometer coupled to a Carlo Erba elemental analyzer at the Environmental Isotope Laboratory, University of Waterloo, Ontario. Resulting measurements are expressed using standard delta notation (δ) as parts per thousand differences with respect to the international reference standards of carbonate rock from the Peedee Belemnite formation for $\delta^{13}C$ (Craig 1957) and atmospheric nitrogen gas for $\delta^{15}N$ (Mariotti 1983). Machine analytical accuracy, respectively, for $\delta^{13}C$ and $\delta^{15}N$ was ± 0.2 ‰ and ± 0.3 ‰ and was determined by repeat analysis (n = 25) of laboratory working standards cross-calibrated to International Atomic Energy Agency standards CH6 for $\delta^{13}C$ and N1 and N2 for $\delta^{15}N$. Duplicate analysis of 1 in 10 samples was used to further assess measurement precision.

To compare among lakes and account for possible anthropogenic variation in stable isotope signatures at the base of the food web (e.g., Post 2002), nitrogen isotopic signatures were baseline corrected. With appropriate estimates of base $\delta^{15}N$ it is possible to determine if observed variation in organism isotopic signatures occurs because of differences in food web structure or because of variation at the base of the food web (Vander Zanden and Rasmussen 1999; Post 2002). Here, baseline correction was accomplished by subtracting the average POM $\delta^{15}N$ signature for each lake from all relevant fish $\delta^{15}N$ signatures. The resulting corrected $\delta^{15}N$ measures, therefore, scale fish and *Diporeia* in terms of trophic distance from the base of the food web and facilitate comparisons among lakes (e.g., Post 2002).

3.2.2 Lipid and DHA Analysis

Total lipid and docosahexaenoic acid (DHA; 22:6n-3) concentrations in individual adult Lake Whitefish samples were analyzed at The National Water Research Institute laboratories of Environment Canada, Burlington, Ontario. DHA is an essential omega-3 fatty acid that occurs in high concentrations in membrane phospholipids and is known to have positive effects on teleost egg, neural and eye development (Bell and Dick 1993; Dalsgaard et al. 2003). Given the important role DHA plays in the nutritional health of fish (Kelly and Kohler 1999; Snyder and Hennessey 2003; Arts and Kohler 2009), DHA has been included in the analysis as a proxy measure of food quality.

Skinless dorsal muscle samples were freeze-dried in preparation for total lipid and DHA analyses. Analysis involved three steps: gravimetric extraction, derivitization, and quantification on an HP6890 gas chromatograph following the methods described in Zellmer et al. (2004). Samples were extracted three times by grinding freeze-dried materials in a 2:1 chloroform:methanol solution (Bligh and Dyer 1959). After centrifugation at 4,000 rpm was used to remove the majority of non-lipid material, the supernatant was transferred to acid-washed, 15-ml centrifuge tubes and rinsed with

34

chloroform:methanol. The centrifuging procedure was followed by a salt wash (0.9% aqueous NaCl

solution) to remove lipophilic proteins before samples were evaporated to 2 ml. From this 2 ml

volume, 200 μL of sample extract were weighed on a Sartorious ME-5 microbalance to provide an

accurate measure of total lipid content. DHA was identified and quantified with a reference to

Supelco's 37 component FAME mix (#47885-U). An internal standard (5 α-cholestane; Sigma-

Aldrich; #C8003) was added to the tissue before extraction to estimate percent recovery during the

extraction procedure. The DHA concentrations are reported as μg FAME/mg dry mass of tissue.

3.2.3 Data Analysis

The size-selective nature of fish sampling precluded the use of von Bertalanffy growth models.

Therefore, linear regression with length as the dependent variable and age as the independent variable

was used to determine growth rate (i.e., slope of length-age regressions) for comparison among

populations.

Indices of resources partitioned to reproduction were estimated using fecundity and the

gonadosomatic index (GSI). Fecundity (F) was calculated using gonad weight (g_w) and estimated

mean wet weight per egg (e_w):

$$(1) \qquad\qquad F = \frac{g_w}{e_w}$$

GSI was computed as the ratio of gonad weight to total fish wet weight (t_w) adjusted for

reproductive tissue (Roff 1992) as:

$$(2) \qquad\qquad GSI = \frac{g_w}{t_w - g_w} \times 100\%$$

GSI was calculated for all Lake Whitefish with the exception of identified spent individuals.

Results obtained from the stable isotope analysis of Lake Whitefish and *Diporeia* samples were

used to determine the Euclidean distance (Δ_{WD}; Krebs 1999) between the two taxa in terms of their

respective isotopic signatures. Euclidean distances for Lake Whitefish in Lake Michigan were determined using mean signatures of *Diporeia* sampled from geographically similar regions. Δ_{WD} was computed as:

$$(3) \qquad \Delta_{WD} = \sqrt{\left(\delta^{13}C_W - \delta^{13}C_D\right)^2 + \left(\delta^{15}N_W - \delta^{15}N_D\right)^2}$$

The subscript W denotes the mean $\delta^{13}C$ and baseline corrected $\delta^{15}N$ signatures of Lake Whitefish and the subscript D denotes the mean $\delta^{13}C$ and baseline corrected $\delta^{15}N$ signatures of *Diporeia*. Taking into consideration the commonly assumed fractionation values of 0.1 for $\delta^{13}C$ and 3.4 for $\delta^{15}N$ (Post 2002), a Δ_{WD} of 3.4 would indicate 100% *Diporeia* consumption.

3.2.4 Statistical Analysis

Statistical analyses were performed using JMP, Version 7 (SAS Institute Inc., Cary, NC). Maximal type I error rates were set at $\alpha = 0.05$ in all analyses. Analysis of covariance (ANCOVA) was used to test for common slopes and intercepts in estimated length-at-age and log fecundity-log body weight regression models. Significant analysis of variance (ANOVA) results were followed by multiple comparisons of means testing using the conservative Tukey's HSD *post hoc* test (Zar 1999) to determine the specifics of among population differences.

Individual fecundity estimates were adjusted for fish body weight (Roff 1992) using the residuals from the log fecundity – log body weight linear regression for each population as body weight was a better predictor of fecundity than length for populations in this study. Residuals from the log fecundity – log body weight regression (hereafter referred to as standardized fecundity) were then plotted against individual log egg diameter to determine if trade-offs exist between egg number and size.

The variance in Lake Whitefish $\delta^{13}C$ and baseline corrected $\delta^{15}N$ signatures were used, respectively as a measure of niche breadth diversity at the base of the food web and trophic diversity

(Layman et al. 2007). Greater variation reflects wider use of available prey resources (Bearhop et al. 2004; Layman et al. 2007). Bartlett's test for variance homogeneity (Bartlett 1937a, 1937b) was applied to determine whether there were significant differences in Lake Whitefish δ^{13}C and baseline corrected δ^{15}N variances among populations and between groups with and without reproductive trade-offs for total lipid and DHA. Welch's t-test or ANOVA was applied when groups had unequal variances (Zar 1999).

3.3 Results

3.3.1 Growth

Estimated models for length-at-age did not share a common slope among populations (ANCOVA, $F_{7, 290} = 5.71$, P < 0.001). Point Pelee and Whitefish Point populations had similar length-at-age slopes (ANCOVA, $F_{1, 55} = 1.77$, P = 0.189), but differed in intercept (ANCOVA, $F_{1, 56} = 4.26$, P = 0.044; Table 3.1). All Lake Michigan populations had similar length-at-age (ANCOVA, $F_{5, 235} = 0.94$, P = 0.454), but differed significantly in intercepts (ANCOVA, $F_{5, 240} = 26.78$, P < 0.001).

3.3.2 Reproductive Investment

GSI (ANOVA, $F_{7, 305} = 16.86$, P < 0.001) varied among populations of Lake Whitefish (Fig. 3.2a). GSI calculated for the Point Pelee population was significantly higher than other populations (Tukey-Kramer post-hoc HSD test, P < 0.05). Whitefish Point GSI values did not separate distinctively from values recorded for the Lake Michigan populations (Tukey-Kramer post-hoc HSD test, P > 0.05). Elk Rapids and Ludington Lake Whitefish had the lowest (Tukey-Kramer post-hoc HSD test, P < 0.05) and similar GSI values.

There was a significant positive relationship between log fecundity and log body weight for all Lake Whitefish spawning populations (Table 3.1). Although a common slope model could not be

estimated (ANCOVA, $F_{7, 297} = 2.23$, $P = 0.032$), populations separated into two homogenous groupings. Populations from Big Bay de Noc, Ludington, Saugatuck, Point Pelee and Whitefish Point composed the first group and possessed a common mean slope (ANCOVA, $F_{4, 167} = 0.90$, $P = 0.468$) that was flatter than the common mean slope (ANCOVA, $F_{2, 130} = 0.52$, $P = 0.597$) estimated for the second group made up of populations from Bailey's Harbor, Naubinway and Elk Rapids. Both groups displayed heterogeneity with respect to intercept estimates (group 1: ANCOVA, $F_{4,171} = 37.00$, $P < 0.001$; group 2: $F_{2,132} = 3.49$, $P = 0.033$). Intercepts from the first group were all higher than the intercepts from the second group.

There were significant negative linear relationships between standardized fecundity and log egg diameter measurements for the Bailey's Harbor, Naubinway, Elk Rapids and Saugatuck populations (Fig. 3.3). All significant models shared a common slope (ANCOVA, $F_{3, 166} = 0.83$, $P = 0.480$; Table 3.1), but differed significantly in regression intercepts (ANCOVA, $F_{3, 169} = 9.81$, $P < 0.001$).

3.3.3 Energy

Log mean percent total lipid (ANOVA, $F_{7, 306} = 43.17$, $P < 0.001$) and DHA (ANOVA, $F_{7, 306} = 24.08$, $P < 0.001$) differed significantly among populations (Fig. 3.2b and Fig. 3.2c). Point Pelee fish had higher mean total lipid values compared to all other populations (Tukey-Kramer post-hoc HSD test, $P < 0.05$). The remaining populations sorted into overlapping groups within which mean total lipid values did not differ (Tukey-Kramer post-hoc HSD test, $P < 0.05$). The first group included: Big Bay de Noc, Ludington and Whitefish Point. The second group included: Bailey's Harbor, Ludington, Naubinway, Saugatuck and Whitefish Point, while the last group, with the lowest total lipid values, included Bailey's Harbor, Elk Rapids, Ludington, Naubinway and Saugatuck.

Mean population measurements of DHA sorted into three homogeneous groupings (Tukey-Kramer post-hoc HSD test, $P < 0.05$; Fig. 3.2c). Bailey's Harbor, Big Bay de Noc, Elk Rapids,

Ludington, Naubinway and Whitefish Point shared the highest DHA concentrations. The Point Pelee population had significantly lower DHA concentrations when compared to all other studied populations (Tukey-Kramer post-hoc HSD, $P < 0.05$).

3.3.4 Diet

Carbon stable isotope variances differed significantly among populations (δ^{13}C: $\chi = 11.45$, $P < 0.001$) but baseline adjusted nitrogen variances did not differ (δ^{15}N: $\chi = 1.20$, $P = 0.300$). The Whitefish Point and Naubinway populations had δ^{13}C variation approximately two-fold greater than that observed in the remaining populations (Table 3.2). Although there were no δ^{15}N variation differences among populations, Whitefish Point had the largest variation. The Point Pelee population showed the lowest variability in δ^{15}N.

Significant differences were also found among population mean δ^{13}C (Welch ANOVA, $F_{7, 116} = 62.50$, $P < 0.001$) and baseline corrected δ^{15}N (ANOVA, $F_{7, 301} = 158.42$, $P < 0.001$) stable isotope values. Along the δ^{15}N axis, populations grouped into five clusters within which mean baseline corrected δ^{15}N values did not differ (Fig. 3.4). Naubinway and Whitefish Point Lake Whitefish had significantly lower mean baseline corrected δ^{15}N than all other populations (Tukey-Kramer post-hoc HSD test, $P < 0.05$). The next lowest cluster included the Bailey's Harbor, Big Bay de Noc and Whitefish Point populations below Ludington. Saugatuck and Elk Rapids formed another trophic grouping, approximately 1 ‰ above the previous group. The Point Pelee population of Lake Whitefish had the highest mean baseline corrected δ^{15}N signature (Tukey-Kramer post-hoc HSD test, $P < 0.05$) that was a full trophic level above the lowest mean signature seen in Naubinway.

Four overlapping δ^{13}C clusters are apparent. The first cluster included the Big Bay de Noc, Ludington, Point Pelee and Saugatuck populations, which had the most negative mean δ^{13}C values (Tukey-Kramer post-hoc HSD test, $P < 0.05$) of all populations. A second cluster included the

Bailey's Harbor, Big Bay de Noc, Point Pelee and Saugatuck populations (Tukey-Kramer post-hoc HSD test, $P < 0.05$) with average mean $\delta^{13}C$ values in the -25.2 to -24.8 ‰ range. The Elk Rapids population differed (Table 3.2) significantly from all other populations (Tukey-Kramer post-hoc HSD test, $P < 0.05$), and was approximately 2 ‰ lower than mean $\delta^{13}C$ values recorded for the Naubinway and Whitefish Point populations (Tukey-Kramer post-hoc HSD test, $P < 0.05$).

Euclidean distances from mean *Diporeia* signatures Δ_{WD} varied by population from the 3 to 4 range consistent with high *Diporeia* consumption for Bailey's Harbor, Big Bay de Noc and Elk Rapids, to low and high values, respectively of 1.36 and 9.16 indicative of low reliance on *Diporeia* as a food source for the Ludington and Whitefish Point populations (Table 3.2 and Fig. 3.4).

3.3.5 Trade-offs, growth and energy

A positive non-significant trend was evident between growth rate and log mean total lipid using all population estimates (ANOVA, $F_{1, 6} = 2.55$, $P = 0.162$; Fig 3.5a). Similarly, a significant positive relationship was observed between GSI and log mean total lipid using all individuals from all populations (ANOVA, $F_{1, 311} = 70.67$, $P < 0.001$; Fig 3.5b).

Populations displaying reproductive tradeoffs in terms of egg size and number included: Bailey's Harbor, Elk Rapids, Naubinway and Saugatuck. The group displaying reproductive trade-offs had significantly lower mean total lipid content in muscle tissue (Welch *t* test, $t_{1, 153} = 7.75$, $P < 0.001$; Fig. 3.5c) and significantly higher DHA concentrations (Welch *t* test, $t_{1, 268} = 2.88$, $P = 0.004$) compared to populations in which there was no trade-off between egg size and number.

No relationship was apparent between log lipid measures and consumption of *Diporeia*. Populations with Δ_{WD} suggesting high consumption of *Diporeia* (e.g., Elk Rapids $\Delta_{WD} = 3.59$ and Bailey's Harbor $\Delta_{WD} = 3.31$), had lower log total lipid means than populations that had Δ_{WD} values

suggesting no consumption of *Diporeia* (e.g., Whitefish Point $\Delta_{WD} = 9.21$ and Point Pelee $\Delta_{WD} = n/a$; Fig. 3.5d).

A comparison between GSI and growth rate among populations (Fig. 3.6) illustrates that the Point Pelee population has both high growth rates and high GSI, whereas the Whitefish Point population invests more in growth than reproduction. The Lake Michigan populations form a cluster, with a negative non-significant trend (ANOVA, $F_{1, 4} = 2.46$, $P = 0.1917$).

3.4 Discussion

As hypothesized, populations with higher growth rates and higher mean reproductive potential have higher energy stores in percent total lipid, but did not evidence any association with DHA concentrations. There was evidence of reproductive trade-offs, with populations having low muscle lipids reducing egg size as egg number increased. Although diet varied among studied populations, there was no evidence to support the hypothesis that high energy reserves were related to *Diporeia* consumption. Therefore, while changes in prey resources have had an effect on Lake Whitefish populations, the impact of declining *Diporeia* abundances alone cannot explain the systemic changes in Lake Whitefish condition and abundance observed across the Great Lakes basin.

3.4.1 Trade-offs, growth and energy

Analyses here suggest that populations in Lake Michigan have less surplus energy available after meeting maintenance requirements than populations in either lakes Erie or Superior and were forced, as a consequence, to make reproductive trade-offs. Reduced surplus energy was manifested in lower somatic growth rates in Lake Michigan populations compared to populations in Lake Erie or Lake Superior. Slower growth in Lake Michigan has also been documented by DeBruyne et al. (2008) who found significant declines in length-at-age across all regions of Lake Michigan between 1980-90 and 1996-2005, particularly in the northern parts of the lake. Length-at-age for all regions of

Lake Michigan in the 1980-90s (DeBruyne et al. 2008) was higher than observed in lakes Erie and Superior from this study, suggesting a dramatic change in growth for Lake Michigan populations. Particularly poor energy investment in growth and reproduction was evident for Bailey's Harbor, Elk Rapids, Naubinway and Saugatuck, with all populations displaying slow to no growth at sampled ages and reproductive trade-offs between egg size and number. Three of the four populations (i.e., Naubinway, Elk Rapids and Bailey's Harbor) displaying trade-offs had a greater rate of fecundity increase with body weight and low initial fecundity as observed by the steeper common slope and low intercepts estimated for the fecundity-weight relationship.

In Lake Michigan, populations appear to be maximizing fecundity and egg size using all available energy resources at the cost of growth. Larger egg sizes tend to be selected for when resource availability is reduced (Hutchings 1991), with ultimate egg size being limited by maternal size (Bell et al. 1977). In some salmonids, e.g., Rainbow Trout (*Oncorhynchus mykiss*), egg size is unaffected by adult food availability and ration limitations are manifested in decreased egg number (Scott 1962). Altering reproductive frequency is another method adopted by some fishes when faced with ration limitations. For example Atlantic Herring (*Clupea harengus*) were found to skip spawning seasons when energetically limited (Kennedy et al. 2010). The low growth and reproductive investment for most Lake Michigan populations suggests Lake Whitefish in Lake Michigan are energetically constrained and have adapted reproductive and growth strategies requiring trade-offs to maximize fitness.

Point Pelee and Whitefish Point populations invested more in growth and reproduction than Lake Michigan populations. Both populations had statistically similar high growth rates, high lipid reserves and they provided no evidence of reproductive trade-offs. During the 1990s, Lake Whitefish in Lake Superior had lower maximum lengths compared to northern Lake Michigan populations (Taylor et al. 1992), possibly as a consequence of low primary productivity, colder temperatures, and

the shorter growing season in Lake Superior (Barbiero and Tuchman 2001). My Lake Superior fish

appeared to invest more energy in somatic growth at each age than Lake Michigan, however,

corresponding GSI values did not differ. Energy intake during winter is generally low for freshwater

fishes (Næsje et al. 2006), with over-winter survival positively related to fish length (Griffiths and

Kirkwood 1995, Heermann et al. 2009). The lack of evidence for reproductive trade-offs in Lake

Whitefish from Whitefish Point suggests they have adapted an energy partitioning strategy favouring

growth over reproduction, possibly as a means of optimizing over-wintering survival. In contrast,

there has not been a significant change in Lake Erie Lake Whitefish length-at-age since 1972 (Lumb

et al. 2007). The high GSI values suggest that Point Pelee fish invest more energy in reproduction for

a given body size compared to other populations, a trend also observed in a comparative study of

Lake Erie and Lake Ontario populations (Lumb et al. 2007). The combination of growth rate and

reproductive investment suggest Lake Erie Lake Whitefish are not energy limited in comparison to

populations from other regions of the Great Lakes, but particularly Lake Michigan populations.

Overall populations with high growth and reproductive investment also tended to have higher

lipid reserves. For example, the Point Pelee and Whitefish Point populations had comparably high

growth, no reproductive trade-offs and higher percent total lipid stored in muscle tissue. Populations

in Lake Michigan, with reproductive trade-offs and lower investment in growth (e.g., Naubinway, Elk

Rapids), tended to have lower lipid stores. Lipids are a primary energy reserve mobilized by teleost

fishes for meeting the energetic requirements of reproduction and are an important component of egg

yolk (Wiegand 1996). Endogenous growth of larval Lake Whitefish has been shown to be positively

related to parental female lipid content and total egg lipid (Brown & Taylor 1992). The importance

of lipids extends to maturation schedules, as specific quantities of mesenteric lipid reserves are

necessary before salmonids mature sexually (Reshetnikov et al. 1970; Thorpe 1986; Adams and

Huntingford 1997). My pre-ovulatory female Lake Whitefish would have previously mobilized

43

muscle lipids to egg yolks, meaning that lipids measured in muscle may be reflective of resources necessary, or are at least available, for over-winter survival. For example, an energy decrease of 34 to 57 % total lipid over the winter period was measured for juvenile Atlantic Salmon (*Salmo salar*) (Næsje et al. 2006). Therefore populations with a higher investment in reproduction, a higher percent lipid stored in muscle tissue, and greater length-at-age must be in better overall condition for over-winter survival.

Although DHA is considered an important indicator of fish health (Arts and Kohler 2009), similar patterns of association between DHA and fish growth and reproductive strategies were not observed. DHA is highly conserved through aquatic food webs, being deposited in phospholipids and preferentially mobilized from muscle tissue for use in ovary development during spawning (Dalsgaard et al. 2003). Nevertheless, there was no relationship between the concentration of DHA stored in muscle tissue and energy investment into growth and reproduction. For example, Point Pelee Lake Whitefish have the lowest DHA concentrations and the highest percent lipid in comparison to all other studied populations. In contrast, the population from Elk Rapids had significantly higher DHA concentrations but was at the low end of the lipid reserve range. Thus, DHA concentrations do not appear to be directly related to condition as measured by lipid levels. Instead DHA levels depend on the prevailing abiotic environmental conditions (e.g., temperature). Polyunsaturated fatty acids play an important role in homeoviscous adaptation of phospholipid membranes (Kelly and Kohler 1999; Snyder and Hennessey 2003; Arts and Kohler 2009). Specifically, unsaturated fatty acids are crucial for maintaining the fluidity necessary for proper functioning of phospholipid membranes (Arts and Kohler 2009 and referencing within). Studies have linked the importance of DHA and other unsaturated fatty acids with fish acclimatization to cold temperatures (Kelly and Kohler 1999; Snyder and Hennessey 2003). Colder temperatures require greater amounts of unsaturated fatty acids (e.g., DHA) to maintain functioning membranes.

Suggested links between temperature and DHA concentrations are consistent with results observed here, with populations from colder environments (e.g., Lake Superior) tending to have greater tissue DHA concentrations than populations from warmer environments (e.g., Lake Erie).

3.4.2 Diet and overall condition

Niche width varied among populations as indicated by the significantly different population carbon stable isotope variances. Within population niche variability (i.e., use of variable prey sources at the base of the food web) was greatest for Whitefish Point and Naubinway. Populations with large niche widths are termed generalist populations and can be composed of all generalist feeders or many specialists (Bearhop et al. 2004). All other populations had a low $\delta^{13}C$ variance, suggesting a low degree of niche diversification and populations with more specialized diets (Bearhop et al. 2004). $\delta^{15}N$ variance was not statistically different among populations meaning that the degree of omnivory was similar for all populations (Bearhop et al. 2004).

Populations display varying affinities for pelagic or littoral food webs at variable trophic levels as indicated by significantly different mean carbon and baseline corrected nitrogen stable isotope values. For example, Whitefish Point and Naubinway populations had significantly higher mean $\delta^{13}C$ values and the lowest mean $\delta^{15}N$ signatures. Accordingly, it could be assumed that Naubinway and Whitefish Point Lake Whitefish mainly consumed littoral prey from lower trophic levels, for example, benthic invertebrates. Harvey et al. (2008) also found that Lake Superior Lake Whitefish were nearshore feeders in Whitefish Bay and that Lake Whitefish $\delta^{13}C$ signatures were spatially variable, suggesting different foraging ecology throughout the lake. Diet data from Lake Michigan populations suggested that Lake Whitefish were feeding on a variety of prey from littoral sources to pelagic sources (Fagan et al. *in review*). An alternate feeding strategy was apparent for Point Pelee fish, a population with the highest $\delta^{15}N$ and low $\delta^{13}C$ signatures, a combination which

suggests pelagic feeding at higher trophic levels than other populations. Without *Diporeia*, Point Pelee Lake Whitefish may be feeding on pelagic food sources such as fish, dreissenid mussels or zooplankton to satisfy energy requirements for high growth, reproduction and investment in lipid storage. These findings concur with those of Lumb et al. (2007) and Cook et al. (2005) who found that Lake Whitefish in Lake Erie have a diverse diet in the absence of *Diporeia* and are able to maintain an overall good condition.

The literature suggests that Lake Whitefish populations began to become physiologically stressed, as manifested by declining growth and condition, subsequent to *Diporeia* abundance declines (Pothoven et al. 2001; Madenjian et al. 2002). In this study, the proximity of Lake Whitefish mean stable carbon and nitrogen isotope signatures to *Diporeia* signatures were not significantly related to measures of lipid stores in muscle tissue or overall fish condition. The lack of association suggests no strong linkages between *Diporeia* consumption and fish condition. For example, Bailey's Harbor and Elk Rapids populations in Lake Michigan had average Euclidean distances (Δ_{WD}) that suggested greater reliance on *Diporeia* consumption, but both populations evidenced poorer growth, reproductive trade-offs and lower lipid stores. It is possible that populations with access to declining *Diporeia* populations are still feeding on the amphipod, but because of decreasing abundances are unable to consume sufficient quantities necessary for growth and reproduction. Populations with higher growth rates and lipid values were not linked isotopically with *Diporeia*, but were observed to have both a pelagic (e.g., Point Pelee) and a littoral diet (e.g., Whitefish Point). Thus, populations may successfully switch from consuming *Diporeia* as the primary prey choice by adopting a variety of feeding tactics.

3.4.3 Conclusion

My results indicate that Lake Michigan Lake Whitefish have lower growth and reproduction, and invest less in lipid stores than populations from lakes Erie and Superior, but that differences in

condition are independent of the type of prey resources used. Given previous evidence of spatially

varied diets (e.g., Harvey et al. 2008), the links between diet and declining condition in Lake

Whitefish may be more complex than the lack of availability of a single prey resource. For example,

where loss of prey resources promotes increased inter-specific competition for food resources, Lake

Whitefish may be competitively inferior and suffer consequent declines in condition. Where loss of

prey resources does not result in increased inter-specific competition, e.g., because of higher local

productivity as in Lake Erie, or where Lake Whitefish themselves are competitively superior, e.g.

colder environments in Lake Superior, Lake Whitefish do not appear to suffer consequent declines in

condition as a result of the loss of a single, albeit historically important, prey resource.

3.5 Figures and Tables

Figure 3.1 Sampling locations for the eight populations of Lake Whitefish (*Coregonus clupeaformis*) used in this study.
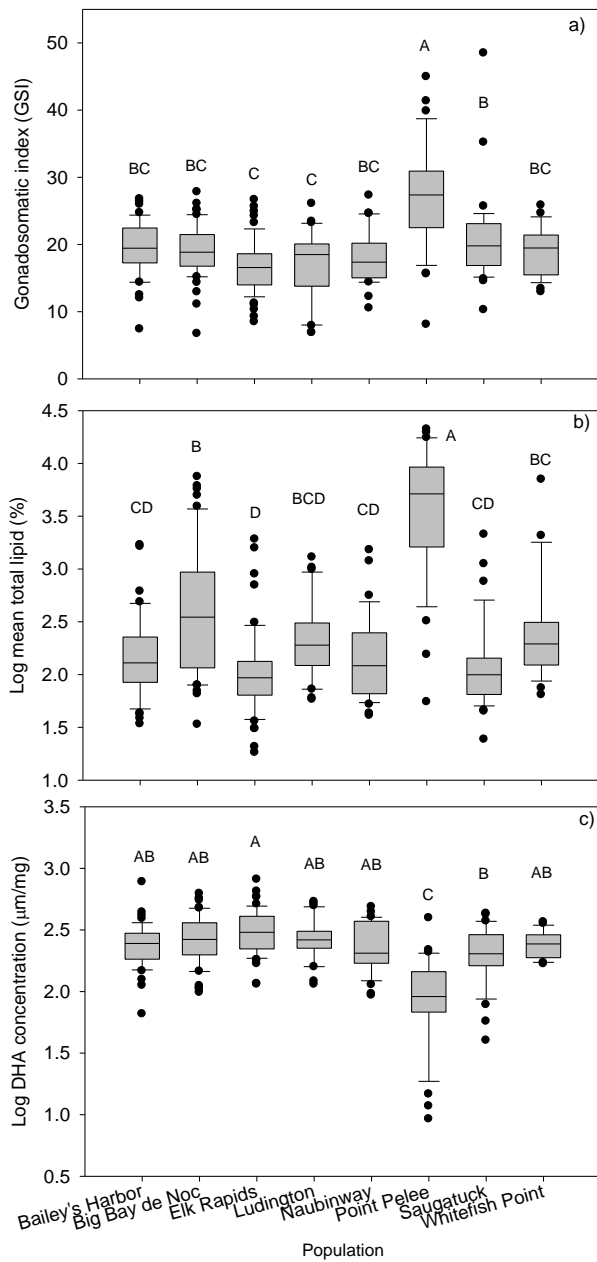
Figure 3.2 Lake Whitefish a) gonadosomatic index, b) log mean percent total muscle lipid, and c) log

concentration of muscle docosahexaenoic acid (DHA) in studied populations. Letters (A, B, C, D)

denote populations with statistically similar means as determined using the Tukey-Kramer post-hoc

HSD test.
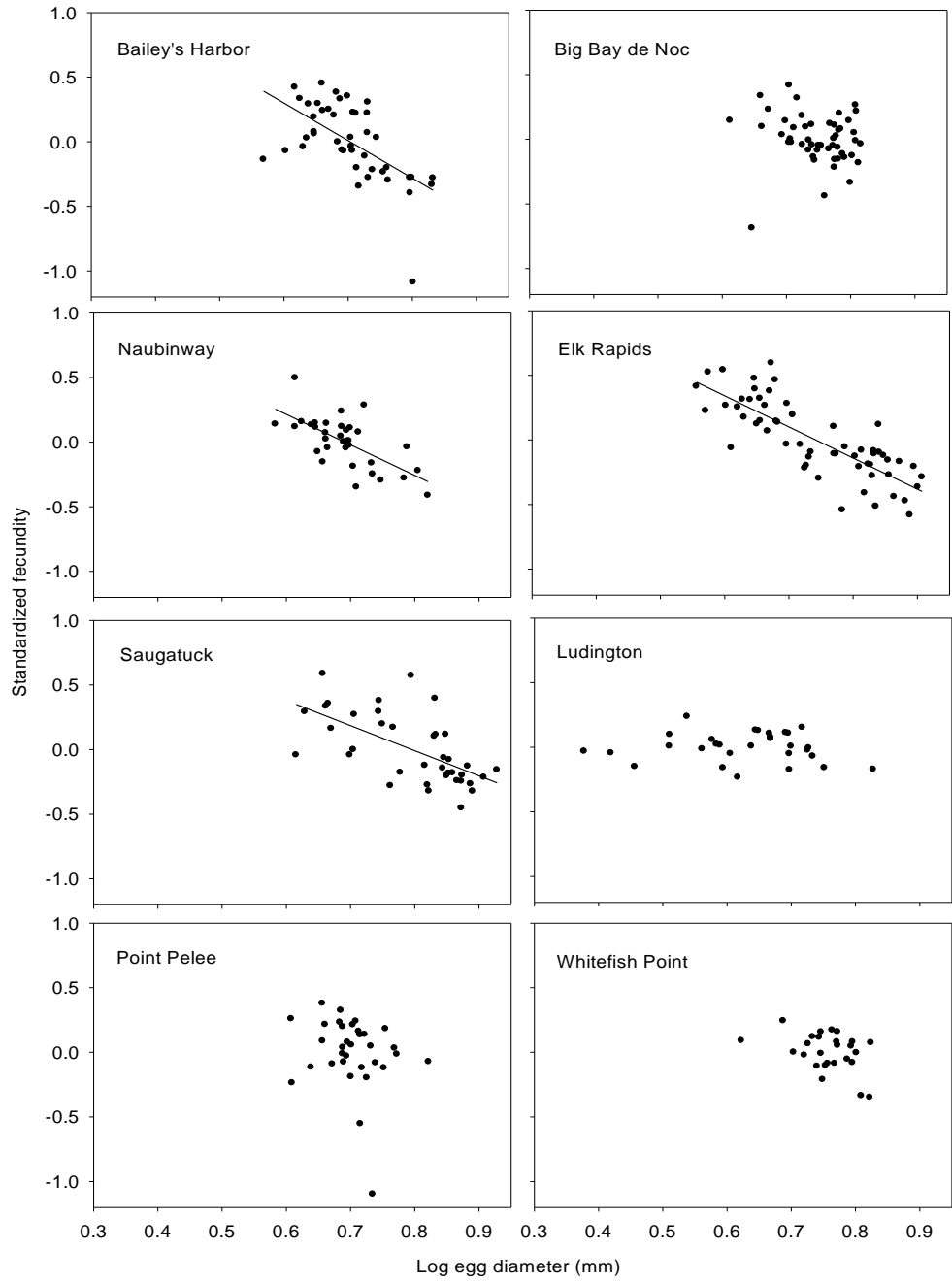
Figure 3.3 Standardized fecundity versus log egg diameter (mm) measurements for each Lake Whitefish population. Populations with significant regressions (P < 0.05) include the estimated model.
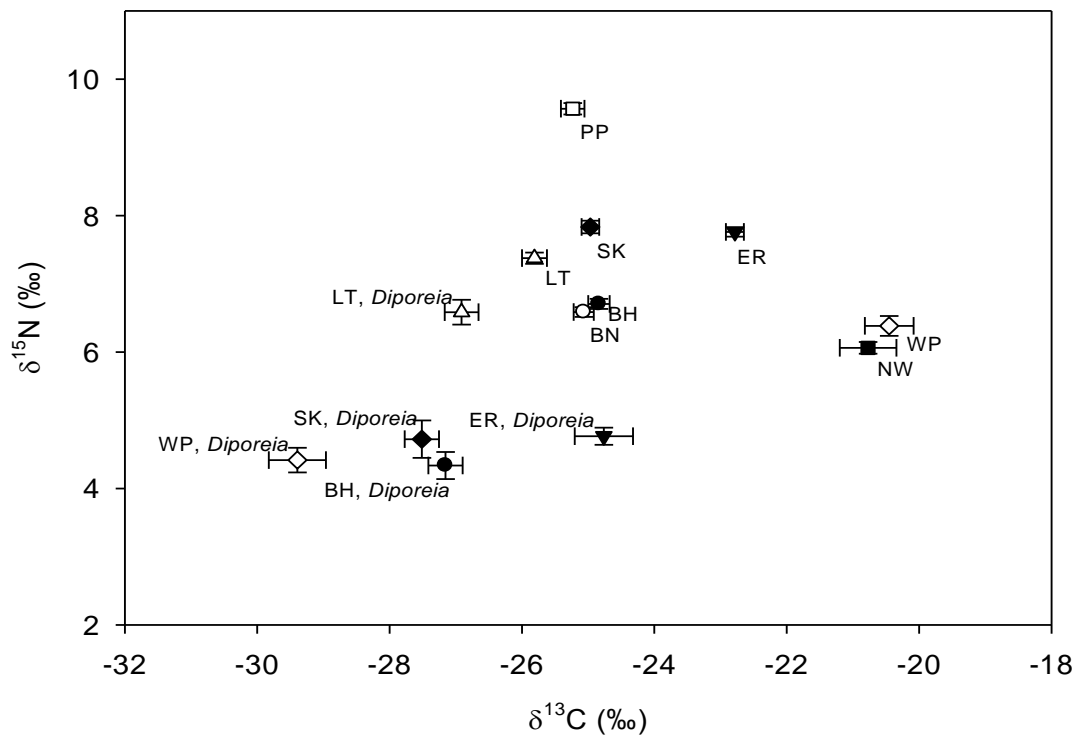
Figure 3.4 Carbon and nitrogen stable isotope signatures (± standard error) for each population of female Lake Whitefish and the corresponding *Diporeia* (labelled) signatures from sampled locations. Populations were identified with labels as follows: Whitefish Point (WP), Point Pelee (PP), Saugatuck (SK), Ludington (LT), Elk Rapids (ER), Naubinway (NW), Big Bay de Noc (BN) and Bailey's Harbor (BH).
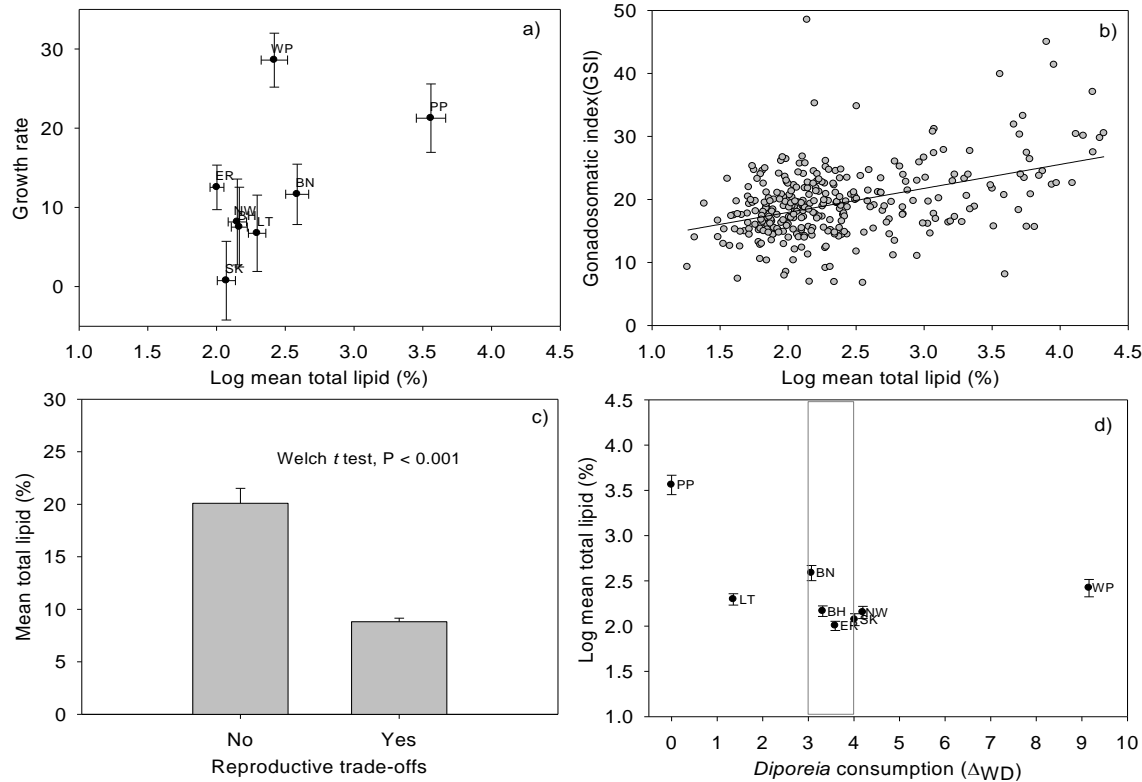
Figure 3.5 Lake Whitefish a) population growth rates and log mean total muscle lipid, b) gonadosomatic index (GSI) and log mean total muscle lipid of all individuals, c) mean total percent muscle lipid of grouped populations: those with significant trade-offs between egg size and number and those without trade-offs, and d) population log mean total muscle lipid and *Diporeia* consumption in terms of Euclidean distance (Δ_{WD}). The grey box highlights populations with high probably of feeding on *Diporeia*. The Point Pelee population was assigned a Δ_{WD} value of 0 as there are no *Diporeia* in Lake Erie. Where possible the value ± standard error was plotted. Populations were identified with labels as follows: Whitefish Point (WP), Point Pelee (PP), Saugatuck (SK), Ludington (LT), Elk Rapids (ER), Naubinway (NW), Big Bay de Noc (BN) and Bailey's Harbor (BH).
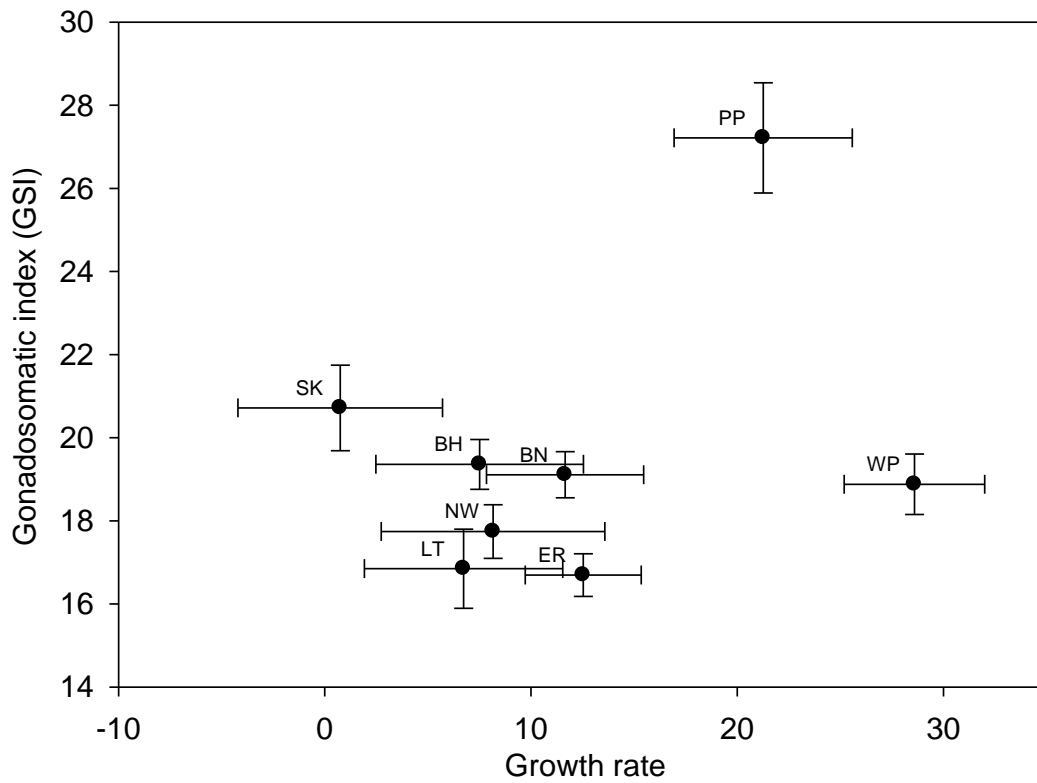
Figure 3.6 Mean gonadosomatic index (GSI) and growth rate for each population (± standard error).

Populations were identified with labels as follows: Whitefish Point (WP), Point Pelee (PP),

Saugatuck (SK), Ludington (LT), Elk Rapids (ER), Naubinway (NW), Big Bay de Noc (BN) and

Bailey's Harbor (BH).

Table 3.1 Estimated length-at-age, log fecundity-weight and standardized log fecundity-egg diameter model regression slope estimates for females in each study population. Confidence limits, upper and lower 95%, are given in parentheses. Populations with a common slope estimate are denoted with a common letter (e.g. A, B) superscript. Significant linear relationships are denoted by *.

Population	n	Growth Length-at-age Slope (95% CI)	Reproduction Log fecundity - weight log a	Slope (95% CI)	Standard. fecundity - egg diam. Slope (95% CI)
Bailey's Harbor	44	7.51 (-2.66, 17.67)	0.97	1.31 (0.89, 1.74)*A	-2.91 (-4.10, -1.71)* A
Big Bay de Noc	50	11.65 (3.99, 19.31)* B	2.10	1.15 (0.90, 1.41)*B	-0.58 (-1.73, 0.58)
Elk Rapids	58	12.53 (6.89, 18.16)* B	-0.22	1.48 (1.18, 1.78)*A	-2.41 (-2.88, -1.93)* A
Ludington	30	6.73 (-3.13, 16.59)	4.31	0.88 (0.62, 1.15)*B	-0.07 (-0.50, 0.36)
Naubinway	34	8.16 (-2.89, 19.21)	-0.88	1.60 (1.30, 1.90)*A	-2.36 (-3.31, -1.41)* A
Point Pelee	33	21.26 (12.44, 30.07)* A	3.54	1.01 (0.71, 1.30)*B	-1.28 (-3.48, 0.91)
Saugatuck	38	0.75 (-9.37, 10.86)	4.09	0.86 (0.32, 1.41)*B	-1.94 (-2.77, -1.11)* A
Whitefish Point	26	28.59 (21.55, 35.62)* A	1.65	1.18 (1.05, 1.32)*B	-1.29 (-2.57, -0.02)

Table 3.2 Female Lake Whitefish stable carbon ($\delta^{13}C$) and baseline corrected nitrogen ($\delta^{15}N$) isotope mean with the coefficient of variation in parentheses and Euclidean distance (Δ_{WD}) between mean Lake Whitefish and *Diporeia* prey in each region. Superscripts denote groups with statistically similar means based on the Tukey-Kramer post-hoc HSD test.

Population	$\delta^{13}C$ (CV)	$\delta^{15}N$ (CV)	Δ_{WD}
Bailey's Harbor	-24.84 (0.04) [C]	6.70 (0.07) [D]	3.31
Big Bay de Noc	-25.07 (0.04) [CD]	6.58 (0.08) [D]	3.07
Elk Rapids	-22.78 (0.05) [B]	7.76 (0.07) [B]	3.59
Ludington	-25.81 (0.04) [D]	7.37 (0.06) [C]	1.36
Naubinway	-20.77 (0.12) [A]	6.06 (0.08) [E]	4.20
Point Pelee	-25.24 (0.04) [CD]	9.57 (0.05) [A]	n/a
Saugatuck	-24.97 (0.03) [CD]	7.83 (0.07) [B]	4.02
Whitefish Point	-20.45 (0.09) [A]	6.38 (0.11) [DE]	9.16

Chapter 4

General Conclusions and Suggestions for Future Research

Reductions in Lake Whitefish growth and condition in the upper Great Lakes have formed the core of much recent fisheries research (e.g., Pothoven et al. 2001; Madenjian et al. 2002; Schneeberger et al. 2005; Pothoven and Nalepa 2006; Pothoven et al. 2006). Theories explaining the changes in condition have been based on the decline in the quality of food available as a result of decreasing *Diporeia* densities in the Great Lakes (Pothoven et al. 2001; Pothoven et al. 2006; Pothoven and Nalepa 2006). This thesis used stable isotope analysis with the aim of determining if there was a plausible link between the declines in Lake Whitefish condition, as indicated in dietary and condition indices, and *Diporeia* abundances for Lake Whitefish populations from around the Great Lakes.

When prey and condition were compared among Lake Michigan Lake Whitefish populations, it was determined that Lake Whitefish exhibited different feeding habits throughout the lake as indicated by distinctive carbon and nitrogen isotope signatures. Trophic niche width and niche space inferred from stable isotope measures also varied among regions. No relationship was found between stable isotope measures and condition metrics (e.g., % muscle lipid, DHA fatty acids). Overall, the results did not substantiate the hypothesis of a causative linkage between Lake Whitefish condition and prey use, particularly the use of *Diporeia*.

When traditional measures of condition did not provide support for the hypothesis that *Diporeia* absences were related to poor Lake Whitefish condition, energy partitioned into growth, reproduction and stored as energy reserves was compared among females from populations of Lake Whitefish from lakes Michigan, Erie and Superior. Analyses suggested that populations investing more energy in growth and reproduction also had more energy stored as muscle lipids. Those populations with low stored muscle lipids displayed reproductive tradeoffs (egg size vs. number) and

56

evidenced little to no growth. Among the studied populations, only those from Lake Michigan provided any evidence of reliance on *Diporeia* as prey. As Lake Michigan populations also tended to be in the poorest condition and/or displayed evidence of reproductive trade-offs symptomatic of nutritional stress, it could not be concluded that *Diporeia* consumption provided more energy for growth, reproduction and stored energy.

While changes in the availability of prey resources has had an effect on Lake Whitefish populations, declining abundances of *Diporeia* alone cannot explain the systemic changes in Lake Whitefish condition across the Great Lakes basin. The stressed condition of populations in Lake Michigan is more likely related to a combination of factors that may include declining *Diporeia* abundances, low overall or alternative prey availability, increases in Lake Whitefish densities, or increased inter-specific competition with other fishes. The Great Lakes are large and dynamic systems where many factors have the potential to affect food web interactions and structure. Complexity in the spatial and temporal structure of Great Lakes food webs make it difficult to link any single change in the ecosystem with an observed effect such as declining Lake Whitefish condition.

Given the complexity observed, management recommendations and suggestions for future research into the factors involved in the declining growth and condition of Lake Whitefish in Lake Michigan should include:

1. Continuous monitoring, quantification and evaluation of changes in primary productivity in the Great Lakes. Primary productivity plays an important role in determining food availability for upper trophic levels and comparable data for all lakes would allow researchers to better understand the factors that influence variations at the base of the food web. The benefits of this research would extend to all Great Lakes food web studies.

2. Evaluation of Lake Michigan benthic invertebrate composition and density to better document prey quality and availability to Lake Whitefish and other competing fishes.

3. Continued monitoring of Lake Whitefish population dynamics within the Great Lakes, including: population density, population growth rate, condition indices (% lipids, fatty acids) and diet composition. The monitoring of population metrics would enable researchers to better quantify Lake Whitefish intra-specific competition and the comparative status of identifiable sub-populations.

4. Quantification of the inter-specific competitive pressures of other fish species on Lake Whitefish within Lake Michigan. Lake Whitefish within Lake Michigan may have experienced increased competitive pressures from other fishes as a result of overall declines in prey resources, including *Diporeia.*

5. The frequency and quantity of Lake Whitefish harvests in Lake Michigan should be reduced until populations are able to stabilize and rebound.

6. Continued effort should be put into avoiding the establishment and spread of exotic freshwater species and the maintenance of native biodiversity within the Great Lakes.

This project is important because it explicitly explored the possibility that declining *Diporeia* abundances may be linked directly to the concurrent declines in Lake Michigan Lake Whitefish. However, declining *Diporeia* abundances are only a piece of the puzzle and the disappearance of *Diporeia* cannot explain observed declines in the condition and growth of Lake Whitefish. It is my opinion that overall food (resource) availability in the Great Lakes, competition among fish species and the levels of Lake Whitefish fisheries exploitation should be considered in the development of management plans for the conservation of native Lake Whitefish populations and the maintenance of native biodiversity within the Great Lakes.

References

Chapter 1

Cook, H.A., Johnson, T.B., Locke, B. and Morrison, B.J. 2005. Status of Lake Whitefish *Coregonus clupeaformis* in Lake Erie. In *Proceedings of a workshop on the dynamics of Lake Whitefish* (Coregonus clupeaformis) *and the amphipod* Diporeia *spp. in the Great Lakes,* L.C. Mohr and T.F. Nalepa, eds., pp. 87–104. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical Report 66.

Dadswell, M.J. 1974. Distribution, ecology and postglacial dispersal of certain crustaceans and fishes in eastern North America. National Museum of Natural Sci., Ottawa, Canada. Publ. Zool. No. 11. 110p.

DeBruyne, R.L., Galarowicz, T.L., Claramunt, R.M. and Clapp, D.F. 2008. Lake Whitefish relative abundance, length-at-age, and condition in Lake Michigan as indicated by fishery-independent surveys. Journal of Great Lakes Research 34: 235-244.

DeNiro, M.J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica Cosmochimica Acta. 45: 341-351.

Dermott, R. and Kerec, D. 1997. Changes to the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979-1993. Canadian Journal of Fisheries and Aquatic Sciences 54: 922-930.

Dermott, R. and Munawar, M. 1993. Invasion of Lake Erie offshore sediments by *Dreissena*, and its ecological implications. Canadian Journal of Fisheries and Aquatic Sciences 50: 2298-2304.

Eadie, B.J. and Robbins, J.A. 2005. Composition and accumulation of recent sediments in Lake Michigan. State of Lake Michigan: ecology, health and management. pp. 89-111. Edited by T. Edsall & M. Munawar.

Ebener, M.P. 1997. Recovery of Lake Whitefish populations in the Great Lakes. Fisheries 22: 18-22.

Freedman, B. 2001. Environmental Science, a Canadian perspective, 2nd edition.

Fuller, K., Shear, H. and Wittig, J. (Eds.). 1995. Great Lakes: an environmental atlas and resource book, 3rd edition. Government of Canada and United States Environmental Protection Agency.

Gardner, W. S., Nalepa, T.F., Frez, W. A., Cichocki, E. A. and Landrum, P. F. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. Canadian Journal of Fisheries and Aquatic Sciences 42: 1827-1832.

Griffiths, R.W., Schloesser, D.W., Leach, J.H. and Kovalak, W.P. 1991. Distribution and dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region. Canadian Journal of Fisheries and Aquatic Sciences 48: 1381.1388.

Hardy, M.B. 1994. The resurgence of Lake Whitefish (*Coregonus clupeaformis*) and its relationship to rainbow smelt and other factors in Lake Erie. M.Sc. Thesis, University of Waterloo, Waterloo, Ontario, Canada.

Hart, J.L. 1931. The food of the Whitefish (*Coregonus clupeaformis*) in Ontario waters, with a note on the parasites. Contr. Can. Biol. Fish. 21: 445-454.

Healey, M.C. 1980. Growth and recruitment in experimentally exploited Lake Whitefish (*Coregonus clupeaformis*) populations. Canadian Journal of Fisheries and Aquatic Sciences 37: 255-267.

Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N. and Howell, T. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 61: 1285-1293.

Hoyle, J.A., Casselman, J.M., Dermott, R., and Schaner, T. 1999. Changes in Lake Whitefish (*Coregonus clupeaformis)* stocks in eastern Lake Ontario following Dreissena mussel invasion. Great Lakes Research Review 4: 5-10.

Ihssen, P.E., Evans, D.O., Christie, W.J., Reckahn, J.A. and DesJardine, R.L. 1981. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of Lake Whitefish (*Coregonus clupeaformis*) in the Great Lakes region. Canadian Journal of Fisheries and Aquatic Sciences 38: 1790-1807.

Kratzer, J.F., Taylor, W.W. and Turner, M. 2007. Changes in fecundity and egg lipid content of Lake Whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986-87 and 2003-05. Journal of Great Lakes Research 33: 922-929.

Lantry, B.F. and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great-Lakes, an interlake comparison. Transactions of the American Fisheries Society 122: 951-976.

Madenjian, C. P., Fahnenstiel, G. L., Johengen, T. H., Nalepa, T.F., Vanderploeg, H. A., Fleischer, G. W., Schneeberger, P.J., Benjamin, D. M., Smith, E. B., Bence, J.R., Rutherford, E. S., Lavis, D. S., Robertson, D. M., Jude, D. J. and Ebener, M. P. 2002. Dynamics of the Lake Michigan food web, 1970–2000. Canadian Journal of Fisheries and Aquatic Sciences 59: 736–753.

Mills, K.H., Gyselman, E.C., Chalanchuk, S.M. and Allan, D.J. 2004. Growth, annual survival, age and length frequencies for unexploited Lake Whitefish populations. Ann. Zool. Fennici 41: 263-270.

Mohr, L.C. and Ebener, M.P. 2005. Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Huron. In *Proceedings of a workshop on the dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the amphipod* Diporeia *spp. In the Great Lakes*, L.C. Mohr and T.F. Nalepa, eds. Ann Arbor, MI. Great Lakes Fisheries Commission Technical Report 66.

Nalepa, T.F., Fanslow, D.L. and Lang, G.A. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshwater Biology 54: 466-479.

Nalepa, T.F., Hartson, D.J., Buchanan, J., Cavaletto, J.F., Lang, G.A. and Lozano, S.J. 2000. Spatial variation in density, mean size and physiological condition of the holartic amphipod *Diporeia* spp. in Lake Michigan. Freshwater Biology 43: 107-119.

Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A. and Lozano, S.J. 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980-1993. Canadian Journal of Fisheries and Aquatic Sciences 55:2402-2413.

Nalepa, T.F., Mohr, L.C., Henderson, B.A., Madenjian, C.P. and Schneeberger, P.J. 2005. Lake Whitefish and *Diporeia* spp. in the Great Lakes: An overview. In *Proceedings of a workshop on the dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the amphipod* Diporeia *spp. in the Great Lakes*, L.C. Mohr and T.F. Nalepa, eds., p. 3-19. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical Report 66.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718.

Pothoven, S.A. and Madenjian, C.P. 2008. Changes in consumption by alewives and Lake Whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. North American. Journal of Fisheries Management 28: 308-320.

Pothoven, S.A., and Nalepa, T.F. 2006. Feeding ecology of Lake Whitefish in Lake Huron. Journal of Great Lakes Research 32: 489-501.

Pothoven, S.A., Nalepa, T.F., Madenjian, C.P., Rediske, R.R., Schneeberger, P.J. and He, J.X. 2006. Energy density of Lake Whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. Environmental Biology of Fishes 76: 151-158.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J. and Brandt, S.B. 2001. Changes in diet and body condition of Lake Whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21: 876-883.

Scharold, J.V., Lozano, S.J. and Corry, T.D. 2004. Status of the amphipod *Diporeia* spp. in Lake Superior, 1994-2000. Journal of Great Lakes Research 30 (Supplement 1): 360-368.

Schneeberger, P.J., Ebener, M.P., Toneys, M. and Peters, P.J. 2005. Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Michigan. In *Proceedings of a workshop on the dynamics of Lake Whitefish* (Coregonus clupeaformis) *and the amphipod* Diporeia *spp. in the Great Lakes*, L.C. Mohr and T.F. Nalepa, eds., pp. 67-86. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical Report 66.

Scott, W.B. and Crossman, E.J. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa.

Taylor, W.W. and Freeberg, M.H. 1984. Effect of food abundance on larval Lake Whitefish, *Coregonus clupeaformis* Mitchill, growth and survival. Journal of Fisheries Biology 25: 733-741.

Chapter 2

Bartlett, M.S. 1937a. Some examples of statistical methods of research in agriculture and applied biology. Journal of the Royal Statistical Society Supplement 4: 137-170.

Bartlett, M.S. 1937b. Properties of sufficiency and statistical tests. Proc. Roy. Statist. Soc. Ser. A 160: 268-282.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A. and Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73: 1007-1012.

Bell, M.V. and Dick, J.R. 1993. The appearance of rods in the eyes of Herring and increased di-docosahexaenoyl molecular species of phospholipids. Journal of the Marine Biological Association of the United Kingdom 73: 679-688.

Bligh, E. G. and Dyer, W. J. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37: 911-917.

Bowers, J.A. 1988. Diel vertical migration of the opossum shrimp *Mysis relicta* in Lake Superior: observations and sampling from the Johnson-sea-link II submersible. Bulletin of Marine Science 43: 730-738.

Cavaletto, J.F. and Gardner, W.S. 1998. Seasonal dynamics of lipids in freshwater benthic

    invertebrates. In *Lipids in Freshwater Ecosystems*, M.T. Arts and B.C. Wainman, eds., pp. 109-

    131 New York, N.Y. Springer.

Cornwell, W.K., Schwilk, D.W. and Ackerly, D.D. 2006. A trait-based test for habitat filtering:

    convex-hull volume. Ecology 87: 1465-1471.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-

    spectrometric analysis of carbon dioxide. Geochimica et Cosmochimica Acta 12: 133-149.

Cummins, K.H. and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological

    energetics. Mitt. Int. Ver. Theor. Angew. Limnol. No. 18.

Dadswell, M.J. 1974. Distribution, ecology and postglacial dispersal of certain crustaceans and fishes

    in eastern North America.. National Museum of Natural Sci., Ottawa, Canada. Publ. Zool. No.

    11. 110p.

Dalsgaard, J., St. John, M., Kattner, G., Muller-Navarra, D. and Hagen, W. 2003. Fatty acid trophic

    markers in the pelagic marine environment. In *Advances in Marine Biology*, A.J. Southward,

    P.A. Tayler, C.M. Young, and L.A. Fuiman, eds., pp. 225-340. New York, N.Y. Academic

    Press.

DeBruyne, R.L., Galarowicz, T.L., Claramunt, R.M. and Clapp, D.F. 2008. Lake Whitefish relative
abundance, length-at-age, and condition in Lake Michigan as indicated by fishery-independent
surveys. Journal of Great Lakes Research 34: 235-244.

Dermott, R. and Kerec, D. 1997. Changes to the deepwater benthos of eastern Lake Erie since the
invasion of *Dreissena*: 1979-1993. Canadian Journal of Fisheries and Aquatic Sciences 54:
922-930.

Driver, E.A., Sugden, L.G. and Kovach, R.J. 1974. Calorific, chemical and physical values of
potential duck foods. Freshwater Biology 4: 281-292.

Ebener, M.P. 1997. Recovery of Lake Whitefish populations in the Great Lakes. Fisheries 22: 18-22.

Eggleton, M.A. and Schramm, J.L., Jr. 2004. Feeding ecology and energetic relationships with habitat
of Blue Catfish, *Ictalurus furcatus*, and Flathead Catfish, *Pylodictis olivaris*, in the lower
Mississippi River, U.S.A. Environ. Biol. Fish 70: 107-121.

Hamilton, S.K., Lewis, W.M. Jr. and Sippel, S.J. 1992. Energy sources for aquatic animals in the
Orinoco River floodplain: evidence from stable isotopes. Oecologia 89: 324-330.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist
100: 419-424.

Ihssen, P.E., Evans, D.O., Christie, W.J., Reckahn, J.A. and DesJardine, R.L. 1981. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of Lake Whitefish (*Coregonus clupeaformis*) in the Great Lakes region. Canadian Journal of Fisheries and Aquatic Sciences 38: 1790-1807.

Johnson, R.L., Blumenshine, S.C. and Coghlan, S.M. 2006. A bioenergetic analysis of factors limiting Brown Trout growth in an Ozark tailwater river. Environmental Biology of Fishes 77: 121-132.

Jones, M.L., Arts, M.T., Faisal, M., Ebener, M.P., Wagner, T., Brendan, T.O., Honeyfield, D. and Wright, G. 2008. Magnitude and potential causes of mortality in four Lake Whitefish populations in Lakes Michigan and Huron: a multidisciplinary approach. Great Lakes Fishery Trust Project Completion Report, Project 2003-06.

Kratzer, J.F., Taylor, W.W. and Turner, M. 2007. Changes in fecundity and egg lipid content of Lake Whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986-87 and 2003-05. Journal of Great Lakes Research 33: 922-929.

Lantry, B.F. and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great-Lakes, an interlake comparison. Transactions of the American Fisheries Society 122: 951-976.

Layman, C. A., Arrington, D.A., Montana, C.G. and Post, D.M. 2007. Can stable isotope ratios provide quantitative measures of trophic diversity within food webs? Ecology 88: 42–48.

Levy, D.A. 1991. Acoustic analysis of diel vertical migration behaviour of *Mysis relicta* and Kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 28: 67-72.

Love, R.M. 1980. The chemical biology of fishes, Vol. 2. 943 pp. New York, N.Y. Academic Press.

Madenjian, C.P., O'Connor, D.V., Pothoven, S.A., Schneeberger, P.J., Rediske, R.R., O'Keefe, J.P., Bergstedt, R.A., Argyle, R.L. and Brandt, S.B. 2006. Evaluation of a Lake Whitefish bioenergetics model. Transactions of the American Fisheries Society 135:61-75.

Marriotti, A. 1983. Atmospheric nitrogen is a reliable standard for natural N-15 abundance measurements. Nature 303: 685-687.

Mortimer, C.H. 1975. Environmental Status of the Lake Michigan Region, 2: Physical Limnology of Lake Michigan, Part 1, Physical characteristics of Lake Michigan and its response to applied forces. ANL/ES-40, Argonne National Laboratory, U.S. Energy Research and Development Administration.

Nalepa, T.F., Fanslow, D.L. and Lang, G.A. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshwater Biology 54: 466.479.

Nalepa, T.F., Hartson, D.J., Buchanan, J., Cavaletto, J.F., Lang, G.A. and Lozano, S.J. 2000. Spatial variation in density, mean size and physiological condition of the holartic amphipod *Diporeia* spp. in Lake Michigan. Freshwater Biology 43: 107-119.

Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A. and Lozano, S.J. 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980-1993. Canadian Journal of Fisheries and Aquatic Sciences 55: 2402-2413.

Phillips, D.L. and Gregg, J.W. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171–179.

Phillips, D.L. and Gregg, J.W. 2003. Source partitioning using stable isotopes: coping with to many sources. Oecologia 136: 261-269.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718.

Pothoven, S.A. and Madenjian, C.P. 2008. Changes in consumption by Alewives and Lake Whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. North American Journal of Fisheries Management 28: 308-320.

Pothoven, S.A. and Nalepa, T.F. 2006. Feeding ecology of Lake Whitefish in Lake Huron. Journal of Great Lakes Research 32: 489-501.

Pothoven, S.A., Fahnenstiel, G.L. and Vanderploeg, H.A. 2004. Spatial distribution, biomass, and population dynamics of *Mysis relicta* in Lake Michigan. Hydrobiologia 522: 291-299.

Pothoven, S.A., Nalepa, T.F., Madenjian, C.P., Rediske, R.R., Schneeberger, P.J. and He, J.X. 2006. Energy density of Lake Whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. Environmental Biology of Fishes 76: 151-158.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J. and Brandt, S.B. 2001. Changes in diet and body condition of Lake Whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21: 876-883.

Rennie, M.D. and Verdon, R. 2008. Development and evaluation of condition indices for the Lake Whitefish. North American Journal of Fishes Management 28: 1270-1293.

Rennie, M.D., Sprules, W.G. and Johnson, T.B. 2009. Resource switching in fish following a major food web disruption. Oecologia 159: 789-802.

Ricklefs, R. E. and Lau, M. 1980. Bias and dispersion of overlap indices: results of some Monte Carlo simulations. Ecology 61:1019-1024.

Schneeberger, P.J., Ebener, M.P., Toneys, M. and Peeters, P.J. 2005. Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Michigan. In: *Proceedings of a workshop on the dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the amphipod* Diporeia *spp. in the Great Lakes*,

L.C. Mohr and T.F. Nalepa, eds., pp. 67-86. Ann Arbor, M.I. Great Lakes Fisheries
Commission Technical Report 66.

Smith E. P. and Zaret, T.M. 1982. Bias in estimating niche overlap. Ecology 63:1248-1253.

Stephens, D.W. and Krebs, J.R. 1986. Foraging Theory. 262 pp. N.J. Princeton University Press,
Princeton.

Storch, A.J. 2005. The role of invasive zooplankton in the diets of Great Lakes planktivores. Master's
Thesis, State University of New York, Syracuse, N.Y.

Sushchik, N.N., Gladyshev, M.I., Kalachova, G.S., Makhutova, O.N. and Ageev, A.V. 2006.
Comparison of seasonal dynamics of the essential PUFA contents in benthic invertebrates and
Grayling *Thymallus articus* in the Yenisei River. Comparative Biochemistry and Physiology
145: 278-287.

Vander Zanden, M.J. and Rasmussen, J.B. 1999. Primary consumer δ^{13}C and δ^{15}N and trophic
position of aquatic food web studies. Limnology and Oceanography 46: 2061-2066.

Zar, J.H. 1999. Biostatistical analysis. 663 pp. Upper Saddle River, N.J. Prentice-Hall.

Zellmer, I.D., Arts, M.T., Abele, D. and Humbeck, K. 2004. Evidence of sub-lethal damage in
Daphnia (Cladocera) due to solar UV radiation in sub-Arctic ponds. Journal of Arctic,
Antarctic and Alpine Research 36: 370-377.

Chapter 3

Adams, C.E. and Huntingford, F.A. 1997. Growth, maturation and reproductive investment in Arctic

    Char. Journal of Fish Biology 51: 750-759.

Arts, M.T. and Kohler, C.C. 2009. Chapter 10: Health and condition in fish: the influence of lipids on

    membrane competency and immune response, In *Lipids in aquatic ecosystems*. M.T. Arts, M.T.

    Brett, and M. Kainz, eds. New York, N.Y. Springer.

Barbiero, R.P. and Tuchman, M.L. 2001. Results from the U.S. EPA's biological open water

    surveillance program of the Laurentian Great Lakes: I. Introduction and phytoplankton results.

    Journal of Great Lakes Research 27: 134-154.

Bartlett, M.S. 1937a. Some examples of statistical methods of research in agriculture and applied

    biology. Journal of the Royal Statistical Society Supplement 4: 137-170.

Bartlett, M.S. 1937b. Properties of sufficiency and statistical tests. Proc. Roy. Statist. Soc. Ser. A 160:

    268-282.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A. and Macleod, H. 2004. Determining trophic

    niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:

    1007-1012.

Bell, M.V. and Dick, J.R. 1993. The appearance of rods in the eyes of Herring and increased di-
docosahexaenoyl molecular species of phospholipids. Journal of the Marine Biological
Association of the United Kingdom 73: 679-688.

Bell, G.B., Handford, P. and Dietz, C. 1977. Dynamics of an exploited population of Lake Whitefish
(*Coregonus clupeaformis*). Journal of the Fisheries Research Board of Canada 34: 942-953.

Bligh, E. G. and Dyer, W. J. 1959. A rapid method of total lipid extraction and purification. Canadian
Journal of Biochemistry and Physiology 37: 911-917.

Brown, R.W. and Taylor, W.W. 1992. Effects of egg composition and prey density on the larval
growth and survival of Lake Whitefish (*Coregonus clupeaformis* Mitchill). Journal of
Fish Biology 40: 381-394.

Cook, H.A., Johnson, T.B., Locke, B. and Morrison, B.J. 2005. Status of Lake Whitefish *Coregonus
clupeaformis* in Lake Erie. In *Proceedings of a workshop on the dynamics of Lake Whitefish*
(Coregonus clupeaformis) *and the amphipod* Diporeia *spp. in the Great Lakes,* L.C. Mohr and
T.F. Nalepa, eds., pp. 87–104. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical
Report 66.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-
spectrometric analysis of carbon dioxide. Geochimica et Cosmochimica Acta 12: 133-149.

Dalsgaard, J., St. John, M., Kattner, G., Muller-Navarra, D. and Hagen, W. 2003. Fatty acid trophic

  markers in the pelagic marine environment. In *Advances in Marine Biology*, A.J. Southward,

  P.A. Tayler, C.M. Young, and L.A. Fuiman, eds., pp. 225-340. New York, N.Y. Academic

  Press.

DeBruyne, R.L., Galarowicz, T.L., Claramunt, R.M. and Clapp, D.F. 2008. Lake Whitefish relative

  abundance, length-at-age, and condition in Lake Michigan as indicated by fishery-independent

  surveys. Journal of Great Lakes Research 34: 235-244.

Downing, J.A., Plante, C. and Lalonde, S. 1990. Fish production correlated with primary

  productivity, not the morphoedaphic index. Canadian Journal of Fisheries and Aquatic Sciences

  47: 1929-1936.

Ebener, M.P. 1997. Recovery of Lake Whitefish populations in the Great Lakes. Fisheries 22: 18-22.

Elliot, J.M. 1994. Quantitative ecology and the Brown Trout. New York, N.Y. Oxford University

  Press.

Fagan, K.M., Koops, M.A., Arts, M.T., Sutton, T.M. and Power, M. *in review*. Lake Whitefish

  feeding habits in a disrupted system. Chapter 2/Coregonid Symposium Proceedings.

Griffiths, D. and Kirkwood, R. C. 1995. Seasonal variation in growth, mortality and fat stores of

  Roach and Perch in Lough Neagh, Northern Ireland. Journal of Fish Biology 47: 537–554.

Hardy, M.B. 1994. The resurgence of Lake Whitefish (*Coregonus clupeaformis*) and its relationship to Rainbow Smelt and other factors in Lake Erie. M.Sc. Thesis, University of Waterloo, Waterloo, Ontario, Canada.

Harvey, C.J., Ebener, M.P. and White, C.K. 2008. Spatial and ontogenetic variability of Sea Lamprey diets in Lake Superior. Journal of Great Lakes Research 34: 434-449.

Heermann, L., Eriksson, L-O., Magnhagen, C. and Borcherding, J. 2009. Size-dependent energy storage and winter mortality of perch. Ecology of Freshwater Fish 18: 560–571.

Hoyle, J.A., Casselman, J.M., Dermott, R. and Schaner, T. 1999. Changes in Lake Whitefish (*Coregonus clupeaformis)* stocks in eastern Lake Ontario following Dreissena mussel invasion. Great Lakes Research Review 4: 5-10.

Hutchings, J.A. 1991. Fitness consequences of variation in egg size and food abundance in Brook Trout *Salvelinus fontinalis*. Evolution 45:1162–1168.

Kelly, A.M. and Kohler, C.C. 1999. Cold tolerance and fatty acid composition of striped bass, white bass, and their hybrids. North American Journal of Aquaculture 61: 278-285.

Kennedy, J., Skjæraasen, J.E., Nash, R.D.M., Thorsen, A., Slotte, A., Hansen, T. and Kjesbu, O.S. 2010. Do capital breeders like Atlantic Herring (*Clupeea harengus*) exhibit sensitive periods of nutritional control on ovary development and fecundity regulation? Canadian Journal of Aquatic Sciences 67: 16-27.

Kratzer, J.F., Taylor, W.W. and Turner, M. 2007. Changes in fecundity and egg lipid content of Lake Whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986-87 and 2003-05. Journal of Great Lakes Research 33: 922-929.

Krebs, C.J. 1999. Ecological methodology, second edition. Addison-Welsey Eductional Publishers: Don Mills, Ontario, 620 pp.

Layman, C. A., Arrington, D.A., Montana, C.G. and Post, D.M. 2007. Can stable isotope ratios provide quantitative measures of trophic diversity within food webs? Ecology 88: 42-48.

Lumb, C.E., Johnson, T.B., Cook, H.A. and Hoyle, J.A. 2007. Comparison of Lake Whitefish (*Coregonus clupeaformis*) growth, condition, and energy density between lakes Erie and Ontario. Journal of Great Lakes Research 33: 314-325.

Madenjian, C. P., Fahnenstiel, G. L., Johengen, T. H., Nalepa, T.F., Vanderploeg, H. A., Fleischer, G. W., Schneeberger, P.J., Benjamin, D. M., Smith, E. B., Bence, J.R., Rutherford, E. S., Lavis, D. S., Robertson, D. M., Jude, D. J. and Ebener, M. P. 2002. Dynamics of the Lake Michigan food web, 1970–2000. Canadian Journal of Fisheries and Aquatic Sciences 59: 736–753.

Marriotti, A. 1983. Atmospheric nitrogen is a reliable standard for natural N-15 abundance measurements. Nature 303: 685-687.

Mohr, L.C. and Ebener, M.P. 2005. Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Huron. In *Proceedings of a workshop on the dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the amphipod* Diporeia *spp. in the Great Lakes*, L.C. Mohr and T.F. Nalepa, eds. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical Report 66.

Muir, A. M., Ebener, M. P., He, J. X. and J. E. Johnson. 2008. A comparison of the scale and otolith methods of age estimation for Lake Whitefish in Lake Huron. North American Journal of Fisheries Management 28: 625–635.

Næsje, T.F., Thorstad, E.B., Forseth, T., Aursand, M., Saksgård, R. and Finstad, A.G. 2006. Lipid class content as an indicator of critical periods for survival in juvenile Atlantic Salmon (*Salmo salar*). Ecology of Freshwater Fish 15: 572–577.

Nalepa, T.F., Mohr, L.C., Henderson, B.A., Madenjian, C.P. and Schneeberger, P.J. 2005. Lake Whitefish and *Diporeia* spp. in the Great Lakes: An overview. In *Proceedings of a workshop on the dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the amphipod* Diporeia *spp. in the Great Lakes*, L.C. Mohr and T.F. Nalepa, eds., p. 3-19. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical Report 66.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718.

Pothoven, S.A. and Nalepa, T.F. 2006. Feeding ecology of Lake Whitefish in Lake Huron. Journal of Great Lakes Research 32: 489-501.

Pothoven, S.A., Nalepa, T.F., Madenjian, C.P., Rediske, R.R., Schneeberger, P.J. and He, J.X. 2006. Energy density of Lake Whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. Environmental Biology of Fishes 76: 151-158.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J. and Brandt, S.B. 2001. Changes in diet and body condition of Lake Whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21: 876-883.

Reshetnikov, Yu. S., Paranyushkinda, L.P. and Kiyashko, V.I. 1970. Seasonal changes of blood serum protein composition and fat content in whitefishes. Journal of Ichthyology 10: 804-813.

Roff, D.A. 1992. The evolution of life histories: theories and analysis. New York, N.Y. Chapman and Hall.

Schneeberger, P.J., Ebener, M.P., Toneys, M. and Peters, P.J. 2005. Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Michigan. In *Proceedings of a workshop on the dynamics of Lake Whitefish* (Coregonus clupeaformis) *and the amphipod* Diporeia *spp. in the Great Lakes*, L.C. Mohr and T.F. Nalepa, eds., pp. 67-86. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical Report 66.

Scott, D.P. 1962. Effect of food quantity on fecundity of Rainbow Trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 19: 715-731.

Snyder, R.J. and Hennessey, T.M. 2003. Cold tolerance and homeoviscous adaptation in freshwater

    Alewives (*Alosa pseudoharengus*). Fish physiology and Biochemistry 29: 117-126.

Taylor, W.W., Smale, M.A. and Brown, R.W. 1992. An evaluation of size versus age dependent

    maturation of Lake Whitefish stocks in the upper Great Lakes. Polskie Archiwum

    Hydrobiologh 39: 269-277.

Thorpe, J.E. 1986. Age at first maturity in Atlantic Salmon, *Salmo solar*: freshwater period influences

    and conflicts with smolting, p. 7-14. In *Salmonid age at Maturity*, D. J. Meerburg, ed., Can.

    Spec. Publ. Fish. Aquat. Sci. 89.

Vander Zanden, M.J. and Rasmussen, J.B. 1999. Primary consumer δ^{13}C and δ^{15}N and trophic

    position of aquatic food web studies. Limnology and Oceanography 46: 2061-2066.

Wiegand, M.D. 1996. Composition, accumulation and utilization of yolk lipids in teleost fish.

    Reviews in Fish Biology and Fisheries 6: 259-286.

Zar, J.H. 1999. Biostatistical analysis. 663 pp. Upper Saddle River, N.J. Prentice-Hall.

Zellmer, I.D., Arts, M.T., Abele, D. and Humbeck, K. 2004. Evidence of sub-lethal damage in

    Daphnia (Cladocera) due to solar UV radiation in sub-Arctic ponds. Journal of Arctic,

    Antarctic and Alpine Research 36: 370-377.

Chapter 4

Madenjian, C. P., Fahnenstiel, G. L., Johengen, T. H., Nalepa, T.F., Vanderploeg, H. A., Fleischer, G. W., Schneeberger, P.J., Benjamin, D. M., Smith, E. B., Bence, J.R., Rutherford, E. S., Lavis, D. S., Robertson, D. M., Jude, D. J. and Ebener, M. P. 2002. Dynamics of the Lake Michigan food web, 1970–2000. Canadian Journal of Fisheries and Aquatic Sciences 59: 736–753.

Pothoven, S.A. and Nalepa, T.F. 2006. Feeding ecology of Lake Whitefish in Lake Huron. Journal of Great Lakes Research 32: 489-501.

Pothoven, S.A., Nalepa, T.F., Madenjian, C.P., Rediske, R.R., Schneeberger, P.J. and He, J.X. 2006. Energy density of Lake Whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. Environmental Biology of Fishes 76: 151-158.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J. and Brandt, S.B. 2001. Changes in diet and body condition of Lake Whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21: 876-883.

Schneeberger, P.J., Ebener, M.P., Toneys, M. and Peters, P.J. 2005. Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Michigan. In *Proceedings of a workshop on the dynamics of lake whitefish* (Coregonus clupeaformis) *and the amphipod* Diporeia *spp. in the Great Lakes*, L.C. Mohr and T.F. Nalepa, eds., pp. 67-86. Ann Arbor, M.I. Great Lakes Fisheries Commission Technical Report 66.