May 2013

Changes in the Lake Michigan Trophic Structure: As Revealed by Stable C and N Isotopes

Benjamin Turschak
University of Wisconsin-Milwaukee

Recommended Citation

Turschak, Benjamin, "Changes in the Lake Michigan Trophic Structure: As Revealed by Stable C and N Isotopes" (2013). *Theses and Dissertations*. 170.
https://dc.uwm.edu/etd/170

CHANGES IN THE LAKE MICHIGAN TROPHIC STRUCTURE: AS REVEALED BY STABLE C AND N ISOTOPES

by

Benjamin A. Turschak

A Thesis Submitted in
Partial Fulfillment of the
Requirements for the Degree of

Master of Science
in Freshwater Sciences and Technology

at
The University of Wisconsin-Milwaukee
May 2013

ABSTRACT

CHANGES IN THE LAKE MICHIGAN TROPHIC STRUCTURE AS REVEALED BY STABLE C AND N ISOTOPES

by

Benjamin A. Turschak

The University of Wisconsin-Milwaukee, 2013
Under the Supervision of Professor Harvey A. Bootsma

Food web structures which incorporate both slow (nearshore or detrital) and fast (pelagic) energy channels convey stability upon food web biota through asynchrony and multichannel trophic omnivory. Within the Lake Michigan food web, invasive dreissenid mussels have caused rapid changes to food web structure and energy flows. I used stable C and N isotopes and gut content analysis to determine how Lake Michigan food web structure and stability has changed in the past decade, coincident with the expansion of dreissenid mussels and a decrease in pelagic phytoplankton production. Fish and invertebrate samples collected near the port of Milwaukee, WI were analyzed to determine the ^{13}C:^{12}C ($\delta^{13}C$) and ^{15}N:^{14}N ($\delta^{15}N$) ratios. Sampling took place during three distinct periods 2002-2003, 2005-2006 and 2010-2011, and included nearshore, pelagic and profundal fish and invertebrate taxa. $\delta^{13}C$ and $\delta^{15}N$ values were adjusted relative to primary consumers (dreissenid mussels and amphipods) to facilitate meaningful temporal comparison. Enrichment of $\delta^{13}C$ in most food web components over time suggests increased reliance upon a nearshore basal energy source, although the mechanisms remain unclear. The importance of nearshore energy resources may vary spatially depending upon local nearshore benthic productivity. $\delta^{15}N$ results were more variable but further illustrate restructuring of the Lake Michigan food web. Dreissenid mussels appear to have had two opposing effects of both severely altering food web structure through depletion of offshore food availability while simultaneously increasing stability though increased slow energy channel production. Results suggest that the persistence of most species in the lake may be a consequence of multichannel omnivory and increased reliance upon nearshore energy channels despite substantial declines in lake-wide biomass. Management of Lake Michigan fish stocks should consider increased dependence upon this energetic pathway at least for local spatial scales.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

CHAPTER 2: METHODS

CHAPTER 3: RESULTS

CHAPTER 4: DISCUSSION

LIST OF FIGURES

ACKNOWLEDGEMENTS

I would especially like to thank my adviser, Dr. Harvey Bootsma, who patiently guided me through the struggles of studying large lake ecology. Without his expertise and encouragement, this research would not have been possible. I would also like to thank my committee members, Dr. John Janssen and Dr. Jerry Kaster, for providing samples, helpful insights and comments on earlier drafts. Erin Wilcox and many other students and technicians provided a great deal of help with field and lab processing; I am indebted to them for their efforts. Additional thanks go to Sergiusz Czesny, Thomas Höök, and their respective colleagues for collecting and processing samples for stable isotopes and performing gut content analyses. I would also like to extend my gratitude to David Bunnell, Charles Madenjian and David Warner for providing fish and stable isotope data for statistical analyses. Funding for this project was supported by a grant from Wisconsin and Illinois-Indiana NOAA Sea Grant.

CHAPTER 1: INTRODUCTION

1.1 Trophic Omnivory and Invasive Species

In recent decades, it has become increasingly apparent that lateral transfer of materials (e.g. nutrients and energy) between the littoral and pelagic food chains plays a major role in food web dynamics of lakes (Schindler et al., 1996; Polis et al., 1997; Vadeboncouer et al., 2001; Vander Zanden and Vadeboncouer, 2002). Polis and Strong (1996) and Krause et al. (2003) emphasized the importance of multichannel omnivory whereby consumers and predators are supported by the huge diversity of direct and indirect links between parallel food chains and trophic levels. Reciprocal subsidies between habitats can actually increase production and consumer density beyond the apparent capacity of a single focal habitat (Polis et al., 1997; Huxel and McCann, 1998). These subsidies diminish the effect of stressors by bearing the strain across the breadth of the web rather than cascading through a single linear chain (Polis and Strong, 1996).

Multichannel omnivory and/or reciprocal subsidies across the breadth of the food web appear to strongly influence stability. Using the definition taken from Rooney and McCann (2011), stability refers to a continuous measurement of the likelihood of persistence for a group of interacting species. In both model and natural systems, increased stability associated with multichannel omnivory is driven largely by an asynchrony between the slow and fast energy channels and low average link strength (Huxel and McCann, 1998; McCann, 2000; McCann et al., 2005; Rooney et al., 2006; Rooney and McCann, 2011). Slow energy channels dominated by weak links are less susceptible to rapid oscillations and trophic cascades than fast energy channels (McCann, 2000; McCann et al., 2005; Rooney et al., 2006). For example, recalcitrant dissolved organic carbon of the detrital energy reservoir is metabolized and utilized slowly relative to particulate carbon that is represented primarily by plankton (Mann, 1988; Wetzel, 2001; Moore et al., 2004; Rooney and McCann, 2011). This may lead to asynchrony in temporal fluctuations of different energy pathways, resulting in independence of productivity and turnover processes between the fast pelagic channel and the slower detrital or nearshore channels. For large mobile consumers like fish, multichannel omnivory between these asynchronous channels ensures a more stabile energy source and greater overall ecosystem stability (Vander Zanden and Vadeboncouer, 2002; Rooney et al., 2006).

Species invasions have strong potential to modify the natural asymmetric structure of food webs that confers stability by altering fluxes of energy and nutrients (McCann, 2000; Rodriguez, 2006; Rooney et al., 2006). Changes in trophic structure caused by species invasions may result in the pervasive control of a single energy pathway (McCann, 2000; McCann et al., 2005; Rooney et al., 2006). For example, the addition of invasive smallmouth bass in Canadian Shield lakes reduced littoral prey fish abundance. Consequently, native lake trout became more dependent upon pelagic zooplankters and exhibited a decline in trophic position and condition factor (Vander Zanden et al., 1999). Likewise the invasion of cord grass *Spartina* spp. resulted in a major shift of energetic pathways and trophic structure by reducing water movement in coastal tidal flats. Invertebrates became more dependent upon *Spartina* detrital energy channels following reductions to water flow and subsequent reductions in phytoplankton availability (Levin et al., 2006). Invasive freshwater mussels *Dreissena* spp. can capture pelagic energy and nutrients in the nearshore benthos and reduce pelagic productivity. This is thought to reduce the pelagic energy channels while also increasing nearshore benthic primary production (Hecky et al., 2004; Zhu et al., 2006). These examples highlight several ways in which invasive species can alter energy flow through fast and slow energy channels, although impacts vary depending upon the nature of the food web and invading species.

Species invasions alter energy flows through a variety of mechanisms but often these changes result from shifts in the species community composition (Hooper et al., 2005; Rodriguez, 2006). Species richness and abundance can change drastically following modification of habitat (i.e. replacing existing habitats and creating novel habitats; Limen et al. 2005; Schmidt et al. 2007), trophic subsidies (i.e. exploitable prey resources; Ricciardi 2001), and nutrient dynamics following a species invasion (Hecky et al., 2004). Because functional traits of species mediate fluxes of nutrients and other materials through food webs (Hooper et al., 2005), changes in species composition following an invasion alter both energetic pathways and food web linkages.

1.2 Stable C and N Isotope Analyses

Stable isotope analysis is a useful tool to help elucidate changes in energetic pathway and food web linkages following species invasions in aquatic systems (Vander Zanden et al., 1999; Schmidt et al., 2011). Ratios of ^{13}C:^{12}C relative to an international standard ($\delta^{13}C$, hereafter) are typically distinct for benthic and pelagic primary producers with only slight enrichment (0-1‰) following each trophic transfer (Hecky and Hesslein, 1995; Vander Zanden and Rasmussen, 1999). Therefore, $\delta^{13}C$ can act as an indicator of primary energetic source among aquatic consumers. Ratios of ^{15}N:^{14}N relative to atmospheric N ($\delta^{15}N$, hereafter) are typically enriched by 3-4‰ with each trophic transfer and therefore can be used as a continuous measure of trophic position within a food web (Minagawa and Wada, 1984; Peterson and Fry, 1987). Using both $\delta^{13}C$ and $\delta^{15}N$ relative to a baseline, temporal shifts in food webs can be measured to assess the changes in primary energetic pathways and food web linkages following species invasions (Vander Zanden et al., 1999; Schmidt et al., 2007).

Spatiotemporal variation in algal $\delta^{13}C$ and $\delta^{15}N$ results from nutrient or C limitation in addition to preferential uptake. This characteristic creates the useful disparities between benthic and pelagic $\delta^{13}C$ in aquatic systems (Keeley and Sandquist, 1992; France, 1995). In addition, the preferential excretion of isotopically light N results in increased $\delta^{15}N$ with increasing trophic level (Peterson and Fry, 1987). Kinetics of CO_2 diffusion, needed for photosynthetic C fixation, discriminate against $^{13}CO_{2(aq)}$ and result in fractionation between plant tissue and dissolved CO_2 (Hecky and Hesslein, 1995). Within the benthos, boundary layer CO_2 diffusion may be reduced causing periphyton to become C limited (Keeley and Sandquist, 1992). C limitation associated with slow boundary layer diffusion reduces discrimination against ^{13}C among benthic primary producers (Hecky and Hesslein, 1995). This results in a marked disparity between isotopically heavy benthic primary producers and isotopically light pelagic primary producers (France, 1995; Hecky and Hesslein, 1995). Likewise, organisms preferentially excrete isotopically light nitrogenous waste and retain the heavier isotope (Peterson and Fry, 1987). Therefore a consumer’s tissue is incrementally $\delta^{15}N$ enriched relative to its food source.

However, spatiotemporal variability in primary producer δ^{13}C and δ^{15}N can be large both seasonally and between years due to changes in the biogeochemical characteristics of an aquatic system (Zohary et al., 1994; Vander Zanden and Rasmussen, 1999; Ngochera and Bootsma, 2011). Because of this variability, direct comparison of spatially or temporally distinct systems is likely to result in erroneous conclusions. Baseline values are often used to measure against when attempting to make between-system or long term temporal comparisons following a species invasion (Cabana and Rasmussen, 1994; Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999). Typically, long lived primary consumers such as unionid mussels or gastropods provide good isotopic baselines because they temporally integrate seasonal changes in phytoplankton and periphytic algal δ^{13}C and δ^{15}N (Cabana and Rasmussen, 1994; Vander Zanden et al., 1997; Post et al., 2000). Thus it can be assumed that long lived primary consumers possess a δ^{13}C similar to their primary food source with a 3-4‰ enrichment of δ^{15}N. All other organisms in the food web can be measured as the relative distance to baseline primary consumers. This facilitates between system and long term temporal comparisons following a species invasion.

1.3 Changes in the Lake Michigan Food Web

In the past two decades, rapid ecological changes have occurred in the Lake Michigan food web. These changes principally include the establishment of invasive dreissenid mussels, the zebra mussel *Dreissena polymorpha* and more recently the quagga mussel *Dreissena rostriformis bugensis* which has largely replaced the former (Nalepa et al. 2009). Dreissenids—quagga mussels in particular—have reached extremely high densities in Lake Michigan's nearshore and mid depth regions with subsequent effects on lake wide nutrient dynamics and energy flow (Hecky et al., 2004; Zhu et al., 2006; Vanderploeg et al., 2010). Hecky et al. (2004) hypothesized that, because dreissenid mussels filter large volumes of water, they may sequester pelagic nutrients and energy to the nearshore benthos. From 2003-2007, a 17 fold increase in dreissenid biomass in Lake Michigan was observed due to the offshore expansion of quagga mussels (Bunnell et al., 2009). In deeper offshore waters, Vanderploeg et al. (2010) suggested that, during isothermal conditions, offshore mussels have access to the entire water column and create a "mid depth sink" for pelagic nutrients. These changes appear to have resulted in the overall oligotrophication of Lake Michigan and loss of the historically important spring algal bloom (Fahnenstiel et al., 2010; Evans et al., 2011). In addition, declines in primary consumers such as cladoceran zooplankton and the benthic amphipod *Diporeia* have also been coincident with offshore expansion of the dreissenid population and changes in algal productivity (Barbiero et al., 2009; Nalepa et al., 2009; Barbiero et al., 2011a; Barbiero et al., 2011b). Total pelagic and profundal forage fish biomass declined 71% from 2003 to 2007, with the largest declines observed in the bloater and deepwater sculpin populations (Bunnell et al., 2009).

While offshore productivity appears to be declining with the expansion of dreissenid mussels, nearshore benthic productivity has greatly increased. Increased benthic primary productivity has been manifested in the proliferation of the benthic, filamentous alga, *Cladophora* sp. (Bootsma et al., 2004). Field experiments and modeling suggest that dreissenid-mediated changes in nearshore water clarity and phosphorus cycling are largely responsible for increased production of this alga (Auer et al., 2010). In addition to increased benthic algal productivity, nearshore benthic invertebrates such as amphipods and isopods may have directly benefited from the nutrients and energy in dreissenid feces and pseudofeces (Limén et al., 2005). These invertebrates in turn support both native and non-native fishes in the nearshore zone(Pothoven et al., 2000; Janssen and Luebke, 2004). The invasive round goby *Neogobius melanostoma* appears to be one species which has benefited from increased nearshore productivity and now dominates the nearshore fish community (Clapp et al., 2001). Round goby diets primarily include benthic invertebrates, with increasing dependence on dreissenid prey as goby size increases which may have facilitated their proliferation (Creque and Dettmers, 2002; Vanderploeg et al., 2002; Brush et al., 2012). Other disruptions in the nearshore food web include population declines of indigenous fish species, such as yellow perch and mottled sculpin (e.g. Marsden and Robillard, 2004) as a direct effect of round goby (i.e., predation and competition; Janssen and Jude, 2001) or other non-indigenous species (Janssen and Luebke, 2004; Redman et al., 2011).

Nearshore sequestering of nutrients and energy by dreissenid mussels has likely caused major shifts in food web structure and energetic pathways. Understanding the impact of nearshore changes is made difficult by the relative dearth of historical data on the nearshore food web. There is some evidence that new trophic pathways have emerged. For instance, lake whitefish may be relying more on dreissenids as a food source as *Diporeia* populations decline (Pothoven et al., 2001; Rennie et al., 2009; Madenjian et al., 2010). Alewives, the most important prey item for stocked salmonids (Madenjian et al., 2002), have been found to use nearshore chironomid species, especially over nearshore rocky habitat (Kornis and Janssen, 2011). Growing evidence also suggests round goby is a potentially important food source for higher trophic level species, including yellow perch, burbot, and salmonids (Vanderploeg et al., 2002; Johnson et al., 2005; Dietrich et al., 2006; Truemper et al., 2006; Hensler et al., 2008; Jacobs et al., 2010). These new pathways serve as a conduit through which carbon fixed in nearshore benthos becomes available to an upper food web historically reliant upon pelagic energy.

1.4 Objectives and Hypotheses

The magnitude of changes occurring in the nearshore zone has likely impacted the entire Lake Michigan food web, although drawing direct evidence remains difficult (Madenjian et al., 2002; Nalepa et al., 2009). From a management perspective, understanding whether the increased importance of the nearshore benthic energy pathway may compensate for the apparent loss of energy from the pelagic zone is a critical question. Furthermore, addressing this question will begin to help us understand how food web trophic structure and stability respond to species invasions in a Laurentian Great Lake. The objective of this study was to determine whether the Lake Michigan fish community has become significantly more dependent upon nearshore benthic energy in response to major offshore oligotrophication and nearshore benthification following the dreissenid invasion. To do this, stable C and N isotopes were used as indicators of major energetic pathways and trophic level during the period of dreissenid invasion. Several hypotheses are addressed within this objective: 1) increases in $\delta^{13}C$ among pelagic and profundal fishes, which historically derived the majority of their energy from phytoplankton, has resulted from increased dependence upon nearshore energy sources, 2) changes in $\delta^{13}C$ signatures of nearshore fishes, which historically derived the majority of their energy from nearshore C, have changed little during the dreissenid proliferation due to increased nearshore productivity and higher maintained benthic invertebrate biomasses, and 3) the ability of Lake Michigan fishes to incorporate productive nearshore energy pathways, though multichannel omnivory, has helped to maintain stability of populations despite fluctuations associated with pelagic energy channels.

CHAPTER 2: METHODS

2.1 Study Sites and Sample Collection

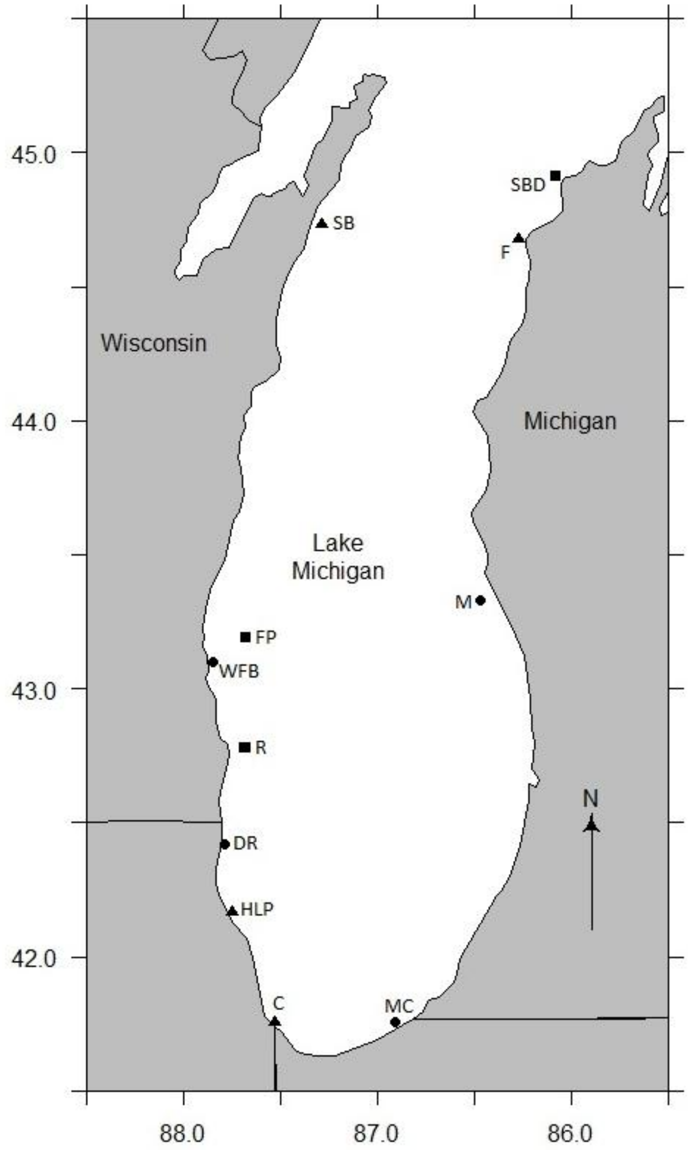

Figure 1. 2010-2011 Lake Michigan study sites measured in decimal degrees North and West. Triangles indicate sites with rocky substrate, circles indicate sites with sandy substrate, and squares indicate mixed soft or hard substrates. Nearshore sites including Sturgeon Bay, WI (SB), Fox Point, WI (FP), Whitefish Bay, WI (WFB), Highland Park, IL (HLP), Dead River, IL (DR), Calumet, IN (C), Michigan City, IN (MC), Muskegon, MI (M), Frankfort, MI (F), and Sleeping Bear Dunes, MI (SBD) were typically sampled in May, July, and September at 3 m, 8 m, and 15 m depths. Offshore study sites including Sturgeon Bay, WI, Fox Point, WI, Racine, WI (R), and Frankfort, MI and were sampled in 50-110 m of water.

Phytoplankton, benthic algae, invertebrates and fishes were collected from Lake Michigan during two time periods following the invasion of dreissenid mussels, 2002-2003, and 2010-2012. These periods correspond with the early expansion (2002-2003) and highest observed lake-wide abundance (2010-2012) for quagga mussels (Nalepa et al., 2009). 2002-2003 sampling occurred in the Lake Michigan nearshore and offshore regions with a particular focus on areas near Milwaukee, WI. In 2010-2012, sample collection occurred as part of a nearshore food web project which included 10 study sites in the Lake Michigan nearshore zone (<16 m; Figure 1 excluding Racine). Nearshore study sites were sampled at three depths (3-5 m, 7-10 m and 15-16 m) comprising a mix of rock, sand and soft sediment. Nearshore sampling occurred three times annually in May, July and September, 2010 and 2011. Additional sampling occurred at 4 offshore (50-110 m) sites: including Sturgeon Bay, WI, Fox Point, WI, Racine, WI, and Frankfort, MI (Figure 1). Offshore sites were sampled irregularly between 2010 and 2012 as part of other projects or to provide supplementary fish and invertebrate samples which may have been missed in nearshore sampling.

Sample collection methods for invertebrates and fish varied with site depth and substrate type. Nearshore invertebrates, amphipods (*Gammarus* and *Echinogammarus* spp.*)*, Isopoda, Chironomidae larvae and *D. rostiformis bugensis,* were collected using a ponar grab over soft sediment or by scuba divers performing quantitative benthic scrapes over rock substrates. Collection of invertebrates was done in triplicate for each date and depth being sampled. Offshore invertebrates, *D. rostiformis bugensis* profunda, *Diporeia* sp., and *Mysis diluviana,* were collected qualitatively using a combination of ponar, zooplankton tows and bottom trawling. Fish sampling included alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), brown trout (*Salmo trutta*), chinook salmon (*Oncorhynchus tshawytscha*), deepwater sculpin (*Myoxocephalus thompsonii*), lake trout (*Salvelinus namaycush*), longnose dace (*Rhinichthys cataractae cataractae*), rainbow smelt (*Osmerus mordax*), round goby (*Neogobius melanostomus*), slimy sculpin (*Cottus cognatus*), spottail shiner (*Notropis hudsonius*), and yellow perch (*Perca flavescens*).

Fish from 2002-2003 were collected using a variety of techniques including gillnets, bottom trawling, and angling. 2010-2012 nearshore fish samples were collected using gillnets. Supplemental fish from the 2010-2012 time periods were collected by otter trawling and angling. For alewife, bloater, and rainbow smelt, additional samples from a central time period (2005-2006) were also provided by the USGS Great Lakes Science Center in Ann Arbor, Michigan, from annual mid water trawling surveys.

2.2 Sample Processing

Stable isotope measurements of tissue C and N concentration were made at the University of Wisconsin-Milwaukee School of Freshwater Sciences. Stable isotope samples were either processed immediately or frozen in the laboratory until analysis. Ponar grab and benthic scrape replicates were sorted by taxon and each taxonomic category present was subsampled for further analysis. Hard shelled mollusks including dreissenids were dissected to remove soft tissue. Individual fish were typically homogenized in the laboratory and a 3-4 mg subsample (dry weight) was saved for analysis. For large fishes greater than 250 mm, a dorsal muscle tissue sample was collected and homogenized.

Paired t-tests were used to test for differences between fish homogenate and dorsal muscle tissue for three species, alewife, round goby, and spottail shiner. There were no significant differences between the $\delta^{13}C$ of homogenate and dorsal muscle when these three species were analyzed individually (t_3=-2.59, P=0.122; t_3=1.10, P=0.385; t_3=-3.44, P=0.074; respectively) or together (t_9=-0.06, P=0.952). Conversely, $\delta^{15}N$ of homogenate and dorsal muscle was significantly different (t_9=-3.21, P=0.011) although when only a single species was tested, there was no significant difference for alewife (t_3=-3.077, P=0.091) or spottail shiner (t_3=-1.11, P=0.381) δ^{15}N. Only round goby showed a significant difference between δ^{15}N of muscle tissue and homogenate (t_3=-4.44, P=0.047). The mean difference in round goby muscle tissue (8.949‰) and homogenate (8.787‰) δ^{15}N was small albeit significant. Given the similarities between both muscle and homogenate among all species, I felt justified in combining these tissue types for analyses. Invertebrate and fish tissues were lyophilized and again homogenized. For each sample, 3-4 mg of the dried homogenate was then packed in tin capsules for stable isotope analysis.

Stable isotope measurements and measurements of tissue C and N concentrations were made at the School of Freshwater Sciences using an isotope ratio mass spectrometer (Finnigan MAT delta S SIR-MS, with elemental analyzer front end and ConFlo II interface). After every 12th sample, an acetanilide control was run to ensure instrument calibration. ^{13}C:^{12}C ratios (δ^{13}C values) were measured relative to the PDB carbonate standard, and δ^{15}N values were measured relative to the ^{15}N:^{14}N ratio of air. Results were expressed in per mil (‰) differences between the isotope ratio of the sample and that of the standard, using the formula:

$$\delta^{13}C\ or\ \delta^{15}N = \left(\frac{R_{Sample}}{R_{Standard}} - 1\right) \times 1000$$

where $R = {}^{13}C/{}^{12}C\ for\ \delta^{13}C$ and $R = {}^{15}N/{}^{14}N\ for\ \delta^{15}$N (Appendix A).

In 2011, benthic invertebrate (excluding dreissenid mussels) and zooplankton biomass was calculated using the percent C obtained from the gas chromatograph peak areas. This allowed us to calculate the average mass of C per individual. Biomass was then calculated using the following formula:

$$Biomass\ (mg\ C\ m^{-2}) = \frac{mg\ C}{indvidual} * \frac{no.individuals}{m^2}$$

This facilitated comparisons between seasonal biomass fluctuations of benthic invertebrates and zooplankton, which represent slow and fast energy channels of the nearshore and offshore waters near Milwaukee, WI.

2.3 Sample Corrections

Because lipids are ^{13}C depleted relative to muscle (Peterson and Fry, 1987; Post et al., 2007), correction equations were developed to determine lipid-extracted δ^{13}C values. This was done on a species specific basis to reduce interspecific variability associated with generic correction equations (Fagan et al., 2011). In order to develop the correction equation, stable isotope analyses were conducted before and after tissue lipid extraction. At least six samples of each species were selected for lipid extraction. The samples included a broad range of C:N ratios. This range in C:N ratio reflects a range of lipid content in a tissue sample, with higher values indicating higher lipid content (Post et al., 2007). Lipids were extracted by mixing a 2:1 chloroform-methanol solution with the dried homogenate. The mixture was agitated periodically for 30 minutes then centrifuged for 10 minutes at 4000 rpm and the supernatant was decanted. This process was repeated three times to ensure all lipids were removed from the tissue. The tissue was then allowed to dry under a fume hood overnight and stable isotope analysis was rerun. The lipid correction equation was then determined as:

$$\delta^{13}C_{PL} = \delta^{13}C_L - m * (C{:}N_L - \overline{C{:}N_{PL}}) - b \text{ (Appendix B)}$$

where $\delta^{13}C_L$ is the $\delta^{13}C$ of a sample prior to lipid extraction, $C{:}N_L$ is the C:N mass ratio of a sample prior to lipid extraction, $\overline{C{:}N_{PL}}$ is the average C:N ratio for all samples of a given species following lipid extraction, and m and b are the slope and intercept, respectively, of a simple linear relationship between $\Delta\mathrm{C{:}N}$ (i.e. $\mathrm{C{:}N_L} - \overline{\mathrm{C{:}N_{PL}}}$) and $\Delta\delta^{13}\mathrm{C}$ (i.e. $\delta^{13}\mathrm{C_L} - \delta^{13}\mathrm{C_{PL}}$) for a given species. Small sample sizes or small ranges in C:N ratios for brown trout, bloater, deepwater sculpin, and chinook salmon precluded development of lipid extraction equations so the Post et al. (2007) correction was applied to these species. A paired t-test was used to test the difference between our lipid correction and the generic correction proposed by Post et al. (2007) for all other species. Results suggest that the Post et al. (2007) lipid corrected δ^{13}C values were statistically indistinguishable from our correction equation results (t_{57}=0.002, P=0.4991). Therefore, the Post et al. (2007) correction equation was used for species that precluded lipid extraction.

For temporal comparisons, δ^{13}C and δ^{15}N of each species were determined relative to a primary consumer, nearshore dreissenid mussels, for each time period (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999). By integrating short term temporal variation in isotopes near the base of the food web, dreissenids create a baseline from which the rest of the food web can be measured and thereby facilitate long term temporal comparisons of trophic structure. To minimize spatial variation among primary consumers, only those dreissenids collected from 8-10 m of water near Milwaukee, WI were used to generate baseline data for the three time periods, 2002-2003, 2005-2006, and 2010-2012.

Baseline changes in $\delta^{15}N$ varied substantially more in the offshore zone than in the nearshore zone between 2002-2003 and 2010-2012. Offshore *D.r. bugensis* $\delta^{15}N$ increased 2.10‰ while nearshore amphipods $\delta^{15}N$ decreased 1.13‰. Therefore, a fish which derived considerably more energy from pelagic sources in 2002-2003 than it did in 2010-2012 would be expected to exhibit a shift to lower $\delta^{15}N$ because of baseline isotopic differences between these two sources. However, this shift reflects a change in energy source, not trophic level. Because of this nearshore-pelagic difference in the baseline $\delta^{15}N$ shift over time, $\delta^{15}N$ was converted to trophic level (TL). TL for each taxa was determined according to the proportion of energy it derived from pelagic phytoplankton versus nearshore primary production. This allowed us to standardize a taxon's trophic level along the nearshore-pelagic continuum. TL was determined for each taxa using the following equation modified from Post et al. (2000):

$$TL = 2 + \frac{(\delta^{15}N_{taxa} - [\delta^{15}N_{profundal\ mussel} * \propto + \delta^{15}N_{amphipod} * (1 - \propto)])}{3.4} \text{ (Appendix C)}$$

where α is the proportion of carbon in the focal taxa stemming from pelagic phytoplankton and calculated:

$$\propto = \frac{(\delta^{13}C_{taxa} - \delta^{13}C_{amphipod})}{(\delta^{13}C_{profundal\ mussel} - \delta^{13}C_{amphipod})} \text{ (Appendix C)}$$

For organisms with $\delta^{13}C$ greater than that of $\delta^{13}C_{amphipod}$, α was assumed to be 0.

Temporal comparisons were made using samples collected from the same location in Lake Michigan to minimize artifacts due to spatial variability in isotopic composition. Typically, this was limited to the sites on the western side of Lake Michigan's southern basin including Fox Point, WI, Whitefish Bay, WI and Racine, WI. For some pelagic planktivores including alewife, bloater, and rainbow smelt, temporal comparisons included samples collected lake wide to increase sample sizes. For alewife (>100 mm), 2-way ANOVA using $\delta^{13}C$ or $\delta^{15}N$ as the dependent variables and location (6 locations; Figure 1) and depth (3 depths; 3 m, 8 m, 15 m) as the independent variables were performed to determine if significant differences existed among study sites within a given time period. Bloater (>150 mm) from Sturgeon Bay, WI and Frankfort, MI were collected in 110m of water and were also compared using a t-test to assess spatial differences. Neither 2-way ANOVA nor t-test was performed on rainbow smelt due to low samples sizes at most sites. Results suggested no difference existed among sample locations or depths for alewife ($\delta^{13}C$: $F_{5,29}$=2.401, P=0.0613; $F_{2,29}$=0.454, P=0.6392; $\delta^{15}N$: $F_{5,29}$=1.089, P=0.388, $F_{2,29}$=0.941, P=0.941) or between sample location for bloater (t_{57}=-1.25, P=0.2161). Therefore it was also assumed that there was no spatial difference for rainbow smelt in later analyses.

2.4 Statistical Analysis of Stable Isotope Data

For individual fish species, ANCOVA was used to test differences in $\delta^{13}C$ and $\delta^{15}N$ between time periods using total length as the covariate. Data were normalized using log transformation and length was removed from the analysis if it was not significant. Techniques proposed by Layman et al. (2007) and by Schmidt et al. (2007)

were used to describe community wide changes in isotope-inferred niche space and trophic structure following the invasion of dreissenid mussels. Layman et al. (2007) proposed 6 metrics including $\delta^{15}N$ (or TL) range, $\delta^{13}C$ range, total area, mean distance to a centroid (average $\delta^{13}C$ and trophic level of all the taxa in the food web), mean nearest neighbor distance and standard deviation of nearest neighbor distance with $\delta^{13}C$ and $\delta^{15}N$ biplot data. $\delta^{15}N$ range and $\delta^{13}C$ range provided information about the number of trophic levels and the breadth of basal energy resources, respectively. Total area refers to the convex hull area encompassing all taxa on the $\delta^{13}C$ and trophic position biplot. This metric provided information about the size of the combined trophic niche space which the study taxa occupied and the amount of trophic diversity. Mean Euclidean distance to the centroid and mean Euclidean nearest neighbor distance provided a measure of the degree of trophic diversity and proximity of trophic positions in niche space. Finally, standard deviation of nearest neighbor distance indicated the uniformity of the taxa density in the food web. Lower values of this metric indicated a more uniform distribution of trophic positions. Together these metrics allowed us to make temporal comparison of food web length and breadth as well as trophic diversity and niche overlap. Additionally Schmidt et al. (2007), proposed using circular statistics to assess the uniformity of changes occurring in a food web. Following this method, Rayleigh's test was used to determine if the angle of change for each species on a $\delta^{13}C$ and $\delta^{15}N$ biplot (i.e. niche space) between 2002-2003 and 2010-2012 was consistent. The nearshore fish community and offshore pelagic and profundal fish community were tested separately using circular statistics. Fish with α values > 50% prior to the offshore expansion of dreissenids were considered offshore and this was validated by surveys of the offshore fish community (Madenjian et al., 2012). Fish species that exhibited ontogenetic diet shifts in $\delta^{13}C$ and $\delta^{15}N$ (based upon ANCOVA results) were subdivided into separate size classes for circular statistics.

2.5 Stomach Content Analysis

Stomach content analyses for comparison with stable isotope results were also performed on a number of fish species collected from 2010-2012 including alewife, bloater, rainbow smelt, round goby, and yellow perch. Round goby and yellow perch were subdivided into three size classes due to significant ontogenetic shifts in diet revealed by the stable isotope analysis. Yellow perch size classes include <70 mm, 70-150 mm, and >150 mm and round goby size classes include <60 mm, 60-100 mm, and >100 mm. Stomachs were removed and dissected for all species, excluding round goby for which the entire digestive tract was removed and dissected. Gut contents were identified to the lowest possible taxonomic classification. Each prey category was counted and results were presented as percent occurrence in the diet (no. of individuals with prey item in the diet/total no. of individuals). This provided a measure of a species ability to utilize nearshore prey resources.

CHAPTER 3: RESULTS

3.1 Offshore Invertebrate and Fish Community

In order to make temporal comparisons between 2002-2003 and 2010-2012, offshore dreissenid mussels were used to assess baseline changes in isotopic composition. Mussel $\delta^{13}C$ became enriched by less than 1‰ over this period, although changes in $\delta^{15}N$ were more substantial (2002-2003: $\delta^{13}C$=-27.44, $\delta^{15}N$=6.8; 2010-2012: $\delta^{13}C$=-26.95 $\delta^{15}N$=8.90). The change in offshore dreissenid $\delta^{15}N$ likely reflects changes in the Lake Michigan nitrogen dynamics that alter the $\delta^{15}N$ of all food web components. Therefore, normalization to baseline values was necessary for temporal comparisons. Changes observed in dreissenids were relatively small compared to other profundal invertebrates including *Diporeia* and *Mysis*, which both shifted toward heavier $\delta^{13}C$ and $\delta^{15}N$. $\delta^{13}C$ in particular became significantly enriched for both *Diporeia* and *Mysis* (Figure 2). Both species also exhibited increased trophic level measured relative to the primary consumer baseline, although this change was not significant (Figure 2).

Several species of pelagic prey fish, alewife, bloater, and rainbow smelt, were compared during three periods, 2002-2003, 2005-2006, and 2010-2012, to determine whether temporal isotopic changes were continuous. All three species exhibited progressive isotopic changes in time with respect to both $\delta^{13}C$ and $\delta^{15}N$ although small bloater deviated from this pattern (Figure 3). Ontogenetic and temporal changes for pelagic prey fishes were also compared statistically using ANCOVA (Appendix D). Alewife and bloater $\delta^{13}C$ decreased with total length but increased significantly with time (Figure 4a and Figure 4c, respectively).

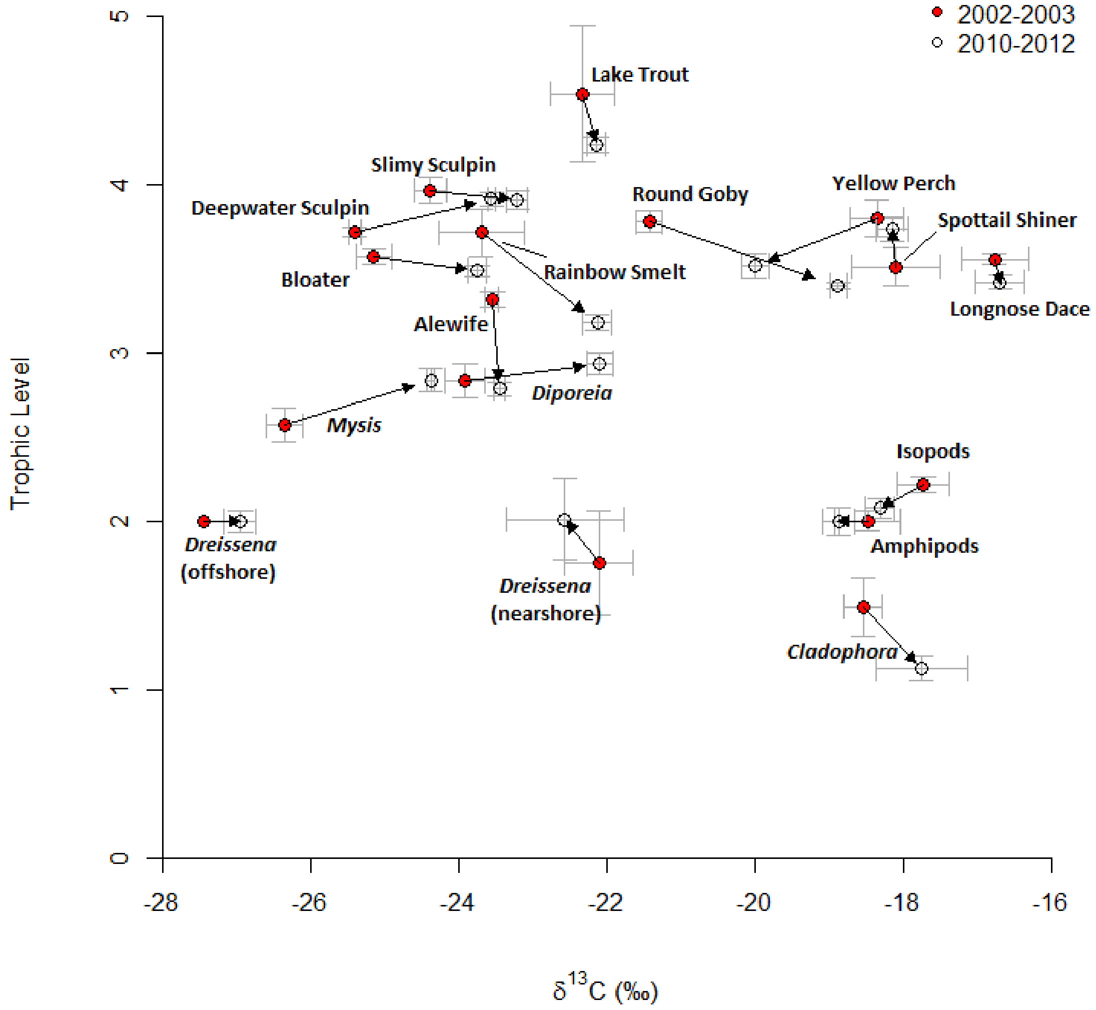

Figure 2. Stable isotope food web biplot illustrating δ^{13}C and trophic level of Lake Michigan fishes and invertebrates during two time periods, 2002-2003 (closed symbols) and 2010-2012 (open symbols). Trophic level was measured relative to offshore (80-100 m) *Dreissena* and nearshore (8-10 m) amphipods which were both assumed to occupy a trophic level of 2. Arrows represent the magnitude and direction of change in niche space for each taxa between the two time periods. Actual values δ^{13}C and trophic level values are given in Appendix A and Appendix C, respectively.

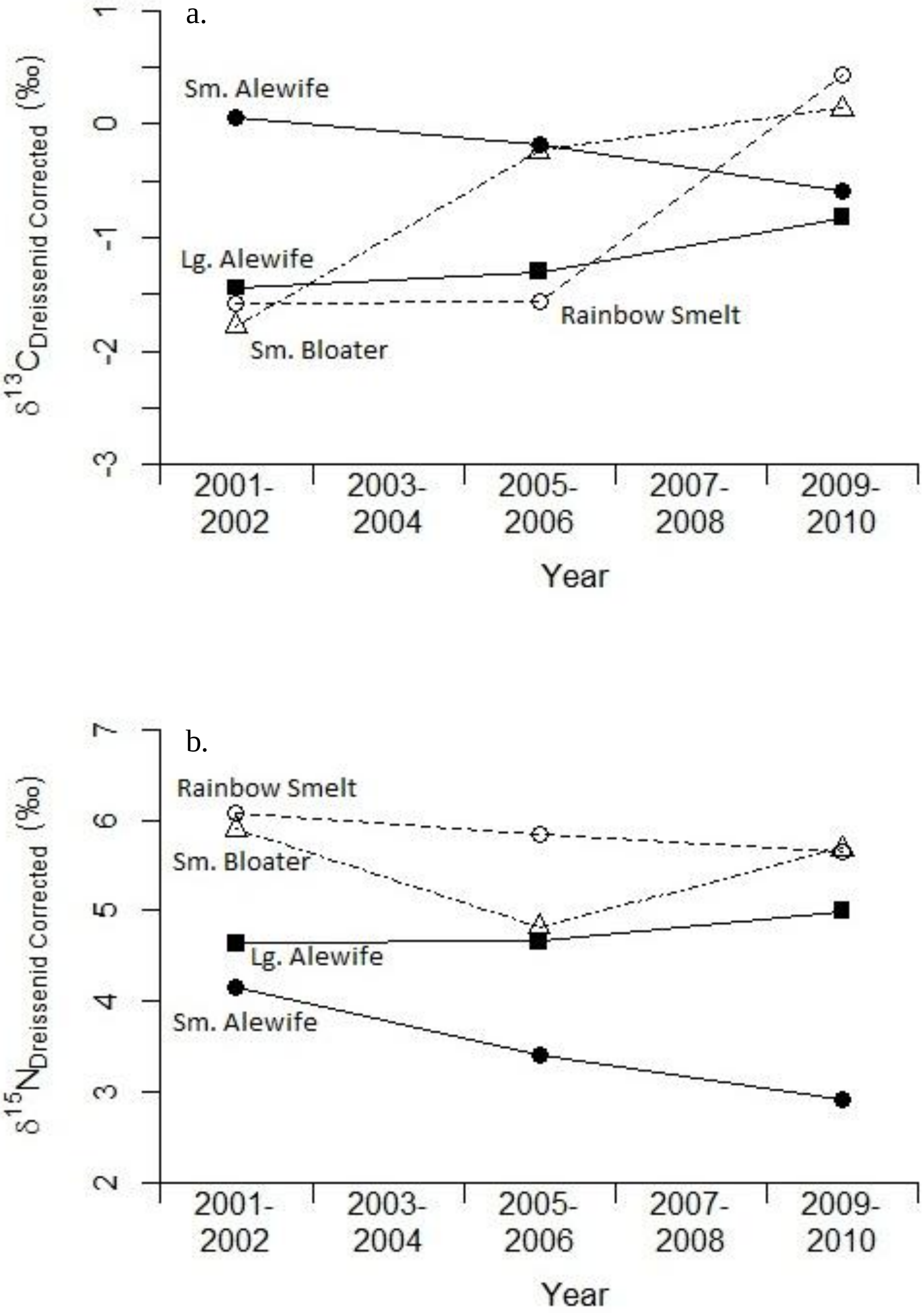

Figure 3. δ^{13}C (a) and δ^{15}N (b) of large alewife (Lg. Alewife), small alewife (Sm. Alewife), small bloater (Sm. Bloater) and rainbow smelt for three distinct time periods (2002-2002, 2005-2006 and 2010-2012) during the proliferation of dreissenid mussels illustrating the progressive isotopic change of pelagic fishes. δ^{13}C and δ^{15}N values of fishes are adjusted relative to nearshore dreissenid mussel baseline. Actual values δ^{13}C and δ^{15}N values are given in Appendix A.

Conversely, rainbow smelt $\delta^{13}C$ did not change with increasing total length but did increase over time (Figure 4e). For alewife and bloater $\delta^{15}N$, a significant interaction between the independent variables, year and length, existed. This relationship is illustrated by a lower relative $\delta^{15}N$ at total lengths <100 mm and higher relative $\delta^{15}N$ at total lengths >100 mm for both species during 2010-2012 (Figure 4b and Figure 4d, respectively). However, $\delta^{15}N$ increased with increasing total length for all alewife and bloater size classes and all study years. No significant temporal or ontogenetic change in rainbow smelt $\delta^{15}N$ was observed (Figure 4f).

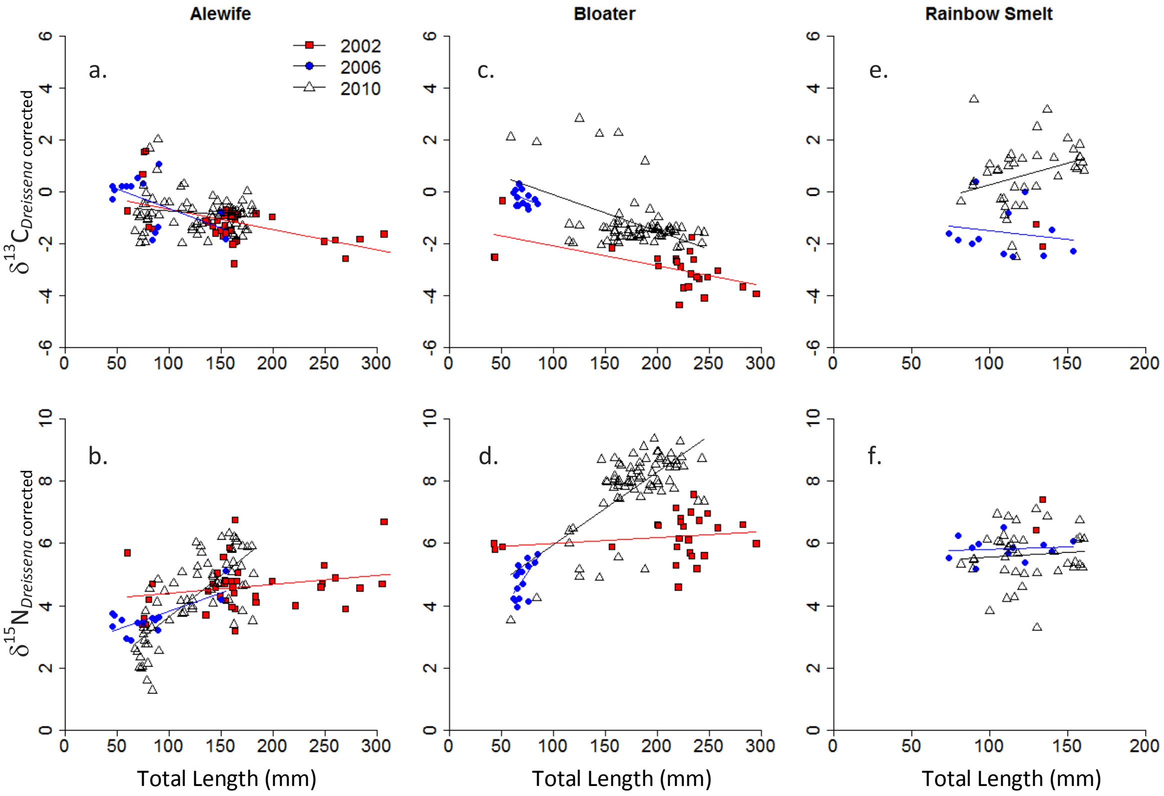

Figure 4. Linear regression plots of total length versus $\delta^{13}C$ (upper) and $\delta^{15}N$ (lower) measured relative to nearshore (8-10 m) dreissenid mussels for pelagic fishes alewife (a and b), bloater (c and d), and rainbow smelt (e and f). Nearshore dreissenid mussels were used because offshore dreissenids and nearshore amphipods were not available for baseline data during all three time periods. ANCOVA summary statistics presented in Appendix D.

Diets collected from pelagic prey fishes from 2010 to 2012 were used to help validate stable isotope results. Frequency of occurrence of benthic invertebrates, particularly chironomid species and small zoobenthos, suggest high importance of these taxonomic categories (Figure 5). However, pelagic zooplankton were also present in a large fraction of pelagic prey fish diets. Occurrence of prey items varied on a species specific basis. In alewife stomachs, chironomid species were present most frequently, followed by pelagic zooplankton and other small zoobenthos (Figure 5). Bloater diets most frequently contained small zoobenthic taxa such as chydorids and harpacticoids followed by pelagic zooplankton and other assorted taxa (Figure 5). Dreissenids, although not common, were present with greater frequency in bloater stomachs than other pelagic prey fishes (Figure 5). Rainbow smelt diets most frequently contained chironomid species followed by pelagic zooplankton and small zoobenthos (Figure 5).

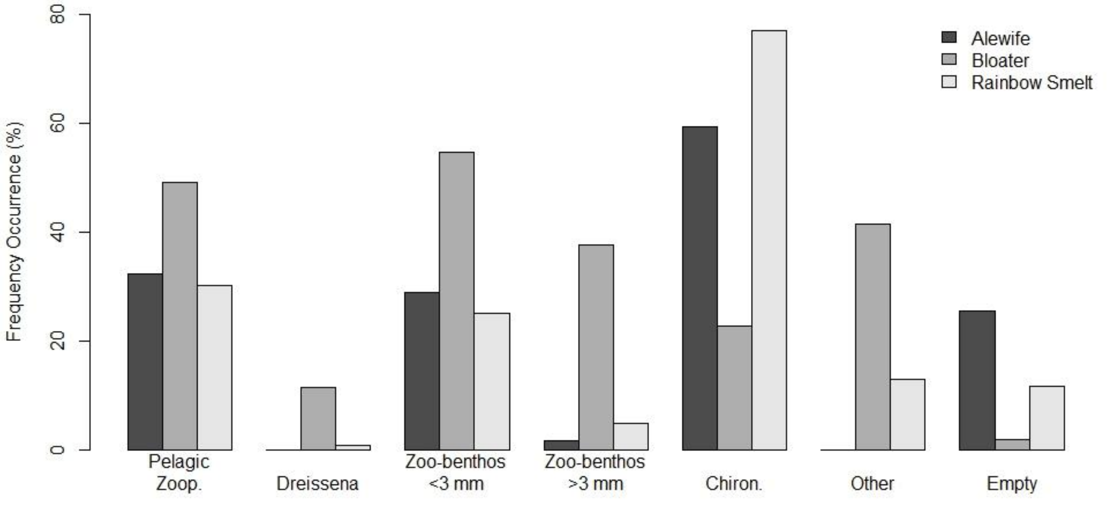

Figure 5. Frequency of occurrence of pelagic prey fish diet items Samples were collected from both rock and sand habitat types in less than 15m of water during April to September of 2010-2012. Items classified as “Other” include parasites, *Hemimysis*, terrestrial invertebrates, and unidentifiable material.

Among profundal deepwater and slimy sculpin, isotope signatures varied significantly with total length and time (Appendix D). Temporal changes for these species were consistent with isotopic changes observed among the pelagic prey fishes (Figure 2) although ontogenetic changes differed on a species specific basis. Deepwater sculpin $\delta^{13}C$ increased significantly with increasing total length and between early and latter time periods (Figure 6a). Slimy sculpin $\delta^{13}C$ decreased significantly with increasing total length, and there was a significant increase in $\delta^{13}C$ between the early and latter time period (Figure 6c). $\delta^{15}N$ did not vary significantly with total length for either deepwater or slimy sculpin (Figure 6b and Figure 6d, respectively). However, a significant increase in $\delta^{15}N$ was observed for both species over time (Figure 6b and Figure 6d, respectively).

Temporal isotopic shifts among lake trout were similar although less pronounced than those observed for pelagic/profundal prey fishes (Figure 2; Appendix D). Apparent shifts to heavier $\delta^{13}C$ and lighter $\delta^{15}N$ were observed in this study, although these changes were not significant (Figure 6e and Figure 6f, respectively). Small lake trout from 2002-2003 exhibited a broad range of $\delta^{13}C$ relative to larger lake trout. Small lake trout <500 mm total length were not captured in 2010 to 2012 so a temporal comparison was not possible. With increasing total length among lake trout, $\delta^{13}C$ decreased toward a more pelagic signal although this change was not significant (Figure 6e). $\delta^{15}N$, however, increased significantly with increasing length suggesting an ontogenetic shift in feeding behavior (Figure 6f).

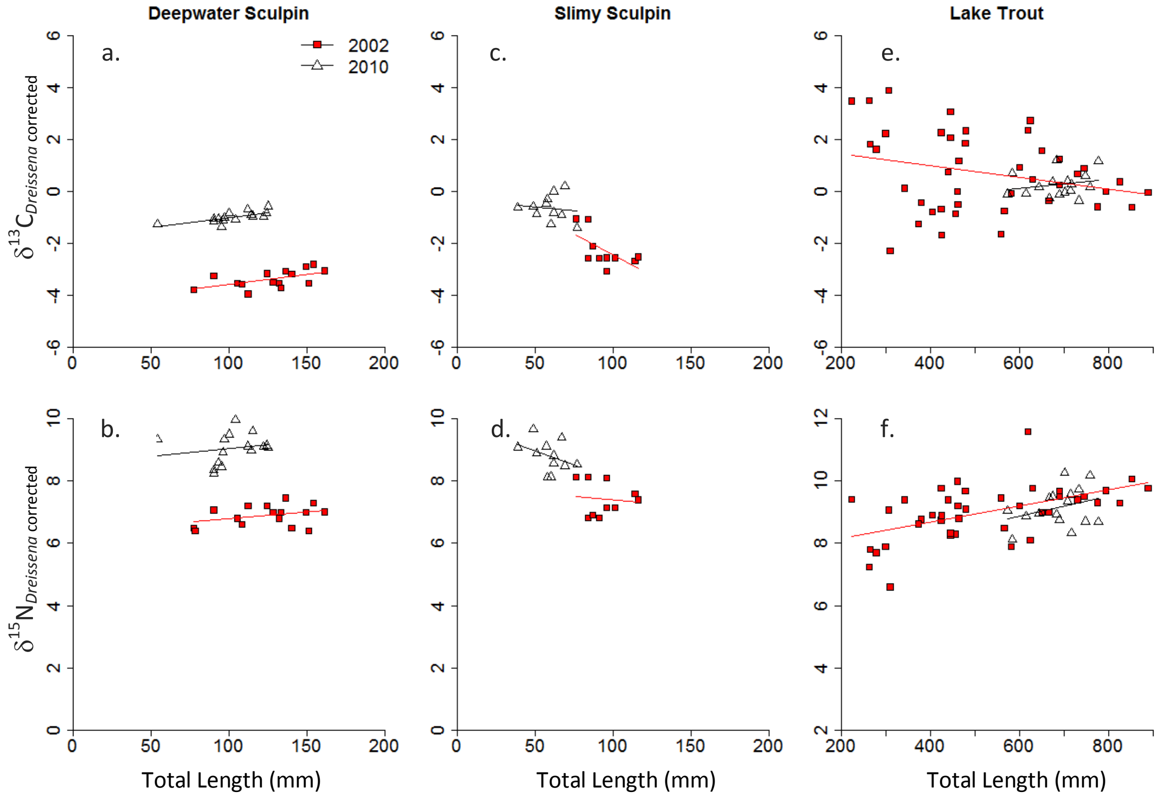

Figure 6. Simple linear regression plots of total length versus $\delta^{13}C$ (upper) and $\delta^{15}N$ (lower) measured relative to nearshore (8-10 m) dreissenid mussels for deepwater sculpin (a and b), slimy sculpin (c and d), and lake trout (e and f).

3.2 Nearshore Fish and Invertebrate Community

Nearshore invertebrates exhibited relatively small temporal shifts in isotopic composition compared to offshore invertebrate taxa. Nearshore amphipods, which were used to determine a nearshore isotopic baseline, exhibited only minor shifts with respect to both $\delta^{13}C$ and $\delta^{15}N$ (2002-2003: $\delta^{13}C$=-18.43, $\delta^{15}N$=4.67; 2010-2012: $\delta^{13}C$=-18.87 $\delta^{15}N$=3.54). Likewise, changes in nearshore dreissenid mussels and isopod taxa were minor compared to those changes observed among profundal invertebrates. For both taxa, no significant changes in the $\delta^{13}C$ or trophic level were observed (Figure 2).

Among the nearshore fishes, temporal trends in isotopic signal varied among species and were less consistent than those of the offshore fish communities (Figure 2; Appendix D). Round goby exhibited a significant shift to heavier $\delta^{13}C$ and lighter $\delta^{15}N$ (Figure 7a and Figure 7b, respectively). $\delta^{13}C$ of round goby decreased significantly with increasing total length while $\delta^{15}N$ showed little ontogenetic change (Figure 7a and Figure 7b, respectively). Conversely, yellow perch was one of few species that actually shifted significantly toward lighter $\delta^{13}C$ over time (Figure 7c). The magnitude of this change was greatest among yellow perch <70 mm although all sizes shifted toward more pelagic $\delta^{13}C$. In addition, yellow perch $\delta^{13}C$ increased significantly with total length (Figure 7c). Yellow perch $\delta^{15}N$ also increased significantly with increasing total length although there was no significant change temporally (Figure 7d).

Among nearshore fishes, diets of round goby (Figure 8a) and yellow perch (Figure 8b) from 2010-2012 were analyzed. Based on stable isotope results, both species exhibited strong ontogenetic shifts in δ^{13}C indicating a change in primary energetic source, so these species were divided into separate size classes to better elucidate feeding relationships. Small round goby (< 60 mm) diets most frequently contained small zoobenthic taxa followed by chironomid species and dreissenid mussels. Medium round goby (60-100 mm) diets most frequently contained chironomid species followed by small zoobenthic taxa and dreissenids. Among large round goby (>100 mm), the importance of chironomids and small zoobenthos declined while frequency of dreissenids in the diet increased. In addition, the frequency of occurrence of larger zoobenthic invertebrates

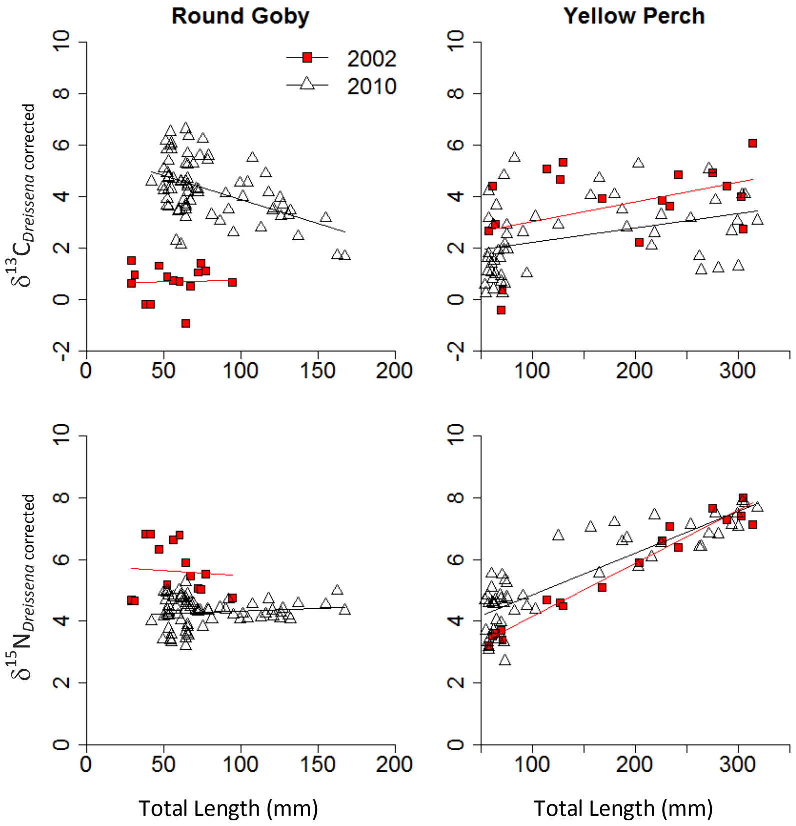

Figure 7. Simple linear regression plots of total length versus δ^{13}C (upper) and δ^{15}N (lower) measured relative to nearshore (8-10 m) dreissenid mussels for round goby (a and b) and yellow perch (c and d).

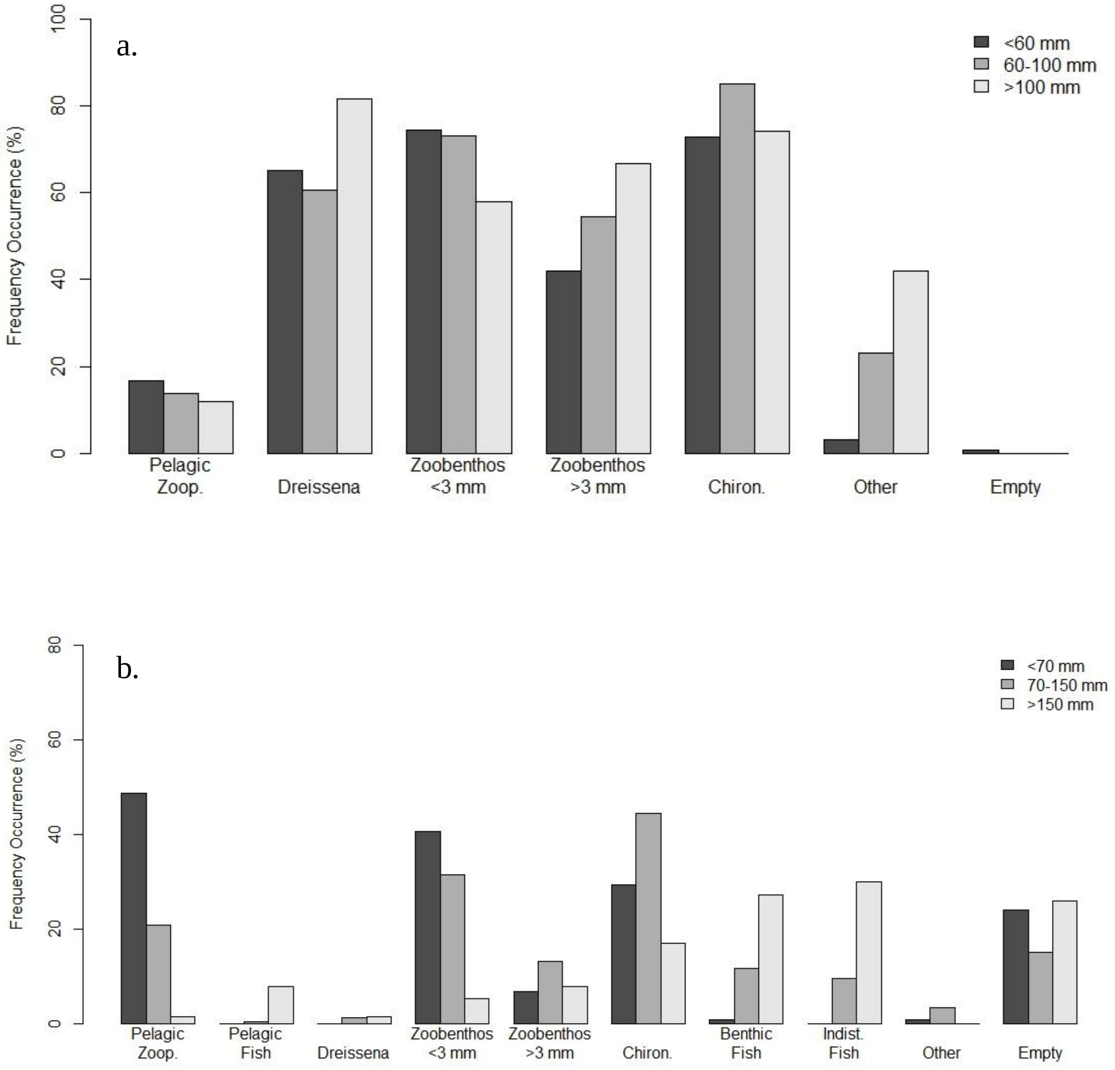

Figure 8. Frequency of occurrence of round goby diet items (a) and yellow perch diet items (b). Samples were collected from both rock and sand habitat types in less than 15m of water during April to September of 2010-2012. Items classified as “Other” include parasites, *Hemimysis*, terrestrial invertebrates, and unidentifiable fish and other matter.

was typically lower than that of other common prey items but increased consistently with increasing size class (Figure 8a). For small yellow perch (<70 mm), pelagic zooplankton occurred most frequently in diets followed by small zoobenthic taxa and chironomid species. There was a reduction in pelagic zooplankton and small zoobenthic taxa occurrence in medium yellow perch diets, while chironomid occurrence increased. The largest size class of yellow perch (>150 mm) showed a marked reduction in the presence of all invertebrate taxa and a switch to piscivory. Large yellow perch diets most frequently contained other fishes followed by chironomid species (Figure 8b).

3.3 Community Wide Changes in Niche Space and Trophic Structure

Major isotopic shifts among the Lake Michigan invertebrate and fish communities occurred between the early transition from zebra to quagga mussels (2002-2003) and the later quagga invasion (2010-2012; Appendix E). Trophic level range increased by 5.50%

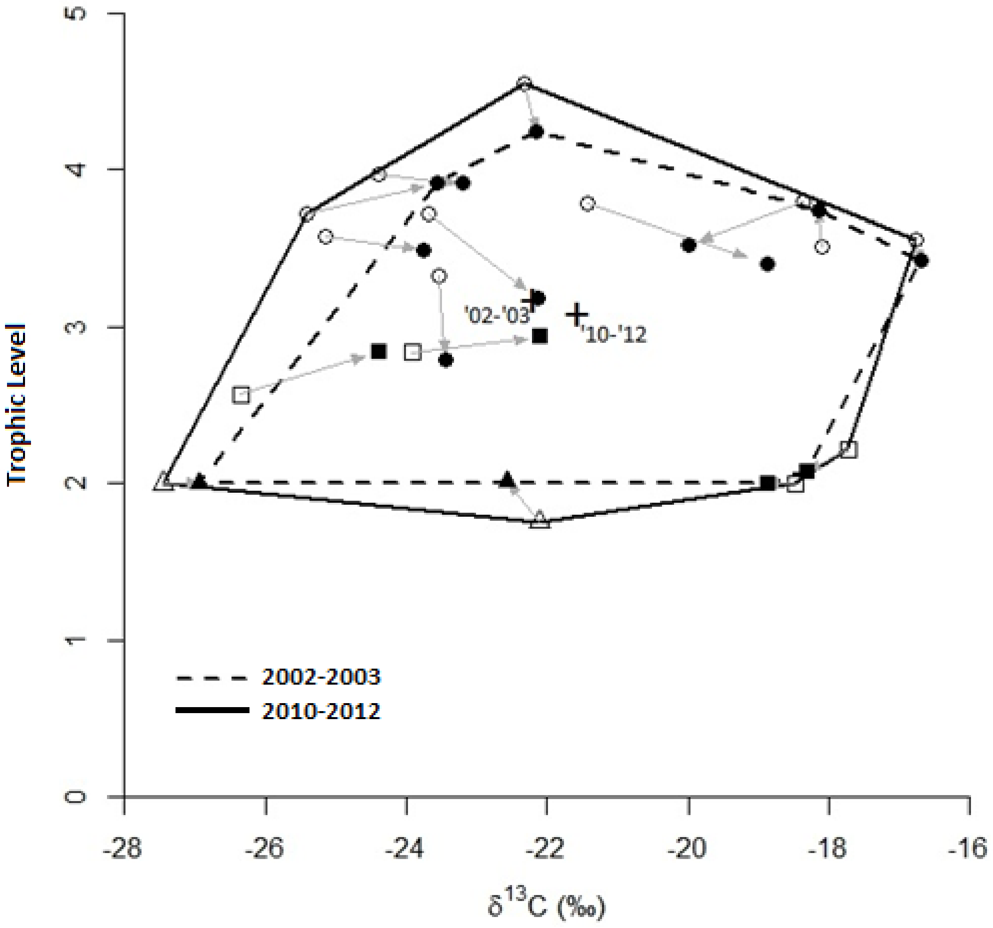

Figure 9. Stable isotope food web biplot illustrating $\delta^{13}C$ and trophic level of Lake Michigan fishes (circles), invertebrates (squares), and dreissenid mussels (triangles) during two time periods, 2002-2003 (open symbols) and 2010-2012 (closed symbols). A trophic level is assumed to be equivalent to a 3.4‰ difference in $\delta^{15}N$ and was measured relative to offshore *D.r. bugensis* (80-100 m) and nearshore (8-10 m) amphipods which were assumed to occupy a trophic level of 2. Arrows represent the magnitude and direction of change in niche space for each taxa between the two time periods. The polygons represents the convex hull area encompassing all 2002-2003 taxa (solid outline) and 2010-2012 taxa (dashed outline) with respective food web centroid (crosses) in $\delta^{13}C$ and $\delta^{15}N$ niche space.

suggesting a slight increase in number of trophic transfers between the lowest taxa (*Cladophora*) and the highest taxa (lake trout). However, a 3.96% decline in $\delta^{13}C$ range suggests a decrease in the breadth of basal energy sources. Convex hull area encompassing all taxa in the stable isotope biplot declined by 5.71% due to reduced $\delta^{13}C$ range. Mean centroid distance (-5.95%) and mean nearest neighbor distance (-12.10%) declined with the compression of the convex hull area and $\delta^{13}C$ range. However, the standard deviation of nearest neighbor distance increased by 25.38% indicating a broader dispersal of taxa within trophic niche space (Figure 9).

Circular statistics reveal a uniform and significant (Z=0.6767, P=0.007; Figure 10a) directional shift in niche space was observed for the pelagic and profundal fish community (Appendix E). The direction of change in niche space indicates greater reliance upon nearshore energy sources and corroborates the declines in $\delta^{13}C$ range and convex hull area. All offshore species and size classes, with the exception of small alewife, shifted toward more enriched $\delta^{13}C$. In contrast, the nearshore fish community revealed no significant uniform shifts in niche space (Z=0.0759, P=0.9631; Figure 10b). For example, all size classes of yellow perch shifted toward a more offshore pelagic $\delta^{13}C$ signal, while all size classes of round goby shifted toward an enriched nearshore $\delta^{13}C$ signal.

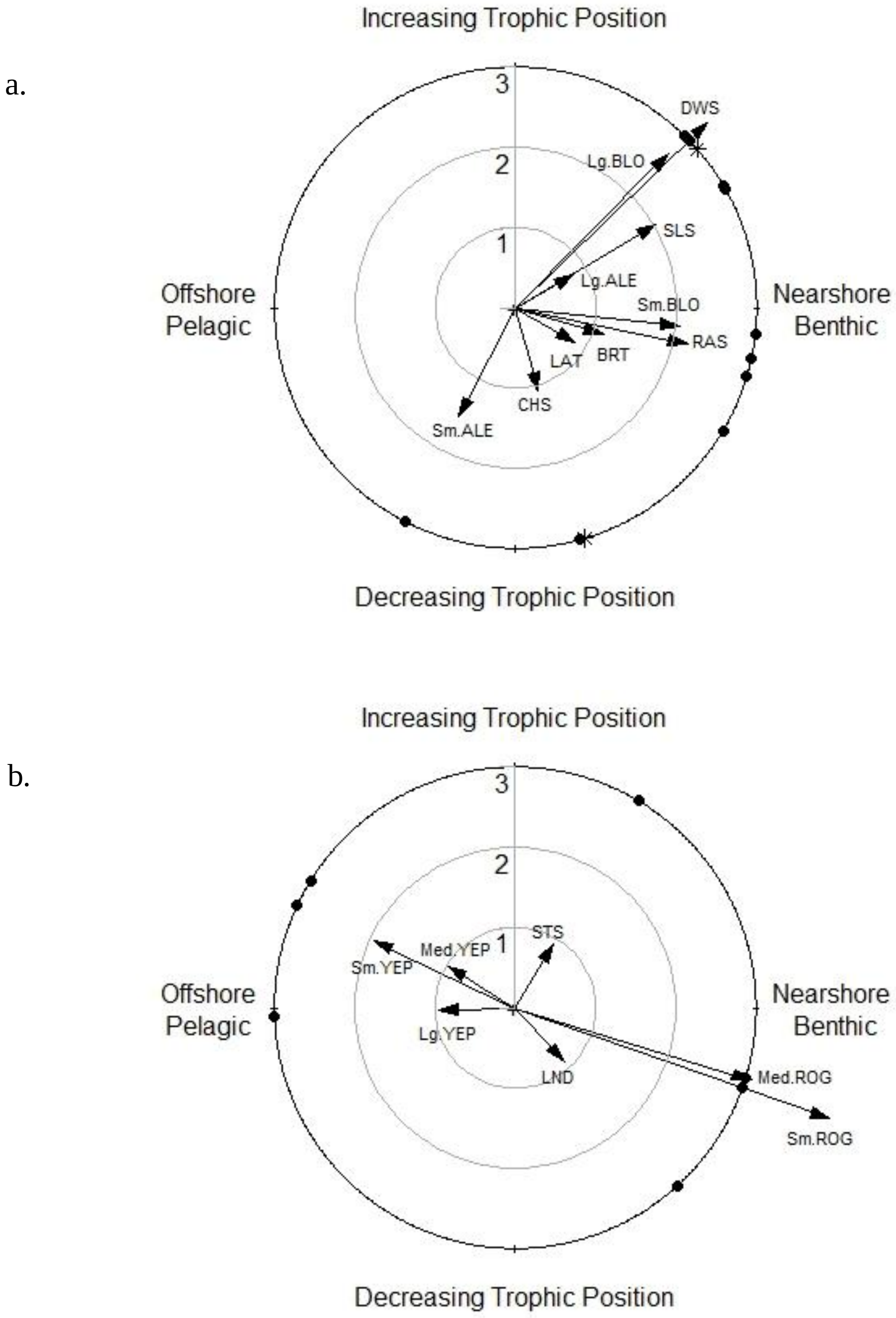

Figure 10. Arrow diagrams illustrating the angular change in δ^{13}C and δ^{15}N niche space between to time periods, 2002-2003 and 2010-2012. Each arrow represents the average direction and magnitude of change for an individual fish species between these two time periods. Gray concentric circles illustrate magnitude of change (‰) and asterisks indicate the 95% confidence intervals around the angular mean. Changes in the pelagic/profundal fish community (a) and nearshore fish community (b) are represented separately because the dreissenid invasion was expected to affect these communities differently.

CHAPTER 4: DISCUSSION

4.1 Offshore Food Web Changes

Changes within the Lake Michigan fish and invertebrate community, particularly the offshore communities, were surprisingly consistent among species over the study period. However, the exact mechanism driving this apparent shift to heavier $\delta^{13}C$ remains unclear and may vary between species. It is widely established that enriched $\delta^{13}C$ corresponds to increased dependence upon nearshore basal energy resources such as periphytic algae (Fry and Parker, 1979; Hecky and Hesslein, 1995; Bootsma et al., 1996) or increased algal growth rates (Laws et al., 1995; Burkhardt et al., 1999). Relatively minor changes in isotopic composition of plankton feeding dreissenid mussels and nearshore benthic feeding amphipods suggest similarly small temporal changes in $\delta^{13}C$ at the level of primary producers. Therefore its seems likely that the source of enriched $\delta^{13}C$ among higher consumers has resulted from increased reliance upon the nearshore food web and not from higher algal growth rates which would also affect the primary consumer baseline. (Vander Zanden and Rasmussen, 1999). Increased production of *Cladophora* and other benthic algae, including periphytic diatoms, occurring in the nearshore zone following the proliferation of dreissenid mussels support this hypothesis (Bootsma et al., 2004; Auer et al., 2010). However, the mechanisms by which offshore fishes and invertebrates may benefit from nearshore benthic algal growth are not obvious.

Other studies of Great Lakes fishes have suggested increased dependence upon nearshore energy pathways following the proliferation of dreissenid mussels, although these studies have focused on specific species (Rennie et al., 2009; Madenjian et al., 2010; Kornis and Janssen, 2011). Some work, however, has begun to suggest community-wide changes in diet and relatively higher catch rates in the nearshore zone following species invasions and subsequent ecosystem changes (Hondorp et al., 2005; Riley and Adams, 2010). Given the diversity of feeding ecology and habitat preferences among Lake Michigan fishes, it would seem unlikely that ubiquitous shifts in $\delta^{13}C$ have been driven by the same mechanism for the entire pelagic and profundal prey fish communities (Davis et al., 2005).

Plausible sources of enriched $\delta^{13}C$ in basal food resources include smaller phytoplankton taxa (Laws et al., 1995; Rau et al., 1996; Popp et al., 1998) and nearshore periphytic algae (France, 1995; Hecky and Hesslein, 1995). Small phytoplankton have relatively large surface area to volume ratios and correspondingly greater CO_2 diffusion rate and C limitation (Rau et al., 1996). As CO_2 becomes limiting, discrimination against the heavier C isotope decreases (Hecky and Hesslein, 1995). Therefore $\delta^{13}C$ in small phytoplankton may become enriched relative to larger taxa. Given the increased relative abundance of small cyanobacteria and chlorophytes and decreases in large diatoms in Lake Michigan (Fahnenstiel et al., 2010), shifts to heavier $\delta^{13}C$ in phytoplankton might be expected. However, stable isotope results suggest very little change in dreissenid mussels, which primarily feed on phytoplankton, suggesting this mechanism is unlikely. Thus the source of enriched $\delta^{13}C$ is more likely nearshore benthic algae such as *Cladophora* or benthic diatoms.

Nearshore benthic algal production has greatly benefited from increased light and nutrients in the nearshore benthos with subsequent sloughing during the fall (Bootsma et al., 2004; Auer et al., 2010). To determine whether nearshore benthic algae might make a significant contribution to the offshore organic C pool, *Cladophora* biomass measurements and estimates of areal distribution were used to estimate total annual benthic algal production. Peak *Cladophora* biomass in 2011 was 252 ± 92 g m^{-2} (mean dry weight ± 1 s.d.) in the nearshore zone (<15 m) near Milwaukee, WI based upon scuba benthic scrapes. *Cladophora* was measured to be 20% C by dry mass. For the estimates presented here, areal coverage was assumed to be 24% in the Lake Michigan nearshore zone excluding Green Bay (Brooks et al., 2012). Based upon these values, annual lake wide contributions could be conservatively estimated to be near 1200 mg C m^{-2}. This is likely a minimum, as it assumes that *Cladophora* production is equal to the accrual of biomass, and does not account for losses such as sloughing that may occur during the accrual period. Historic C deposition rates was approximately 23000 mg C m^{-2} yr^{-1} from 1977-1980 (Eadie et al., 1984). However, from 1983-1987 to 2007-2008 there was a 58% decline in annul primary productivity from 240000 to 140000 mg C m^{-2} yr^{-1} following the proliferation of dreissenid mussels (Fahnenstiel et al., 2010). For the purposes of this work estimates of current C deposition were also assumed to be 58% of the historic values measured by Eadie et al. (1984). This estimate is also conservative because the spring bloom, which was dominated by large diatoms and is now absent, likely contributed disproportionately more to algal deposition than other seasons (Fitzgerald and Gardner, 1993). Given these assumptions, 2011 *Cladophora* contribution is approximately 9% of the estimated annual C deposition resulting from settling phytoplankton in 2007-2008. Based upon a single source $\delta^{13}C$ mixing model, *Diporeia* would need to derive ~20% more C from periphytic algae to cause the observed shift in

δ^{13}C. Although this is substantially more than 9%, it is possible that localized contributions of periphytic algae are ~20% for offshore areas adjacent to areas of high nearshore productivity such as the area sampled for this study. Therefore, it seems plausible that local nearshore algal production may be contributing substantially to offshore detrital energy pools with resulting increases in δ^{13}C among profundal invertebrates such as *Diporeia* and *Mysis* (Marzolf, 1965; Guiguer and Barton, 2002).

Isotopic shifts in the profundal fish community, particularly deepwater and slimy sculpin, have likely mirrored those changes observed in *Diporeia* and *Mysis*. Deepwater and slimy sculpin were collected in water >55 m deep. It would be unlikely that these fish are feeding directly upon nearshore prey resources due to their habitat and feeding preferences (Kraft and Kitchell, 1986; Davis et al., 2005; Hondorp et al., 2005). Slimy sculpin preferentially feed upon *Diporeia* whereas deepwater sculpin are more reliant upon both *Diporeia* and *Mysis* (Kraft and Kitchell, 1986; Davis et al., 2005; Hondorp et al., 2005; Hondorp et al., 2011). This pattern is also observed in the 2002-2003 isotope results. Deepwater sculpin reflected the more depleted δ^{13}C of *Mysis* while slimy sculpin reflected the more enriched δ^{13}C of *Diporeia*. By 2010-2012, both sculpin species shifted significantly toward heavier δ^{13}C reflecting changes observed in their profundal invertebrate prey. Interestingly, stable isotope results suggested increased interspecific diet overlap in 2010-2012 relative to 2002-2003, consistent with other researchers hypotheses and decreasing invertebrate abundance (Nalepa et al., 2009; Hondorp et al., 2011). This adds to the growing body of evidence explaining the declining energy density of sculpins in Lakes Huron and Michigan (Hondorp et al., 2005; Pothoven et al., 2010; Hondorp et al., 2011).

Among major constituents of the Lake Michigan pelagic prey fish community, shifts in isotopic composition may also reflect the increases in the δ^{13}C of *Diporeia* and *Mysis*. Alewife, bloaters and rainbow smelt are largely reliant upon zooplankton, but relatively large contributions of *Diporeia,* and *Mysis* have also been observed, particularly in bloater and rainbow smelt (Wells and Beeton, 1963; Davis et al., 2005). Declining abundance of *Diporeia*, which are lipid rich, has resulted in reduced energy density among some Lake Michigan fishes (Madenjian et al., 2000; Madenjian et al., 2006). The isotope data presented here further corroborates historic diet data indicating the importance of profundal invertebrates in the diet of pelagic prey fishes. However, small alewife and bloater diets collected from the pelagic zone in Lake Michigan suggest an overwhelming reliance upon zooplankton (Wells and Beeton, 1963; Davis et al., 2005). This relationship may have become more exaggerated with declining *Diporeia* density in the profundal benthos (Hondorp et al., 2005; Nalepa et al., 2009). Following the offshore expansion of dreissenid mussels, small alewives have seemingly become dependent upon a more pelagic energy pathway, opposing changes observed among all other pelagic and profundal prey fishes. This shift may have resulted from increased dependence upon zooplankton. The relatively large ontogenetic shift in diet for both alewife and bloater as revealed by stable isotopes may be an indication of diet switching as these fishes become less reliant upon nearshore prey resources and switch to alternative prey like offshore zooplankton, *Diporeia* or *Mysis* with increasing size. The large change in the relationship between increasing length and δ^{15}N for bloater and alewife also suggested diet switching. Apparently, alewife and bloater are more dependent on lower trophic level prey at small sizes and more dependent on higher trophic level prey at large sizes than in the past. This may be in response to ecosystem changes such as the differential shift in $\delta^{15}N$ baseline in the nearshore verses offshore food web. More gut content analyses and stable isotope analysis on invertebrate prey will help explain this shift more clearly.

$\delta^{13}C$ enrichment of pelagic planktivores, such as alewife, bloater, and rainbow smelt. may have also resulted from increased direct dependence upon nearshore prey items. Gut content analyses conducted in this study and by other investigators suggests that chironomid taxa from the nearshore benthos may be an important source of energy among alewives (Kornis and Janssen, 2011). Chironomid taxa were encountered more frequently than zooplankton in alewife and rainbow smelt diets. Other small zoobenthos, including harpacticoid copepods and chydorids, were also frequently found in diets. Of all fishes compared in this study, bloaters were the only species with dreissenids in their guts. But they also most frequently contained non-chironomid benthic invertebrates. Bottom feeding strategies of bloater may even offer them a competitive advantage over other fishes as the nearshore benthos becomes more productive (Janssen, 1978; Crowder and Binkowski, 1983). One major caveat to this finding is that most fish for this study were collected from the nearshore zone which may have biased their gut contents toward nearshore prey. Furthermore, temporal sampling of diets occurred in May, July, and September and may not be representative of long-term feeding preferences. Nevertheless, it is clear that pelagic prey fishes are quite capable of capturing and utilizing nearshore prey items consistent with observed isotopic shifts and corresponding ecosystem changes.

Large lake trout have exhibited little change in isotopic composition relative to the pelagic and profundal prey fish community. Some recent evidence has suggests that lake trout may be utilizing nearshore energy channels in other lakes (Johnson et al., 2005; Dietrich et al., 2006) but the results of this study provide little evidence of this. Although temporally enriched $\delta^{13}C$ and depleted $\delta^{15}N$ were observed, these changes were not significant. The magnitude and direction of this change is very similar to that of alewife and may indicate increased reliance upon this prey resource. Jacobs et al. (in press) suggest that chinook salmon have become increasingly reliant upon alewife prey in response to major declines in other prey fish populations (Bunnell et al., 2011; Madenjian et al., 2012). It is possible that a similar change has occurred with respect to lake trout. Ontogenetic changes in lake trout $\delta^{15}N$ are apparent with increasing size in 2002-2003 and 2010-2012 illustrating a clear increase in trophic level with increasing size. Unfortunately, no lake trout <500 mm were captured in the 2010-2012 sampling but 2002-2003 sampling indicates a broad range of $\delta^{13}C$ in small lake trout. Additional sampling of small lake trout may reveal significant temporal changes in the $\delta^{13}C$-length relationship.

4.2 Nearshore Food Web Changes

Significant isotopic changes in the nearshore fish community were apparent for the invasive round goby and yellow perch. Enrichment of round goby $\delta^{13}C$ suggested increased reliance upon a food web based on benthic algal production. This change seems paradoxical because round goby are known to be benthic predators (Jude and Reider, 1992; Vanderploeg et al., 2002). One plausible explanation for this shift could be a switch from dreissenid mussels, which have $\delta^{13}C$ similar to that of phytoplankton, to increased reliance upon non-dreissenid benthic invertebrates (Brush et al., 2012). Round goby selectively feed upon small dreissenid mussels and may actually change the local size class frequencies of dreissenids (Barton et al., 2005). Therefore depletion of the preferred size class of this food source over time may have resulted in a compensatory switch to increased reliance upon alternative prey. Likewise increased reliance upon non-dreissenid benthic invertebrates may have also resulted in interspecific competition with yellow perch and help explain the shift to depleted $\delta^{13}C$ for all yellow perch size classes. Round goby are a known competitor of native fishes (French III and Jude, 2001; Janssen and Jude, 2001) and stable isotope results provide early evidence of competitive interaction between these two species. Diet data collected for this study indicate the prevalence of pelagic zooplankton, particularly among small and intermediate size classes of yellow perch, further corroborating stable isotope results. Significant increases were observed in yellow perch $\delta^{15}N$ with total length illustrating increasing trophic level. This relationship was consistent temporally and supports gut content analyses illustrating the increased importance of fishes in the diet of large yellow perch.

4.3 Multichannel Omnivory and Lake Michigan Food Web Stability

Stability in aquatic food webs is driven by food web structure which incorporates slow nearshore benthic or detrital energy pathways and faster pelagic energy pathways (Polis et al., 1997; Vander Zanden and Vadeboncouer, 2002; Rooney et al., 2006; Rooney and McCann, 2011). Within Lake Michigan, food web structure has been modified by dreissenid mussels, which are thought to sequester allochthonus and pelagic energy in the nearshore benthos (Fahnenstiel et al., 1995; Hecky et al., 2004). In this study, nearshore benthic invertebrate and pelagic zooplankton biomass were used illustrate the relative importance of the nearshore benthic energy pathway and the pelagic energy pathway, respectively. Seasonal fluctuations in 2011 benthic invertebrate (excluding dreissenids) and pelagic zooplankton areal C concentration were observed. However, benthic invertebrates exhibited consistently higher areal C concentration throughout the study with seasonal lows (193 mg C m^{-2}) occurring in July and seasonal highs (711 mg C m^{-2}) occurring in late May (Figure 11a). Conversely zooplankton C concentration rose quickly in June and July, peaked in August (223 mg C m^{-2}), but again approached very low concentrations during the cold water period in late fall (Figure 11a). From a stability perspective the consistently higher areal C biomass present in the nearshore benthos may provide a consistent source of energy to Lake Michigan fishes which are capable of utilizing this energy pathway. Furthermore this would promote stability among fish populations historically dependent upon pelagic energy sources such as zooplankton, which are subject to rapid seasonal oscillations in biomass and approach very low biomass in the winter.

The effect of changing energy pathways on food web stability can be described with respect to the biomass of pelagic and profundal fish communities as well. Based upon α values calculated for individual species, considerably less C was derived from the fast pelagic energy channel in 2010-2012 than in 2002-2003 (Figure 11b). This shift in time corresponded to reports documenting declines in Lake Michigan prey fish biomass based upon bottom trawl surveys (Bunnell et al., 2011; Madenjian et al., 2012). The largest shifts in α were observed in deepwater sculpin (-19.4%), rainbow smelt (-18.0%) and bloater (-13.2%) while alewife was the only species for which α increased (1.6%)

(Figure 11b). Typically, the largest changes in α corresponded to the largest declines in average biomass from 1974-2004 to 2010. By 2010, biomass of deepwater sculpin, rainbow smelt and bloater declined to 8.4-8.6% of their 1974-2004 average. Slimy sculpin biomass was very low throughout the bottom trawl time series but biomass for this species doubled from the 1974-2004 average to 2010 (Figure 11b). Alewife biomass declined to 16.9% of the 1974-2004 average biomass by 2010. This relatively smaller shift in alewife population size relative to bloater, deepwater sculpin and rainbow smelt corresponds to the least shift in $\delta^{13}C$ among pelagic or profundal prey fishes. In addition, alewife possessed the most nearshore signal of all the common pelagic and profundal prey fishes prior to the population explosion of dreissenid mussels. Taken together, these data suggest that alewife biomass may be more stable over time because this species is best suited to novel nearshore benthic energy pathways. Diet analysis of alewives has also begun to demonstrate the importance of nearshore prey items (Janssen and Luebke, 2004; Kornis and Janssen, 2011). In contrast to alewife, bloater and deepwater sculpin exhibited some of the largest shifts toward nearshore or detrital $\delta^{13}C$ and were most dependent upon pelagic phytoplankton based C prior to the proliferation of dreissenid mussels. In addition, these species also exhibited the greatest declines in biomass from 1973-2004 accounting for the majority of lost biomass in Lake Michigan pelagic and profundal prey fishes (Bunnell et al., 2011; Madenjian et al., 2012). These results provide some preliminary evidence that those species better suited to multichannel trophic omnivory, such as alewife, are able to maintain higher relative biomass than those species which are highly dependent upon the fast energy channel. Other explanations for the observed changes exist and may be having interacting effects with these observed patterns although conclusive evidence is sparse (Madenjian et al., 2002; Bunnell et al., 2006; Bunnell et al., 2009).

Although the large biomass declines of many species in the lake suggests that food web stability (i.e. the likelihood of persistence for a group of interacting species) is decreasing (Taylor, 1992; Rooney and McCann, 2011), I propose a conceptual model in which the persistence of many species is a reflection of their ability to feed across multiple energy channels. Among the highly speciated Laurentian Great Lakes coregonines (i.e. freshwater whitefishes), those species sharing the most similar niche space were either extirpated or are now threatened following anthropogenic perturbations (Schmidt et al., 2011). Highly specialized feeding or depth preferences made these species especially susceptible to stressors. Among the Lake Michigan fish community, multichannel trophic omnivory is apparent through the transitional period following the establishment of dreissenid mussels. Shifting from preferred energy channels has been described frequently for fishes and may have allowed most species described in this study to persist despite major reductions in phytoplankton abundance albeit lower densities (Hodgeson and Kitchell, 1987; Schindler and Scheuerell, 2002; Vander Zanden and Vadeboncouer, 2002).

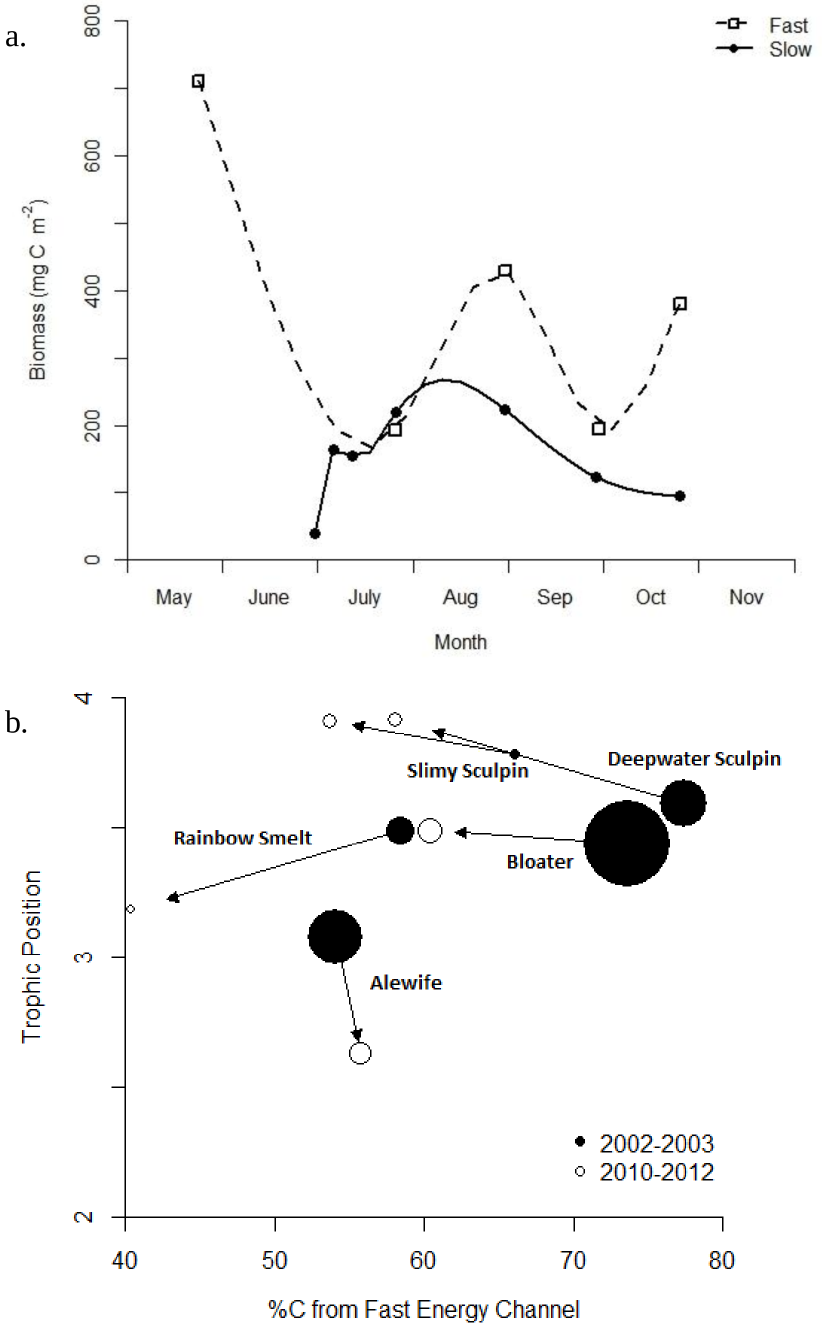

Figure 11 a. 2011 areal C biomass over time from nearshore benthic invertebrates excluding dreissenid mussels (10 m) and pelagic zooplankton (70 m) in Lake Michigan near Milwaukee, WI. **b.** Biplot of the percent C derived from the fast pelagic energy channel versus trophic position for the Lake Michigan pelagic and profundal prey fishes from 2002-2003 to 2010-2012. Area of each point is proportional to USGS estimated lake-wide biomass (kt) for these species. Biomass estimates are taken from the published 1974-2004 average and 2010 biomass for the earlier (solid circles) and later periods (open circles), respectively (Bunnell et al., 2011).

4.4 Conclusions

The Lake Michigan food web appears to have been greatly affected by the dreissenid mussel invasion and subsequent reductions in the spring phytoplankton bloom. Reductions in pelagic and profundal invertebrate and fish biomasses are consistent with dreissenid mediated declines in the fast energy channel. However, dreissenids have also increased water clarity and sequestered nutrients and energy in the nearshore and mid-depth regions of the lake, thereby augmenting the slow nearshore energy channel through increased benthic algal and invertebrate productivity. Contributions of nearshore productivity to much of the Lake Michigan food web have likely mitigated the impact of the major pelagic energy channel declines. Dreissenids have depleted offshore food availability, which in itself would destabilize pelagic food web structure. However, dreissenids have also fostered greater nearshore production, and this has helped to maintain food web stability, to the extent the food web as a whole has been able to benefit from this new energy source. Therefore dreissenid mussels appear to have had two opposing effects of both severely altering food web structure while simultaneously increasing stability though increased slow energy channel production.

The pathways through which nearshore basal energy sources are reaching upper trophic levels remains unknown but may have included increased inputs of benthic algae to the offshore detrital energy pool, direct dependence upon nearshore prey items, or some combination of both. Pathways of nearshore energy transfer probably vary on a species specific basis, depending on physiological feeding strategies and habitat preferences (Janssen, 1978; Kraft and Kitchell, 1986). Likewise, inputs of nearshore basal energy into the pelagic food web may vary spatially in Lake Michigan. The rocky nearshore habitats of Lake Michigan's western side have greater densities of dreissenid mussels and associated benthic algae and invertebrate communities (Gonzalez and Burkart, 2004; Hecky et al., 2004; Auer et al., 2010; Vanderploeg et al., 2010; Kornis and Janssen, 2011). The efforts of this study were focused largely on the western side of Lake Michigan, particularly near Milwaukee, WI. Some fish taxa including alewife and bloater were collected from around the entire Lake Michigan basin but statistical tests indicated relatively minor spatial differences for these species. Other fish taxa such as round goby varied greatly from one side of the lake to the other so temporal comparisons were restricted to the areas near Milwaukee, WI. Therefore caution should be exercised when extrapolating these results to the entire Lake Michigan fish community. Long term temporal patterns may be very different in locations such as Lake Michigan south eastern shore where gradual sloping, sandy substrates dominate and dreissenid densities are much lower in the nearshore.

This is one of the first studies (e.g. Schmidt et al. 2007) illustrating a consistent community-wide shift in isotopic composition in response to a species invasion or ecosystem stressor. Results provide empirical evidence that food web structure can be altered in response to a species invasion, with the negative impacts on stability being mitigated by increased reliance on slow energy pathways. These data support the hypothesis that—despite structural changes—some degree of stability has been maintained through multichannel omninvory and greater reliance on slow energy pathways. The Lake Michigan invertebrate and fish communities have continued to persist albeit major declines in biomass have been observed. However, further stress may exceed the system's ability to compensate and result in extirpations and altered steady states (Scheffer et al., 2001). Dreissenid populations do not appear to have reached steady state (Nalepa et al., 2009), and so the food web is likely still in a state of transition. Pairing these results with more accurate assessments of populations, at least for local scales, may help managers quantify the relative importance of nearshore energy contributions to the whole lake and create better numerical models for Lake Michigan fish population dynamics.

REFERENCES

Auer, M.T., L.M. Tomlinson, S.N. Higgins, S.Y. Malkin, E.T. Howell and H.A. Bootsma. 2010. Great Lakes Cladophora in the 21st century: same algae, different ecosystem. *J. Great Lakes Res.* 36: 248-255.

Barbiero, R.P., D.B. Bunnell, D.C. Rockwell and M.C. Tuchman. 2009. Recent increases in the large glacial-relict calanoid *Limnocalanus macrurus* in Lake Michigan. *J. Great Lakes Res.* 35: 285-292.

Barbiero, R.P., B.M. Lesht and G.J. Warren. 2011a. Evidence for bottom-up control of recent shifts in the pelagic food web of Lake Huron. *J. Great Lakes Res.* 37: 78-85.

Barbiero, R.P., K. Schmude, B.M. Lesht, C.M. Riseng, G.J. Warren and M.C. Tuchman. 2011b. Trends in *Diporeia* populations across the Laurentian Great Lakes, 1997-2009. *J. Great Lakes Res.* 37: 9-17.

Barton, D.R., R.A. Johnson, L. Campbell, J. Petruniak and M. Patterson. 2005. Effects of Round Gobies (Neogoius melanstomus) on Dreissenid Mussels and Other Invertebrates in Eastern Lake Erie, 2002-2004. *J. Great Lakes Res.* 31 (Suppl. 2): 252-261.

Bootsma, H., R.E. Hecky, R.H. Hesslein and G.F. Turner. 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotope analysis. *Ecology*. 77: 1286-1290.

Bootsma, H.A., E.B. Young and J.A. Berges. 2004. *Cladophora* research and management in the Great Lakes. Milwaukee.

Brooks, C.J., M. Sayers, R. Schuman, M.T. Auer, G. Meadows, N. Jessee and N. Grimm. 2012. Mapping and monitoring the extent of *Cladophora* and submerged aquatic vegetation in the Great Lakes using multi-resolution, multi-temporal satellite imagery. 55th Annual Conference on Great Lakes Research, International Association of Great Lakes Research. Cornwall, Ontario.

Brush, J.M., A.T. Fisk, N.E. Hussey and T.B. Johnson. 2012. Spatial and seasonal variability in the diet of round goby (Neogobius melanostomus): stable isotopes indicate that stomach contents overestimate the importance of dreissenids. *Can. J. Fish. Aquat. Sci.* 69: 573-586.

Bunnell, D.B., C.P. Madenjian and R.M. Claramunt. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 63: 2434-2446.

Bunnell, D.B., C.P. Madenjian, J.D. Holuszko, J.V. Adams and J.R.P. French III. 2009. Expansion of *Dreissena* into offshore waters of Lake Michigan and potential impacts on fish populations. *J. Great Lakes Res.* 2009: 74-80.

Bunnell, D.B., C.P. Madenjian, J.D. Holuszko, T.J. Desorcie and J.V. Adams. 2011. Status and trends of the prey fish populations in Lake Michigan, 2010. Lake Michigan Fishery Commission Meeting. Ypsilanti, MI.

Burkhardt, S., U. Riebesell and I. Zondervan. 1999. Effects of growth rate, CO_2 concentration, and cell size on stable carbon isotope fractionation in marine phytoplankton. *Geochimica et Cosmochimica Acta*. 63: 3729-3741.

Cabana, G. and J.B. Rasmussen. 1994. Modelling food chain structure and contaminent bioaccumulation using stable nitrogen isotopes. *Letters to Nature*. 372: 255-257.

Cabana, G. and J.B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Ecology*. 93: 10844-10847.

Clapp, D.F., P.J. Schneeberger, D.J. Jude, G. Madison and C. Pistis. 2001. Monitoring round goby (Neogobius melanostomus) population expansion in eastern and northern Lake Michigan. *J. Great Lakes Res.* 27: 335-341.

Creque, S.M. and J.M. Dettmers. 2002. Growth and Survival of Neashore Fishes in Lake Michigan. Illinois Natural History Survey.

Crowder, L.B. and F.P. Binkowski. 1983. Foraging behaviors and the interaction of alewife, *Alosa pseudoharengus*, and bloater, *Coregonus hoyi*. *Environ. Biol. Fish.* 8: 2.

Davis, B.M., J.F. Savino and L.M. Ogilvie. 2005. Diet niches of forage fish in Lake MIchigan. *Advanc. Limnolol.* 60: 261-275.

Dietrich, J.P., B.J. Morrison and J.A. Hoyle. 2006. Alternative Ecological Pathways in the Eastern Lake Ontario Food Web--Round Goby in the Diet of Lake Trout. *J. Great Lakes Res.* 32: 395-400.

Eadie, B.J., R.L. Chambers, W.S. Gardner and G.L. Bell. 1984. Sediment trap studies in Lake Michigan: resuspension and chemical fluxes in the southern basin. *J. Great Lakes Res.* 10: 307-321.

Evans, M.A., G. Fahnenstiel and D. Scavia. 2011. Incidental oligotrophication of North American Great Lakes. *Environmental Science and Technology*. 45: 3279-3303.

Fagan, K.A., M.A. Koops, M.T. Arts and M. Power. 2011. Assessing the utility of C:N ratios for predicting lipid content in fishes. *Can. J. Fish. Aquat. Sci.* 68: 374-385.

Fahnenstiel, G., S. Pothoven, H. Vanderploeg, D. Klarer, T. Nalepa and D. Scavia. 2010. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. *J. Great Lakes Res.* 36: 20-29.

Fahnenstiel, G.L., T.B. Bridgeman, G.A. Lang, M.J. McCormick and T.F. Nalepa. 1995. Phytoplankton productivity in Saginaw Bay, Lake Huron: Effects of zebra mussel (*Dreissena polymorpha*) colonization. *J. Great Lakes Res.* 21: 465-475.

Fitzgerald, S.A. and W.S. Gardner. 1993. An algal carbon budget for pelagic-benthic coupling in Lake Michigan. *Limnol. Oceanogr.* 38: 547-560.

France, R.L. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol. Oceanogr.* 40: 1310-1313.

French III, J.R.P. and D.J. Jude. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *J. Great Lakes Res.* 27: 300-311.

Fry, B. and P.L. Parker. 1979. Animal diet in Texas seagrass meadows: δ^{13}C evidence for the importance of benthic plants. *Esturine and Coastal Marine Science*. 8: 499-509.

Gonzalez, M.J. and G.A. Burkart. 2004. Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species, *Gammarus fasciatus* and *Echinogammarus ischnus*. *J. Great Lakes Res.* 30: 100-113.

Guiguer, K.R.R.A. and D.R. Barton. 2002. The trophic role of *Diporeia* (Amphipoda) in Colpoys Bay (Georgian Bay) benthic food web: a stable isotope approach. *J. Great Lakes Res.* 28: 228-239.

Hecky, R.E. and R.H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *J. N. Benthol. Soc.* 14: 631-653.

Hecky, R.E., R.E.H. Smith, D.R. Baron, S.J. Guildford, W.D. Taylor, M.N. Charlton and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61: 1285-1293.

Hensler, S.R., D.J. Jude and J. He. 2008. Burbot growth and diets in Lakes Michigan and Huron: an ongoing shift from native species to round gobies. *American Fisheries Society Symposium*. 59: 91-110.

Hodgeson, J.R. and J.F. Kitchell. 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). *American Midland Naturalist*. 118: 323-336.

Hondorp, D.W., S.A. Pothoven and S.B. Brandt. 2005. Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in Southeast Lake Michigan. *Transactions of the American Fisheries Society*. 134: 588-601.

Hondorp, D.W., S.A. Pothoven and S.B. Brandt. 2011. Feeding selectivity of slimy sculpin *Cottus cognatus* and deepwater sculpin *Myoxocephalus thompsoni* in southeast Lake MIchigan: Implications for species coexistence. *J. Great Lakes Res.* 37: 165-172.

Hooper, D.U., I. Chapin, F.S., J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A.J. Symstad, J. Vandermeer and D.A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*. 75: 3-35.

Huxel, G.R. and K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. *The American Naturalist*. 152: 460-469.

Jacobs, G.R., C.P. Madenjian, D.B. Bunnell and J.D. Holuszko. 2010. Diet of lake trout and burbot in Northern Lake Michigan during spring: Evidence of ecological interaction. *J. Great Lakes Res.* 36: 312-317.

Janssen, J. 1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes *Coregonus hoyi* and *C. artedii*. *J. Fish. Res. Board Can.* 35:

Janssen, J. and D.J. Jude. 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *J. Great Lakes Res.* 27: 319-328.

Janssen, J. and M.A. Luebke. 2004. Preference for rocky habitat by age-0 yellow perch and alewives. *J. Great Lakes Res.* 30: 93-99.

Johnson, T.B., D.B. Bunnell and C.T. Knight. 2005. A Potential New Energy Pathway in Central Lake Erie: the Round Goby Connection. *J. Great Lakes Res.* 31: 238-251.

Jude, D.J. and R.H. Reider. 1992. Establishment of Gobidae in the Great Lakes Basin. *Can. J. Fish. Aquat. Sci.* 49: 416-421.

Keeley, J.E. and D.R. Sandquist. 1992. Carbon: freshwater plants. *Plant, Cell and Environment*. 15: 1051-1035.

Kornis, M.S. and J. Janssen. 2011. Linking emergent midges to alewife (*Alosa pseudoharengus*) preference for rocky habitat in Lake Michigan littoral zones. *J. Great Lakes Res.* 37: 561-566.

Kraft, C.E. and J.F. Kitchell. 1986. Partioning of food resources by sculpins in Lake Michigan. *Environ. Biol. Fish.* 16: 309-316.

Krause, A.E., K.A. Frank, D.M. Mason, R.E. Ulanowicz and W.W. Taylor. 2003. Compartments revealed in food-web structure. *Letters to Nature*. 426: 282-285.

Laws, E.A., B.N. Popp, R.R. Bidigare, M.C. Kennicutt and S.A. Mackro. 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretiocal considerations and experimental results. *Geochimica et Cosmochimica Acta*. 56: 1131-1138.

Layman, C.A., D.A. Arrington, C.G. Montana and D.M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *ecology*. 88: 42-48.

Levin, L.A., C. Neira and E.D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. *Ecology*.

Limen, H., v.O. C.A.D. and H.J. MacIsaac. 2005. Food partitioning between the amphipods *Echinogammarus ischnis, Gammarus faciatus,* and *Hyalella azteca* as revelaed by stable Isotopes. *J. Great Lakes Res.* 31: 97-104.

Limén, H., C.D.A. van Overdijk and H.J. MacIsaac. 2005. Food partitioning between the amphipods Echinogammarus ischnus, Gammarus fasciatus, and Hyalella azteca as revealed by stable isotopes. *J. Great Lakes Res.* 31: 97-104.

Madenjian, C.P., D.B. Bunnell, T.J. Desorcie, M.A. Chriscinske, M.J. Kostich and J.V. Adams. 2012. Status and trends of prey fish populations in Lake Michigan, 2011. Lake Michigan Fishery Commission Meeting. Windsor, ON.

Madenjian, C.P., R.F. Elliott, T.J. Desorcie, R.M. Stedman, D.V. O'Connor and D.V. Rottiers. 2000. Lipid concentrations in Lake Michigan fishes: seasonal, spatial, ontogenic, and long-term trends. *J. Great Lakes Res.* 26: 427-444.

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

Madenjian, C.P., S.A. Pothoven, J.M. Dettmers and J.D. Holuszko. 2006. Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. *Can. J. Fish. Aquat. Sci.* 63: 891-902.

Madenjian, C.P., S.A. Pothoven, P.J. Schneeberger, M.P. Ebener, L.C. Mohr, T.F. Nalepa and J.R. Bence. 2010. Dreissenid mussels are not a "dead end" in Great Lakes food webs. *J. Great Lakes Res.* 36: 73-77.

Mann, K.H. 1988. Production and use of detritus in various freshwater, esturine, and coastal marine ecosystems. *Limnol. Oceanogr.* 33: 910-930.

Marsden, J.E. and S.R. Robillard. 2004. Decline of yellow perch in southwestern Lake Michigan, 1987-1997. *North American Journal of Fisheries Management*. 24: 952-966.

Marzolf, R. 1965. Substrate relations of the burrowing amphipod *Pontoporeia affinis* in Lake Michigan. *Ecology*. 5: 580-592.

McCann, K.S. 2000. The diversity-stability debate. *Nature*. 405: 428-433.

McCann, K.S., J.B. Rasmussen and J. Umbanhowar. 2005. The dynamic of spatially coupled food webs. *Ecology Letters*. 8: 513-523.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of δ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. *Geochimica et Cosmochimica Acta*. 48: 1135-1140.

Moore, J.C., E.L. Berlow, D.C. Coleman, P.C. de Ruiter, Q. Dong, A. Hastings, N.C. Johnson, K.S. McCann, K. Melville, P.J. Morin, K. Nadelhoffer, A.D. Rosemond, D.M. Post, J.L. Sabo, K.M. Scow, M.J. Vanni and D.H. Wall. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters*. 7: 584-600.

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

Ngochera, M.J. and H.A. Bootsma. 2011. Temporal trends of phytoplankton and zooplankton stable isotope composition in tropical Lake Malawi. *J. Great Lakes Res.* 37: 45-53.

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18: 293-320.

Polis, G.A., W.B. Anderson and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28: 289-316.

Polis, G.A. and D.R. Strong. 1996. Food web complexity and community dynamics. *The American Naturalist*. 147: 813-846.

Popp, B.N., E.A. Laws, R.R. Bidigare, J.E. Dore, K.L. Hanson and S.G. Wakeham. 1998. Effect of phytoplankton cell geometry on carbon isotope fractionation. *Geochimica et Cosmochimica Acta*. 62: 69-77.

Post, D.M., C.A. Layman, D.A. Arrington, G. Takimoto, J. Quattrochi and C.G. Montana. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*. 152: 179-189.

Post, D.M., M.L. Pace and N.G. Hairston Jr. 2000. Ecosystem size determines food-chain length in lakes. *Letters to Nature*. 405: 1047-1049.

Pothoven, S., T. Nalepa, P. Schneeberger and S. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. *North American Journal of Fisheries Mangaement.* 21: 876-883.

Pothoven, S.A., D.W. Hondorp and T.F. Nalepa. 2010. Declines in deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia* spp. in lakes Huron and Michigan. *Ecology of Freshwater Fish*. 20: 14-22.

Pothoven, S.A., T.F. Nalepa and S.B. Brandt. 2000. Age-0 and Age-1 yellow perch diet in southeastern Lake Michigan. *J. Great Lakes Res.* 26: 235-239.

Rau, G.H., U. Riebesell and D. Wolf-Gladrow. 1996. A model of photosynthetic ^{13}C fractionation by marine phytoplankton based on diffusive molecular CO_2 uptake. *Marine Ecology Progress Series*. 133: 275-285.

Redman, R.A., S.J. Czesny, J.M. Dettmers, M.J. Weber and D. Makauskas. 2011. Old tales in recent context: current perspective on yellow perch recruitment in Lake Michigan. *Transactions of the American Fisheries Society*. 140: 1277-1289.

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

Ricciardi, A. 2001. Facilitative interactions among aquatic invaers: is an "invasional meltdown" occuring in the Great Lakes? *Can. J. Fish. Aquat. Sci.* 58: 2513-2525.

Riley, S.C. and J.V. Adams. 2010. Long-term trends in habitat use of offshore dermersal fishes in western Lake Huron suggest large scale ecosystem change. *Transactions of the American Fisheries Society*. 139: 1322-1334.

Rodriguez, L.F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions*. 8: 927-939.

Rooney, N., K. McCann, G. Gellner and J.C. Moore. 2006. Structural asymetry and the stability of diverse food webs. *Nature*. 442: 265-269.

Rooney, N. and K.S. McCann. 2011. Integrating food web diversity, structure and stability. *Trends Ecol. Evol.* 27: 40-46.

Scheffer, M., S. Carpenter, J.A. Foley, C. Folke and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature*. 413: 591-596.

Schindler, D.E., S.R. Carpenter, K.L. Cottingham, X. He, J.R. Hodgeson, J.F. Kitchell and P.A. Soranno. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. In: Polis, G. A. and Winemiller, K. O. (eds), Food Webs: Integration of Patterns and Dynamics. Chapham & Hall: pp. 96-105.

Schindler, D.E. and M.D. Scheuerell. 2002. Habitat coupling in lake ecosystems. *Oikos*. 98: 177-189.

Schmidt, S.N., C.J. Harvey and M.J. Vander Zanden. 2011. Historical and contemporary trophic niche partitioning among the Laurentian Great Lakes coregonines. *Ecological Applications*. 21: 888-896.

Schmidt, S.N., J.D. Olden, C.T. Solomon and M.J. Vander Zanden. 2007. Quantitative approaches to the analysis of stable isotope food web data. *Ecology*. 88: 2793-2802.

Taylor, A.D. 1992. Deterministic stability analysis can predict the dynamics of some stochastic population models. *Journal of Animal Ecology*. 61: 241-248.

Truemper, H.A., T.E. Lauer, T.S. McComish and R.A. Edgell. 2006. Response of yellow perch diet to a changing forage base in southern Lake Michigan, 1984-2002. *J. Great Lakes Res.* 32: 806-816.

Vadeboncouer, Y., M.J. Vander Zanden and D.M. Lodge. 2001. Putting the lake back together: Reintegrating benthic pathways into lake food web models. *Bioscience*. 52: 44-54.

Vander Zanden, M.J., G. Cabana and J.B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ^{15}N) and literature dietary data. *Can. J. Fish. Aquat. Sci.* 54: 1142-1158.

Vander Zanden, M.J., J.M. Casselman and J.B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Letters to Nature*. 401: 464-467.

Vander Zanden, M.J. and J.B. Rasmussen. 1999. Primary consumer δ^{13}C and δ^{15}N and the trophic position of aquatic consumers. *Ecology*. 80: 1395-1404.

Vander Zanden, M.J. and Y. Vadeboncouer. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*. 83: 2152-2161.

Vanderploeg, H., J.R. Liebig, T. Nalepa, G. Fahnenstiel and S. Pothoven. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *J. Great Lakes Res.* 36: 50-59.

Vanderploeg, H.A., T.F. Nalepa, D.J. Jude, E.L. Mills, K.T. Holeck, J.R. Liebig, I.A. Grigorovich and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci*. 59: 1209-1228.

Wells, L. and A.M. Beeton. 1963. Food of the bloater, *Coregonus hoyi*, in Lake Michigan. *Transactions of the American Fisheries Society*. 92: 245-255.

Wetzel, R.G. 2001. Limnology: Lake and River Ecosystems. 3rd Edition. *Academic Press, San Diego, California.*

Zhu, B., D.G. Fitzgerald, C.M. Mayer, L.G. Rudstam and E.L. Mills. 2006. Alteration of ecosystem function by zebra mussels in Onieda Lake: Impacts on submerged macrophytes. *Ecosystems*. 9: 1017-1028.

Zohary, T., J. Erez, M. Gophen, I. Berman-Frank and M. Stiller. 1994. Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. *Limnol. Oceanogr.* 39: 1030-1043.

APPENDIX A

Mean δ^{13}C and δ^{15}N ± 1 S.E.of Lake Michigan Fishes and Invertebrates

	2002-2003			2005-2006			2010-2012		
Offshore Species	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N
Alewife (<100 mm)	6	-22.05 ± 0.57	9.07 ± 0.37	12	-21.80 ± 0.26	7.42 ± 0.08	22	-23.16 ± 0.22	7.02 ± 0.21
Alewife (>100 mm)	32	-23.54 ± 0.09	9.54 ± 0.12	2	-22.91 ± 0.50	8.66 ± 0.45	53	-23.38 ± 0.08	9.11 ± 0.15
Bloater (<100 mm)	3	-23.89 ± 0.72	10.80 ± 0.06	15	-21.85 ± 0.08	8.82 ± 0.15	9	-22.43 ± 0.69	9.79 ± 0.53
Bloater (>100 mm)	25	-25.30 ± 0.24	11.10 ± 0.14				61	-23.94 ± 0.09	12.15 ± 0.13
Rainbow Smelt	4	-23.69 ± 0.58	10.97 ± 0.57	12	-23.18 ± 0.28	9.83 ± 0.11	48	-22.13 ± 0.19	9.75 ± 0.11
Deepwater Sculpin	18	-25.40 ± 0.09	11.72 ± 0.09				15	-23.56 ± 0.05	13.16 ± 0.12
Slimy Sculpin	10	-23.40 ± 0.77	12.43 ± 0.41				11	-23.21 ± 0.15	12.91 ± 0.15
Brown Trout	1	-22.52 ± NA	12.11 ± NA				9	-21.99 ± 0.18	11.03 ± 0.12
Chinook Salmon	1	-22.58 ± NA	13.50 ± NA				4	-22.79 ± 0.15	11.79 ± 0.20
Lake Trout (>500 mm)	12	-21.82 ± 0.28	13.98 ± 0.15				21	-22.14 ± 0.13	13.33 ± 0.16
Diporeia	11	-23.91 ± 0.26	8.08 ±0.31				2	-22.09 ± 0.18	8.86 ± 0.08
Mysis	5	-26.35 ± 0.25	8.25 ± 0.42				3	-24.38 ± 0.06	10.05 ± 0.23
Nearshore Species									
Round Goby (<60 mm)	8	-21.39 ± 0.22	10.63 ± 0.36				35	-18.05 ± 0.17	8.49 ± 0.11
Round Goby (60-100 mm)	7	-21.46 ± 0.28	10.40 ± 0.26				85	-19.09 ± 0.14	8.74 ± 0.08
Round Goby (>100 mm)							25	-19.30 ± 0.25	8.53 ± 0.06
Yellow Perch (<70 mm)	3	-18.76 ± 0.54	8.33 ± 0.12				18	-20.87 ± 0.26	8.32 ± 0.17
Yellow Perch (70-150 mm)	5	-19.09 ± 1.25	9.08 ± 0.26				15	-20.30 ± 0.39	8.75 ± 0.24
Yellow Perch (>150 mm)	12	-17.94 ± 0.30	11.73 ± 0.23				26	-19.23 ± 0.23	10.92 ± 0.12
Longnose Dace	6	-16.76 ± 0.45	9.74 ± 0.11				9	-16.69 ± 0.33	8.37 ± 0.14
Spottail Shiner	4	-18.10 ± 0.60	9.58 ± 0.39				15	-18.15 ± 0.22	9.48 ± 0.24
Mottled Sculpin	6	-16.62 ± 0.36	9.98 ±0.19						
Amphipod	6	-15.98 ± 0.20	4.25 ± 0.36				11	-16.09 ± 0.37	3.54 ± 0.23
Isopod	9	-15.08 ± 0.38	5.19 ± 0.16				12	-15.35 ± 0.36	3.85 ± 0.20
Cladophora	9	-18.54 ± 0.25	2.71 ± 0.59				12	-17.76 ± 0.62	0.89 ± 0.14

Mean δ^{13}C and δ^{15}N ± 1 S.E.of Lake Michigan Fishes Relative to Nearshore Driessenid Mussels

	2002-2003			2005-2006			2010-2012		
Offshore Species	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N
Alewife (<100 mm)	6	0.05 ± 0.57	4.17 ± 0.37	12	-0.19 ± 0.26	3.42 ± 0.28	22	-0.60 ± 0.22	2.91 ± 0.21
Alewife (>100 mm)	32	-1.44 ± 0.09	4.64 ± 0.12	2	-1.30 ± 0.50	4.66 ± 0.64	53	-0.82 ± 0.08	5.00 ± 0.15
Bloater (<100 mm)	3	-1.79 ± 0.72	5.90 ± 0.06	15	-0.24 ± 0.08	4.82 ± 0.57	9	0.13 ± 0.69	5.68 ± 0.53
Bloater (>100 mm)	25	-3.20 ± 0.24	6.20 ± 0.14				61	-1.38 ± 0.09	8.04 ± 0.13
Rainbow Smelt	4	-1.59 ± 0.58	6.07 ± 0.57	12	-1.57 ± 0.28	5.83 ± 0.37	48	0.43 ± 0.19	5.64 ± 0.11
Deepwater Sculpin	18	-3.30 ± 0.09	6.82 ± 0.09				15	-1.00 ± 0.05	9.05 ± 0.12
Slimy Sculpin	10	-2.28 ± 0.22	7.83 ± 0.43				11	-0.65 ± 0.15	8.80 ± 0.15
Lake Trout (>500 mm)	12	-0.22 ± 0.44	9.60 ± 0.20				21	0.42 ± 0.13	9.22 ± 0.16
Nearshore Species									
Round Goby (<60 mm)	8	0.71 ± 0.22	5.73 ± 0.36				35	4.51 ± 0.17	4.38 ± 0.11
Round Goby (60-100 mm)	7	0.64 ± 0.28	5.50 ± 0.26				85	3.47 ± 0.14	4.63 ± 0.08
Yellow Perch (<70 mm)	3	3.34 ± 0.54	3.43 ± 0.12				18	1.69 ± 0.26	4.21 ± 0.17
Yellow Perch (70-150 mm)	5	3.01 ± 1.25	4.18 ± 0.26				15	2.26 ± 0.39	4.64 ± 0.24
Yellow Perch (>150 mm)	12	4.16 ± 0.30	6.83 ± 0.23				26	3.33 ± 0.23	6.81 ± 0.12
Spottail Shiner	4	4.00 ± 0.60	4.68 ± 0.39				15	4.41 ± 0.22	5.37 ± 0.24
Longnose Dace	6	5.34 ± 0.45	4.84 ± 0.11				9	5.87 ± 0.33	4.26 ± 0.14

Note: Values in this table correspond to those used for ANCOVA and Circular Statistics

APPENDIX B

Species Specific Lipid Correction Equations

Offshore Species	2002-2003 Mean C:N	2010-2012 Mean C:N	Correction Equation	R^2
Alewife	5.67	4.81	$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-3.66)*1.077+0.5828]$	0.8661
Rainbow Smelt	4.45	4.43	$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-3.91)*1.190+0.4622]$	0.9362
Slimy Sculpin	5.56	4.13	$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-3.78)*1.514+0.2328]$	0.9983
Lake Trout	6.69	5.52	$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-3.69)*1.020+0.6709]$	0.8599
Invertebrates*			$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-3.83)*0.6426+0.8971]$	0.7984
Nearshore Species				
Round Goby	4.59	4.28	$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-3.54)*0.342+0.3132]$	0.9813
Yellow Perch	4.41	4.41	$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-4.00)*0.8163+0.6623]$	0.9386
Spottail Shiner	4.84	4.74	$\delta^{13}C_{\text{Lipid Corrected}} = \delta^{13}C+[(C:N-3.77)*0.891+0.3263]$	0.9586

*Invertebrates included *Diporeia, Mysis,* and zooplankton taxa covering a broad range of C:N ratios.

Note: R^2 values measure the relationship between correction equation and measured lipid free values.

The generic correction equation from Post et al. (2007) was used for those species not listed here.

APPENDIX C

Mean α and Trophic Level of Fish and Invertebrates Represented in Figure 2

	2002-2003			2010-2012		
Offshore Species	n	α	Trophic Level	n	α	Trophic Level
ALE	38	0.54	3.08	84	0.56	2.63
Bloater	28	0.74	3.44	70	0.60	3.49
RAS	4	0.58	3.49	48	0.40	3.18
DWS	18	0.77	3.59	15	0.58	3.92
SLS	10	0.66	3.78	11	0.54	3.91
BRT	1	0.45	3.90	9	0.39	3.59
CHS	1	0.46	4.31	4	0.49	3.66
LAT	33	0.38	4.38	21	0.41	4.24
Diporeia	11	0.61	2.62	2	0.40	2.93
Mysis	5	0.88	2.50	3	0.68	2.84
Nearshore Species						
ROG	15	0.33	3.51	145	0.06	3.40
YEP	20	0.06	3.69	59	0.16	3.52
LND	6	0.00	3.49	9	0.00	3.42
STS	4	0.04	3.42	15	0.01	3.74
Amphipod	4	0.04	1.81	11	0.04	1.94
Isopod	9	0.02	2.14	12	0.01	2.08
Nearshore Quagga	5	0.41	1.48	3	0.46	2.01
Cladophora	9	0.03	1.40	12	0.06	1.13

Note: Offshore dreissenids were assumed to have an α of 1 and trophic level of 2
2002-2003: δ^{13}C=-27.44, δ^{15}N=6.8; 2010-2012: δ^{13}C=-26.95 δ^{15}N=8.90

Nearshore amphipods were assumed to have an α of 0 and trophic level of 2
2002-2003: δ^{13}C=-18.43, δ^{15}N=4.67; 2010-2012: δ^{13}C=-18.87 δ^{15}N=3.54

APPENDIX D

Analysis of Covariance Summary Statistics

					Full Model (Factors)						Reduced Model (Factors)			
Species	**Dependent**	**Degrees of Freedom**			**Year**		**Length**		**Year*Length**		**Year**		**Length**	
	Isotope	Length	Year	Error	F	P	F	P	F	P	F	P	F	P
Alewife	C	1	2	112	7.1800	0.0012	17.4850	0.0001	2.8450	0.0623	6.9550	0.0014	16.9370	0.0001
	N	1	2	113	8.3320	0.0004	52.1490	0.0000	28.0680	0.0000				
Bloater	C	1	2	103	78.7250	< 2e-16	33.3060	0.0000	0.1950	0.8230	79.9500	< 2e-16	33.8300	0.0000
	N	1	2	104	97.4300	< 2e-16	39.1500	0.0000	17.9700	0.0000				
Rainbow Smelt	C	1	1	47	39.6360	0.0000	1.7970	0.1870	2.4520	0.1240	38.4720	0.0000	1.7440	0.1930
	N	1	1	49	0.9160	0.3430	0.3280	0.5690	0.0180	0.8930	0.9340	0.3380	0.3350	0.5650
Deepwater Sculpin	C	1	1	26	500.4110	< 2e-16	12.8520	0.0014	1.0190	0.3221	500.0600	< 2e-16	12.8400	0.0013
	N	1	1	27	224.0380	0.0000	2.1960	0.1500	0.0000	0.9830	232.3320	0.0000	2.2770	0.1420
Slimy Sculpin	C	1	1	17	49.9920	0.0000	4.8380	0.0420	1.8090	0.1960	47.8400	0.0000	4.6300	0.0452
	N	1	1	17	35.7260	0.0000	0.7470	0.4000	0.3760	0.5480	37.0080	0.0000	0.7740	0.3910
Lake Trout	C	1	1	53	0.5930	0.4450	1.8160	0.1840	0.3280	0.5690	0.6000	0.4420	1.8390	0.1810
	N	1	1	53	0.7050	0.4050	17.8630	0.0001	0.0330	0.8560	0.7180	0.4010	18.1890	0.0001
Round Goby	C	1	1	85	256.5050	< 2e-16	17.4510	0.0001	1.8750	0.1750	253.9200	< 2e-16	17.2800	0.0001
	N	1	1	85	64.9250	0.0000	0.6770	0.4130	0.2890	0.5920	65.4660	0.0000	0.6820	0.4110
Yellow Perch	C	1	1	68	6.9860	0.0102	13.3080	0.0005	0.3310	0.5667	7.0550	0.0098	13.4380	0.0005
	N	1	1	68	0.3380	0.5631	230.4490	<2e-16	3.6160	0.0615	0.3250	0.5700	222.0320	<2e-16

APPENDIX E

Lake Michigan Food Web Metrics

Metric	**Year**		**Percent**
	2002-2003	2010-2012	**Change**
δ^{15}N Range	11.79	12.44	5.50%
δ^{13}C Range	10.68	10.25	-3.96%
Total Convex Hull Area	74.00	69.78	-5.71%
Mean Centroid Distance	4.28	4.03	-5.95%
Mean Nearest Neighbor Distance	1.58	1.39	-12.10%
Mean St. Dev. of Nearest Neighbor Distance	0.74	0.93	25.38%

Note: The various metrics presented here are unit less and meant only to facilitate relative comparisons

Summary of Circular Statistics

Metric	**Pelagic Fishes**	**Benthic Fishes**
Mean Angle (Radians)	3.58	3.48
Upper 95% C.I. (Radians)	0.719	NA
Lower 95% C.I. (Radians)	-1.28	NA
Rayleigh's Test Statistic	0.6767	0.0759
P value	0.007	0.963