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ASSESSING THE TROPHIC POSITIONS OF LAKE MICHIGAN FISHES USING STABLE CARBON AND NITROGEN ISOTOPES

by

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ABSTRACT

ASSESSING THE TROPHIC POSITIONS OF LAKE MICHIGAN FISHES USING STABLE CARBON AND NITROGEN ISOTOPES

by

Benjamin A. Turschak

The University of Wisconsin-Milwaukee, 2021
Under the supervision of Professor Harvey A. Bootsma

Lake Michigan is the second largest Laurentian Great Lake and is characterized by broad spatiotemporal variation in ecosystem processes such as nutrient cycling and energy flow. Variation in ecosystem processes—such as those induced by invasive dreissenid mussels—and subsequent changes in the spatiotemporal distribution of resources (i.e. prey or habitat) has resulted in major changes in Lake Michigan's fish community. The ability of fish species to cope with spatiotemporal resource dynamics is at least partially dependent on their ability to shift apparent trophic position along various resource gradients. The objectives of this research were to quantify trophic positions of Lake Michigan fishes following major ecosystem changes and identify potential mechanisms responsible for spatiotemporal variation.

To address these objectives, stable C and N isotopes were used to quantify the trophic position of many common Lake Michigan fish species. Consumer stable C and N isotopes vary as a function of resource reliance and primary energetic pathways (e.g. pelagic, profundal, and nearshore benthic). Therefore, isotopic composition was quantified to determine the relative importance of various energetic pathways and prey resources to Lake Michigan fish species. In some instances, isotopic variation could be evaluated relative to environmental resource

gradients and facilitated assessment of species and community level trophic responses over those gradients.

The trophic positions of common nearshore fish species were evaluated across the Lake Michigan basin. Mixing models were used to evaluate the relative importance of various prey sources and energetic pathways to each species across the basin. Differences in prey sources and primary energetic pathway varied as a function of water clarity for some nearshore fishes. It is likely that regional water clarity, derived from remote sensed $K_d(490)$, affects the relative importance of pelagic versus nearshore benthic primary and secondary production with resultant impacts on diets and primary energy sources for some nearshore species. For other nearshore species, there was nearly ubiquitous reliance on pelagic energy pathways regardless of water clarity or relative importance of nearshore benthic energy pathways.

Among the Lake Michigan salmonine community, trophic position was assessed during a period when preferred alewife (*Alosa pseudoharengus*) prey abundance and size structure was changing. Isotopic niche area and mixing models were used to quantify reliance on alewife and alternate prey sources. When the alewife population was small and dominated by larger individuals, some salmonines relied more heavily on alternate prey sources and energy pathways. Conversely, at higher alewife abundance and smaller size composition, most salmonines shifted their diet to greater reliance on this abundant prey source. Differential trophic responses of the salmonine community to alewife population dynamics highlighted variable capacity for reliance on alternate energy pathways and potential for niche partitioning among this predator community.

Unlike many fish species, abundance of cisco (*Coregonus artedi*) is apparently increasing in Lake Michigan and condition remains high. Much is unknown about the trophic ecology of this

population and the mechanisms for its recent expansion. The trophic position and diet of this species were assessed relative to other common Lake Michigan fishes using measures of isotopic niche area and diet mixing models. It appears that cisco currently occupy the trophic role of a pelagic predator similar to Pacific salmonines (*Oncorhynchus spp.*) and brown trout (*Salmo trutta*). Despite apparently stronger reliance on pelagic prey, cisco exhibited considerable reliance on alternate nearshore benthic energetic pathways as well. Ability to use multiple energetic pathways may have aided their ongoing population expansion.

Nearshore fishes, salmonines, and cisco exhibited varying degrees of reliance on alternate prey and energetic pathways. In the case of certain nearshore fishes and salmonines, reliance on alternate prey sources was apparent over spatial and temporal resource gradients, respectively. Reliance on alternate energetic pathways likely conveys stability to these fish populations resulting from the asynchrony of production across dominant energetic pathways. Species reliant on a single energetic pathway are likely subject to stronger fluctuations in available prey resources. Sustaining important fisheries and maintaining ecosystem function in midst of ongoing ecological change may benefit from consideration of the ability of fish species to rely on alternate energetic pathways.

To my parents, who encouraged my interest in nature and enabled my fishy pursuits from a young age.

To my son, Jonah, whose insatiable wonder at the natural world (and frequent interruptions during a COVID-19 era of working from home) helped me maintain perspective on the true importance of work in natural resources. You have helped me more than you will ever know.

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Chapter 1. Background

Lake Michigan Food Web

The Lake Michigan ecosystem and corresponding fish community has undergone periods of drastic change resulting from multiple anthropogenic stressors including habitat degradation, overfishing, and introduction of non-native species (Smith 1968; Eshenroder and Burnham-Curtis 1999; Bunnell et al. 2012). Over the past two decades, the invasion and subsequent population expansion of dreissenid mussels has emerged as a primary mechanism for ongoing change. Combined with reductions in nutrient loading, dreissenids have caused major changes to energy flow (e.g. benthic-pelagic coupling) resulting in the redistribution of biomass and energy flow through many food web compartments (Hecky et al. 2004; Mida et al. 2010; Vanderploeg et al. 2010a; Evans et al. 2011; Li et al. 2020). Because dreissenids can efficiently filter phytoplankton from the water column and sequester nutrients and energy in the benthos, they have reduced pelagic primary production, changed phytoplankton community composition, and changed the relative importance of seasonal algal blooms (Hecky et al. 2004; Fahnenstiel et al. 2010; Kerfoot et al. 2010a; Vanderploeg et al. 2010a). Coincident or resultant changes in the pelagic and profundal invertebrate community such as the loss of *Diporeia* and shifts in zooplankton community composition have likely reduced trophic transfer efficiency and further exacerbated declines in pelagic primary production for Lake Michigan fishes (Nalepa et al. 2009; Barbiero et al. 2011; Madenjian et al. 2015). While pelagic primary production and trophic efficiency has been reduced, nearshore-benthic primary production has increased in Lake Michigan over the same period. Dreissenid filtering has increased water clarity and sequestration of pelagic nutrients to the benthos resulting in greater benthic primary production (Hecky et al. 2004; Auer et al. 2010; Brooks et al. 2015). Secondary production, in terms of non-dreissenid benthic invertebrate biomass, also appears to respond positively to greater benthic primary productivity and increased habitat complexity associated with dreissenid mussel beds (Janssen et al. 2005 and references therein). Increased nearshore primary and secondary production may support some fish species in Lake Michigan, potentially offsetting declines in pelagic energy pathways (Madenjian et al. 2010).

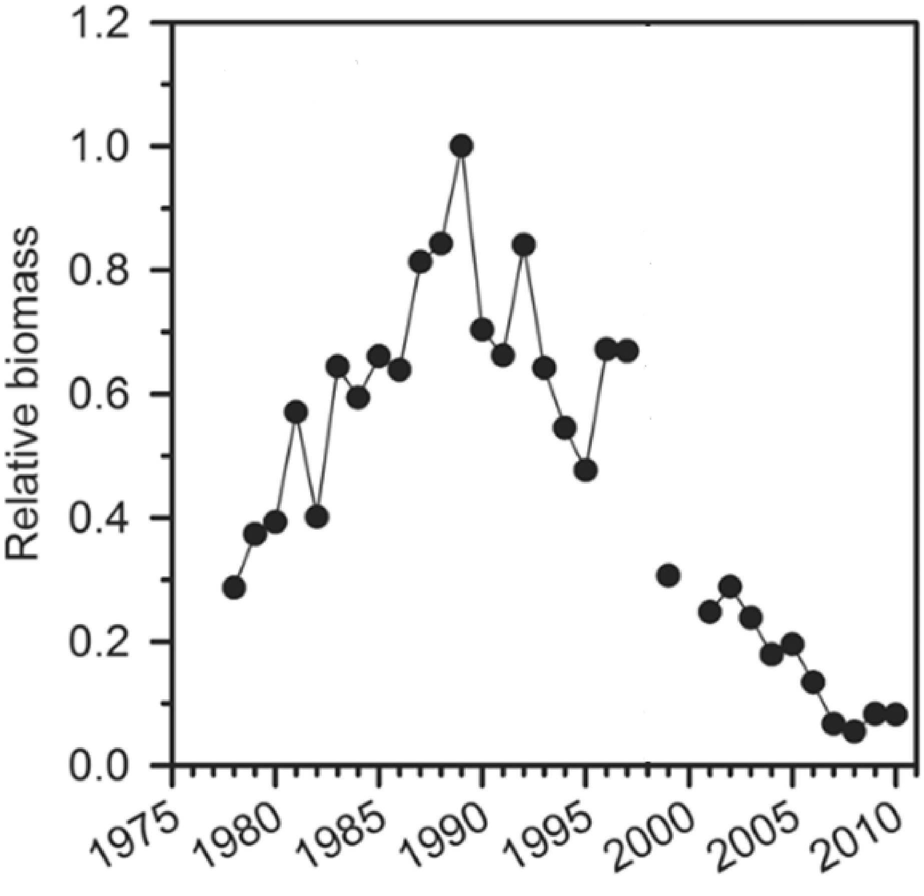

Figure 1.1. Time series of relative biomass of pelagic and profundal prey fishes captured in U.S. Geological Survey annual bottom trawl survey. Figure reproduced from Bunnell et al. (2014).

Major changes in benthic-pelagic coupling and primary production are increasingly well understood but much uncertainty remains about the effect of these changes on the fish community. Energy density, and weight at age has declined for several species of key management interest including the alewife (*Alosa pseudoharengus*), and lake whitefish

(*Coregonus clupeaformis)* which is consistent with the loss of *Diporeia* and subsequent changes in the diets of these species (Pothoven et al. 2006; Madenjian et al. 2015). Furthermore, biomass of most pelagic and profundal forage fishes has declined synchronously with changes in nutrient loading and redirection of nearshore energy to the benthos (Fig. 1.1; Bunnell et al. 2014). Though biomass of salmonine predators is largely regulated with stocking, growth of Pacific salmonines *(Oncorhynchus spp.*), including Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss)*, also appear to be closely linked to changes in preferred alewife prey biomass. In addition, Chinook salmon growth appears to be subject to density dependence suggestive of limited prey availability relative to population size (B. Turschak, MDNR, unpublished). Unlike Pacific salmonines, biomass of Lake Trout (*Salvelinus namaycush*) has increased over this time with relatively little change in growth rate (Seider and Caroffino 2020; Matthias, B., MSU Quantitative Fisheries Center, unpublished). Likewise, cisco (*Coregonus artedi)* in northeastern Lake Michigan appear to be experiencing a population expansion (based upon survey catch per effort CPE and angler catch rates) and exhibit high growth relative to other extant Great Lakes cisco populations (Fig. 1.2; Claramunt et al. 2019). Reliance on nearshore round goby (*Neogobius melanostomus*) prey by lake trout and cisco may explain apparent increased biomass and sustained growth rates (Breaker et al. 2020; Leonhardt et al. 2020). Differential directional responses in growth and biomass observed among fish species over the past two decades demonstrate that large scale changes in ecosystems processes (i.e.

nutrient cycling and energy flow) may be offset by stabilizing mechanisms for some species which remain poorly understood or quantified (Madenjian et al. 2015; Ives et al. 2018).

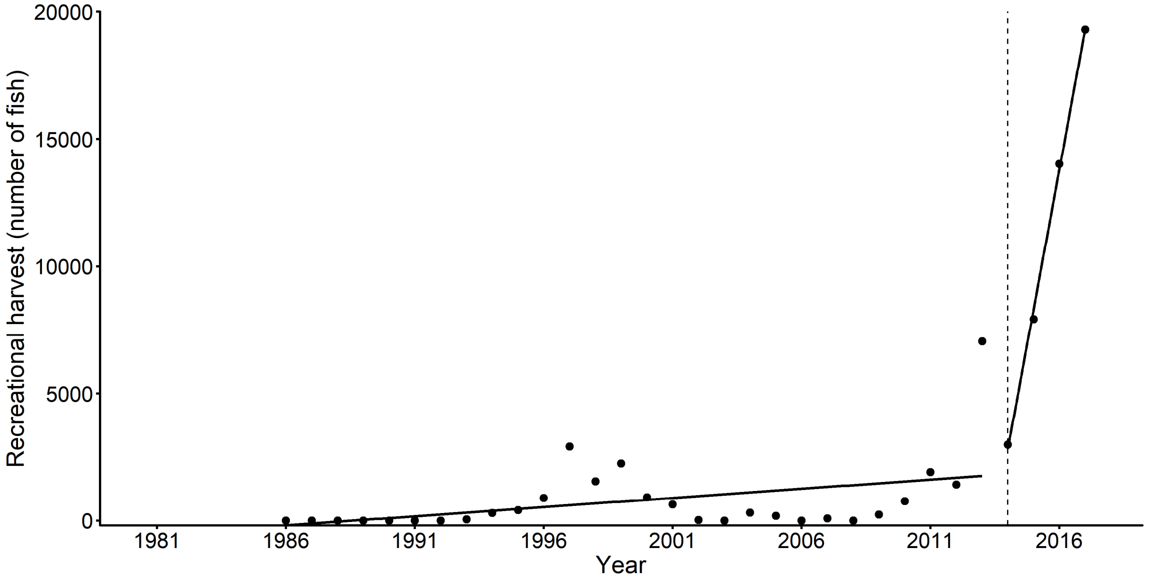

Figure 1.2. Time series of recreation cisco harvest in Michigan waters of Lake Michigan from annual creel census. Vertical hashed line indicates the series break point corresponding to increased catch rates. Figure reproduced from Claramunt et al. (2019).

Use of alternate energy or resource pathways (i.e. nearshore, pelagic, and profundal) may stabilize populations following perturbations such as major changes in trophic structure which in turn may increase the adaptive capacity of food webs (Ives et al. 2018). Reliance on multiple resource pathways helps to stabilize populations resulting from the independence or asynchrony of productivity patterns (Rooney et al. 2006; Rooney and McCann 2012; McMeans et al. 2015). Therefore, the differential population dynamics or growth rates of Lake Michigan fishes may correspond to differences in reliance on alternate resources, especially those independent of depressed pelagic energy pathways. Relatively few studies of Laurentian Great Lakes fishes have evaluated differential resource use across spatial or temporal gradients that are large enough to characterize reliance on alternate energy pathways (Rennie et al. 2009; Rush et al. 2012; Turschak et al. 2014b; Fera et al. 2017). As a result, evaluation of trophic position or resource reliance is often focused on spatial or temporal scales over which resources have remained relatively constrained resulting in a myopic view of resource usage by species of interest. Evaluating variation in trophic position relative to broader spatiotemporal resource gradients is a necessary step toward understanding the ability of species to cope with changes in trophic structure and characterize the adaptive capacity of the Lake Michigan food web (Ives et al. 2018).

Stable C and N Isotopes

Studies of stable C and N isotopes provide a useful means for quantifying changes in trophic structure of aquatic communities and are among the most used isotopes in ecological studies. Stable C isotope ratios (expressed as $\delta^{13}C$) vary broadly among primary producers but are relatively conserved (<1 ‰) during trophic transfer (Bootsma et al., 1996; France, 1995b; Hecky and Hesslein, 1995). At the base of a food web, stable nitrogen isotope ratios (expressed as $\delta^{15}N$) can vary according to the form of nitrogen assimilated. Above that base, $\delta^{15}N$ increases incrementally by 3-4‰ with each trophic transfer (Minagawa and Wada 1984; Vander Zanden et al. 1997). $\delta^{15}N$ is also enriched in profundal organisms in the Great Lakes and oceans due to ^{15}N enrichment of phytoplankton during the settling process (Altabet 1988; Ostrom et al. 1998; Sierszen et al. 2006). Thus, in aquatic systems $\delta^{13}C$ and $\delta^{15}N$ are used to determine primary energetic pathways (i.e., benthic or pelagic) as well as trophic level and/or depth distribution of consumers, respectively (Turschak and Bootsma 2015; Kornis et al. 2020).

Measurements of $\delta^{13}C$ and $\delta^{15}N$ can be used to quantify variation in resource use of fishes relative to spatiotemporal environmental resource gradients. In the Laurentian Great Lakes, application of stable isotopes to characterize broad scale changes in trophic position has provided evidence for increased reliance on nearshore energy pathways following reductions in pelagic primary productivity and dreissenid mediated ecosystem changes. Turschak et al. (2014) found that the pelagic/profundal invertebrate and forage fish community of Lake Michigan increased reliance on nearshore/benthic energy resources from 2002-2012. Greater reliance on nearshore energy sources has also been measured for large bodied Great Lakes fishes including lake whitefish (1950s-2006; Rennie et al. 2009; Fera et al. 2017) and lake trout (1995-2008; Rush et al. 2012) using stable isotopes. While these studies highlight the ability of some species to shift resource reliance in response to redirection of pelagic energy nearshore, additional work is needed to characterize trophic positions of other important fish species and examine isotopic variation in the context of important resource gradients.

Challenges to Fisheries Management

Changes in the Lake Michigan ecosystem have occurred rapidly since the establishment of the Lake Michigan Fish Community Objectives (FCO; circa 1995) which serve to guide and unify diverse fisheries management activities under common objectives. In addition to fisheries goals derived from the International Joint Commission's Great Lakes Water Quality Agreement and the Great Lakes Fish Commission's Joint Plan, the primary goal of the FCO is to "*Restore and maintain the biological integrity of the fish community so that production of desirable fish is sustainable and ecologically efficient*". However, rapid changes corresponding to declines in pelagic productivity and increased nearshore productivity have outpaced evaluation and subsequent understanding of changes in the trophic structure of the fish community. In particular, food web structure described in the FCO focuses almost entirely on pelagic energy pathways (phytoplankton → *Diporeia*/*Mysis*/zooplankton → forage fishes → piscivores) and fish production potential derived from this pathway. While this was likely an appropriate simplification at the time, outcomes of ongoing management activities must now consider the ability or inability of fish species to use alternate energy pathways. Fish communities capable of reliance on alternate energy pathways will then support greater adaptive capacity of the Lake Michigan food web in the midst of ongoing ecological changes (Ives et al. 2018).

Research Objectives and Questions

Research Objective

Use stable C and N isotopes to quantify the trophic positions of Lake Michigan fishes following major ecosystem changes and identify potential mechanisms responsible for spatiotemporal variation. To address this objective, the research provided hereafter addresses three research questions.

Research Question 1

What is the magnitude of spatial variation in trophic position of Lake Michigan nearshore fishes and what are potential mechanisms for variation? Nearshore fishes link nearshore primary and secondary production to recreationally important top predators and, in some cases (e.g. yellow perch, *Perca flavescen*s), are themselves recreationally important. However, little work has been done to quantify the importance of various energy pathways to important Lake Michigan nearshore fish species around the basin. Observed diets of nearshore fishes suggest spatial differences (Happel et al. 2015b, 2015a; Foley et al. 2017) but explicit quantification of trophic position and proportional nearshore benthic energy use (relative to pelagic energy use) is needed to understand trophic flexibility of these species to ongoing ecosystem perturbations. Given the degree of spatial variation in diets, potential exists to identify explanatory covariates using existing broad scale physical, chemical, or biological monitoring data (i.e. satellite remote sensing). Identification of explanatory variables may help to elucidate mechanisms for spatial variation and evaluate trophic flexibility of nearshore species in the future.

Research Question 2

How do the diets of Lake Michigan salmonines respond to changes in forage fish abundance and size structure? Lake Michigan salmonines support an economically important recreation fishery while maintaining top-down control of invasive forage fishes such as the alewife and, to a lesser extent, rainbow smelt (*Osmerus mordax*) and round goby (Melstrom et al. 2013; Tsehaye et al. 2014a, 2014b; Raynor and Phaneuf 2020). As such, this community is subject to intensive management via harvest regulations and supplemental stocking targeted at maximizing fishery potential while sustaining continued recruitment of their preferred alewife prey (Claramunt et al. 2012). Past diet studies have ubiquitously demonstrated that diets of all Lake Michigan salmonines are dominated by alewives (Stewart et al. 1981; Rand et al. 1993; Savitz 2009), but some salmonine species have demonstrated regional and/or seasonal reliance on alternate prey resources such as terrestrial invertebrates, rainbow smelt, and round goby (Happel et al. 2018, 2020; Leonhardt et al. 2020). Use of alternate prey sources may help support fishery potential during periods of low and variable alewife recruitment (as observed since the early 2000s). However, multiyear lakewide diet studies are relatively less common and have largely ignored abundance and size structure of the prey fish community as it relates to predators. Therefore, the trophic flexibility of each species to changes in forage abundance and size structure remains a critical unknown for continued management particularly as alewife abundance remains near record lows levels.

Research Question 3

What trophic role does a resurgent cisco population occupy in the changing Lake Michigan food web? A remnant population of cisco located in/near Grand Traverse Bay, Michigan, began a population expansion in Northeastern Lake Michigan around 2011 (Claramunt et al. 2019).

While much uncertainty exists regarding the specific mechanisms for this population and range expansion, their large size and piscivorous diet seem to suggest that this population of cisco occupy a trophic role unique from that of most other Great Lakes cisco populations (i.e. Lakes Huron, Ontario and Superior are dominated by smaller zooplanktivorous forms; Breaker et al. 2020). Little effort has been made to characterize the trophic role of Lake Michigan cisco in the context of the broader Lake Michigan fish community. However, improved understanding of their role in the Lake Michigan food web may offer clues about their recent success during a period when congener (e.g. bloater and lake whitefish) populations have remained suppressed or continued to decline (Bunnell et al. 2020; Seider and Caroffino 2020).

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Chapter 2. Spatial Variation In Trophic Structure Of Nearshore Fishes In Lake Michigan As It Relates To Water Clarity[1]

Abstract

Nearshore water clarity, as measured by remotely sensed $K_d(490)$, and stable C and N isotopes of several nearshore fishes differed across the Lake Michigan basin. $\delta^{13}C$ of Round Goby, Yellow Perch, and Spottail Shiner were depleted in the southeast where water clarity was low relative to the southwest where water clarity was greater. Bayesian analyses were used to evaluate spatial variation in diet composition and quantify the relationship between water clarity and the proportional importance of pelagic energy in fish diets. Water clarity in nearshore areas is likely related to variable riverine inputs, resuspension, and upwelling processes. While these processes may not directly impact $\delta^{13}C$ or $\delta^{15}N$ of nearshore fishes, we hypothesize that water clarity differentially affects benthic and pelagic algal production. Lower water clarity in the benthos and subsequently lower benthic productivity may be related to regional diet differences and increased reliance on pelagic energy sources. Mobile fishes such as Alewife may not be in isotopic equilibrium with regional prey sources and depart from spatial patterns observed in other nearshore fishes.

Introduction

Ecologists recognize that ecosystem processes (e.g. primary production, nutrient cycling, energy flow) change along environmental gradients over broad spatial scales (Vannote et al. 1980; Turner 1989; Polis et al. 1997; Allan 2004). With technological advances in Geographic

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Information Systems (GIS) and remote sensing techniques, it has become easier to assess how large scale patterns in ecosystem structure and function are related to terrestrial and aquatic physiography (Turner 1989; Levin 1992; West et al. 2010). However, it remains difficult to assess dynamic ecosystem processes such as energy flow and nutrient cycling over broad spatial scales, and how these processes are affected by physical and geochemical gradients, particularly when the process of interest is variable over short time scales (Turner 1989).

Large lakes and their surrounding catchments often cover broad geographic regions with diverse land-use, geology, and drainage regimes (Robertson 1997). Lake Michigan, the second largest Laurentian Great Lake (58,030 km^2), is influenced strongly by wind driven physical processes and internal chemical cycling. The lake's nearshore environment is highly variable, due to spatial differences in bathymetry, shoreline structure, bottom type, and riverine inputs (Boyce 1974, Eadie et al. 1984; Conley et al. 1988; Janssen et al. 2005). As a result, there is a range of environmental gradients much larger than observed in most small lakes. As such, it is to be expected that food web structure and energy flow pathways will also vary both spatially and temporally.

Several studies of nearshore fishes in Lake Michigan have investigated spatial heterogeneity in diets using multiple indicators including fatty acids, gut content analysis, and stable isotopes (Happel et al. 2015a; 2015b; Foley et al. 2017). These studies suggest that spatial variation in physical conditions such as fluvial input and substrate type as well as regional differences in primary production pathways may result in regional diet differences (Happel et al. 2015a; 2015b; Foley et al. 2017). Despite apparent spatial variation in nearshore fish diets and energy pathways, it remains unclear how this variation may be related to broader scale physical or geochemical gradients.

While stable C and N isotope ratios are extremely useful for determining energy flow pathways within aquatic food webs (Hecky and Hesslein 1995; Vadeboncoeur et al. 2002), they can also be used to gain insight into biogeochemical processes, including nutrient loading, nutrient cycling, and carbon fixation (Hama et al. 1983; Ostrom et al. 1997; Kumar et al. 2011), which in turn reflect physical properties and processes such as land use, water clarity, river discharge, and substrate type. Therefore, a detailed analysis of stable C and N isotope ratios (expressed as $\delta^{13}C$ and $\delta^{15}N$, respectively) can provide insight into the relationships between physical environmental gradients and food web structure over broad spatial scales (West et al. 2010). Stable isotope ratios vary as a result of isotopic fractionation, a process by which the isotope ratios of reactants and products diverge during chemical reactions (Peterson and Fry 1987). For aquatic organisms, $\delta^{13}C$ can be used to trace the relative contribution of isotopically heavy benthic primary producers and isotopically light pelagic primary producers to higher trophic levels (France 1995; Hecky and Hesslein 1995; Bootsma et al. 1996). $\delta^{15}N$ increases in a stepwise fashion with each trophic transfer which makes it a useful measure of consumer trophic level (DeNiro and Epstein 1981; Vander Zanden and Rasmussen 1999). Because isotopic fractionation is a mechanistic process, spatial patterns in stable isotopic composition of material (e.g. nutrient or detritus) or organisms can be used to infer spatial differences in ecosystem processes such as nutrient cycling and energy flow (Bowen et al. 2010), especially when spatial variation in stable isotope ratios are measured against a temporally integrated trophic baseline (Vander Zanden and Rasmussen 1999; Post 2002).

Independent spatial metrics that can be measured remotely, such as temperature, chlorophyll *a*, and turbidity, can be combined with stable isotope data to provide a powerful means of detecting and explaining large scale gradients in ecosystem processes (Radabaugh et al.

2013). Turbidity, which can be inferred from the diffuse light attenuation coefficient at 490 nm [K_d(490)] (Yousef et al. 2016), is particularly useful in that it reflects several key properties and processes that can influence nearshore energy flow, including the distribution of river plumes, sediment resuspension, and the relative availability of light to planktonic versus benthic algae (Vadeboncoeur et al. 2003; Rao and Schwab 2007; Lohrenz et al. 2008a). The distinction between planktonic and benthic production has become especially important in Lake Michigan, where the former has decreased in the past few decades (Fahnenstiel et al. 2010) while the latter has increased (Auer et al. 2010; Brooks et al. 2014), with apparent effects on much of the food web (Turschak et al. 2014).

In this study, we examine spatial patterns in stable C and N isotopes of several common fishes across 8 study sites throughout Lake Michigan's nearshore zone. Fish species included two native species (yellow perch *Perca flavescens* and spottail shiner *Notropis hudsonis)* and two non-native species (round goby *Neogobius melanstomus* and alewife *Alosa pseudoharengus*) with variable life histories and feeding ecologies. We hypothesized that the relative importance of pelagic versus benthic energy pathways and diets among nearshore fishes in Lake Michigan reflect broad spatial variation in water clarity. Furthermore, we hypothesized that spatial patterns in the relative importance of pelagic vs benthic energy pathways among species would vary according to their life-history and feeding ecologies. Diet compositions of each species across study sites was inferred using stable isotope analysis. In addition, spatial isotopic differences were compared with spatial patterns of water clarity [K_d(490)] as derived from satellite imagery. This approach allowed us to determine the degree to which spatial variation in primary production pathway (i.e. benthic vs. pelagic) and nearshore trophic structure are related to spatial patterns of water clarity in this large lake.

Methods

Sample Collection

Biological samples were collected from 8 study sites located in the nearshore zone of Lake Michigan, 2-15 m depth (Fig. 2.1). These sites varied widely with respect to surrounding land use, substrate type, and hydrodynamics. Most sites were sampled on three occasions (May, July, September) in 2010 and 2011 with supplemental collection occurring intermittently among sites and years.

Collection methods are the same as described by Foley et al. (2017) and Happel et al. (2015a; 2015b). Briefly, fish and invertebrates were collected using a variety of techniques depending on the target taxa and substrate being sampled. Fish were collected with micromesh (6 and 8 mm bar) and larger experimental gillnet sets (12.7, 19.1, and 25.5 mm bar) set at 2-5 m, 8-10 m, and 15-16 m depths. In rocky nearshore areas, benthic invertebrates were collected by scuba divers performing benthic scrapes (400 cm^2) on large rocks. Over soft sediments, benthic invertebrates were collected using a Ponar grab. In the case of both benthic scrapes and Ponar grabs, triplicate samples were collected for each sample date and location. Zooplankton were collected by performing triplicate vertical daytime tows with 64 μm zooplankton net at each date and location.

Sample Processing

Fish and invertebrate samples were placed on ice in the field and then sorted immediately upon arrival in the laboratory. After sorting, samples were frozen at -28°C until processing could be completed. Guts were removed from all fish samples. Fish <250 mm were homogenized whole after the gut was removed whereas fish >250 mm had a dorsal muscle tissue plug removed and homogenized. Paired comparison of whole-body tissue homogenate and dorsal muscle tissue plug stable isotopes have revealed little difference and so we felt justified in treating these data similarly (Turschak 2013). Benthic invertebrates were sorted by taxon into pooled samples from each site, date, and replicate, and then analyzed whole. Bulk zooplankton samples were also pooled from each site, date, and replicate, and then analyzed. Soft tissue was dissected from shell material of dreissenid mussels. Fish and invertebrate samples were then lyophilized, and 3-4 mg of the dried homogenate packed into tin capsules for stable C and N isotope analysis.

Stable isotope measurements were made using the methods described in Turschak and Bootsma (2015), and Ngochera and Bootsma (2011). Briefly, isotope concentrations were measured using an isotope ratio mass spectrometer (Finnigan MAT delta S SIR-MS) with elemental analyzer front end and ConFlo II interface. Carbon calibration was done with NIST standard RM 8542 (sucrose, $\delta^{13}C=-10.47$) and a NIST-traceable standard (glycine, $\delta^{13}C=-33.63$). Nitrogen calibration was with NIST standard RM 8547 (IAEA-N1 ammonium sulfate, $\delta^{1}5N=0.4$), NIST standard RM 8548 (IAEA-N_2 ammonium sulfate, $\delta^{15}N=20.3$), and a NIST-traceable ammonium chloride standard ($\delta^{15}N=-8.9$). During sample runs, an acetanilide control sample was run every twelfth sample and analyzed for ^{13}C:^{12}C and ^{15}N:^{14}N ratios. Instrument precision was ±0.2‰ for both C and N isotopes based upon acetanilide controls. All stable isotope results are expressed in δ notation (i.e. $\delta^{13}C$ and $\delta^{15}N$) as per mil (‰) differences between the isotope ratio of the sample and that of the international standard (PDB carbonate and atmospheric air for $\delta^{13}C$ and $\delta^{15}N$, respectively). Taxa specific lipid-corrections were applied to $\delta^{13}C$ values following the equations described in Turschak and Bootsma (2015) to reduce variability associated with consumer tissue lipid content.

Data Analysis

MODIS satellite images of Lake Michigan were collected for 2010 and 2011 and then loaded into R (version 3.2.3, R Foundation for Statistical Computing) with the "ncdf4" software package. Using this software, we extracted the georeferenced level 2 $K_d(490)$ data for each image, which represents the diffuse attenuation of downwelling light at a wavelength of 490 nm following a fourth-order polynomial fit of 488 nm (blue) and 555 nm (green) remotely-sensed reflectance in NASA's NOMAD dataset (Werdell and Bailey 2005). While this algorithm is based on primarily open ocean type (Case 1) waters where optical constituents are assumed to be co-varying, it has been shown to be valid for determination of *in situ* $K_d(490)$ in the Great Lakes, particularly Lake Michigan (Yousef et al. 2016). For Lake Michigan, we used this product as a surrogate measure of turbidity in the water column with the assumption that trends observed are primarily due to changes in the optical properties of the water column. While this study was not designed to validate satellite observations or recommend a new approach for analyzing remote imagery, we did consider the distribution of remote sensing reflectance (R_{rs}) spectra in Lake Michigan available on NASA's SeaBASS data archive relative to the NASA bio-Optical Marine Algorithm Data set (NOMAD) used to derive the coefficients used in the algorithm retrieving $K_d(490)$ from MODIS Aqua data to ensure we were operating within a similar optical space. Excluding observations in highly eutrophic areas not considered here (e.g. southern Green Bay), Lake Michigan R_{rs} spectra fell predominantly around the median NOMAD R_{rs} values, and between the 25% and 75% quantiles of the NOMAD dataset (Appendix A.1). Lake Michigan stations fell well within the distribution of the NOMAD dataset without a statistically significant bias towards any region of the NOMAD dataset. From this, we assumed we were operating within a similar optical space and proceeded to use satellite derived $K_d(490)$ as an indicator of water column light availability over the study period.

MODIS image data were matched to study site locations with a Euclidean nearest neighbor approximation. The nine 1 km^2 image pixels (3 x 3 grid) centered around each study site were found and then averaged to produce a daily $K_d(490)$ value for all eight study sites in each image (Bailey and Werdell 2006). Although one image per day was captured for Lake Michigan, cloud cover over study locations resulted in missing data for certain sites on certain dates. The median and median absolute deviation (mad) of all cloud free images for each study site from 2010 and 2011 were calculated. Median and median absolute deviation were used to characterize central tendency and variance instead of mean and standard deviation because $K_d(490)$ data were not normally distributed; these metrics give less weight to extreme values that are typically anomalous and inaccurate in remotely sensed data sets.

Because study sites were in nearshore regions, some pixel values had to be excluded due to proximity to shore, resulting in less than 9 pixels, with an average of 4.3 pixels for all applied values. There is potential for bottom effects (e.g. light reflected from bottom substrate) in retrieved pixels; however, we were not able to determine the degree to which satellite derived measurements were influenced by bottom reflectance. For the sake of simplicity, we assume that bottom effects were negligible. Potential errors in data interpretation due to this assumption are discussed below. For graphical representation, only (e.g. Fig. 2.1), images with <90% cloud cover were interpolated to a fixed grid (0.01° x 0.01° grid cells) over Lake Michigan using an inverse distance weighted interpolation algorithm (Fig. 2.1).

We quantified the diets of nearshore fishes across sites using a Bayesian mixing model approach. The “MixSIAR” package (Stock and Semmens 2013) built for R was used to quantify dietary proportions of prey sources using $\delta^{13}C$ and $\delta^{15}N$ as tracers, region as a random effect factor, and total length as a covariate. Potential prey sources for each species were the same as those used in Turschak and Bootsma (2015) but isotope ratios of prey were site-specific. In addition to source isotope data, trophic enrichment factors (mean ± sd) of 0.4 ± 1.3 for $\delta^{13}C$ and 3.4 ± 1.0 for $\delta^{15}N$ were provided as model inputs (Post 2002). We used default vague prior probability distributions with three Markov chain Monte Carlo (MCMC) simulations of 1,000,000 iterations. The burn-in period for each iteration chain was set at 500,000 and the subsequent values were thinned by a factor of 500. Chain convergence was checked using the Gelman-Rubin and Geweke diagnostic tests. If chains had not converged, a second model run was performed with three chains of length 3,000,000, burn-in period of 1,500,000, and thinned by a factor of 500.

We additionally attempted to quantify the relationship between dietary proportions from benthic and pelagic sources with water clarity (as measured by daily $K_d(490)$) at each sample location and total length of individual fish. To prepare the data for these calculations, a correction factor was first applied to the $\delta^{13}C$ values of fish to account for trophic discrimination such that $\delta^{13}C_{TDF} = \delta^{13}C_{fish} - \Delta$, where Δ is described by the following equation (Ives et al. 2013):

$$\Delta = TDF_C \left[\frac{(\delta^{15}N_{fish} - \delta^{15}N_{pc})}{TDF_N}\right].$$

Trophic discrimination factors represent the average per mil shift in $\delta^{13}C$ and $\delta^{15}N$ (TDF_C = 0.4‰ and TDF_N = 3.4‰, respectively) resulting from fractionation that occurs from one trophic level to the next (Post 2002). $\delta^{15}N_{pc}$ is the overall baseline $\delta^{15}N$ calculated as the mean $\delta^{15}N$ of both benthic and pelagic primary consumers (i.e. amphipods, isopods, chironomids, oligochaetes, and dreissenid mussels). The pelagic source and benthic source model inputs were dreissenid mussels and non-dreissenid benthic invertebrates (amphipods, isopods, chironomids and oligochaetes), respectively. Although not all fish consume these source groups directly, relatively long-lived primary consumers (e.g. mussels) serve as time-integrated representatives of basal pelagic and benthic δ^{13}C sources (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999; Post et al. 2000). Because not all benthic taxa were present at all sites, the benthic source was calculated using an unweighted combined average δ^{13}C of all amphipods, isopods, chironomids and oligochaetes and the pelagic source was calculated using the average δ^{13}C of nearshore (<15 m depth) dreissenid mussels.

With consumer δ^{13}C values adjusted for trophic discrimination and benthic and pelagic sources established, we then extended the Bayesian mixing model of the "MixSIAR" package to incorporate a hierarchical region-specific intercept that is a function of water clarity with the additive covariate of individual fish total length. Thus, we characterize dietary proportions at two levels (i.e., split-plot design). The first level describes variation in dietary proportion across total length.

$$f(y) \sim Normal(\beta_{0x} + \beta_1 * \mathrm{TL}_i)$$

Where *f*(*y*) is the centered log ratio (CLR) transformation of the relative contributions of each energy source (benthic or pelagic) and using δ^{13}C as a single tracer. Here, the benthic source was calculated using the regional average δ^{13}C of all amphipods, isopods, chironomids and oligochaetes and the pelagic source was calculated using the regional average δ^{13}C of nearshore (<15 m depth) dreissenid mussels. β_{0x} is the region-specific intercept, β_1 is the coefficient of total length, and TL_i is the total length of individual i. The second level of the model describes variation in dietary proportion across regions as a function of $K_d(490)$.

$$\beta_{0x} \sim Normal(\beta_2 + \beta_3 * \mu_x, \sigma)$$

Where β_2 is the intercept describing the global mean composition in CLR space, β_3 describes the effects of mean $K_d(490)$ value on the overall mean composition, μ_x is the mean $K_d(490)$value at region x, and σ is the standard deviation of the region specific intercept. An additional consideration is daily measurements of $K_d(490)$ in each region and its associated uncertainty. To account for variation in $K_d(490)$, we integrated a second model to describe the $K_d(490)$ values at each site. Estimation of the mean $K_d(490)$ value (μ_x) and its uncertainty at each region was accomplished by incorporating the individual $K_d(490)$ values at each region into the model.

$$\mathrm{Kd}_{xi} \sim Lognormal(\mu_x, \tau_x)$$

Where Kd_{xi} are the observed daily $K_d(490)$ values in region x, and τ_x is the standard deviation of $K_d(490)$ values at region x on a log scale. Thus, parameter estimates represent the joint posterior probability distribution that incorporate individual variation in dietary composition with the effect of total length and region effects that are a function of $K_d(490)$ values.

We used default vague prior probability distributions in MixSIAR (Stock and Semmens 2013) for the region random effects model. Additional parameters for the $K_d(490)$ were also given vague prior probability distributions (β_2 was given a vague Dirichlet prior on the transformed composition; β_3 and μ_x were given independent normal distributions with mean = 0 and precision = 0.001; and σ and τ_x were given independent gamma distributions with shape and rate = 0.001 with three MCMC simulations of 2,505,000 total iterations. The burn-in period for each iteration chain was set at 5,000 and the subsequent values were thinned by a factor of 50 for a total of 50,000 saved iterations. Chain convergence was checked using the Gelman-Rubin and Geweke diagnostic tests.

Results

Median light extinction coefficients as measured by $K_d(490)$ varied across study sites in 2010 and 2011 (Median = 0.14 - 0.61 m^{-1}; Table 2.1; Fig. 2.1) with the lowest values in the southwestern basin (sites 2 and 3) and highest in the southeastern basin (sites 6 and 7). Furthermore, variation in $K_d(490)$ differed among study sites (MAD = 0.04-0.73 m^{-1}) with lower variation observed at the southwestern study sites (sites 2 and 3) than at the southeastern study sites (sites 6 and 7; Table 2.1; Fig. 2.1). Greater $K_d(490)$ median and MAD were observed in the southeastern study sites particularly during the spring and summer of 2010 and 2011 (Table 2.1).

Regional patterns were also observed in the $\delta^{13}C$ and $\delta^{15}N$ of nearshore fishes (Fig. 2.2a-h). In particular, round goby (Fig. 2.2a), yellow perch (Fig. 2.2c) and spottail shiner (Fig. 2.2e) $\delta^{13}C$ exhibited spatial differences which were nearly directly inverse to that of $K_d(490)$ with relatively high values in the southwestern basin and lower values in the southeastern basin. Differences in mean $\delta^{13}C$ among study sites differed by as much as 5.38‰, 2.66‰, and 3.97‰ for round goby, yellow perch, and spottail shiners, respectively, between southwest and southeast study sites (Fig. 2a, 2c and 2e). Only alewife diverged from this spatial pattern with relatively uniform $\delta^{13}C$ or <1.41‰ mean differences among all sites (Fig. 2g). By comparison, the $\delta^{15}N$ of most nearshore species did not vary as much as $\delta^{13}C$ nor did it vary in a spatially consistent manner across our study sites (Fig. 2.2b, 2.2d, and 2.2f). Round goby (Fig. 2.2b), yellow perch

(Fig. 2.2d), and spottail shiner (Fig. 2.2f) mean $\delta^{15}N$ varied by less than 1.32‰ among study sites. Interestingly, only alewife exhibited larger regional variation (3.90‰) in $\delta^{15}N$ which was driven by the depleted $\delta^{15}N$ at site 1 (Sturgeon Bay) compared to the other sites (Fig. 2.2h). $\delta^{15}N$ values this low were not observed in any other fish species sampled in this study.

Bayesian mixing model results indicated both regional and ontogenetic differences in the diets of nearshore fishes (Fig. 2.3-2.6). Round goby relied more on benthic invertebrates at western and northern study sites, 1-4 and 8, relative to south eastern study sites, 5-7, where dreissenid mussels were a more important diet item (Fig. 2.3). For example, round goby posterior diet proportions of benthic invertebrates were 0.361 (95% CI = 0.282 to 0.447) greater at site 2 (Milwaukee) in the southwest than at site 6 (Saugatuck) in the southeast. Furthermore, there was a strong ontogenetic shift to greater reliance on nearshore dreissenid mussels with increasing total length across all study sites (Fig. 2.3). The proportion of alewife prey in yellow perch posterior diet estimates were more than 0.28 (95% CI = -0.02 to 0.60) greater at site 7 (Muskegon) than at all other study sites (Fig. 2.4). Similar ontogenetic patterns were observed for yellow perch across study sites with a high degree of zooplanktivory at small sizes then transitioning to benthic invertebrates and fish prey at intermediate and larger sizes, respectively (Fig. 2.4). The proportion of benthic invertebrate prey in spottail shiner posterior diet estimates were more than 0.28 (95% CI = -0.226 to 0.570) greater at site 2 (Milwaukee) than at all other study sites (Fig. 2.4) but there were no strong or consistent ontogenetic shifts among study sites (Fig. 2.5). Alewives appear to have similar diets across study sites except for site 1 and 2 (Sturgeon Bay and Milwaukee) where posterior diet proportions of offshore cladocerans are more than 0.38 (95% CI = 0.145 to 0.702) and 0.15 (95% CI = -0.515 to 0.773) greater than at all other study sites (Fig. 2.6), respectively. Among study sites, alewives were relatively more reliant on nearshore zooplankton at small sizes then transitioned to offshore cladocerans and offshore copepod prey at intermediate and larger sizes, respectively (Fig. 2.6).

The proportion of pelagic energy (α) assimilated by nearshore fishes increased as a function of both increasing total length and increasing $K_d(490)$ among all nearshore fishes (Fig. 2.7). For example, posterior predictions of round goby α increased by 0.215 (95% CI = 0.09 to 0.38) across a range of sizes from 25 mm to 125 mm while fixing $K_d(490)$ at 0.15 m^{-1}. Likewise, at a fixed total length of 75 mm, round goby α increased by 0.728 (95% CI = 0.337 to 0.895) over a range of $K_d(490)$ values from 0.15-0.75 m^{-1} (Fig. 2.7b). Yellow perch and spottail shiner exhibited similar changes in α resulting from increasing $K_d(490)$ however the effect of total length on α was relatively smaller in these species. α increased by 0.355 (95% CI = 0.134 to 0.539 ; Fig. 2.7d-f) for yellow perch (150 mm) and by 0.481 (95% CI = 0.199 to 0.703; Fig. 2.7g-i)) for spottail shiners (100 mm) over a range of $K_d(490)$ values (0.15-0.75 m^{-1}). Posterior predictions for small alewife (50 mm) α increased greatly by 0.960 (95% CI = 0.362 to 1.00) over a range $K_d(490)$ values (0.15-0.75 m^{-1}, Fig. 2.7j)). However, at larger sizes (e.g. 150mm) alewife α varied little over a range of $K_d(490)$ and remained very near 1 (Fig 2.7k-l).

Discussion

To our knowledge, this is the first paper to use satellite observations to explain spatial patterns in the food web structure and diets of nearshore fishes in a large lake. Results indicate that this approach can offer valuable insight into explaining spatial variability in isotopic composition and trophic structure. By combining remotely sensed $K_d(490)$ with traditional methods of stable isotope ecology, we were able to quantify the relationship between water clarity and trophic structure for fishes with variable life history strategies. In particular, the proportion of pelagic energy (α) of several species of nearshore fishes in Lake Michigan varied strongly as a function of $K_d(490)$ and moderately as a function of total length. Furthermore, the specific diet components of Lake Michigan fishes also varied regionally and may be related to water clarity as measured by $K_d(490)$.

$K_d(490)$ was greatest in the southeastern portion of Lake Michigan and lowest in the southwestern portion of the basin, consistent with recent trends in remotely-sensed estimates of Secchi depth and suspended minerals (Shuchman et al. 2006; Binding et al. 2015). The spatial differences in $K_d(490)$ are likely the result of variation in fluvial inputs, frequency of resuspension events, upwelling events and/or differences in phytoplankton abundance. Several major rivers including the St. Joseph River, Kalamazoo River, Grand River, and Muskegon River terminate in the southeastern portion of Lake Michigan between sites 5 and 7 draining a large catchment area of agricultural and urban land use (Robertson 1997). By contrast, the catchment along the southwestern portion of Lake Michigan includes several moderate to small rivers which drain relatively smaller agricultural and urban catchment areas (Robertson 1997). Therefore, it is probable that sediment being carried from rivers in the southeastern basin increase the nearshore mean annual turbidity between sites 5 and 7 relative to the southwest region where the watershed is smaller (Lohrenz et al. 2004). Likewise, frequent sediment resuspension events in southeast Lake Michigan likely contribute to the higher apparent turbidity in this region (Eadie et al. 1984; 2002, Mortimer 1988; Schwab et al. 2006). These resuspension events can be very large; one major event can resuspend as much fine sediment as total annual inputs to the entire lake basin (Eadie et al. 1990; 2002). By contrast, upwelling events are more common on the western shore of Lake Michigan, due to prevailing westerly winds (Boyce 1974; Plattner et al. 2006). These upwelling events typically carry clear, nutrient rich hypolimnetic water to the surface, which may stimulate increased primary production (Haffner et al. 1984; Dunstall et al. 1990; Lesht et al. 2002). A combination of major fluvial input, resuspension and upwelling may be occurring simultaneously given their episodic nature which makes disentangling their effects difficult. In general, however, higher median and MAD $K_d(490)$ in the southeast basin, particularly during the spring and summer, suggest more frequent episodic turbidity events in this region relative to the southwestern basin (Table 2.1).

River plumes can decrease local water clarity and may offer one possible explanation for the apparent linkage between $K_d(490)$ and the enriched $\delta^{13}C$ of round goby, yellow perch and spottail shiners in southwestern Lake Michigan relative to the southeast (Lohrenz et al. 2004). Fluvial seston inputs, particularly in the southeastern basin, are ^{13}C depleted relative to Lake Michigan seston (Larson et al. 2012; Marko et al. 2013). Therefore, if large quantities of fluvial particulate organic carbon are entering the nearshore food web in the southeastern region, it would be reasonable to expect lower $\delta^{13}C$ compared to the southwest where fluvial carbon input is likely much lower. Although large spatial variation in $\delta^{13}C$ was apparent, we observed little spatial variability in $\delta^{15}N$ of round goby, yellow perch and spottail shiners among study sites. Larson et al. (2012) also observed low variability in the $\delta^{15}N$ of Lake Michigan nearshore consumers near river mouths, in contrast to relatively high $\delta^{15}N$ variability for river seston and biota. Similarly, Peterson et al. (2007) concluded that the isotopic composition of biota in open nearshore habitats near tributary mouths is influenced minimally by tributary inputs. Given the relatively small range of $\delta^{15}N$ values we observed in nearshore fishes, it seems unlikely that fluvial seston is making a significant direct contribution to the nearshore food web though indirect effects on productivity may be an important factor (Lohrenz et al. 2004; 2008a; Kerfoot et al. 2010).

Alternatively, we suggest that spatial variation in nearshore fish $\delta^{13}C$ is likely related to regional water clarity and its effects on benthic versus pelagic energy pathways. $K_d(490)$ values are directly related to water clarity and to the attenuation of photosynthetically available radiation (PAR) (Pierson et al. 2008). Though reduced water clarity affects both benthic and pelagic primary producers, the effects are proportionately greater on the former (McCauley et al. 1989; Vadeboncoeur et al. 2003). We made regional estimates of $K_d(PAR)$ following a relationship for the Baltic Sea—a coastal (Case 2) system (Pierson et al. 2008). Using 2010-2011 median $K_d(490)$ extinction coefficients for our lowest light attenuation site (site 3; 0.14) and highest light attenuation site (site 6; 0.61) as input, produced $K_d(PAR)$ values of 0.18 and 0.48, respectively. These $K_d(PAR)$ values suggest a typical photic depth ($Zeu=4.6/K_d(PAR)$) of 25.6 and 9.6m, respectively (Kirk 1994). Considering these typical conditions and a fixed depth of 10 m (i.e. the mid-point for most of our nearshore sampling), site 3 consistently has light available to the benthos while site 6 generally does not receive appreciable light in the benthic layer. Other studies have empirically corroborated these estimates and have shown increased benthic algal production in southwestern Lake Michigan particularly near sites 2 and 3 and a paucity of benthic algal production near southeast study sites 5-7 (Auer et al. 2010; Brooks et al. 2015). Because benthic primary producers tend to be more ^{13}C enriched than phytoplankton (France 1995; Hecky and Hesslein 1995), generalist consumers that can take advantage of benthic energy pathways are likely to also possess heavier $\delta^{13}C$ signals. In the southeastern region of Lake Michigan, light limitation likely has a proportionately larger effect on the $\delta^{13}C$ of benthic algae than on phytoplankton resulting in the convergence of benthic and pelagic energy sources (Vadeboncoeur et al. 2003; Chandra et al. 2005). Conversely, the combination of both higher water clarity and rocky substrate in the southwestern region may facilitate increased benthic primary production and greater food web reliance on enriched benthic $\delta^{13}C$ sources (Janssen et al. 2005; Shuchman et al. 2006; Kornis and Janssen 2011).

If benthic production is indeed lower in nearshore regions with higher $K_d(490)$, then increased nearshore fish α values at higher $K_d(490)$ sites suggests that primary production rates not only influence the productivity of higher trophic levels, but also the trophic structure (Melack 1976; Ware and Thomson 2005). Indeed, combining Bayesian posterior estimates of α for high clarity sites 2-4 in the southwest and low clarity sites 5-7 in the southeast and evaluating the differences reveals greater reliance on pelagic energy in the southeast for round goby, yellow perch and spottail shiner. Therefore, it seems probable that increased light attenuation or lower water clarity is related to reduced energy flow through the benthic energy pathway and greater reliance on pelagic energy pathways. Other studies have also shown that the transition from littoral periphyton production to pelagic phytoplankton production results in generalist littoral consumers becoming more dependent on pelagic energy sources in smaller lakes (Vadeboncoeur et al. 2003; Chandra et al. 2005). These patterns were observed along gradients of increasing total phosphorus and reduced water clarity corresponding to cultural eutrophication (Vadeboncoeur et al. 2003; Chandra et al. 2005). While Lake Michigan has undergone oligotrophication resulting from invasive dreissenid mussels, spatial heterogeneity in nearshore water clarity with subsequent effects on productivity processes are likely related to similar differences in regional trophic structure and energy flows.

Mixing model results estimating proportions of specific diets items generally support the finding that nearshore fishes are more dependent on pelagic energy pathways at lower water clarity sites in the southeast although site specific variation is apparent. Round gobies, in particular, responded to increased $K_d(490)$ by shifting to greater reliance on a pelagic energy pathway. Our results indicate that this difference corresponds to increased reliance on dreissenid mussels at southeastern study sites where $K_d(490)$ is greatest and is consistent with fatty acid and gut content data collected in a parallel study (Fig. 2.6, Foley et al. 2017). This shift may be related to decreased availability of non-dreissenid benthic invertebrates in the southeast relative to the southwest where benthic primary production is greater (Happel et al. 2015a; 2015b; Foley et al. 2017). Diet switching from soft-bodied benthic invertebrates to dreissenid mussels was also apparent for round goby and resulted in the most marked ontogenetic shift from benthic to pelagic energy pathway among the species included in this study. This result is consistent with other studies which have observed greater consumption of dreissenids by large round gobies (Turschak and Bootsma 2015; Foley et al. 2017).

By comparison, α values of yellow perch and spottail shiners also indicated greater reliance on pelagic energy pathways as $K_d(490)$ increased although ontogenetic shifts in primary energetic pathway were not as strong. Mixing models for yellow perch revealed higher reliance on non-dreissenid benthic invertebrate prey at southwestern sites 2 and 3 and much lower benthic invertebrate contributions at southeastern site 7 where $K_d(490)$ was higher. This diet pattern was similar to the findings of Happel et al. (2015a). Despite this, mixing model results of yellow perch from site 6 in the east were not different than western sites, perhaps in response to localized substrate (rocky) which can dominate diet patterns (Happel et al. 2015a). Ontogenetic diet shifts from invertebrates to fishes were very apparent for yellow perch and have been documented in other studies (Turschak and Bootsma 2015). Similar to yellow perch, spottail shiner mixing models revealed a strong reliance on non-dreissenid benthic invertebrates at site 2 in the southwest, comparable to the findings of Happel et al. (2015b) but generally little ontogenetic shift in diet proportions across the size range observed in this study.

Alewife α varied much more at small sizes than at larger sizes in this study. Although our results indicate a large effect of increasing $K_d(490)$ on the α of small alewife , this pattern is highly variable and is likely due to the high variability among individuals and across study sites at this size. Larger alewife exhibited strong reliance on pelagic energy source across a range of $K_d(490)$ values. We expect that this lower spatial variability arises from the high mobility of this species relative to other nearshore fishes which are more likely to remain in a small geographic area following the larval drift period (Ray and Corkum 2001; Beletsky et al. 2007; Glover et al. 2008). By making relatively large lateral nearshore-offshore movements, diel vertical movements, and perhaps broader regional movements, alewives effectively integrate any spatial variation in isotopic baseline. Our methodology, which assesses consumer α using a $\delta^{13}C$ mixing model with regional benthic and pelagic primary consumers endmembers, is likely inappropriate for alewife because they are not in isotopic equilibrium with these regional baselines.

Increased reliance on nearshore benthic energy sources has been documented in the Lake Michigan food web as a result of declining offshore productivity and increased nearshore productivity (Hecky et al. 2004; Fahnenstiel et al. 2010; Vanderploeg et al. 2010b; Turschak et al. 2014a). However, it is well established that nearshore areas are highly variable in physical conditions including water clarity (Janssen et al. 2005; Lohrenz et al. 2008b; Brooks et al. 2015) and the results of this study suggest that nearshore fishes' primary energetic pathways and diets respond to variation in these local conditions. Nearshore fishes such as the round goby can serve as conduits through which nearshore energy is transferred to higher trophic levels (Johnson et al. 2005; Dietrich et al. 2006; Foley et al. 2017). Therefore, by responding to regional differences in physical conditions and, by extension, dominant primary production pathways, nearshore fishes may be able to facilitate the transfer of energy from lower trophic levels to higher trophic levels across a broad range of nearshore conditions. This energy transfer may be very important in the midst of declining offshore productivity.

The spatial extent of this work consists of only a subset of nearshore areas in the Lake Michigan basin and is limited in coverage of nearshore areas in the northern basin and open water areas. While this is still valuable given the growing importance of nearshore areas in the Laurentian Great Lakes (Hecky et al. 2004; Turschak et al. 2014), more spatially comprehensive surveys of isotopic data are needed for the entire lake basin. These surveys could be used to create isoscapes which could then be paired with existing physical and biogeochemical data from empirical data sets, models, or remote sensing (Bowen et al. 2010; West et al. 2010). Combining isoscapes with other spatial data can provide a more mechanistic understanding of how energy and nutrients flow through the food web across a range of large scale physical gradients such as water clarity (Bowen et al. 2010). Such data will also serve as valuable baseline data for future studies addressing the impact of nutrient loading, species invasion and climate change over broad spatial scales (Radabaugh et al. 2013).

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Table 2.1. Seasonal Kd(490) sample size (number of cloud free images), median, and median absolute deviation (MAD) for 8 nearshore study sites (Fig. 2.1) in 2010 (top), and 2011 (middle) as well as total Kd(490) sample size, median, and MAD for combined 2010 and 2011.

Study Site	Winter 10			Spring 10			Summer 10			Fall 10		
	n	median	MAD	n	median	MAD	n	median	MAD	n	median	MAD
1. Sturgeon Bay	38	0.11	0.04	35	0.24	0.24	46	0.21	0.20	34	0.19	0.11
2. Milwaukee	24	0.14	0.04	24	0.13	0.06	44	0.14	0.05	37	0.14	0.03
3. Highland Park	22	0.15	0.04	33	0.14	0.05	49	0.14	0.04	33	0.14	0.03
4. Calumet	15	0.17	0.05	28	0.19	0.07	44	0.24	0.09	32	0.20	0.03
5. Michigan City	12	0.10	0.04	37	0.25	0.18	53	0.20	0.16	33	0.20	0.03
6. Saugatuck	23	0.23	0.21	33	2.56	2.95	46	1.92	2.42	32	0.25	0.16
7. Muskegon	22	0.34	0.35	31	3.40	3.99	46	1.53	2.00	22	0.39	0.36
8. Sleeping Bear	31	0.11	0.05	48	0.19	0.15	54	0.34	0.29	25	0.23	0.19
	Winter 11			Spring 11			Summer 11			Fall 11		
	n	median	MAD	n	mean	MAD	n	median	MAD	n	median	MAD
1. Sturgeon Bay	34	0.10	0.03	34	1.05	1.40	52	1.88	2.53	33	0.23	0.14
2. Milwaukee	22	0.12	0.04	23	0.19	0.09	41	0.15	0.06	33	0.14	0.05
3. Highland Park	19	0.18	0.05	23	0.16	0.06	41	0.14	0.03	36	0.15	0.05
4. Calumet	8	0.14	0.09	12	0.21	0.11	32	0.26	0.10	22	0.20	0.04
5. Michigan City	14	0.23	0.05	17	0.22	0.07	42	0.27	0.13	27	0.19	0.06
6. Saugatuck	23	0.43	0.35	24	1.40	1.43	47	1.96	2.56	29	0.18	0.06
7. Muskegon	20	0.22	0.12	26	1.34	1.44	49	2.19	2.42	28	0.26	0.11
8. Sleeping Bear	24	0.10	0.03	33	0.19	0.11	55	0.32	0.29	25	0.13	0.06
	Overall											
	n	median	MAD									
1. Sturgeon Bay	306	0.20	0.17									
2. Milwaukee	248	0.14	0.05									
3. Highland Park	256	0.14	0.04									
4. Calumet	193	0.20	0.06									
5. Michigan City	235	0.21	0.11									
6. Saugatuck	257	0.61	0.72									
7. Muskegon	244	0.60	0.73									
8. Sleeping Bear	295	0.20	0.15									

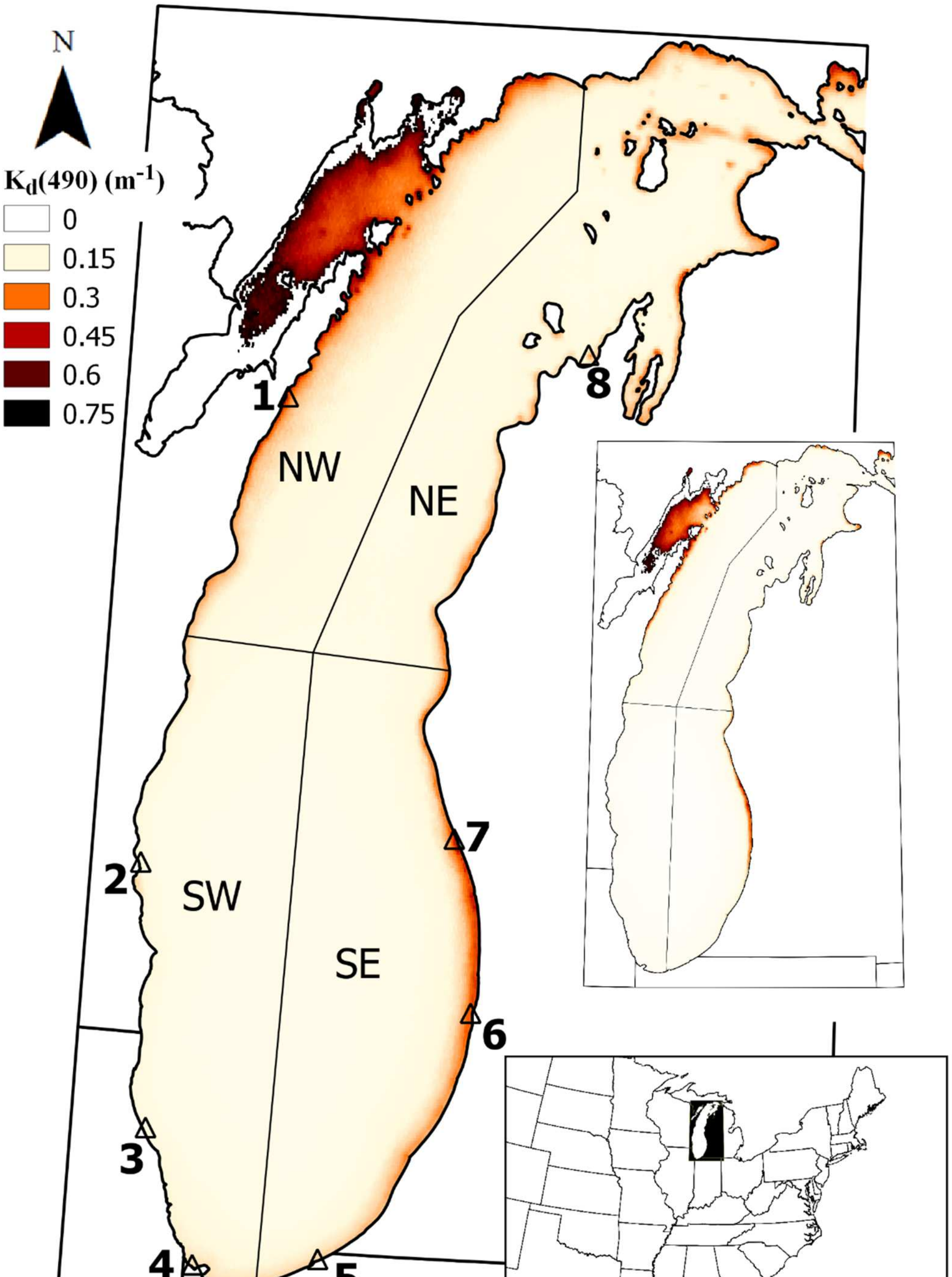

Figure 2.1. Lake Michigan nearshore study sites overlaid on $K_d(490)$ (m^{-1}) median and median absolute deviation (upper right inlay) derived from MODIS Aqua imagery acquired from Jan. 1, 2010 - Dec. 31, 2011 shown on the same color scale. Higher values and warmer colors indicate lower water clarity. Site names are as follows: 1) Sturgeon Bay, WI, 2) Milwaukee, WI, 3) Dead River, IL, 4) Calumet, IL, 5) Michigan City, IN, 6) Saugatuck, MI, 7) Muskegon, MI, and 8) Good Harbor Bay, MI.

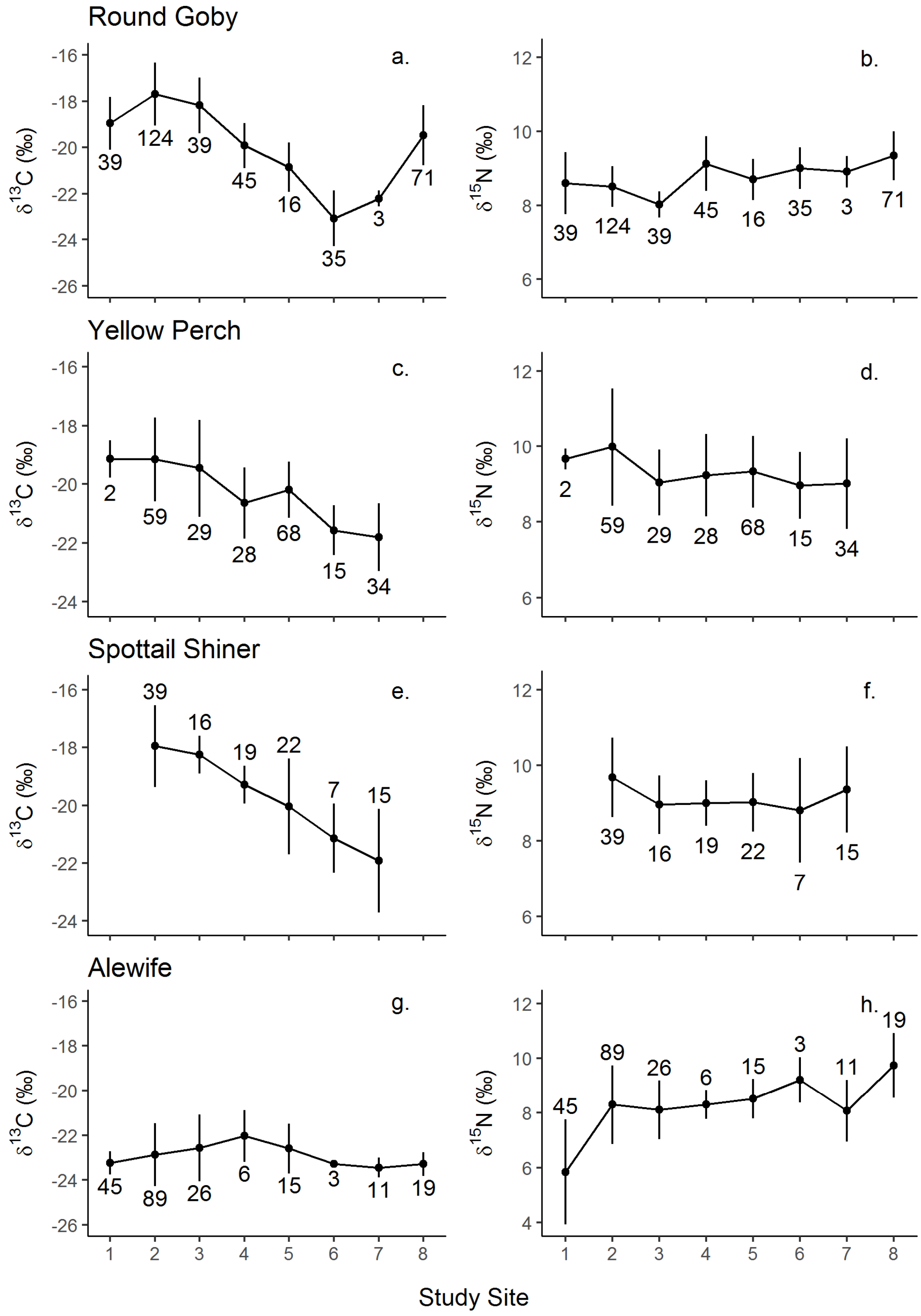

Figure 2.2. Mean $\delta^{13}C$ (± sd, left panels) and $\delta^{15}N$ (± sd, right panels) for round goby (a and b), yellow perch (c and d), spottail shiner (e and f), and alewife (g and h) at the eight study sites shown in Fig. 2.1. Sample sizes for each data point are shown.

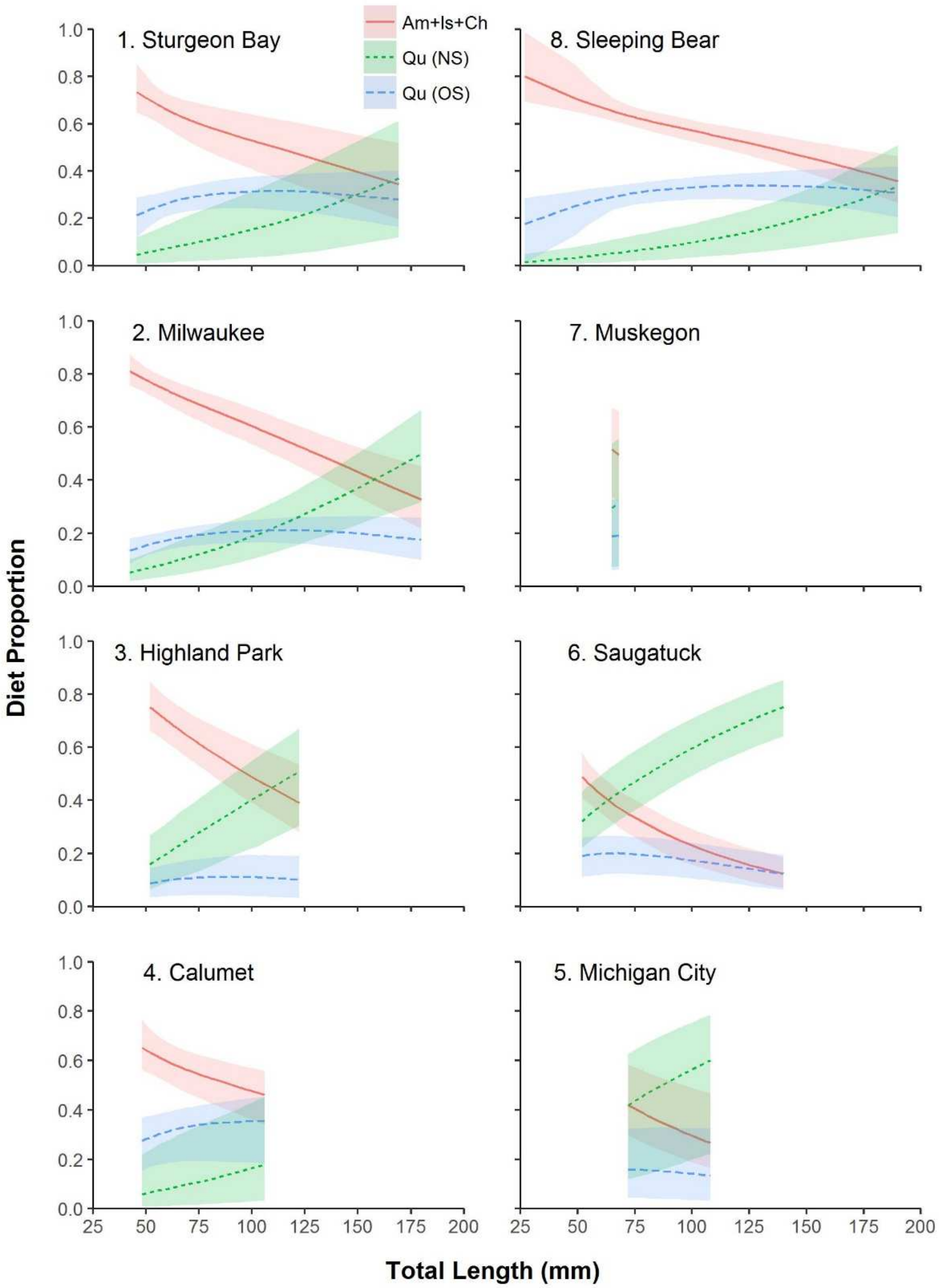

Figure 2.3. $\delta^{13}C$ and $\delta^{15}N$ mixing model predictions of dietary proportions as a function of total length (mm) for round goby at nearshore study sites 1-8. Lines represent the mean of the posterior probability distribution and the shaded area represent the bounds of the 95% credible interval of the predicted diet proportion. Line type and colors correspond to specific prey categories (Am+Is+Ch, amphipods, isopods, and chironomids; Qu (NS), nearshore quagga mussels; Qu (OS), offshore quagga mussels).

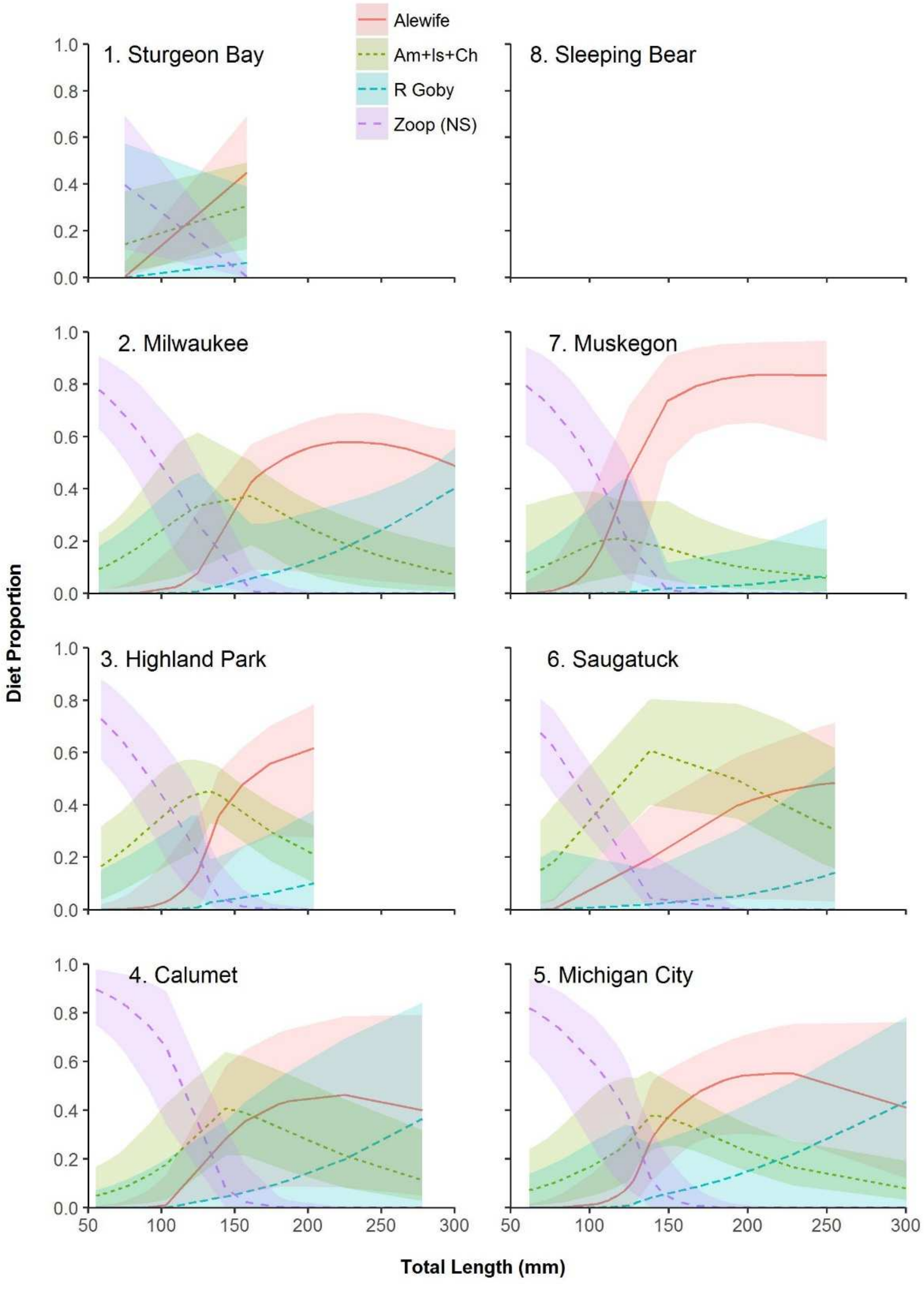

Figure 2.4. $\delta^{13}C$ and $\delta^{15}N$ mixing model predictions of dietary proportions as a function of total length (mm) for yellow perch at nearshore study sites 1-8. Lines represent the mean of the posterior probability distribution and the shaded area represent the bounds of the 95% credible interval of the predicted diet proportion. Line type and colors correspond to specific prey categories (Alewife, Alewife; Am+Is+Ch, amphipods, isopods, and chironomids; R. Goby, Round Goby; NS Zoop, nearshore bulk zooplankton).

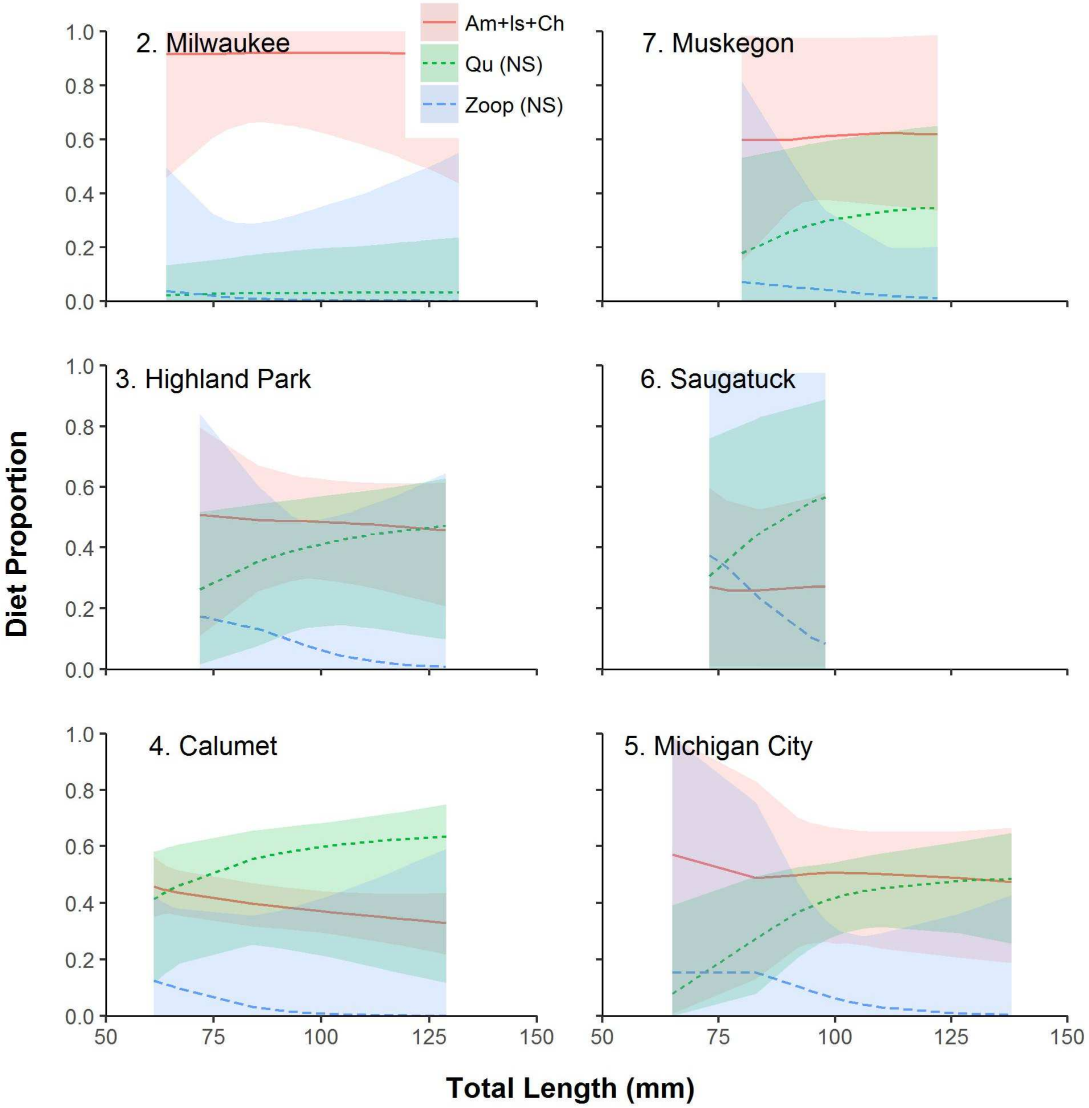

Figure 2.5. $\delta^{13}C$ and $\delta^{15}N$ mixing model predictions of dietary proportions as a function of total length (mm) for spottail shiner at nearshore study sites 1-8. Lines represent the mean of the posterior probability distribution and the shaded area represent the bounds of the 95% credible interval of the predicted diet proportion. Line type and colors correspond to specific prey categories (Am+Is+Ch, amphipods, isopods, and chironomids; Qu (NS), nearshore quagga mussels; NS Zoop, nearshore bulk zooplankton).

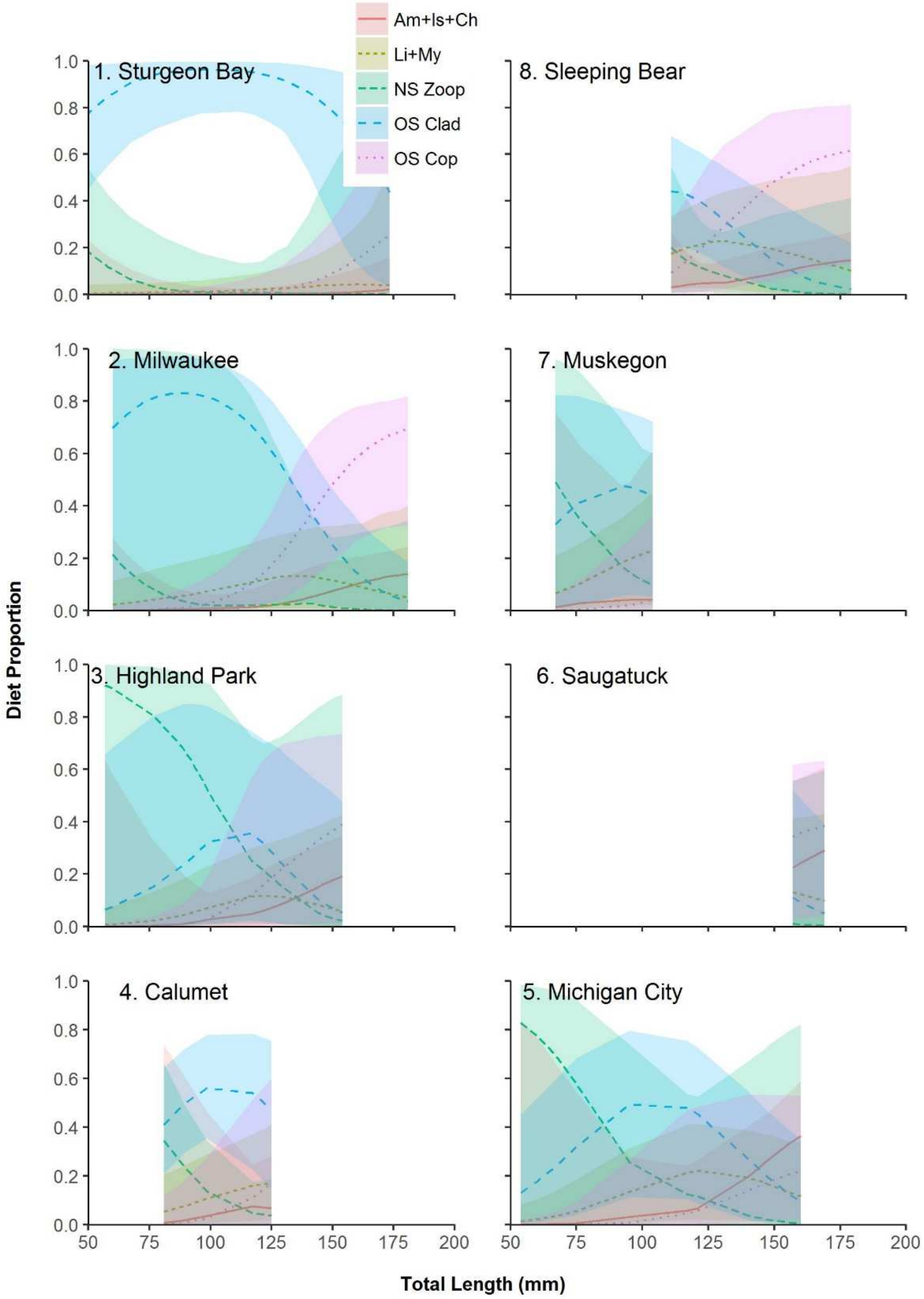

Figure 2.6. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for alewife at nearshore study sites 1-8. Lines represent the mean of the posterior probability distribution and the shaded area represent the bounds of the 95% credible interval of the predicted diet proportion. Line type and colors correspond to specific prey categories (Am+Is+Ch, amphipods, isopods, and chironomids; Li+My, *Limnocalanus* and *Mysis*; NS Zoop, nearshore bulk zooplankton; OS Clad, offshore cladocerans; OS Cop, offshore copepods).

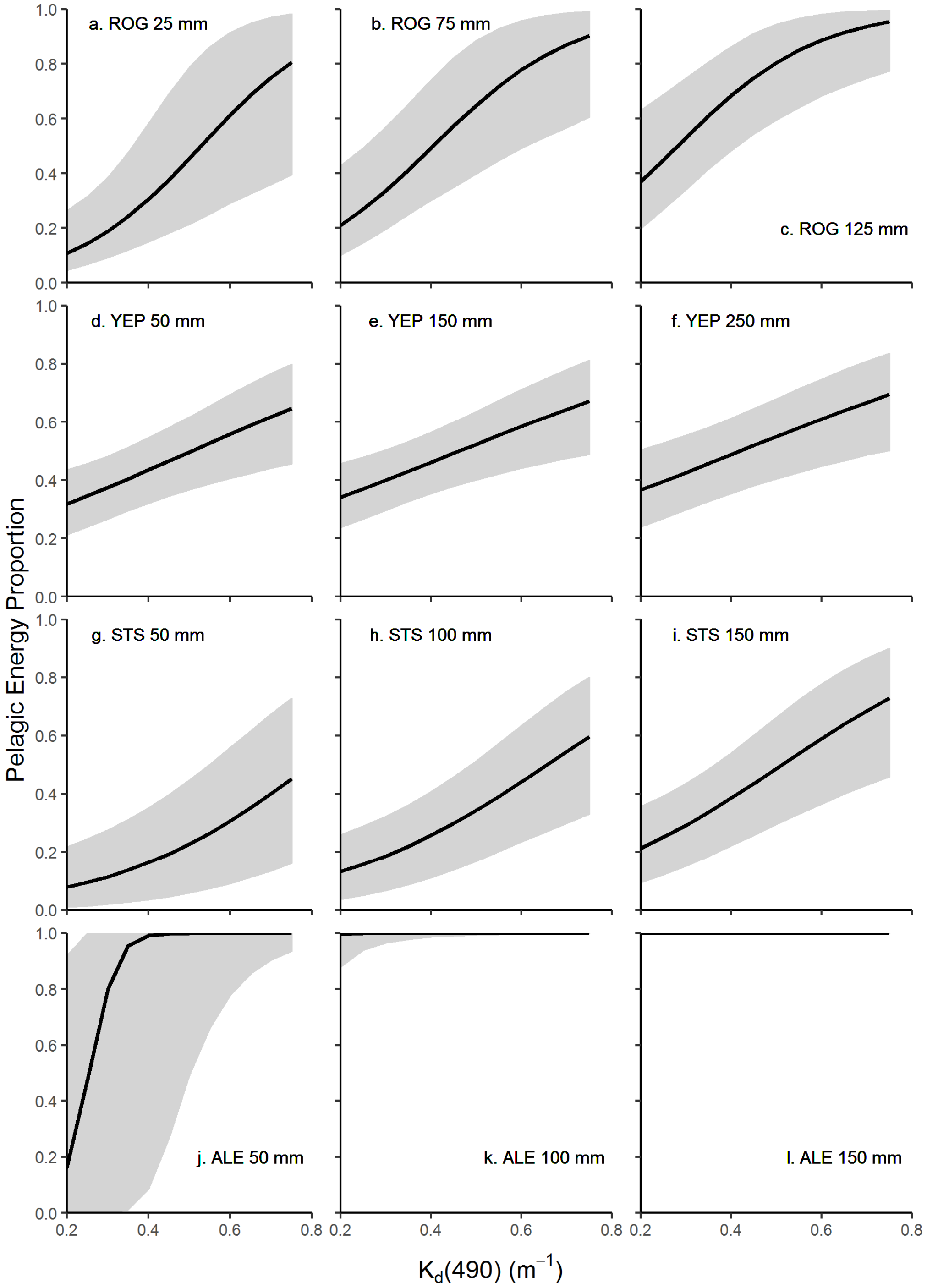

Figure 2.7. Model predictions of the proportion of energy from pelagic sources as a function of $K_d(490)$ for round goby (ROG: a-c), spottail shiner (STS: d-f), yellow perch (YEP: g-i) and alewife (ALE: j-l) at variable total lengths (mm). The range of $K_d(490)$ values were selected to encompass the observed range in medians. Higher $K_d(490)$ indicates lower water clarity. Solid lines represent the median of the posterior probability distribution and the shaded area represent the bounds of the 95% credible interval of the predicted pelagic energy proportion.

Chapter 3. Temporal Variation in the Niche Partitioning of Lake Michigan Salmonines as it Relates to Alewife Abundance and Size Structure.[2]

Abstract

Stable isotope analyses offer a useful means for quantifying ecological niche dimensions, though few studies have examined isotopic response of an ecological community with respect to resource gradients such as fluctuations in prey availability. Stable carbon and nitrogen isotopes were measured for Lake Michigan salmonines and their prey collected from 2014 to 2016. Bayesian ellipse and mixing model analyses were used to quantify isotopic niche characteristics and diets, respectively, among species and years. During the three-year study period, abundance and size structure of preferred alewife prey changed substantially and offered an opportunity to explore predator isotopic niche response and diet shifts along a prey resource gradient. Results suggested increased reliance on alewives, especially small alewives, over the study period and were consistent with greater availability of this prey. However, differential use of alewife size classes and alternative prey sources by salmonine predators was apparent, which suggested possible resource partitioning. Characterization of ecological niche overlaps using stable isotopes likely requires consideration of shared resource availability as well as specific prey and habitat.

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[2] Turschak, B.A., C.R. Bronte, S. Czesny, B. Gerig, A. Happel, T.O. Höök, M.K. Kornis, B.S. Leonhardt, B.G. Matthias, J. Rinchard, D. Warner, H. Bootsma. *Accepted*. Temporal Variation in the Niche Partitioning of Lake Michigan Salmonines as it Relates to Alewife Abundance and Size Structure. Can J. Fish. Aquat. Sci.

Introduction

Multiple descriptions of a niche have been given over the past century, but G. Evelyn Hutchinson formalized the now widely known concept of an ecological niche (Hutchinson 1957). The “Hutchinsonian” niche is described as an abstract multidimensional space representing the multiple biotic and abiotic environmental variables required for a population to persist (Hutchinson 1957). This ecological niche concept laid much of the foundation for understanding how species may coexist within a given community, including theoretical and quantitative descriptions of niche breadth and niche partitioning. However, quantification of a species’ niche or resource requirements remains challenging (reviewed by Holt, 2009).

A growing number of studies have attempted to use stable isotope analyses to quantify multiple dimensions of an organism’s ecological niche (e.g. Kornis et al., 2020; Layman et al., 2007; Schmidt et al., 2011; Yuille et al., 2015). Stable isotope ratios (e.g., $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, or δD) of an organism’s tissue vary because of differential mixing and fractionation of heavy and light isotopes associated with environmental gradients and physiological processes (e.g., primary production, geology, temperature, hydrology, diet, trophic level, growth, and metabolic activity; Peterson and Fry, 1987). Therefore, biotic resource use as well as the abiotic environment experienced by an organism affect mixing and fractionation processes, with resultant variation in isotopic signature. Because mixing and fractionation are mechanistic processes, quantifying an organism’s position along various stable isotope gradients provides a continuous measure of that organism’s environment and resource use (Vander Zanden and Vadeboncouer 2002; Bowen et al. 2010; Turschak et al. 2019). In this way, the isotopic range that an organism occupies along various isotopic axes, referred to as its ‘isotopic niche’, is somewhat analogous to the multidimensional ecological niche of that organism (Layman et al. 2007; Newsome et al. 2007;

Jackson et al. 2011; Swanson et al. 2015). Examining intra- and inter-specific species variation in isotopic niche facilitates bivariate or multivariate comparisons of multiple resource overlaps. These comparisons are similar to classical Gaussian examples that demonstrated resource use overlaps of theoretical species along a single resource gradient (May and MacArthur 1972). For instance, studies of Laurentian Great Lakes fish assemblages have been used to quantify the degree of spatial and dietary overlap among native and introduced salmonines as well as niche partitioning of historic and extant coregonines (Schmidt et al. 2011; Gerig et al. 2018; Mumby et al. 2018; Kornis et al. 2020)

Interpretation of isotopic niche overlap and estimates of resource use derived from stable isotope studies can be difficult to interpret in ecological terms (Matthews and Mazumder 2004; Newsome et al. 2007; Hoeinghaus and Zeug 2008). In many instances, resources of interest are not isotopically distinct. Therefore, resolution of resource or prey use by an organism may reflect only resource use generalities rather than providing specific resource or prey uses (Phillips et al. 2005). Likewise, consumer species using distinct prey sources that are isotopically similar may appear to have artificially high degrees of niche overlap owing to the inability of an isotopic niche to resolve ecological niche dimensions. Even when prey sources are isotopically distinct, complexities arise when interpreting ecological niche from stable isotope data because these data reflect only the realized ecological niche at the spatiotemporal scale of the study rather than the full fundamental niche of that organism (France 1995b; Hecky and Hesslein 1995a; Vander Zanden and Rasmussen 1999; Post 2002). For instance, during times when a preferred prey is abundant, all predator species may consume that prey resulting in a high degree of apparent niche overlap (Liem 1980; Robinson and Wilson 1998; Yuille et al. 2015). Conversely when preferred prey are less abundant, those same predators may adopt more species-specific feeding behaviors resulting in lower apparent niche overlap (Liem 1980; Robinson and Wilson 1998; Yuille et al. 2015). Discerning potential for niche overlap when shared resources are limited or quantifying degree of generalist versus specialist foraging among a community of organisms is often the goal of stable isotope studies (e.g. Bootsma et al. 1996; Genner et al. 1999). However, isotopic niche area and position are likely to vary across multiple environmental or resource gradients, so quantifying potential for niche overlap or resource switching ideally requires examination of isotopic niche parameters along these various gradients.

Stable carbon and nitrogen (hereafter C and N, respectively) isotopes are among the mostly commonly used isotopes in ecological studies. Stable C isotope ratios (expressed as $\delta^{13}C$) vary broadly among primary producers but are relatively conserved (<1 ‰) during trophic transfer (Bootsma et al., 1996; France, 1995b; Hecky and Hesslein, 1995). At the base of a food web, stable nitrogen isotope ratios (expressed as $\delta^{15}N$) can vary according to the form of nitrogen assimilated. Above that base, $\delta^{15}N$ increases incrementally by 3-4 ‰ with each trophic transfer (Minagawa and Wada 1984; Vander Zanden et al. 1997). $\delta^{15}N$ is also enriched in profundal organisms in the Great Lakes and oceans due to ^{15}N enrichment in settling phytoplankton (Altabet 1988; Ostrom et al. 1998; Sierszen et al. 2006). Thus, in aquatic systems $\delta^{13}C$ and $\delta^{15}N$ are used to determine primary energetic pathway (i.e., benthic or pelagic) and trophic level and/or depth distribution of consumers, respectively (Turschak and Bootsma 2015; Kornis et al. 2020).

We sought to examine $\delta^{13}C$ and $\delta^{15}N$ isotopic niche overlap as it relates to the diets of Lake Michigan salmonines. Lake Michigan, a Laurentian Great Lake, has a salmonine community comprised of native lake trout *Salvelinus namaycush*, as well as introduced Pacific salmonines *Oncorhynchus* spp. (Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss*), and brown trout *Salmo trutta*. Diet studies of these species spanning decades have yielded unequivocal evidence that the invasive pelagic planktivore alewife *Alosa pseudoharengus* is the primary prey for all salmonines in Lake Michigan (Jude et al. 1987; Stewart and Ibarra 1991; Rand et al. 1993; Warner et al. 2008; Savitz 2009; Jacobs et al. 2010, 2013; Happel et al. 2018; Leonhardt et al. 2020). The extent of alternate prey use is lower than observed in systems without alewife prey (e.g. (Roseman et al. 2014) but still varies among species. For instance, Chinook salmon appear almost exclusively reliant on alewives, whereas steelhead and coho salmon diets have varied to include larger proportions of invertebrate prey as well (Jacobs et al. 2013; Leonhardt et al. 2020). Lake trout and brown trout, while still highly dependent on alewives, also obtain large proportions of their diets from round goby *Neogobius melanostomus*, an invasive benthivorous prey species (Kornis et al. 2017; Happel et al. 2018; Leonhardt et al. 2020).

The degree of dependence on alewife prey and hence potential for dietary niche overlap likely also varies spatiotemporally for Lake Michigan salmonines (Happel et al. 2018, 2020; Leonhardt et al. 2020). Early diet studies of Lake Michigan salmonines suggested very high degrees of dietary overlap corresponding to an abundant alewife population with multiple ages well represented in the diet (Jude et al. 1987; Stewart and Ibarra 1991; Jacobs et al. 2013). However, alewife and other pelagic forage fish have declined substantially, corresponding with sustained high consumptive demand by salmonine predators, which may have been further exacerbated by major declines in the abundance of the native amphipod *Diporeia* (Madenjian et al. 2002, 2006, 2015; Tsehaye et al. 2014b, 2014a). The age structure of the current alewife population is highly truncated with relatively few old fish in any given year. Recruitment has also been variable and observed to be low in most years since 2013 (Vidal et al. 2019; Bunnell et al. 2020). With major long-term declines in pelagic prey fish biomass, some salmonine predators have been able to use alternative benthic or terrestrial energy pathways, which are decoupled from pelagic energy pathways (Johnson et al. 2005b; Dietrich et al. 2006b; Rennie et al. 2009; He et al. 2015; Fera et al. 2017). The degree of species-specific dependence on these alternative pathways seems to correspond to long-term lakewide declines in pelagic alewife, as well as the size structure of locally available alewives among seasons (Roseman et al. 2014; He et al. 2015; Happel et al. 2018; Leonhardt et al. 2020).

Stable C and N isotope data for Lake Michigan salmonines were available for the 3-year period from 2014 to 2016, during which time lakewide alewife density increased markedly, and size structure shifted from larger to smaller individuals (Fig. 3.1; D. Warner personal communication; Bunnell et al., 2020; Legler 2020;). Estimates of numeric and biomass density increased substantially from a record low density of primarily larger individuals in 2014 to numerically more abundant but smaller individuals in 2015 and 2016. This transition corresponds to the recruitment of age-0 fish (approximately < 100mm) in both 2015 and 2016 detected by the August lakewide hydroacoustic survey (Fig. 3.1; Bunnell et al. 2020). During this same period, we collected muscle tissue from Lake Michigan salmonines and analyzed them for stable isotopes. This provided the opportunity to 1) characterize salmonine isotopic niche areas and positions as well as intra- and inter-species overlaps across a temporal resource gradient and 2) use stable isotope mixing models to evaluate temporal and regional diet differences as they might relate to alewife density and size structure. Our objectives were to determine whether stable C and N isotopes were able to resolve changes in realized dietary niche area among species and, if so, the degree of niche partitioning and diet flexibility among these species along a dietary resource gradient.

Methods

Sample Collection

Stable isotope samples and biometric data were collected from the five most prevalent species of Lake Michigan salmonine (n=2,057) in 2014-2016. Most salmonine samples were collected from recreationally harvested fish as part of the U.S. Fish and Wildlife Service Great Lakes Mass Marking Program (Bronte et al. 2012). Detailed stable isotope sampling strategy and methodology from the Mass Marking Program are given by Kornis et al. (2020), where tissue samples were collected from angler catches at fish cleaning stations and at recreational fishing tournaments at 28 port cities around Lake Michigan. In 2014, samples were collected from June-September, and in 2015 and 2016 samples were collected from April-September. Supplemental lake trout samples were also collected in 2016 as part of several independent gill net (38-152 mm stretch mesh) sampling efforts led by the Michigan Department of Natural Resources (Eastern Lake Michigan), Wisconsin Department of Natural Resources (Southwestern Lake Michigan), and Little Traverse Bay Band of Odawa Indians (Northeastern Lake Michigan). In addition to biometric data (e.g., total length and weight), small (< 10 g) skin-free dorsal muscle tissue plugs for stable isotope analysis, and stomachs, were removed from all salmonines sampled and were stored at -20^{o}C until they could be processed in the laboratory.

Forage fishes and invertebrate prey samples (n = 581) were collected in 2014-2016 using a variety of methods. In 2014 and 2015, forage fishes and invertebrates were captured in September bottom trawl surveys conducted by the U.S. Geological Survey at their seven index sites around Lake Michigan (Bunnell et al. 2020). Dorsal muscle tissue plugs were collected from forage fish and stored frozen until samples could be processed in the laboratory. Aquatic invertebrates *Mysis relicta* and *Bythotrephes longimanus* were collected using vertical plankton net (500 μm) tows and individuals were pooled according to taxa after each tow and stored frozen. In 2016, forage fish samples were collected from May to October using a combination of bottom trawls and micromesh gillnets (6-12 mm stretch mesh). Forage fish sampling was performed by the University of Wisconsin-Milwaukee, Purdue University, Illinois Natural History Survey, NOAA Great Lakes Environmental Research Laboratory, and Little Traverse Bay Band of Odawa Indians in 2016. Prey fishes collected in 2016 were frozen whole prior to laboratory analyses. Terrestrial invertebrates, which were an important component of steelhead observed diets in 2016 (Leonhardt et al. 2020), were removed from diets during gut content analyses, subset, and then set aside in desiccators for subsequent stable isotope analysis.

Protocols for sample collection and euthanasia were reviewed and approved by the University of Wisconsin-Milwaukee Institutional Animal Care and Use Committee following guidelines from the American Association for Laboratory Animal Science.

Sample Processing and Analysis

Laboratory processing and stable isotope analysis were done independently in each year of the study period. Forage fish homogenates, salmonine dorsal muscle plugs, and whole invertebrates were dried in 1.5ml polypropylene microcentrifuge tubes using drying oven at 60°C for 48 h (2014) or were lyophilized (2015-2016) in polystyrene weighing boats. Dried samples were homogenized by grinding with a mortar and pestle (2014) or by chopping into a fine powder using surgical scissors or razor blades (2015-2016). Subsamples of dried tissue homogenate (0.8-1.2 mg) were then packed into a tin capsule for subsequent stable isotope analyses. In 2014, samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the UC-Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer (EA) front-end coupled with a PDZ Europa 20-20 isotope ratio mass spectrometer (IRMS). In 2015, samples were analyzed at the Center for Environmental Science and Technology, University of Notre Dame using an EA (Costech, Valencia, CA) coupled to a Delta Plus IRMS (Thermo Scientific, Waltham, MA). In 2016, samples were analyzed at the School of Freshwater Sciences, University of Wisconsin-Milwaukee using an elemental analyzer front end (ECS 4010, Costech Instruments, Valencia, CA) coupled with a Delta V Plus IRMS (Thermo Fisher, Bremen). For each sample year, isotope ratios were adjusted after each sample run using a 3-point standard curve and known NIST laboratory standards. During all sample runs, an acetanilide control sample was analyzed for ^{13}C:^{12}C and ^{15}N:^{14}N ratios after every 12th sample to ensure precision of IRMSs used for each sample year ($\delta^{13}C$ SD = 0.20 and $\delta^{15}N$ SD $\leq$ 0.20). All stable isotope results were expressed in per mil (‰) differences between the isotope ratio of the sample and that of the standard (PDB carbonate or atmospheric air for $\delta^{13}C$ and $\delta^{15}N$, respectively), using the formula: $\delta^{13}C$ or $\delta^{15}N$ = $(R_{sample}/R_{Standard}-1) \times 1000$, where R = $^{13}C/^{12}C$ for $\delta^{13}C$ and R = $^{15}N/^{14}N$ for $\delta^{15}N$.

Data Processing and Analysis

All $\delta^{13}C$ values of salmonine predators and prey were corrected for lipid content, and $\delta^{13}C$ values presented hereafter reflect lipid-corrected values. Lipid-correction for most species was done using Lake Michigan species-specific equations and coefficients developed and described in Appendix B of Turschak et al. (2014) and Turschak (2013). Correction coefficients were updated for salmonines and some prey by Kornis et al. (2020) and these updated coefficients were used for all applicable species. However, species-specific correction equations were not developed for several taxa including bloater *Coregonus hoyi*, *Bythotrephes*, and terrestrial invertebrates. For these taxa, the generic correction equations of Post et al. (2007) were used in place of species-specific corrections.

For analysis purposes, salmonine stable isotope samples from each of the various ports were grouped into four major quadrants of the lake (i.e., Northwest-NW, Southwest-SW, Southeast-SE, and Northeast-NE) as described in Turschak et al. (2018). Analysis regions were selected *a priori* based on expected spatial variability observed in previous Lake Michigan stable isotope studies (Happel et al. 2015a; Foley et al. 2017; Turschak et al. 2019). However, regional trophic baseline corrections were not made for salmonine predators. Given broad horizontal and/or vertical (profundal/pelagic) movements of salmonine predators in the Laurentian Great Lakes, most are unlikely to reach isotopic equilibrium with regional or depth specific isotopic values (Adlerstein et al., 2008, 2007a, 2007b; Bronte et al., 2007; Clark et al., 2017; Haynes et al., 1986; Schmalz et al., 2002; and Michigan Department of Natural Resources unpublished data). Therefore, imposing regional differences in baseline isotope signatures on predators caught within each region is likely to result in artificial regional differences that obscure true differences in predator isotopic niche (Vander Zanden and Rasmussen 1999; Post 2002; Foley et al. 2014; Turschak et al. 2019).

Sample sizes of prey taxa and size classes of interest (prey sources, hereafter) were variable among years and seasons, so these data were pooled together to produce lake-wide, three-year (2014-2016) mean and variance estimates of $\delta^{13}C$ and $\delta^{15}N$. For forage fishes, size structure and sample size collected for analyses during opportunistic sampling reflected natural lakewide size structure and abundance. Therefore, this study was unable to collect all possible prey sources for all years and seasons and required data pooling. Given known ontogenetic variation in stable isotope signatures (Turschak and Bootsma 2015; Mumby et al. 2017) and changes in size structure for certain prey species (e.g. alewife) over the study period (Bunnell et al. 2020), interannual variation among prey source $\delta^{13}C$ and $\delta^{15}N$ probably reflected the variable size structure and availability of prey sources during various collections. To provide equal weight to annual $\delta^{13}C$ and $\delta^{15}N$ mean and variance estimates despite unbalanced annual collections, a resampling procedure was used when prey source data was available for multiple years. Using prey source specific annual mean and SD values, normal distributions were generated and randomly resampled (n = 1000) for each year. Annual resampled $\delta^{13}C$ and $\delta^{15}N$ distributions for each species were combined and the mean and SD was recalculated to produce a three-year pooled value wherein mean and variance for each year was given equal weight. This procedure incorporated prey source variance observed across all study years, seasons, and regions and allowed us to minimize biases associated with unbalanced sampling of prey source isotopic data.

Quantitative statistical analyses of stable isotope data were performed in R version 3.5.1 (The R Foundation for Statistical Computing). Diet proportions of salmonines were determined using the MixSIAR package (Stock and Semmens, 2016) stable isotope mixing models. MixSIAR models were modified from the standard rjags package to operate using the runjags package in R which better facilitated parallel processing (i.e., 4 cores) and extension of MCMC (Markov chain Monte Carlo) chain length without having to restart model runs. These modified MixSIAR models were structured with collection year as a random factor, region as a nested random factor, and consumer total length as a continuous covariate. Informative prior Dirichlet distributions were used based on wet weight diet proportions observed in salmonine diets in 2015 and 2016 (Leonhardt et al. 2020). Prior distributions varied with species but were held constant among years and regions included in this study. Apart from round goby, which were included as a nearshore/benthic endmember in all models, predator-specific prey sources that made up less than 2% by weight in 2015-2016 observed annual lake-wide diet proportions were not included as potential sources in mixing models (Leonhardt et al. 2020). $\delta^{13}C$ and $\delta^{15}N$ trophic discrimination factors (mean ± SD) of 0.4 ± 1.3 and 3.4 ± 1.0, respectively, were also provided as model inputs (Post 2002). Models were run with 4 parallel MCMC chains of length 50,000. Burn-in length was 20,000 and chains were thinned by 10. Model convergence was evaluated visually using trace plots and quantitatively using the Gelman-Rubin Diagnostic. If the Gelman-Rubin Diagnostic exceed 1.05 for more than 5% of parameter estimates, the model was extended by an additional 50,000 iterations with the same burn-in length and thinning. The model was revaluated using the Gelman-Rubin Diagnostic and iteratively extended as described above until this diagnostic indicated fewer than 5% of parameter estimates exceeded 1.05.

Isotopic niche area expressed as Bayesian Standard Ellipse Area (SEA_B) and overlap were assessed using the SIBER (Jackson et al. 2011) and nicheROVER (Swanson et al. 2015) packages in R, respectively, by fitting 95% Bayesian ellipses to $\delta^{13}C$ and $\delta^{15}N$ biplot data. Ellipses were fit to each year-species combination to assess interannual variation in isotopic niche area within a salmonine species (e.g. Species A Year 1 x Species A Year 2 x Species A Year 3) and among salmonine species (e.g. Species A Year 1 x Species B Year 1 x Species C Year 1). Isotopic niche overlap was also evaluated among species on an interannual basis to better understand potential for ecological interactions from one year to the next (e.g. Species A $\cap$ Species B Year 1 x Species A $\cap$ Species B Year 2 x Species A $\cap$ Species B Year 3).

Results

Isotopic Niche Size and Overlap

Lake Michigan salmonines occupied a broad range in the stable C and N isotope biplot ($\delta^{13}C$: -26‰ - -20‰; $\delta^{15}N$: 8‰-15‰) with niche area and interspecific overlap varied among species (Fig. 3.2 lower left panel and Fig. 3.3). When all data years were combined, non-Pacific salmonines, brown trout and lake trout, occupied the largest isotopic niche areas (Fig. 3.2 lower left panel). The large isotopic niche of brown trout encompassed much of the area occupied by other salmonines and resulted in a high degree of apparent isotopic niche overlap (60-97%, Fig. 3.2 lower panels and Fig. 3.3). While lake trout also occupied a large isotopic niche area, they occupied the most unique area, with enriched $\delta^{15}N$ relative to other salmonines (Fig. 3.2 lower panels). As a result, lake trout had the least overlap with other salmonines (11-55%; Fig. 3.2 lower panels and Fig. 3.3). Pacific salmonines occupied smaller isotopic niche areas and there was greater niche overlap among these congeners (Fig. 3.2 lower panels and Fig. 3.3). Chinook salmon had the largest niche area of Pacific salmonines, with the smaller niche areas of steelhead and coho salmon mostly contained within the Chinook salmon niche area (coho: 87%; steelhead: 89% overlap with Chinook salmon; Fig. 3.2 lower panels and Fig. 3.3). Coho salmon and steelhead occupied the smallest niche areas of all salmonines, which resulted in a very low degree of overlap with lake trout and brown trout, although overlap between coho salmon and steelhead was large (88-90%; Fig. 3.2 lower panels and Fig. 3.3).

Within individual years, niche area and degree of overlap among species varied relative to the more general patterns that were observed when all study years were combined (Fig. 3.2 and Fig. 3.3). Isotopic niche area for all salmonines except coho salmon declined from 2014 to 2015 and then increased again in 2016 with magnitude of interannual shifts variable among species (Fig. 3.2 left panels). Coho salmon—the only species to deviate from this pattern—also exhibited the least interannual variation in niche area from 2014-2016 (95% CI: 0.824-1.672‰$^{2)}$. Conversely, brown trout and steelhead exhibited the largest change in niche area over the study period (95% CI: 1.44-3.49‰^{2} and 0.67-2.13‰^{2}, respectively; Fig. 3.2 left panels). Species-specific niche areas also shifted downward (lower $\delta^{15}N$) from 2014 to 2016. This was especially apparent for brown trout, lake trout, and Chinook salmon and less pronounced for coho salmon and steelhead (Fig. 3.2 left panels). All species were ^{13}C-enriched in 2015 relative to 2014 and 2016 (Fig. 3.2 left panels). Magnitude and direction of interannual shifts in both niche area and location were different among Lake Michigan salmonines (Fig. 3.2 left panels). Interannual changes in niche area and position were asymmetric among salmonine species and resulted in interannual differences in interspecific niche overlap (Fig. 3.2 lower panels). These changes are depicted in detail in Fig. 3.3.

Isotope Diet Mixing Models

Estimated brown trout diets shifted with increased total length as well as among study years (Fig. 3.4 and Fig. 3.5). Differences in brown trout diet among years were greater than relatively moderate regional differences within years. Among all years, large alewife ≥100 mm increased in dietary importance with increasing brown trout total length. However, large alewives were a larger overall proportion of brown trout diets in 2014 than they were in 2015 and 2016. Small alewives <100 mm, by comparison increased in dietary importance from 2014 to 2016 despite variable ontogenetic diet patterns among years and regions for this prey item. Large and small alewives were the most important diet component for brown trout in all years with substantial contributions of round goby and terrestrial invertebrates to diets at small sizes, particularly in 2015.

Estimated lake trout diets had the greatest regional diet differences of any Lake Michigan salmonine which also varied ontogenetically and interannually (Fig. 3.4 and Fig. 3.6). Among all years, large alewives dominated lake trout diets, except for lake trout from northwest Lake Michigan in 2015, which were apparently more reliant on round goby over the relatively smaller range of sizes that were available in that region. With increases in total length, lake trout appeared to transition to greater reliance on profundal prey fish like bloater and became less reliant on large alewife. Small alewives contributed less than other prey types to lake trout diets (< 20%) among years and regions and their contribution to lake trout diets varied little with changes in lake trout total length. Reliance on round goby varied little with length of lake trout but varied both interannually and regionally. For example, in 2015 round goby contributed more to regional diets than in other years. Round gobies were apparently also of relatively high importance to lake trout diets in the northwest region, intermediate in the eastern regions, and least important in the southwest region.

Estimated Chinook salmon diets shifted from relatively high reliance on small alewives to large alewives with increasing total length (Fig. 3.4 and Fig. 3.7). The relative importance of small and large alewives remained similar regionally within a given year but interannual differences were apparent. Greater importance of small alewives across all Chinook salmon sizes was observed in 2016, while all sizes of Chinook salmon were relatively more reliant on large alewives in 2014 and 2015. Round goby contributed relatively little to Chinook salmon diets, with greatest reliance on this prey occurring for small Chinook salmon in 2014.

Like Chinook salmon, estimated coho salmon diets varied little regionally but ontogenetic and interannual differences were apparent (Fig. 3.4 and Fig. 3.8). Small alewives dominated coho salmon diets in 2014 and 2015, particularly for coho salmon <600 mm. As coho salmon total length increased, small alewife prey were replaced with a combination of large alewives, *Bythotrephes*, *Mysis*, and round goby. By contrast, small alewives appeared to make up a smaller proportion of coho salmon diets in 2016. Instead, diet of small coho salmon shifted to strong reliance on terrestrial invertebrates and diet of larger coho shifted to greater reliance on

Bythotrephes in 2016. In all years, large alewives, *Mysis*, and round goby appeared to contribute relatively little to coho diets but importance of these prey increased slightly with increased total length. Much greater uncertainty in mixing model diet proportions was observed for coho salmon than other salmonines.

Like the other Pacific Salmonines, estimated steelhead diets were very similar regionally despite strong ontogenetic and interannual variation (Fig. 3.4 and Fig. 3.9). In 2014 and 2015, terrestrial invertebrates comprised a major component of steelhead diets, particularly at small total lengths. As steelhead total length increased, diets transitioned from terrestrial invertebrates to strong reliance on large alewives. Unlike 2014 and 2015, steelhead diets in 2016 were almost entirely dominated by small alewives with very little reliance on other prey. From 2014-2016, there was a substantial increase in contributions of small alewives to steelhead diets and a subsequent decrease in terrestrial invertebrates and large alewives. Round goby also contributed relatively more to steelhead diets in 2015, as was observed for other salmonines.

Discussion

The magnitude and direction of species-specific interannual changes in isotopic niche area and position, as well as trophic overlap among salmonine species, were consistent with shifts in abundance and size structure of the Lake Michigan alewife population and resulting consumption of potential alternative prey items. This study focused on the effects of changes in alewife density and size structure because this prey is highly preferred by Lake Michigan salmonines (Happel et al. 2020; Leonhardt et al. 2020). However, when preferred prey density is low or alternate prey density is very high, generalist predators may switch feeding to alternate prey and energy pathways (Robinson and Wilson 1998; Hayden et al. 2014; McMeans et al. 2015). Species-specific shifts in isotopic niche area and position will then be a function of the alternate prey resource pools (and their isotopic position) available to the predator based on its specific foraging locations, preferences, physiology and/or behavior (Matthews and Mazumder 2006; Weidel et al. 2011; Mumby et al. 2018; Kornis et al. 2020). Therefore, asymmetric isotopic niche responses can be observed among predators through variable use of alternate prey given density and size structure of a preferred shared prey. By combining diet mixing models with isotopic niche overlap, we were able to determine that each salmonine species exhibited a dietary response that is unique to that species and yet seemingly consistent with lake wide changes in preferred prey density and size structure.

Over the study period, niche area and position as well as diet mixing model results for brown trout, Chinook salmon, and steelhead suggested a shift to greater reliance on small alewives <100 mm and less reliance on large alewives ≥100 mm. One probable cause for this change is the increased availability of small alewives from improved recruitment in 2015 following very low recruitment in 2013 and 2014 (Fig. 3.1; Bunnell et al., 2020). That this event is not immediately reflected in the isotopic composition of predators is likely due to their preference for alewives larger than 50-125 mm (Leonhardt et al., 2020). It is likely that young-of-year (YOY) alewives are poorly selected for by salmonines until late summer in Lake Michigan based on alewife growth rates and possible advection from nursery habitats (Höök et al. 2006, 2007; Höök and Pothoven 2009). Given the seasonally delayed availability of young alewife as potential prey and the relatively slow isotopic turnover rates of large adult salmonines (several months or more; Trueman et al., 2005; Vander Zanden et al., 2015), there may be a substantial temporal lag in the predator isotopic response to changes in small alewife availability. Rate of isotopic response will be dependent on the time/season that YOY alewife become selected for by a given predator, and the rate of isotopic incorporation which varies as a function of predator catabolic turnover and growth (Weidel et al. 2011; Vander Zanden et al. 2015). Our results suggest that switching to small alewives (or isotopically similar prey) is somewhat apparent for steelhead in 2015, whereas this response is lagged for brown trout and Chinook salmon until 2016. This may be because steelhead are known to forage higher in the water column than other salmonines (Haynes et al. 1986; Aultman and Haynes 1993). The warmer temperatures at these shallower depths will increase catabolic turnover and growth, and also allow them to more frequently encounter small alewives that are distributed higher in the water column at smaller sizes (Brandt 1980).

Mixing model results did not reflect similar increases in reliance on small alewives for coho salmon over the study period. Coho salmon consistently occupied the smallest niche area across years, and their isotopic niche position suggests a heavy reliance on small alewife. However, isotopic mixing model results were highly variable and included large proportions of invertebrate prey as well as small alewife. This is likely the result of the large number of isotopically similar prey sources included in the coho salmon mixing model. Similarity of isotopic sources limits a mixing model’s ability to resolve diet differences and results in prey proportion estimates with greater variability and uncertainty (Phillips et al. 2005; Parnell et al. 2010). Given this limitation, it is difficult to precisely assess how coho salmon diets responded to the changes in the alewife density and size structure. Previous studies and ongoing research have demonstrated a strong correlation between age-1 coho salmon growth rates and availability of small alewives, which suggests the high importance of this prey when its available (O’Gorman et al., 1987; Michigan DNR unpublished data).

Lake trout consistently occupied some of the largest niche areas (surpassed only by brown trout) but were the least closely associated with small alewives in the isotope biplots.

Enriched $\delta^{15}N$ of lake trout is likely the result of reliance on the enriched $\delta^{15}N$ profundal energy pathway and associated deeper dwelling prey such as bloater or sculpins (Turschak and Bootsma 2015; Kornis et al. 2020), as well as round gobies and large alewives that were enriched in $\delta^{15}N$ relative to small alewife. Small alewives also prefer warmer surface waters where lake trout, which prefer colder water, are unlikely to encounter them as prey (Wismer and Christie 1987; Bergstedt et al. 2012; Negus and Bergstedt 2012). Indeed, mixing model results suggest low importance of small alewife prey for lake trout. Nevertheless, niche area for lake trout did shift toward lower $\delta^{15}N$ from 2014 to 2016. Mixing model results suggest that this shift is the result of greater reliance on large alewives, which also increased in abundance in 2016 following 2015 recruitment (Bunnell et al. 2020), and a corresponding reduced reliance on bloater and round goby.

Except for Chinook salmon, which are nearly obligate alewife predators in Lake Michigan (Jacobs et al. 2013; Leonhardt et al. 2020), isotopic mixing models suggested that Lake Michigan salmonines shifted to greater reliance on round goby in 2015, as indicated by enriched $\delta^{13}C$ among many individual salmonines in 2015 relative 2014 and 2016. Although round gobies were the only ^{13}C-enriched nearshore/benthic endmember included in mixing models, it is possible that the ^{13}C-enrichment of salmonines in 2015 reflects greater reliance on other nearshore prey. However, round goby are hyper-abundant in shallow, rocky, nearshore, benthos of Lake Michigan during the summer and likely make a seasonal migration offshore to overwinter in the offshore profundal region (reviewed by Kornis et al., 2012). Given abundance and seasonal distributions, it is likely that round gobies are the primary conduit of enriched nearshore benthic $\delta^{13}C$ to salmonines. Indeed, recent diets studies have shown substantial reliance on this prey by lake trout and brown trout as well as occasional reliance by some Pacific salmonines (Johnson et al. 2005b; Dietrich et al. 2006b; Roseman et al. 2014; Happel et al. 2020; Leonhardt et al. 2020). Whether round goby are the primary nearshore prey source for salmonines or not, increased reliance on nearshore energy pathways in response to declining offshore pelagic energy pathways has been noted in Great Lakes fishes (Rennie et al. 2009; Turschak et al. 2014b). Salmonine charter angling effort and harvest of some Lake Michigan salmonines has also shifted to nearshore waters following major food web changes (Simpson et al. 2016). Furthermore, the shift toward nearshore energy sources coincides with the lowest biomass of alewives since forage fish monitoring began in 1962 (Predator-Prey Ratio model results from the Lake Michigan Salmonid Working Group)(Bunnell et al. 2020). By spring of 2015, much of the relatively strong 2010 and 2012 alewife year classes were likely lost to predation (Tsehaye et al. 2014a, 2014b; Madenjian et al. 2015) and negligible recruitment occurred again until the summers of 2015 and 2016. This means that alewife density would have been at an all-time low prior to the late summer or fall of 2015, at which time YOY alewife recruits would have reached sizes and offshore distributions susceptible to greater salmonine predation. Given the late season recruitment of alewives in 2015, it is likely that salmonines would have been somewhat more reliant on alternate prey sources for much of that year. Furthermore, relatively slow isotopic response times in salmonine muscle tissue may have led to a protracted alternate prey source signal (i.e., enriched $\delta^{13}C$ nearshore/benthic sources) even as alewife became more abundant in 2015 (Trueman et al. 2005; Höök et al. 2006, 2007; Vander Zanden et al. 2015)

In addition to increased reliance on nearshore/benthic energy sources in 2015, mixing model results for brown trout, steelhead and coho salmon (particularly smaller individuals of these species) suggests some reliance on invertebrate prey. Reliance on invertebrate prey was greatest in 2014 and 2015 and coincides with low alewife abundance prior to the recruitment event which occurred in 2015. Terrestrial invertebrates are commonly observed in Lake Michigan salmonine diets, especially steelhead (Rand et al. 1993; Leonhardt et al. 2020) and are often associated with surface feeding in thermal bars which entrain large numbers of terrestrial invertebrates in the spring and early summer (Haynes et al. 1986; Aultman and Haynes 1993; Höök et al. 2004). Other invertebrates commonly found in salmonine diets include the large predatory cladoceran, *Bythotrephes, longimanus* and the larger glacial relict *Mysis relicta* (Leonhardt et al. 2020). Poor growth rates of coho salmon during years of low small alewife abundance suggest that diet switching to a lower energy density prey such as invertebrates is likely among small coho salmon, and offers further evidence that invertebrates are more common prey at low alewife densities (O'Gorman et al., 1987; Michigan DNR unpublished data).

Species-specific responses over the study period were consistent with changes observed in alewife density and size structure, although reliance on alternative prey was variable and could be characterized as either generalist or specialist at the level of predator populations. For example, brown trout and lake trout collected in this study appeared to be generalists with respect to prey selection and foraging location. This is evidenced by greater intraspecific isotopic variation (i.e. large isotopic niche areas) and diets that included large proportions of alternate prey such as round goby when alewife abundance was lowest prior to the 2015 recruitment event. Both species used nearshore benthic prey (i.e. more ^{13}C-enriched), however, brown trout had lower $\delta^{15}N$ than lake trout, which suggests that they fed higher in the water column than the more profundal lake trout. Steelhead and coho salmon appeared to also be prey generalists but exhibited lower intraspecific isotopic variation than brown trout and lake trout. Lower isotopic variation among steelhead and coho salmon may have been driven, at least in part, by specialization with respect to foraging location. Steelhead transitioned from high reliance on terrestrial invertebrates in 2014 to much greater reliance on small alewives in 2015 and 2016 which suggests that this species was likely very surface oriented but opportunistic with respect to available prey near the surface. Likewise, coho salmon appeared to have a diet comprised of a suite of epilimnetic/metalimnetic invertebrate prey as well as small alewives. The Chinook salmon, by comparison, may have specialized with respect to both prey and foraging location, with a strong preference for alewife and limited use of alternate terrestrial or benthic prey sources observed in other species' diets.

The use of stable isotopes to characterize ecological niche specialization (or lack thereof), presents some difficulties that are apparent in this study. Quantifying ecological niche breadth of a predator using stable isotopes is dependent on the isotopic differences observed among possible prey sources. For instance, ontogenetic increases in alewife $\delta^{15}N$ and decreases in $\delta^{13}C$ have been noted in several studies (Turschak and Bootsma 2015; Mumby et al. 2017). Therefore, a species such as Chinook salmon, which preys upon multiple size classes of alewives (Leonhardt et al. 2020), may exhibit a relatively large isotopic niche breadth despite high reliance (i.e. specialization) on a single isotopically variable prey. Similarly, high reliance on a prey source with spatially distinct isotopic signature (e.g. round goby; Foley et al., 2017; Turschak et al., 2018) may also result in large apparent isotopic niche area if spatial movements of the predator are also limited (Kornis et al. 2020). In the case of Lake Michigan salmonines, horizontal and/or vertical movements for most are likely large enough that prey source spatial variation is integrated in the predator's isotopic signature (Adlerstein et al., 2008, 2007a, 2007b; Bronte et al., 2007; Clark et al., 2017; Haynes et al., 1986; Schmalz et al., 2002; and Michigan DNR unpublished data). However, extent of isotopic integration of spatially explicit prey sources is likely variable among species (Kornis et al. 2020) and warrants further testing in the Great Lakes. Conversely, distinct prey sources that are isotopically similar present the opposite problem. For instance, coho salmon exhibit a more diverse observed diet than Chinook salmon (i.e. broader ecological niche) yet have a comparably smaller isotopic niche area (Kornis et al. 2020; Leonhardt et al. 2020). Because isotopic niche area reflects variation among individuals in a population, it is also possible that isotopic similarity among individual generalists (i.e. individuals with large observed diet breadth) in a population will yield a small isotopic niche area of the population (Bolnick et al. 2003). Newsome et al. (2007) reviewed some of these challenges associated with the use of stable isotopes to characterize ecological niche and suggest that converting consumer isotopic values into diet proportions is a useful approach. Use of isotope mixing model results in this study provide a means of exploring variation in isotopic niche area with respect to trophic ecology and support the findings of Newsome et al. (2007). .

A second challenge in using stable isotopes to characterize ecological niche results from availability of highly abundant preferred prey. In Lake Michigan, we observed a high degree of isotopic niche overlap among salmonines that appears to be primarily associated with reliance on alewife prey, as observed in many previous diet studies (e.g. Jude et al., 1987; Leonhardt et al., 2020; Stewart and Ibarra, 1991). If it were assumed that isotopic niches of two sympatric populations were analogous to ecological niches of those populations, high isotopic niche overlap would indicate strong potential for competition and low overlap would indicate niche partitioning among species. However, because of preferential alewife predation (Leonhardt et al. 2020), high overlap may not necessarily indicate competition but rather an abundance of this prey (Robinson and Wilson 1998; Golcher-Benavides and Wagner 2019). It appears that salmonine species switch from preferential feeding on alewives to alternative prey (e.g.

terrestrial invertebrates and round goby) as alewife abundance dwindles or as size structure changes. The threshold for prey switching may vary among salmonines, with Chinook apparently tolerating very low alewife abundance whereas Lake Trout may use alternate prey even at relatively higher small alewife abundance. Use of alternate prey by Lake Michigan salmonines may offer some evidence for how this community of predators partitions available prey by means of species-specific foraging locations or behaviors (e.g., nearshore benthic, surface, or profundal) when preferred prey are scarce. However, this also means that consideration must be given to resources gradients when examining potential for competition using stable isotopes.

Species-specific responses to changes in resource availability can be dissimilar and subsequently result in changes in potential interspecific interactions as revealed by isotopic niche overlaps among those species. Differential use of alternate prey resource pools (i.e., pelagic, profundal, nearshore/benthic, and terrestrial) is likely to aid sympatry among the Lake Michigan salmonine community, particularly if dynamics of those resource pools are decoupled from one-another (i.e., asymmetric) (Rooney et al. 2006; Rooney and McCann 2012). However, use of alternate resources may also allow this community to sustain itself at levels which are detrimental to the preferred alewife prey population. Compensatory declines in predator abundance resulting from low alewife abundance may be offset by these alternate resource subsidies (Schindler et al. 1996; Polis et al. 1997; Vander Zanden and Vadeboncouer 2002). For example, following the population collapse of alewives in Lake Huron in the early 2000s, high predation pressure by lake trout—facilitated by reliance on alternate round goby prey—has maintained suppression of the alewife population (He et al. 2015).

Assessing niche overlap and potential for competition using stable isotope analyses has become a common practice in ecological studies, particularly with the growing availability of analytical tools catering to these needs (see Gerig et al., 2018; Kornis et al., 2020; Mumby et al., 2018 as examples from the Laurentian Great Lakes). However, little work has been done to explore how intraspecific niche areas and positions vary along resources gradients such as prey availability (McMeans et al. 2015). The isotopic niche of an organism reflects the discrete set of resource conditions within the spatiotemporal domain of a study. While analyses of niche overlap offer valuable insight into shared or differential resource use within a community, they are probably limited with respect to quantifying the actual potential for competition without also considering availability of shared resources. By decomposing isotopic niche area and position into specific prey proportions along a shared resource gradient using mixing models, changes in resource use and alternate resource subsidies become more apparent. Future work may consider incorporating resource gradients or other environmental gradients as explanatory variables in mixing models. This would aid in understanding and predicting potential for competition among species under different scenarios. Given the relatively short temporal scope of this study (3 years) and covariation among variables (i.e. alewife abundance increased proportionately with decreasing size), it was not possible to develop a statistically robust mixing model that included these explanatory variables.

Understanding how ecological communities partition available resources along environmental gradients is important as ecosystems cope with continued changes resulting from species invasions, habitat degradations, climate change and other anthropogenic stressors (McMeans et al. 2015). Findings of this study add to literature suggesting that stable isotopes offer a useful means of understanding both species specific and community level response to spatiotemporal environmental gradients (Schmidt et al. 2009, 2011; Turschak et al. 2014b, 2019). This work is novel in that it helps to quantify asymmetric diet response of a predator community to changes in a preferred prey resource. Niche area and position as they relate to specific diet proportions can be examined in the context of specific prey resource gradients or other environmental gradients. We focused on resource gradients associated with a single preferred prey source, however, a similar approach might be used to explore multiple environmental gradients including density of other prey and predators. Future work incorporating multiple environmental gradients as explanatory variables into mixing models will aid in understanding how species are able to cope with continued ecological changes and may aid resource managers in making decisions to mitigate loss of ecological function or economic value associated with these changes.

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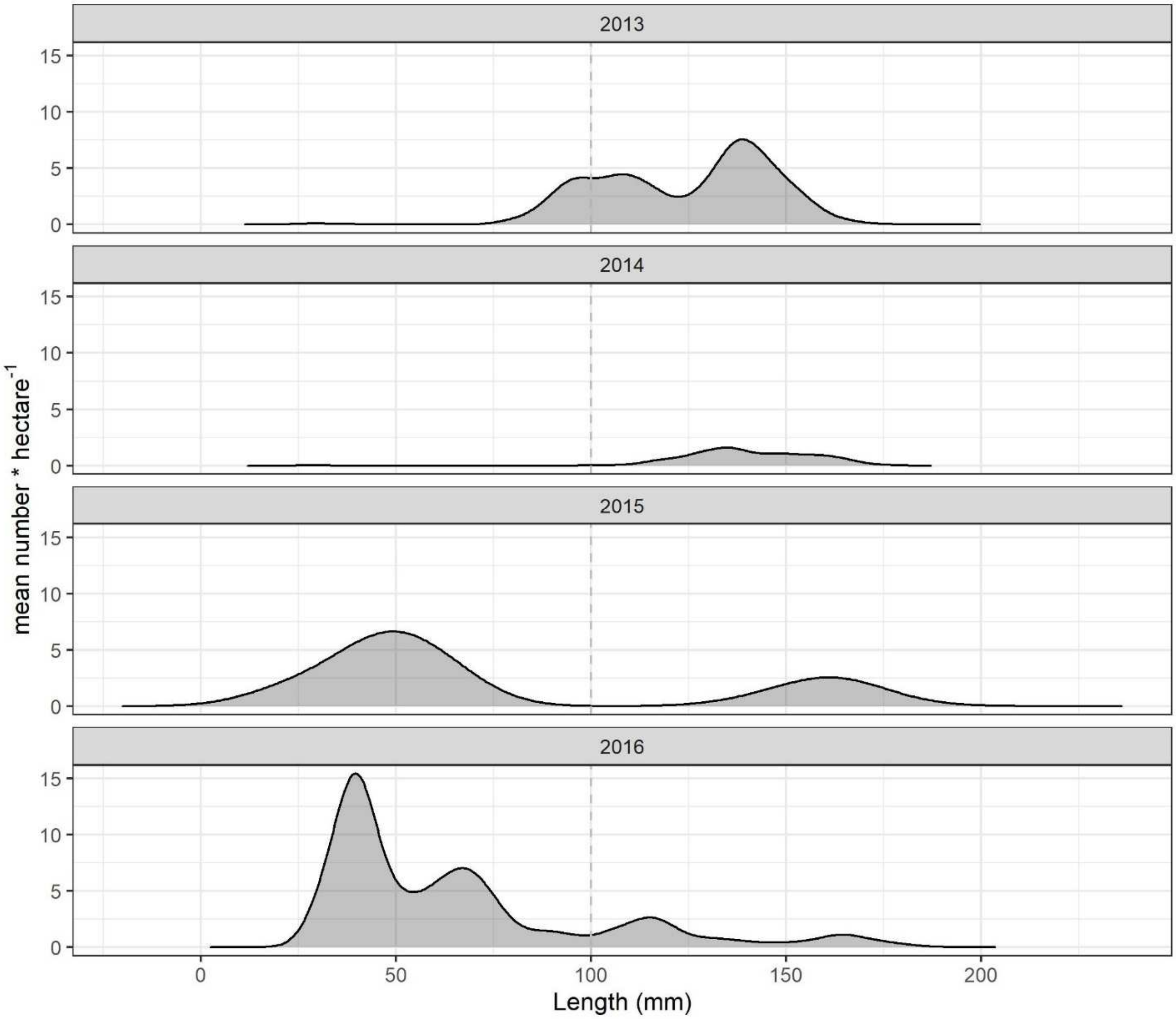

Figure 3.1. Lake Michigan alewife length density distribution scaled by average lakewide areal density of alewives from 2013 to 2016 (D. Warner personal communication; Data Source: Lake Michigan Hydroacoustic Survey). Cutoff for discrete alewife size classes used in this study are indicated by the vertical dashed lines: small alewives < 100 mm and large alewives ≥ 100 mm, or ≈ age 0 and ≈ age 1+, respectively, during the August hydroacoustic survey.

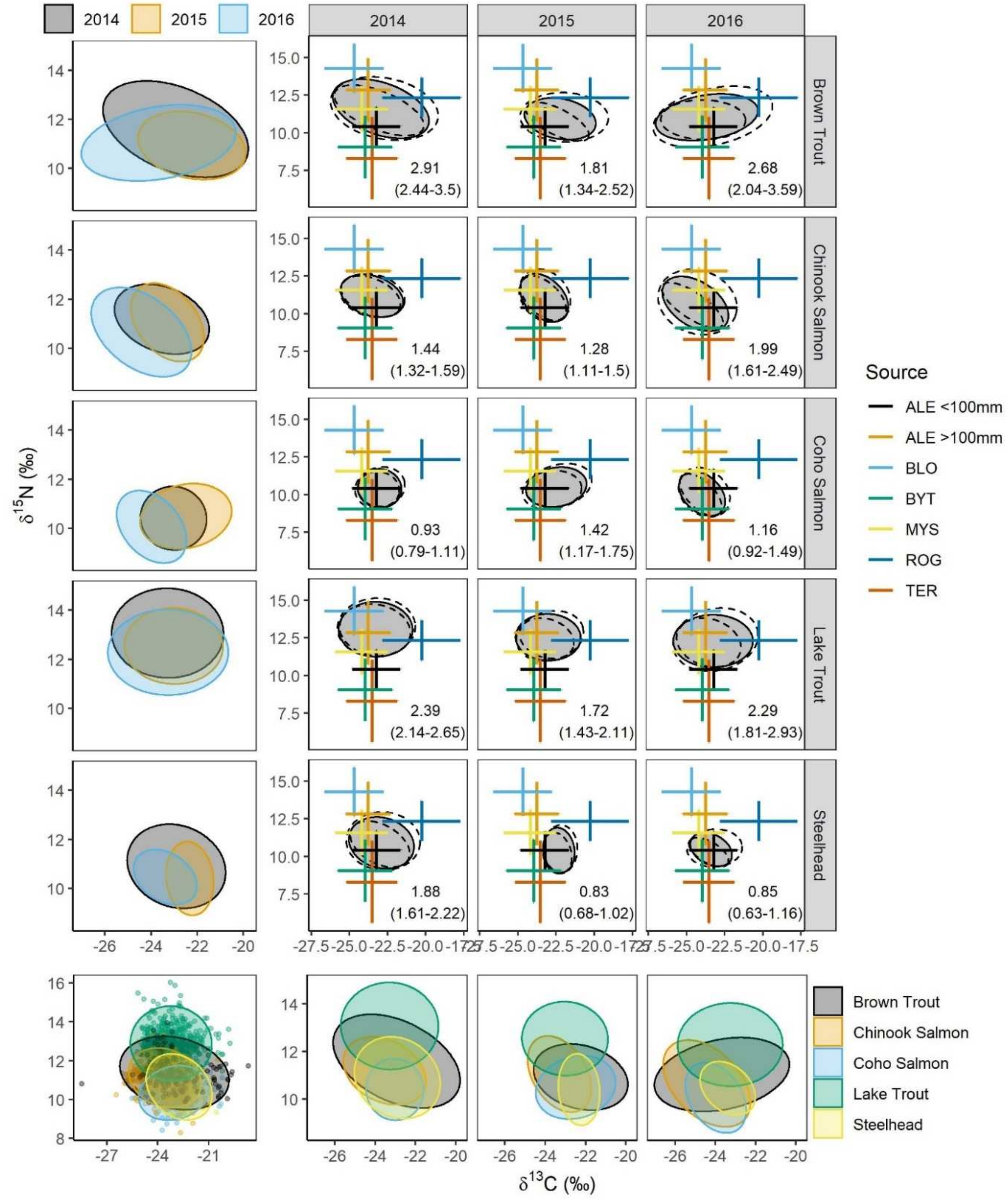

Figure 3.2. Median 95% δ^{13}C and δ^{15}N isotopic niche for Lake Michigan salmonines from 2014-2016. Left panels (upper five) depict interannual differences in isotopic niche position and size for individual salmonine species. Lower panels (right three) depict interspecific isotopic niche area and niche overlap among salmonine species within individual study years. Lower-left most panel depicts interspecific isotopic niche area and niche overlap for all study years combined with individual data points shown to illustrate ellipse fitting. Block of panels in the upper right depict individual species-year combinations with trophic-adjusted prey position and standard deviation (δ^{13}C: +0.8 +/- 1.3; δ^{15}N: +3.4 +/- 1.0) overlaid as colored cross bars. Dashed lines indicate the upper and lower 95% credible intervals around the shaded median ellipse and the text indicates median ellipse area (95% credible interval)

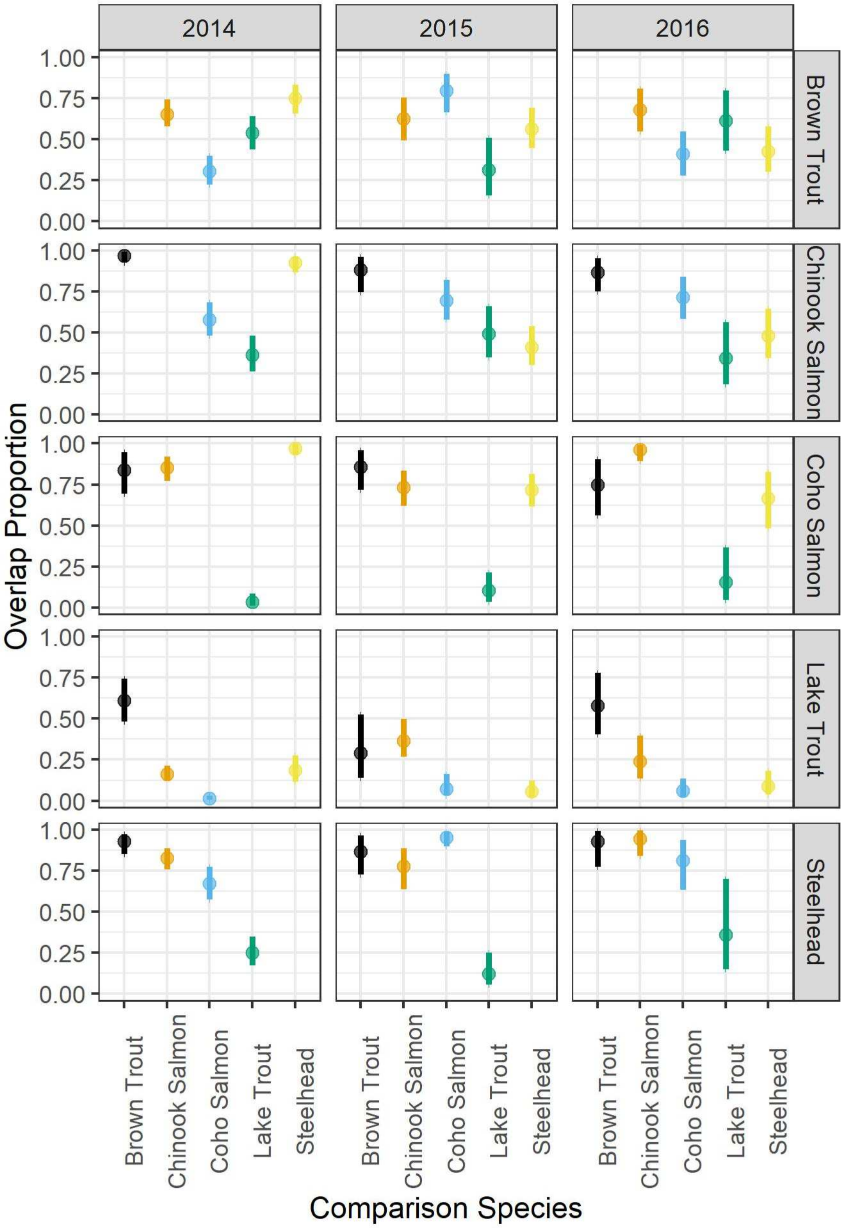

Figure 3.3 Pairwise median (95% credible interval) $\delta^{13}C$ and $\delta^{15}N$ isotopic niche overlap among species expressed as a percentage of overlap in species-specific 95% isotopic niche region shown in Fig. 3.2. Horizontal panels (2014-2016) indicate the year for which the pairwise comparisons are being made and vertical panels indicate the reference species. Pairwise comparisons are directional and are expressed relative to the reference species. For example, an individual from comparison species A (x-axis) has XX% probability of occurring within reference species B's (vertical panels) isotopic niche region.

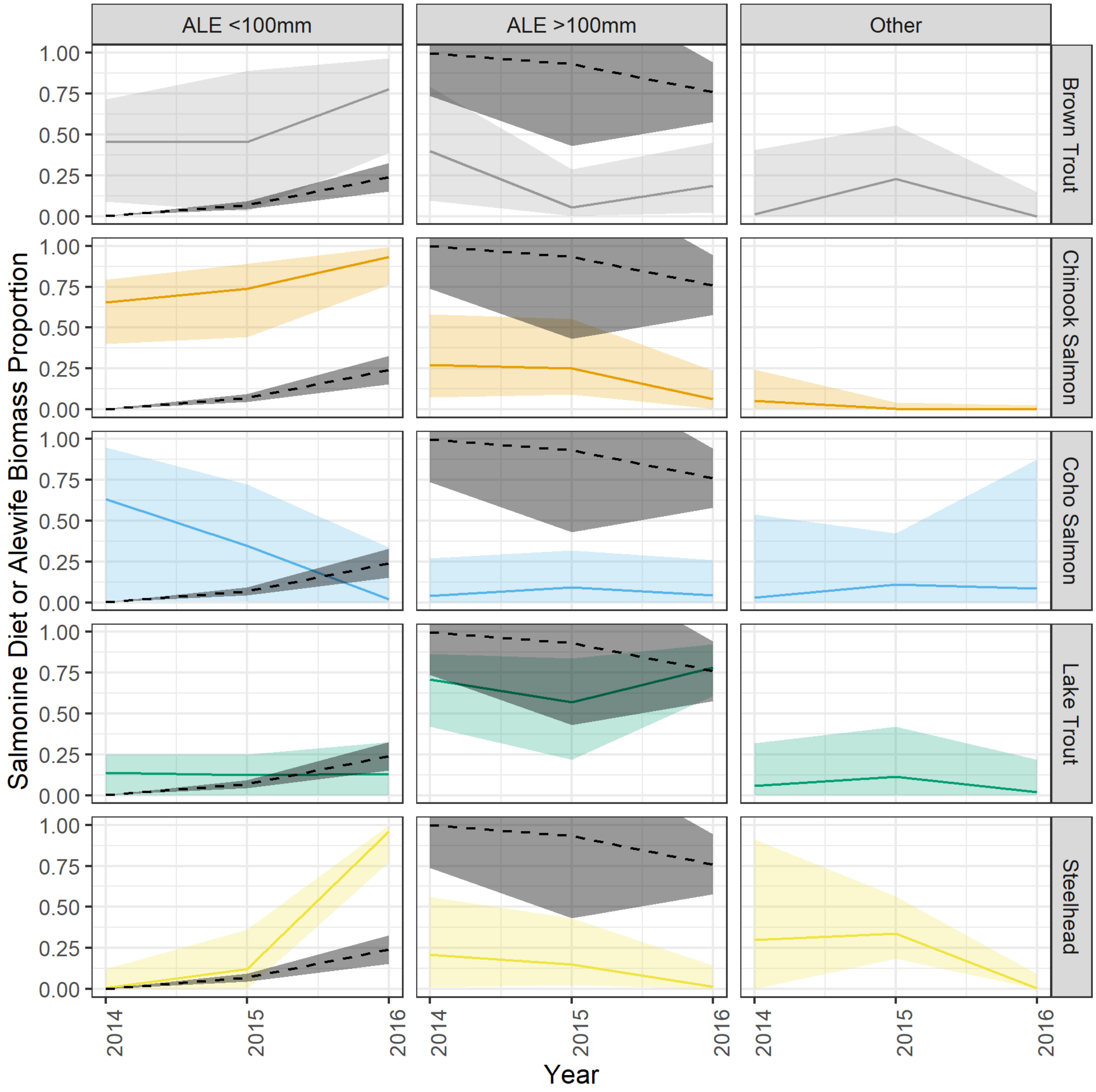

Figure 3.4. Estimates (median and 95% credible interval) of small alewife (left panels), large alewife (middle panels), and all other potential prey (right panels) to the lakewide diets of salmonine predators over the study period (Solid lines and light gray or colored shading; Brown Trout: light gray; Chinook Salmon: orange; Coho Salmon: blue; Lake Trout: green; Steelhead: yellow). Lakewide biomass (mean and standard error) of alewife size classes as a proportion of total lakewide alewife biomass measured by the August hydroacoustic survey are overlayed for comparison (Dashed lines and dark gray shading; D. Warner personal communication; see methods in Adams 2018 and Warner et al. 2019).

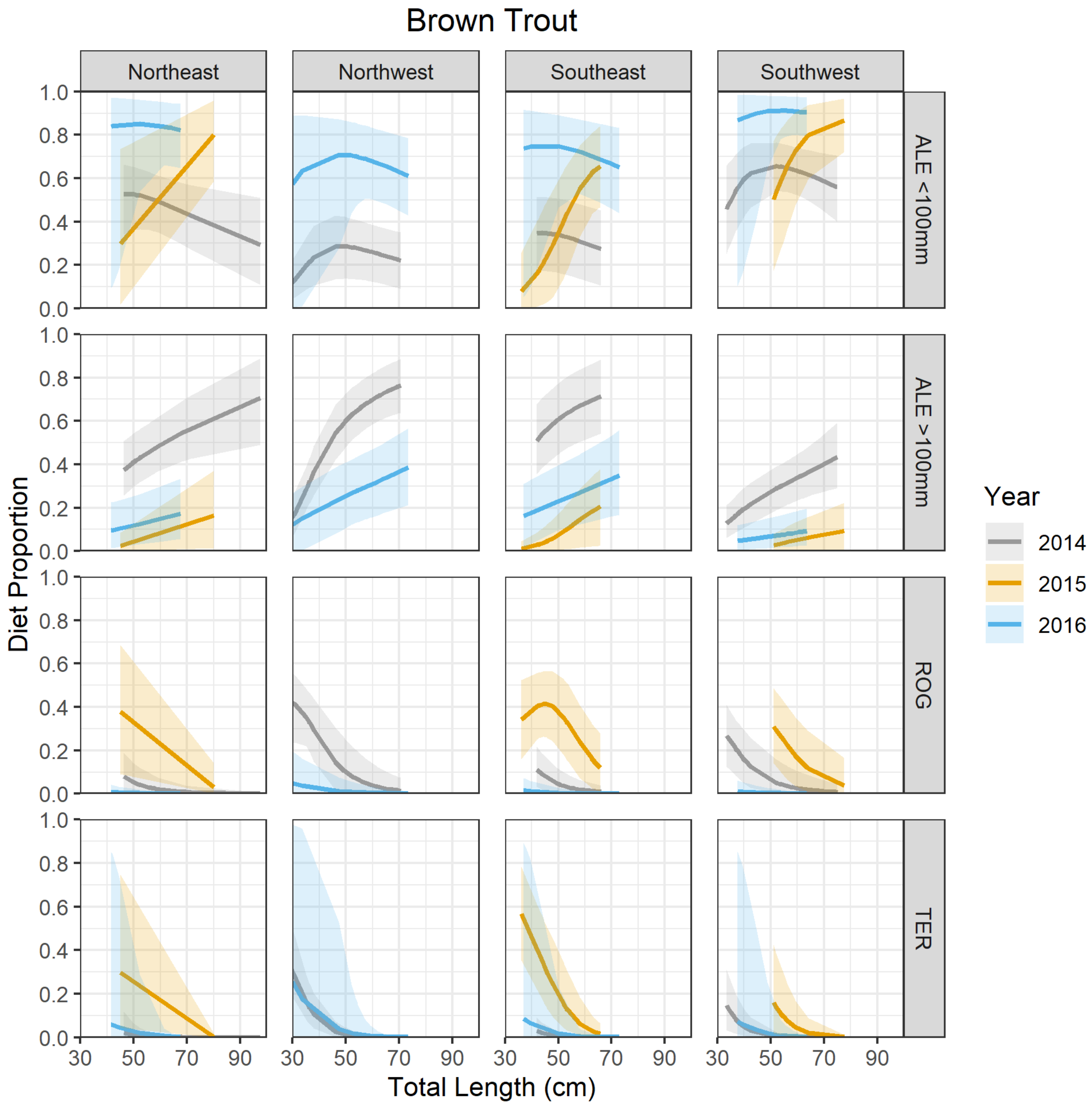

Figure 3.5. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for brown trout. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE < 100 mm: small alewives; ALE > 100 mm: large alewives; ROG: round goby) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colors correspond to specific study years (2014-2016).

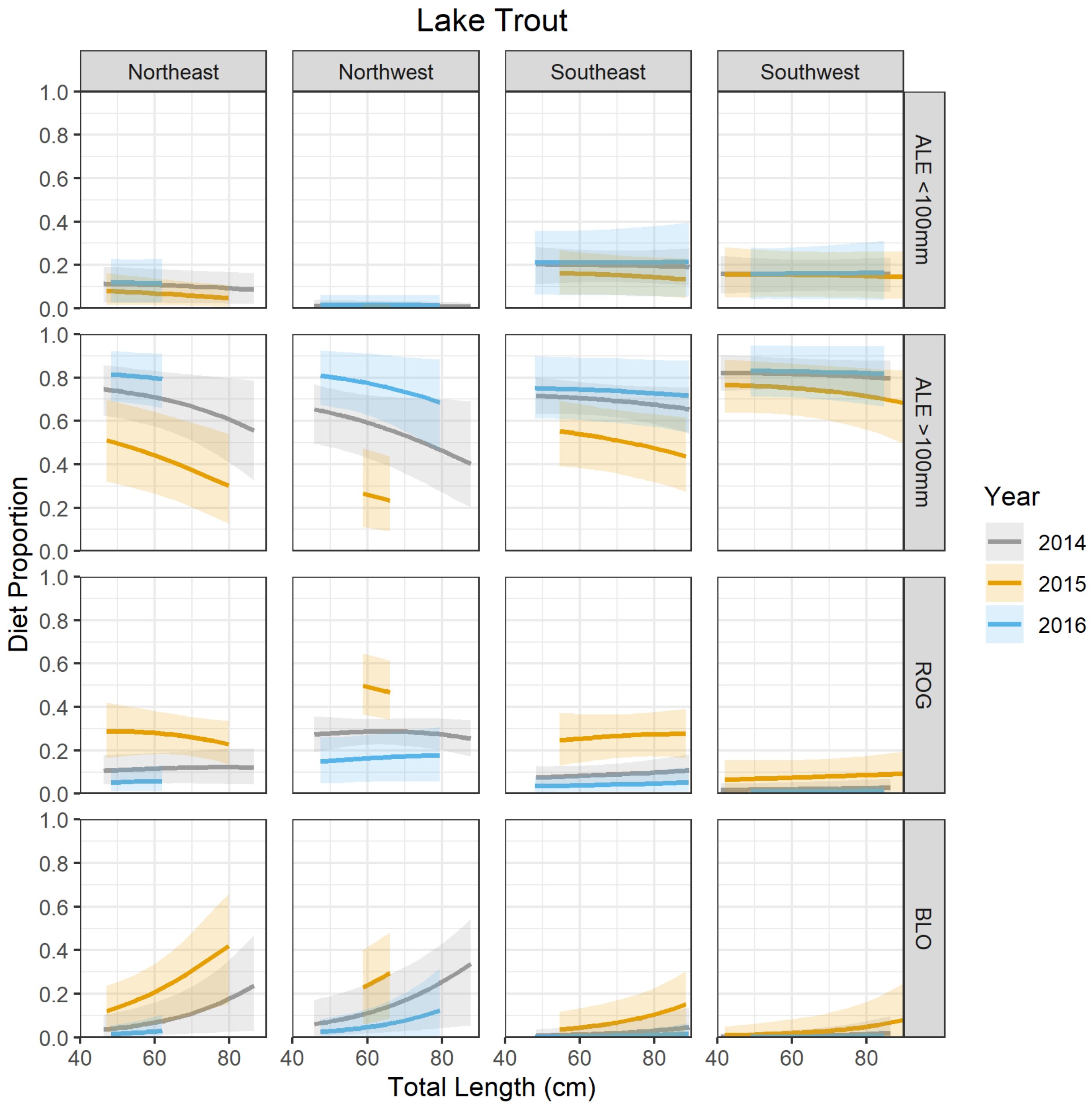

Figure 3.6. $\delta^{13}C$ and $\delta^{15}N$ mixing model predictions of dietary proportions as a function of total length (mm) for Chinook salmon. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE < 100 mm: small alewives; ALE > 100 mm: large alewives; ROG: round goby; and TER: terrestrial invertebrates) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colors correspond to specific study years (2014-2016).

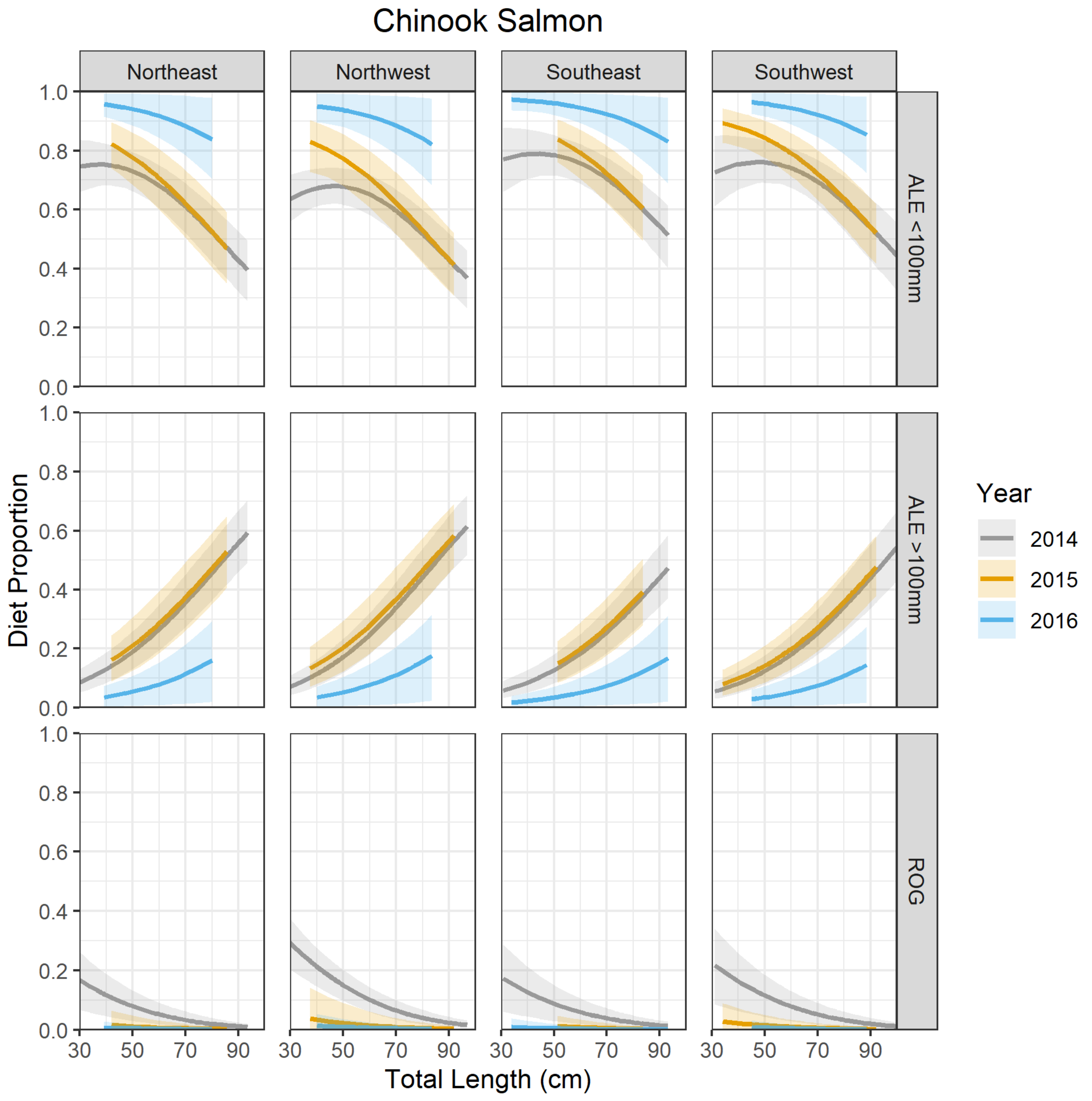

Figure 3.7. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for coho salmon. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE < 100 mm: small alewives; ALE > 100 mm: large alewives; BYT: *Bythotrephes*; MYS: *Mysis*; ROG: round goby; and TER: terrestrial invertebrates) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colors correspond to specific study years (2014-2016).

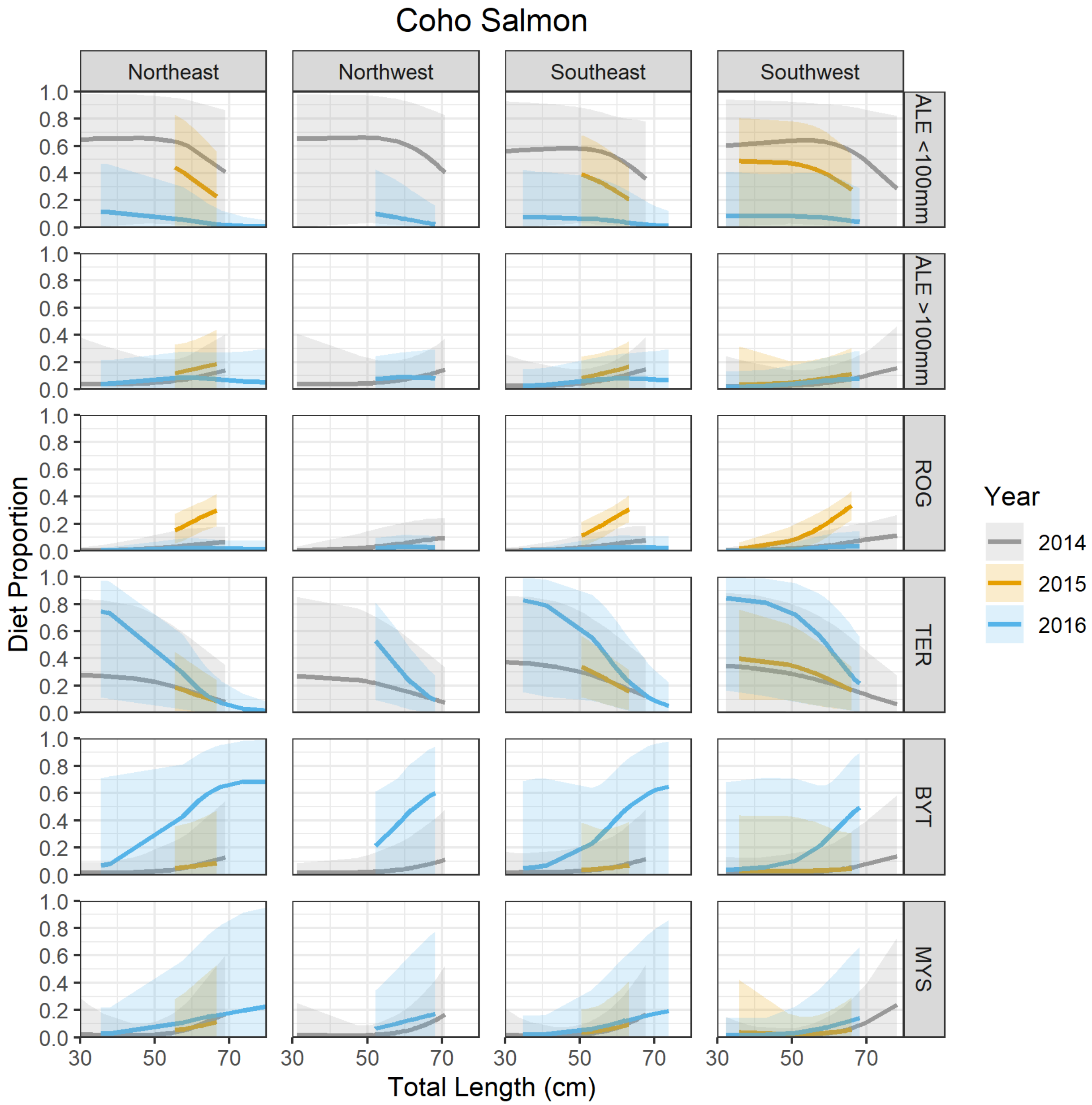

Figure 3.8. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for coho salmon. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE < 100 mm: small alewives; ALE > 100 mm: large alewives; BYT: Bythotrephes; MYS: Mysis; ROG: round goby; and TER: terrestrial invertebrates) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colors correspond to specific study years (2014-2016).

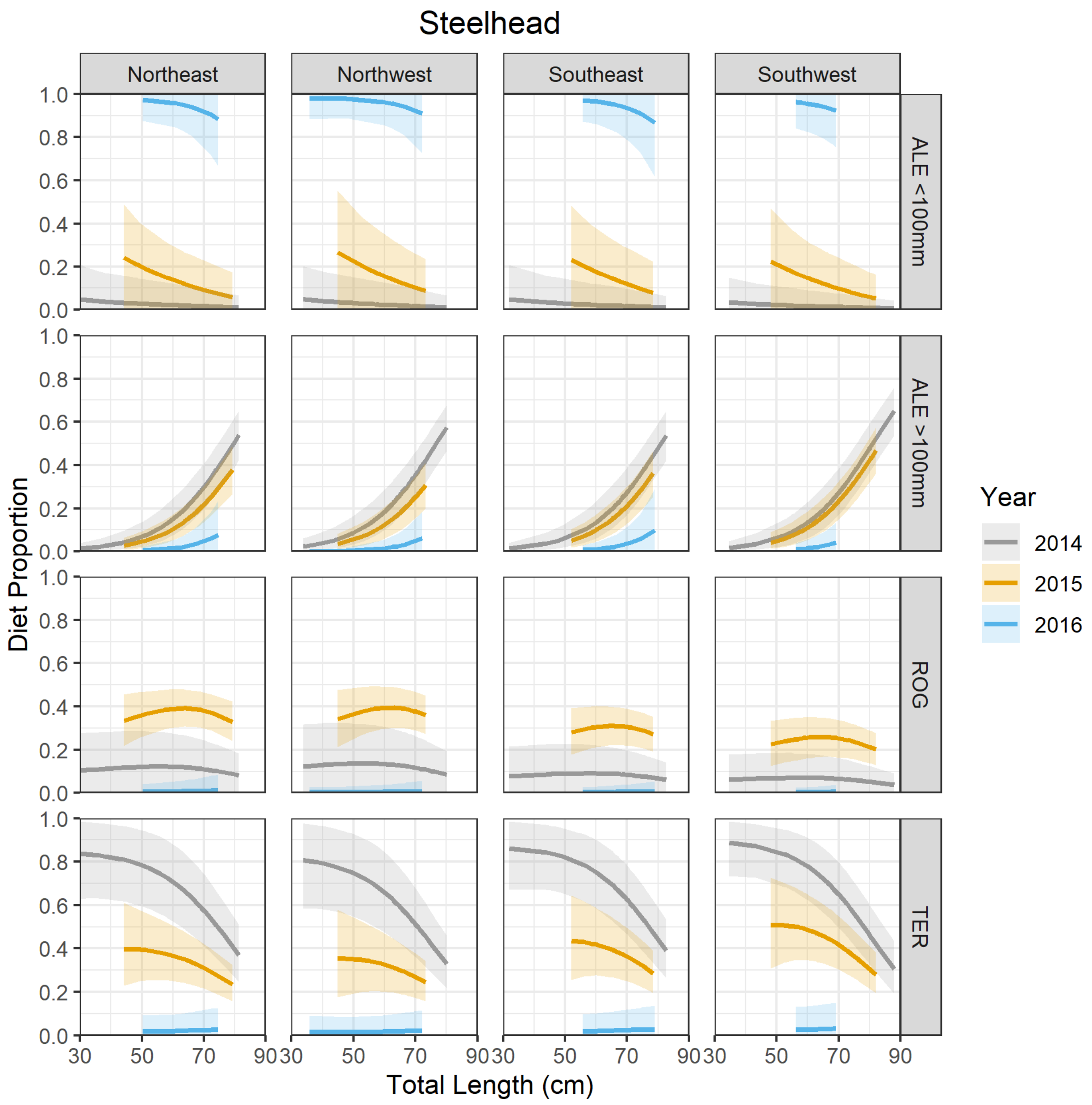

Figure 3.9. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for steelhead. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE < 100 mm: small alewives; ALE > 100 mm: large alewives; ROG: round goby; and TER: terrestrial invertebrates) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colors correspond to specific study years (2014-2016).

Chapter 4. Examining the Trophic Ecology of Lake Michigan's Resurgent Cisco Population with Stable C and N Isotopes[3]

Abstract

Lake Michigan's remnant cisco (*Coregonus artedi*) population is amid an expansion (2011-present) following near extirpation by the 1970s. Strong evidence of piscivory derived from observed diet analyses suggests that this population may occupy a unique trophic role relative to other Laurentian Great Lake and north temperate lake cisco populations. To verify their trophic role in the Lake Michigan food web, cisco and their prey were collected over a period from 2015-2020 for stable C and N isotope analyses. Leveraging existing stable isotope datasets for Lake Michigan, the trophic position of cisco was assessed by quantifying the isotopic niche space occupied by cisco relative to common salmonine predators and prey fish species. Diet mixing models were then constructed to estimate the relative importance of potential prey sources to cisco diets. Results suggest that cisco occupy an isotopic niche extremely similar to that of Lake Michigan salmonines and are more dissimilar to Lake Michigan prey fish species. Mixing models suggest greater relative importance of pelagic prey sources to cisco diets than expected based on previous descriptions of observed diets, although discerning the relative importance of isotopically similar pelagic prey sources may require further investigation. Under ecological conditions present in Lake Michigan at the time of this study, it appears that cisco occupy the trophic role of a pelagic piscivore but derive a considerable portion of their diet from nearshore benthic round goby as well.

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[3] Turschak, B.A., J.L. Jonas, C. LaFaver, J.B. Smith, B.S. Breaker, C.R. Bronte, D.B. Bunnell, M.S. Kornis, K.L. Pangle, and H.A. Bootsma. *In prep*. Examining the trophic ecology of Lake Michigan's resurgent cisco population with stable C and N isotopes. To be submitted to J. Great Lakes Res.

Introduction

Cisco (*Coregonus artedi*) populations in Lake Michigan are experiencing a recovery after being nearly extirpated (Claramunt et al., 2019). Increased catch rates in fishery independent surveys, commercial fisheries, and recreational fisheries concurrently indicate increasing abundance at ports in northeastern Lake Michigan near Grand Traverse Bay (Claramunt et al. 2019). Cisco also appear to be expanding their distribution in Lake Michigan with increased observations in fishery independent gillnet surveys and pier fisheries from ports extending into the southern basin near Benton Harbor, MI (Michigan Department of Natural Resources, unpublished data). However, the ecological factors that contributed to recent population recoveries remain uncertain, as does the trophic role of cisco in a vastly different Lake Michigan ecosystem (Madenjian et al. 2015).

Throughout the late-1800s and early 1900s, Lake Michigan supported an important commercial fishery for cisco which, at its peak, reached nearly 11 million kg harvested per year. Harvest rates declined rapidly thereafter and averaged nearly 2.2 million kg per year from 1923 to 1938 (Brown et al., 1999; Wells and McLain, 1973). Large-scale declines in coregonine populations continued into the 1970s and were likely associated with over-harvest, adverse interactions with invasive species, and environmental degradation (Smith 1968; Wells and McLain 1973; Crowder 1980; Myers et al. 2009). While the importance of individual stressors or interactions among stressors remain somewhat unclear (Madenjian et al. 2008, 2011), cisco were nearly extirpated from each of the lower Great Lakes (i.e. all Laurentian Great Lakes except for Lake Superior) by the 1970s (Eshenroder and Burnham-Curtis 1999; George 2019).

Prior to large-scale population declines, cisco likely played an important role in food webs of the Laurentian Great Lakes, functioning as shallow-water pelagic invertivores (George

2019). Observations of stomach contents from cisco collected in Lake Superior and smaller north temperate lakes have, with few exceptions, described cisco as consumers of zooplankton (e.g. cladocerans, and cyclopoid and calanoid copepods) and macroinvertebrates (e.g. *Mysis relicta* and chironomid dipterans; Stockwell et al. 2010; Anderson et al. 2011; Gamble et al. 2011b, 2011a; Ahrenstorff et al. 2013; Keeler et al. 2015; Eshenroder et al. 2016). Piscivory has been infrequently observed and annual contributions of fish to diets of cisco have been presumed to be relatively low (Hoff et al., 1997; Hrabik et al. 1998). Findings from historic populations of cisco in Lake Michigan support assumptions of planktivory. Bulk stable C and N isotopes from archived specimens of Lake Michigan and Lake Superior cisco collected during the early 1900s, were used to evaluate trophic level and the depth of water occupied (Schmidt et al. 2011). Isotopic evaluations indicated that cisco historically occupied trophic levels similar to that of planktivorous deep water coregonines (Schmidt et al., 2011). Analyses additionally indicated that cisco (and lake whitefish) occupied depth ranges shallower than those occupied by other prevalent coregonines in the lakes (Schmidt et al. 2011).

The trophic ecology of Lake Michigan cisco under contemporary ecological conditions is likely different from historic Lake Michigan populations and other extant Laurentian Great Lake and north temperate lake populations (Breaker et al. 2020). Recent observations of cisco stomach contents in Lake Michigan indicated a surprisingly high degree of piscivory and reliance on invasive prey species, including round goby (*Neogobius melanostomus)*, alewife (*Alosa pseudoharengus*), and *Bythotrephes* (Breaker et al. 2020). Contributions of benthic round gobies to cisco diets were especially large, followed by contributions of pelagic *Bythotrephes*, alewives and surface oriented pupal/adult dipterans. The degree of dietary reliance on round goby was unexpected; goby tend to be benthically oriented and prefer warm water temperatures whereas cisco are thought to be pelagically oriented and prefer lower temperatures (Smith 1956; Lee and Johnson 2005; Breaker et al. 2020). These results provided evidence that Lake Michigan cisco are much more piscivorous than indicated previously and demonstrated greater foraging plasticity and reliance on benthic energy pathways. However, cisco diets were largely derived from bottom gill nets set in nearshore areas during periods when the lake was isothermal or weakly stratified (Breaker et al., 2020). As a result, biases may be associated with location, gear used, or the timing of sampling events. Understanding of cisco trophic position derived from observed diets may be augmented by use of ecological tracers such as stable isotopes which reflect long-term diet reliance including under-sampled seasons (e.g. winter and mid-summer thermally stratified seasons) and spatial distributions (e.g. open-water suspended).

Stable C and N isotopes provide a commonly used metric for tracing energy flow, quantifying trophic position, and estimating dietary composition of aquatic organisms (France 1995; Bootsma et al. 1996; Vander Zanden and Vadeboncouer 2002; Newsome et al. 2007). Discrimination of ^{13}C uptake during photosynthesis and variation in environmental isotope abundance results in broad differences in stable C isotope ratios (expressed as δ^{13}C) between benthic and pelagic primary producers (France 1995; Hecky and Hesslein 1995; Vander Zanden and Vadeboncouer 2002). Relatively little (<1‰) additional fractionation of δ^{13}C occurs during trophic transfer from primary producers to consumers (France 1995; Hecky and Hesslein 1995; Post 2002). Therefore, δ^{13}C provides a good metric of primary energetic pathway (i.e. benthic vs. pelagic) among aquatic consumers (Hecky and Hesslein 1995; Vadeboncoeur et al. 2002). Unlike δ^{13}C, stable N isotope ratios (expressed as δ^{15}N) are enriched (3-4‰) with each trophic transfer resulting from discrimination against ^{15}N during elimination of nitrogenous waste and subsequent retention of the heavier isotope in consumer tissues (Minagawa and Wada 1984;

Peterson and Fry 1987). Thus, $\delta^{15}N$ increases in a stepwise manner from the base of the food web and provides a continuous measure of consumer trophic level (Minagawa and Wada 1984; Vander Zanden and Rasmussen 1999). Consumer $\delta^{13}C$ and $\delta^{15}N$ represent a mixture of isotopic signatures derived from dietary sources which are integrated into consumer tissues through catabolic turnover and growth processes (Vander Zanden et al. 2015; Stock et al. 2018). Because these metabolic processes are relatively slow, consumer tissues can be used to quantify trophic position and diet mixtures over longer time scales (months) than traditional observed diets (hours-days) (Weidel et al. 2011; Hayden et al. 2014; Vander Zanden et al. 2015). Existing data sets and studies of stable C and N isotope compositions have provided insights into contemporary food web structure and energy flow (Turschak et al. 2014; Turschak and Bootsma 2015; Turschak et al. 2019; Kornis et al. 2020). Specifically stable isotopes have been used to address resource partitioning or overlap among nearshore and offshore fish communities and reconstruct time-integrated diets of these fishes (Turschak et al. 2019; Kornis et al. 2020).

To characterize the trophic role of cisco relative to other Lake Michigan fishes and verify conclusions from stomach content analyses, we collected cisco tissues for stable C and N isotopic analyses from 2015-2020. Previous large-scale isotopic analyses of Lake Michigan's contemporary food web did not include cisco. Updating existing isotopic datasets with cisco facilitated an evaluation of relative trophic similarity between cisco and other Lake Michigan fishes with more well-known trophic ecologies. Furthermore, because better long-term integration of the cisco's trophic role can be obtained through isotopic analyses, this method can be used to verify observed diets or identify potential biases resulting from shorter integration times (Hayden et al. 2014; Futia et al. 2021). For instance, anecdotal evidence from recreational anglers suggests that alewives were more important in cisco diets obtained from mid-summer and over-winter fisheries during periods when fishery-independent sampling was low. Therefore, the collection of stable isotope data from cisco provided a timely opportunity to address two primary objectives: 1) identify the trophic role of the expanding Lake Michigan cisco population relative to previously modeled common predator and prey fishes (Turschak et al. 2019; Kornis et al. 2020), and 2) quantify the time-integrated diet proportions of Lake Michigan cisco for comparison with recent observed stomach contents.

Methods

Sample Collection and Processing

Lake Michigan cisco, as well as prey fishes and invertebrates commonly encountered in cisco diets (Breaker et al. 2020), were collected from 2015-2020. Collection dates and locations ranged from May-December and occurred at several locations in northeastern Lake Michigan where densities were high enough to consistently encounter cisco during surveys (Fig. 4.1). Cisco were collected using graded mesh (25.4-152.4 mm) fishery independent bottom set gillnets. Two species of prey fish (i.e. round goby and alewife) were also collected using bottom set small mesh gillnets (round goby and alewife; 6.0-38.1 mm) or minnow traps (round goby). After collection, fish samples were transported back to the laboratory where biological data (e.g., total length and total weight) were recorded. Benthic invertebrates including dipteran *Chironomidae*, were collected by scuba benthic scrapes over rocky substrate at a depth of 5-20 m near Good Harbor Bay, MI in 2016 (Fig. 4.1). At the laboratory, invertebrate samples were sorted into taxon specific groups (e.g. Chironomids) and a composite sample of multiple individuals was created for each sampling event. For cisco, skin-free dorsal muscle tissue plugs were removed and stored frozen for subsequent stable isotope analyses. Probable prey sources including prey fishes and invertebrates were frozen whole for subsequent processing and stable isotope analyses.

Sample preparation and stable isotope analyses were performed at the School of Freshwater Sciences, University of Wisconsin-Milwaukee. Individual whole prey fish were homogenized in a blender before additional processing occurred. Frozen cisco dorsal tissue plugs, prey fish homogenates, and whole invertebrates were lyophilized in polystyrene weighing boats. Dried samples were chopped into a fine powder using surgical scissors and razor blades. Subsamples of dried homogenates (0.5-1.0 g) were then packed in tin capsules for subsequent isotope analysis using an elemental analyzer (ECS 4010, Costech Instruments, Valencia, CA) coupled with a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher, Bremen). Isotope ratios were adjusted after each sample run using a 2-point standard curve and known NIST laboratory standards. An acetanilide control sample was analyzed for $\delta^{13}C$ and $\delta^{15}N$ ratios after every 12th sample to ensure instrument precision ($\delta^{13}C$ SD = 0.20 and $\delta^{15}N$ SD $\leq$ 0.20). All stable isotope results were expressed in per mil (‰) differences between the isotope ratio of the sample and that of the standard (PDB carbonate or atmospheric air for $\delta^{13}C$ and $\delta^{15}N$, respectively), using the formula: $\delta^{13}C$ or $\delta^{15}N = (R_{sample}/R_{Standard}-1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ for $\delta^{13}C$ and $R = {}^{15}N/{}^{14}N$ for $\delta^{15}N$.

Stable C and N isotope data for Lake Michigan salmonine predator fishes, common prey fishes, and some invertebrate taxa, compiled for prior studies (*ca* 2014-2016), were used to augment the cisco and prey dataset collected for this study (Fig. 4.1). These prior studies collected each of the five salmonine species common in Lake Michigan including brown trout *Salmo trutta*, Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *Oncorhynchus kisutch*, lake trout *Salvelinus namaycush*, and steelhead *Oncorhynchus mykiss* to help characterize the trophic role of these species. Additionally, stable C and N isotope data from common prey fish and invertebrate taxa including alewives, bloater *Coregonus hoyi*, deepwater sculpin *Myxocephalus thompsonii*, rainbow smelt *Osmerus mordax*, round goby, and slimy sculpin *Cottus cognatus* were also collected to support diet mixing models of Lake Michigan salmonines. Regional stable C and N isotopic variation in salmonines and alewives is low in Lake Michigan so lakewide data from prior studies were retained for subsequent analyses (Fig. 4.1; Turschak et al. 2019; Kornis et al. 2020). For other prey taxa, regional variation is known to be higher or has not been formally analyzed (Happel et al. 2015b, 2015a; Foley et al. 2017; Turschak et al. 2019). As a result, data for all other prey taxa were subset to include only records from the focal study area in northeastern Lake Michigan (Fig. 4.1). Sample preparation and isotope analyses used in previous stable isotope studies are like those described herein, and specific details can be found in Ch. 2.

Data Processing and Analysis

Because lipids are ^{13}C depleted, bulk δ^{13}C was normalized for lipid content using mass C:N ratios (Pinnegar and Polunin 1999; Post et al. 2007; Newsome et al. 2014). δ^{13}C values presented hereafter reflect lipid-normalized values. Post et al. (2007) lipid normalization equations were used for cisco, bloater, deepwater sculpin, and invertebrate species because Lake Michigan species-specific lipid normalization equations were not available. For all other taxa included in this study, species-specific normalization equations and coefficients developed and described in Appendix B of Turschak et al. (2014) and Turschak (2013) were applied. Normalization coefficients were updated for many Lake Michigan fishes by Kornis et al. (2020) and these updated coefficients were used in normalizations of all non-cisco fish taxa.

To address the first study objective, the “isotopic niche” or the position of cisco in $\delta^{13}C$ and $\delta^{15}N$ biplots were quantified by fitting Bayesian ellipses to the data (Swanson et al. 2015; Kornis et al. 2020). Isotopic niche of Lake Michigan cisco, salmonines, and prey fishes were quantified by fitting 95% Bayesian ellipses to $\delta^{13}C$ and $\delta^{15}N$ biplot data. Isotopic niche, as measured by Bayesian ellipses, indicate the region of the $\delta^{13}C$ and $\delta^{15}N$ biplot space where a randomly selected individual has a 95% probability of occurring (Swanson et al. 2015). Because stable isotope composition of consumers varies with environmental resource use (e.g. prey sources or prey size), position of a consumer along various isotopic axes is somewhat analogous to the multidimensional ecological niche of that consumer (Layman et al. 2007; Newsome et al. 2007; Jackson et al. 2011; Swanson et al. 2015). Theoretically, larger isotopic niche areas represent broader resource usage whereas small niche areas indicate limited resource usage (Layman et al. 2007; Jackson et al. 2011). Likewise, broader isotopic niche overlap among species may indicate greater interspecific resource overlap whereas separation among isotopic niches indicates reliance on isotopically distinct resources. To quantify species-specific isotopic niche area, Bayesian Standard Ellipse Area (SEA_B) was calculated using the SIBER package in R (Jackson et al. 2011). In addition, pairwise isotopic niche overlaps between cisco and common predator and prey fishes were used to help quantify trophic similarities. Niche overlap between cisco and other Lake Michigan fishes were quantified using the nicheROVER (Swanson et al. 2015) package in R version 4.0.2 (The R Foundation for Statistical Computing).

To address the second study objective, Bayesian isotopic mixing models were used to estimate the time-integrated diet proportions of expected diet sources. Bayesian mixing models offer a distinct advantage over simple linear mixing models through incorporation of uncertainty in mathematically undetermined systems (Prey Sources > Isotopic Tracers + 1; Parnell et al.

2010) as well as through incorporation of prior diet data (Stock et al. 2018). Mixing models were performed in R version 4.0.2 using the MixSIAR package (Stock and Semmens, 2016). However, MixSIAR models were modified from the standard rjags package to operate using the runjags package in R which facilitated parallel processing (i.e., 4 cores) and extension of MCMC (Markov chain Monte Carlo) chain length without having to restart model runs. These modified MixSIAR models were structured with consumer total length as a continuous covariate and uninformative prior Dirichlet distributions for diet proportions. $\delta^{13}C$ and $\delta^{15}N$ trophic discrimination factors (TDF; mean ± SD) of 0.4 ± 1.3 and 3.4 ± 1.0, respectively, were provided as model inputs (Post 2002). Models were run with 4 parallel MCMC chains of length 50,000. Burn-in length was 20,000 and chains were thinned by 10. Model convergence was evaluated visually using trace plots and quantitatively using the Gelman-Rubin Diagnostic. If the Gelman-Rubin Diagnostic exceed 1.05 for more than 5% of parameter estimates, the model was extended by an additional 50,000 iterations with the same burn-in length and thinning. The model was revaluated using the Gelman-Rubin Diagnostic and iteratively extended as described above until this diagnostic indicated fewer than 5% of parameter estimates exceeded 1.05 and trace plots appeared well mixed.

If Bayesian isotopic mixing models produced bimodal posterior diet proportions for two or more isotopically similar prey resources and failed to reach convergence criteria, prey sources were combined *a priori* and the model was rerun (Phillips and Gregg 2003; Ward et al. 2011). Combining isotopically similar prey sources was done using a resampling approach. A random normal distribution of 1000 samples with the same mean and standard deviation $\delta^{13}C$ and $\delta^{15}N$ as each prey source was generated. $\delta^{13}C$ and $\delta^{15}N$ distributions from each prey source were then combined. From the combined distributions, $\delta^{13}C$ and $\delta^{15}N$ means and standard deviations were recalculated such that each prey source was equally weighted.

Important prey sources included in diet mixing models were derived from 2014-2019 observed annual lake-wide cisco diet proportions. The most important prey sources by mass in observed diets and subsequent sources for diet mixing models, were round goby, *Bythotrephes*, alewives, and dipteran chironomids (Breaker et al. 2020). Prey sources that made up less than 1% by mass were not included as potential sources in mixing models (Breaker et al. 2020). Only alewives and round goby <100 mm were observed in cisco diets due to apparent cisco gape limitation (Breaker et al. 2020). Because alewives and round goby are known to have ontogenetic diet shifts and corresponding shifts in isotopic signatures, prey source $\delta^{13}C$ and $\delta^{15}N$ data were reduced to include only those individuals less than 100 mm (Turschak and Bootsma 2015; Mumby et al. 2017). *Bythotrephes* were not sampled for this study and published values from Lake Michigan were used instead (Driscoll et al. 2015). Prey sources were normalized to account for trophic discrimination using the same methods applied in the MixSIAR package where TDF normalized source means, and standard deviations are calculated as $\mu_{source} + \mu_{TDF}$ and $\sqrt{\sigma_{source}^2 + \sigma_{TDF}^2}$, respectively, for both $\delta^{13}C$ and $\delta^{15}N$. TDF normalized prey sources were plotted to ensure that cisco consumers generally occupied the geometric region bounding TDF normalized prey sources (i.e. isotopic mixing space). This also facilitated easier visualization of cisco isotopic resource reliance such that TDF normalized sources nearer to cisco consumers are likely more important in their diets.

Results

Cisco Isotopic Niche Area and Overlap

Cisco occupied an area of the $\delta^{13}C$ and $\delta^{15}N$ biplot similar to most Lake Michigan salmonines (Fig. 4.2). Pairwise isotopic niche overlap indicated high probability that a randomly selected cisco would occur in the isotopic niche space of brown trout and Pacific salmonines and lower relative probability of occurring in the niche space of lake trout (Fig. 4.2). Cisco had a 96% median probability (95% CI: 95-99%) of occurring within the niche space occupied by brown trout (Fig. 4.3). Because brown trout occupied a larger isotopic niche area (measured as SEA_B) than cisco, the median probability of brown trout occurring in the niche space of a cisco was somewhat lower at only 82% (95% CI: 74-89%; Fig. 4.2; Appendix B.1). Cisco occupied an isotopic niche space very similar to that of Chinook salmon with a 90% median probability (95% CI: 85-94%) of occurring within the Chinook salmon niche space (Fig. 4.3). Conversely, the smaller niche area of Chinook salmon corresponded to an even greater directional probability (Med: 96%; 95% CI: 62-98%) of occurrence inside cisco's isotopic niche space (Fig. 4.2; Appendix B.1). Cisco had an 85% probability (95% CI: 77%-91%) of occurring in the niche space of Steelhead (Fig. 4.3). Like Chinook salmon, steelhead also occupied a very similar, albeit smaller, isotopic niche area than cisco which corresponded to an increased median probability (Med: 93%; 95% CI: 87-96%) of occurrence inside cisco's niche space (Fig. 4.2; Appendix B.1). Among brown trout and Pacific salmonines, cisco had the lowest median probability (Med: 76%; 95% CI: 68-83%) of occurring in the niche space occupied by coho salmon (Fig. 4.3). Coho salmon occupied the smallest niche area which was largely contained within the isotopic niche space occupied cisco (Fig. 4.2; Appendix B.1). As a result, coho salmon had a greater median probability of occurring within cisco's isotopic niche space (Med: 91%;

95% CI: 84-96%; Appendix B.1). Unlike brown trout and Pacific salmonines, cisco had only a 41% (95% CI: 32-52%) median probability of occurring in the niche space occupied by lake trout which were enriched with respect to $\delta^{15}N$ relative to cisco and other salmonines (Fig. 4.2; Fig. 4.3). Lake trout occupied a somewhat larger niche area than cisco and median directional probability of lake trout occurring in the niche space of cisco was correspondingly lower (Med: 28%; 95% CI: 20-38%; Fig. 4.2; Appendix B.1).

Cisco also had a lower probability of occurring in the niche space occupied by Lake Michigan prey fishes than Pacific salmonines (*Oncorhynchus spp.*) and brown trout (Fig 4.2 and Fig. 4.4). Among pairwise prey fish comparisons, cisco had the highest median probability (Med: 72%, 95% CI: 32-95%) of occurring in the niche space occupied by round goby (Fig. 4.5). In contrast, round goby had a much larger niche area and correspondingly lower probability (Med:15%, 95% CI: 7-25%) of occupying the same niche space as cisco (Fig. 4.4; Appendix B.2). Relative to round goby, cisco had a somewhat lower probability of occurring in the same niche space as other prey fishes including rainbow smelt (Med: 57%, 95% CI: 27-82%), deepwater sculpin (Med: 49%; 95% CI: 33-68), slimy sculpin (Med: 49%; 95% CI: 32-68), and large alewives (Med: 42%; 95% CI: 25-61; Fig. 4.5). Rainbow smelt occupied a larger niche area than cisco and had a lower median directional probability of occurring in the isotopic niche space of cisco (Med: 25%, 95% CI: 13-40%; Fig. 5.4; Appendix B.2). Deepwater sculpin also occupied a slightly larger niche area than cisco but had a higher median directional probability (Med: 56, 95% CI: 41-70%) of occurring in the niche space of cisco (Fig. 4.4; Appendix B.2). Large alewives had an isotopic niche area very similar to that of cisco and slightly lower median directional probability of occurring in the same niche space (Med: 29%, 95% CI: 19-41%; Fig. 4.4; Appendix 2). Among prey fishes, slimy sculpin had smallest isotopic niche area and highest median directional probability of occurring in the niche space of cisco (Med: 62%, 95% CI: 42-79%; Fig. 4.4; Appendix B.2). Cisco had very low probability of occurring in the same niche space as bloater (Med: 17%, 95% CI: 9-30%) and small alewives (Med: 0%, 95% CI: 0-4%; Fig. 4.5). Both bloater and small alewives had a slightly smaller isotopic niche area than cisco and correspondingly higher directional probability of occurring in the same niche space (Med: 33%, 95% CI: 18-51% and Med: 1%, 95% CI: 0-12%, respectively; Fig. 4.4; Appendix B.2).

Isotope Diet Mixing Models

TDF normalized prey sources used in cisco diet mixing models occupied several distinct regions of the $\delta^{13}C$ and $\delta^{15}N$ biplot (Fig. 4.6). Small alewives (<100 mm) and *Bythotrephes* possessed low $\delta^{13}C$ and intermediate $\delta^{15}N$ relative to other prey sources (Fig. 4.6). Although mean $\delta^{15}N$ and $\delta^{13}C$ was lower for *Bythotrephes*, isotopic distributions for small alewives and *Bythotrephes* overlapped substantially (Fig. 4.6). Mean differences in $\delta^{13}C$ and $\delta^{15}N$ for these two species were 0.29‰ (SD: ± 2.18‰) and 1.77‰ (SD: ±2.55‰), respectively. The mixing model relying on small alewives and *Bythotrephes* as separate sources produced bimodal posterior diet proportions and failed to reach convergence criteria. Due to their relatively high isotopic overlap, small alewife and *Bythotrephes* prey sources were pooled together as a combined source for subsequent isotopic mixing models. Benthic invertebrates were the most isotopically distinct prey source resulting from their relatively high $\delta^{13}C$ and low $\delta^{15}N$ values (Fig. 4.6). Finally, small round goby (<100 mm) had an intermediate $\delta^{13}C$ and the highest $\delta^{15}N$ among potential prey sources (Fig. 4.6). Cisco were isotopically most similar to small alewives, followed by *Bythotrephes*, round goby, and benthic invertebrates after TDF adjustment of prey $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 4.6).

Isotopic mixing models used to describe time-integrated cisco diets suggested strong reliance on small alewife and/or *Bythotrephes* prey followed by lower reliance on round goby prey, and very low reliance on benthic invertebrates (Fig. 4.7). Diets proportions changed ontogenetically with increased reliance on round goby and decreased reliance on small alewives and *Bythotrephes* as total length increased (Fig. 4.7). Ontogenetic diets shifts from small alewife and *Bythotrephes* to small round goby corresponded to elevated $\delta^{15}N$ among larger cisco (Fig. 4.6) Mean diet proportions of small alewives and/or *Bythotrephes* was 74% (95% CI: 66-82%), 63% (95% CI: 56-70%), and 56% (95% CI: 46-65%) for minimum (25.0 cm), median (44.5 cm), and maximum (56.1 cm) cisco total lengths, respectively. Mean diet proportion of round goby was 25% (95% CI: 18-34%), 36% (95% CI: 30-43%), and 44% (95% CI: 34-54%) for minimum, median, and maximum cisco total lengths, respectively. Mean diet proportion of benthic invertebrates were consistently <1% (95% CI: 0-3%) across the range of cisco total lengths.

Discussion

Measurements of $\delta^{13}C$ and $\delta^{15}N$ seem to indicate that Lake Michigan cisco occupy the trophic role of a pelagic piscivore as evidenced by their isotopic similarity to salmonines. By comparing cisco isotopic niche position to that of know pelagic piscivores and common prey fish species, it is apparent that cisco have the highest probability of occupying the same niche space as Pacific salmonines and brown trout, relying on similar prey resources as these other piscivores. By overlaying TDF normalized prey sources onto isotopic niches of cisco, Pacific salmonines, and brown trout, it is evident that each of these five species exhibits a high degree of overlap with small alewife prey suggesting that this may be a shared prey source within the piscivore community. Indeed, studies using observed diet, stable isotopes, and fatty acids have demonstrated ubiquitous preference for alewife prey among Lake Michigan salmonines (Happel et al. 2020; Leonhardt et al. 2020; Ch. 2). Similar to salmonines, cisco diet mixing models also estimate high reliance on alewife or isotopically similar pelagic prey such as *Bythotrephes* especially at small to mid-range total lengths from 25-44.5 cm observed in this study.

Small alewives and *Bythotrephes* were the only pelagic prey sources considered in diet mixing models used in this study. Diet studies of cisco in the Laurentian Great Lakes or inland lakes with invertebrate communities containing similar invertebrate assemblages indicate strong reliance on zooplankton and macroinvertebrates including calanoid and cyclopoid copepods, cladocerans, and *Mysis* (Stockwell et al. 2010; Anderson et al. 2011; Gamble et al. 2011b, 2011a; Ahrenstorff et al. 2013; Keeler et al. 2015; Eshenroder et al. 2016; Ridgway et al. 2020). Some of these invertebrate taxa including *Mysis*, and the calanoid *Limnocalanus macrurus*, are known to be ^{15}N enriched due to trophic omnivory and/or bacterial ^{15}N enrichment of algal energy sources during the settling process (Altabet 1988; Ostrom et al. 1998; Altabet et al. 1999; Vander Zanden et al. 1999; Sierszen et al. 2006; Driscoll et al. 2015). If cisco were to derive substantial energy from these ^{15}N enriched pelagic invertebrate prey sources, their δ^{15}N would be relatively high and their trophic role herein may be falsely interpreted as a pelagic piscivores. For instance, forage fishes with strong dietary reliance on *Mysis* and *Limnocalanus,* such as deepwater and slimy sculpin have δ^{15}N values which may be greater than Pacific salmonines predators in Lake Michigan (Turschak and Bootsma 2015). Nevertheless, it seems extremely unlikely that *Mysis* or *Limnocalanus* comprise a large proportion of Lake Michigan cisco diets as evidenced by their low isotopic niche overlap with pelagic and profundal prey fish species relative to salmonines. Furthermore, analyses of observed diets in Lake Michigan cisco found very low contributions of these prey items (<1% by count and by mass) in 725 diets spanning dates from April 1-Dec 30 and across similar collection locations used in this study (Breaker et al. 2020). Therefore, it seems most likely that pelagic prey used by Lake Michigan cisco are small alewives and/or *Bythotrephes*.

Though reliance on pelagic prey sources by cisco is evident from isotopic data collected in this study, discerning the specific diet proportions of isotopically similar pelagic prey remains difficult. Predatory *Bythotrephes* shared substantial isotopic overlap with small alewives in Lake Michigan likely due to both species' shared reliance on pelagic zooplankton prey sources (Schulz and Yurista 1998; Pangle and Peacor 2009; Bunnell et al. 2011, 2015; Vanderploeg et al. 2012). As a result of isotopic overlap, mixing models were unable to accurately apportion cisco diet mixtures to these two prey sources resulting in failure to meet model convergence criteria. Combining small alewife and *Bythotrephes* into a single pelagic prey source *a priori* resulted in model convergence and greatly improved diagnostics but precluded resolving specific diet proportions for these sources. However, considering the relatively better alignment of TDF normalized small alewife prey (and known alewife predators) with cisco in the stable isotope biplot, it seems more probable that a greater proportion of cisco diets are derived from small alewives than *Bythotrephes*. Likewise the relatively lower isotopic niche overlap of cisco with pelagic prey fishes such as alewives and rainbow smelt that prey upon *Bythotrephes* offers further evidence that small alewives are of greater importance in cisco diets (Bunnell et al. 2015).

Stable isotope results corroborate the potential importance of piscivory (i.e. small alewives and round gobies) for Lake Michigan cisco, but the higher relative importance of pelagic prey sources was somewhat inconsistent with observed diet studies (Breaker et al. 2020). Observed diet study results indicated approximately 29% by mass of diets pooled across season and location were derived from small alewife (14%) and *Bythotrephes* (15%). Conversely, round gobies were nearly double the importance of pelagic prey items and made up 57% of observed diets by mass. Because the size range of cisco collected for this study included a higher proportion of small fish (<40 cm) than the observed diet study, mixing model diet proportions for only fish ≥40 cm were estimated to ensure ontogenetic diet comparability between studies. Using only this subset of larger fish, estimates of mean diet proportion were 61% (95% CI: 51-69%) for small alewife/*Bythotrephes*, and 39% (95% CI: 31-48%) for round goby with negligible (0%) contributions from benthic invertebrates including chironomid dipterans. These results are nearly opposite the pattern present in observed diets with respect to benthic-pelagic energy reliance.

One possible explanation for discrepancies between observed diet proportions and stable isotope mixing models may have resulted from misspecification of source isotopic composition or TDFs. Due to the opportunistic nature of sampling, simultaneous collections of cisco and prey sources rarely occurred. Therefore, the isotopic signature of prey source populations included in isotopic mixing models may not have been representative of the prey populations consumed by cisco. Likewise, TDFs were derived from published values and were not measured directly for each prey source. Studies have found considerable variation in TDFs between sources and consumers which may result in erroneous estimates of diet proportions (Caut et al. 2009). The additive effect of poorly specified prey isotopic signatures and/or TDFs should be a misalignment of TDF normalized prey sources from cisco in the $\delta^{13}C$ and $\delta^{15}N$ biplot and subsequent misassignment of cisco diet proportions. This explanation seems very improbable considering the close alignment salmonines and known alewife prey apparent in our study results (Happel et al. 2020; Leonhardt et al. 2020). TDF normalized small alewife align directly over the niche space of all Pacific salmonines and brown trout and meet *a priori* expectations given known salmonine preference for alewife prey (Jacobs et al. 2013; Happel et al. 2020; Leonhardt et al. 2020). Likewise, round gobies serve as an important alternate prey for salmonines, especially brown trout and lake trout, and the range of TDF normalized round goby values also exhibit considerable overlap with those of known predator species (Happel et al. 2018, 2020; Luo et al. 2019; Leonhardt et al. 2020).

Alternatively, discrepancies between observed diet proportions and stable isotope mixing models may be associated with differential integration times. Isotopic analyses of dorsal muscle tissue likely reflect diet consumed over months or longer depending on catabolic turnover, growth, and fish size (Weidel et al. 2011; Vander Zanden et al. 2015). Conversely, while providing much greater taxonomic resolution, observed diets represent feeding over hours to days which makes them relatively more subject to collection biases associated with time of day, season, or sampling location (Hyslop 1980; Pinnegar and Polunin 1999; Baker et al. 2014; Futia et al. 2021). Contemporary cisco diet analyses on Lake Michigan have relied largely on fish collected from bottom set gillnets (≈80% of diets) particularly during the spring and fall (≈93% of diets) during isothermal or weakly stratified conditions (Apr-Jun and Oct-Dec) (Breaker et al. 2020). Under these conditions, cisco are likely to exhibit thermal habitat overlaps with round goby. Additionally, bottom set gillnets may select for benthically oriented individuals which may be feeding on round goby while missing pelagically oriented conspecifics. Preliminary depth and temperature data, gathered from internal acoustic transmitting tags in Lake Michigan cisco from 2019-2020, indicate a substantial increase in median depth occupancy from June to July with thermal occupancy temperatures occurring at 8-15°C in July (D. Hondorp, unpublished data). Increasing depth and observed temperature occupancy range from June through July, likely corresponds to the onset and strengthening of thermal stratification and orientation to the metalimnion. In extant Lake Superior and historic Lake Michigan populations, cisco also typically occupy thermal zones at or below the metalimnion during the stratified period (Smith 1956; Stockwell et al. 2010). Conversely, thermal preferences of round goby (≈22ºC) are much greater than observed for cisco with normal summer distributions in warm, shallow nearshore areas (Johnson et al. 2005; Kornis et al. 2012; Carlson et al. 2021). As a result, it is unlikely that these two species would exhibit substantial thermal habitat overlap during this stratified period. Furthermore, growth and catabolic turnover of cisco should be greatest during relatively warmer stratified conditions and likely correspond to increased consumptive demand at this time (Pauly 1990; Weidel et al. 2011; Vander Zanden et al. 2015). Therefore, diets during stratified conditions likely represent a larger fraction of annual prey consumption. Given the relative paucity of observed diets collected during strongly stratified conditions (Jul-Sep), it is plausible that contribution of pelagic prey, required to meet energetic demands, are underrepresented in existing diet studies. Likewise, the proportional contributions of round goby may then be overestimated in cisco observed diets.

Stable isotope results presented herein reflect Lake Michigan cisco diets and apparent trophic role given ecological conditions and prey availability at the time of collection (2017-2020). Therefore, it is possible that continued ecological changes to the Lake Michigan food web, particularly reductions in pelagic energy pathways, will result in corresponding changes in cisco's apparent trophic role. For instance, even a community of diverse trophic specialists (e.g. African cichlids) may consume a single energetically preferred prey resource if it becomes sufficiently abundant (Liem 1980; Robinson and Wilson 1998; Golcher-Benavides and Wagner 2019). Use of a hyperabundant or highly preferred prey resource may suggest high trophic similarity but does not reflect the ability of a community to partition available alternate resource subsidies when preferred or hyperabundant prey are absent (Robinson and Wilson 1998). In Lake Michigan, population estimates of small (i.e. yearling) alewife abundance (at Jan 1), derived from statistical catch at age modelling, indicates an increasing trend in yearling recruitment from 2015-2019 (Appendix B.3). High dietary reliance on small alewives by cisco over the study period may reflect higher relative abundance of this prey source. Similarly diets of Lake Michigan salmonine predators also remain largely comprised of alewives and offer further evidence of sustained availability and recruitment of this preferred prey resource over the study period (Leonhardt et al. 2020; B. Roth unpblished data). Nevertheless, alewife recruitment in Lake Michigan since the early 2000s has been somewhat unstable whereas round goby, *Bythotrephes*, and chironomid dipterans may serve as relatively more consistent seasonal energy subsidies when alewife recruitment is low (Madenjian et al. 2005; Höök et al. 2007; Collingsworth et al. 2014). Indeed, dietary plasticity of cisco observed in Lake Michigan and across their range distribution highlights the ability of this group to utilize diverse prey types (Breaker et al. 2020; Ridgway et al. 2020). Therefore, the isotopic niche overlap of cisco with Lake Michigan salmonines may correspond to only a narrow range of resource availability and does not account for the apparent trophic flexibility of this species across a broader range of resources. Rather, these study results reflect one potential extreme of cisco trophic niche.

Whether alewives constitute a large proportion of Lake Michigan cisco diets should be of particular interest to ongoing Lake Michigan fisheries management. Restoration of cisco and other coregonines has emphasized restoring ecological function, particularly through habitat coupling (i.e. benthic-pelagic and littoral-profundal), following the declines of historic populations (Bronte et al. 2017). With respect to cisco, however, the extant population appears to now occupy an isotopic niche very similar to the salmonine community in Lake Michigan and may provide similar ecological function as this existing community. Results of this study are somewhat equivocal in discerning reliance on small alewives and only reflect trophic niche over a narrow range of resource availability. However, if isotopic niche overlap with salmonines is the result of a shared alewife prey resource, interests in restoring ecological function via cisco restoration may be somewhat misguided and at odds with other Lake Michigan fish community objectives (Eshenroder et al. 1995). For instance, management aimed at maintaining a diverse salmonine community supported by pelagic prey fish may become more challenging if the preferred pelagic prey fish, alewives, are increasingly preyed upon by an expanding cisco population (Eshenroder et al. 1995). Alternately, fisheries supported by multiple energy pathways may be needed following oligotrophication of Lake Michigan's offshore waters and subsequent declines in many pelagic and profundal invertebrates and prey fishes (Evans et al. 2011; Bronte et al. 2017; Ives et al. 2018). The dietary plasticity of cisco, including reliance on multiple energy pathways (e.g. pelagic and benthic) and novel invasive species such as round goby and *Bythotrephes*, may subsidize cisco diets and help maintain population stability despite declining or fluctuating pelagic alewife abundance (Vander Zanden and Vadeboncouer 2002; Rooney et al. 2006; Rooney and McCann 2011). Results of this study suggest that periodic spatiotemporal surveillance of cisco diets and evaluation of their trophic role in the novel and changing Lake Michigan food web may be necessary to monitor and predict responses to continued ecosystem changes and potential management activities.

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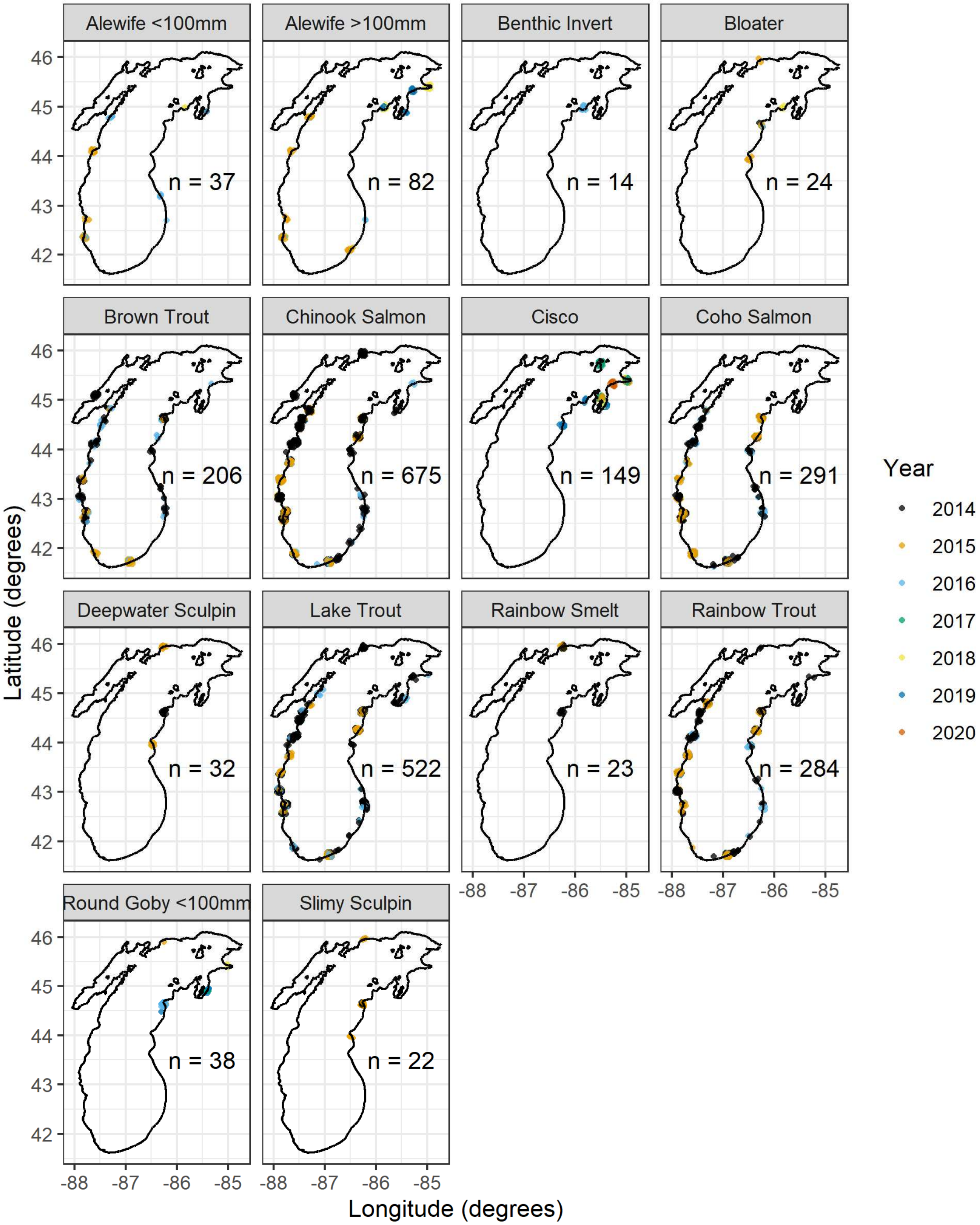

Figure 4.1. Maps of Lake Michigan depicting the spatial distribution of $\delta^{13}C$ and $\delta^{15}N$ samples used for analyses. Panels depict species-specific spatial sampling distributions and colors indicate the year that samples were collected. Species-specific samples sizes are included as text in each panel.

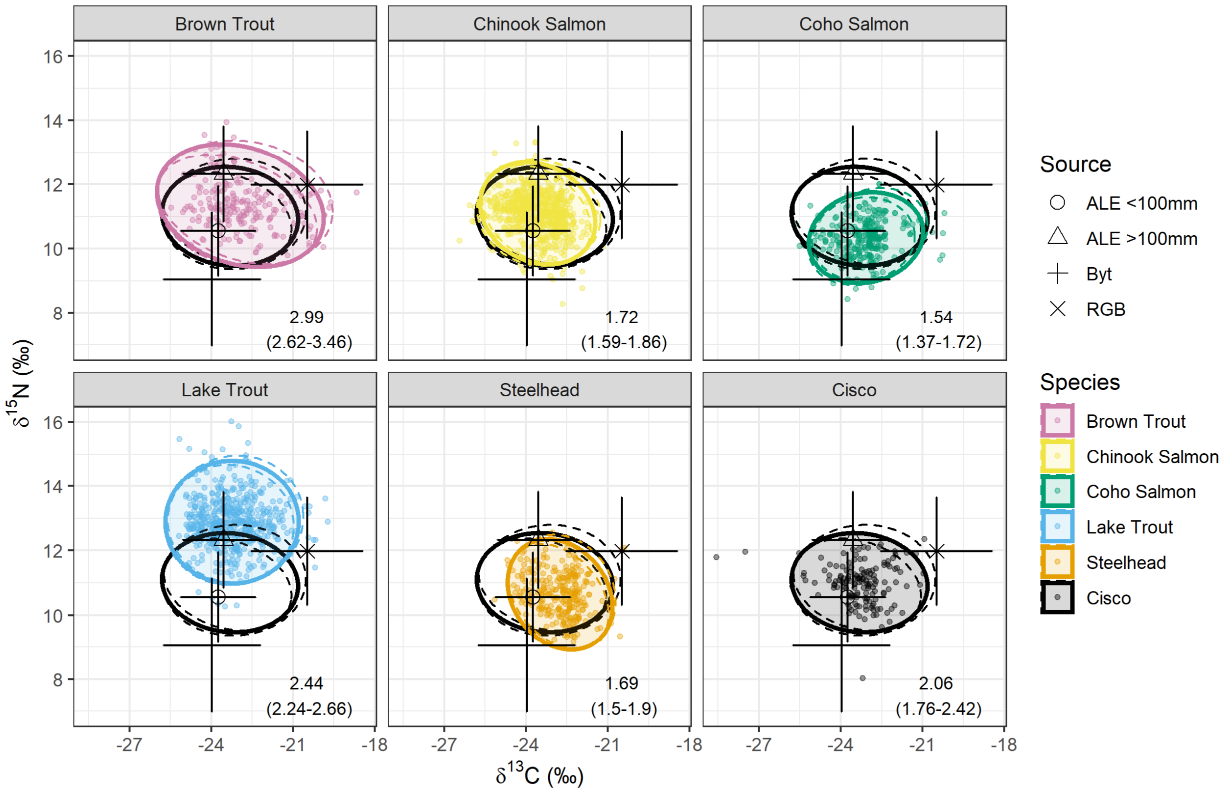

Figure 4.2. Colored and black ellipses indicate the median 95% δ^{13}C and δ^{15}N isotopic niche for Lake Michigan salmonines and cisco, respectively, from 2014-2020. Dashed lines indicate the upper and lower 95% credible intervals around the shaded median ellipse and the text indicates SEA$_B$ median ellipse area (95% credible interval). Colored points depict individuals from a given salmonine species and black points with cross bars represent TDF normalized prey position and standard deviation (δ^{13}C: +0.8 ± 1.3; δ^{15}N: +3.4 ± 1.0).

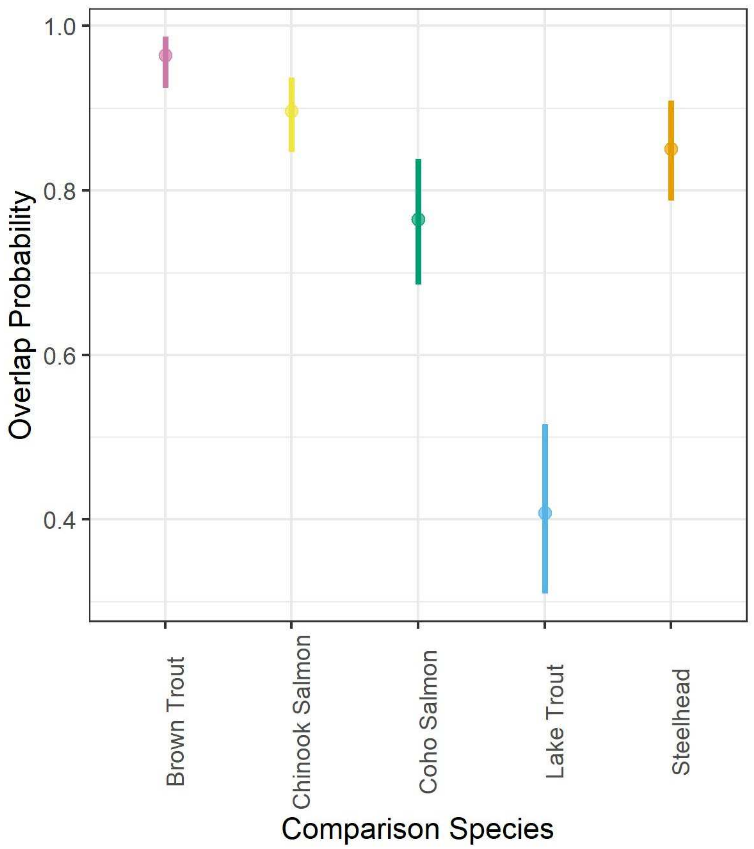

Figure 4.3. Median (95% credible interval) probability that a cisco will occur in the ^{13}C and δ^{15}N isotopic niche space of common Lake Michigan salmonine species.

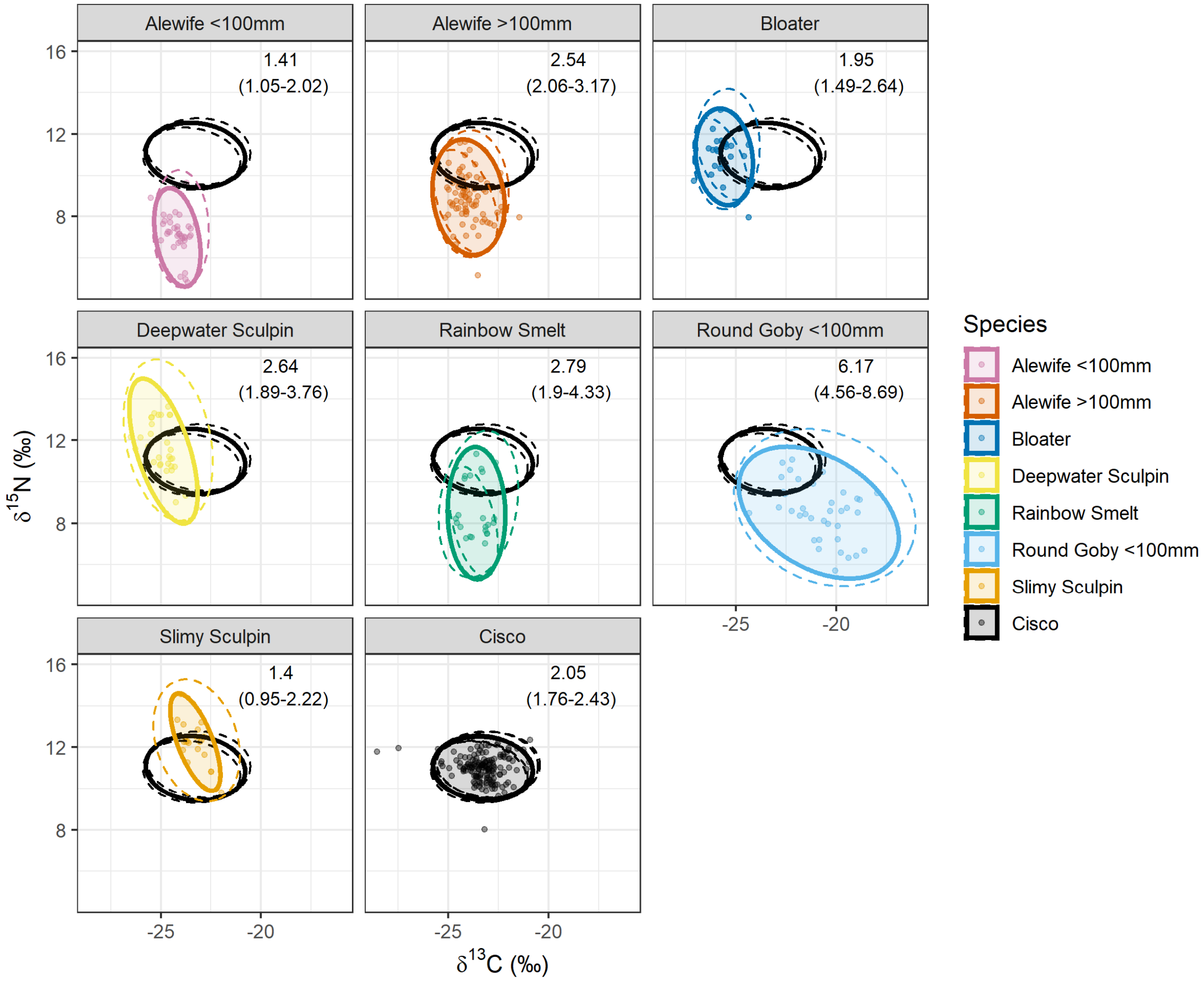

Figure 4.4. Colored and black ellipses indicate the median 95% $\delta^{13}C$ and $\delta^{15}N$ isotopic niche for Lake Michigan prey fishes and cisco, respectively, from 2014-2020. Dashed lines indicate the upper and lower 95% credible intervals around the shaded median ellipse and the text indicates SEA_B median ellipse area (95% credible interval). Colored points depict individuals from a given prey fish species.

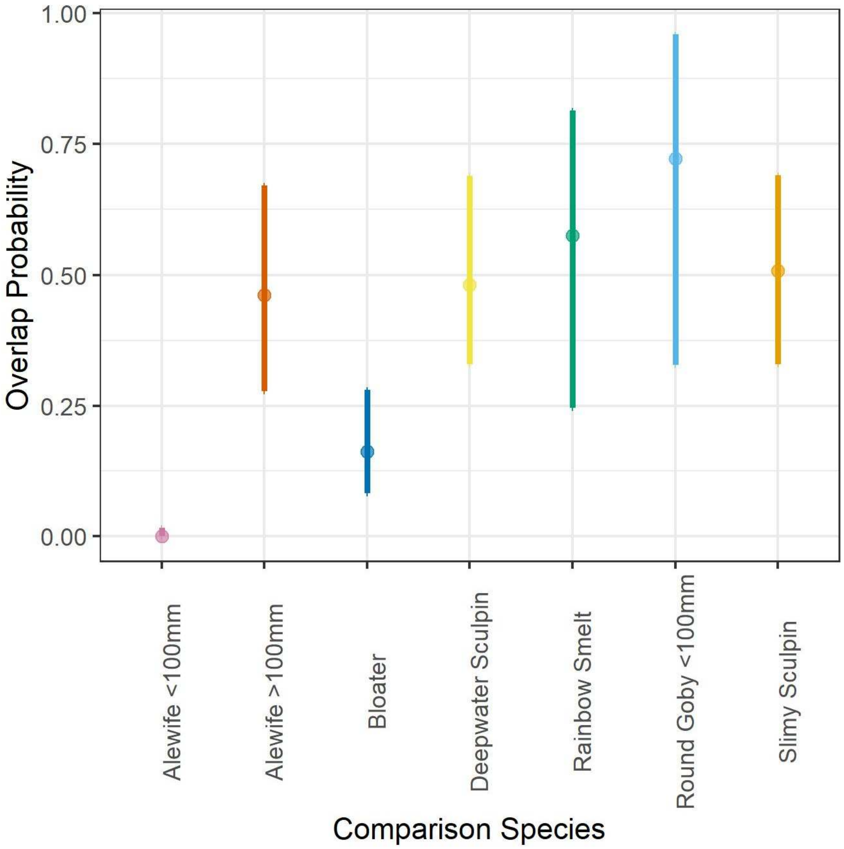

Figure 4.5. Median (95% credible interval) probability that a cisco will occur in the ^{13}C and δ^{15}N isotopic niche space of common Lake Michigan prey fish species.

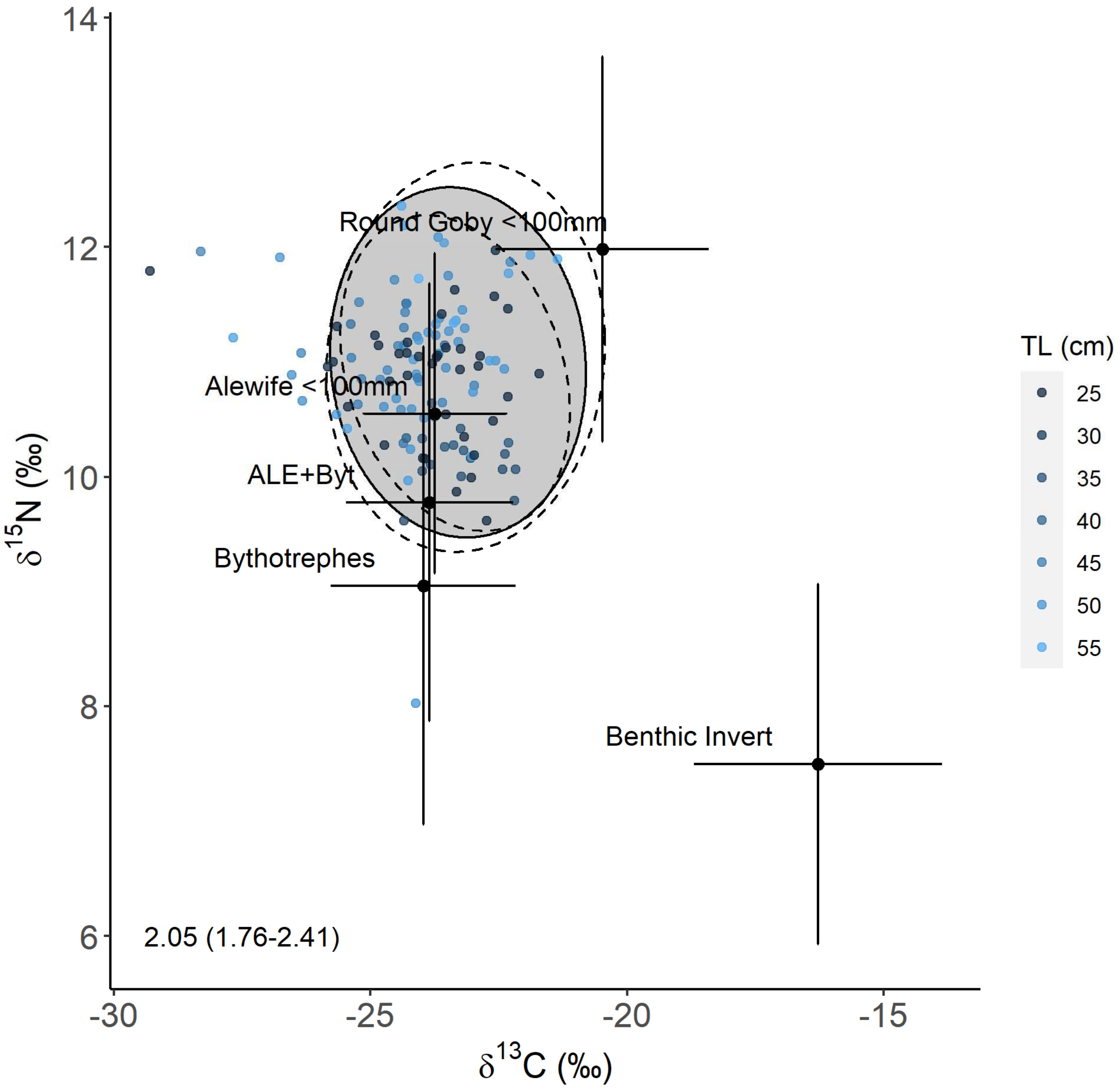

Figure 4.6. Shaded ellipse indicates the median 95% $\delta^{13}C$ and $\delta^{15}N$ isotopic niche for Lake Michigan cisco and dashed lines indicate the upper and lower 95% credible intervals around the shaded median ellipse. Blue shaded points represent individual cisco with darker points indicating shorter total length individuals and brighter points indicating longer total length individuals. Black points with cross bars represent TDF normalized prey position and standard deviation ($\delta^{13}C$: +0.8 ± 1.3; $\delta^{15}N$: +3.4 ± 1.0) for common cisco prey sources derived from Breaker et al. (2020) as well as pooled Alewife <100mm and *Bythotrephes*, (ALE+Byt).

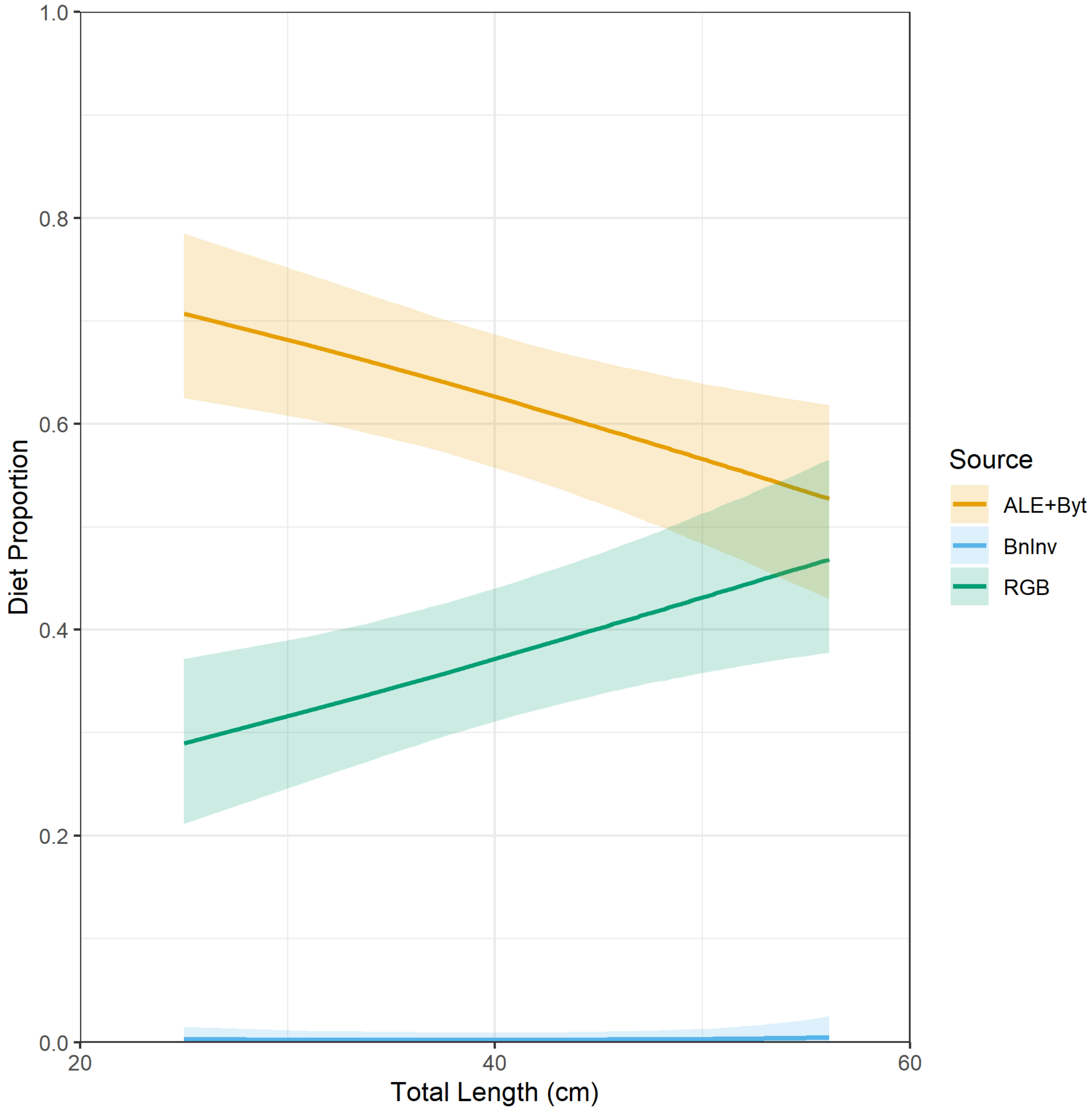

Figure 4.7. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for Lake Michigan cisco. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Colors correspond to specific prey sources (ALE+Byt, pooled Alewife <100mm and *Bythotrephes*; BnInv, soft-bodied benthic invertebrates; RGB, Round Goby <100 mm).

Chapter 5. Summary and Conclusions

Describing the resource reliance and trophic position of Lake Michigan fishes in the context of natural environmental gradients has been a unifying theme throughout the preceding chapters. Oligotrophication of the offshore waters of Lake Michigan (and other Laurentian Great Lakes) has corresponded to reductions in major pelagic resources including most invertebrate and prey fish taxa (Evans et al. 2011; Bunnell et al. 2014). Meanwhile, sequestration of pelagic nutrients and energy in the nearshore benthos has stimulated regional primary and secondary production (Hecky et al. 2004; Janssen et al. 2005; Auer et al. 2010). This redistribution of energy through the food web can be expected to differentially affect the trophic position of fishes corresponding to species-specific abilities to cope with reduced pelagic energy and/or use nearshore benthic resources (Madenjian et al. 2015; Ives et al. 2018). However, most studies characterizing the trophic ecology of Great Lakes fishes are necessarily limited in spatial and temporal scope and therefore only reflect patterns in prey resource use corresponding to a narrow range of resource availabilities. Understanding and predicting the adaptive capacity of Lake Michigan's food web to ongoing ecological changes requires improved understanding of species-specific trophic position relative to resource gradients. Natural variation in resource gradients (e.g. benthic primary and secondary production or pelagic prey fish production) were identified over the spatial and temporal scope of the preceding chapters and provided an opportunity to examine fish trophic positions in the context of those gradients.

Benthic primary and secondary production has generally increased in the nearshore waters of Lake Michigan but the relative importance of this energetic pathway to the nearshore fish community is variable among locations and species (Hecky et al. 2004; Auer et al. 2010; Brooks et al. 2015; Happel et al. 2015b, 2015a; Foley et al. 2017). Spatial variation in reliance on nearshore benthic energy pathways among nearshore fishes likely corresponds to variation in the relative importance of this pathway (Ch. 2). This is in turn mediated by physical conditions of the nearshore region at any given location. For instance, at locations where water clarity and subsequent nearshore benthic primary and secondary production is relatively high, some nearshore fishes correspondingly increase reliance on benthic prey. Conversely, where water clarity is lower and benthic production is inhibited, the relative importance of pelagic production is greater, and some nearshore fishes respond with increased reliance on pelagic prey sources. However, the trophic response of fish species to nearshore productivity gradients is not ubiquitous. At one extreme, alewives (*Alosa pseudoharengus*) exhibit strong reliance on pelagic energy resources regardless of the relative importance of this energetic pathway. At the opposite extreme, round goby (*Neogobius melanostomus*) are apparently able to switch from pelagic to benthic energy reliance by making a diet shift from dreissenid mussels to soft-bodied benthic invertebrates, respectively.

Temporal variation in pelagic prey fish production seems to be a more important driver of the relative importance of alternate energetic pathways for the Lake Michigan salmonine community (Ch. 3). Because salmonines are able to make broad scale spatial movements over relatively short time periods, regional variation in the relative importance of nearshore versus offshore production is less important than lakewide interannual variation in alewife abundance and size structure (Adlerstein et al., 2008, 2007a, 2007b; Bronte et al., 2007; Clark et al., 2017; Haynes et al., 1986; Schmalz et al., 2002; and Michigan Department of Natural Resources unpublished data). Pelagic alewives remain the preferred prey of salmonines (Jacobs et al. 2013; Happel et al. 2020; Leonhardt et al. 2020) but, during periods when abundance or preferred size classes are low, salmonines exhibit varying degrees of reliance on alternate energetic pathways

(Ch. 3). Generally, salmonines relied more heavily on alternate energetic pathways (e.g. terrestrial and nearshore benthic) when small alewife abundance was low. However, responses were species-specifics and dependent on abilities to use alternate prey sources and thresholds for prey switching. For instance, low small alewife abundance from 2014 until early 2015 corresponded to greater reliance on alternate nearshore, profundal, or terrestrial prey sources among brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and steelhead (*Oncorhynchus mykiss*). Conversely, Chinook salmon (*Oncorhynchus tshawytscha*) exhibited little capacity to rely on alternate energetic pathways via diet switching. Variation in Chinook salmon diets corresponded to only changes in available alewife sizes.

Unlike nearshore fish and salmonine communities, the spatial and temporal distribution of samples precluded evaluation of cisco (*Coregonus artedi*) resource reliance across broad resource gradients (Ch. 4). Nevertheless, reliance on multiple energetic pathways is readily apparent for Lake Michigan cisco and likely helped facilitate their ongoing population expansion (Claramunt et al. 2019; Breaker et al. 2020). Much like salmonines, cisco are largely reliant on pelagic prey but also derive considerable energy from alternate nearshore benthic pathways (Ch. 4). It seems likely that reliance on round goby should provide a seasonally stable prey subsidy when pelagic alewife or *Bythotrephes longimanus* prey are limited (Kornis et al. 2012; Breaker et al. 2020). In this way, cisco provide a striking example of trophic flexibility for a species undergoing a natural population expansion (i.e. no supplemental stocking). This population level response is in stark contrast to other pelagic fish species, including the congener bloater (*Coregonus hoyi*), which have undergone large declines coincident with cisco expansion (Bunnell et al. 2014, 2020).

Taken together, the preceding chapters quantitatively demonstrate differential reliance on alternate energy pathways by Lake Michigan fishes. Because nearshore benthic primary and secondary production likely varies asynchronously with pelagic production, nearshore fishes capable of reliance on nearshore-benthic energy pathways may experience greater stability in prey resources and potentially greater population and recruitment stability (Rooney et al. 2006; Rooney and McCann 2012; McMeans et al. 2015). For prey fishes, reliance on alternate energy pathways appears to be driven by prey switching and reliance on regionally abundant pelagic or benthic invertebrate prey. Among salmonine and cisco predators, reliance on alternate energy pathways occurs both directly through diet switching and indirectly via prey source diet switching. Steelhead, for instance, derive large proportions of their diets from terrestrial energy pathways through direct predation on terrestrial insects. Conversely, indirect reliance on alternate energy pathways by lake trout, brown trout, and cisco is apparent through predation on round goby which differentially rely more on nearshore benthic energy sources where regional benthic production is higher. Both direct and indirect reliance on alternate energy pathways should help stabilize Lake Michigan fishes because prey population dynamics will be decoupled from one-another (Vander Zanden and Vadeboncouer 2002; Rooney et al. 2006; Rooney and McCann 2012; McMeans et al. 2015). However stronger reliance on a single pelagic energy pathway, as observed with alewives and obligate alewife predators such as Chinook salmon, may result in greater instability of these populations.

Stable C and N isotope analyses served as the basis for time-integrated measures of primary energetic pathway and/or resource reliance described above. Isotopic dissimilarity between pelagic, profundal, and nearshore benthic isotopic baselines facilitated relatively clear delineation of major energetic pathways to Lake Michigan fishes (France 1995; Ostrom et al.

1997; Altabet et al. 1999; Vander Zanden and Vadeboncouer 2002; Sierszen et al. 2006; Turschak and Bootsma 2015). Variation in these isotopic baselines resulted in subsequent variation in isotopic niche areas corresponding to reliance on one or more major energetic pathways (Jackson et al. 2011; Layman et al. 2012; Swanson et al. 2015). Isotopic niche areas of Lake Michigan fishes were then decomposed into specific diet proportions using Bayesian mixing models which quantified variation in energetic pathway and/or resource reliance. Finally, incorporation of covariates and explanatory factors (e.g. total length, water clarity, year, and region) into mixing models were used to help describe variation in resource reliance associated with specific resource gradients (Stock et al. 2018).

Despite their demonstrated utility, the preceding chapters also highlight a need for caution when applying stable isotope analyses to understand resource reliance and trophic position of fishes in large lakes. First, isotopic baselines need to be considered at a spatial scale appropriate to the species of interest (Vander Zanden and Rasmussen 1999; Post 2002; Radabaugh et al. 2013). When evaluating the relative importance of major energetic pathways to fish species, isotopic endmembers (e.g. soft-bodies benthic invertebrates and dreissenid mussels) should be collected over a spatial scale corresponding to the expected regional distribution of the species of interest. For localized nearshore fish populations, isotopic baselines may need to be specific to study locations (Ch. 2). Conversely, highly mobile species such as pelagic alewives, salmonines, and cisco are likely never at isotopic equilibrium with local isotopic baselines and therefore may be better suited to use of broader regional or lakewide baselines (Ch. 3 and Ch. 4). Second, descriptions of the fish trophic position or trophic ecology derived from stable isotopes reflect environmental resource gradients over the spatiotemporal domain of the study. This is demonstrated by shared reliance on alewife prey by salmonines when relative abundance of this preferred prey source is high. However, when alewife abundance is low, resource partitioning becomes more apparent. Thus, resource reliance or trophic position by a species may be difficult to extrapolate outside the range of conditions present during the study. Finally, the accuracy and precision of diet proportions derived from mixing models depends on accurate assignment of prey sources and trophic discrimination factors (TDFs). Inclusion of realistic variance estimates around prey source and TDF means helps to ensure that the range of model estimated diet proportions contains true population means (Semmens et al. 2013; Newsome et al. 2014). Furthermore, inclusion of proper prey sources in mixing models may benefit from careful consideration of observed diets. When possible, use of informative priors derived from observed diets may also improve estimates of diet proportions particularly when mixing models are unable to resolve differences in isotopically similar prey sources (Semmens et al. 2013; Stock et al. 2018).

Continued periodic surveillance of the stable isotope composition of Lake Michigan fishes would help fisheries managers anticipate how species will respond to ongoing ecological changes and corresponding availability of resources. While this work identified several potential resource gradients, expanding existing stable isotope datasets may facilitate direct incorporation of spatiotemporal explanatory variables into isotopic mixing models. Analyses of nearshore benthic versus pelagic resource reliance provided in Ch. 2 offers a simple framework for incorporation of remote sensed spatial data as a predictor of resource reliance using stable isotope mixing models. Conversely, the limited temporal scope and covariance of explanatory variables (e.g. alewife abundance and size structure) in Ch. 3 precluded their direct incorporation into salmonine mixing models. However, continued surveillance of both predator and prey stable isotope data coupled with ongoing estimates of prey abundance and size structure could be used to estimate diet proportions as a function of prey availability. These types of analyses and may then help to parameterize ecological or decision support models used to assess risks associated ecological changes (e.g. species invasions and climate change) or impacts of management actions (e.g. nutrient abatement and predator stocking) (e.g. Kao et al. 2015, 2018). Furthermore differential reliance on multiple energy pathways by the fishes, derived from continued stable isotope analyses, should be informative to understanding adaptive capacity of the Lake Michigan food web to ongoing ecological changes (Ives et al. 2018).

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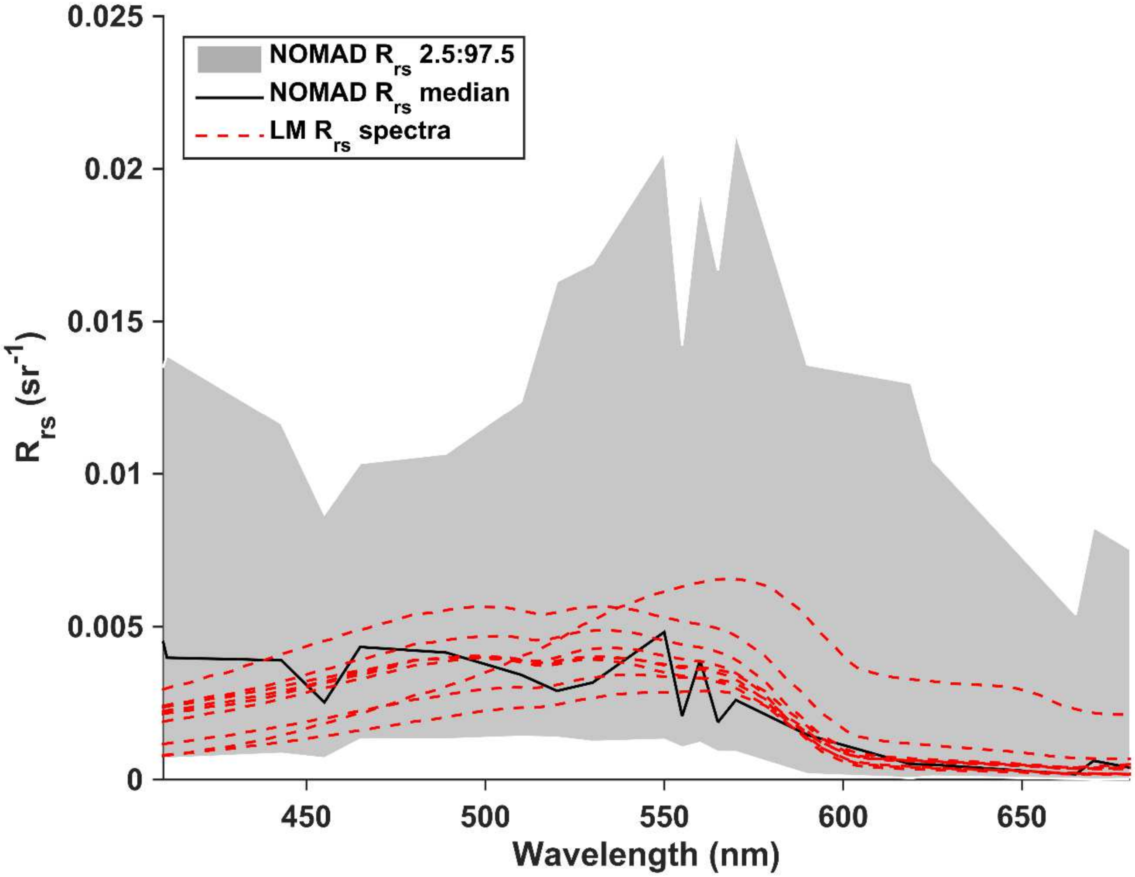
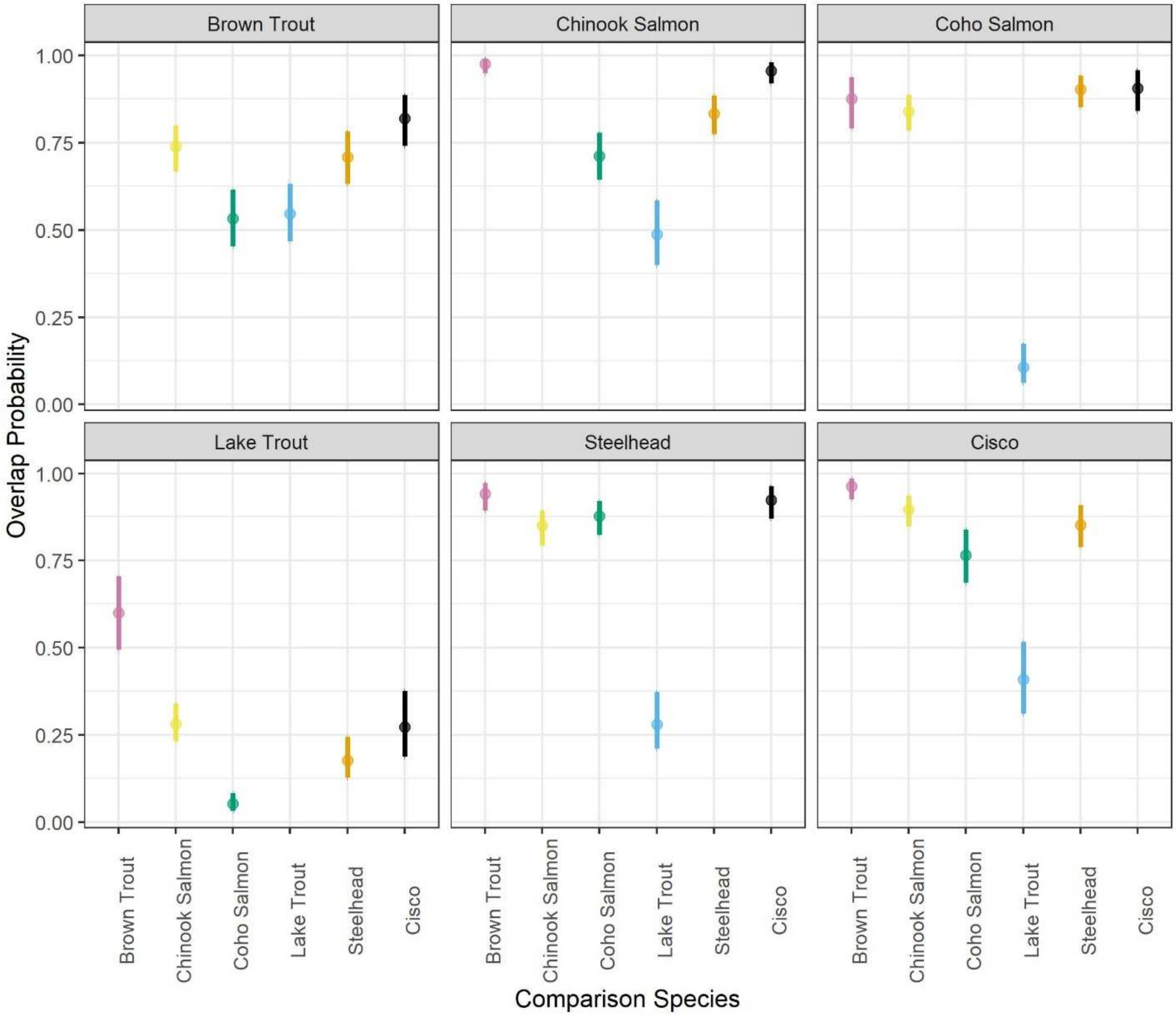
Appendix A. Supplemental Material for Chapter 2

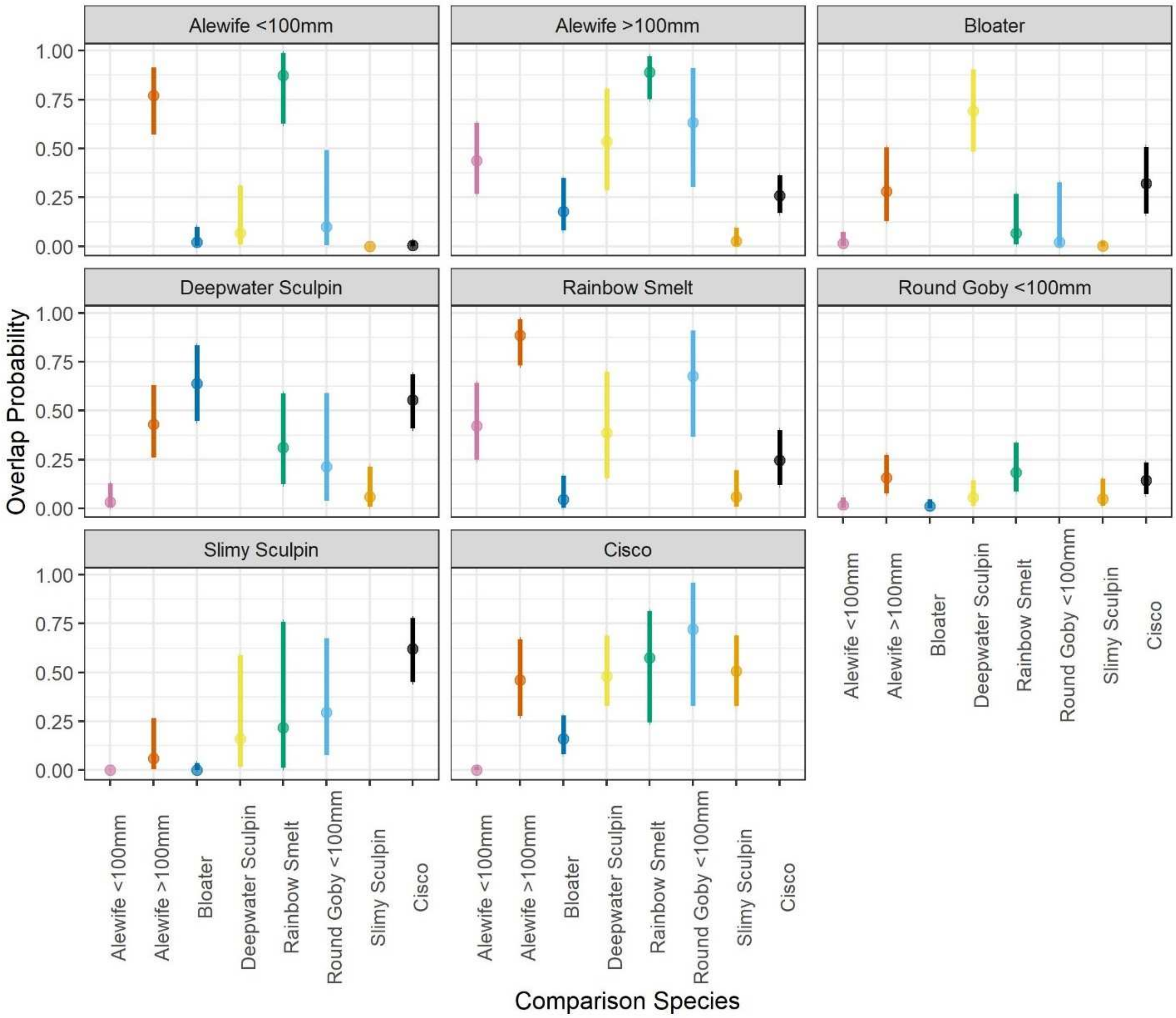


Appendix A. 1. Statistical range (2.5% and 97.5% quantiles, shaded gray) and median (black line) of NOMAD R_{rs} spectra relative to Lake Michigan R_{rs} spectra (red dashed lines) available on SeaBASS.

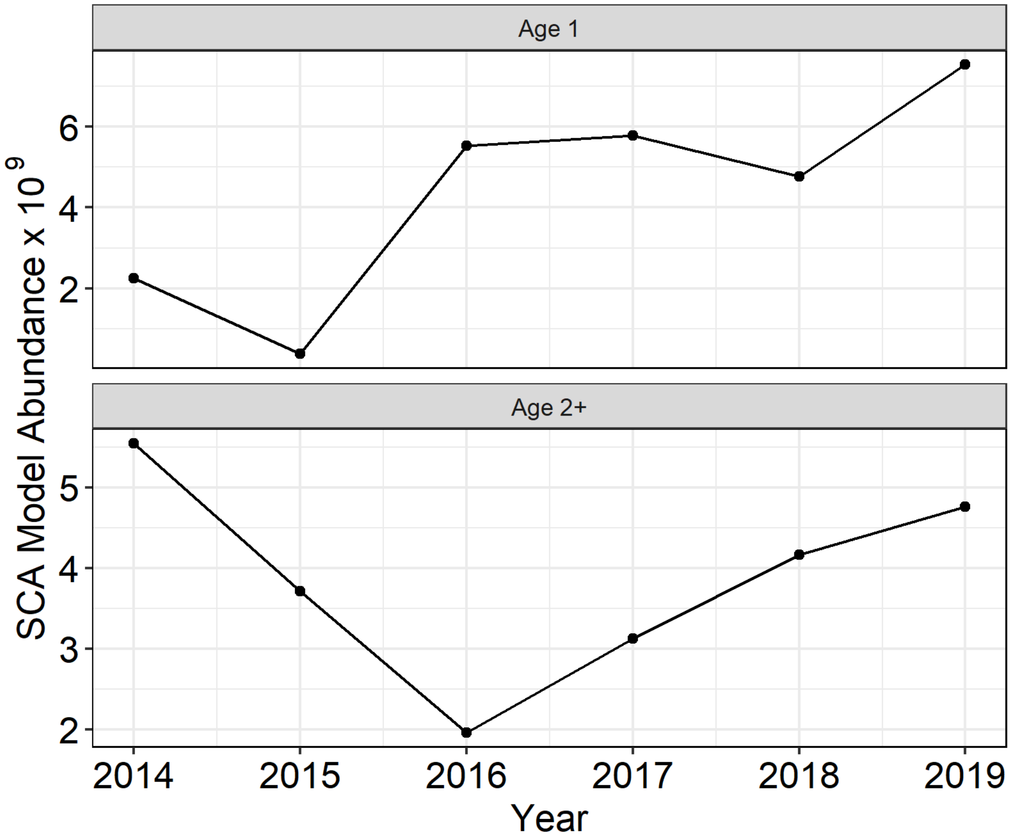
Appendix B. Supplemental Material for Chapter 4



Appendix B. 1. Probability of isotopic niche overlap for Lake Michigan salmonines and cisco. Points depict median (95% credible interval) probability of an individual from species A (panel titles) occurring in the δ^{13}C and δ^{15}N isotopic niche space of comparison species B (x-axis).



Appendix B. 2. Probability of isotopic niche overlap for Lake Michigan prey fishes and cisco. Points depict median (95% credible interval) probability of an individual from species A (panel titles) occurring in the $\delta^{13}C$ and $\delta^{15}N$ isotopic niche space of comparison species B (x-axis).



Appendix B. 3. Lake Michigan alewife abundance at age 1 (top) and ages 2+ (bottom) on Jan 1 of 2014-2019 derived from statistical catch at age (SCA) model estimates. SCA models were developed by Tsehaye (2014)and are updated annually by the Lake Michigan Technical Committee's Salmonid Working Group.

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Turschak, B.A., C.R. Bronte, S. Czesny, B. Gerig, A. Happel, T. Hook, M.S. Kornis, B.S. Leonhardt, B.G. Matthias, J.R. Rinchard, D.M. Warner, and H.A. Bootsma. Accepted. Temporal variation in the niche partitioning of Lake Michigan salmonines as it relates to alewife abundance and size structure. Canadian Journal of Fisheries and Aquatic Sciences.

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Happel, A., B.S. Leonhardt, T. Hook, H. Bootsma, C.R. Bronte, M.S. Kornis, S. Czesny, B. Turschak, C. Maier, J. Rinchard. 2020. J. Great Lakes Res. 46(6): 1689-1701.

Anderson, M., B. Turschak, S. Czesny, J.L. Jonas. 2019. Quantitative methods to reconstruct length and weight of Great Lakes prey fishes from dietary observations of partially digested prey. J. Great Lakes Res. 45(6): 1228-1240.

Bunnell, D.B., D.M. Warner, C.P. Madenjian, B. Turschak, P. Armenio, T. Desorcie. 2020. Status and Trend of Pelagic and Benthic Prey Fish Populations in Lake Michigan, 2019. A report to the Great Lakes Fishery Commission, Lake Michigan Committee Meeting, Ypsilanti, MI 2020.

Warner, D.M., K. Phillips, B. Turschak, D. Hanson, J. Smith. 2019. Status of Pelagic Prey Fishes in Lake Michigan, 2018. A report to the Great Lakes Fishery Commission, Lake Michigan Committee Meeting, Ypsilanti, MI 2019.

Turschak, B.A., S. Czesny, J.C. Doll, B.K. Grunert, T.O. Hook, J. Janssen, H.A. Bootsma. 2018. Spatial Variation in Trophic Structure of Nearshore Fishes in Lake Michigan as it Relates to Water Clarity. Canadian Journal of Fisheries and Aquatic Sciences. (doi: 10.1139/cjfas-2017-0390)

Turschak, B.A., H.A. Bootsma. 2015. Lake Michigan Trophic Structure as Revealed by Stable C and N Isotopes. J. Great Lakes Res., 41 SUPPL. 3, pp. 185-196 (doi:10.1016/j.jglr.2015.04.004).

Turschak, B.A., D. Bunnell, S. Czesny, T.O. Hook, J. Janssen, D. Warner, H.A. Bootsma. 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology. 95(4), pp. 1243-1252 (doi: 10.1890/13-0329.1).

Turschak, B.A., A.H. Moerke, B.I. Evans. 2011. Spatial and seasonal patterns in the crustacean zooplankton community of the St. Marys River. J. Great Lakes Res., 37 SUPPL. 2, pp. 21-27.

Selected Presentations

Turschak, B.A. and D. Clapp. 2021. Spawning Site Selection by Lake Trout and Lake Whitefish on Good Harbor Reef: Reef Restoration and Dreissenid Mussel Removal. 2021. A Presentation to the Great Lakes Fishery Commission, Lake Michigan Committee Virtual Meeting, 2021.

Turschak, B.A., C. Bronte, S. Czesny, B. Gerig, A. Happel, T.O. Hook, M. Kornis, B. Leonhardt, B. Matthias, J. Rinchard, D. Warner, and H.A. Bootsma. 2020. Dietary Niche of Lake Michigan Salmonines as it Relates to Alewife Population Structure. International Association of Great Lakes Research Virtual Conference (Oral Presentation).

Turschak, B.A. and D. Clapp. 2021. Lake Trout and Whitefish Spawning Site Selection on Good Harbor Reef. NPS Sleeping Bear Dunes Virtual Research Symposium (Oral Presentation).

Turschak, B.A., C. Bronte, S. Czesny, B. Gerig, T.O. Hook, M. Kornis, B. Leonhardt, D. Warner, H.A. Bootsma. 2019. Diet and Niche Overlap of Lake Michigan Piscivorous

Fishes as Revealed by Stable Isotopes. Midwest Fish and Wildlife Conference, Cleveland, OH (Oral Presentation).

Turschak, B.A., C.R. Bronte, S. Czesny, T.O. Höök, M.S. Kornis, B. Leonhardt, J. Janssen, and H.A. Bootsma. 2018. Using Stable C and N isotopes to Assess Diets of Lake Michigan Salmonines: Implications for Ongoing Management. Midwest Fish and Wildlife Conference, Milwaukee, WI (Oral Presentation).

Turschak, B.A., H.A. Bootsma, M. Kornis, C.R. Bronte, S. Czesny, B. Gerig, T.O. Höök, B. Leonhardt, J. Rinchard, and D. Warner. 2019. Diet and Niche Overlap of Lake Michigan Piscivorous Fishes as Revealed by Stable Isotopes. International Association of Great Lakes Research Conference, College at Brockport, State University of New York, NY (Oral Presentation given by M. Kornis).

Kornis, M. and B. Turschak. 2018. Salmon and Trout Diets in Lake Michigan. A Presentation to the Great Lakes Fishery Commission, Lake Michigan Committee, Sault Ste. Marie, ON.

Turschak, B.A. and H.A. Bootsma 2017. Using Stable C and N Isotopes to Characterize Large-Scale Spatial and Temporal Variation in the Diets of Lake Michigan Fishes. Midwest Fish and Wildlife Conference, Lincoln, NE (Oral Presentation).

Turschak, B.A., B. Grunert, H.A. Bootsma. 2017. Effects of Ecology and Biogeochemistry on the stable isotopes of nearshore fishes in Lake Michigan. International Association of Great Lakes Research Conference, Detroit, MI (Oral Presentation).

Turschak, B.A. and H.A. Bootsma. 2015. Assessing the Potential Role of Round Goby as a Conduit for Avian Botulism. Society for Freshwater Science Conference, Milwaukee, WI (Oral Presentation).

Turschak, B.A. Changes in the Lake Michigan Food Web as Revealed by Stable C and N Isotopes. Lake Michigan Fisheries Forum, Lakeland College, Cleveland, WI, (Oral Presentation).

Turschak, B.A. 2014. Beneath the Waves: A Historical and Contemporary Perspective the Great Lakes Open Water Fishery. Educational public seminar series at the Milwaukee Co. Sailing Center, Milwaukee, WI, (Oral Presentation).

Turschak, B.A. and H.A. Bootsma. Spatial Variability in the Trophic Structure of Lake Michigan Fishes as Revealed by Stable C and N Isotopes. International Association of Great Lakes Research Conference, McMaster University, Hamilton, ON, (Oral Presentation).

Turschak, B.A. and H.A. Bootsma. 2013. Changes in the Lake Michigan Trophic Structure as Revealed by Stable C and N Isotopes. International Association of Great Lakes Research Conference, Purdue University, West Lafayette, IN, (Oral Presentation).

Turschak, B.A. 2012. Invasive Species and the Lake Michigan Food Web. Educational public seminar series, Milwaukee Co. Sailing Center, Milwaukee, WI (Oral Presentation).

Turschak, B.A. and H.A. Bootsma. 2012. Food Web Changes in Lake Michigan as Revealed by Stable C and N Isotopes. International Association of Great Lakes Research Conference, Cornwall, ON (Oral Presentation).

Selected Grants and Projects

Fetzer, W., A. Briggs, L. Loken, B. Turschak, J. Vander Zanden, D. Warner, B. Weidel. Quantifying energy sources supporting Great Lakes Prey Fish. Great Lake Fisheries Trust. 2020.

Hondorp, D.W., B. Turschak, N. Barton, E. Olsen, J. Jonas, K. Donner, J. Smith, and M. Herbert. Spawning Site Selection by Lake Whitefish in Northeast Lake Michigan. Great Lakes Fish and Wildlife Restoration Act. 2020.

Hondorp, D.W., B. Turschak, N. Barton, E. Olsen, J. Jonas, K. Donner, J. Smith, and M. Herbert. Stock structure and interactions of Lake Whitefish in Grand Traverse Bay and Adjacent Areas of Lake Michigan. Great Lake Fisheries Trust. 2020.

Hondorp, D.W., B. Turschak, J. Jonas, K. Donner, J. Smith. Migration and Spawning Behaviors of Adult Cisco in Grand Traverse Bay, Lake Michigan. Great Lakes Fishery Trust. Great Lakes Fish and Wildlife Restoration Act. 2019.

Roth, B. C. Bronte, M. Kornis, J. Jonas, D. O'Keefe, R. Clark, J. He, E. Roseman, K. Donner, B. Turschak, N. Barton. A comprehensive evaluation and comparison of the food webs of lakes Michigan and Huron using predator diets and stable isotopes. Great Lakes Fishery Trust: Proposal #2018.1783.

GLRI Collaborative Project between the NPS and MDNR. Research Lake Michigan Nearshore Ecosystem Changes: Cooperative Agreement for Coastal Management in Great Lakes Parks. 2018.

United States Fish and Wildlife Service (Federal Aid in Sport Fish Restoration); Assessment 230485: Assessment of salmonine populations and their prey in Michigan waters of Lake Michigan. Department of Interior, Sport Fish Restoration Program. 2018-2021.

Selected Honors and Awards

Kohler Trust for Clean Water Fellowship Recipient (2021)

Distinguished Graduate Student Fellowship Recipient (2017)

Janice Lee Fenske Memorial Award Finalist (2017)

School of Freshwater Sciences Student Travel Award (2016)

Great Lakes Foundation Fellowship (2016)

JGLR Top 25 Most Cited Authors of 2011 Recipient

UWM Dutton's Fellowship Recipient (2010)