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The influence of body size and season on the feeding ecology of three freshwater fishes with different diets in Lake Erie

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ABSTRACT

Isotopic niche and length-isotope relationships were quantified across the body size of three similarly-sized fish species with different feeding strategies as adults (benthivore: freshwater drum, *Aplodinotus grunniens*; piscivore: walleye, *Sander vitreus*; and omnivore: white perch, *Morone americana*) in Lake Erie's western basin using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$. Stable isotopes demonstrated that resource utilization changed with body size for all three species and length-isotope relationships varied with season. Isotopic niche overlap was lower when modelled with three isotopes ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) than with two ($\delta^{13}C$ and $\delta^{15}N$), providing greater resolution of feeding ecology among the species. Based on isotopic niches, there was significant overlap in resource use among species and size classes in spring, but overlap decreased in the fall for both. In this study, freshwater fish species with different adult feeding strategies partition resources through different mechanisms that vary through body size and season. Isotopes supported the generally identified feeding ecology of each species but demonstrated that each species underwent significant changes in feeding ecology with increasing body size. Changes in isotopes across season, and body size for each species demonstrate the need for a more thorough understanding of how resource use changes with body size and season in freshwater fish.

Introduction

The feeding ecology of an organism is influenced by numerous factors over the course of its life. These factors include, but are not limited to, prey choice and habitat use (Post, 2003; Werner and Gilliam, 1984), resulting from trade-offs between resource availability, interspecific competition, and predation risk (Sánchez-Hernández et al., 2018; Werner and Hall, 1988), and is strongly correlated with both body size and ontogeny (Sánchez-Hernández et al., 2018). Diet in fish is often regulated by gape size, with a transition from smaller to larger prey as an individual grows. For example, juvenile piscivore fish typically feed on zooplankton or small invertebrates but switch to larger invertebrates and fish as they become larger (Amundsen et al., 2003; Galarowicz et al., 2006; Post, 2003). Less is known about shifts in resource use in other feeding guilds (e.g. planktivores, benthivores), but there is evidence to suggest that piscivores are not the only group that undergo changes in niche due to increasing body size (Ng et al., 2008; Werner and Hall, 1988; White, 1985).

Shifts in diet associated with changes in habitat use indicate a trade-off between optimal foraging, environmental conditions, and survival (Byström et al., 2004; Galarowicz et al., 2006; Werner and Gilliam, 1984). Smaller individuals are more vulnerable to predation and may use different habitat (e.g., food resources, temperatures, etc.) than larger conspecifics to avoid predators. Bluegill (*Lepomis macrochirus*) have been shown to shift from a predominately littoral (e.g. macroinvertebrates) to a pelagic diet (e.g. zooplankton) at a discrete size threshold to maximize prey quality and minimize both predation risk and resource competition with the closely related pumpkinseed sunfish (*Lepomis gibbosus*; Werner and Hall, 1988). As well, under high predation risk, individuals cannot be as selective about prey items (i.e. greater diversity of prey within their diet), which would result in larger niche exploitation by the population (Eklöv and Svanbak, 2006).

Feeding ecology can also be influenced by resource partitioning, likely to reduce resource competition within communities (Ross, 1986; Schoener, 1974), or can be the result of past interactions. Coregonids within the Laurentian Great Lakes (hereafter Great Lakes) partition habitat resources among species and morphotypes by depth while foraging for similar prey found across a depth gradient (Schmidt et al., 2011). Resource partitioning among species may also change with body size. Such changes in resource use (e.g. habitat, diet) due to increasing body size are often trade-offs that optimize the benefit of better resources (e.g. temperature, larger prey) and minimize negative

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interactions with other species (e.g. competition, predation; Sánchez-Hernández et al., 2018; Werner and Gilliam, 1984; Werner and Hall, 1988). For example, a fish that feeds on benthic prey at small sizes but switches to a pelagic diet when it reaches a size threshold will alter diet (i.e. different prey) and the species it interacts with (i.e. different predators or competitors; Byström et al., 2003; Werner and Gilliam, 1984; Werner and Hall, 1988). The size threshold where shifts in resource use occur are likely related to gape size, which restricts the size of prey an individual can consume, and predation risk, which affects an individual's foraging behavior (e.g. use habitat with more shelter; Sánchez-Hernández et al., 2018). Given gape size restrictions, similarly sized fish could feed on similar diet items while experiencing comparable predation risk (Mittelbach, 1984). As a result, smaller individuals of a species may partition resources differently than larger fish because the species it interacts with have changed.

Seasonal changes in prey availability may affect the feeding ecology of species as they shift their resource use to take advantage of abundant prey. Shifts in prey consumption based on season are well-documented throughout marine and freshwater ecosystems (Eloranta et al., 2010; Gopalan et al., 1998; Xue et al., 2005). Adult fish may shift their diet to take advantage of seasonally abundant prey (e.g. eggs, fish larvae, etc.; Brush et al., 2012; Ng et al., 2008). In juvenile fishes, seasonal shifts in diet are usually a trade-off between prey abundance, and increasing body size, allowing individuals to target larger prey (Gopalan et al., 1998). As a result, it is important to consider seasonal changes in the availability of prey when looking at changes in resource use caused by increasing body size.

Despite the possibility of changes in feeding ecology driven by body size and season, adult life stages are usually the primary factor defining a species ecological role or niche, despite that being the period when individuals experience the least growth (Sánchez-Hernández et al., 2018). Moreover, most research conducted on variation of feeding ecology in piscivores focuses on the early life history or until the switch to piscivory has occurred (e.g. larval, fry and early juvenile stages) and often does not investigate further changes as the fish continues to grow (Mittelbach and Persson, 1998; Sánchez-Hernández et al., 2018). Given that the Great Lakes, and other aquatic ecosystems around the world, have experienced substantial ecosystem changes to trophic interactions and energetic pathways, knowledge of changes in resource use and niche overlap as a result of increasing body size is needed to better predict future ecosystem changes (Sánchez-Hernández et al., 2018).

Stable isotopes provide a metric to quantify feeding ecology, as isotope values reflect diet and habitat use (Fry, 2007; Layman et al., 2007; Newsome et al., 2007) and niche can be quantified through estimation of isotopic niche using two or three isotopes (Jackson et al., 2011; Swanson et al., 2015). Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes have been used as indicators of habitat use and trophic position, respectively, in both aquatic and terrestrial ecosystems (Boecklen et al., 2011; Nawrocki et al., 2016; Post, 2002). Sulphur stable isotopes (δ^{34}S) are used predominately to quantify marine versus freshwater habitat use, but recently they have been used to differentiate between open water and benthic habitats in freshwater ecosystems (Colborne et al., 2016; Croisetière et al., 2009; Newsome et al., 2007). Increases in δ^{15}N often correspond with increases in relative trophic position (Newsome et al., 2007; VanderZanden et al., 1997). Low values of δ^{13}C are often interpreted as an individual having a higher dependence on pelagic prey, with higher values suggesting increased use of littoral resources (Croisetière et al., 2009; Newsome et al., 2007). Recent literature suggests that high values of δ^{34}S indicate use of open-water (i.e. pelagic) resources, and lower values indicate increased use of benthic resources (Colborne et al., 2016; Croisetière et al., 2009). While two isotope niche analysis is most commonly used, recent research suggests that three isotopes can provide better resolution, especially when there is little difference in δ^{13}C and δ^{15}N between sources (Colborne et al., 2016; Peterson and Howarth, 1987; Phillips and Gregg, 2003; Swanson et al., 2015).

Given the need to understand how aquatic food webs are changing as a result of anthropogenic stressors, it is important to establish the current state of the ecosystem and determine whether factors such as body size and seasonality have an impact on the relationships between different species within the food web. To this end, the goal of this research was to quantify the effects of body size and season on the trophic ecology of three freshwater fishes with different feeding strategies in Lake Erie's western basin using stable isotopes. Key baseline species were also collected and analyzed for δ^{15}N, δ^{13}C, and δ^{34}S to evaluate habitat difference in isotope values and allow for habitat use comparison between size classes and among fish species. We hypothesized that these species will partition resources within similar size classes among species and between size classes within species; such strategies would be indicated by low degrees of overlap in isotopic niche.

Methods

Study system and species

Lake Erie is large (25,700 km^2) and home to over 130 fish species (Hartman, 1972; International Joint Commission, 2014). The western basin of the lake is shallow and highly productive, potentially giving species the chance to feed on similar prey items. Three common, widespread, and large bodied (average total length ≥200 mm) fish species were selected to investigate changes in isotopic niche and resource use with body size and season: freshwater drum, a benthivore (*Aplodinotus grunniens*; Bur, 1982, 1984); walleye, a piscivore, (*Sander vitreus*; Mittelbach and Persson, 1998; Scott and Crossman, 1998); and, white perch, an omnivore (*Morone Americana*; Guzzo et al., 2013; Stanley and Danie, 1983).

These three species are phylogenetically different, but inhabit similar regions, and may use similar habitats and prey at different periods of their life histories. Freshwater drum in Lake Erie undergo three distinct transitions in diet from pelagic zooplankton as larvae, to benthic invertebrates at lengths <150 mm in total length, returning to a pelagic diet at lengths between 150 and 350 mm, and reverting back to a predominantly benthic diets at lengths ≥350 mm (Table 1; Bur, 1982; French and Bur, 1996; Gopalan et al., 1998; Morrison et al., 1997). White perch are generalist omnivores with a preference for zooplankton at total lengths smaller than 200 mm and fish as their size increases (Table 1; Schaeffer and Margraf, 1986; Scott and Crossman, 1998; Stanley and Danie, 1983). Walleye feed on a mixture of zooplankton, benthic invertebrates, and fish until they reach total lengths of ~80 mm, after which walleye transition to a diet consisting solely of fish by the time they are 150 mm in length (Table 1; Galarowicz et al., 2006; Hartman and Margraf, 1992; Mittelbach and Persson, 1998).

There is little information on habitat shifts for these species in Lake Erie based on body size, however, changes in diet are often highly correlated with changes in habitat use (Sánchez-Hernández et al., 2018; Werner and Gilliam, 1984; Werner and Hall, 1988). As a result, freshwater drum likely utilize benthic habitat at lengths <150 mm and >350 mm, and use pelagic habitat between lengths of 150–350 mm (Bur, 1982; French and Bur, 1996; Gopalan et al., 1998; Morrison et al., 1997). White perch and walleye probably use predominantly pelagic habitat at all sizes (Hartman and Margraf, 1992; Mittelbach and Persson, 1998; Schaeffer and Margraf, 1986; Scott and Crossman, 1998; Stanley and Danie, 1983).

Lower trophic level species including seston, dreissinid mussels (*Dreissena* spp.), and benthic invertebrates were collected to provide baseline indicators of habitat isotope signatures because they are relatively sessile and less affected by movement and growth than fish. For example, benthic invertebrates would provide δ^{13}C and δ^{34}S values for benthic/littoral habitat, and seston would provide a pelagic δ^{13}C and δ^{34}S. Because dreissenid mussels are benthic filter feeders that consume both suspended littoral and benthic algae, their isotope values would be intermediate of benthic invertebrates and seston (Campbell et al., 2009;

Table 1
Feeding guild, key life history traits (hatch length, total length at Age 1: TL_{Age1}, maximum total length: TL_{max}) and diet of three species (freshwater drum, walleye, and white perch) within Lake Erie's western basin. References for each trait are indicated by letters in superscripts and listed below.

Species	Feeding guild	TL_{Age1} (mm)	TL_{max} (mm)	Diet
Freshwater Drum	Benthivore^{a,b}	157^{a,d}	750^{d}	**Young of the year (YOY-Age 1, < 150 mm):** initially zooplankton (primarily cladoceran), with increasing dependence on benthic invertebrates (primarily chironomids), **Age 1–5 (150–350 mm):** benthic invertebrates (chironomids), zooplankton (cladoceran), fish **Age 6+ (> 350 mm):** decapods, small Bivalvia, fish, dreissenid mussels ^{a,b,e,f,o}
Walleye	Piscivore^{a,g,h}	206^{a,g}	790^{a,g}	**YOY (< 200 mm):** zooplankton, and benthic invertebrates, before transitioning to fish **Age 1+ (>200 mm):** Fish predominately, some benthic invertebrates ^{a,f,j,p}
White Perch	Omnivore^{g,k,l,m}	87^{a,g}	483^{a,g,m}	**YOY – Age 3 (< 200 mm):** Zooplankton, benthic invertebrates, insect larvae **Age 3+ (> 200 mm)** Zooplankton, benthic invertebrates, fish eggs, fish, dreissenid mussels^{a,f,k,l,n}

References: a) Scott and Crossman, 1998; b) Bur, 1982; c) Swedburg and Walburg, 1970; d) Bur, 1984; e) French and Bur, 1996; f) Corkum, 2010; g) Mittelbach and Persson, 1998; h) Overman and Parrish, 2001; i) Hartman and Margraf, 1992; j) VanderZanden et al., 1997; k) Guzzo et al., 2013; l) Schaeffer and Margraf, 1986; m) Stanley and Danie, 1983; n) Parrish and Margraf, 1990; o) Morrison et al., 1997; p) Galarowicz et al., 2006

Garton et al., 2005). These values can then be compared to the fish to determine approximately which habitats they are using.

Sample collection

Walleye ($n = 73$), white perch ($n = 64$), and freshwater drum ($n = 136$) were collected from the western basin of Lake Erie during the annual fish community trawl surveys conducted by the Ohio Department of Natural Resources (ODNR), the United States Geological Survey (Lake Erie Biological Station), and Ontario Ministry of Natural Resources and Forestry (OMNRF) during May, June, August, September, and November 2016. Upon capture, all fish were euthanized in compliance with the protocols of the government agency conducting the trawls and with the Canadian Council on Animal Care's policies. Seston was collected bi-weekly from June to September, and dreissenid mussels (*Dreissena* spp.) and benthic invertebrates (Chironomidae and *Hexagenia* spp.) were collected between August and September from four sites in the western basin to allow for the comparison of the three fish species. Fish samples were kept on ice and transported to the Great Lakes Institute for Environmental Research (GLIER) at the University of Windsor and stored at −20 °C for later sample preparation. Prior to dissection, fish were thawed, the total length and weight of each fish measured, and a skinless white muscle sample was taken between the pectoral and dorsal fins for stable isotope analysis.

Stable isotope analysis: sulphur, carbon, and nitrogen

All muscle samples were lyophilized at −48 °C and 133×10^3 mbar for 48 h, and then homogenized into a fine powder by hand using a mortar and pestle or dissection scissors. For sulphur ($\delta^{34}S$), freeze-dried samples were weighed into tin cups (sample mass 6000–6500 μg) without any further processing. Samples for $\delta^{13}C$ and $\delta^{15}N$ were lipid extracted using a 2:1 chloroform:methanol mixture (Colborne et al., 2016; Nawrocki et al., 2016) to eliminate the bias in $\delta^{13}C$ in fish muscle compared to pure protein (Boecklen et al., 2011; Fry et al., 2003). Samples for $\delta^{13}C$ and $\delta^{15}N$ analysis were weighed into tin cups for a final mass of 400–600 μg.

Carbon and nitrogen isotopic composition were determined using a Delta V Advantage Thermoscientific Continuous Flow Mass Spectrometer (Thermo Scientific, Bremen, Germany) coupled to a 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA). Sulphur isotopic composition was analyzed on a Delta V Plus Thermoscientific Continuous Flow Mass Spectrometer (Thermo Scientific, Bremen, Germany) coupled to a 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA) in the GLIER Chemical Tracers Laboratory.

Instrument accuracy throughout the period of sample analysis, as measured by NIST standards, was within 0.3‰ (NIST 8554, NIST 8555, and NIST 8529) of certified values for $\delta^{34}S$, 0.2‰ (NIST 8547, NIST 8573 and NIST 8574) for $\delta^{15}N$, and 0.1‰ (NIST 8573, 8542, and 8544) for $\delta^{13}C$. Precision of $\delta^{13}C$ and $\delta^{15}N$ based on four laboratory standards (NIST 1577c, tilapia muscle, USGS 40 and Urea ($n = 104$ for each)), run every 12 samples, was 0.2‰, and precision of $\delta^{34}S$, measured by five internal laboratory standards (NIST 1577c, NIST 8529, NIST 8555, tilapia muscle, and USGS 42; $n = 18$ for each), run every 10 samples, was ≤0.3‰. Sample reproducibility of $\delta^{13}C$ and $\delta^{15}N$ sample tissue replicates (measured in triplicate every 10 samples) was ±0.1‰ ($n = 83$), and reproducibility for $\delta^{34}S$ (run in duplicate for every eighth sample) was ± 0.1‰ ($n = 12$), which was within the acceptable range for all isotopes (± 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, and ± 0.3‰ for $\delta^{34}S$).

Statistical analysis

Because ANOVA assumptions of normality and homoscedasticity were not met, Kruskal-Wallis tests were conducted to compare seasonal isotope values for each species to determine if there were seasonal shifts in isotopes values for each species and isotope. All species had significant seasonal differences in $\delta^{15}N$ (Kruskal-Wallis: $\chi^2 \geq 27.5$, $p \leq 0.001$), white perch had seasonal differences for $\delta^{13}C$ ($\chi^2 = 7.2$, $p = 0.01$) and freshwater drum showed seasonal differences in $\delta^{34}S$ ($\chi^2 = 14.2$, $p = 0.001$); therefore, samples were grouped by the season they were collected in. Thus, samples collected in May and June (hereafter spring) and samples collected in August, September, and November (hereafter fall) were grouped together. Seston was collected in both seasons, however, benthic invertebrates and dreissenid mussels were only collected during the fall.

Linear and polynomial relationships between each isotope ($\delta^{13}C$, $\delta^{15}N$, or $\delta^{34}S$) and total length for each species were assessed using least squares regressions in R version 3.4 (R Core Team, 2017). Polynomial regressions were selected when R^2 and F values significantly improved compared to linear regression test statistics. Residuals for significant isotope-length relationships were normally distributed (Shapiro-Wilks test, $p > 0.2$).

Fish were grouped into three size classes (small: <200 mm, medium: 200–400 mm, and large: >400 mm) for further statistical analysis; as isotopic niche reflects data from groups, there was no appropriate regression method. No white perch larger than 350 mm were caught during the sample period, so no large size class (>400 mm) exists for the species within our analysis. Additionally, because large fish (>400 mm) did not experience seasonal changes in isotope values, the large size class was treated as a single group in all further statistical analyses to reduce the number of groups being compared and simplify the interpretation of results. Size classes were chosen so that fish that had similar sizes, predation risk, and opportunity to eat similar prey items could be compared. Predation risk and size of prey consumed are closely linked with body size (Sánchez-Hernández et al., 2018); therefore, choosing size classes would help reduce species differences related to these variables. However, these size classes do not precisely capture variation in predation risk within and between species because of ontogenetic and intraspecific variation in morphology (e.g. body depth). The size class ranges were chosen to maximize the number of samples per size and species; they also reflect expected changes in resource use by freshwater drum and white perch (Bur, 1982; Guzzo et al., 2013; Morrison et al., 1997; Stanley and Danie, 1983).

Isotopic niche was assessed using the SIBER and nicheROVER packages in R version 3.4 (Jackson et al., 2011; R Core Team, 2017; Swanson et al., 2015). Standard ellipses area (SEA_B) was calculated in SIBER (Stable Isotope Bayesian Ellipses in R) to summarize niche size along the carbon-nitrogen ($\delta^{13}C$-$\delta^{15}N$), the carbon-sulphur ($\delta^{13}C$-$\delta^{34}S$), and the sulphur-nitrogen ($\delta^{34}S$-$\delta^{15}N$) axis within species and among species (Jackson et al., 2011). The nicheROVER package was used to model the degree of niche overlap in two ways: 1) two isotopes using $\delta^{13}C$ and $\delta^{15}N$, the isotopes most frequently used in niche and foraging studies, and; 2) a three isotope model incorporating $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ (Swanson et al., 2015). We considered niche overlap to be biologically significant if it was >60% based on the criteria used for niches and stomach contents (e.g. Pianka's niche overlap index, Schoener's diet overlap index; Cabral et al., 2002; Gopalan et al., 1998; Pianka, 1973, 1974).

Results

Carbon stable isotopes in baseline samples (e.g. benthic invertebrates and seston) ranged from −24.2 ± 0.3‰ (mean ± 1 SE, $n = 14$) in dreissenid mussels to −29.8 ± 0.9‰ ($n = 3$) in chironomids, and most were lower than the three fish species (Table 2), indicating the habitats the fish were feeding in were probably sampled since $\delta^{13}C$ increases slightly with trophic position (Post, 2002; Vander Zanden et al., 1999). This was reinforced by baseline $\delta^{34}S$ values, which is not affected by trophic position, and ranged from −1.4 ± 0.4‰ in chironomids to 6.0 ± 0.6‰ in fall seston, overlapping the range of $\delta^{34}S$ in the fish species (0.4–3.5‰; Table 2). Sulphur isotopes ($\delta^{34}S$) were lower in baseline species that are associated with benthic habitat (i.e. *Hexagenia* spp., and chiromomids), and higher in baseline species associated with pelagic habitat (i.e. seston). Dreissenid mussels had $\delta^{34}S$ values intermediate to seston and the benthic invertebrates sampled, likely due to its dependence on phytoplankton as a food source. Baseline $\delta^{15}N$ were around half those measured in the fish species and ranged from 6.1 ± 0.5‰ ($n = 7$) in spring seston to 9.0 ± 0.3‰ ($n = 5$) in *Hexagenia* spp. in the fall (Table 2).

Relationships between stable isotopes and total length by season

Freshwater drum showed a significant increase then decrease in $\delta^{13}C$ with total length during the spring months, but no relationship existed between total length and $\delta^{13}C$ during the fall (Fig. 1a). This indicates that, during the spring, benthic prey is likely important for freshwater drum when they are intermediate lengths (i.e. 250–450 mm) but that they exhibit a preference for pelagic prey at smaller and larger lengths. Freshwater drum $\delta^{15}N$ decreased with total length during the spring (Fig. 1b), suggesting a decrease in trophic position with length. During the fall, freshwater drum $\delta^{15}N$ increased with total length to ~350 mm in length but then decreased (Fig. 1b). Sulphur ($\delta^{34}S$) had no significant relationship with total length in either season for freshwater drum (Fig. 1c).

Walleye showed no significant relationship between total length and $\delta^{13}C$ or $\delta^{15}N$ during the spring, but both isotopes increased significantly with length during the fall (Fig. 2a-b). This implies an increase in trophic position with length and a slight increase in dependence on benthic prey with length during the fall. Sulphur ($\delta^{34}S$) exhibited no significant relationship with total length for either season in walleye (Fig. 2c).

White perch showed no relationship for $\delta^{13}C$ with total length for either season (Fig. 3a), nor for $\delta^{15}N$ or $\delta^{34}S$ during the spring (Fig. 3b-c). White perch had significant increases in $\delta^{15}N$ and $\delta^{34}S$ with total length during the fall (Fig. 3b-c), suggesting that larger fish had higher tropic positions and greater reliance on pelagic prey during the fall months than smaller fish.

Isotopic niche overlap

In general, overlap between niches was much higher when modelled using two isotopes ($\delta^{13}C$ and $\delta^{15}N$) versus three isotopes ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$; Table 3). This was true for all niche overlap (e.g. intra and interspecific overlap) but was greatest when comparing among species in the medium size class, which had large overlaps (mean ± SE; spring: 70.7 ± 9.8%, fall: 52.4 ± 12.0%) in both seasons when only $\delta^{13}C$ and $\delta^{15}N$ were used to model niche, and little overlap when all three isotopes were used (mean ± SE; spring: 10.3 ± 3.6%, fall: 6.2 ± 4.5%; Table 3). Additionally, while both seasons had similar degrees of overlap on average (mean ± SE; two isotopes: 48.6 ± 4.3 and 41.1 ± 5.1%, three-isotopes: 24.4 ± 3.9 and 15.4 ± 4.4% in spring and fall respectively), there was generally less overlap during the fall than during the spring with a few exceptions (Table 3, Fig. 4a-i).

Walleye and white perch both experienced high intraspecific overlap on average in spring for both the two and three isotope models (> 60% with two isotopes, > 50% with three), whereas freshwater drum showed moderate to little intraspecific overlap during the spring (< 25%, Table 3). During the fall, walleye also had high intraspecific overlap (> 50% for both models) on average, whereas white perch had little (two isotopes: 15.8 ± 11.4%, three isotopes: ND, Table 3). Freshwater drum had high intraspecific overlap for the two-isotope model (mean

Table 2
Stable isotopes (mean ± 1 SE) for baseline species, freshwater drum, walleye, and white perch in the western basin of Lake Erie over two seasons (spring: May to June; fall: July to September). All baseline samples are pooled samples of multiple individuals from various sample dates and sites. Dashes indicate no data is available.

Species	Size class	Total length (mm)	Spring					Fall				
			n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n	$\delta^{34}S$ (‰)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n	$\delta^{34}S$ (‰)
Baseline	*Chironomidae*	–	–	–	–	–	–	3	−29.8 ± 0.9	7.2 ± 0.5	3	−1.4 ± 0.4
	Dreissenidae	–	–	–	–	–	–	14	−24.2 ± 0.3	7.6 ± 0.2	6	3.0 ± 0.1
	Hexagenia	–	–	–	–	–	–	5	−25.2 ± 0.4	9.0 ± 0.3	5	2.0 ± 0.3
	Seston	–	8	−28.0 ± 0.5	6.1 ± 0.2	6	4.7 ± 0.2	35	−25.0 ± 0.2	7.5 ± 0.2	7	6.0 ± 0.6
Freshwater Drum	*Small*	125 ± 6	7	−24.4 ± 0.6	16.9 ± 0.5	6	1.6 ± 0.9	34	−21.7 ± 0.1	13.7 ± 0.2	9	2.6 ± 0.2
	Medium	315 ± 6	22	−21.5 ± 0.2	17.2 ± 0.1	9	0.4 ± 0.4	23	−21.6 ± 0.2	15.9 ± 0.1	6	1.7 ± 0.5
	Large	473 ± 8	20	−22.0 ± 0.2	15.0 ± 0.3	11	2.5 ± 0.3	30	−21.5 ± 0.2	14.7 ± 0.2	7	2.5 ± 0.1
	Average	**316 ± 13**	**49**	**−22.1 ± 0.2**	**16.3 ± 0.2**	**26**	**1.6 ± 0.3**	**87**	**−21.6 ± 0.1**	**14.6 ± 0.1**	**22**	**2.3 ± 0.2**
Walleye	*Small*	178 ± 4	16	−21.2 ± 0.1	17.5 ± 0.1	8	3.3 ± 0.1	2	−21.8 ± 0.2	15.1 ± 0.2	2	4.1 ± 0.3
	Medium	286 ± 9	20	−21.6 ± 0.1	17.3 ± 0.1	8	3.3 ± 0.4	15	−21.7 ± 0.1	15.8 ± 0.1	6	3.5 ± 0.2
	Large	525 ± 19	6	−21.2 ± 0.3	17.1 ± 0.2	6	3.2 ± 0.3	14	−21.4 ± 0.2	16.8 ± 0.3	10	3.5 ± 0.1
	Average	**325 ± 17**	**42**	**−21.4 ± 0.1**	**17.4 ± 0.1**	**22**	**3.3 ± 0.2**	**31**	**−21.5 ± 0.1**	**16.2 ± 0.2**	**18**	**3.6 ± 0.1**
White Perch	*Small*	121 ± 7	31	−22.1 ± 0.2	16.8 ± 0.2	14	2.7 ± 0.5	10	−22.8 ± 0.2	14.0 ± 0.2	5	1.2 ± 0.6
	Medium	242 ± 7	20	−22.1 ± 0.1	16.9 ± 0.1	9	2.9 ± 0.3	3	−21.8 ± 0.2	15.1 ± 0.4	3	3.3 ± 0.3
	Average	**165 ± 9**	**51**	**−22.1 ± 0.1**	**16.8 ± 0.1**	**23**	**2.8 ± 0.3**	**13**	**−22.6 ± 0.2**	**14.2 ± 0.2**	**8**	**2.0 ± 0.5**

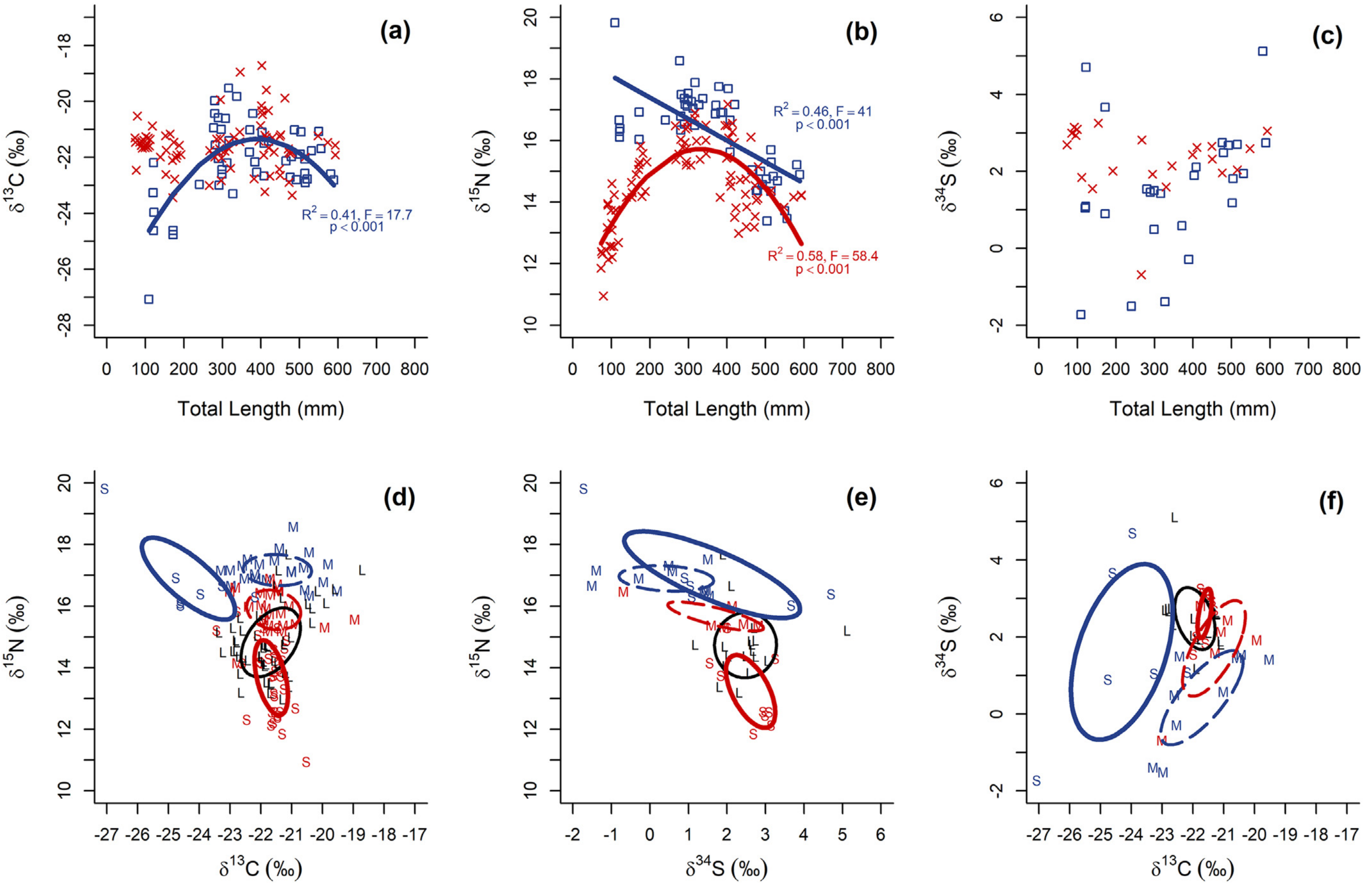

Fig. 1. Isotope relationships with length (a-c) and isotopic niche plots (d-f) for freshwater drum. a-c: Trends in isotope values with total length (a: δ^{13}C, b: δ^{15}N, and c: δ^{34}S) of freshwater drum across two seasons (spring: blue squares; fall: red x's). Significant relationships between isotope values and length are indicated by solid lines. d-f: SIBER standard ellipses estimating isotopic niche (d: δ^{13}C-δ^{15}N, e: δ^{34}S-δ^{15}N, f: δ^{13}C-δ^{34}S) for three sizes of freshwater drum (small: $<$ 200 mm, S's and thick solid lines; medium: 200–400 mm, M's and dashed lines; large: $>$ 400 mm, L's and thin solid lines) across two seasons (spring: blue, fall: red, pooled data (large fish only): black) represented by SIBER standard ellipses.

± SE, 59.2 ± 9.6%) in fall, but when modelled with three isotopes, overlap was only half that (27.6 ± 11.1%, Table 3).

All three species experienced similar mean interspecific overlap overall regardless of season or model type (i.e. two vs. three isotopes; Table 3). However, when comparing interspecific niche overlap within size classes, small fish ($<$ 200 mm) experienced more overlap in spring than the other size classes in the three-isotope model (Table 3). Medium fish experienced the greatest amount of overlap among species during spring than the other size classes in the two-isotope model. During the fall, isotopic niche overlap increased with increasing size classes in both the two-isotope and three-isotope models (Table 3).

Discussion

These three species of large bodied freshwater fish of Lake Erie had unique resource utilization strategies across body size based on isotopic niches using three stable isotopes, demonstrating some resource partitioning through both habitat use and trophic position. However, some size and species combinations had significant niche overlap in the spring, suggesting that there could be competition for resources at various life stages and seasons, or they consume abundant prey types that could support multiple consumers without resource partitioning. In the fall, there was minimal isotopic niche overlap, indicating species had different resource use during this period. These results largely confirm identified feeding ecologies associated with the adult life stage of each of the three fish species but demonstrate the value of considering the influence of body size on trophic ecology.

While baseline δ^{15}N was similar across season, all fish species had significantly lower δ^{15}N in the fall than during the spring, and suggests that they were feeding on lower trophic level prey between spring and fall. Walleye and white perch were feeding at a higher trophic position than freshwater drum in both seasons, which conforms with what is known about the diet of the species. Lower δ^{15}N, or trophic position, in the fall could reflect the importance of late spring and early summer algal blooms and associated zooplankton and larval fish as prey, compared to a winter and early spring diet with limited access to these lower trophic level diet items, as seen in other studies (Eloranta et al., 2010; Gopalan et al., 1998; Xue et al., 2005). However, it is difficult to make inferences about this because diet information for winter and early spring are lacking in Lake Erie and the Great Lakes in general. Seasonal movement could also contribute to the differences observed between seasons in δ^{15}N, because movement to the central and eastern basin of Lake Erie in fall has been documented for walleye (Raby et al., 2018), and is believed to occur for freshwater drum and white perch based on management surveys (Y. Zhao, personal communication, March 15, 2019).

Sources of carbon were consistent across season, size, and fish species with a few exceptions (e.g. small freshwater drum) based on δ^{13}C, and indicates all three species were feeding on prey that had a similar carbon source, or that their prey's diet shared a carbon source given variation in δ^{15}N. Baseline seston δ^{13}C increased slightly from spring to fall, but was very variable and ranged across 4‰ in spring and 11‰ during the fall, which confounds inferences about habitat use and diet in the fish. The increase in δ^{13}C between baseline and fish species is consistent with the trophic increases of δ^{15}N and did not vary seasonally. The lack

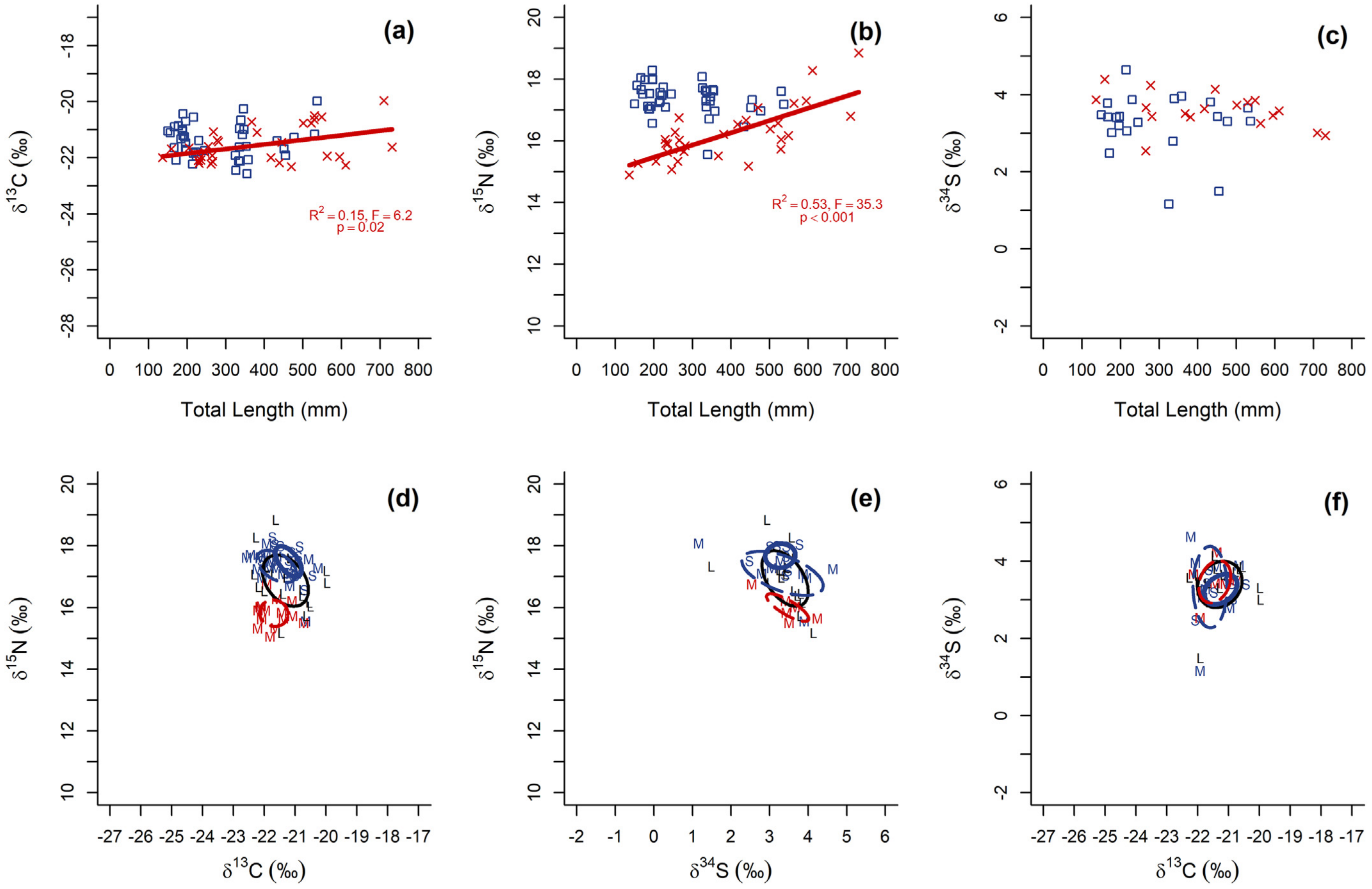

Fig. 2. Relationships of isotope values with total length (a-c), and estimates of isotopic niche (d-f) of walleye. a-c: Length-isotope relationships (a: $\delta^{13}C$, b: $\delta^{15}N$, and c: $\delta^{34}S$) of walleye across two seasons (spring: blue squares, fall: red x's). d-f: Isotopic niche (d: $\delta^{13}C$-$\delta^{15}N$, e: $\delta^{34}S$-$\delta^{15}N$, f: $\delta^{13}C$-$\delta^{34}S$) of three size classes of walleye (small: < 200 mm, S's and thick solid lines; medium: 200–400 mm, M's and dashed lines; large: > 400 mm, L's and thin solid lines) in two seasons (spring: blue, fall: red, pooled data [large fish only]: black) represented by SIBER standard ellipses.

of seasonal change in fish $\delta^{13}C$ could be explained by feeding in the same habitat, prey sharing diet items, or reflect a lack of variation of $\delta^{13}C$ in the resources consumed (Phillips and Gregg, 2003). Given the shallow depths across the western basin of Lake Erie, and pelagic-benthic coupling among species described in other studies (Morrison et al., 2000; Schindler and Scheuerell, 2002; Vadeboncoeur et al., 2002), habitat differences in $\delta^{13}C$ normally seen in lakes may not apply in this system. Indeed, Guzzo et al. (2011, 2013) measured similar values of $\delta^{13}C$ for seston, dreissenid mussels, and white perch in Lake Erie's western basin to those presented in the current study, and Garton et al. (2005) also obtained similar seston $\delta^{13}C$ values in an earlier study. Better temporal resolution of $\delta^{13}C$ within habitats of Lake Erie would help interpret these results, as would variation between basins given the seasonal movements of these fish species.

Sulphur ($\delta^{34}S$) showed greater separation between baseline and fish species than $\delta^{13}C$, which suggests these fish species did have some differences in habitat use and diet that were not reflected in the more commonly used $\delta^{13}C$. Unfortunately, understanding of $\delta^{34}S$ dynamics in freshwater ecosystems and within organisms of Lake Erie is limited, but is growing. Croisetière et al. (2009) found that freshwater organisms feeding in open water (i.e. pelagically) had higher $\delta^{34}S$ values than those associated with benthic habitat, consistent with observed $\delta^{34}S$ in baseline species in this study. However, Colborne et al. (2016) did not observe this pattern in pelagic and benthic forage fish of Lake Ontario and a review on isotope ecology suggested higher $\delta^{34}S$ was associated with benthic feeding (Newsome et al., 2007), opposite to the trends found here and in Croisetière et al. (2009). Clearly, there is a need to better understand the dynamics of $\delta^{34}S$ in freshwater systems but this does not preclude comparing isotopic trends among the study species here. Indeed, including a third isotope ($\delta^{34}S$) into the analysis provided greater separation of species niche and trophic relationships in Lake Erie fish, at least with defining relative niche space, consistent with other recent papers that have used this isotope or another tracer such as fatty acids (Brewster et al., 2016; Colborne et al., 2016; Ofukany et al., 2014; Solomon et al., 2011). Because niches are multidimensional by nature, if significant overlap occurs on two axes it is possible that they diverge on another (Hutchinson, 1959; Ross, 1986), as Colborne et al. (2016) demonstrated with lake trout (*Salvelinus namaycush*) in Lake Ontario. Croisetière et al. (2009) also better differentiated between benthic and pelagic algae in freshwater boreal lakes when using $\delta^{34}S$ in addition to $\delta^{13}C$. To this end, the addition of a third isotope ($\delta^{34}S$) to the analysis in the present study showed that freshwater drum used more benthic resources (lower $\delta^{34}S$) than the other two species, a trend not observed in the two isotope model. Given that freshwater drum are bentho-pelagic predators and prefer benthic prey (e.g. benthic invertebrates; Bur, 1982), and this was not picked up in the two-isotope model, it seems likely that the addition of $\delta^{34}S$ improved the accuracy of the calculated isotopic niches among these three species in Lake Erie. However, further research is warranted to determine the accuracy of isotope models incorporating three or more tracers into their analysis.

The pattern of isotopic niche across size classes and season in freshwater drum demonstrates how defining a species ecological role based on expected adult feeding ecology can lead to generalizations which obscure changes in a species trophic ecology. Freshwater drum are considered a primarily benthic species (Bur, 1982; Scott and Crossman, 1998), and yet isotopes in this study suggest there are two length ranges (< 200 mm and > 400 mm) where they have isotopic niches which indicate

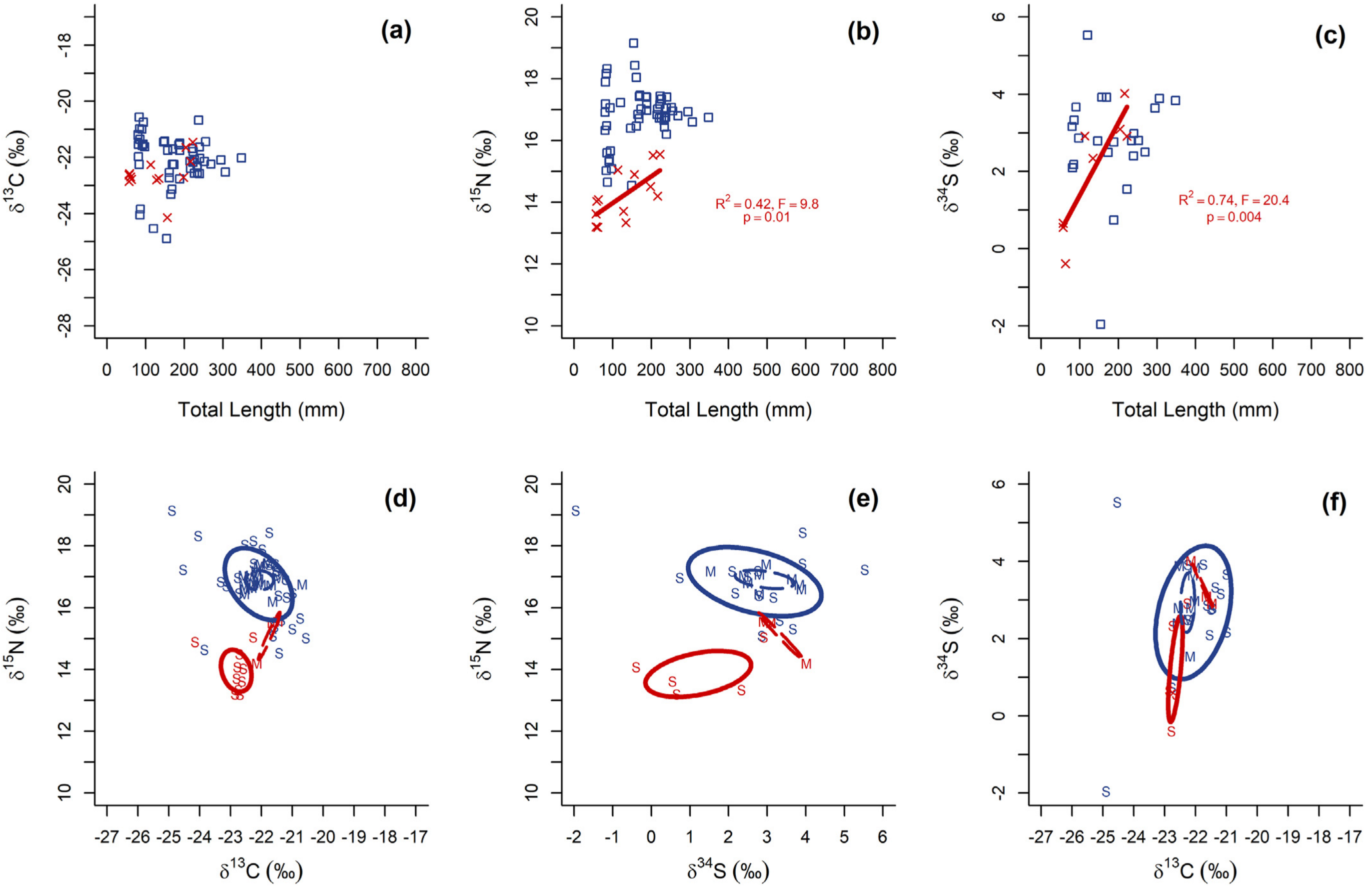

Fig. 3. Length-isotope relationships (a-c) and isotopic niche (d-f) of white perch in two seasons. (d-f). The trends of isotope values with total length (a: δ^{13}C, b: δ^{15}N, c: δ^{34}S) in two seasons (spring: blue squares, fall: red x's). d-f: Isotopic niche estimated by SIBER standard ellipses (SEA_B; d: δ^{13}C-δ^{15}N, e: δ^{34}S-δ^{15}N, f: δ^{13}C-δ^{34}S) across size classes (small: < 200 mm, S's and solid lines; medium: 200–400 mm, M's and dashed lines) of white perch in two seasons (spring: blue, fall: red) represented by SIBER standard ellipses.

a higher dependence on pelagic prey during the spring. Small freshwater drum (< 150 mm) have a high reliance on zooplankton in the spring before they transition to benthic invertebrates as a primary diet item (Bur, 1982; Gopalan et al., 1998), consistent with δ^{34}S and δ^{13}C in this study. Past research also found that large freshwater drum (> 350 mm) fed heavily on dreissenid mussels after their invasion into Lake Erie in 1987, which have higher δ^{34}S (i.e. more pelagic) compared with other benthic invertebrates (e.g. Chironomidae, *Hexagenia* spp.). This could mean that, while freshwater drum are feeding predominately within benthic habitats, their isotopic signature is reflecting the pelagic signature of dreissenid mussels which feed on pelagic phytoplankton (French and Bur, 1996; Morrison et al., 1997). Freshwater drum trophic position (δ^{15}N) declined with increasing size during the spring, which could be the result of large freshwater drum consuming low trophic level organisms such as dreissenid mussels as shown by baseline δ^{34}S within this study and previous research within Lake Erie (French and Bur, 1996; Morrison et al., 1997). Conversely, fall freshwater drum experienced an increase in δ^{15}N until they were ~250–300 mm in length, and then declined again at larger sizes. Bur (1982) suggested that small fish were an important component of the diet of 250–400 mm freshwater drum, which could explain the high trophic position of the medium size class in this study. These changes in trophic position and habitat use with size are likely driven by gape size limitation, resulting in a threshold effect on the resources (i.e. types of prey, habitat) used by individuals, and highlight the importance of having a more comprehensive understanding of a species ecological role across different sizes.

Table 3

Isotopic niche overlap (%, mean ± SE) modelled with two isotopes (δ^{13}C and δ^{15}N) and three isotopes (δ^{13}C, δ^{15}N, and δ^{34}S) for freshwater drum, walleye and white perch across two seasons. Intraspecific isotopic niche overlap is the average degree of overlap between size classes of a species (i.e. within a species). Interspecific isotopic niche overlap is the average degree of overlap a species has with other species across all size classes (i.e. among species). Within size class niche overlap is the average degree of interspecific overlap among species within a single size class.
Dashes indicate no data.

	Two isotopes		Three isotopes	
	Spring	Fall	Spring	Fall
Intraspecific niche overlap				
Freshwater Drum	25.2 ± 5.6	59.2 ± 9.6	13.9 ± 4.6	27.6 ± 11.1
Wallleye	75.6 ± 9.2	52.5 ± 26.1	50.7 ± 11.7	50.4 ± 38.2
White Perch	64.3 ± 35.8	15.8 ± 11.4	53.6 ± 46.3	–
Interspecific niche overlap				
Freshwater Drum	42.9 ± 5.8	46.3 ± 7.0	14.1 ± 3.4	10.7 ± 4.4
Walleye	46.6 ± 6.3	36.7 ± 8.2	19.2 ± 5.1	8.5 ± 4.2
White Perch	53.9 ± 6.2	31.0 ± 7.5	31.3 ± 6.4	6.2 ± 4.8
Within size class niche overlap				
Small	34.0 ± 15.0	39.6 ± 10.2	25.0 ± 13.5	0.6 ± 0.2
Medium	70.7 ± 9.8	52.4 ± 12.0	10.3 ± 3.6	6.2 ± 4.5
Large	49.7 ± 16.6	49.7 ± 16.6	18.5 ± 8.3	18.5 ± 8.3
Mean Total Overlap	**48.6 ± 4.3**	**41.1 ± 5.1**	**24.4 ± 3.9**	**15.4 ± 4.4**

Walleye showed minimal shifts in isotopic niche with increasing size, which suggests that as a population their diet and resource use is fairly consistent throughout their lives. While no isotopes showed any significant trends with size during the spring, δ^{15}N and δ^{13}C increased significantly with body size during the fall, indicating an increase in trophic position and the use of benthic or littoral resources as fish got larger. The lack of trends in isotopes with body size during the spring, could be the result of a high abundance of prey (e.g. zooplankton, larval

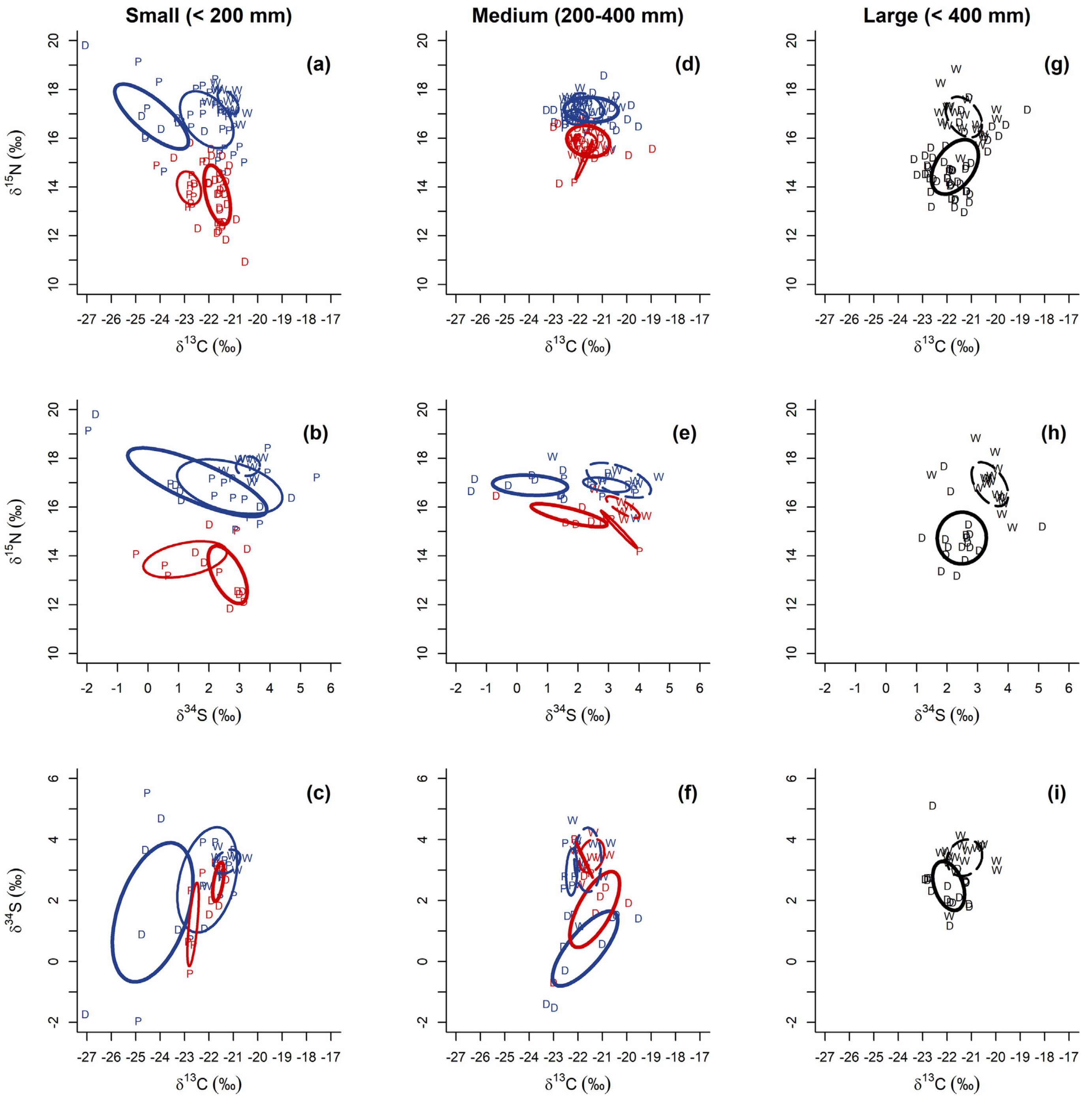

Fig. 4. SIBER stable isotope ellipses estimating the variation in niche among species (freshwater drum: D's and thick solid lines, walleye: W's and dashed lines, and white perch: P's and thin solid lines) and seasons (spring: blue, fall: red, year-round: black) at different size classes (Small <200 mm [a-c], Medium 200-400 mm [d-f], and Large >400 mm [g-i]) for $\delta^{13}C$ and $\delta^{15}N$ (top), $\delta^{34}S$ and $\delta^{15}N$ (middle), and $\delta^{13}C$ and $\delta^{34}S$ (bottom). Ellipses represent the standard ellipses area (SEA_B) of each niche. No large white perch or small fall walleye were caught during the study period; thus, they were omitted from the analysis.

fish, fish eggs) in the system during the spring and early summer due to the spring algal bloom, allowing conspecifics to target isotopically similar abundant prey (Pothoven et al., 2009; Wu and Culver, 1992). Walleye shift to a piscivorous diet at small sizes (~20–80 mm; Galarowicz et al., 2006; Graeb et al., 2005), and because juvenile piscivores often feed on larval fish that are isotopically similar to their parents (Vander Zanden et al., 2004), a trend of increasing trophic position with body size during the spring could be masked as a result. During the fall, increases in trophic position with body size could be related to a reduction in the abundance of small prey (e.g. larval fish), and the gape limitation of smaller individuals, restricting their diet to smaller prey fish or large benthic invertebrates (Gopalan et al., 1998; Wu and Culver, 1992). Additionally, increasing $\delta^{13}C$ reflected an increase in benthic or littoral resource use and could indicate increased mobility in larger fish which allows them to use a larger area to forage within (i.e. habitat coupling; Schindler and Scheuerell, 2002; Vadeboncoeur et al., 2002). Overall, the patterns (or lack thereof) of resource use as measured by stable isotopes with body size show the significance of seasonal differences in prey abundance in shaping a species niche.

White perch had consistent resource use across size classes during the spring, however, niche area decreased significantly with increasing size (e.g. $\delta^{13}C$ and $\delta^{15}N$ niche area, small: 3.8‰^{2}, medium: 0.5‰^{2}), suggesting that small white perch as a population are generalists (i.e. consume a wide variety of prey) but are specialists (i.e. consume limited diet items) at an individual level (Nawrocki et al., 2016; Quevedo et al., 2009), and that as they get larger their diets become more similar. Indeed, this can be observed in Fig. 3, with smaller individuals exhibiting a large variation in isotopes which decreases as fish get larger. Additionally, white perch was the only species to exhibit a significant increase in pelagic habitat use with length, as indicated by δ^{34}S during the fall. This agrees with what is known about the feeding ecology of white perch, as small white perch often feed on a combination of benthic invertebrates and zooplankton, but fish and zooplankton become more important diet items as they grow larger (Guzzo et al., 2013; Parrish and Margraf, 1990; Scott and Crossman, 1998).

Isotopic niche overlap among species was smaller in the fall than in the spring, demonstrating the importance of resource availability for fish species in Lake Erie, and likely other freshwater ecosystems, consistent with past research (Brush et al., 2012; Pothoven et al., 2009; Stockwell et al., 2014). In this study, the decline in interspecific niche overlap with size during the spring could be the result of a combination of factors such as small fish foraging on similar diet items due to gape size limitations (Schael et al., 1991), or small fish using similar habitat to avoid predation (Werner and Gilliam, 1984). Medium and large fish will have mostly escaped predation risk and be less gape size limited than smaller conspecifics, which means they have more freedom to use their preferred habitats and prey, allowing them to partition resources more effectively (Morrison et al., 1997; Overman and Parrish, 2001; Schael et al., 1991). Niche overlap increased with size among species in the fall, conceivably due to a greater abundance of prey such as larval fish, zooplankton, or benthic invertebrates during the late spring and early summer months because of the spring phytoplankton bloom and spawning season. This could indicate resources are less limiting during the spring, allowing for species diets and resource use to overlap more without encountering inter- or intra-specific competition (Pothoven et al., 2009; Wu and Culver, 1992).

While the three studied fish species partitioned resources in Lake Erie based on stable isotopes, how they partitioned resources (i.e. trophic position, habitat) changed depending on size class, highlighting the importance of body size in determining isotopic niche. As expected based on their described feeding ecology in past research (Bur, 1982; Hartman and Margraf, 1992), large fish (> 400 mm) partitioned resources through both trophic position and habitat (δ^{15}N, δ^{34}S), with freshwater drum occupying a lower trophic position (lower δ^{15}N) and using more benthic resources (lower δ^{34}S) than walleye. Similar patterns of resource partitioning were observed in small fish, with one key difference; small freshwater drum appeared to be using more pelagic resources than white perch and walleye compared with baseline δ^{13}C and δ^{34}S during the spring, although they had more benthic δ^{13}C and δ^{34}S during the fall. These changes in niche from spring to fall are consistent with diet studies on young-of-the year white perch and freshwater drum in Lake Erie which indicated that, while both species undergo a diet shift from zooplankton to benthic invertebrates, freshwater drum shift to foraging on benthic invertebrates earlier in the season than white perch, and that there is minimal overlap within their diets as a result (Gopalan et al., 1998). Medium fishes in our study partitioned resources predominantly through habitat use (δ^{13}C, δ^{34}S), with little differentiation between niche through trophic position, unlike the other two size classes. Medium freshwater drum had a δ^{34}S value close to benthic invertebrates (Chironimidae, *Hexagenia* spp., and Dreissenidae) and white perch had the most pelagic δ^{13}C value compared with seston which agrees with what is known about the feeding ecology of both freshwater drum and white perch (Bur, 1982; Parrish and Margraf, 1990). In many cases, differences in resource use among species across size classes would have gone unnoticed if δ^{34}S had been omitted from analysis because the three species had similar δ^{13}C (e.g. medium and large size classes).

Conclusions

In this study, we found evidence that fish species with similar sizes as adults but with differing foraging ecologies partitioned resources but this varied seasonally and with changing body size. Less niche overlap in fall suggested that resource partitioning was more important at this time, but also suggest that resource availability could play a role in trophic interactions among these species. Intraspecific resource utilization within species demonstrated that generalizing a species ecological role based on adult (e.g. large body size) foraging ecology could mask important changes in a species foraging ecology at smaller sizes. Additionally, changes in niche area may indicate shifts in resource use at the population level because smaller individuals may feed on a wide variety of prey as a population and specialize on the individual level (generalist population, large niche area) but diet becomes more similar at the individual level at larger sizes indicated by smaller niche size. Finally, as is consistent with other recent studies (e.g. Solomon et al., 2011; Ofukany et al., 2014; Colborne et al., 2016), the addition of a third isotope to our analysis improved the resolution of trophic and species relationships observed.

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References

Amundsen, P.A., Bøhn, T., Popova, O.A., Staldvik, F.J., Reshetnikov, Y.S., Kashulin, N.A., Lukin, A.A., 2003. Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. Hydrobiologia 497, 109–119. https://doi.org/10.1023/A:1025465705717.

Boecklen, W.J., Yarnes, C.T., Cook, B.A., James, A.C., 2011. On the use of stable isotopes in trophic ecology. Annu. Rev. Ecol. Evol. Syst. 42, 411–440. https://doi.org/10.1146/annurev-ecolsys-102209-144726.

Brewster, J.D., Giraldo, C., Swanson, H., Walkusz, W., Loewen, T.N., Reist, J.D., Stern, G.A., Loseto, L.L., 2016. Ecological niche of coastal Beaufort Sea fishes defined by stable isotopes and fatty acids. Mar. Ecol. Prog. Ser. 559, 159–173. https://doi.org/10.3354/meps11887.

Brush, J.M., Fisk, A.T., Hussey, N.E., Johnson, T.B., Sprules, W.G., 2012. Spatial and seasonal variability in the diet of round goby (*Neogobius melanostomus*): stable isotopes indicate that stomach contents overestimate the importance of dreissenids. Can. J. Fish. Aquat. Sci. 69, 573–586. https://doi.org/10.1139/f2012-001.

Bur, M.T., 1982. Food of freshwater drum in western Lake Erie. J. Great Lakes Res. 8, 672–675. https://doi.org/10.1016/S0380-1330(82)72007-6.

Bur, M.T., 1984. Growth, reproduction, mortality, distribution, and biomass of freshwater drum in Lake Erie. J. Great Lakes Res. 10, 48–58. https://doi.org/10.1016/S0380-1330(84)71806-5.

Byström, P., Persson, L., Wahlström, E., Westman, E., 2003. Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. J. Anim. Ecol. 72, 156–168. https://doi.org/10.1046/j.1365-2656.2003.00681.x.

Byström, P., Andersson, J., Persson, L., De Roos, A.M., 2004. Risk limitation and foraging-predation resource and habitat use in young Arctic char. Oikos 104, 109–121.

Cabral, H.N., Lopes, M., Loeper, R., 2002. Trophic niche overlap between flatfishes in a nursery area on the Portuguese coast. Sci. Mar. 66, 293–300. https://doi.org/10.3989/scimar.2002.66n3293.

Campbell, L.M., Thacker, R., Barton, D., Muir, D.C.G., Greenwood, D., Hecky, R.E., 2009. Re-engineering the eastern Lake Erie littoral food web: the trophic function of non-indigenous Ponto-Caspian species. J. Great Lakes Res. 35, 224–231. https://doi.org/10.1016/j.jglr.2009.02.002.

Colborne, S.F., Rush, S.A., Paterson, G., Johnson, T.B., Lantry, B.F., Fisk, A.T., 2016. Estimates of lake trout (*Salvelinus namaycush*) diet in Lake Ontario using two and three isotope mixing models. J. Great Lakes Res. 42, 695–702. https://doi.org/10.1016/j.jglr.2016.03.010.

Corkum, L., 2010. Fishes of Essex County and Surrounding Waters. Essex County Field Naturalists' Club, Windsor.

Croisetière, L., Hare, L., Tessier, A., Cabana, G., 2009. Sulphur stable isotopes can distinguish trophic dependence on sediments and plankton in boreal lakes. Freshw. Biol. 54, 1006–1015. https://doi.org/10.1111/j.1365-2427.2008.02147.x.

Eklöv, P., Svanbak, R., 2006. Predation risk influences adaptive morphological variation in fish populations. Am. Nat. 167, 440–452. https://doi.org/10.1086/499544.

Eloranta, A.P., Kahilainen, K.K., Jones, R.I., 2010. Seasonal and ontogenetic shifts in the diet of Arctic charr Salvelinus alpinus in a subarctic lake. J. Fish Biol. 77, 80–97. https://doi.org/10.1111/j.1095-8649.2010.02656.x.

French, J.R.P., Bur, M.T., 1996. The effect of zebra mussel consumption on growth of freshwater drum in Lake Erie. J. Freshw. Ecol. 11, 283–289. https://doi.org/10.1080/02705060.1996.9664450.

Fry, B., 2007. Stable Isotope Ecology. Springer Science, New York.

Fry, B., Baltz, D.M., Benfield, M.C., Fleeger, J.W., Gace, A., Haas, H.L., Quiñones-Rivera, Z.J., 2003. Stable isotope indicators of movement and residency for brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. Estuaries 26, 82–97. https://doi.org/10.1007/BF02691696.

Galarowicz, T.L., Adams, J.A., Wahl, D.H., 2006. The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. Can. J. Fish. Aquat. Sci. 63, 1722–1733. https://doi.org/10.1139/f06-073.

Garton, D.W., Payne, C.D., Montoya, J.P., 2005. Flexible diet and trophic position of dreissenid mussels as inferred from stable isotopes of carbon and nitrogen. Can. J. Fish. Aquat. Sci. 62, 1119–1129. https://doi.org/10.1139/f05-025.

Gopalan, G., Culver, D.A., Wu, L., Trauben, B.K., 1998. Effects of recent ecosystem changes on the recruitment of young-of-the-year fish in western Lake Erie. Can. J. Fish. Aquat. Sci. 55, 2572–2579. https://doi.org/10.1139/f98-130.

Graeb, B.D., Galarowicz, T., Wahl, D.H., Dettmers, J.M., Simpson, M.J., 2005. Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators. Can. J. Fish. Aquat. Sci. 62, 2010–2020. https://doi.org/10.1139/f05-112.

Guzzo, M.M., Haffner, G.D., Sorge, S., Rush, S.A., Fisk, A.T., 2011. Spatial and temporal variabilities of δ^{13}C and δ^{15}N within lower trophic levels of a large lake: implications for estimating trophic relationships of consumers. Hydrobiologia 675, 41–53. https://doi.org/10.1007/s10750-011-0794-1.

Guzzo, M.M., Haffner, G.D., Legler, N.D., Rush, S.A., Fisk, A.T., 2013. Fifty years later: trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. Biol. Invasions 15, 1695–1711. https://doi.org/10.1007/s10530-012-0401-z.

Hartman, W.L., 1972. Lake Erie: effects of exploitation, environmental changes and new species on the fishery resources. J. Fish. Res. Board Canada 29, 899–912.

Hartman, K.J., Margraf, F.J., 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. Trans. Am. Fish. Soc. 121, 245–260. https://doi.org/10.1577/1548-8659(1992)121<0245.

Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93, 145–159.

International Joint Commission, 2014. A Balanced Diet for Lake Erie: Reducing Phosphorus Loadings and Harmful Algal Blooms (Report of the Lake Erie Ecosystem Priority).

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Layman, C., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88, 42–48.

Mittelbach, G.G., 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65, 499–513.

Mittelbach, G.G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences. Can. J. Fish. Aquat. Sci. 55, 1454–1465. https://doi.org/10.1139/cjfas-55-6-1454.

Morrison, T.W., Lynch, W.E., Dabrowski, K., 1997. Predation on zebra mussels by freshwater drum and yellow perch in western Lake Erie. J. Great Lakes Res. 23, 177–189. https://doi.org/10.1016/S0380-1330(97)70895-5.

Morrison, H.A., Whittle, D.M., Haffner, G.D., 2000. The relative importance of species invasions and sediment disturbance in regulating chemical dynamics in western Lake Erie. Ecol. Model. 125, 279–294. https://doi.org/10.1016/S0304-3800(99)00189-1.

Nawrocki, B., Colborne, S.F., Yurkowski, D.J., Fisk, A.T., 2016. Foraging ecology of bowfin (*Amia calva*), in the Lake Huron-Erie Corridor of the Laurentian Great Lakes: individual specialists in generalist populations. J. Great Lakes Res. 42, 1452–1460. https://doi.org/10.1016/j.jglr.2016.08.002.

Newsome, S.D., del Rio, C.M., Bearhop, S., Phillips, D.L., 2007. A niche for isotope ecology. Front. Ecol. Environ. 5, 429–436. https://doi.org/10.1890/060150.01.

Ng, C.A., Berg, M.B., Jude, D.J., Janssen, J., Charlebois, P.M., Amaral, L.A., Gray, K., 2008. Chemical amplification in an invaded food web: seasonality and ontogeny in a high-biomas, low-diversity ecosystem. Environ. Toxicol. Chem. 27, 2186–2195.

Ofukany, A.F.A., Wassenaar, L.I., Bond, A.L., Hobson, K.A., 2014. Defining fish community structure in Lake Winnipeg using stable isotopes (δ^{13}C, δ^{15}N, δ^{34}S): implications for monitoring ecological responses and trophodynamics of mercury & other trace elements. Sci. Total Environ. 497–498, 239–249. https://doi.org/10.1016/j.scitotenv.2014.07.125.

Overman, N.C., Parrish, D.L., 2001. Stable isotope composition of walleye: ^{15}N accumulation with age and area-specific differences in δ^{13}C. Can. J. Fish. Aquat. Sci. 58, 1253–1260. https://doi.org/10.1139/cjfas-58-6-1253.

Parrish, D., Margraf, J., 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined from feeding and growth. Can. J. Fish. Aquat. Sci. 47, 1779–1787.

Peterson, B.J., Howarth, R.W., 1987. Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island. Georgia. Limnol. Oceanogr. 32, 1195–1213. https://doi.org/10.4319/lo.1987.32.6.1195.

Phillips, D.L., Gregg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136, 261–269. https://doi.org/10.1007/s00442-003-1218-3.

Pianka, E.R., 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 1, 1–8.

Pianka, E.R., 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. 71, 2141–2145. https://doi.org/10.1073/pnas.71.5.2141.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. [1] 83, 703–718, https://doi.org/10.2307/3071875.

Post, D.M., 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. Ecology 84, 1298–1310.

Pothoven, S.A., Vanderploeg, H.A., Ludsin, S.A., Höök, T.O., Brandt, S.B., 2009. Feeding ecology of emerald shiners and rainbow smelt in Central Lake Erie. J. Great Lakes Res. 35, 190–198. https://doi.org/10.1016/j.jglr.2008.11.011.

Quevedo, M., Svanbäck, R., Eklöv, P., 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. Ecology 90, 2263–2274.

R Core Team, 2017. R: A Language and Environment for Statistical Computing.

Raby, G.D., Vandergoot, C.S., Hayden, T.A., Faust, M.D., Kraus, R.T., Dettmers, J.M., Cooke, S.J., Zhao, Y., Fisk, A.T., Krueger, C.C., 2018. Does behavioural thermoregulation underlie seasonal movements in Lake Erie walleye? Can. J. Fish. Aquat. Sci. 496, 1–9. https://doi.org/10.1139/cjfas-2017-0145.

Ross, S.T., 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 1986, 352–388.

Sánchez-Hernández, J., Nunn, A.D., Adams, C.E., Amundsen, P.A., 2018. Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. Biol. Rev. 94, 539–554. https://doi.org/10.1111/brv.12468.

Schaeffer, J.S., Margraf, F.J., 1986. Food of white perch (*Morone americana*) and potential for competition with yellow perch (*Perca flavescens*) in Lake Erie. Ohio J. Sci. 86, 26–29.

Schael, D.M., Rudstam, L.G., Post, J.R., 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). Can. J. Fish. Aquat. Sci. 48, 1919–1925. https://doi.org/10.1139/f91-228.

Schindler, D.E., Scheuerell, M.D., 2002. Habitat coupling in lake ecosystems. Oikos 98, 177–189.

Schmidt, S.N., Harvey, C.J., Vander Zanden, M.J., 2011. Historical and contemporary trophic niche partitioning among Laurentian Great Lakes coregonines. Ecol. Appl. 21, 888–896.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science (80-.). 185, 27–39.

Scott, W.B., Crossman, E.J., 1998. Freshwater Fishes of Canada. 5th ed. Galt House Publications Ltd, Oakville.

Solomon, C.T., Carpenter, S.R., Clayton, M.K., Cole, J.J., Coloso, J.J., Pace, M.L., Vander Zanden, M.J., Weidel, B.C., 2011. Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope Bayesian mixing model. Ecology 92, 1115–1125. https://doi.org/10.1890/i0012-9658-92-5-1115.

Stanley, J.G., Danie, D.S., 1983. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (North Atlantic) - White Perch (Lafayette).

Stockwell, J.D., Yule, D.L., Hrabik, T.R., Sierszen, M.E., Isaac, E.J., 2014. Habitat coupling in a large lake system: delivery of an energy subsidy by an offshore planktivore to the nearshore zone of Lake Superior. Freshw. Biol. 59, 1197–1212. https://doi.org/10.1111/fwb.12340.

Swanson, H.K., Lysy, M., Power, M., Stasko, A.D., Johnson, J.D., Reist, J.D., 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. Ecology 96, 318–324.

Swedburg, D.V., Walburg, C.H., 1970. Spawning and early life history of the freshwater drum in Lewis and Clark Lake, Missouri River. Trans. Am. Fish. Soc. 99, 560–570. https://doi.org/10.1577/1548-8659(1970)99<560:SAELHO>2.0.CO;2.

Vadeboncoeur, Y., Vander Zanden, M.J., Lodge, D.M., 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. Bioscience 52, 44. https://doi.org/10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2.

Vander Zanden, M.J., Casselman, J.M., Rasmussen, J.B., 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401, 464–467. https://doi.org/10.1038/46762.

Vander Zanden, M.J., Cabana, G., Rasmussen, J.B., 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ^{15}N) and literature dietary data. Can. J. Fish. Aquat. Sci. 54, 1142–1158. https://doi.org/10.1139/f97-016.

Vander Zanden, M.J., Hulshof, M., Ridgway, M.S., Rasmussen, J.B., 2004. Application of stable isotope techniques to trophic studies of age-0 smallmouth bass. Trans. Am. Fish. Soc. 127, 729–739. https://doi.org/10.1577/1548-8659(1998)127<0729:AOSITT>2.0.CO;2.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Ecology 15, 393–425.

Werner, E.E., Hall, D.J., 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69, 1352–1366.

White, T.C.R., 1985. When is a herbivore not a herbivore? Oecologia 67, 596–597. https://doi.org/10.1007/BF00790034.

Wu, L., Culver, D.A., 1992. Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): a size-related response to zooplankton density. Can. J. Fish. Aquat. Sci. 49, 1932–1937. https://doi.org/10.1139/f92-214.

Xue, Y., Jin, X., Zhang, B., Liang, Z., 2005. Seasonal, diel and ontogenetic variation in feeding patterns of small yellow croaker in the Central Yellow Sea. J. Fish Biol. 67, 33–50. https://doi.org/10.1111/j.0022-1112.2005.00677.x.