Journal of Great Lakes Research 42 (2016) 1452–1460

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Foraging ecology of Bowfin (*Amia calva*), in the Lake Huron–Erie Corridor of the Laurentian Great Lakes: Individual specialists in generalist populations

Brent Nawrocki, Scott F. Colborne *, David J. Yurkowski, Aaron T. Fisk

Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada

ARTICLE INFO

Article history:
Received 13 January 2016
Accepted 2 August 2016
Available online 18 August 2016

Communicated by Michael Sierszen

Index words:
Bowfin
Foraging ecology
Individual specialization

ABSTRACT

The foraging ecology of bowfin (*Amia calva*) is relatively unknown in the Laurentian Great Lakes despite comparable abundances to other piscivorous predators. We investigated bowfin foraging ecology by determining trophic position, isotopic niche size, dietary proportions, and the degree of individual specialization at two locations in the Lake Huron–Erie Corridor using carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes and stomach content analysis. Trophic position did not differ between Mitchell's Bay (4.2) and Peche Island (4.3) using $\delta^{15}N$, but both sites had large ranges in individual estimates (range = 2.8). Bowfin isotopic niche size was large across site, season, and tissue, suggesting a generalist feeding strategy at the population level. However, bowfin had greater between-individual than within-individual variation accounting for 72% and 88% of total niche size at Mitchell's Bay and Peche Island, respectively, suggesting specialist feeding strategies at the individual level. Stable isotope mixing models for Peche Island showed high proportions of crayfish (54%) and small fish (*Cyprinidae* spp., *Lepomis* spp.; 38%) in their diet, consistent with high stomach content prevalence for crayfish (spring = 75%, fall = 10%) and small fishes (spring = 19%, fall = 33%) at Peche Island. Overall, our analysis of bowfin suggests a complex foraging ecology with bowfin acting as generalist predators at the species level but exhibiting a high degree of individual specialization, warranting further study to assess their trophic role in this diverse ecosystem of conservation concern.

Introduction

The Laurentian Great Lakes are characterized by a high degree of biodiversity, numerous top predator fish species, and complex trophic interactions relative to other temperate freshwater systems (Baustian et al., 2014; Jude and Pappas, 1992). As well, the Great Lakes support a $7 billion dollar (USD) annual fishery that primarily focuses on high trophic level piscivorous fish species, e.g., walleye (*Sander vitreus*) and Chinook salmon (*Oncorhynchus tshawytsha*) (Landsman et al., 2011). Over the past two centuries, the Great Lakes watershed has been a focal point of human activities and associated stressors, including over-harvesting of species such as lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*; O'Brien et al., 2014; Regier et al., 1999), the introduction of numerous aquatic invasive species (e.g., *Dreissena polymorpha*; Nalepa et al., 1996), changes to nutrient budgets and productivity (Dove and Chapra, 2015), and the introduction of toxic chemicals (e.g., polychlorinated biphenyls; Baustian et al., 2014). The cumulative effects of these stressors likely have major implications to the stability of Great Lakes food webs (O'Brien et al., 2014).

Understanding the foraging ecology of higher trophic level species is fundamental to quantifying the trophic structure of food webs and understanding the resilience and stability of ecosystems (McCann et al., 1998), particularly those facing anthropogenic stressors (Vander Zanden et al., 1999a). High trophic level species, including piscivores, can act as a trophic stabilizing force within fish communities (Scarnecchia, 1992), in part because they may be able to fill ecological niches in the absence of other predator species because of their dietary flexibility (Baustian et al., 2014). Despite the integral role piscivorous predators may play in the Great Lakes, the foraging ecology of many of these species remain poorly characterized.

Bowfin (*Amia calva*), a piscivorous predator with abundances in the Great Lakes comparable to other predators including northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) (Lapointe, 2014), have rarely been studied, likely due to the perception that they are a "nuisance fish" and the belief that they are not economically or ecologically relevant (Koch et al., 2009; Mundahl et al., 1998). This species is the only remaining species of the order Amiiformes, dating back more than 150 million years. Stomach content analyses in other regions, e.g., rivers in the Atlantic coastal region (Ashley and Rachels, 1999), and habitat types, e.g., freshwater rivers and estuaries (Jordan and Arrington, 2001, 2014; Mundahl et al., 1998), describe bowfin as generalists that feed on a variety of small forage fish and benthic invertebrates, especially crayfish (*Humilis* spp.). However, other studies experimentally introduced bowfin to a small temperate lake in an unsuccessful attempt to minimize overgrazing by bluegill (*Lepomis machrochirus*), suggesting that bowfin may selectively consume crayfish and small minnows and not consume a wide range of prey as

---

* Corresponding author. Tel.: +1 519 253 3000x4730.
E-mail address: scolbor@uwindsor.ca (S.F. Colborne).

http://dx.doi.org/10.1016/j.jglr.2016.08.002
0380-1330/© 2016 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

previously believed (Breder, 1928; Mundahl et al., 1998). However, it is not known whether bowfin exhibit generalist foraging strategies at the individual or population level. Populations that are described as generalists may actually be composed of individuals that use a much smaller subset of the available resources and, therefore, are more accurately described as resource specialists (e.g., Bolnick et al., 2002, 2003). Assessing the foraging ecology of bowfin may provide insight into the role of this understudied, yet abundant predatory fish in the Great Lakes.

Many diet studies of fish, including bowfin outside of the Great Lakes (Ashley and Rachels, 1999; Jordan and Arrington, 2001, 2014), have relied on stomach content analysis to provide quantitative estimates of prey items and assess specific short-term diet. Stomach contents can provide a quantitative "snapshot" of what an individual has most recently consumed through direct examination of prey items; however, stomach content analysis is subject to multiple biases including empty stomachs, differential prey digestion rates, and identification issues due to digestion (Hyslop, 1980). It is now common to use both stomach contents and stable isotope analysis (SIA) to overcome some of the stomach content biases and to infer diet over longer time scales, i.e., weeks to months depending on the tissue sampled, providing insight into how resource use changes over time (Boecklen et al., 2011). Stable isotopes of carbon (δ^{13}C) are used to indicate energy source because on average they change by <1‰ between trophic levels (e.g., Vander Zanden and Rasmussen, 2001) and differ between primary production pathways, e.g., C3 and C4 plants (Fry, 2007). In temperate freshwater systems, δ^{13}C is used as an indicator of littoral macrophyte or pelagic phytoplankton sources of primary productivity (Newsome et al., 2007). Stable nitrogen isotopes (δ^{15}N) are used to estimate trophic position (TP) because it predictably increases between prey and consumer (Post, 2002), with a gradual decline in the δ^{15}N increase (diet-tissue discrimination factor; DTDF) between consumers and prey at higher trophic levels (Hussey et al., 2014). Thus, in temperate freshwater systems, δ^{15}N and δ^{13}C provide information about both energy source/habitat use and vertical food web position for an individual or population, and this information can be combined to model and compare the isotopic niche size, a proxy for comparing the ecological niche of individuals and populations (Layman et al., 2007; Newsome et al., 2009). Stable isotopes can also be used in mixing models to estimate individual niche variation (Newsome et al., 2009) and dietary proportions of specific prey species (Stock and Semmens, 2013).

The objective of this study was to assess bowfin foraging ecology within the Laurentian Great Lakes, specifically within the Lake Huron–Erie Corridor, using a combination of stomach content and stable isotope analyses of muscle and liver tissue. Based on dietary studies in other regions we expected the Great Lakes population of bowfin to exhibit generalist foraging patterns with diets that included a diverse assortment of small forage fish and benthic invertebrates. We also expected that, if bowfin exhibited a generalist foraging tactic, there would be similar trophic positions and diets across sites and over the primary foraging period of the year, i.e., spring to summer, which required sampling bowfin from multiple sites and at multiple time periods. We tested these predictions by determining bowfin (i) trophic position, (ii) isotopic niche size and variation, (iii) quantitative prey consumption, and (iv) degree of individual specialization for two sites along the Huron-Erie Corridor over two seasons.

Methods

Study sites and sample collection

Bowfin were collected at two sites in the Lake Huron–Erie Corridor: (1) the head of the Detroit River at the south side of Peche Island (~42.35°N, 82.92°W) in spring (20 April to 20 June 2014; $n = 12$, 2 male and 10 female) and fall (20 September to 14 November 2014; $n = 11$, 6 male and 5 female), and (2) the northeastern basin of Lake St. Clair at Mitchell's Bay (42.48°N, 82.42°W) in fall only (19–25 October 2014; $n = 23$, 14 male and 9 female). Both sites are highly productive nearshore habitats with well-mixed water columns, have seasonally constant water flow, and are well-regarded for recreational fishing due to the high biodiversity of game fish (Baustian et al., 2014; Hondorp et al., 2014). Mitchell's Bay is a wetland region with an average depth of 3.4 m, dense macrophyte growth, stagnant water, and a combination of terrestrial and aquatic species (Leach, 1991), as compared to waters around Peche Island that are morphologically similar to lakes with both a littoral and pelagic habitat and is more influenced by urbanization (Lapointe, 2014).

Bowfin and their potential prey items were collected using a single anode boat electrofisher with a direct current of 4.0 A with a pulse frequency of 30–60 Hz. Zebra mussels (*Dreissena polymorpha*) were collected using a ponar sampler. All fish were euthanized with an overdose of tricaine methanesulfonate (MS-222) solution, approximately 75 mg MS-222 per 1 L of water. Total length (bowfin size range: 35–70 cm) and mass were measured for each fish, i.e., bowfin and prey fish, and a 1 cm^3 sample of muscle tissue was removed anterior to the dorsal fin and stored frozen at −20 °C until stable isotope analysis. The entire liver was also collected, as well as whole stomachs which were removed and frozen for diet analysis.

Stomach content analysis

To estimate the contribution of specific prey types to bowfin diet, we used stomach content analysis. Prey species were identified to the lowest possible taxonomic level and % frequency of occurrence (%F, the occurrence of a specific prey type across all stomachs), % by number (%N, the amount of a particular prey species in relation to all prey species across all stomachs), and percentage by weight (%W, the percent weight contribution of a particular species across total mass of all prey species in all stomachs) were used to determine the Index of Relative Importance (IRI) for each prey type (Hyslop, 1980) and is expressed on a percent basis (%IRI) (e.g., Brush et al., 2012; Cortes et al., 1996) using the equations:

$$IRI = (\%N \times \%W) + \%F \tag{1}$$

and

$$\%IRI_i = \frac{100\, IRI_i}{\sum_{i=1}^{n} IRI_i} \tag{2}$$

Dietary trophic position (TP_{SCA}) from stomach contents was calculated for each bowfin sampling group (Peche Island—spring, Peche Island—fall, Mitchell's Bay—fall) using the equation:

$$TP_{SCA} = 1 + \left(\sum_{i=1}^{x} \%IRI_i \, x \, TP_i \right) \tag{3}$$

where literature TPs of prey items (TP_i), as well as proportional %IRI values for each corresponding prey item ($\%IRI_i$) are summed for each bowfin group (Cortes, 1999). Unidentifiable material present in the stomachs of bowfin was not included in TP_{SCA} calculations.

Stable isotope analysis

All samples were lyophilized at −48 °C and 133 × 10^3 mbar for 48 h, and homogenized by hand using a mortar and pestle. Lipids are depleted in ^{13}C relative to pure protein samples, a potential bias when interpreting δ^{13}C values (Bligh and Dyer, 1959; Post et al., 2007); to remove this effect, lipids were extracted from the homogenized fish tissues using a 2:1 chloroform:methanol mixture after which samples were dried and re-ground by hand. Samples were then weighed into tin cups to obtain a final sample mass of 400–600 µg. The carbon and nitrogen isotopic compositions of each sample 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) in the Trophic Ecology Laboratory at the Great Lakes Institute for Environmental Research, University of Windsor. Stable isotope values are reported as units per mil (δ) and were calculated using the equation:

$$\delta X = \left(\left[\frac{Rsample}{Rstandard}\right] - 1\right) \times 1000$$

where X represents ^{13}C or ^{15}N and R is represented by ^{13}C:^{12}C and ^{15}N:^{14}N.

Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (AIR) were used as standard reference materials for δ^{13}C and δ^{15}N, respectively. Values of NIST standards run during the analysis of samples for this study for δ^{15}N were within 0.1‰ (NIST 8573), 0.4‰ (NIST 8548), and <0.1‰ (NIST 8549), and for δ^{13}C were within 0.2‰ (NIST 8542) and 0.1‰ (NIST 8573) of certified values. Precision for laboratory standards (NIST 1577c and tilapia muscle ($n = 221$ for each)), run after every 12 samples, were 0.1‰ for δ^{13}C and 0.2‰ for δ^{15}N. The sample reproducibility of replicate tissue samples (every 10 samples analyzed in triplicate) was within the acceptable ±0.2‰ range (0.1‰ for δ^{13}C and 0.1‰ for δ^{15}N, $n = 30$).

Mixing model diet contributions

A Bayesian stable isotope mixing model (MixSIAR, v 3.0.1; Stock and Semmens, 2013) was used to estimate proportional diet contributions of candidate prey types of bowfin at Peche Island. Mitchell's Bay was not included in the MixSIAR model due to limited prey sample numbers to accurately determine the model "source" variable. The "source" variables in the models were represented by the mean (±1 SD) and sample size of δ^{13}C and δ^{15}N values of common prey species. Individual t-tests were performed for each prey species to determine if there were significant differences in either δ^{13}C or δ^{15}N between spring and fall at Peche Island. Due to the similar δ^{13}C and δ^{15}N values for both bowfin muscle tissue and prey species (Student's t-tests, all $P > 0.06$, see ESM Table S1) between Peche Island sampling periods, we assumed seasonal consistency of all bowfin muscle tissue and prey species (see below), including crayfish and juvenile largemouth bass (*Micropterus salmoides*), which were not collected during both seasons. ANOVAs with Tukey's post hoc comparisons were used to determine differences in δ^{13}C and δ^{15}N values between the prey species collected. Based on previous studies (Ashley and Rachels, 1999; Jordan and Arrington, 2001, 2014), as well as the data we collected from stomach contents, we selected bluegill, pumpkinseed (*Lepomis gibbosus*), spottail shiner (*Notropis hudsonius*), crayfish, and juvenile largemouth bass as candidate prey species to be included in isotope mixing models of Peche Island bowfin. Northern pike, not a diet item of bowfin, was selected as a control.

The MixSIAR models were built using the candidate prey species and assumptions about the relationships between the isotopic values of a consumer and the food it consumes, i.e., DTDF. Based on multiple freshwater fish species from temperate environments, a DTDF of 0.47‰ for δ^{13}C values (Vander Zanden and Rasmussen, 2001) and 3.4‰ for δ^{15}N values were used for each prey species (Post, 2002). Each MixSIAR model was run for 5 chains, 10,000 iterations, and all results are presented as mean values with 95% Bayesian credibility intervals (95% BCI).

Trophic position estimates using stable isotopes

Trophic position estimates based on δ^{15}N stable isotopes ($TP_{\delta 15N}$) were determined for individual bowfin from each season and site using a variable DTDF model for white muscle tissue (see Hussey et al., 2014, for details). We based our estimates on a model that incorporates the decrease in Δ^{15}N with increasing dietary δ^{15}N, i.e., those generally associated with higher trophic levels. Trophic position was calculated using the equation:

$$TP_{\delta 15N} = \frac{\log\left(\delta^{15}N_{lim} - \delta^{15}N_{baseline}\right) - \log\left(\delta^{15}N_{lim} - \delta^{15}N_{consumer}\right)}{k} + TP_{baseline} \tag{4}$$

where the isotopic composition of each consumer is represented by $\delta^{15}N_{consumer}$, $\delta^{15}N_{baseline}$ is the mean composition of a known baseline consumer, and $TP_{baseline}$ represents the known TP of the baseline group (Hussey et al., 2014). Here we used the δ^{15}N values of zebra mussels, which were assigned a TP = 2 based on their classification as primary consumers (Vander Zanden et al., 1999b; Post, 2002). $\delta^{15}N_{lim}$ is the value at which nitrogen (^{15}N and ^{14}N) uptake is balanced by nitrogen excretion (i.e., $\Delta^{15}N = 0$ with each trophic level) and k is the rate at which $\delta^{15}N_{consumer}$ approaches $\delta^{15}N_{lim}$. Based on Hussey et al. (2014), we used values of 21.93 and 0.14 to represent $\delta^{15}N_{lim}$ and k, respectively.

All bowfin stable isotope data were determined to have normal distributions and equal variances using Shapiro–Wilk's tests and Levene's test, respectively. Individual t-tests found no significant differences in δ^{13}C (Student's t-test, $t_{21} = -0.6$; $P = 0.3$) or δ^{15}N ($t_{21} = 0.8$; $P = 0.2$) between the two seasons at Peche Island, for white muscle tissue (i.e., long isotopic turnover rate; Boecklen et al., 2011), thus eliminating season as a factor and allowing all samples to be grouped by site (Peche Island or Mitchell's Bay). However, bowfin liver δ^{15}N at Peche Island differed between seasons (Student's t-test, $t_{21} = 2.6$; $P = 0.01$), thus liver data were not combined by season. Analysis of covariance (ANCOVA) was used to compare bowfin TP across site with total body length as a covariate, as well as to compare δ^{13}C to body length with site as a covariate.

Isotopic niche area

To estimate the isotopic niche space occupied by bowfin at each site and sampling period, we used the SIBER (Stable Isotope Bayesian Ellipses in R) analysis package in SIAR v. 4.2 (Parnell et al., 2015) to generate standard ellipse areas (SEA_C) that represent the core 40% of the individuals measured (Jackson et al., 2011; Guzzo et al., 2013). The use of SEA_C provides insight into the positioning and orientation of ellipse area in two-dimensional isotopic space. We then estimated the niche size for each group, as well for baseline species zebra mussels, to then test for differences in niche size between locations and season using Bayesian inference that measured the standard ellipse (SEA_C) area over 10,000 iterations (SEA_B; Jackson et al., 2011). The niche size estimates are reported as the mean SEA_B values with 50, 75, and 95% Bayesian credibility intervals (BCI). We then used SEA_B to estimate the probability of niche size from group one being smaller than group two. We calculated the proportion of posterior estimates that were smaller than the other group relative to the total number posterior estimates (1×10^5).

Individual specialization

To test the degree of individual specialization in bowfin from both sites, we used linear mixed models to assess the effects of sex, total body length, and tissue type on bowfin δ^{13}C and δ^{15}N values. We corrected δ^{13}C and δ^{15}N values in bowfin white muscle and liver using mean diet-tissue discrimination factors established for fish (0.47‰ for δ^{13}C and 3.4 ‰ for δ^{15}N in white muscle—Post, 2002; Vander Zanden and Rasmussen, 2001; and 0.77‰ for δ^{13}C and 1.65‰ for δ^{15}N in liver—Caut et al., 2009) prior to analysis to eliminate the effect of tissue-specific differences. Tissue type represented the time scale of isotopic turnover for muscle (long-term turnover tissue) and liver (short-term turnover tissue). Due to repeated sampling per individual and to avoid pseudo-repeatability, sample ID was included as a random effect with fixed effects including sex, total body length, and tissue type. For each population and element, we used variance component analysis from the linear mixed models in the random effect term (i.e., fish ID) to estimate total observed variability in bowfin δ^{13}C and δ^{15}N values (total isotopic niche width—TINW) by summing the average intercept variability (i.e., between individual component; BIC) and the average isotopic variance within an individual (i.e., residual variability and within individual component; WIC). Variance components for δ^{13}C and δ^{15}N of each population were summed similar to Newsome et al. (2009, 2015) and Yurkowski et al. (2016). When BIC proportions were greater than WIC proportions, it indicated specialization among individuals, while a greater WIC than BIC suggests generalization across the population. The degree of individual specialization was calculated by the WIC/TINW ratio where values closer to 0 represent a high degree of individual specialization, values of 1 represent generalist foraging tactics. We interpret values ≤0.5 to represent individual specialization (Newsome et al., 2015).

All statistical analyses were performed using the statistical software package "R" (R Core Team, 2015). Linear mixed-effects models were performed using the nlme package v. 3.1–118 with $\alpha = 0.05$ (Pinheiro et al., 2015).

Results

Stomach contents

Of the 46 stomachs examined for stomach content analysis, 70% had measurable stomach contents ($n = 32$). The %IRI of bowfin stomach contents indicated that crayfish were the most prevalent prey item in the Peche Island (spring) group (%IRI = 75), while unidentifiable material accounted for the greatest %IRI contribution for both Peche Island (fall) (%IRI = 56) and Mitchell's Bay (fall) (%IRI = 39) (Table 1). The presence of vertebral columns within the unidentified material suggests the consumption of smaller fish species, but further identification was not possible. Crayfish were the only species to be present in bowfin stomachs across all three sampling groups, though the %IRI values varied (Mitchell's Bay—fall %IRI = 39 and Peche Island—fall = 10). Other prey items such as bluegill, pumpkinseed, juvenile largemouth bass, juvenile northern pike, juvenile bowfin, and yellow perch (*Perca flavescens*) were found in the stomach contents; however, they all had %IRI values <10 (see Table 1 for individual species %IRI).

Diet estimates from stable isotope mixing model

Individual t-tests of each candidate prey species revealed no significant intraspecific differences in δ^{13}C or δ^{15}N values of prey between seasons. One-way ANOVAs with Tukey's post hoc comparisons showed interspecific significant differences between prey types for either δ^{13}C or δ^{15}N (Table 4). Stable isotope mixing models (MixSIAR) of Peche Island bowfin estimated crayfish to be the largest dietary contributor (mean = 54%; 95% BCI = 16–80%), while juvenile largemouth bass and northern pike (control) were negligible in dietary proportions (mean ≤ 0.05% for each species; Table 4).

Trophic position estimates

Sex and body length did not significantly influence muscle δ^{15}N at Peche Island (ANCOVA, $F_{1,7} = 0.2$; $P = 0.6$) and Mitchell's Bay ($F_{1,19} = 0.5$; $P = 0.5$) in fall and were not considered in TP analysis. Due to the sex bias for Peche Island—spring bowfin, only body length did not significantly influence muscle δ^{15}N (ANOVA, $F_{1,10} = 0.001$; $P = 0.9$). There were significant differences in δ^{13}C with respect to standard body length ($F_{1,39} = 71.3$; $P < 0.001$), which were driven by differences in Peche Island—fall and Mitchell's Bay—spring (Tukey's HSD, $t = 5.9$, $P < 0.001$) and Peche Island—spring and Mitchell's Bay—fall ($t = 4.5$, $P < 0.001$). Estimates of Bowfin TP_{SCA} were similar across season and site (Peche Island—spring = 4.1, fall = 4.0; Mitchell's Bay—fall = 4.2). $TP_{\delta15N}$ were comparable to TP_{SCA} values and were not significantly

Table 1
Stomach contents of bowfin (*Amia calva*) collected at Peche Island in spring and fall, and Mitchell's Bay in fall. Prey number (%N), prey frequency (%F), and prey weight (%W) were all used to calculate an Index of Relative Importance (%IRI). Unidentifiable material was not included in %IRI calculation. See Methods for details.

Species	Functional feeding group	Literature trophic position	Peche Isle—spring ($n = 12$)				Peche Isle—fall ($n = 11$)				Mitchell's Bay—fall ($n = 23$)			
			%N	*%F*	*%W*	%IRI	*%N*	*%F*	*%W*	%IRI	*%N*	*%F*	*%W*	%IRI
Banded killifish[a]	Insectivores	3.3[1]	0	0	0	0	0	0	0	0	8.3	8.3	2.9	1.7
Spottail shiner[b]		2.7[2]	0.3	8.3	0.5	0.5	17.7	25.0	6.4	9.5	0	0	0	0
Yellow bullhead[c]		3.8[3]	0	0	0	0	0	0	0	0	16.7	16.7	13.8	9.0
Spotfin shiner[d]	Zoobenthivores	2.5[2]	0	0	0	0	5.9	12.5	7.4	2.6	0	0	0	0
Crayfish[e]		3.0[2]	44.8	50.0	36.4	75.1	17.7	12.5	34.4	10.3	33.3	33.3	33.2	39.1
Bluegill[f]	Omnivores	3.2[4]	7.1	16.7	36.4	11.9	0	0	0	0	0	0	0	0
Pumpkinseed[g]		3.3[2]	4.2	16.7	19.1	7.1	0	0	0	0	0	0	0	0
Round goby[h]		3.2[5]	0	0	0	0	29.4	25.0	23.7	21.0	8.3	8.3	1.1	1.4
Bowfin (juvenile)[i]	Piscivores	3.9[4]	0	0	0	0	0	0	0	0	8.3	8.3	6.4	2.2
Largemouth bass (juvenile)[j]		3.5[2]	25.0	8.3	3.2	3.9	0	0	0	0	8.3	8.3	5.0	2.0
Northern pike (juvenile)[k]		4.2[4]	3.1	8.3	0.4	0.5	0	0	0	0	0	0	0	0
Yellow perch[l]		3.7[2]	0	0	0	0	0	0	0	0	8.3	8.3	25.2	4.9
Unidentifiable material	–	–	0.6	8.3	4.1	1.0	29.4	62.5	28.1	56.7	41.7	41.7	12.5	39.8

[a] *Fundulus diaphanous.*
[b] *Notropis hudsonius.*
[c] *Ameirurus natalis.*
[d] *Cyprinella spiroptera.*
[e] *Humilis spp..*
[f] *Lepomis macrochirus.*
[g] *Lepomis gibbosus.*
[h] *Neogobius melanostomus.*
[i] *Amia calva.*
[j] *Micropterus salmoides.*
[k] *Esox Lucius.*
[l] *Perca flavescens.*
[1] Froese and Pauly, 2000.
[2] Vander Zanden et al., 1997.
[3] Turner, 1966.
[4] McLeod et al., 2015.
[5] Brush et al., 2012.

different between Peche Island ($TP_{\delta 15N} = 4.3$) and Mitchell's Bay ($TP_{\delta 15N} = 4.2$; $F_{1,42} = 1.57$, $P = 0.33$; Table 2), and there was no evidence of an interaction effect between TP and total body length ($F_{1,42} = 1.74$, $P = 0.19$). $TP_{\delta 15N}$ estimates ranged from 3.5 to 6.0 at Peche Island and 3.3–5.2 at Mitchell's Bay (Fig. 1).

Isotopic niche metrics

Stable isotopes of bowfin white muscle tissue at Peche Island had the smallest range in $\delta^{13}C$ (CR = 7.2‰) and the largest range in $\delta^{15}N$ (NR = 6‰), while the largest CR and smallest NR values were at Mitchell's Bay (CR = 8.6‰, NR = 4.6‰) (Table 2, Fig. 2a). In comparison, the lowest liver CR and NR values were at Peche Island (fall) (CR = 4.0‰, NR = 3.8‰), while the highest CR and NR ranges were at Peche Island (spring) (CR = 9.3‰) and Mitchell's Bay (NR = 6.2‰), respectively (Table 2, Fig. 2b).

Isotopic niche size estimates (SEA_B) varied between sites and was supported by a predictable pattern of increasing $\delta^{15}N$ between zebra mussels (baseline indicator) and bowfin at both Peche Island and Mitchell's Bay (Fig. 2.a, b). This inclusion of baseline zebra mussel stable isotopes provides context in regards to the orientation and positioning of bowfin within isotopic niche space relative to trophic level. Additionally, isotopic niche orientation (i.e., shape) remained consistent between bowfin muscle and liver tissue at both locations (Fig. 2.a, b). The probability that Peche Island bowfin niche size estimates (SEA_B) using muscle had smaller niche areas than Mitchell's Bay was 88% (Fig. 3.a). In comparison, Peche Island bowfin liver niche size was estimated to be smaller than Mitchell's Bay in only 11% of simulations for either season, while Peche Island (spring) was estimated to be smaller than Peche Island (fall) in 3% of simulations (Fig. 3b).

Individual specialization

The total BIC was larger than the WIC for both Mitchell's Bay (total intercept variance = 5.82) and Peche Island (total intercept variance = 5.04) accounting for 72% and 88% of total observed variability (TINW), respectively (Table 3). Bowfin TINW was larger at Mitchell's Bay (8.09) than at Peche Island (5.75) (Table 3). The degree of individual specialization (WIC/TINW) for both the Mitchell's Bay and Peche Island populations was high (0.28 and 0.12) indicating high levels of individual specialization in both populations (Table 3).

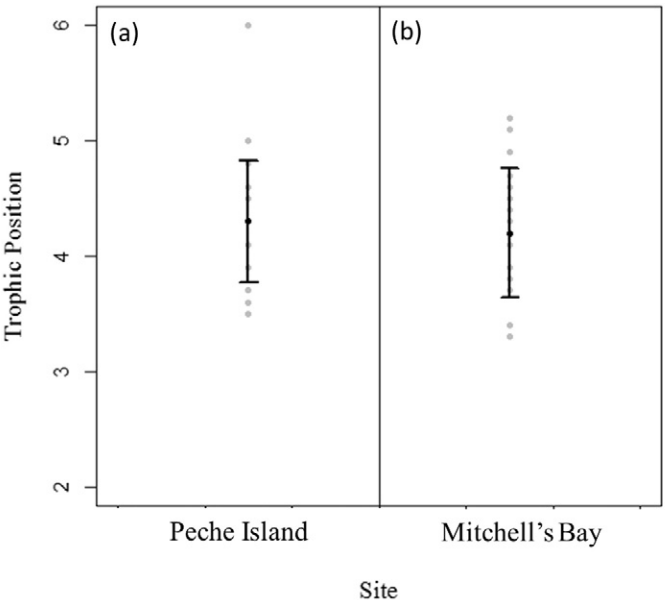

Fig. 1. Trophic position of individuals (grey dots) and means (± 1 SD, black dots) of bowfin (*Amia calva*) white muscle tissue at (a) Peche Island and (b) Mitchell's Bay in the Lake Huron–Erie Corridor.

Discussion

Here we focused on feeding ecology of the bowfin, an understudied yet abundant predator species within the Huron–Erie Corridor and across the Great Lakes. We found that bowfin exhibited spatially consistent feeding patterns between two disparate sites (Peche Island—deeper water riverine habitat; Mitchell's Bay—shallow marsh-like habitat), and temporally based on seasonal sampling and SIA of liver and muscle. Although bowfin consumed a variety of prey types, they mainly focused on crayfish and smaller forage fish. The overall large isotopic niche widths of bowfin suggested a generalized feeding strategy at the population level, but there was evidence of individual diet specialization. Based on stable isotopes and stomach contents, bowfin occupied a TP of slightly higher than 4, but with a wide range in individual values (range 3.2–6), consistent with an individual specialist feeding strategy. Our analyses suggest that bowfin can utilize a range of prey types, occupy different trophic roles (low or high TP), and would likely be resilient to changes in the Great Lakes food web.

In general, stomach content and stable isotope analyses demonstrated that feeding ecology of the bowfin was comparable across space and time in the Huron–Erie Corridor, although crayfish were most common in the stomachs during the spring sampling period. Despite this consistency, bowfin had a large isotopic niche (SEA_B) with values 2–4 times larger than other piscivorous predators in this system, including

Table 2
Stable isotopes values of $\delta^{13}C$ and $\delta^{15}N$, trophic position, and estimated standard ellipse areas (SEA_B) of bowfin (*Amia calva*) and zebra mussels (*Dreissena polymorpha*) collected at two sampling locations, Peche Island and Mitchell's Bay, in the Lake Huron–Erie Corridor. CR and NR represent ranges in $\delta^{13}C$ and $\delta^{15}N$. All stable isotope and $\delta^{15}N$-based trophic position values are reported as mean ± 1 SD. Dietary position reported as a single value for Peche Island (spring and fall) and Mitchell's Bay based on prey across all stomach contents (see Methods).

Site	n	White muscle							Liver				
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	CR (‰)	NR (‰)	$\delta^{15}N$-based Trophic Position	Dietary trophic position	**SEA_B (‰)**	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	CR (‰)	NR (‰)	**SEA_B (‰)**
Bowfin (*Amia calva*)													
Peche Island Spring	12	−16.7 ± 1.8	13.3 ± 1.3	7.2	6.0	4.3 ± 0.5	4.1	6.7	−17.4 ± 2.4	13.6 ± 1.0	9.3	3.9	7.9
Fall	11						4.0		−15.9 ± 1.1	12.5 ± 1.1	4.0	3.8	3.2
Mitchell's Bay	23	−21.7 ± 2.4	14.3 ± 1.4	8.6	4.6	4.2 ± 0.6	4.2	9.3	−20.7 ± 2.7	14.9 ± 1.5	9.1	6.2	12.7
Zebra mussel (*Dreissena polymorpha*)													
Peche Island[*]	16	−22.2 ± 0.8	3.97 ± 0.9	3.0	2.6	**N/A**	**N/A**	1.6	**N/A**	**N/A**	**N/A**	**N/A**	0.77[a] 0.13[b]
Mitchell's Bay	8	−21.5 ± 1.8	6.8 ± 0.3	6.0	0.8	**N/A**	**N/A**	1.5	**N/A**	**N/A**	**N/A**	**N/A**	**N/A**

[*] Zebra mussel $\delta^{15}N$ values were significantly different across season, thus an average of the two sampling groups were taken for both $\delta^{13}C$ and $\delta^{15}N$ when using zebra mussels as baseline for bowfin muscle tissue.

[a] Peche Island (spring) muscle tissue SEA_B

[b] Peche Island (fall) muscle tissue SEA_B.

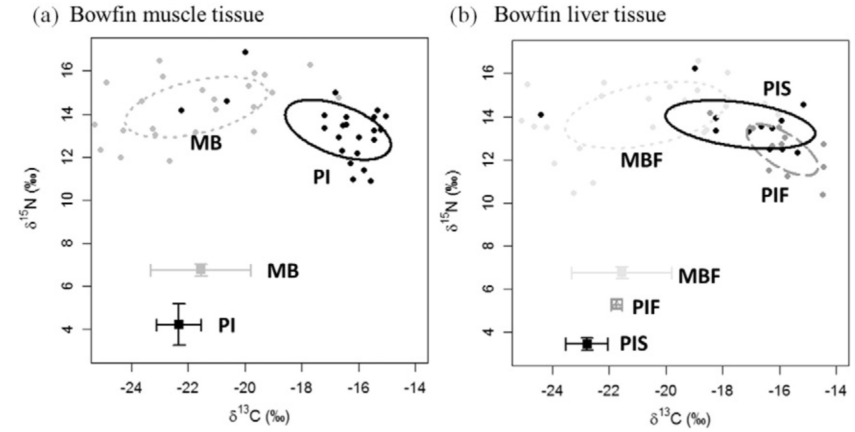

Fig. 2. (a) Stable isotope bi-plot showing isotopic niche areas of bowfin (*Amia calva*) white muscle tissue (SEA_C) for Peche Island (PI; black dots and ellipse) and Mitchell's Bay (MB; grey dots and hashed ellipse). Zebra mussels (*Dreissena polymorpha*) are represented by a black dot (mean ± 1 SD) at Peche Island and a grey dot (mean ± 1 SD) at Mitchell's Bay. Fig. 2. (b) Isotopic niche areas of bowfin liver tissue (SEA_C) and zebra mussels for each sampling group (Peche Island—spring; PIS, Peche Island—fall; PIF, Mitchell's Bay—fall; MBF) in the Lake Huron–Erie Corridor. Black dots and solid ellipses represent bowfin at Peche Island (spring), while dark grey dots, hashed ellipses represent Peche Island (fall) bowfin and zebra mussels, respectively. The light grey dots, dotted ellipses represent Mitchell's Bay bowfin and zebra mussels.

largemouth bass, northern pike, walleye, muskellunge, and longnose gar (*Lepisoteus osseus*) (Nawrocki, 2015). Consistent with isotopic niche size, bowfin had a much wider range of individual $TP_{\delta 15N}$ values (TP range = 2.8) than other predators in the Huron–Erie Corridor, such as largemouth bass (TP range = 1.7) and northern Pike (TP range = 1.3), although values were comparable to longnose gar (TP range = 2.3) (Nawrocki and Fisk, University of Windsor, 2015, unpublished data). This would imply that individual bowfin target specific prey items consistently through time, but that the overall range of items consumed by the population is also consistent through time and space. This scenario suggests that bowfin exhibit intraspecific resource partitioning, potentially through the use of small, home ranges within these habitats. Bowfin TP estimates using stable isotope and stomach content analyses were lower than largemouth bass (TP = 4.6) and longnose gar (TP = 5.1) collected at Peche Island during the same period as this study (Nawrocki and Fisk, University of Windsor, 2015 unpublished data). The large ranges in bowfin TP suggest a high degree of omnivory, i.e., consumption of prey from multiple trophic levels or food chains at the population level, and are supported by similar literature mean TP estimates of 3.8 and large TP ranges across different populations in North America (Froese and Pauly, 2000). The relationship between $\delta^{13}C$ and body length at Mitchell's Bay, but not at Peche Island, may also be suggestive of size-related prey preference after ontogenetic shifts from juveniles to adults.

Despite similar TPs for bowfin at Peche Island and Mitchell's Bay, there was variation in the ellipse positioning, relative to baseline dressenid mussels, of the isotopic niches (SEAc) between these sites. These different ellipse positions at each site suggest either bowfin utilizing different prey types at our sampling sites or variation related to baseline isotopic variation between the sites (Fry, 2007; Guzzo et al., 2011). While there were differences in the positioning of ellipses between sites, isotopic niche orientation and size remained consistent across tissue type at each site. In addition to similar niche size, estimates of individual specialization within bowfin populations were consistent across sampling sites, suggesting that individual bowfin diet is seasonally consistent (Newsome et al., 2009). This is further supported by large $\delta^{13}C$ ranges across both tissue and site and may be attributed to individual specialization in bowfin populations being driven by discrete habitat utilization. Finally, stomach contents indicate similar total diversity of prey species between sampling sites and seasons which is more consistent with baseline isotopic variation driving differences in isotopic niche rather than different prey communities at Peche Island and Mitchell's Bay.

Diet metrics used in this study, i.e., stomach contents and stable isotope mixing models, indicated that bowfin consumed a variety of smaller prey species. These patterns were seasonally consistent at Peche Island with isotope mixing models estimating the diet contributions of bluegill, pumpkinseed, and spottail shiners to vary by ≤6%. Furthermore, crayfish and small fish (e.g., spottail shiners, bluegill) were major diet contributors at Peche Island across both stomach contents and mixing models. However, crayfish contribution to diet was much higher based on stomach contents as compared to isotope mixing models, but this could be related to a stomach content bias that results in an overestimation of slower to digest hard-shelled prey items, i.e., crayfish carapace, thus driving a higher %IRI value of crayfish in diet (Shimose et al., 2006; Yeager et al., 2014). In comparison, Mitchell's Bay bowfin consumed mainly crayfish and round goby (*Neogobius melanostomus*) based on stomach content analysis, suggesting that short-term diet is consistent in consumption of small fishes and invertebrates. Stomach content estimates of bowfin collected in the fall were dominated by unidentifiable material, limiting our ability to accurately identify closely related taxa and estimate short-term diet of an individual at that time (Hyslop, 1980); however, the presence of small vertebral columns likely suggests the unidentified material were mainly smaller fishes (e.g., Cyprinidae , *Neogobius* spp.).

In other parts of North America, bowfin consume a wide variety of prey (e.g., Berry, 1955; Scarnecchia, 1992; Ashley and Rachels, 1999; Jordan and Arrington, 2001), consistent with our results. A population of bowfin in the Kissimmee River (FL, USA) exhibited diet flexibility in response to seasonal fluctuations in the abundance of various prey species, suggesting that populations of bowfin are able to adjust to seasonal prey availability (Jordan and Arrington, 2014). Additionally, bowfin have been found to consume both large quantities and a diversity of prey types (Mundahl et al., 1998); and when compared to largemouth bass, bowfin demonstrate a faster ability to respond to variation in prey availability (Jordan and Arrington, 2014). The consistency between short-term stomach content analysis in other regions, as well as the diet and longer-term isotope analyses completed here, indicate that in many areas of their distribution, bowfin consume a variety of large benthic invertebrates, e.g., crayfish and smaller fishes (e.g., *Lepomis* spp.), and show plasticity in diet. Our results suggest that this high variability in diet at the population level is driven by high degrees of prey specialization at the individual level. These findings of dietary plasticity as a species may be relevant in further understanding Great Lakes trophic structure, as it relates to the ability of bowfin to adapt to continuing anthropogenic stressors, changing prey abundances (Lapointe, 2014), and the alteration of existing trophic linkages (Schindler and Scheuerell, 2002; Tunney et al., 2012).

To understand the ecological role of bowfin within the Great Lakes, it is necessary to also consider their feeding patterns relative to other

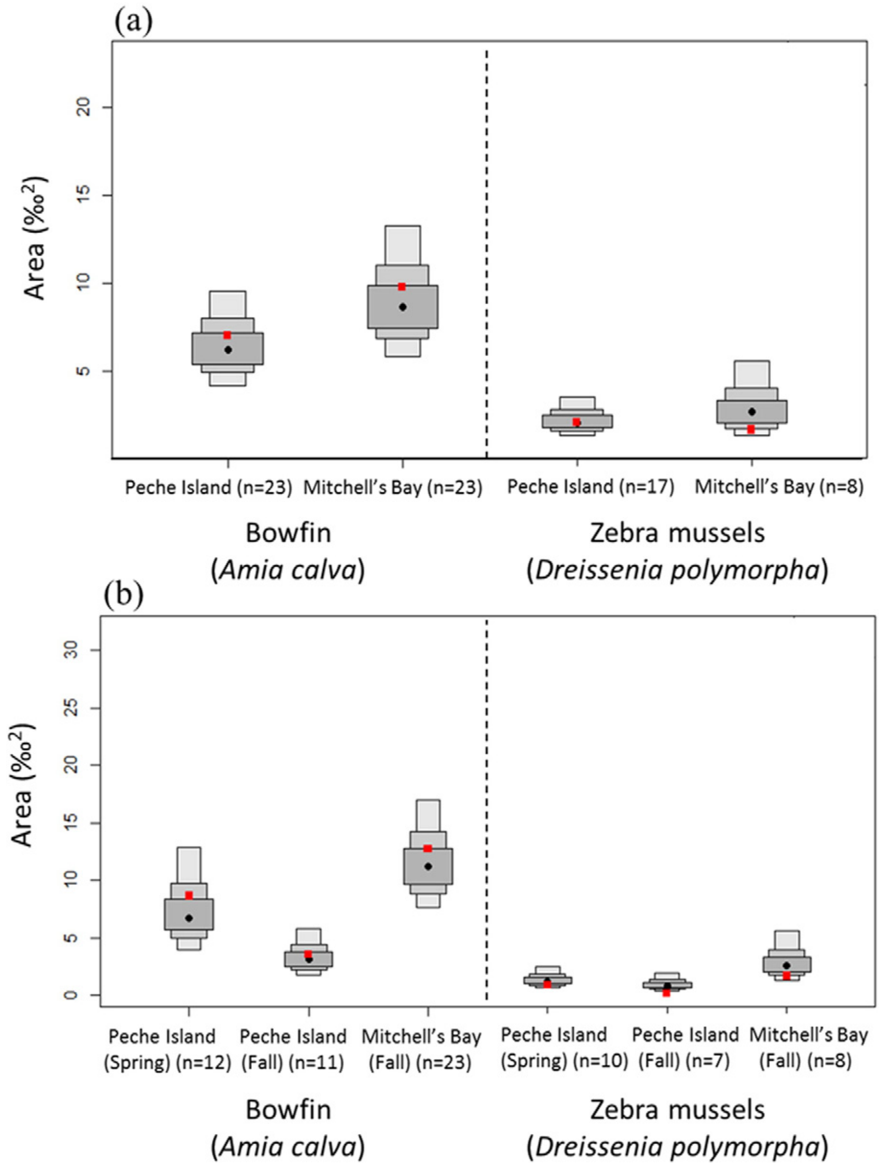

Fig. 3. (a) Density plots presenting the mean and Bayesian credibility intervals (BCIs) for standard ellipse areas (*SEA$_B$*) of bowfin (*Amia calva*) white muscle tissue and zebra mussels (*Dreissena polymorpha*) at Peche Island and Mitchell's Bay in the Lake Huron–Erie Corridor. The black dots correspond to mean SEA$_{B,}$ the squares (red in online version) represent SEA$_{C,}$ and the grey boxes represent BCIs of 50, 75, and 95%; (b) Density plots presenting the mean and Bayesian credibility intervals (BCIs) for standard ellipse areas (*SEA$_B$*) of Bowfin (*Amia calva*) liver tissue and zebra mussels (*Dreissena polymorpha*) at each sampling group (Peche Island—spring, Peche Island—fall, Mitchell's Bay—fall) in the Lake Huron–Erie Corridor. The black dots correspond to mean SEA$_B$, the red dots represent SEA$_C$, and the grey boxes represent BCIs of 50, 75, and 95%.

piscivorous fish found in the region. Largemouth bass exhibit dietary plasticity across areas in the Great Lakes (Hodgson and Kitchell, 1987), while walleye consume fewer prey types, e.g., emerald shiner (*Notropis atherinoides*) (Carreon-Martinez et al., 2011). Even though these other piscivores may be viewed as generalists across the scale of entire Great Lakes region, the local specialization of foraging tactics may allow them to be more susceptible to nutritional stress, fluctuating prey abundances, intra-guild predation, or competition (Hourston, 1952; Hoyle et al., 2012; Kapuscinski et al., 2011). In comparison to other piscivorous predators in the Great Lakes, bowfin have greater

Table 3

Variance component analysis from linear mixed-effects analysis for bowfin δ^{13}C and δ^{15}N values at Mitchell's Bay and Peche Island. Total isotopic niche width (TINW) is the sum of the intercept and residual variances for both δ^{13}C and δ^{15}N. Total intercept variance (BIC, between individual component) and total residual variance (WIC, within individual component) were determined by summing the intercept and residual variances for both δ^{13}C and δ^{15}N. Proportion of WIC and BIC explained (%) was calculated by dividing total intercept variance and total residual variance by TINW. (*) denotes greater BIC than WIC, indicating specialization.

Location	δ^{13}C (‰)			δ^{15}N (‰)			Total intercept variance (BIC)	Total residual variance (WIC)	TINW
	Intercept variance	Residual variance	Conditional r^2	Intercept variance	Residual variance	Conditional r^2			
Mitchell's Bay	5.03	1.34	0.82	0.79	0.93	0.57	5.82 (72%)*	2.27 (28%)	8.09
Peche Island	3.77	0.34	0.93	1.27	0.37	0.80	5.04 (88%)*	0.71 (12%)	5.75

Table 4

Model parameters ($\delta^{13}C$ and $\delta^{15}N$) for bowfin (*Amia calva*) diet estimates at Peche Island in spring and fall 2014 using MixSIAR. Seasonal prey item $\delta^{13}C$ and $\delta^{15}N$ values were grouped together as there were no significant differences in values across season. All stable isotopes are reported as mean ± 1 SD. Mean diet proportion estimates are reported with 95% Bayesian credibility intervals (BCI). Separate one-way ANOVA models were used to compare isotopic compositions of prey species (dependent variable: $\delta^{13}C$ or $\delta^{15}N$; independent variable: species) with Tukey's HSD post hoc comparisons. Superscript letters indicate prey species with similar isotopic values for mean $\delta^{13}C$ or $\delta^{15}N$ based on post hoc comparisons.

Prey species	Prey item			Bowfin MixSIAR
	Model parameters			
	n	$\delta^{13}C$	$\delta^{15}N$	Mean diet proportion (95% BCI)
Bluegill	22	-16.3 ± 1.2^{a}	11.1 ± 0.9^{a}	0.1 (0.01–0.3)
Crayfish	10	$-17.9 \pm 1.3^{b,c}$	$9.6 \pm 0.7^{b,c}$	0.54 (0.16–0.8)
Largemouth bass (juvenile)	7	$-17.0 \pm 0.9^{a,c,d}$	14.2 ± 0.9^{d}	0.03 (0.01–0.12)
Pumpkinseed	14	$-15.7 \pm 1.8^{a,d}$	$10.5 \pm 0.8^{a,c}$	0.12 (0.04–0.36)
Spottail shiner	20	$-18.5 \pm 1.2^{b,c}$	10.6 ± 0.7^{a}	0.16 (0.04–0.51)
Northern pike	27	$-17.0 \pm 1.0^{a,c,d}$	13.8 ± 0.71^{d}	0.04 (0.01–0.13)

niche widths than largemouth bass, walleye, longnose gar, northern pike, and muskellunge, providing incentive to take a broader community approach to compare bowfin with other higher trophic level species to characterize niche overlap and, ultimately, trophic structure (Nawrocki, 2015).

In conclusion, we illustrate that bowfin within the Huron–Erie Corridor consume a diverse number of prey species that remain relatively consistent between season (spring and fall) and locations which differ in environmental characteristics. The broad niche sizes and TP ranges of bowfin at the population level, as well as a high degree of resource specialization or dietary consistency at the individual level, also support the assumption that bowfin are omnivorous as a population, consuming prey across different habitat zones and trophic levels, ultimately suggesting great trophic complexity in this understudied fish species.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2016.08.002.

Acknowledgments

We thank A. Weidl, C. Lee, J. Mumby, P. Rivers, H. Pettitt-Wade, K. Gammie-Janisse, S. Kessel, M. Beaudry, T. Leadley, and J. Del Papa for assistance in the field, A.J. Hussey for guidance on stable isotope analysis, and K. Wellband for help with R-Studio. This research was funded by an NSERC Discovery Grant to A.T.F. and the Alex S. Davidson Great Lakes Stewardship to B.N.

References

Ashley, K.W., Rachels, R.T., 1999. Food habits of bowfin in the Black and Lumber Rivers, North Carolina. Proc. Annu. Conf. Southeast Assoc. Fish and Wildl. Agencies 53, 50–60.

Baustian, M.M., Mavrommati, G., Dreelin, E.A., Esselman, P., Schultze, S.R., Qian, L., Gim Aw, T., Luo, L., Rose, J.B., 2014. A one hundred year review of the socioeconomic and ecological systems of Lake. St. Clair, North America. J. Great Lakes Res. 40 (2), 15–26.

Berry, F.H., 1955. Food of mudfish *Amia calva* in Lake Newman, Florida, in relation to its management. Quart. J. Florida Acad. Sci. 18 (1), 69.

Bligh, E.G., Dyer, W.J., 1959. A rapid method for total lipid extraction and purification. Can. J. Biochem. Physiol. 37 (8), 911–917.

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.

Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M., Svanback, R., 2002. Measuring individual-level resource specialization. Ecology 83 (10), 2936–2941.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M.L., 2003. The ecology of individuals: Incidence and implications of individual specialization. Am. Soc. Nat. 161 (1), 1–28.

Breder, C.M., 1928. On the appetite of *Amiatus calva* (Linnaeus). Copeia 54-56.

Brush, J.M., Fisk, A.T., Hussey, N.E., Johnson, T.B., 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.

Carreon-Martinez, L., Johnson, T.B., Ludsin, S.A., Heath, D.D., 2011. Utilization of stomach content DNA to determine diet diversity in piscivorous fishes. J. Fish Biol. 78 (4), 1170–1179.

Caut, S., Angulo, E., Courchamp, F., 2009. Variation in discrimination factors (Δ15Nand Δ13C): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. 46, 443–453.

Cortes, E., 1999. Standardized diet compositions and trophic levels of sharks. ICES J. Mar. Sci. 56, 707–717.

Cortes, E., Manire, C.A., Hueter, R.E., 1996. Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in southwest Florida. Bull. Mar. Sci. 58 (2), 353–367.

Dove, A., Chapra, S.C., 2015. Long-term trends of nutrients and trophic response variables for the Great Lakes. Limnol. Oceanogr. 00, 1–35.

Froese, R., Pauly, D., 2000. Fish Base 2000: Concepts, Design and Data Sources.

Fry, B., 2007. Stable Isotope Ecology. Springer Science & Business Media.

Guzzo, M.M., Haffner, G.D., Sorge, S., Rush, S.A., Fisk, A.T., 2011. Spatial and temporal variabilities of $\delta^{13}C$ and $\delta^{15}N$ within lower trophic levels of a large lake: implications for estimating trophic relationships of consumers. Hydrobiologia 675, 41–53.

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.

Hodgson, J.R., Kitchell, J.F., 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). Am. Midl. Nat. 118 (2), 323–336.

Hondorp, D.W., Roseman, E.F., Manny, B.A., 2014. An ecological basis for future fish habitat restoration efforts in the Huron–Erie Corridor. J. Great Lakes Res. 40 (2), 23–30.

Hourston, A.S., 1952. The food and growth of maskinonge (*Esox masquinongy* Mitchill) in Canadian waters. J. Fish. Res. Board Can. 8 (5), 347–368.

Hoyle, J.A., Bowlby, J.N., Brousseau, C.M., Johnson, T.B., Morrison, B.J., Randall, R.G., 2012. Fish community structure in the Bay of Quinte, Lake Ontario: the influence of nutrient levels and invasive species. Aquat. Ecosyst. Health Manag. 15 (4), 370–379.

Hussey, N.E., Macneil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F., Cliff, G., Wintner, S.P., Fennessy, S.T., Fisk, A.T., 2014. Rescaling the trophic structure of marine food webs. Ecol. Lett. 17, 239–250.

Hyslop, E.J., 1980. Stomach contents analysis-a review of methods and their application. J. Fish Biol. 17, 411–417.

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.

Jordan, F., Arrington, D.A., 2001. Weak trophic interactions between large predatory fishes and herpetofauna in the channelized Kissimmee River, Florida, USA. Wetlands 21 (1), 155–159.

Jordan, F., Arrington, D.A., 2014. Piscivore responses to enhancement of the channelized Kissimmee River, Florida, USA. Restor. Ecol. 22 (3), 418–425.

Jude, D.J., Pappas, J., 1992. Fish utilization of Great Lakes coastal wetlands. J. Great Lakes Res. 18 (4), 651–657.

Kapuscinski, K.L., Farrell, J.M., Murry, B.A., 2011. Feeding strategies and diets of young-of-the-year muskellunge from two large river ecosystems. N. Am. J. Fish Manag. 32, 635–644.

Koch, J.D., Quist, M.C., Hansen, K.A., Jones, G.A., 2009. Population dynamics and potential management of bowfin (*Amia calva*) in the Mississippi River. J. Appl. Ichthyol. 25, 545–550.

Landsman, S.J., Nguyen, V.M., Gutowksy, L.F.G., Gobin, J., Cook, K.V., Binder, T.R., McLaughlin, R.L., Cooke, S.J., 2011. Fish movement and migration studies in the Laurentian Great Lakes: Research trends and knowledge gaps. J. Great Lakes Res. 37, 365–379.

Lapointe, N.W.R., 2014. Effects of shoreline type, riparian zone and instream microhabitat on fish species richness and abundance in the Detroit River. J. Great Lakes Res. 40 (1), 62–68.

Layman, C.A., Arrington, D.A., Montana, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88 (1), 42–48.

Leach, J.H., 1991. Biota of Lake St. Clair: Habitat evaluation and environmental assessment. Hydrobiologia 219, 187–202.

McCann, K., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. Nature 395, 794–798.

McLeod, A.M., Arnot, J.A., Borga, K., Selck, H., Kashian, D.R., Krause, A., Paterson, G., Haffner, G.D., Drouillard, K.G., 2015. Quantifying uncertainty in the trophic magnification factor related to spatial movements of organisms in a food web. Integr. Environ. Assess. Manag. 9999 (9999), 1–13.

Mundahl, N.D., Melnytshuk, C., Spielman, D.K., Harkins, J.P., Funk, K., Bilicki, A.M., 1998. Effectiveness of bowfin as a predator on bluegill in a vegetated lake. N. Am. J. Fish Manag. 18, 286–294.

Nalepa, T.F., Hartson, D.J., Gostenik, G.W., Fanslow, D.L., Lang, G.A., 1996. Changes in the freshwater mussel community of Lake St. Clair: From unionidae to *Dreissena polymorpha* in eight years. J. Great Lakes Res. 22 (2), 354–369.

Nawrocki, B., 2015. Food Web Metrics of Piscivorous Predators in the Lake-Huron Erie Corridor Using Stable Isotopes (Electronic Theses and Dissertations. Paper 5435).

Newsome, S.D., Martinez del Rio, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5 (8), 429–436.

Newsome, S.D., Tinker, M.T., Monson, D.H., Oftedal, O.V., Ralls, K., Staedler, M.M., Fogel, M.L., Estes, J.A., 2009. Using stable isotope to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90, 961–974.

Newsome, S.D., Tinker, M.T., Gill, V.A., Hoyt, Z.N., Doroff, A., Nichol, L., Bodkin, J.R., 2015. The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. Oecologia 178, 45–59.

O'Brien, T.P., Taylor, W.W., Roseman, E.F., Madenjian, C.P., Riley, S.C., 2014. Ecological factors affecting rainbow smelt recruitment in the main basin of Lake Huron, 1976-2010. Trans. Am. Fish. Soc. 143, 784–795.

Parnell, A.C., Jackson, A.L., R Core Team, 2015. *Stable Isotope Bayesian Ellipses in R* package version 4.2.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2015. NLME: Linear and Nonlinear Mixed Effects Models. R package version 3. pp. 1–121.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83 (3), 703–718.

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

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Regier, H.A., Whillans, T.H., Christie, W.J., Bocking, S.A., 1999. Over-fishing in the Great Lakes: the context and history of the controversy. Aquat. Ecosyst. Health Manag. 2, 239–248.

Scarnecchia, D.L., 1992. A reappraisal of gars and bowfins in fishery management. Fisheries 17 (5), 6–10.

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

Shimose, T., Shono, H., Yokawa, K., Saito, H., Tachihara, K., 2006. Food and feeding habits of blue marlin, *Makaira nigricans*, around Yonaguni Island, southwestern Japan. Bull. Mar. Sci. 79 (3), 761–775.

Stock, B.C., Semmens, B.X., 2013. MixSIAR GUI User Manual [computer program]. Version version 1.0.

Tunney, T.D., McCann, K.S., Lester, N.P., Shuter, B.J., 2012. Food web expansion and contraction in response to changing environmental conditions. Nat. Commun. 3 (1105), 1–9.

Turner, J.L., 1966. Distribution and food habits of ictalurid fishes in the Sacramento–San Joaquin Delta. In: Turner, J.L., Kelley, D.W. (Eds.), Ecological Studies of the Sacramento–San Joaquin Delta, Part II. Cal. Dept. Fish Bull., pp. 130–143

Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. 46 (8), 2061–2066.

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.

Vander Zanden, M.J., Casselman, J.M., Rasmussen, J.B., 1999a. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401, 464–467.

Vander Zanden, M.J., Shuter, B.J., Lester, N.P., Rasmussen, J.B., 1999b. Patterns of food chain length in lakes: a stable isotope study. Am. Nat. 154 (4), 406–411.

Yeager, L.A., Layman, C.A., Hammerschlag-Peyer, C.M., 2014. Diet variation of a generalist fish predator, grey snapper *Lutjanus griseus*, across an estuarine gradient: trade-offs of quantity for quality? J. Fish Biol. 85, 264–277.

Yurkowski, D.J., Ferguson, S., Choy, E.S., Loseto, L.L., Brown, T.M., Muir, D.C.G., Semeniuk, C.A.D., Fisk, A.T., 2016. Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. Ecol. Evol. 6, 1666–1678.