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ORIGINAL PAPER

Fifty years later: trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie

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Abstract Since the introduction of white perch (*Morone americana*) into Lake Erie over 50 years ago, the population size of native yellow perch (*Perca flavescens*) has decreased up to 79 % and significant changes to the ecosystem have occurred. We examined long-term population estimates and used stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) paired with stomach content analysis to quantify the trophic ecology and niche overlap of adult yellow perch and white perch in the western basin of Lake Erie. We found that changes in yellow perch abundance since 1979 appeared to be better correlated with changes in fishery exploitation rates than with food competition effects from white perch. At the time of this study, yellow perch were found to have higher δ^{13}C values, indicating greater utilization of benthic food resources than white perch, and white perch occupied higher trophic positions based on δ^{15}N. The diets of both species varied spatially and seasonally based on stable isotopes and stomach contents, likely driven by changes in prey abundance. Comparison of niche widths using stable isotope population metrics and Schoener diet similarity index suggested a low to moderate degree of niche overlap between species. Isotopic niches of white perch were generally larger than those of yellow perch demonstrating broader resource utilization by this non-indigenous species. We submit that isotopic niche overlap comparisons are more appropriate for studies seeking to understand interactions among populations over course temporal scales, while diet overlap indices, such as the Schoener index provide a means to study fine-scale interactions such as ontogenetic and seasonal diet shifts.

Keywords Yellow perch · White perch · Stomach content analysis · Diet · Stable isotopes · Laurentian Great Lakes · Niche width · Food web · Population metrics

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Introduction

The spread of non-indigenous species (NIS) to new ecosystems is becoming increasingly common in many regions of our planet (Vitousek et al. 1997; Mack et al. 2000). The majority of NIS introductions are attributed to human activities associated with international trade (Mack and Lonsdale 2001; Levine and D'antonio 2003) and as a result introductions are occurring over unprecedented spatial and temporal scales, particularly in large aquatic ecosystems (Cohen and Carlton 1998; Ruiz et al. 2000; Ricciardi 2006). Many successful NIS are classified as trophic generalists (Marvier et al. 2004), characterized by their wide ecological tolerance and diets, allowing them to be highly successful in new habitats (Sax and Brown 2000; Polo-Cavia et al. 2008). Once established, NIS generalists have the potential to displace native specialist species, leading to biotic homogenization and having cascading effects on existing food webs and altering ecosystem function (McKinney and Lockwood 1999; Sakai et al. 2001; Olden et al. 2004; Bruno and Cardinale 2008). As a result, many scientists and lake managers recognize the importance in understanding the role of non-indigenous species in shaping food web structure and dynamics.

The Laurentian Great Lakes have experienced over 180 successful NIS introductions (Holeck et al. 2004), compromising the structure and biological integrity of their food webs (Mills et al. 1994; Ricciardi and MacIsaac 2000). For example, the food web of Lake Huron has undergone substantial changes as a result of introduced species. Sea lamprey (*Petromyzon marinus*) were a critical factor in the population declines of lake trout (*Salvelinus namaycush*), burbot (*Lota lota*), lake whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus artedi*) (Great Lakes Fishery Commission 1995, 2007a, b). Alewife prey on yellow perch (*Perca flavescens*) and lake trout fry and new NIS such as dreissenid mussels have been associated with a 90 % reduction in cladocerans, a key food source to many pelagic-yearling fish (Great Lakes Fishery Commission 2007b). While all Great Lakes food webs experienced the introduction of NIS, not all have resulted in major collapses of native predatory fish populations.

Despite being home to several NIS species, the western basin of Lake Erie continues to support one of North America's largest freshwater fisheries (DFO 2006). One important NIS in western Lake Erie is the white perch (*Morone americana*), an estuarine fish native to the east coast of North America (Scott and Crossman 1973). White perch were first collected in Lake Erie in 1953, proliferated in the mid-1970s, and became abundant in the western Lake Erie in 1982 (Larsen 1954; Parrish and Margraf 1990; Fig. 1). Based on the examination of stomach contents of white perch and yellow perch from western Lake Erie during the 1980s, researchers concluded that newly introduced white perch could have negative effects on native yellow perch (Schaeffer and Margraf 1986a, b; Parrish and Margraf 1994). Since these early diet studies there have been substantial changes to the benthic community of the western basin of Lake Erie. Dreissenid mussels colonized and spread throughout the lake and now comprise 80–90 % of the benthic biomass (Tyson and Knight 2001). Round goby (*Neogobius melanostomus*) became established, increasing the predation pressure on the eggs of predatory fish species (Roseman et al. 2006). Large benthic invertebrates such as *Hexagenia*, caddisfly nymphs (Trichoptera) and amphipods have re-colonized the western basin and have been linked to increased growth and recruitment of yellow perch (*Perca flavescens*) (Tyson and Knight 2001). In spite of the return of large benthos, a key food source for yellow perch, stocks in western Lake Erie have not returned to population sizes seen before the

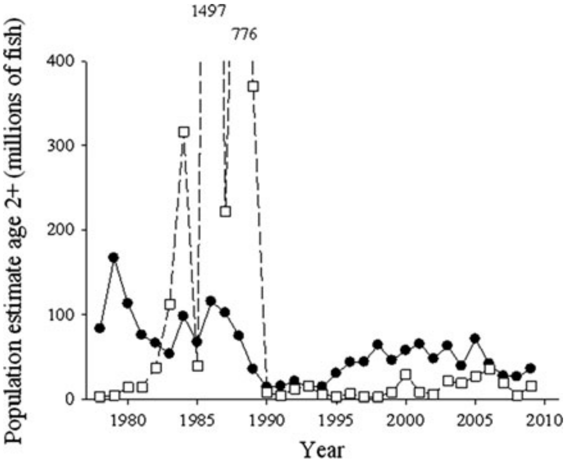


Fig. 1 Populations estimates of adult (age 2+) yellow perch (*black circles*) and white perch (*white squares*) in the western basin of Lake Erie from 1978 through 2009 (Yellow Perch Task Group 2011; Ontario Ministry of Natural Resources unpublished data)

establishment of white perch (Yellow Perch Task Group 2011; Fig. 1). This raises questions regarding the health of yellow perch populations in the basin and suggests that in addition to understanding recruitment dynamics, there is a need to better understand potential interactions with sympatric NIS species.

This study applies contemporary stable isotope approaches with stomach content analysis to assess the trophic ecology and niche overlap of yellow and white perch across the western basin of Lake Erie. Stable isotope analysis is widely applied in ecological research to understand the effects of NIS on food webs (Vander Zanden et al. 1999; Jackson et al. 2012). Naturally occurring stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) reveal distinct aspects of a consumer's long-term trophic niche by providing a time- and space-integrated representation of dietary carbon sources and relative trophic position (Peterson and Fry 1987; DeNiro and Epstein 1981; Layman and Allgeier 2012). Recently, quantitative metrics and statistical frameworks have been developed for examining stable isotope variation among defined groups, understanding trophic diversity and quantifying niche space (Layman et al. 2007; Turner et al. 2010; Hammerschlag-Peyer et al. 2011; Jackson et al. 2011). These tools allow for a better characterization of the ecological role of generalist species and their potential effects on native species and their food webs. Despite their wide use, stable isotopes do have limitations; estimates of trophic position are highly dependent on the diet-tissue discrimination factor, which can vary among species and with environmental conditions (Post 2002; Power et al. 2003; Martinez del Rio et al. 2009); isotope turnover in muscle of adult fish species is often on the scale of several months, potentially missing temporal diet changes (Perga and Gerdeaux 2005) and isotope analysis lacks fine-scale taxonomic resolution particularly in complex food webs (Johnson et al. 2002). Therefore, stomach content analysis is often used in complement of stable isotope analysis, as it provides a snapshot of a consumer's diet at the time of capture (Bearhop et al. 2004) and allows for detailed taxonomic characterization of diet.

The objectives of the present study were to: (1) quantify the carbon sources, trophic positions and isotopic niches of adult yellow perch and white perch from the western basin of Lake Erie using stable isotopes; and, (2) quantify the degree of diet overlap between adult yellow perch and white perch in western Lake Erie using stomach content analysis. As well, we quantify changes in the population sizes of adult yellow perch and white perch in the western basin of Lake Erie since 1979. Knowledge of these interactions provides important insight on how sympatric native and introduced fish species coexist and will contribute to lake management strategies, including conserving commercially valuable native fish communities potentially threatened by interactions with NIS.

Methods

Study site

This study took place in the western basin of Lake Erie, a shallow (average depth 7.5 m, maximum depth 10 m), flat basin making up the western third of Lake Erie. The western basin is classified as mesotrophic (Kane et al. 2009), and is vertically mixed with little evidence of summer stratification. The western basin of Lake Erie is spatially complex in terms of its overlying water masses (e.g., water chemistry), a result of tributary and connecting channel inputs. The basin has two major water inputs, the Detroit and Maumee rivers. Although the Detroit River's mean annual discharge is more than 35 times that of the Maumee (5,100 and 135 m^3s^{-1}), the Maumee River contributes ~35 % of the total phosphorus load to the basin (Ditoro et al. 1987; Baker and Richards 2002; Dolan and McGunagle 2005). The relatively warm nutrient-rich waters of the Maumee River plume remain as a distinct water mass, which circulates counter-clockwise in the southwest portion of the lake. The Detroit River provides a much larger flow of relatively cool, nutrient limited water and its plume extends well out into the basin (Reichert et al. 2010; Fig. 2). Differences in the contributing water from the Maumee and Detroit rivers provide spatial and seasonal subsidies of nutrients and energy, but also contribute to environmental heterogeneity with respect to water temperatures, phytoplankton and zooplankton dynamics and fish assemblages (Barbiero et al. 2001; Barbiero and Tuchman 2001; Reichert et al. 2010). These physical and biophysical attributes provide important spawning, nursery habitats and forage bases for numerous native fish species including yellow perch (Zhao et al. 2009; Reichert et al. 2010).

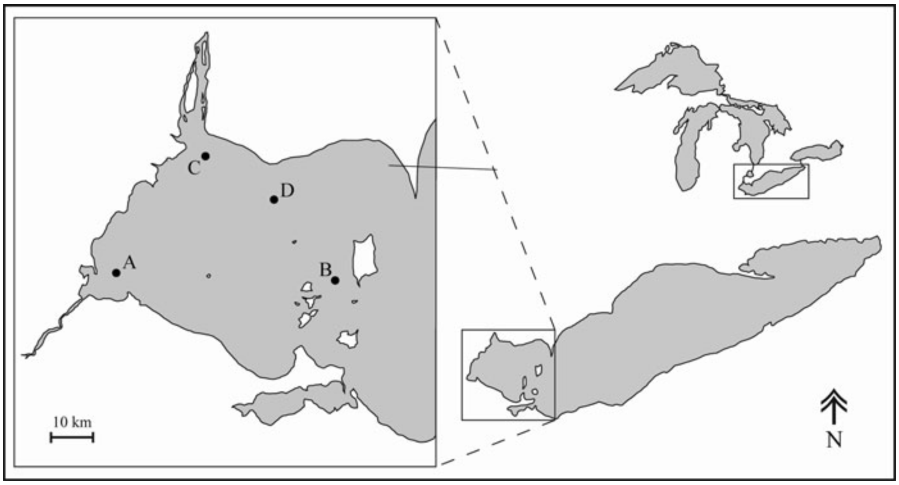


Fig. 2 Location of sampling areas in the western basin of Lake Erie. *A* Maumee River Plume, *B* Bass Islands, *C* Detroit River Plume, *D* Middle Sister Island

Population size estimates

Yearly population abundances of age 2 + yellow perch were obtained from the report of the Yellow Perch Task Group (2011). We estimated population abundances for age 2 + white perch ($N_{\text{white perch}}$) based on the assumption that this species has equal catchability and survival to yellow perch, using the following equation:

$$N_{\text{whiteperch}} = N_{\text{yellowperch}} \times (\text{CPUE white perch}/\text{CPUE yellow perch})$$

where $N_{\text{yellow perch}}$ are abundance estimates from the Yellow Perch Task Group (2011), and CPUE values for white perch and yellow perch were derived from standardized protocols (for protocols see: Ontario Ministry of Natural Resources 2012) using annual index gill netting and bottom trawls (Ontario Ministry of Natural Resources unpublished data).

Stable isotope analysis

Fishes and zebra mussels used for stable isotope analysis were collected using bottom trawls and gill nets deployed monthly at each sampling area (Fig. 2) from May to September of 2009 as part of the Ontario Ministry of Natural Resources and Ohio Department of Natural Resources summer inter-agency trawls (Tyson et al. 2006). Dreissenid mussels were collected to provide baseline δ^{13}C and δ^{15}N data at each sampling location. Dreissenid mussels are sessile, filter feeders that are longer lived than plankton, and, therefore, provide site- specific and time-integrated stable isotope values of organisms at the base of the food web. This allows for differences in basal stable isotope values to be taken into account when comparing carbon sources and trophic position among fish species and locations (Post 2002). Both dressenid mussels and fishes (total lengths (TL) recorded) were frozen whole and brought back to lab. In the lab, zebra mussels were shucked to remove shells, rinsed with distilled water, and then pooled into single samples of 5–10 individuals of similar size to achieve sufficient sample for analysis and frozen at −20 °C. Individual fish dorsal muscle plugs were removed and frozen at −20 °C.

Samples for stable isotope analysis (see Table 1 for isotope values and sample sizes) were freeze-dried, ground and analyzed using a Delta V Advantage isotope ratio mass spectrometer (Thermo Electron Corporation, Bremen, Germany) and 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA). Stable isotope values are conveyed in δ notation where $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standard reference material was Pee Dee Belemnite carbonate for CO_2 and atmospheric nitrogen for N_2. Three different lab and one NIST (8414) reference standards were used for quantification of stable isotope and element percentage after every 12 samples, and

Table 1 Comparison of stable isotope ratios and total length (mean ± SD) of yellow perch, white perch, and zebra mussels collected during spring and fall at four sites in the western basin of Lake Erie

Site	Species	Season	n	$\delta^{13}C$	$\delta^{15}N$	Total Length
Detroit	Yellow perch	Spring	10	−21.30 ± 1.6	12.32 ± 0.67	16.2 ± 2.7
		Fall	8	−20.97 ± 0.4	12.97 ± 0.4	16.3 ± 1.8
	White perch	Spring	10	−22.34 ± 0.9	14.39 ± 1.0	18.2 ± 4.0
		Fall	8	−22.50 ± 0.5	14.69 ± 0.6	18.7 ± 4.6
	Dreissenids	Spring	3	−23.26 ± 0.2	6.82 ± 0.2	
		Fall	6	−22.62 ± 0.3	6.66 ± 0.3	
Middle Sister	Yellow perch	Spring	10	−21.91 ± 1.3	12.35 ± 1.0	17.2 ± 2.6
		Fall	6	−21.20 ± 0.1	12.87 ± 0.1	17.2 ± 1.7
	White perch	Spring	13	−22.38 ± 0.8	13.50 ± 1.0	14.7 ± 3.8
		Fall	10	−22.97 ± 0.7	13.33 ± 1.0	16.7 ± 2.2
	Dreissenids	Spring	3	−25.12 ± 0.2	6.87 ± 0.2	
		Fall	6	−22.25 ± 1.1	6.35 ± 0.5	
Maumee	Yellow perch	Spring	19	−21.97 ± 0.5	13.30 ± 0.6	15.8 ± 2.2
		Fall	8	−22.47 ± 0.6	12.69 ± 0.4	15.3 ± 1.8
	White perch	Spring	15	−22.84 ± 1.2	14.68 ± 0.8	16.8 ± 2.8
		Fall	10	−22.35 ± 0.6	13.25 ± 0.5	13.9 ± 1.4
	Dreissenids	Spring	3	−26.56 ± 0.1	8.07 ± 0.1	
		Fall	6	−24.53 ± 2.1	8.25 ± 0.9	
Bass	Yellow perch	Spring	18	−21.79 ± 0.5	13.70 ± 0.6	16.2 ± 1.7
		Fall	8	−22.37 ± 0.3	13.58 ± 0.8	15.2 ± 2.0
	White perch	Spring	14	−23.04 ± 0.6	14.67 ± 0.5	16.4 ± 3.2
		Fall	9	−21.97 ± 1.7	13.81 ± 0.5	17.5 ± 3.9
	Dreissenids	Spring	3	−25.32 ± 0.2	10.10 ± 0.1	
		Fall	8	−24.33 ± 1.8	8.01 ± 1.1	

every tenth sample was run in triplicate to assess within-run precision. Analytical precision, based on the standard deviation of an internal lab (fish muscle) and NIST standard 8414 (bovine liver) for $\delta^{15}N$ ($n = 55$/standard), were 0.16 and 0.20 ‰, respectively, and for $\delta^{13}C$ were 0.05 and 0.07 ‰, respectively. Analysis of NIST standards (sucrose and ammonium sulphate; $n = 3$ for each) generated values that were within 0.01 and 0.07 ‰ of certified values for $\delta^{15}N$ and $\delta^{13}C$, respectively.

Statistical analysis

All statistical analyses were performed using the statistical package R (Version 2.14.2; R Development Core Team 2012). Before the analysis, all stable isotope data were tested for normality and homogeneity of variance using probability plots, box plots and multivariate normality tests where applicable. Stable isotope data were divided into spring (May and June) and fall (August and September) to capture changes in diet and isotope variation through the open water season (Guzzo et al. 2011). Sampling locations were treated separately to provide insight into the feeding ecology of species across our study sites, which vary physically and biologically from one another (Guzzo et al. 2011).

We used MANOVA to test for the effects of species, site, and season on stable isotope values of yellow and white perch. We then used ANOVA to specify significant differences found in MANOVA to $\delta^{13}C$ and $\delta^{15}N$.

This study used quantitative population metrics calculated from stable isotope data to assess trophic ecology and niche overlap of yellow and white perch. These population metrics were first developed by Layman et al. (2007) and further enhanced by Jackson et al. (2011). We used the package *stable isotope*

Bayesian ellipses in R (SIBER) in the R statistical computing packing (R Development Core Team 2012) to calculate these metrics. Stable isotope values from individual yellow and white perch sampled were used in these calculations, which were bootstrapped to 10,000 iterations and indicated with the subscript "b" (Jackson et al. 2012). The *nitrogen range* (NR_b) and *carbon range* (CR_b) represent the range of δ^{13}C and δ^{15}N within a population and, therefore, quantify the total range of δ^{13}C and δ^{15}N exploited by each population. CR_b describes the breath of food sources being consumed by a specific population, while NR_b provides insight into the vertical feeding behavior in the food web and nitrogen sources of populations (Layman et al. 2007; Jackson et al. 2011, 2012). We calculated standard ellipse areas (*SEA*) using the variance and covariance of bivariate isotope data to contain approximately 40 % of data to represent a core isotopic niche for each population, which is not sensitive to sample size. *SEA* were then corrected (SEA_c) to minimize bias caused by small sample sizes by using an (n − 2) correction on the denominator (Jackson et al. 2011, 2012) using the equation:

$$\mathrm{SEA_c} = \mathrm{SEA} \times [(\mathrm{n}-1)/(\mathrm{n}-2)].$$

The SEA_c was then be used to calculate the degree of isotopic niche overlap, representing a quantitative measure of dietary similarity between populations. We consider a significant overlap to be >0.6, the same criteria used in the Schoener diet overlap index (Schoener 1968). We then used a Bayesian approach (SEA_b) as described in Jackson et al. (2011) to obtain confidence intervals for isotopic niche areas. These confidence intervals allow for statistical comparisons of the sizes of isotope niche widths among populations. See Jackson et al. (2011) for detailed methodology on calculation of population metrics, Layman et al. (2007) for description of the original community metrics and Jackson et al. (2012) for an example of the use of these population metrics on biological data.

Stomach content analysis

Stomach content data were obtained from both Legler (2008) and USGS (2010) and were reevaluated to allow for appropriate comparisons (i.e. fishes of same size range, collected from similar sampling locations) with corresponding stable isotope analyses. Fishes from Legler (2008) were collected for stomach content analyses from both the Maumee and Detroit River plumes during May and/or June of years 2006 and 2007 and USGS (2010) collected from all four sampling locations May, June, Aug and September of 2009. Stomach content data obtained from Legler (2008) were in the form of as frequency of occurrence and average percent composition by volume. Data obtained from USGS (2010) were in the form of counts and frequency of occurrence. For detailed information on collection and analyses of these diet data refer to Legler (2008) and USGS (2010).

Using the Legler (2008) data, we estimated diet similarity between species using Schoener diet overlap index (Schoener 1968):

$$\mathrm{D} = 1 - {}^{1}\!/_{2} - \sum\left(\left|\rho_{\mathrm{ij}} - \rho_{\mathrm{ik}}\right|\right),$$

where D is the index value, p_{ij} and p_{ik} is the relative proportion, on a volume basis, of each prey item i for species j and k, respectively. The index value of diet overlap can range from 0, indicating no overlap, to 1, indicating complete overlap between the two species being compared. Index values >0.6 indicate significant dietary overlap (Schoener 1968; Zaret and Rand 1971; Mathur 1977). Diets were summarized for yellow perch with total lengths ranging only 94–245 mm, and for white perch with TLs ranging 83–265 mm to match those TLs used for the corresponding stable isotope analyses. We did not calculate Schoener diet overlap index using the USGS diet data, because the proportions of the diet constituents on a volume or weight basis were not available.

Results

Yellow perch and white perch population size

After becoming abundant in Lake Erie in the early 1980s, the population size of adult white perch in the lake's western basin continued to grow exponentially through 1986, when the population size peaked at 1.5 billion fish (Fig. 1). The population size of adult yellow perch remained relatively high during 1978–1986, but then substantially declined 1986–1990. Adult white perch population size dramatically decreased between 1986 and 1990. Since 1990, the adult yellow perch population peaked at 65 million fish in 2005 and fell to approximately 35 million fish by 2009. The adult white perch population size has remained relatively low since 1990 (Fig. 1).

Stable isotopes values

The results of MANOVA revealed significant effects of species, sampling area, and season on the stable isotope values of dorsal muscle from yellow and white perch (Table 2). Results of ANOVA found yellow and white perch to differ in both their mean $\delta^{13}C$ and $\delta^{15}N$ values, with yellow perch having higher $\delta^{13}C$ and lower $\delta^{15}N$ values than white perch across all sampling areas (Tables 1, 2). The $\delta^{13}C$ and $\delta^{15}N$ values of both yellow and white perch were found to differ significantly among sites, however, only $\delta^{15}N$ values were found to be significantly affected by season (Table 2). Mean $\delta^{13}C$ and $\delta^{15}N$ values of yellow perch increased from spring to fall at Detroit River and Middle Sister Island, but decreased over that same period at Maumee River and Bass Island. White perch $\delta^{13}C$ and $\delta^{15}N$ values exhibited the opposite seasonal trends, except for at Detroit River, where their $\delta^{15}N$ also increased from spring to fall (Table 1).

Isotopic population metrics

The SEA_c of yellow and white perch showed overlap during spring at Detroit River and Middle Sister Island and in fall at Maumee River and Bass Island (Fig. 3). Of these situations where the SEA_c overlapped, only that at Middle Sister in spring was deemed significant (>0.60; Table 3). There was no overlap in SEA_c between yellow and white perch at Maumee River or Bass Island in the spring season or at Detroit River and Middle Sister during fall (Fig. 3; Table 3). The size of SEA_c varied with site and season for both yellow and white perch. Generally, yellow perch SEA_c were larger at Detroit River and Middle Sister Island and during the spring season, while white perch SEA_c were highly variable among sites and seasons (Fig. 3; Table 3). Using confidence intervals obtained from Bayesian estimation of isotopic niche size (SEA_b) we found isotopic niches of white perch to be significant larger than those of yellow perch at Maumee River in spring ($P = 0.03$) and Middle Sister Island in fall ($P = 0.04$), with all other comparisons showing no difference in among species (Fig. 4).

The NR_b values of white perch were higher than those of yellow perch across all sampling areas and

Table 2 MANOVA and ANOVA results, testing differences in the values of the stable isotopes $\delta^{13}C$ and $\delta^{15}N$ among yellow perch and white perch at four sampling locations for spring and fall seasons in western Lake Erie

MANOVA ($\delta^{13}C - \delta^{15}N$)	*df*	Pillai trace	F	Num *df*	*P*
Species	1	0.314	38.59	2	<0.001*
Site	3	0.269	8.84	6	<0.001*
Season	1	0.067	6.05	2	0.003*
Residuals	170				
ANOVA ($\delta^{13}C$)	***df***	**Sum sq**	**Mean sq**	**F value**	***P***
Species	1	28.38	33.71	33.71	<0.001*
Site	3	8.615	2.872	3.411	0.02*
Season	1	0.273	0.273	0.325	0.57
Residuals	170	143.15	0.842		
ANOVA ($\delta^{15}N$)	***df***	**Sum sq**	**Mean sq**	**F value**	***P***
Species	1	34.61	34.62	59.89	<0.001*
Site	3	24.95	8.318	14.39	<0.001*
Season	1	7.012	7.012	12.13	<0.001*
Residuals	170	98.26	0.578		

* A significant effect

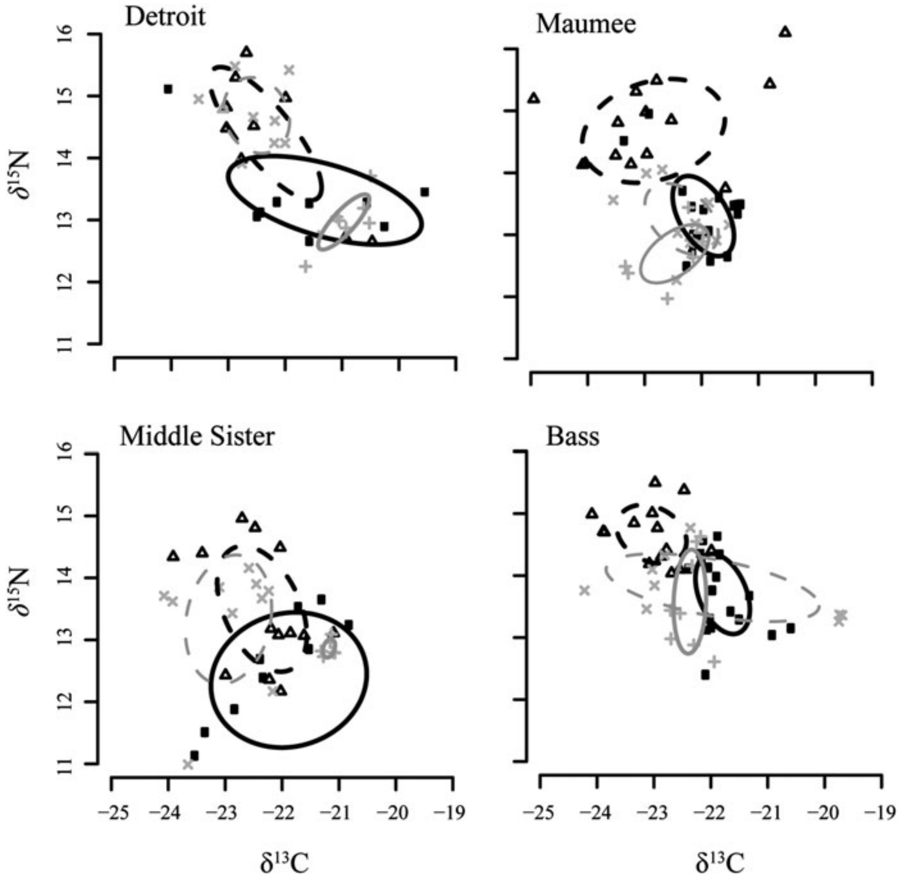


Fig. 3 Stable isotope bi-plot for each sampling area, illustrating the isotopic niches of yellow and white perch collected in spring (*black symbols and lines*) and fall (*grey symbols and lines*) 2009. Lines enclose standard ellipse areas (SEA_c) for each season for yellow perch (*solid lines*) and white perch (*dashed lines*) represent the total niche area occupied by each species. Individual data points for yellow perch collected in spring are represented by *solid squares* and in fall by grey crosses. White perch collected in spring are represented by *open triangles* and in fall by "x"

seasons, except Bass Island in spring. Differences in CR_b among the species were much more variable (Table 3). During both seasons yellow and white perch consistently had higher NR_b and CR_b at Detroit River and Middle Sister Island compared to Maumee River and Bass Island (Table 3).

Stomach content analysis

Stomach content data from USGS (2010) were summarized as frequency of occurrence from a total of 123 yellow perch (94–245 mm TL) and 80 white perch (83–265 mm TL). During spring, zooplankton and benthic invertebrates were the most common diet item and fish and fish eggs the least common for both species. Zooplankton was found to be present in all white perch stomachs sampled in spring, at all sampling locations, while the presence of zooplankton ranged from 33.4 to 100 % in yellow perch. Dreissenids were also found to be an important diet item for yellow perch in spring, and was present in 22.3–56.3 % of fish analyzed (Table 4—*top*). During fall, zooplankton was not present in the diets of yellow perch at any sampling location, however, it remained in the diets of white perch (0–100 %). Benthic invertebrates remained a important diet item for both yellow (41.6–100 %) and white perch (100 %—all locations) and the presence of fishes also increased the diets of both species during the fall season (0–58.3 % for yellow perch, 0–42.9 % for white perch). Dreissenids remained an important diet item for yellow perch in the fall (Table 4—*top*).

Stomach content data from Legler (2008) were summarized from a total of 277 yellow perch (94–245 mm TL) and 325 white perch (83–265 mm TL) using frequency of occurrence and average percent composition by volume. These data existed only for the Detroit and Maumee River plumes for fishes collected in spring, and sample sizes were much larger per site than those from USGS (Table 4—*top/bottom*). Based on frequency of occurrence, zooplankton was found more commonly in the stomachs of

Table 3 Comparison of stable isotope population metrics and Schoener overlap index for yellow perch and white perch from four sites in the western basin of Lake Erie grouped by season caught

Season	Site	Species	NR_b	CR_b	SEA_c	SIBER Overlap	Schoener Overlap	
							2006	2007
Spring	Detroit	Yellow perch	2.74	3.77	3.20	0.54	0.57	0.55
		White perch	2.77	3.55	1.95			
	Middle sister	Yellow perch	2.59	2.06	4.67	0.88*		
		White perch	2.74	2.86	2.28			
	Maumee	Yellow perch	2.04	1.95	0.95	0	0.45	0.58
		White perch	2.79	1.96	3.20			
	Bass	Yellow perch	1.65	1.55	0.88	0		
		White perch	1.44	1.70	0.89			
Fall	Detroit	Yellow perch	2.76	2.63	0.36	0		
		White perch	2.91	2.87	1.10			
	Middle Sister	Yellow perch	1.93	3.32	0.05	0		
		White perch	2.18	2.87	2.44			
	Maumee	Yellow perch	1.63	1.58	0.75	0.29		
		White perch	1.79	1.26	1.06			
	Bass	Yellow perch	1.63	2.53	0.75	0.45		
		White perch	2.26	2.59	2.72			

n sample size used to calculate metrics, NR_b δ^{15}N range, CR_b δ^{13}C range, SEA_c standard ellipse area, *SIBER overlap* fraction ranging from 0 to 1 represents the amount of standard ellipse area overlap between yellow and white perch, *Schoener overlap* fraction ranging from 0 to 1 represents the amount of diet similarity between yellow perch and white perch based on stomach content from Legler (2008)

* A significant diet overlap ($D > 0.60$) for SIBER or Schoener index

white perch, while yellow perch stomachs included more benthic invertebrates and dreissenids (Table 4—*bottom*). Legler (2008) data summarized as percent by volume provided a means to understand the relative importance of each diet item to yellow and white perch. The stomach contents of yellow perch in spring were dominated in volume by benthic invertebrates at Detroit River, while zooplankton, benthic invertebrates and dressenids were all important at Maumee River. White perch diets were comprised of mostly zooplankton and benthic invertebrates at both sites, with dreissenids also of important at Maumee River (Fig. 5). Schoener diet index from Legler (2008) data indicated the no significant diet overlap of yellow and white perch in both Detroit River and Maumee River Plumes during spring (Table 3).

Discussion

As is the case with many successful NIS, white perch have been described as a generalist species with a wide ecological niche and tolerance for a wide range of environmental conditions (Stanley and Danie 1983; Wong et al. 1999). These characteristics have contributed to the success this estuarine species has had in establishing in many inland systems of North America, such as the Laurentian Great Lakes (Christie 1972; Busch et al. 1977; Boileau 1985). Using δ^{13}C and δ^{15}N and subsequent isotopic population metrics along with complementary stomach content data, we compared the trophic ecology and diet of adults of white perch to native yellow perch in the western basin of Lake Erie, a system where these sympatric species have co-existed for over fifty years. As well, index gillnetting data were used to assess temporal trends in yellow perch and white perch abundance. Herein, we discuss the results of our analyses with a focus on the following: (1) spatial and seasonal differences in relative diet among species indicated by stable isotopes and stomach content analysis; (2) isotopic population metrics and niche and diet overlap of yellow perch and white perch; (3) comparison of the application of stable isotopes and stomach content

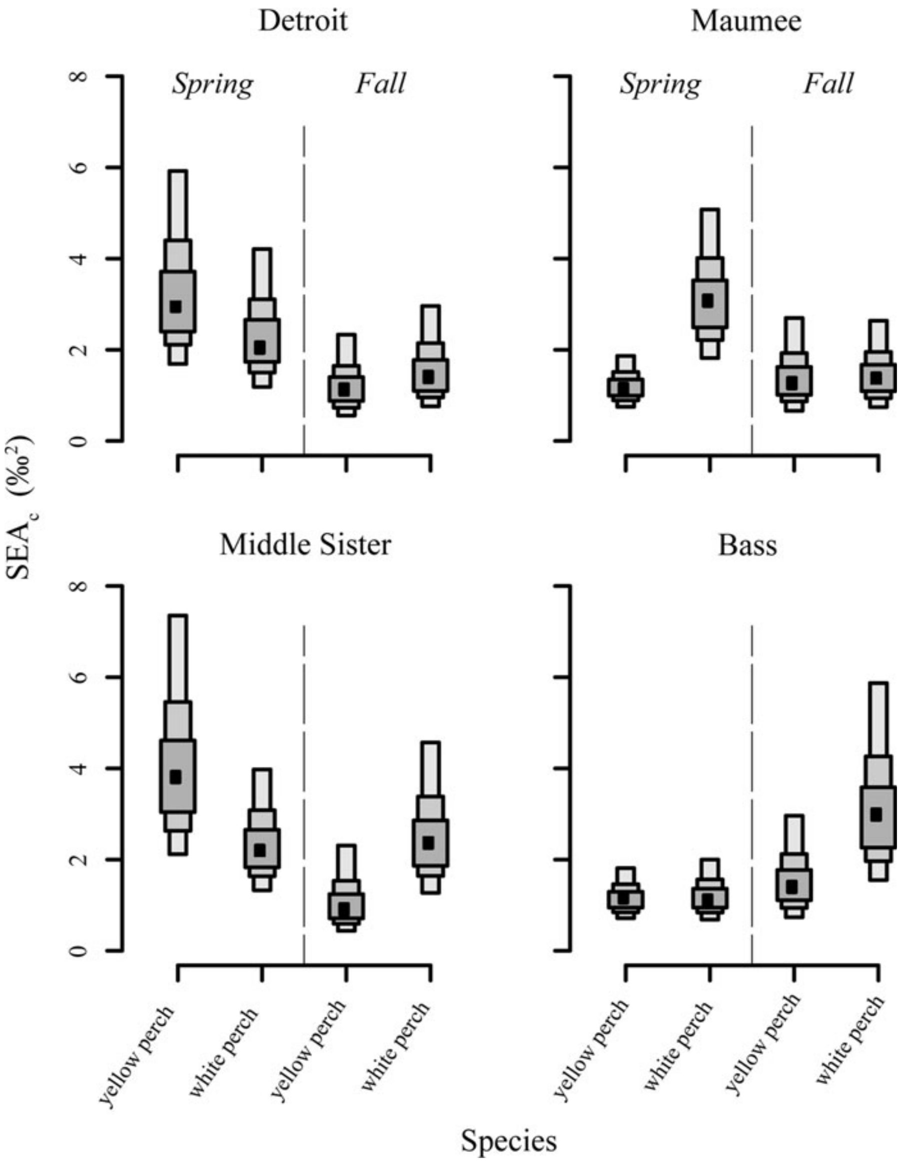


Fig. 4 Density plot presenting the Bayesian estimates of confidence intervals for standard ellipses areas. *Black squares* correspond to means and grey boxes represent confidence intervals of 50, 75 and 95 % confidence intervals for both yellow perch and white perch at all four sampling areas

analyses to assess relative diet of sympatric fish species; and (4) potential causes for reduced populations of yellow since the introduction of white perch in the basin.

The relative trophic ecology and diet of yellow perch and white perch varied with season in the western basin of Lake Erie. Mean values of δ^{13}C of yellow perch in spring were higher than those of white perch at all sampling locations. These differences in δ^{13}C among species were most pronounced at Bass Island (1.25 ‰) and least pronounced at Middle Sister Island (0.47 ‰). White perch had higher δ^{15}N values than yellow perch across all sampling locations during spring, and these differences were highest at Detroit River (2.07 ‰) and lowest at Bass Island (0.97 %). These isotope values suggest that yellow perch relied on a more benthic carbon source and fed at lower trophic positions than white perch during spring across the basin. The potential movement of fishes across sampling locations could blur differences in stable isotope values between sampling location, as lower trophic level isotope values are known to vary between these sites (Guzzo et al. 2011), and, thus, makes interpretations related to isotopes more conservative. Stomach content data, particularly those of Legler (2008), support results of stable isotope analysis,

Table 4 *Top*—diets expressed as frequency of occurrence (%) for yellow perch and white perch collected from Detroit River Plume, Middle Sister Island, Maumee River Plume and Bass Island areas within Lake Erie's western basin during years 2009 (USGS 2009). *Bottom*—diets expressed as mean (years 2006 and 2007) frequency of occurrence (%) for yellow perch and white perch collected from the Detroit and Maumee river plumes within Lake Erie's western basin (Legler 2008). Yellow perch TLs ranged from 94 to 245 mm and white perch TLs ranged from 83 to 265 mm

Season	Prey category [data from USGS (2010)]	Yellow perch				White perch			
		Detroit (n = 18)	Middle sister (n = 19)	Maumee (n = 16)	Bass (n = 18)	Detroit (n = 16)	Middle sister (n = 15)	Maumee (n = 14)	Bass (n = 12)
Spring	Zooplankton	33.4	100	100	38.9	100	100	100	100
	Benthic Invertebrates*	100	100	100	100	37.7	100	100	100
	Fishes	16.7	15.8	6.3	5.6	6.3	0	0	0
	Fish Eggs	22.2	0	6.3	0	12.5	13.3	7.1	0
	Dreissenids	22.3	36.9	56.3	44.4	12.5	13.4	0	16.7
		(n = 20)	(n = 12)	(n = 14)	(n = 6)	(n = 6)	(n = 5)	(n = 7)	(n = 5)
Fall	Zooplankton	0	0	0	0	0	40	42.9	100
	Benthic Invertebrates*	100	41.6	100	50	100	100	100	100
	Fishes	25	58.3	28.6	0	33.3	0	42.9	0
	Fish Eggs	0	0	0	0	0	0	0	0
	Dreissenids	30	25	14.2	50	16.7	20	0	40

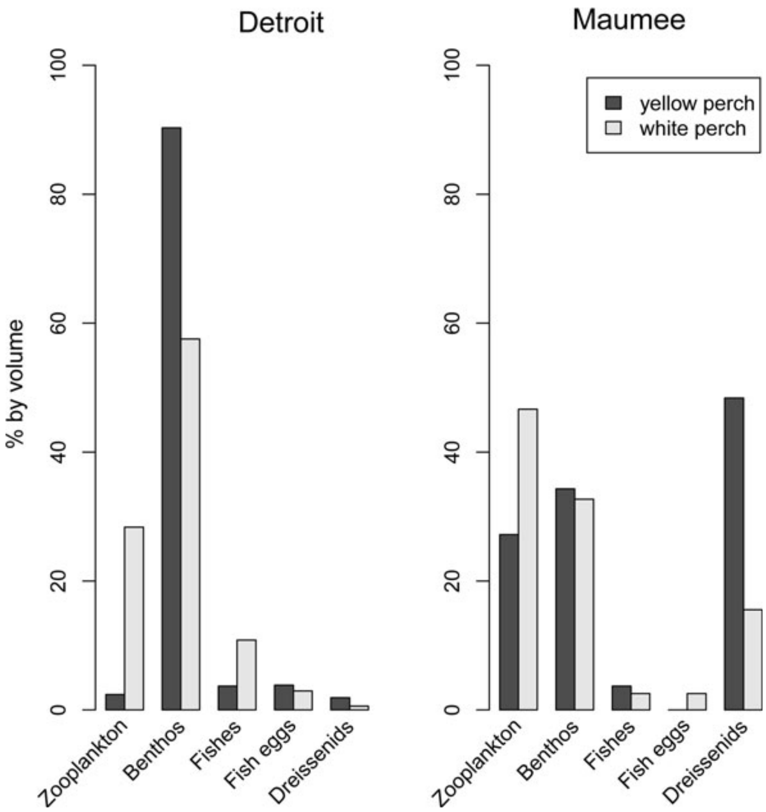
Season	Prey category (data from Legler (2008))	Detroit		Maumee	
		Yellow perch (n = 103)	White perch (n = 174)	Yellow perch (n = 174)	White perch (n = 151)
Spring	Zooplankton	1.3	30.4	17.3	51.3
	Benthic invertebrates	100	90.8	78.2	59.8
	Fishes	4.6	12.4	4.5	4.4
	Fish eggs	8.4	6.5	0	5.4
	Dreissenids	2.4	1.6	78.1	25.2

[a] n denotes sample size

indicating yellow perch ate more benthic invertebrates and dreissenids, while white perch relied more on zooplankton. Garton et al. (2005) found zooplankton in the western basin of Lake Erie to be higher in δ^{15}N and lower in δ^{13}C than dreissenids, which was in accord with our results from both stable isotopes and diet analysis indicating that white perch are more reliant on zooplankton than yellow perch. The higher trophic position of white perch compared with that of yellow perch may have also been due, in part, to a higher proportion of fishes (including fish eggs) in the diet of white perch than in yellow perch diet. The Legler (2008) diet data showed that the proportion of fishes in white perch diet was slightly higher than that for yellow perch, but these data were just for spring. Fall sampling, along with detailed stomach content analysis, should be performed to determine whether the higher proportion of fishes in the diets of white perch persists into fall months.

Yellow perch and white perch have been documented to undergo similar seasonal diet shifts in the western basin of Lake Erie (Parrish and Margraf 1994). These similarities are likely a result of variations in prey communities and the opportunistic feeding behaviours of these two sympatric species. In late summer, young-of-the-year minnows (*Cyprinidae*) become more available (Duncan et al. 2011) as zooplankton abundance typically begins to decline in lakes (Gopalan et al. 1998). Our diet analysis suggests yellow perch and white perch diets are quite similar in

Fig. 5 Comparison of the diets of yellow perch and white perch expressed as average percent composition by volume. Values are means of years 2006 and 2007 (Legler 2008)



fall, with fishes and benthic invertebrates found in similar amounts in the stomachs of the two species. One major difference is white perch's continued consumption of zooplankton (USGS 2010), which may provide explanation for higher δ^{15}N values of white perch. This continued consumption of zooplankton, despite its decreased abundance might be a result of physical constraints (gape position) on benthic foraging by white perch (Parrish and Margraf 1990). While, this is not evident from our diet analysis, we point out that sample sizes for our fall diet analysis were small, and thus may not accurately depict differences in diet between these two species. Additonally, we suggest that frequency of occurrence data (USGS 2010) may provide insight into diet breadth, while diet by volume (Legler 2008) provides relative importance of various diet items to each species.

Stomach contents varied among sampling locations, providing some explanation for differences in δ^{13}C and δ^{15}N among sites. Yellow perch, white perch, and zebra mussels all followed similar isotopic trends and had higher δ^{13}C values at Detroit River and Middle Sister Island relative to Maumee River and Bass Island, indicative of a more benthic source of carbon. This is consistent with our diet data that showed both yellow perch and white perch consume more zooplankton in the Maumee River plume and increased benthic invertebrates and fishes in Detroit River plume. This is also consistent with prey availability, as soft-rayed fishes are found in higher abundances in Detroit River Pplume compared to Maumee River plume (Forage Task Group 2010). Differences in fish isotope values and diet among sites could also result from baseline differences in isotopic values between Detroit and Maumee rivers. Lower food web species, such as young-of-year fishes and dreissenids from Maumee River plume, have been shown to exhibit lower δ^{13}C and higher δ^{15}N values due to crop and inorganic fertilizer runoff, while Detroit River exhibits higher δ^{13}C and lower δ^{15}N values (Table 1; Guzzo et al. 2011). However, given the relative differences in stable isotope values between the yellow perch and white perch and differences in stomach contents across sampling areas, the feeding ecology of these fish species appears to vary across the western basin of Lake Erie.

The use of stable isotope-derived population metrics provided a novel means to quantify feeding interactions among yellow perch and white perch. In general, white perch were found to have larger isotopic niches than yellow perch, which is in agreement with previous work that found that white perch tend to have broad, plastic diets (Zuerlein 1981; Stanley and Danie 1983; Couture and Watzin 2008). These results are consistent with the idea that NIS have broader diets, and in turn larger niche widths than their native counterparts (Lodge 1993; Moyle and Light 1996). While the isotopic niches of white perch were larger in most cases, there were some spatial and seasonal complexities. For example, in spring, yellow perch had larger isotopic niches at both Detroit River and Middle Sister Island. This may have been the result of increased consumption of dreissenids (USGS data), which can have highly variable δ^{13}C values (Guzzo et al. 2011) in combination with consumption of zooplankton by white perch. As expected, species with isotopic niches often had larger NR_b and CR_b, however, there were some exceptions, particularly when differences in isotopic niches among species were less pronounced. NR_b and CR_b varied spatially and seasonally, again suggesting that resource utilization is influenced by local habitat characteristics and possibly prey availability.

Both stable isotope and stomach content analyses indicated a low to moderate degree of niche (or diet) overlap between yellow perch and white perch in the western basin of Lake Erie. The results of stable isotope analysis revealed that SIBER overlap was less than 0.60 in seven of the eight comparisons of site and seasons; an overlap index value greater than 0.60 is sufficiently high to warrant the potential for feeding competition and is indicative of a significant niche overlap. Only at Middle Sister Island in the spring did the stable isotope based SIBER overlap exceed 0.60. Moreover, the average SIBER overlap index value was only 0.27; this value is indicative of a low to moderate degree of niche (or diet) overlap. In addition, results of MANOVA and ANOVA indicated highly significant differences between yellow perch and white perch in western Lake Erie with regard to their stable isotope values. Furthermore, the Schoener diet overlap indices calculated from the Legler (2008) data for all four combinations of site (Maumee River plume and Detroit River plume) and year (2006 and 2007) were less than 0.60; the average across these combinations was 0.54. Thus, stomach content analysis results corroborated the results of stable isotope analysis. Finally, we submit that isotopic niche overlap comparisons are more appropriate for studies seeking to understand interactions among populations over coarse temporal scales, while diet overlap indices, such as the Schoener index, provide a means to study fine-scale interactions such as ontogenetic and seasonal diet shifts.

There are a number of limitations and weaknesses to the application of stable isotopes to quantify and compare trophic ecology among sympatric fish species. First, to relate stable isotopes in a species to its diet requires accurate diet-tissue discrimination factors, which represent the change in isotope values between a predator and it's prey. These diet-tissue discrimination factors have been shown to vary with species (Martinez del Rio et al. 2009), tissue (Bearhop et al. 2002), diet quality (Vanderklift and Ponsard 2003), isotope value in food (Caut et al. 2009, Dennis et al. 2010), and environment (Power et al. 2003) among other things. Stable isotopes, particularly those of muscle from adult fishes are subject to slow turnover (Perga and Gerdeaux 2005), and thus may not provide accurate depictions of the diet of fishes at the time of capture. Additionally, stable isotopes at the base of food webs are subject to spatial and temporal variation in large lakes (Guzzo et al. 2011) that can confound their interpretation.

Often the addition of stomach content analysis to studies of trophic ecology provides a means of ground-truth of the stable isotope values. Stomach content analysis, however, is not without limitations and only provides a snapshot of diet previous to the time of capture, limited by empty stomachs and biased by low sample sizes (Bearhop et al. 2004). Despite employing both isotope and stomach content analyses in this study, specific questions remain regarding the spatial complexities in feeding interactions among these species. To answer these questions, we recommend that future studies consider studying habitat use through acoustic telemetry with comparisons to prey abundance and spatially explicit stomach content to further understand the relationship between these two fish species across the basin.

Yellow perch populations in the western basin of Lake Erie declined substantially since 1979 and eventually hit record lows in 1991 (Freeman et al. 1996), casting serious concerns regarding yellow perch stocks. It would seem logical that these observed decreases in yellow perch could have been related to the increased competitive pressure exhibited by rapidly increasing populations of non-indigenous white perch. This idea was furthered by work that suggested that white perch were limiting the growth of yellow perch through food competition (Hayward and Margraf 1987; Parrish 1988; Parrish and Margraf 1990, 1991, 1994) and that the species showed similar temporal patterns of resource use in Lake Erie (Schaeffer and Margraf 1986a, b; Parrish and Margraf 1994). However, examination of the findings of Parrish and Margraf (1990, 1991) and Schaeffer and Margraf (1986a, b), combined with population size, recruitment, and exploitation rates in western Lake Erie during 1975–2009 (Yellow Perch Task Group 2011) do not support the idea that competitive pressure alone led to decreases in yellow perch stocks. First, the average diet overlap indices from Parrish and Margraf (1991) and Schaeffer and Margraf (1986a, b) were both <0.60, suggesting no significant diet overlap (Schoener 1968) between yellow perch and white perch. A laboratory study on the feeding of yellow perch and white perch concluded that the species were equally capable of feeding on zooplankton (Parrish and Margraf 1991), and, therefore, even with low densities of benthic invertebrates in western Lake Erie at the time (Hayward 1988), yellow perch and white perch could utilize other prey sources. Additionally, examination of time series data for age-2 recruitment estimates of yellow perch suggested that newly introduced white perch did not negatively affect yellow perch survival (Yellow Perch Task Group 2011). If white perch were out-competing yellow perch for food, so that yellow perch recruitment was affected, then yellow perch survival should have begun to decrease starting in 1982 when white perch abundance increased. This was not the case, as yellow perch year-class strength continued to be strong in 1982, 1984 and, 1985 (Yellow Perch Task Group 2011). Large decreases in yellow perch populations 1988–1990 and 2005–2009 both coincided with increases in exploitation rates, while increases in populations in the late 1990s and early 2000s related to decreases in exploitation by the fishery (Yellow Perch Task Group 2011). Therefore, changes in fishery pressure, rather than competition with white perch, would appear to better describe historical changes in the adult yellow perch population in the western basin of Lake Erie.

We recognize that recruitment of fishes, such as yellow perch and white perch is determined in the first year of life, so focusing this paper on adults has likely missed the period when trophic overlap between the two species would most affect survival. Previous publications have shown young-of-year yellow perch and white perch to have overlapping diets and undergo similar seasonal ontogenetic diet shifts to benthic foods associated with decreases in zooplankton abundance (Gopalan et al. 1998). Therefore, we suggest further studies evaluating the effects of feeding interactions on young-of-year fishes to better elucidate mechanisms governing recruitment of these two species.

Although the Lake Erie ecosystem has undergone major changes since the 1980s, our results indicated that yellow perch and white perch in the western basin of Lake Erie have maintained some degree of separation in occupied niches and in diet. During the 1990s, dreissenid mussels and the round goby, invaders from the Ponto-Caspian region, became well established in Lake Erie and the native burrowing mayfly population recovered in Lake Erie's western basin. Our stable isotope data showed that the ecological niches occupied by yellow perch and white perch during 2009 were significantly different from one another. Our stomach content analysis revealed that the diet overlap between yellow perch and white perch in western Lake Erie was only at a low to moderate level, thereby, corroborating our stable isotope analysis. Furthermore, the stomach content analyses of the 1980s also indicated that the diet overlap between yellow perch and white perch from Lake Erie was not significant (Schaeffer and Margraf 1986a; Parrish and Margraf 1990, 1991). Therefore, yellow perch and white perch in western Lake Erie have appeared to maintain a moderate degree of diet overlap for nearly 30 years. These results suggested that feeding competition between these two species was not the cause of changes in yellow perch population sizes over time. Instead, changes in fishery exploitation rates may have been partly responsible for the changes observed in the adult yellow perch population size over time. New stressors, such as climate change and introductions of new NIS (e.g., Asian carps), may eventually disrupt the ecological balance existing between yellow perch and white perch populations in western Lake Erie; such disruptions have been discussed, theoretically, by Bohn and Amundsen (2001).

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References

Baker DB, Richards RP (2002) Phosphorus budgets and riverine phosphorus export in northwestern Ohio watersheds. J Environ Qual 31:96–108

Barbiero RP, Tuchman ML (2001) Results from the US EPA's biological open water surveillance program of the Laurentian Great Lakes: I. Introduction and phytoplankton results. J Great Lakes Res 27:134–154

Barbiero RP, Little RE, Tuchman ML (2001) Results from the US EPA's biological open water surveillance program of the Laurentian Great Lakes: III. Crustacean zooplankton. J Great Lakes Res 27:167–184

Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen an carbon stable isotopes in avian blood and feathers. Physiol Biochem Zool 75:451–458

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012

Bohn T, Amundsen PA (2001) The competitive edge of an invading specialist. Ecology 82:2150–2163

Boileau MG (1985) The expansion of white perch, *Morone americana*, in the lower Great Lakes. Fisheries 10:6–10

Bruno JF, Cardinale BJ (2008) Cascading effects of predator richness. Front Ecol Environ 6:539–546

Busch WN, Davies DH, Nepszy SJ (1977) Establishment of white perch, *Morone americana*, in Lake Erie. J Fish Res Board Can 34:1039–1041

Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors (δ^{13}C and δ^{15}N): the effect of diet isotope values and applications for diet reconstruction. J Appl Ecol 46:443–453

Christie WJ (1972) Lake Ontario—effects of exploitation, introductions, and eutrophication on salmonid community. J Fish Res Board Can 29:913–929

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Couture SC, Watzin MC (2008) Diet of invasive adult white perch (*Morone americana*) and their effects on the zooplankton community in Missisquoi Bay, Lake Champlain. J Great Lakes Res 34:485–494

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Dennis CA, MacNeil MA, Rosati JY, Pitcher TE, Fisk AT (2010) Diet discrimination factors are inversely related to δ^{13}C and δ^{15}N values of food for fish under controlled conditions. Rapid Commun Mass Sp 24:3515–3520

DFO (2006) Canadian fisheries statistics, 2005. Fisheries and Oceans Canada, Ottawa

Ditoro DM, Thomas NA, Herdendorf CE, Winfield RP, Connolly JP (1987) A post audit of a lake eutrophication model. J Great Lakes Res 13:801–825

Dolan DM, Mcgunagle KP (2005) Lake Erie total phosphorus loading analysis and update: 1996–2002. J Great Lakes Res 31:11–22

Duncan JM, Marschner CA, Gonzalez MJ (2011) Diet partitioning, habitat preference and behavioral interactions between juvenile yellow perch and Round Goby in nearshore areas of Lake Erie. J Great Lakes Res 37:101–110

Forage Task Group (2010) Report of the Lake Erie forage task group. Presented to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission, Ann Arbor

Freeman M, Dietz P, Kayle K, Kenyon R, Knight C, Thomas M (1996) Report of the Lake Erie yellow perch task group. Great Lakes Fishery Commission, Ann Arbor

Garton DW, Payne CD, Montoya JP (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

Gopalan G, Culver DA, Lin W, Trauben BK (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

Great Lakes Fishery Commission (1995) Fish community objectives for Lake Huron. Great Lakes Fishery Commission, Ann Arbor

Great Lakes Fishery Commission (2007a) Strategy and options for promoting the rehabilitation of ciscoes in Lake Huron. Great Lakes Fishery Commission, Ann Arbor

Great Lakes Fishery Commission (2007b) Environmental objectives for Lake Huron. Great Lakes Fishery Commission, Ann Arbor

Guzzo MM, Haffner GD, Sorge S, Rush SA, Fisk AT (2011) Spatial and temporal variability 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

Hammerschlag-Peyer C, Yeager LA, Araujo MS, Layman CA (2011) A hypothesis-testing framework for studies investigating ontogenetic niche shift using stable isotope ratios. PLOS One. doi:10.1371/journal.pone.0027104

Hayward RS (1988) Eutrophication effects on bioenergetic conditions for Lake Erie yellow perch. Ph. D. Thesis, The Ohio State University

Hayward RS, Margraf FJ (1987) Eutrophication effects on prey size and food available to yellow perch in Lake Erie Trans. Am Fish Soc 116:210–223

Holeck KT, Mills EL, Macisaac HJ, Dochoda MR, Colautti RI, Ricciardi A (2004) Bridging troubled waters: biological invasions, transoceanic shipping, and the Laurentian Great Lakes. Bioscience 54:919–929

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602

Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLoS One 7(2):e31757. doi:10.1371/journal.pone.0031757

Johnson BM, Martinez PJ, Stockwell JD (2002) Tracking trophic interactions in coldwater reservoirs using naturally occurring stable isotopes. Trans Am Fish Soc 131:1–13

Kane DD, Gordon SI, Munawar M, Charlton MN, Culver DA (2009) The Planktonic Index of Biotic Integrity (P-IBI): an approach for assessing lake ecosystem health. Ecol Indic 9:1234–1247

Larsen A (1954) First record of the white perch (*Morone americana*) in Lake Erie. Copeia 1954:154

Layman CA, Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. Mar Ecol Prog Ser 448:131–141

Layman CA, Arrington DA, Montana CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Legler ND (2008) Effects of Lake Erie habitat variation and digestion rate on feeding in freshwater fishes. M.Sc. Thesis, University of Windsor

Levine JM, D'antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8:133–137

Mack RN, Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for. Bioscience 51:95–102

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Martinez del Rio C, Wolf N, Carleton SA, Gannes LZ (2009) Isotopic ecology ten years after a call for more laboratory experiments. Biol Rev Camb Philos Soc 84:91–111

Marvier M, Kareiva P, Neubert MG (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Anal 24:869–878

Mathur D (1977) Food habits and competitive relationships of the bandfish shiner in Halawakee Creek, Alabama. Am Midl Nat 97:89–100

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Mills EL, Leach JH, Carlton JT, Secor CL (1994) Exotic species and the integrity of the Great Lakes- lessons from the past. Bioscience 44:666–676

Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. Biol Cons 78: 149–162

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. Trends Ecol Evol 19:18–24

Ontario Ministry of Natural Resources (2012) 2011 Status of major stocks. Lake Erie Management Unit, ISSN 1718-4924 (Print), ISBN 978-1-4435-8983-3 (Print, 2011 ed.), ISSN 1925-5454 (Online), ISBN 978-1-4435-8984-0 (PDF, 2011 ed.). 79 pp

Parrish DL (1988) The white perch and its interactions with yellow perch in Lake Erie. Ph. D. Thesis The Ohio State University

Parrish DL, Margraf FJ (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

Parrish DL, Margraf FL (1991) Prey selectivity by age-0 white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in laboratory experiments. Can J Fish Aquat Sci 48:607–610

Parrish DL, Margraf FJ (1994) Spatial and temporal patterns of food use by white perch and yellow perch in Lake Erie. J Freshwater Ecol 9:29–35

Perga ME, Gerdeaux D (2005) Are fish what they eat' all year round? Oecologia 144:598–606

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Polo-Cavia N, Lopez P, Martin J (2008) Interspecific differences in responses to predation risk may confer competitive advantages to invasive freshwater turtle species. Ethology 114:115–123

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

Power M, Guiguer KRRA, Barton DR (2003) Effects of temperature on isotopic enrichment in *Daphnia magna*: implications for aquatic food web studies. Rapid Commun Mass Sp 17:1619–1625

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reichert JM, Fryer BJ, Pangle KL, Johnson TB, Tyson JT, Drelich AB, Ludsin SA (2010) River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. Can J Fish Aquat Sci 67:987–1004

Ricciardi A (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Divers and Distrib 12:425–433

Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol Evol 15:62–65

Roseman EF, Taylor WW, Hayes DB, Hanes AL, Francis JT (2006) Predation on walleye eggs by fish on reefs in Western Lake Erie. J Great Lakes Res 32:415–423

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North

America: apparent patterns, processes, and biases. Annu Rev Eco Syst 31:481–531

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Eco Syst 32:305–332

Sax DF, Brown JH (2000) The paradox of invasion. Global Eco Biogeogr 9:363–371

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

Schaeffer JS, Margraf FJ (1986b) Population characteristics of the invading white perch (*Morone americana*) in western Lake Erie. J Great Lakes Res 12:127–131

Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726

Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. Bull Fish Res Board Can 184:966

Stanley JG, Danie DS (1983) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic-white perch). USFW, Division of Biological Services. FWS/OBS-82/11.7

Turner TF, Collyer ML, Krabbenhoft TJ (2010) A general hypothesis-testing framework for stable isotope ratios in ecological studies. Ecology 91:2227–2233

Tyson JT, Knight RL (2001) Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. T Am Fish Soc 130:766–782

Tyson JT, Johnson TB, Knight CT, Bur MT (2006) Intercalibration of research survey vessels on Lake Erie. N Am J Fish Manag 26:559–570

United States Geological Survey (2010) Fisheries research and monitoring activities of the Lake Erie Biological Station, 2009. Sandusky, Ohio

Vander Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464–467

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer δ^{15}N enrichment: a meta analysis. Oecologia 136:169–182

Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. NZ J Ecol 21:1–16

Wong RK, Noble RL, Jackson JR, VanHorn S (1999) White perch invasion of B. Everett Jordan Reservoir, North Carolina. Proc Annu Conf Southeast Assoc Fish Wildl Agencies 53:12–169

Yellow Perch Task Group (2011) Report of the Lake Erie Yellow Perch task group. Presented to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission, Ann Arbor

Zaret TM, Rand AS (1971) Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336–342

Zhao YM, Jones ML, Shuter BJ, Roseman EF (2009) A biophysical model of Lake Erie walleye (*Sander vitreus*) explains interannual variations in recruitment. Can J Fish Aquat Sci 66:114–125

Zuerlein G (1981) The white perch in Nebraska. Nebraska Game and Parks Commission. Tech. Ser. 8. Lincoln