MR TAYLOR J SENEGAL (Orcid ID : 0000-0001-7344-2879)
DR STEVEN A. POTHOVEN (Orcid ID : 0000-0002-7992-5422)

Article type   : Original articles

Title: Stable isotopes and morphology reveal spatial and annual patterns in trophic reliance of an invertivorous juvenile fish

Authors: Taylor J. Senegal[1]*, Timothy M. Sesterhenn[1,2], Charles R. Roswell[1,3], Steven A. Pothoven[4], Tomas O. Höök[1,5]

[1]Purdue University, Department of Forestry and Natural Resources; [2]Morningside College; [3]Illinois Natural History Survey; [4]National Oceanic and Atmospheric Administration; [5]Illinois-Indiana Sea Grant

***Corresponding author:** tsenegal13@gmail.com; 715 W. State Street, West Lafayette, IN 47907; (909)262-3627

Running Title: Trophic variation of yellow perch in Saginaw Bay

Abstract

Ecological studies have traditionally treated fish species or populations as homogenous groups; however, numerous studies have shown that intrapopulation variation in resource use is widespread. Within-species diet differences are evident in small and large freshwater systems, and may influence trophic and population dynamics. In a previous study of young yellow perch, spatial intrapopulation diet variation was observed for stomach contents, a relatively short-term diet indicator. In the current study, we build upon the earlier study of yellow perch in Saginaw Bay, Lake Huron, and assess patterns of long-term diet indicators (stable isotopes and morphology) to assess consistency of diet variation over time and improve characterization of trophic differences among sites. Specifically, we analyzed soft tissue samples for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios, and used geometric morphometrics to describe morphological variation of young yellow perch. While both isotopes displayed significant spatial differences, $\delta^{15}N$ values demonstrated a much clearer separation among sites, with greater $\delta^{15}N$ values for yellow perch collected closer to the mouth of the Saginaw River. Morphological variation also was more apparent among sites rather than between years or months, with more streamlined yellow perch morphologies evident at sites where they consumed high proportions of zooplankton relative to benthic invertebrates. Somewhat unexpectedly, soft tissue $\delta^{13}C$ values varied strongly between the two study years; however, the ultimate cause of such inter-annual variation in $\delta^{13}C$ is unclear. These long-term indicators showed consistent spatial differences, which suggests that individual fish are using resources at a particular site long enough to reflect a stable isotope or morphological signal. Yellow perch production at different locations seemingly relies on different prey resources, suggesting that annual variation in dominant trophic pathways may alter the performance of yellow perch at each location.

Keywords: trophic ecology, intrapopulation variation, yellow perch, stable isotope, morphology, Saginaw Bay

Introduction

Traditionally, ecological studies have described resource use patterns at the species or population level, with the assumption that individual differences are relatively unimportant. However, numerous studies, including those summarized by Bolnick et al. (2003), have shown that treatment of conspecifics as homogenous groups is inappropriate and intrapopulation variation in resource use is widespread. Individual differences in ecological attributes (e.g., prey preferences, foraging strategies, and susceptibility to predation) may strongly influence population dynamics (e.g., Araújo, Bolnick, & Layman, 2011). Such individual differences occur in a wide range of taxa (Bolnick et al., 2003), with fish being one of the most studied taxonomic groups (see review in Araújo et al., 2011).

Fish resource use patterns have commonly been generalized at the population level (e.g., Madenjian et al., 2002), but several studies have examined intrapopulation variation (e.g., Quevedo et al., 2009). Within-species diet differences of fish occur in both large and small freshwater systems, and often exhibit spatial patterns within a waterbody. For example, within glacial lakes, diets of age-0 largemouth bass *Micropterus salmoides* varied spatially and were influenced by local (e.g., vegetation) characteristics (Middaugh, Foley, & Höök, 2013). Diets of Eurasian perch *Perca fluviatilis* in a small Swedish lake varied between littoral and pelagic habitats (Svanbäck & Persson, 2004). In larger systems, such as the Laurentian Great Lakes, similar patterns have emerged. Yellow perch *Perca flavescens* and round goby *Neogobius melanostomus* diets varied along a broad spatial gradient in Lake Michigan, where fish consumed more benthic prey items along the western shoreline and relied more on pelagic prey and pelagic trophic pathways in the east (Foley et al., 2017; Happel et al., 2015).

As an example of within-population trophic variation, Roswell et al. (2013) observed interindividual diet variation of age-0 yellow perch in Saginaw Bay, Lake Huron in 2009 and 2010. These authors demonstrated clear spatial diet variation (likely related to prey availability), and also documented spatially variable selectivity and specialization on either zooplankton or benthic prey (Figure 1). Though available prey densities (zooplankters and benthic invertebrates) varied among years, patterns of spatial diet variation remained consistent (Roswell et al., 2013). It is, however, unclear if these spatial intrapopulation diet differences are consistent when considering diet indicators that reflect more long term resource use by individual fish. Roswell et al. (2013) examined stomach contents, which is a commonly used index of diet (Hyslop, 1980) that allows for detailed identification and enumeration of diet items. However, stomach content analysis is a short-term indicator of diet and may not reflect long-term feeding. Moreover, this index may not accurately reflect prey assimilated by fish and may be biased by variable digestion rates of hard and soft tissues (e.g., Brush et al., 2012; Kionka and Windell, 1972; MacDonald et al., 1982). In short, stomach content analysis only reflects a “snapshot” of trophic utilization, and it is plausible that Roswell et al.'s (2013) observations of spatial differences reflect individuals feeding at a particular location for a short period of time and then moving. That is, observations by Roswell et al. (2013) may not reflect different groups of fish relying on distinct resources for extended periods of time.

In contrast to stomach content analysis, several other measures of trophic reliance, such as stable isotopes, reflect assimilated diet and resource use on a longer timescale (Peterson & Fry, 1987). Isotopic turnover rates vary depending upon various factors (e.g., growth rate and environmental conditions), but generally provide dietary information on a scale of weeks to months as opposed to days (Weidel, Carpenter, Kitchell, & Vander Zanden, 2011). Since isotopic values are predictably transferred from diet to consumer (Budge et al., 2008), stable isotopes in soft tissues, like carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), are commonly used to study foraging ecology (Post, 2002). Specifically, isotope values are typically standardized and reported as δ values; ratios of heavy to light isotopes relative to international measurement standards. $\delta^{13}C$ values of soft tissues in part reflect sources of primary production (i.e., carbon source) assimilated by a consumer (DeNiro & Epstein, 1978; Peterson & Fry, 1987; Post, 2002). While $\delta^{15}N$ values of soft tissues are often used to estimate trophic position due to consistent isotopic discrimination between trophic levels (Deniro & Epstein, 1980; Post, 2002), they also can reflect source of nitrogen. For example, agricultural inputs, which often have distinct isotopic values, were found to be strongly influential on $\delta^{15}N$ values of aquatic consumers in receiving water bodies (Larson, Richardson, Vallazza, & Nelson, 2013). Thus, in large lakes, spatial differences in allochthonous inputs (e.g., increasing distance from rivermouth) in $\delta^{15}N$ values may be reflected in the soft tissues of fish.

Intrapopulation diet variation also may result in morphological variation. Morphology can be considered a foraging and habitat indicator because habitat and resource use may influence the body form of fish, in particular, young, developing fish (Skulason & Smith, 1995; Svanbäck & Eklöv, 2003). Morphological variation is well documented in Eurasian perch and both habitat and differential foraging appear to influence morphology of this species (Hjelm & Johansson, 2003; Svanbäck & Eklöv, 2002, 2003). In several lakes, Eurasian perch residing in the littoral zone typically feed on benthic macroinvertebrates, while fish in the pelagic zone are zooplanktivorous or piscivorous. Variation along the littoral-pelagic axis is similarly reflected in morphology. Eurasian perch in littoral habitat are deeper-bodied and thus better suited for maneuverability in structurally complex habitat. In contrast, the fusiform body of fish in pelagic habitat reduces drag in an open environment (Hjelm, Svanback, Bystrom, Persson, & Wahistrom, 2001; Svanbäck & Eklöv, 2002, 2003). In addition, Eurasian perch in littoral habitats often exhibit mouths directed downwards, opposite the terminal or upturned mouths of perch in pelagic habitats (Svanbäck & Eklöv, 2002). While not as well-studied as congeneric Eurasian perch, morphologies of young yellow perch also appear to respond to habitat and foraging differences (Malinich, 2019). Thus, prolonged utilization of resources in a specific area may be reflected by these long-term diet indicators.

In addition to spatial differences, temporal patterns (e.g., seasonal, annual) may also contribute to differences in consumer morphologies and stable isotope ratios. Seasonal shifts in prey availability (e.g., Roswell et al., 2013) and consumption patterns (e.g., Hrycik et al., 2018) may influence not only isotope composition, but also foraging behavior and morphological variation. Variation in $\delta^{13}C$ values of producers is partially attributable to taxonomic composition and differences in how producers incorporate different C isotopes (Bernasconi, Barbieri, Simona, & Dec, 1997; Cifuentes, Sharp, & Fogel, 1988; Hodell & Schelske, 1998). The relative abundance of primary producers typically varies seasonally and may vary annually, and such temporal shifts can lead primary and secondary consumers to rely on different primary producers and reflect different $\delta^{13}C$ values over time. $\delta^{15}N$ values are influenced by N uptake, nitrification, denitrification, and degradation of organic matter (Brandes & Devol, 1997; Mariotti et al., 1981; Teranes & Bernasconi, 2000), all of which vary over time. Carbon and nitrogen stable isotope ratios of plankton may also change during decomposition, with $\delta^{13}C$ decreasing by about 1.6 ‰ over 110 days and $\delta^{15}N$ values cumulatively changing by +0.2 ‰ and -2.8 ‰ under oxic and anoxic conditions, respectively (Lehmann, Bernasconi, Barbieri, & McKenzie, 2002). Since decomposition patterns and oxygen conditions may vary temporally, these processes can contribute to seasonal and annual differences in stable isotope ratios of consumers. Temporally variable loading of carbon and nitrogen to aquatic systems, as well as shifts in the magnitude of primary production, can contribute to seasonal and annual differences in stable isotope ratios. The magnitude of autochthonous primary production, and its contribution relative to allochthonous production, is often higher in the summer, resulting in higher $\delta^{13}C$ values (e.g., Lehmann et al., 2004). Lacustrine nitrogen isotopic composition is strongly influenced by external nitrogen loading (Ostrom, Long, Bell, & Beals, 1998; Teranes & Bernasconi, 2000), and increased relative contribution of allochthonous inputs in winter increases $\delta^{15}N$ values (e.g., Lehmann et al., 2004). Finally, many of these processes that may contribute to temporal differences in consumer stable isotope ratios and morphologies may also differ across space, and thereby simultaneously influence spatial and temporal variation in consumer stable isotope ratios and morphologies.

Yellow perch is an ecologically and economically prominent fish species in the Laurentian Great Lakes. Recruitment of yellow perch in Saginaw Bay was poor in the early 2000s (Ivan et al. 2011; Fielder & Thomas, 2014) and may have been partially attributed to diet leading to low growth rates and increased susceptibility to size-selective predators (Roswell et al. 2014). In examining early life dynamics of yellow perch in Saginaw Bay, Roswell et al. (2013) documented spatial intrapopulation variation of yellow perch stomach contents and speculated that such differences could temper population-wide variability in survival and recruitment of age-0 yellow perch. However, given the short time horizon reflected by stomach contents and the potential of fish to move among locations, it is unclear to what extent these findings reflect different groups of fish relying on distinct resources for extended periods of time. Diet indicators that reflect longer term foraging patterns and trophic assimilation may be more appropriate for assessing the consistency of trophic variation over time (Vinson & Budy, 2011). To this end, we employed two long-term diet and habitat-use indicators, stable isotopes of soft tissue and morphology, to reexamine age-0 yellow perch collected concomitant with individual yellow perch collected by Roswell et al. (2013) in 2009 and 2010 and elucidate the consistency of spatiotemporal variation of their diets. While a variety of processes may contribute to spatio-temporal variation of consumer morphologies and stable isotope ratios (as described above), our primary aim was to evaluate the extent of spatio-temporal variation of consumer morphologies and stable isotope ratios and not explicitly evaluate the mechanisms leading to such potential variation. Nonetheless, because the sites in this study differed in distance from the Saginaw River input and Roswell et al. (2013) documented yellow perch feeding on different prey items at these sites, we expected spatial variation in both isotopic values and morphology. Furthermore, we anticipated moderate annual variation in both indicators consistent with annual changes in observed relative prey densities (zooplankton to benthic invertebrates) between 2009 and 2010 (Roswell et al., 2013).

Methods

Fish collection

We collected age-0 yellow perch in August and September of 2009 and 2010. We sampled three sites (SB-2, -10, -14) in Saginaw Bay, Lake Huron, which differed in terms of depth, substrate, relative availability of different invertebrate prey, and consumption patterns of age-0 yellow perch (Table 1; Figures 1 and 2). Detailed methods can be found in (Roswell et al., 2013; Roswell, Pothoven, & Höök, 2014). In brief, we towed a 7.6-m semi-balloon bottom trawl with 13-mm stretched-mesh cod-end for 10 min at approximately 1.3 ms^{-1} (1-5 trawl tows per site-date sampling event). During each month, we collected samples from all sites within a 3-day period. After collection, we placed fish in coolers with ice and then stored samples at -20°C. Age-0 yellow perch were differentiated from all other age classes through clear divisions in length frequency data (C. Roswell, unpublished data). In the laboratory, we thawed, weighed and measured fish for total length. Roswell et al. (2013, 2014) analyzed stomach contents of yellow perch collected during 2009 and 2010. We subsequently analyzed morphology and stable isotope ratios of individuals collected concomitantly (i.e., in the same trawl tows), but these were different individuals than those analyzed for stomach contents. All research presented in the manuscript was conducted in accordance with all applicable laws and rules set forth by governments and institutions and all necessary permits were acquired when the research was conducted, including a Scientific Collector's Permit from the State of Michigan. This work was approved under Purdue Animal Care and Use Committee's Protocol 1112000400.

Morphology

After thawing fish, we captured images for morphological analysis. We placed individual fish on a bed of beads, oriented them facing to the left, and refrained from moving the camera setup between photographs. We captured photographs with a Panasonic TS5 camera and placed 15 digital landmarks (J. Olsson & Eklöv, 2005; Jens Olsson, Svanbäck, & Eklöv, 2006) on the images using tpsDIG2w64, a software program for digitizing landmarks on images (Figure 3; Adams, Rohlf, & Slice, 2004). We analyzed fish images with MorphoJ, a program that employs geometric morphometrics to quantify shape variation (Klingenberg, 2011). We performed a Procrustes fit on the landmarks to remove influence of size, orientation and rotation on the true shape of the image (Adams, Rohlf, & Slice, 2013). To account for allometric effects, we regressed Procrustes coordinates against individual centroid size, and we used the resulting regression residuals for all subsequent analyses (Klingenberg, 2011).

We performed permutational multivariate analysis of variance (perMANOVA) with 10,000 permutations on centroid size-Procrustes coordinate regression residuals to examine morphological variation among all sites. We lacked samples from site SB-14 during September of 2010 (see Table 1). Senegal (2019) demonstrated that due to significant month effects, it was inappropriate to group samples across months. Therefore, to maintain a balanced design, we conducted three separate perMANOVAs: a) excluding SB-14, b) excluding 2010, and c) excluding September. Site was a factor in each of these perMANOVAs, while month (a and b) and year (a and c) were a factor in two out of the three perMANOVAs.

In addition, we analyzed shape differences (Mahalanobis distance, MD) between site pairs (i.e., SB-10 vs SB-14, SB-10 vs SB-2, and SB-2 vs SB-14) with discriminant function analysis (DFA) based on centroid size - Procrustes coordinate regression residuals (Hirsch, Eklöv, & Svanbäck, 2013; Jens Olsson et al., 2006). We created wireframe plots associated with DFA results to visualize morphological variation between site pairs. While we also visualized morphological differences between years and months (Supporting Information Figure S1), we focused on site differences since we expected these differences to be greatest based upon diet differences (Figure 1).

Stable Isotopes

After removing stomachs, we dried whole fish at 70 °C and placed samples in individual vials. Samples were ground by mortar and pestle, and then analyzed for carbon and nitrogen stable isotope ratios with an NC2500 elemental analyzer plumbed into a Thermo Delta V isotope ratio mass spectrometer (IRMS). Tissue samples had a consistently low C:N ratio (mean 1.9±0.17) and we intended to use isotope ratio values to estimate contributions of coarse prey categories (i.e., benthic or pelagic), so we did not perform a mathematical lipid correction on values (Post et al., 2007). We measured C and N isotope values relative to the Vienna Pee Dee belemnite and atmospheric N_2 standards, respectively, via two-point calibration using the CBT (an animal standard) and KCRN (a plant standard) reference materials. Soft tissue isotopic analysis occurred at the Cornell University Stable Isotope Laboratory. We report stable isotope ratios as delta (δ) values, or per mil (‰) = $((R_{sample}/R_{standard})-1) \times 10^3$, where $R_{standard}$ is one of the international standards previously mentioned.

We plotted the mean ± SE $\delta^{13}C$ and $\delta^{15}N$ of soft tissues in a stable isotope biplot. Initial inspection of the data showed distinct site differences for $\delta^{15}N$ and temporal differences for $\delta^{13}C$. In addition, individual size can have strong influence on isotopic composition. Thus, we performed univariate tests using analysis of covariance (ANCOVA) with individual length as a covariate. Similar to morphological analyses, we lacked samples from SB-14 during September 2010 and thus we conducted three separate analyses: a) excluding SB-14, b) excluding 2010, and c) excluding September. For each ANCOVA, we initially included all relevant factors (including site, year, month, and length), as well as all two-way interaction terms. For final models, we subsequently excluded insignificant interaction terms. All statistical analyses were performed in R (R Core Team, 2019).

Results

Fish collection

In total, we collected and analyzed 139 age-0 yellow perch for morphology (n = 139) and stable isotope ratios (n = 80; Table 1). However, no fish were available for September of 2010 at SB-14. Yellow perch total length ranged from 41-75 mm (average = 57.4 mm).

Morphology

Again, due to lack of samples from SB-14 during September of 2010 we conducted three separate perMANOVAs to compare morphologies across sites. The perMANOVA excluding SB-14 was the only such test that identified significant factors; both site ($R^2_{1,110}$=0.03, P=0.008) and year ($R^2_{1,110}$=0.03, P=0.024) were significant. When excluding 2010 or September data, no factors in the perMANOVAs were significant (Table 2). DFA results displayed significant morphological differences between fish from SB-10 and SB-2 (MD=2.68, P<0.001), and between fish from SB-10 and SB-14 (MD=3.89, P<0.001). In contrast, fish from SB-2 and SB-14 had no significant morphological difference (MD=1.58, P=0.079). DFA wireframe plots of average shape differences also suggested morphological distinction of fish from SB-10. SB-10 fish appeared deeper-bodied, while fish from SB-2 and SB-14 were more fusiform (Figure 4).

Stable Isotopes

Biplots of yellow perch isotope ratios showed relatively high $\delta^{13}C$ values in 2010 and relatively low $\delta^{15}N$ values at sites further from the Saginaw River input (Figure 5). Again, we conducted three separate ANCOVAs to account for the lack of data from SB-14 in September 2010. Though $\delta^{13}C$ values were significantly influenced by site, year, month, and length and $\delta^{15}N$ values were significantly influenced by site and month among analyses (Table 3), year consistently had the strongest effect on $\delta^{13}C$ values and site consistently had the strongest effect on $\delta^{15}N$ values. In the analysis excluding SB-14, month had an interactive effect with site ($F_{1,62}=10.89$, $P=0.002$) and year ($F_{1,62}=13.97$, $P<0.001$) on $\delta^{13}C$ values. When September was removed, there was a significant interaction between year and length ($F_{1,34}=12.98$, $P=0.001$) on $\delta^{15}N$ values.

Discussion

Long-term habitat and trophic indicators, stable isotopes and morphology, displayed intrapopulation variation among age-0 yellow perch in Saginaw Bay. As expected, spatial variation was evident in stable isotope values and morphology. While both isotope ratios displayed significant spatial differences, $\delta^{15}N$ values demonstrated a much clearer separation among sites. Morphological variation also was more apparent among sites rather than between years or months. Somewhat unexpectedly, however, yellow perch $\delta^{13}C$ values displayed much greater inter-annual variation than spatial variation.

Spatial Patterns

Stable isotopes and morphology spatial patterns were generally consistent with stomach content patterns observed by Roswell et al. (2013). Yellow perch from SB-2 and SB-14 had stomach contents primarily consisting of zooplankton, while fish from SB-10 had a greater proportion of benthic macroinvertebrates in their stomach contents (Figure 1). Despite variable zooplankter and benthic macroinvertebrate densities between years, these stomach content spatial patterns remained generally consistent (Roswell et al., 2013). The same spatial differences were reflected by stable isotopes and morphology, with yellow perch collected at SB-10 distinguished from those at the other two sites. These consistent spatial patterns across both short- and long-term diet indicators suggest that fish likely remain and forage in the same location for prolonged periods.

Potential drivers of spatio-temporal differences in prey densities and diet variation include spatially and temporally variable riverine discharge and water current patterns within Saginaw Bay. The Saginaw River is the primary tributary flowing into Saginaw Bay, delivering approximately 78% of total phosphorous to the bay and producing a river plume that typically travels counter-clockwise in the bay (Sesterhenn et al., 2014; Stow & Höök, 2013). Total phosphorus and chlorophyll *a* concentrations are relatively high in the river plume and generally have a stronger effect on the southeast side of inner Saginaw Bay, where sites SB-2 and SB-14 are located. In contrast, SB-10 is located near the outer bay and may be subject to influences in addition to the Saginaw River. The Au Gres River discharges northeast of SB-10 into the outer bay and circulation models suggest this riverine input may affect this site (Stow & Höök, 2013). Moreover, influxes from outer Saginaw Bay and Lake Huron proper may intermittently influence this location.

Yellow perch from sites closer to the Saginaw River mouth had higher δ^{15}N values. This pattern may be related to increased contribution and influence of allochthonous input for these more inner bay sites (Lehmann, Bernasconi, McKenzie, et al., 2004). Tributaries containing agricultural or urban runoff are typically enriched in ^{15}N (Larson et al., 2013), which is reflected in fish δ^{15}N values (Vandermyde & Whitledge, 2008). The drainage basin of Saginaw Bay encompasses over 22,000 km^2 of industrial, urban, and agricultural land (Millie et al., 2006), of which about half is predominantly agricultural (Fales et al., 2016). Considering the southeastern position of SB-2 and SB-14 and the general counter-clockwise flow of the Saginaw River plume (Stow & Höök, 2013), observed spatial patterns of age-0 yellow perch δ^{15}N values are consistent with expectations based upon the assumed influence of a large, agriculturally-dominant watershed. Decomposition of settled plankton may also affect the δ^{15}N values of particle-feeding invertebrates. Decomposition occurring under anoxic conditions can lead to greater decreases in particulate δ^{15}N than decomposition under oxic conditions (Lehmann et al. 2002). Plausibly, the combination of greater depth, thermal stratification and silt substrate at SB-10 may have contributed to anoxic decomposition at this site which may be reflected in relatively low consumer δ^{15}N values.

Differences in δ^{13}C of organic matter can be attributed to long-term variation in phosphorous availability and primary productivity (Schelske & Hodell, 1991). Saginaw Bay has a relatively large phosphorus reservoir within bottom sediments. The inner bay is subject to strong winds and heavy mixing, which causes resuspension of inorganic phosphorus and the possibility of conversion to soluble reactive phosphorous (Hawley et al., 2014). Furthermore, primary production may be influenced by variable water clarity, and thus light penetration, caused by variable discharge or resuspended sediments (Hawley et al., 2014; Turschak et al., 2018). In short, spatial and temporal heterogeneity in environmental conditions may impact dominant primary production and energy pathways contributing to growth of young yellow perch.

Stable isotope values have frequently been used to distinguish between allochthonous and autochthonous inputs (Carpenter et al., 2005; Solomon, Carpenter, Cole, & Pace, 2008). For example, Lehmann et al. (2004) observed variation in isotopic composition in Lake Lugano, a large eutrophic lake on the border of Switzerland and Italy. Increased primary productivity and phytoplankton biomass was associated with higher δ^{13}C values of surface water particulate organic carbon and dissolved inorganic carbon; carbon isotope values subsequently decreased with lower primary productivity (Lehmann, Bernasconi, McKenzie, et al., 2004). Within each year, the range of δ^{13}C values overlapped substantially among sites, but on average we observed that δ^{13}C was lower for yellow perch from SB-10 (Figure 5). This site is closer to outer Saginaw Bay, less influenced by the Saginaw River and consistently experiences lower primary productivity than the two more inner bay sites.

In freshwater environments, δ^{13}C values can be used to differentiate between littoral, benthic and pelagic production because primary producers in the littoral and benthic zones (e.g., algae, detritus) are typically enriched in ^{13}C compared to producers in the pelagic zone (e.g., France, 1995; Hecky & Hesslein, 1995). However, soft tissue δ^{13}C values in the present study did not reflect this pattern. Site SB-10 is deeper than SB-2 and SB-14 and is characterized by silt substrate, whereas SB-2 and SB-14 is characterized by cobble and sand, respectively. While SB-2 and SB-14 contained relatively high densities of *Dreissena* spp. mussels, SB-2 contained relatively high densities of benthic invertebrates preferred by yellow perch, such as chironomids, and these prey were actively selected and consumed by yellow perch at SB-10 (Figure 1; Roswell et al. 2013). Based on these patterns, we expected yellow perch δ^{13}C values to be relatively high at SB-10. While $\delta^{13}C$ values overlapped among sites, they were on average lower for yellow perch from SB-10 (Figure 5). We did not design our study to evaluate mechanisms contributing to this unexpected pattern. However, it is possible that within year spatial differences in $\delta^{13}C$ are primarily related to spatial differences in allochthonous inputs, the influence of Lake Huron proper, and dominant primary producers, rather than differences in the type of prey consumed across sites. In fact, differences in the type of prey consumed among sites may have served to temper differences in observed yellow perch $\delta^{13}C$ among sites.

Morphological variation of fish between benthic and pelagic habitats is well documented (e.g., Eurasian perch, Hjelm and Johansson, 2003; Svanbäck and Eklöv, 2003, 2002). Yellow perch with more benthivorous diets (i.e., SB-10) were deeper-bodied, which is consistent for fish foraging on the bottom. In contrast, yellow perch with more pelagic diets (i.e., SB-2 and SB-14) were more fusiform with a thinner caudal peduncle, which allows for more efficient cruising. Mouth position, which is associated with foraging strategy, was inconsistent with previous studies (e.g., Langerhans et al., 2003; Parker et al., 2009). Yellow perch from SB-10 had upturned mouths, which is typically indicative of a pelagic diet; fish collected at SB-2 and SB-14 had downturned mouths, indicative of benthic foraging. Despite disagreement between mouth position and feeding mode, mouth position may be influenced by unknown characteristics of habitat structure (Olsson & Eklöv, 2005) or growth rate (Olsson et al., 2006).

Interannual Patterns

In our study, yellow perch soft tissue $\delta^{13}C$ values increased approximately 2‰ from 2009 to 2010. Unlike clear seasonal patterns of $\delta^{13}C$ values (e.g., Lehmann et al., 2004b), annual patterns are not necessarily as straightforward to interpret. $\delta^{13}C$ values of particulate organic carbon often do not directly correlate with annual primary productivity because of variable inputs of terrestrial organic matter (e.g., Lehmann et al., 2004a). Estimated total phosphorus loading from the Saginaw River decreased from 2009 to 2010, but total phosphorus concentrations in the inner bay remained relatively stable (Stow & Höök, 2013). Thus, the annual increase of $\delta^{13}C$ values observed in our study is not consistent with changes in phosphorous concentrations. However, greater chlorophyll *a* concentrations were observed in 2010 (Stow & Höök, 2013) and suggest increased autochthonous production, which typically results in higher $\delta^{13}C$ values (Post, 2002; Vander Zanden, Chandra, Park, Vadeboncoeur, & Goldman, 2006).

Annual differences in internal and external nutrient loading also could favor the differential production of benthic invertebrates and zooplankters. Available densities of benthic invertebrates in Saginaw Bay generally increased from 2009 to 2010 (Roswell et al., 2013). This was especially true at site SB-10, where yellow perch fed primarily on benthic invertebrates. In contrast, peak late summer zooplankton densities decreased from 2009 to 2010 (see SB-2 and SB-14 in Figure 1). Diets consisting of a greater proportion of benthic invertebrates typically have relatively high $\delta^{13}C$ values (Post, 2002), and thus the increase in yellow perch $\delta^{13}C$ values from 2009 to 2010 are consistent with changes in available prey. However, this shift was generally not reflected in stomach content of age-0 yellow perch (Figure 1; Roswell et al., 2013). Stomach contents were fairly similar between the two years. Moreover, even at sites SB-2 and SB-14, where yellow perch fed overwhelmingly on zooplankton, the annual shift in $\delta^{13}C$ values was still evident. In short, while the increased availability of benthic prey may be reflective of a similar system driver as the annual shift in yellow perch $\delta^{13}C$ values, the mechanisms leading to this shift in prey availability and the ultimate cause of increased yellow perch $\delta^{13}C$ values in Saginaw Bay are unclear.

Conclusion

Consistent spatial variation of long-term foraging indicators (i.e., stable isotopes and morphology), together with stomach content analysis, supports the notion that age-0 yellow perch consistently foraged in a relatively local area (Roswell et al., 2013). Realized yellow perch stable isotope ratios and morphologies were likely partially attributable to different foraging strategies among sites and partially responsive to variable allochthonous inputs and differential primary production pathways. The use of different resources (i.e., benthic or pelagic) in different areas of Saginaw Bay may suggest yellow perch groups are somewhat distinct. Yellow perch display inter-annually variable recruitment success in Saginaw Bay (Ivan, Höök, Thomas, & Fielder, 2011). However, year to year variation in allochthonous input, autochthonous production and the relative availability of benthic and pelagic prey in different areas of the bay may allow spatially distinct groups of young yellow perch to differentially thrive across years and temper bay-wide recruitment variation. In addition to spatial patterns, we observed a pronounced shift in yellow perch $\delta^{13}C$ values among years. We speculate that this shift may be related to annual variation in the relative importance of bay-wide production pathways. Yellow perch production at different locations seemingly relies on different production pathways, suggesting that annual variation in dominant production pathways may alter the relative contribution of yellow perch from different locations.

Acknowledgements

The authors thank the students and technicians involved with sample collection and analysis. The authors thank the staff at the Cornell University Stable Isotope Laboratory (COIL) for soft tissue analysis. Figure 1 was developed with the assistance of Carolyn Foley. Figure 3 was illustrated by Tim Malinich. This paper was greatly improved from comments from two anonymous reviewers. The project was funded by an award from the National Oceanic and Atmospheric Administration's (NOAA) Center for Sponsored Coastal Ocean Research and Purdue University's Department of Forestry and Natural Resources.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceived and designed the investigation: TMS, SAP, TOH. Performed field and/or laboratory work: TMS, CRR, SAP. Analyzed the data: TJS, TMS, TOH. Contributed materials, reagents, and/or analysis tools: TJS, TMS, SAP, TOH. Wrote the paper: TJS, TMS, CRR, SAP, TOH.

Data Availability Statement

Fish sampling data and statistical results are available from the corresponding author.

References

Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: ten years of progress following the "revolution." *Ital. J. Zool*, *71*, 5–16.

Adams, D. C., Rohlf, F. J., & Slice, D. E. (2013). A field comes of age: Geometric morphometrics in the 21st century. *Ecology, Evolution and Organismal Biology Publications Ecology Evolution and Organismal Biology*, *24*(1), 7–14. Retrieved from http://lib.dr.iastate.edu/eeob_ag_pubs

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Bernasconi, S. M., Barbieri, A., Simona, M., & Dec, N. (1997). Carbon and nitrogen isotope variations in sedimenting organic matter in Lake Lugano. *Limnology*, *42*(8), 1755–1765.

Bolnick, D. I., Svanbäck, 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. Nat*, *161*(1), 1–28.

Brandes, J. A., & Devol, A. H. (1997). Isotopic fractionation of oxygen and nitrogen in coastal marine sediments. *Geochimica et Cosmochimica Acta*, *61*(9), 1793–1801.

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. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(3), 573–586. https://doi.org/10.1139/f2012-001

Budge, S. M., Wooller, M. J., Springer, A. M., Iverson, S. J., McRoy, C. P., & Divoky, G. J. (2008). Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. *Oecologia*, *157*, 117–129. https://doi.org/10.1007/s00442-008-1053-7

Carpenter, S. R., Hodgson, J. R., Kritzberg, E. S., Cole, J. J., Bade, D. L., Pace, M. L., … Bastviken, D. (2005). Ecosystem subsidies: Terrestrial support of aquatic food webs from 13C addition to contrasting lakes. *Ecology*, *86*(10), 2737–2750. https://doi.org/10.1890/04-1282

Cifuentes, L. A., Sharp, J. H., & Fogel, M. L. (1988). Stable carbon and nitrogen in the isotope biogeochemistry Delaware estuary. *Limnology and Oceanography*, *33*(5), 1102–1115.

Deniro, M. J., & Epstein, S. (1980). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, *45*, 341–351. https://doi.org/10.1016/0016-7037(81)90244-1

DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, *42*, 495–506.

Fales, M., Dell, R., Herbert, M. E., Sowa, S. P., Asher, J., O'Neil, G., … Wickerham, B. (2016). Making the leap from science to implementation: Strategic agricultural conservation in Michigan's Saginaw Bay watershed. *Journal of Great Lakes Research*, *42*, 1372–1385. https://doi.org/10.1016/j.jglr.2016.09.010

Fielder, D. G., & Thomas, M. V. (2014). Status and trends of the fish community of Saginaw Bay, Lake Huron 2005-2011. In *Michigan Department of Natural Resources, Fisheries Research Reports, Lansing, MI.*

Foley, C. J., Henebry, M. L., Happel, A., Bootsma, H. A., Czesny, S. J., Janssen, J., … Höök, T. O. (2017). Patterns of integration of invasive round goby *Neogobius melanostomus* into a nearshore freshwater food web. *Food Webs*. https://doi.org/10.1016/j.fooweb.2016.10.001

France, R. L. (1995). Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnology and Oceanography*, *40*(7), 1310–1313. https://doi.org/10.4319/lo.1995.40.7.1310

Happel, A., Creque, S., Rinchard, J., Höök, T., Bootsma, H., Janssen, J., … Czesny, S. (2015). Exploring yellow perch diets in Lake Michigan through stomach content, fatty acids, and stable isotope ratios. *Journal of Great Lakes Research*, *41*(3), 172–178. https://doi.org/10.1016/j.jglr.2015.03.025

Hawley, N., Redder, T., Beletsky, R., Verhamme, E., Beletsky, D., & DePinto, J. V. (2014). Sediment resuspension in Saginaw Bay. *Journal of Great Lakes Research*, *40*(S1), 18–27. https://doi.org/10.1016/j.jglr.2013.11.010

Hecky, R. E., & Hesslein, R. H. (1995). Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society*, *14*(4), 631–653.

Hirsch, P. E., Eklöv, P., & Svanbäck, R. (2013). Indirect trophic interactions with an invasive species affect phenotypic divergence in a top consumer. *Oecologia*, *172*, 245–256. https://doi.org/10.1007/s00442-013-2611-1

Hjelm, J., & Johansson, F. (2003). Temporal variation in feeding morphology and size-structured population dynamics in fishes. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1522), 1407–1412. https://doi.org/10.1098/rspb.2003.2376

Hjelm, J., Svanback, R., Bystrom, P., Persson, L., & Wahistrom, E. (2001). Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos*, *95*(2), 311–323.

Hodell, D. A., & Schelske, C. L. (1998). Production, sedimentation, and isotopic composition of organic matter in Lake Ontario. *Limnology*, *43*(2), 200–214. Retrieved from https://aslopubs.onlinelibrary.wiley.com/doi/pdf/10.4319/lo.1998.43.2.0200

Hrycik, A. R., Collingsworth, P. D., Rogers, M. W., Guffey, S. C., & Höök, T. O. (2018). Seasonal trophic variation of yellow perch exceeds spatial variation in a large lake basin. *Journal of Great Lakes Research*, *44*(2), 299–310. https://doi.org/10.1016/j.jglr.2018.01.007

Hyslop, E. J. (1980). Stomach contents analysis - a review of methods and their application. *Journal of Fish Biology*, *17*, 411–429.

Ivan, L. N., Höök, T. O., Thomas, M. V., & Fielder, D. G. (2011). Long-term and interannual dynamics of walleye and yellow perch in Saginaw Bay, Lake Huron. *Transactions of the American Fisheries Society*, *140*(4), 1078–1092. https://doi.org/10.1080/00028487.2011.603976

Kionka, B. C., & Windell, J. T. (1972). Differential movement of digestible and indigestible food fractions in rainbow trout *Salmo gairdneri*. *Transactions of the American Fisheries Society*, *101*(1), 112–115. https://doi.org/10.1577/1548-8659(1972)101<112

Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources*, *11*, 353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x

Langerhans, R. B., Layman, C. A., Langerhans, A. K., & Dewitt, T. J. (2003). Habitat-associated morphological divergence in two Neotropical fish species. *Biological Journal of the Linnean Society*, *80*, 689–698.

Larson, J. H., Richardson, W. B., Vallazza, J. M., & Nelson, J. C. (2013). Rivermouth alteration of agricultural impacts on consumer tissue δ15N. *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0069313

Lehmann, M. F., Bernasconi, S. M., Barbieri, A., & McKenzie, J. A. (2002). Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. *Geochimica et Cosmochimica Acta*, *66*(20), 3573–3584. https://doi.org/10.1016/S0016-7037(02)00968-7

Lehmann, M. F., Bernasconi, S. M., Barbieri, A., Simona, M., & McKenzie, J. A. (2004). Interannual variation of the isotopic composition of sedimenting organic carbon and nitrogen in Lake Lugano: A long-term sediment trap study. *Limnology and Oceanography*, *49*(3), 839–849. https://doi.org/10.4319/lo.2004.49.3.0839

Lehmann, M. F., Bernasconi, S. M., McKenzie, J. A., Barbieri, A., Simona, M., & Veronesi, M. (2004). Seasonal variation of the δ13C and δ15N of particulate and dissolved carbon and nitrogen in Lake Lugano: Constraints on biogeochemical cycling in a eutrophic lake. *Limnology and Oceanography*, *49*(2), 415–429. https://doi.org/10.4319/lo.2004.49.2.0415

MacDonald, J. S., Waiwood, K. G., & Green, R. H. (1982). Rates of digestion of different prey in Atlantic cod *Gadus morhua*, ocean pout *Macrozoarces americanus*, winter flounder *Pseudopleuronectes amerkanus*, and American plaice *Hippoglossoides platessoides*. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*, 651–659.

Madenjian, C. P., Fahnenstiel, G. L., Johengen, T. H., Nalepa, T. F., Vanderploeg, H. A., Fleischer, G. W., … Ebener, M. P. (2002). Dynamics of the Lake Michigan food web, 1970-2000. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(4), 736–753. https://doi.org/10.1139/f02-044

Malinich, T. M. (2019). *Intraspecific variation in freshwater fishes; Insights into trophic relationships, morphology and bioaccumulation*.

Mariotti, A., Germon, J. C., Hubert, P., Kaiser, P., Letolle, R., Tardieux, A., & Tardieux, P. (1981). Experimental determination of nitrogen kinetic isotope fractionation: Some principles; Illustration for the denitrification and nitrification processes. *Plant and Soil*, *62*, 413–430. https://doi.org/10.1007/BF02374138

Middaugh, C. R., Foley, C. J., & Höök, T. O. (2013). Local and lake-scale habitat effects on abundance, lengths, and diets of age-0 largemouth bass and bluegill in Indiana temperate lakes. *Transactions of the American Fisheries Society*, *142*(6), 1576–1589. https://doi.org/10.1080/00028487.2013.820218

Millie, D. F., Weckman, G. R., Pigg, R. J., Tester, P. A., Dyble, J., Litaker, R. W., … Fahnenstiel, G. L. (2006). Modeling phytoplankton abundance in Saginaw Bay, Lake Huron: Using artificial neural networks to discern functional influence of environmental variables and relevance to a Great Lakes observing system. *Journal of Phycology*, *42*, 336–349. https://doi.org/10.1111/j.1529-8817.2006.00209.x

Olsson, J., & Eklöv, P. (2005). Habitat structure, feeding mode and morphological reversibility: Factors influencing phenotypic plasticity in perch. *Evolutionary Ecology Research*, *7*, 1109–1123.

Olsson, Jens, Svanbäck, R., & Eklöv, P. (2006). Growth rate constrain morphological divergence when driven by competition. *Oikos*, *115*, 15–22. https://doi.org/10.1111/j.2006.0030-1299.14965.x

Ostrom, N. E., Long, D. T., Bell, E. M., & Beals, T. (1998). The origin and cycling of particulate and sedimentary organic matter and nitrate in Lake Superior. *Chemical Geology*, *152*(1–2), 13–28. https://doi.org/10.1016/S0009-2541(98)00093-X

Parker, A. D., Stepien, C. A., Sepulveda-Villet, O. J., Ruehl, C. B., & Uzarski, D. G. (2009). The interplay of morphology, habitat, resource use, and genetic relationships in young yellow perch. *Transactions of the American Fisheries Society*, *138*(4), 899–914. https://doi.org/10.1577/T08-093.1

Peterson, B. J., & Fry, B. (1987). Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics*, *18*, 293–320.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, *83*(3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montaña, C. G. (2007). Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, *152*(1), 179–189. https://doi.org/10.1007/s00442-006-0630-x

Quevedo, M., Svanbäck, R., & Eklöv, P. (2009). Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology*, *90*(8), 2263–2274.

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Roswell, C. R., Pothoven, S. A., & Höök, T. O. (2013). Spatio-temporal, ontogenetic and interindividual variation of age-0 diets in a population of yellow perch. *Ecology of Freshwater Fish*. https://doi.org/10.1111/eff.12041

Roswell, C. R., Pothoven, S. A., & Höök, T. O. (2014). Patterns of age-0 yellow perch growth, diets, and mortality in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research*, *40*(S1), 123–132. https://doi.org/10.1016/j.jglr.2014.01.008

Schelske, C. L., & Hodell, D. A. (1991). Recent changes in productivity and climate of Lake

Ontario detected by isotopic analysis of sediments. *Methods*, *36*(5), 961–975.

Senegal, T. J. (2019). *Trophic ecology and habitat occupancy of yellow perch in nearshore Lake Michigan and Saginaw Bay, Lake Huron*.

Sesterhenn, T. M., Roswell, C. R., Stein, S. R., Klaver, P., Verhamme, E., Pothoven, S. A., & Höök, T. O. (2014). Modeling the implications of multiple hatching sites for larval dynamics in the resurgent Saginaw Bay walleye population. *Journal of Great Lakes Research*, *40*(S1), 113–122. https://doi.org/10.1016/j.jglr.2013.09.022

Skulason, S., & Smith, T. B. (1995). Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*. https://doi.org/10.1016/S0169-5347(00)89135-1

Solomon, C. T., Carpenter, S. R., Cole, J. J., & Pace, M. L. (2008). Support of benthic invertebrates by detrital resources and current autochthonous primary production: Results from a whole-lake13C addition. *Freshwater Biology*, *53*(1), 42–54. https://doi.org/10.1111/j.1365-2427.2007.01866.x

Stow, C. A., & Höök, T. O. (2013). *NOAA Technical Memorandum GLERL-160: Saginaw Bay Multiple Stressors Summary Report*. Retrieved from www.glerl.noaa.gov.

Svanbäck, R., & Eklöv, P. (2002). Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia*, *131*(1), 61–70. https://doi.org/10.1007/s00442-001-0861-9

Svanbäck, R., & Eklöv, P. (2003). Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *OIKOS*, *102*, 273–284.

Svanbäck, R., & Persson, L. (2004). Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *Journal of Animal Ecology*, *73*, 973–982.

Teranes, J. L., & Bernasconi, S. M. (2000). The record of nitrate and productivity utilization limitation provided by 15N values in lake organic matter-A study of sediment from trap and core sediments Switzerland. *Limnology and Oceanography*, *45*(4), 801–813.

Turschak, B. A., Janssen, J., Grunert, B. K., Czesny, S., Doll, J. C., Höök, T. O., & Bootsma, H. A. (2018). Spatial variation in trophic structure of nearshore fishes in Lake Michigan as it relates to water clarity. *Canadian Journal of Fisheries and Aquatic Sciences*, *377*(April 2018), 1–14. https://doi.org/10.1139/cjfas-2017-0390

Vander Zanden, M. J., Chandra, S., Park, S.-K., Vadeboncoeur, Y., & Goldman, C. R. (2006).

Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(12), 2608–2620. https://doi.org/10.1139/f06-148

Vandermyde, J. M., & Whitledge, G. W. (2008). Otolith δ15N distinguishes fish from forested and agricultural streams in southern Illinois. *Journal of Freshwater Ecology*, *23*(2), 333–336. https://doi.org/10.1080/02705060.2008.9664206

Vinson, M. R., & Budy, P. (2011). Sources of variability and comparability between salmonid stomach contents and isotopic analyses: Study design lessons and recommendations. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(1), 137–151. https://doi.org/10.1139/F10-117

Weidel, B. C., Carpenter, S. R., Kitchell, J. F., & Vander Zanden, M. J. (2011). Rates and components of carbon turnover in fish muscle: insights from bioenergetics models and a whole-lake 13 C addition. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(3), 387–399. https://doi.org/10.1139/f10-158

Table 1. Yellow perch collection overview with site, site characteristics (depth, substrate [Sub]), year, month, and day-of-year (DOY). Abundances (*n*) for stable isotope (SI) and morphological (Morpho) analyses.

Site	Characteristics	Year	Month	DOY	SI (*n*)	Morpho (*n*)
SB-2	Depth: 3.9 m	2009	August	216, 217, 222	7	9
	Sub: Rocky/ large cobble		September	244, 245	14	24
		2010	August	222, 223	8	19
			September	266	6	29
SB-10	Depth: 12.2 m	2009	August	216, 217, 222	4	4
	Sub: Silt/ muck		September	244, 245	5	6
		2010	August	222, 223	6	10

			September	266	9	10
SB-14	Depth: 3.8 m	2009	August	216, 217, 222	9	12
	Sub: Sand		September	244, 245	6	7
		2010	August	222, 223	6	9
			September	266	0	0

Table 2. perMANOVA results for morphometric analyses. Results from three separate analyses: a) excluding SB-14, b) excluding 2010, and c) excluding September. Factors include: site, year, and month. Significant results ($P<0.05$) in bold. Excluded data represented by "--".

		Site	Year	Month
a)	R^2	**0.03**	**0.03**	0.02
	P	**0.008**	**0.024**	0.108
	df	**1,110**	**1,110**	1,110
b)	R^2	0.08	--	0.01
	P	0.063	--	0.397
	df	3,70	--	1,70
c)	R^2	0.05	0.01	--
	P	0.130	0.414	--
	df	2,62	1,62	--

Table 3. ANCOVA results for yellow perch carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes. Results from three separate analyses: a) excluding SB-14, b) excluding 2010, and c) excluding September. Factors include: site, year, month, length, site-month interaction, year-month interaction, and year-length interaction. Significant results ($P<0.05$) in bold. Excluded data represented by "--".

			Site	Year	Month	Length	Site:Month	Year:Month	Year:Length
a)	$\delta^{13}C$	F	5.93	193.89	21.74	0.54	10.89	13.97	--
		P	**0.018**	**<0.001**	**<0.001**	0.466	**0.002**	**<0.001**	
		df	1, 62	1, 62	1, 62	1, 62	1, 62	1, 62	
	$\delta^{15}N$	F	58.23	0.71	2.87	1.18	--	--	--
		P	**<0.001**	0.402	0.095	0.281			
		df	1, 64	1, 64	1, 64	1, 64			
b)	$\delta^{13}C$	F	4.98	--	31.78	0.94	--	--	--
		P	**0.012**		**<0.001**	0.339			
		df	2, 40		1, 40	1, 40			
	$\delta^{15}N$	F	11.80	--	8.31	0.36	--	--	--
		P	**<0.001**		**0.006**	0.552			
		df	2, 40		1, 40	1, 40			
c)	$\delta^{13}C$	F	2.12	183.49	--	6.478	--	--	--
		P	0.136	**<0.001**		**0.016**			
		df	2, 35	1, 35		1, 35			
	$\delta^{15}N$	F	12.42	2.54	--	3.00	--	--	12.98
		P	**<0.001**	0.121		0.092			**0.001**
		df	2, 34	1, 34		1, 34			1, 34

Figure legends

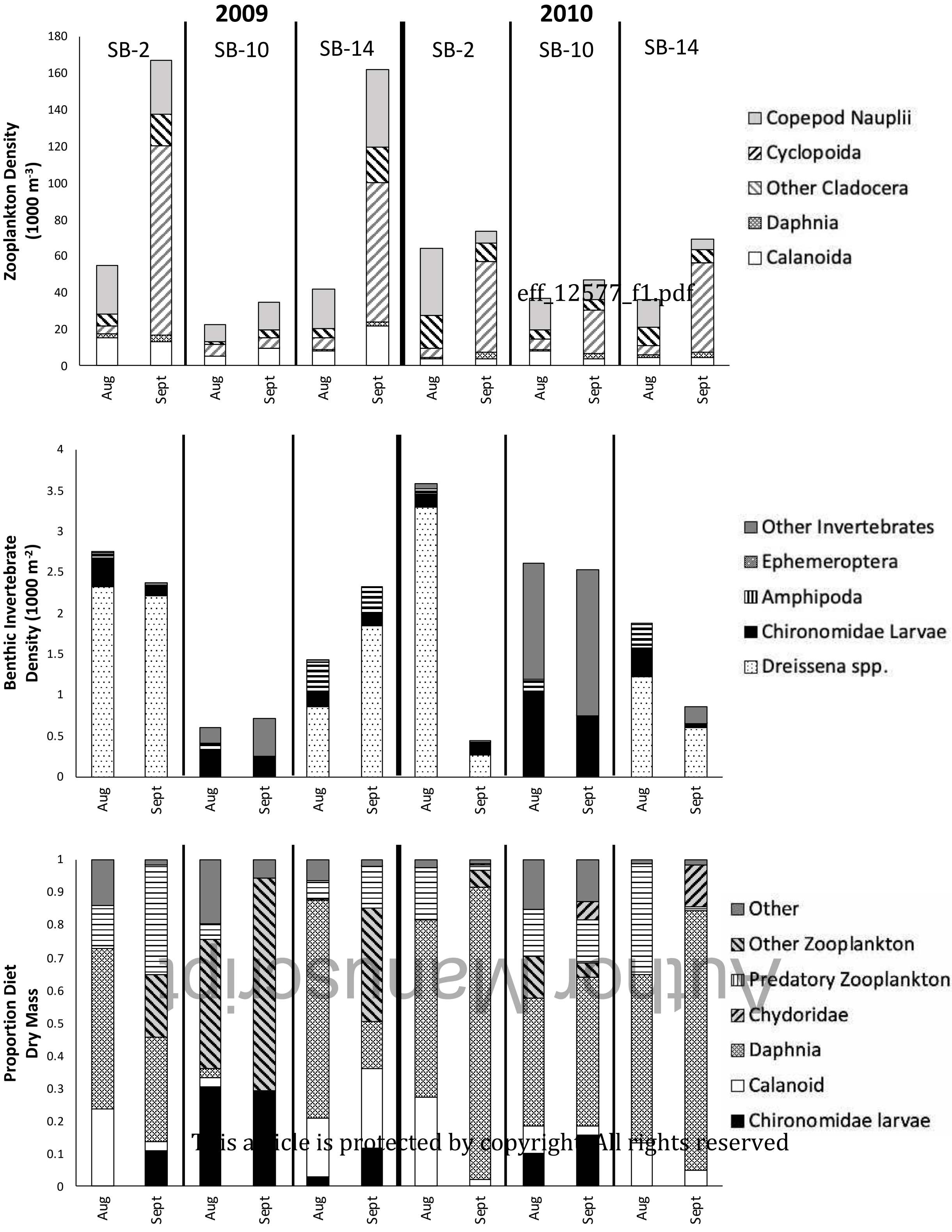
Figure 1. Prey densities of zooplankton (*top row*) and benthic macroinvertebrates (*middle row*), and yellow perch stomach contents by proportional dry mass (*bottom row*). Stomach content categories include: calanoid copepods, Chironomidae larvae, epibenthic Chydoridae, *Daphnia* spp., other, other zooplankton (e.g., *Bosmina*, *Cyclopoida*), and predatory zooplankton (e.g., *Bythotrephes* spp., *Leptodora* spp.). Note that benthic diet items were far more important at site SB-10 than SB-2 and SB-14, while pelagic prey, especially *Daphnia* spp., were more important at SB-2 and SB-14. Data adapted from Roswell et al. (2013).

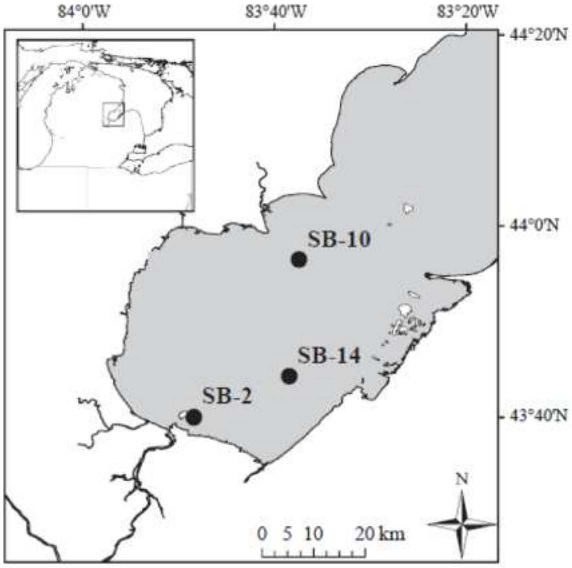
Figure 2. Sampling sites in Saginaw Bay, Lake Huron. Figure adapted from Roswell et al. (2013).

Figure 3. Landmark locations on image of yellow perch for geometric morphometrics.

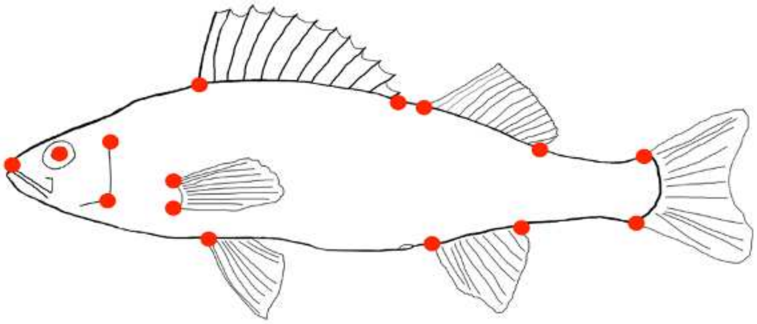
Figure 4. Wireframe plots from discriminant function analysis (DFA) displaying shape differences in average shape between site pairs. Sites denoted by color: (a) SB-10 (black) vs SB-14 (gray); (b) SB-10 (black) vs SB-2 (gray); (c) SB-2 (black) vs SB-14 (gray).

Figure 5. Mean ± SE carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of yellow perch soft tissues. Site denoted by symbol and year denoted by color.

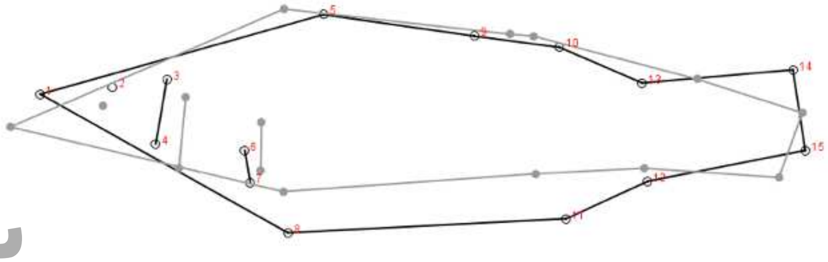

2009
2010
SB-2
SB-10
SB-14
SB-2
SB-10
SB-14
Zooplankton Density (1000 m^{-3})
0
20
40
60
80
100
120
140
160
180
Copepod Nauplii
Cyclopoida
Other Cladocera
Daphnia
Calanoida
Aug
Sept
Benthic Invertebrate Density (1000 m^{-2})
0
0.5
1
1.5
2
2.5
3
3.5
4
Other Invertebrates
Ephemeroptera
Amphipoda
Chironomidae Larvae
Dreissena spp.
Proportion Diet Dry Mass
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Other
Other Zooplankton
Predatory Zooplankton
Chydoridae
Daphnia
Calanoid
Chironomidae larvae



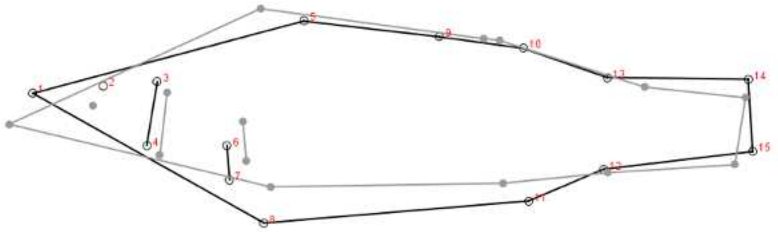
eff_12577_f2.png



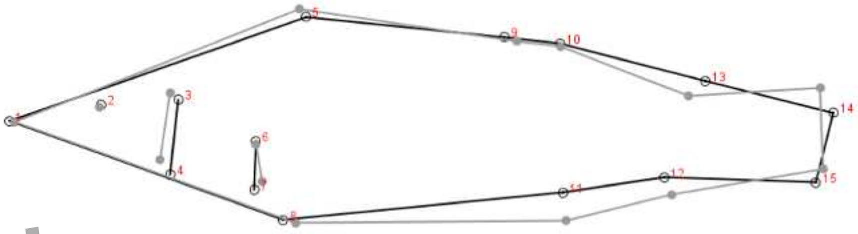
eff_12577_f3.png



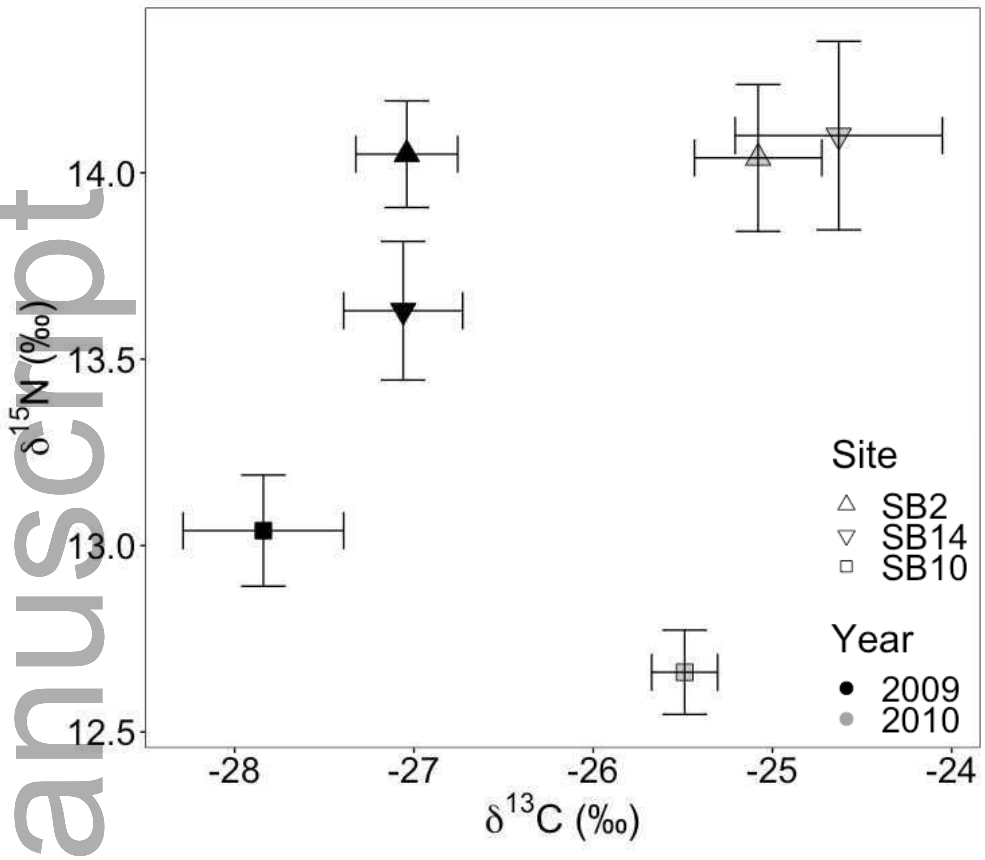
eff_12577_f4a.png



eff_12577_f4b.png



eff_12577_f4c.png



14.0
13.5
13.0
12.5
δ15N (‰)
-28
-27
-26
-25
-24
δ13C (‰)
Site
△ SB2
▽ SB14
□ SB10
Year
● 2009
● 2010

Figure 5.