TROPHIC ECOLOGY AND HABITAT OCCUPANCY OF YELLOW PERCH IN NEARSHORE LAKE MICHIGAN AND SAGINAW BAY, LAKE HURON

by

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ABSTRACT

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Elucidation of habitat and resource use patterns is important for facilitating sustainable management of fisheries. Discrete habitats in large aquatic ecosystems may offer distinct resources and differentially affect performance. Movement of organisms and organic materials links these habitats and potentially leads to spatially complex trophic pathways between basal resources and consumers. Habitat and resource use are commonly explored via two common methods: stable isotopes and morphometric analysis. The first research chapter of this thesis employed both methods to investigate seasonal habitat use of yellow perch *Perca flavescens* in eastern Lake Michigan and connected waterbodies known as drowned river mouth (DRM) lakes. Landmark-based geometric morphometrics was used to compare shape differences among habitats. Stable isotopes of ambient water, otoliths, and soft tissues were compared to differentiate among habitats. Both methods provided evidence of resident nearshore Lake Michigan fish, resident DRM lake fish occupying the littoral zone, and transient Lake Michigan fish occupying the profundal zone of DRM lakes. The majority of transient Lake Michigan fish moved into the profundal zone of DRM lakes in the fall. These results support previously published genetic data of distinct populations of yellow perch in eastern Lake Michigan and connected waterbodies. The second research chapter of this thesis also employed stable isotopes and morphometric analysis, but to investigate the consistency of resource use of age-0 yellow perch in Saginaw Bay, Lake Huron. These methods served as long-term diet indicators, as compared to short-term stomach contents analysis. Both stable isotopes of soft tissues and morphometric analysis showed spatial consistency in variation among sites. Fish from the two sites closer to the tributary input had higher $\delta^{15}N$ values and more fusiform bodies, while fish from the third site further away from the tributary had lower $\delta^{15}N$ values and were deeper-bodied. This spatial variation supports stomach content analysis of age-0 yellow perch from a previously published study. $\delta^{13}C$ ratios displayed annual variation, and while inconsistent with stomach content analysis, was consistent with available prey items. The

findings from this study suggest that young yellow perch in Saginaw Bay have limited movement and forage in a similar area to where they were collected. Previous studies have found discrepancies among indicators and have cautioned generalization of trophic relationships when only relying on a single metric. Agreement between complementary techniques provided additional support to previously-published genetic results and stomach content data, and thereby helped more fully describe habitat use by yellow perch in these systems.

CHAPTER 1. INTRODUCTION

1.1 Introduction

Elucidation of habitat and resource use patterns is important for facilitating sustainable management of fisheries. Discrete habitats in large aquatic ecosystems may offer distinct resources and differentially affect performance (e.g., foraging, spawning conditions, predation refuge). These habitats are often linked by movement of organisms and organic materials, which potentially lead to spatially complex trophic pathways between basal resources and consumers (Solomon et al. 2011). Interfaces between these habitats may experience variable environmental conditions that support increased productivity (Jude and Pappas 1992) and bidirectional movement of resources. Increased understanding of habitat and resource use improve understanding of key ecosystem processes and allow for delineation of fish stocks, thereby informing management strategies.

Two common methods used to study habitat and resource use are stable isotopes and morphological analyses. Both methods include multiple techniques that are capable of addressing a breadth of questions. In fisheries ecology, stable isotopes of soft (e.g., muscle) and hard tissues (e.g., otoliths) are often used to examine habitat use, migration patterns, and trophic energy pathways. Otoliths have been used as indicators of habitat use because they accrete chemicals reflective of the environment and remain metabolically inert (Solomon et al. 2006; Gao and Bean 2008). Carbon isotope ratios ($\delta^{13}C$) in an otolith are influenced by dissolved inorganic processes in ambient water and metabolic processes (Solomon et al. 2006). Oxygen isotope ratios ($\delta^{18}O$) of otoliths, on the other hand, reflect temperature and oxygen stable isotope ratios of ambient water. Soft tissue stable isotopes are frequently used to study foraging ecology because isotopic signatures are predictably transferred from diet to consumer (Budge et al. 2008; Vander Zanden et al. 2016). $\delta^{13}C$ ratios in soft tissue can indicate the dominant source of primary production

supporting a consumer (e.g., benthic, pelagic, terrestrial), while nitrogen stable isotope ratios ($\delta^{15}N$) of soft tissues reflect nitrogen source and abundance (e.g., agricultural runoff; Larson et al., 2013). $\delta^{18}O$ and hydrogen ($\delta^{2}H$) isotope ratios of soft tissues are both affected by diet and ambient water, with $\delta^{2}H$ being more affected by diet and $\delta^{18}O$ being more affected by ambient water (Coulter et al. 2017).

Morphological analysis can be used as a foraging and habitat use indicator because foraging behavior and habitat structure are thought to influence the body shape of a fish (Skulason and Smith 1995; Svanbäck and Eklöv 2003). Fish in lacustrine systems often demonstrate morphological divergence along the littoral-pelagic axis. Species that inhabit littoral or benthic habitat are often deeper-bodied and better suited for high maneuverability in complex environments. In contrast, species occupying pelagic habitat are typically more streamlined, which minimizes drag forces for more efficient cruising. Analysis of body shape traditionally involved linear distances (e.g., length, depth) and their ratios. However, this technique had shortcomings, like the inability to preserve certain geometric relationships (Adams et al. 2013). Geometric morphometrics was developed in the 1980s to capture these relationships and retain more holistic shape information (Adams et al. 2004). Now a commonly used tool, geometric morphometrics can be used to discriminate foraging differences and habitat use within or among populations (Kocovsky et al. 2009). This technique uses a landmark-based approach, in which digital landmarks are individually placed, at the discretion of the user, on fish images. Because no two images are the same, landmarks must be transformed into shape space, most commonly done through a Procrustes fit. The Procrustes fit removes size, orientation, and rotation of the image so that only the true shape remains (Klingenberg 2011). Furthermore, fish often have allometric growth which influences body shape relative to size. This can be corrected by a linear regression

of the Procrustes coordinates on the centroid size of the shape (Klingenberg 2016). The regression residuals are used for all subsequent analyses of shape. Both chapters in this thesis contain a morphometric component, but each uses the method to answer a different question.

This thesis uses stable isotopes and morphological analyses to study habitat and resource use of a native Great Lakes species, yellow perch *Perca flavescens*. Yellow perch is an ecologically and economically prominent fish species in the Great Lakes region and has supported commercial and recreational fisheries (Clapp and Dettmers 2011), though the species' abundance has been variable throughout the past few decades. In southern Lake Michigan, stocks crashed due to a combination of overfishing, poor recruitment, and introduction of nonnative species (Marsden and Robillard 2004). Although commercial fishing of yellow perch was banned in the main basin of Lake Michigan in 1997, stocks have not fully recovered. Similarly, poor recruitment since the 1990s also has led to a decline in yellow perch abundance in Saginaw Bay, Lake Huron (Fielder and Thomas 2006). As a native species, yellow perch serves an important role as prey for piscivorous species (e.g., walleye *Sander vitreus*) and as a predator of forage fish (e.g., alewife *Alosa pseudoharengus*) and invertebrates (Staton et al. 2014). Improved understanding of yellow perch habitat and resource use may help delineate stocks and elucidate production pathways supporting them, which may aid in their management and the management of other native Great Lakes species.

Chapter 2 investigates seasonal habitat occupation by yellow perch in nearshore Lake Michigan and connected drowned river mouth (DRM) lakes. Many fish populations move among habitats on a seasonal basis to take advantage of abundant resources. For some populations, all individuals display consistent seasonal habitat occupation, while in other populations groups of individuals seasonally inhabit different habitats. Relatively recent research has focused on fish

habitat use in nearshore areas and tributaries of the Laurentian Great Lakes. Native and nonnative species are known to migrate between open habitats and protected habitats, such as coastal wetlands and DRM lakes (Brazner et al. 2001; Höök et al. 2007). However, the frequency, timing, and direction of migration is uncertain. Yellow perch inhabit both Lake Michigan and DRM lakes (Janetski et al. 2013); DRM lakes are connecting waterbodies between tributaries and the lake proper, and act somewhat analogous to estuaries (Bhagat and Ruetz 2011). Genetic analyses delineate Lake Michigan yellow perch from DRM lake yellow perch, but also provide supporting evidence of migration by a subset of Lake Michigan yellow perch into the profundal zone of DRM lakes (Chorak et al. 2019).

In this study, we attempted to clarify habitat-use patterns of yellow perch by employing complementary techniques (e.g., morphology, stable isotopes). We used landmark-based geometric morphometrics to examine morphological variation of yellow perch occupying different habitats. We analyzed shape data with multivariate statistics to group and cross-validate known habitat groups. We also performed pairwise comparisons to investigate consistency of shape variation among habitats. In addition to morphometrics, we used stable isotope analysis to determine habitat use. First, we analyzed oxygen and hydrogen stable isotope values of ambient water to determine if habitats were isotopically different. Then, we analyzed carbon and oxygen isotope values of otolith cores to identify natal origins of individual fish. Finally, we quantified carbon, nitrogen, oxygen, and hydrogen stable isotope ratios of muscle tissue to investigate relatively recent habitat use.

Overall, morphometrics and stable isotope analysis supported genetic evidence of distinct yellow perch stocks in Lake Michigan and DRM lakes. Furthermore, a subset of Lake Michigan fish appeared to migrate into the profundal zone of DRM lakes in the fall. Although morphological

variation distinguished among Lake Michigan residents, DRM lake residents, and Lake Michigan migrants, body shape was inconsistent among DRM lakes. Caution must be used when interpreting these results because Lake Michigan fish were preserved differently than DRM lake fish prior to images being taken, which is known to distort body shape (Berbel-Filho et al. 2013; Kočovský 2016). Stable isotope ratios of ambient water ($\delta^{18}O$ and $\delta^{2}H$) from this study, as well as isotope ratios of water and potential prey presented in other studies (Dufour et al. 2005; Stein 2018), show distinctions between Lake Michigan and DRM lakes, as well as among DRM lakes. $\delta^{13}C$, $\delta^{18}O$ and $\delta^{2}H$ values typically increase from tributary to lake proper (Gat et al. 1994; Marko et al. 2013), and followed the same pattern in this study. These habitat differences in stable isotope ratios provided a basis to use stable isotopes of otoliths and muscle to determine habitat use. Otolith core and muscle isotope values distinguished between Lake Michigan and DRM lake residents. Isotopic values of yellow perch collected in the profundal zone of DRM lakes in the fall grouped either with Lake Michigan values or DRM lake values. DRM profundal-caught fish with core and muscle isotopic values similar to Lake Michigan values indicate migration from Lake Michigan, while profundal-caught fish with isotopic values similar to DRM lake values are likely DRM lake residents. We also compared $\delta^{13}C$ and $\delta^{18}O$ values of otoliths and soft tissues of fish from profundal DRM lake zones to identify agreement between habitat-use indicators. In general, fish with core otolith isotopic values indicative of early life in Lake Michigan also had muscle isotopic values indicative of recent life in Lake Michigan. While we can only state that migrant fish moved once, this pattern of consistency suggests fish may make multiple migrations. Knowledge of these seasonal habitat occupancy patterns by yellow perch should be taken into account by managers when estimating population characteristics, such as abundance or fishing mortality.

Chapter 3 investigates the consistency of resource use by young yellow perch in Saginaw Bay, Lake Huron. Ecological studies have traditionally treated species or populations as homogenous groups, however numerous studies have shown that intrapopulation variation in resource use is widespread (Bolnick et al. 2003). Within-species diet differences have been documented in small (Svanbäck and Persson 2004; Middaugh et al. 2013) and large freshwater systems (Happel et al. 2015; Foley et al. 2017) in multiple species. Roswell et al. (2013) observed spatial, interindividual diet variation in stomach contents of age-0 yellow perch in Saginaw Bay. However, stomach contents only provide a short-term measure of diet and cannot explain diet consistency among individuals. Other measures of trophic reliance, such as stable isotopes and morphology, reflect resource use on a longer time scale.

We used stable isotopes of soft tissues and morphological analyses to elucidate the consistency of spatiotemporal variation of age-0 yellow perch diet. We analyzed $\delta^{13}C$ and $\delta^{15}N$ of soft tissues to differentiate assimilated diet from ingested diet found in stomach contents. $\delta^{15}N$ values of yellow perch decreased as the distance from Saginaw River, the primary tributary of Saginaw Bay, increased. $\delta^{13}C$ values of yellow perch were higher in 2010 compared to 2009, which is consistent with a shift in relative prey densities from zooplankton to benthic macroinvertebrates (Roswell et al. 2013). Despite the temporal shift in $\delta^{13}C$ values, spatial diet patterns remained relatively consistent. We used landmark-based geometric morphometrics to describe morphological variation. Again, spatial variation was evident. The two southeast sites, with similar sandy substrate, grouped apart from the third site with rocky structure. Fish from the two southeast sites had fusiform bodies, consistent with a pelagic diet, while fish from the third site were deeper-bodied, which is consistent with a benthivorous diet. The general agreement of multiple diet indicators (stomach contents, stable isotopes, and morphology) indicate prolonged resource use in

an area and distinct trophic reliance among different groups of young yellow perch in Saginaw Bay.

Overall, the use of multiple foraging and habitat indicators helped elucidate resource use and habitat occupancy of yellow perch in two areas of the Great Lakes. Previous studies have found discrepancies among indicators and have cautioned generalization of trophic relationships when only relying on a single metric (e.g., Happel et al., 2015; Leonhardt, 2018). Agreement between complementary techniques provided additional support to previously-published genetic results (Chapter 2) and stomach content data (Chapter 3), and thereby helped more fully describe habitat use by yellow perch in these systems.

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CHAPTER 2. DIFFERENTIAL HABITAT USE PATTERNS OF YELLOW PERCH *PERCA FLAVESCENS* IN EASTERN LAKE MICHIGAN AND CONNECTED DROWNED RIVER MOUTH LAKES

2.1 Introduction

Distinct habitats often provide differential foraging opportunities, spawning conditions, and predation refuge. In marine and large lake ecosystems, multiple distinct habitat types (e.g., pelagic, benthic, nearshore) offer diverse energetic resources (Solomon et al. 2011), but there is nonetheless exchange between these habitats. For example, nearshore zones may be influenced by both offshore waters and tributaries (Morrice et al. 2004), and interfaces between nearshore areas and tributaries serve as potential ecotones, where spatially variable environmental conditions may support increased productivity (Jude and Pappas 1992) and bidirectional movement of fish and resources. Individual fish habitat use in these areas may strongly affect performance (growth, survival, recruitment) and have important implications for fisheries management (e.g., differential regulations across habitats).

A multitude of fish populations move among habitats and occupy different habitats during different seasons. For some populations, seasonal habitat occupation is consistent among individuals, whereas in other populations groups of individuals display distinct habitat occupancy patterns. For example, all individuals in populations of pink salmon *Oncorhynchus gorbuscha* and chum salmon *Oncorhynchus keta* migrate from the ocean into tributaries to spawn (Waples et al. 2001). In contrast, species such as brook trout *Salvelinus fontinalis* (Doucett et al. 2004; Robillard et al. 2011), brown trout *Salmo trutta* (Olsson and Greenberg 2004), steelhead *Oncohynchus mykiss* (McPhee et al. 2007), and white perch *Morone americana* (Kerr et al. 2009) demonstrate patterns of partial migration, with both resident and migrant individuals within a single population.

Several relatively recent studies in the Laurentian Great Lakes have focused on fish habitat use in nearshore areas and their tributaries (e.g., Parker et al., 2009; Schoen et al., 2016; Sierszen et al., 2012). The nearshore zone of eastern Lake Michigan, for instance, is connected to several tributaries by drowned river mouth (DRM) lakes. DRM lakes are coastal habitats created by retreating glaciers and rising lake levels that filled river mouths (Gillett et al. 2015). DRM lakes often contain both open lacustrine zones and coastal wetland habitats (Bhagat and Ruetz 2011). These environments are often relatively productive (Höök et al. 2007; Schoen et al. 2016), provide alternate prey sources (Bhagat and Ruetz 2011), and serve as potentially important spawning and nursery grounds for various fish species (Dufour et al. 2005; Höök et al. 2007, 2008; Bhagat and Ruetz 2011; Janetski and Ruetz 2015).

Native Great Lakes species, such as yellow perch *Perca flavescens*, northern pike *Esox lucius*, lake sturgeon *Acipenser fulvescens*, and several minnow species, as well as nonnative alewife *Alosa pseudoharengus*, are known to migrate between open Great Lake habitats and protected habitats, such as DRM lakes and coastal wetlands (Fortin et al. 1992; Auer 1999; Brazner et al. 2001; Höök et al. 2007; Altenritter et al. 2013). However, uncertainty exists regarding the frequency, timing, and direction of migration. For example, Parker et al. (2009) postulated that yellow perch in DRM lakes migrate from littoral areas to deeper locations within the DRM lake rather than moving to Lake Michigan proper.

Yellow perch occupy both the nearshore region of Lake Michigan and DRM lakes. Stock-recruitment analyses suggest that yellow perch in nearshore Lake Michigan and individual DRM lakes constitute separate stocks (Janetski et al. 2013), but angler accounts and recent genetic analyses propose more complex stock structure and habitat use (Chorak et al. 2019). Yellow perch that are residents of DRM lakes appear to mostly occupy DRM littoral habitat during the summer;

potentially because deeper, profundal areas may become hypoxic (Altenritter et al. 2013; Biddanda et al. 2018; Weinke and Biddanda 2018). Yellow perch that are residents in Lake Michigan likely remain in the nearshore area of the lake proper. Based on genetic analysis, a subset of yellow perch seemingly migrates from Lake Michigan and overwinters within the profundal zone of DRM lakes (Chorak et al. 2019). Thus, yellow perch in the profundal zone of a DRM lake may have migrated from Lake Michigan or originated from the DRM lake itself. Clarification of these habitat-use strategies, including their frequency and consistency, will help better describe spatial structure of fish stocks and resource flow between Great Lakes and their tributaries.

When examining fish stocks and habitat use, a holistic approach employing complementary techniques can increase confidence in elucidating habitat use (Begg and Waldman 1999). Morphometrics, while commonly used in phylogenetic studies and evaluation of fish condition (e.g., nutritional status; Smith et al. 2005), may also discriminate habitat use and foraging differences within or among populations (Kocovsky et al. 2009). Fish populations in lacustrine systems often demonstrate morphological divergence along the littoral-pelagic axis, as seen in yellow perch (Parker et al. 2009a) and congeneric Eurasian perch *Perca fluviatilis* (Svanbäck and Eklöv 2002; Hirsch et al. 2013; Faulks et al. 2015). Perch occupying littoral habitats tend to be deeper-bodied and better suited for high maneuverability and piscivorous feeding. In contrast, perch in a pelagic environment are often more streamlined, minimizing drag forces, and adapted for a planktivorous diet. Therefore, there is potential for morphological differentiation among yellow perch groups occupying different habitats in nearshore Lake Michigan and DRM lakes.

Stable isotope ratios, now a common tool in aquatic ecology, are often used to examine habitat use, migration patterns, and trophic energy pathways. Signatures from hard (e.g., otoliths) or soft (e.g., muscle) tissues can be used to index habitat occupancy, provided there are distinct

isotopic ratios among habitats. Carbon and oxygen isotope ratios of fish otoliths have been used as indicators of natal origin, dietary shifts and habitat use history (Solomon et al. 2006; Gao and Bean 2008). Otoliths, calcified structures used for balance and hearing, grow throughout a fish's lifetime, accrete elements reflective of the environment, and remain metabolically inert, lacking resorption of deposited material. Carbon isotopes within an otolith ($\delta^{13}C_{oto}$) are derived from dissolved inorganic carbon in ambient water and metabolic processes (Solomon et al. 2006), while oxygen isotopes within an otolith ($\delta^{18}O_{oto}$) reflect oxygen stable isotope ratios and temperature of ambient water. Previous studies demonstrated differences in otolith carbon stable isotope ratios between Lake Michigan and tributaries (Dufour et al. 2005, 2008; Rude et al. 2017). Carbon stable isotope ratios of seston have been documented to follow a gradient of ^{13}C-enrichment from tributary to lake proper (Keough et al. 1996; Hoffman et al. 2010; Marko et al. 2013). Oxygen stable isotope values of ambient water remain consistently different between Lake Michigan and DRM lakes such as Muskegon Lake (Dufour et al. 2005; Jameel et al. 2018). Thus, there is potential to use $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ to track habitat use between nearshore Lake Michigan and connecting tributaries.

Stable isotope ratios of soft tissues, in particular $\delta^{13}C$ and $\delta^{15}N$, are often used to study foraging ecology (e.g. Vander Zanden et al. 2016) and trophic relationships within aquatic food webs (Foley et al. 2014; Turschak and Bootsma 2015) because different isotopic signatures are predictably transferred from diet to consumer (Budge et al. 2008). Stable isotopes in soft tissues, like muscle, reflect assimilated food sources over some preceding time period; from two to six months in juvenile and adult fish depending upon tissue turnover (Weidel et al. 2011). Thus, muscle stable isotopes generally provide a more recent index of habitat occupancy than core otolith isotopic values. $\delta^{13}C_{muscle}$ can serve as an indicator of dominant primary production pathways

supporting a consumer (i.e., benthic, pelagic or terrestrial). Consumer stable isotope ratios of nitrogen ($\delta^{15}N_{muscle}$) reflect fractionation of consumed nitrogen isotopes, with baseline $\delta^{15}N$ in an environment reflecting diverse processes, including terrestrial inputs and various internal processes (e.g., denitrification, sediment deposition). Consumer muscle tissue $\delta^{2}H_{muscle}$ and $\delta^{18}O_{muscle}$ values are affected by $\delta^{2}H$ and $\delta^{18}O$ of both diet and ambient water, with $\delta^{2}H_{muscle}$ being more influenced by $\delta^{2}H$ of diet and $\delta^{18}O_{muscle}$ being more influenced by $\delta^{18}O$ of ambient water (Coulter et al. 2017). Stable isotope ratios of hydrogen ($\delta^{2}H_{w}$) and oxygen ($\delta^{18}O_{w}$) of ambient water typically increase from tributary to lake proper as the lighter isotope preferentially evaporates (Gat et al. 1994). Thus, $\delta^{2}H_{muscle}$ and $\delta^{18}O_{muscle}$ can help elucidate recent habitat use and environmental history (Soto et al. 2011; Vander Zanden et al. 2016).

Improved understanding of habitat use for species like yellow perch may aid in their management. Lake Michigan and DRM lake yellow perch populations were previously managed as separate stocks with unique bag limits (MDNR 2016), but this strategy may be inappropriate if inconsistent with habitat use. Accurate descriptions of stock structure and movement are critical to estimating fishing mortality, which will ultimately influence regulation of fishing pressure. Again, genetic evidence suggests a complex stock structure with three distinct habitat-use patterns for yellow perch: Lake Michigan residents, DRM lake residents, and Lake Michigan migrants that overwinter in the profundal zone of DRM lakes (Chorak et al. 2019). However, the relative frequencies of these strategies are unknown, as is the individual consistency of annual habitat use. We employed multiple techniques (geometric morphometrics, otolith stable isotopes, and muscle stable isotopes) to elucidate habitat use among groups of yellow perch in eastern Lake Michigan. We expected concomitant use of these techniques would distinguish between Lake Michigan and littoral DRM lake yellow perch. Furthermore, given that Lake Michigan fish may move into DRM

lakes to overwinter (Chorak et al. 2019), we hypothesized that a proportion of fish collected during fall in the profundal zone of DRM lakes would exhibit morphological and isotopic values (both otolith core and muscle) more similar to Lake Michigan fish than fish collected in DRM lakes during summer or in littoral zones.

2.2 Methods

2.2.1 Sample collection

We collected yellow perch in eastern Lake Michigan during summer (August-September) and fall (October-December) 2015 from two nearshore Lake Michigan sites and five DRM lakes (Lake Charlevoix, Portage Lake, Pentwater Lake, Muskegon Lake, and Lake Macatawa; Table 2.1; Figure 2.1). Note, we used different collection methods as our goal was to collect sufficient fish for analyses and not to index relative abundances across habitats. For DRM lake littoral zones, we randomly selected 200-m transects less than 50 m from shore and no more than 3 m in depth. We then boat electrofished each transect for 20 minutes or until at least 40 yellow perch were collected (Chorak et al. 2019). We defined profundal habitat as the deepest point of the DRM lake where bottom dissolved oxygen was >2 mg/L. We collected fish in DRM lake profundal zones with 5.08- and 7.62-cm stretch-mesh gill nets. The Michigan Department of Natural Resources collected nearshore Lake Michigan fish via trawling and gillnets during their bi-annual yellow perch survey. After collection, fish were weighed and measured for total length. A subset of fish was photographed for morphometric analyses immediately upon collection and all fish were then frozen (–20 °C).

2.2.2 Morphology

Prior to photographing for morphometric analysis, we placed fish on a flat surface with a ruler for scale and fins pinned to expose fin insertions. For fish collected in DRM lakes, we captured images with a Panasonic TS5 camera before freezing samples, whereas fish collected in Lake Michigan were photographed after freezing. Preservation methods such as freezing are known to significantly distort the body shape of fish (Berbel-Filho et al. 2013; Kočovský 2016). Thus, Lake Michigan fish may have preservation-related biases, but comparisons of littoral and profundal-caught fish for DRM lakes should be unbiased as they were preserved identically. We created a TPS file in tpsUtilw64, and placed 18 digital landmarks (Figure 2) in tpsDig2w64 (Zelditch et al. 2004). We removed fish <80 mm (to ensure no young-of-year fish were included) and photos missing landmarks prior to statistical analyses (Webster and Sheets 2010). We used geometric morphometrics to analyze fish images in MorphoJ, which calculates partial warp and uniform scores (Faulks et al. 2015). We performed a Procrustes fit on the scores – a process that translates images to their origin, scales to their centroid size, and minimizes the total sum-of-squares deviations through rotation (Klingenberg 2011; Adams et al. 2013). We corrected for allometry (i.e., shape change due to differences in size) by performing a multivariate regression of shape (i.e., the Procrustes coordinates) on centroid size (Klingenberg 2016). The residuals from this regression were used for subsequent statistical analyses.

2.2.3 Environmental isotope signature

To characterize the isotopic composition of water in nearshore Lake Michigan and DRM lakes, we collected published δ^2H and $\delta^{18}O$ values from Jasechko et al. (2014). Lake Michigan water isotope values are fairly well described and consistent, while DRM lake values are more variable. Thus, to characterize δ^2H_w and $\delta^{18}O_w$ of ambient DRM lake water, we collected two water

samples from all DRM lakes in 2015 and 2018. For each sample, we triple-rinsed a Nalgene™ Certified Wide-Mouth Amber HDPE bottle with ambient water, submerged the bottle under the surface to fill completely, and capped the bottle underwater. We tightly wrapped Parafilm M™ film around the cap to prevent evaporation, then froze samples at –20 °C. Samples were analyzed using a Picarro L2130-I laser analyzer running in discrete sample mode, and data were corrected for memory and through-run drift and calibrated to the VSMOW-SLAP reference scale using the methods described in (Good et al. 2014). Water isotopic analysis occurred at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah.

2.2.4 Otolith

After thawing frozen yellow perch, we obtained sagittal otoliths by removing the gills and cutting the spine with scissors. Then, we used forceps to remove the otoliths and place them in coin envelopes. We selected a subset of otoliths for carbon ($\delta^{13}C_{oto}$) and oxygen ($\delta^{18}O_{oto}$) isotopic analysis. We sonicated otoliths in milli-Q water, marked the origin with mechanical pencil, and embedded them in an Epo-fix block with cyanoacrylate adhesive. After drying at least 24 hours, we cut a 1-mm block around each otolith's origin with an isometric saw, then polished with 3-µm and 1-µm graded polishing paper until the origin was clearly visible. We washed the otoliths in 5% nitric acid and double-rinsed with milli-Q water. We used a 500-µm variable speed dental drill to remove approximately 500 μm^3 of core material. Intra-otolith core samples are expected to represent a period less than the first month of life, as seen in alewife (Dufour et al. 2008) and based on yellow perch otolith growth rates (3µm per day, Reichert 2009). After removal, we weighed the otolith core material and placed it in an acid-washed and ash-glassed exitainer. We converted samples to CO_2 through reaction with orthophosphoric acid, then analyzed the purified gas with a

Thermo Finnigan Gas Bench II coupled to a Delta V or MAT 253 IRMS (Stein 2018). Otolith analyses were conducted at the SIRFER lab.

2.2.5 Muscle

For analysis of muscle tissue isotopic ratios, we removed dorsal muscle plugs with a biopsy plunge, froze the samples at –20 °C for storage, and subsequently dried samples at 70 °C for at least 72 hours prior to analysis. We ground the samples via mortar and pestle and measured C and N isotopic ratios with an NC2500 elemental analyzer plumbed into a Thermo Delta V IRMS. We measured H and O isotopic ratios with a Temperature Conversion elemental analyzer interfaced into an IRMS (e.g., Hrycik et al. 2018). Some studies account for $\delta^{13}C$ and $\delta^{15}N$ variability caused by lipid concentrations by performing lipid extraction or mathematical correction. For aquatic consumers, a lipid concentration greater than 5% (or C:N <3.5) may warrant a correction (Post et al. 2007). Given that muscle samples had a consistently low C:N ratio (average 3.3), and our goal was to study habitat occupancy and not estimate prey consumption, we refrained from performing lipid corrections on muscle stable isotope values. Reference materials used to calibrate measurements included: CBT, KCRN, and an internal deer standard for $\delta^{13}C$ and $\delta^{15}N$, and benzoic acid, CBS, KHS, and an internal keratin standard for $\delta^{2}H$ and $\delta^{18}O$. Isotope ratios for all analyses were measured against the following standards: Vienna Pee Dee belemnite ($\delta^{13}C$), atmospheric N_2 ($\delta^{15}N$), and standard mean ocean water ($\delta^{2}H$ and $\delta^{18}O$). 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.

2.2.6 Statistical analysis

To maximize morphological separation among three habitat groups (nearshore Lake Michigan, littoral and profundal DRM lakes), we applied canonical variate analysis (CVA). Then, we performed discriminant function analysis (DFA) on habitat pairs within sites to discriminate between habitats (based on morphological distances, or Mahalanobis distance, MD) and utilized leave-one-out cross-validation to determine reliability of identification (Klingenberg 2011). Both CVA and DFA were performed on regression residuals to minimize allometric effects.

We visualized stable isotope data with biplots: $\delta^{13}C_{oto}$ vs $\delta^{18}O_{oto}$, $\delta^{13}C_{muscle}$ vs $\delta^{15}N_{muscle}$ and $\delta^{2}H_{muscle}$ vs $\delta^{18}O_{muscle}$. Due to non-normal distribution of data, we used univariate, non-parametric tests to compare means of isotopic values. We were only able to include data from two Lake Michigan sites, so we grouped together all Lake Michigan fish and compared their mean isotopic values with littoral and profundal isotopic values of individual DRM lakes using Mann-Whitney tests. We also used a Mann-Whitney test to compare littoral and profundal mean isotopic values within DRM lakes. Due to sample size, only Lake Charlevoix, Pentwater Lake and Muskegon Lake were used for within-lake comparisons. Given multiple hypothesis tests and our aim to balance statistical power with minimization of Type I errors, we determined significance at two critical values, marginal ($\alpha = 0.05$) and high ($\alpha = 0.005$).

2.2.7 Individual otolith – muscle relationships

We assessed agreement of early life and recent habitat use of individual yellow perch by comparing individual otolith and muscle $\delta^{13}C$ and $\delta^{18}O$ values. We visualized the data for each isotope with biplots (e.g., $\delta^{13}C_{oto}$ vs $\delta^{13}C_{muscle}$) and performed a Spearman rank correlation test to determine if there was agreement between isotopic values of natal origin and recent habitat use. Further, we considered profundal-caught fish for this analysis because these individuals, as

suggested by genetic analysis (Chorak et al. 2019), likely exhibit movement between habitats unlike resident yellow perch in Lake Michigan and the littoral zone of DRM lakes. We limited these correlations to profundal-caught fish from DRM lakes with sufficient samples sizes (i.e., only Lake Charlevoix, Pentwater Lake, Muskegon Lake). We performed six correlation tests total – one for each DRM lake for each isotope. All analyses were performed in R (R Core Team 2019).

2.3 Results

2.3.1 Sample collection

In total, 474 yellow perch were analyzed for morphometrics, 126 for otolith stable isotopes, and 174 for muscle stable isotopes (Table 2.1). Lake Michigan fish were collected in nearshore areas near Charlevoix and Portage and were subsequently grouped together for plotting and statistical analyses. All yellow perch collected in Portage Lake were from the littoral zone. Since only two fish with otolith data were collected in the littoral zone of Lake Macatawa, they were not included in otolith stable statistical isotope analyses. Total length of yellow perch ranged from 80-343 mm (average = 188.0 mm).

2.3.2 Morphology

Canonical variate analysis axes CVI and CV2 represent 43.4% and 27.1% of morphological variation, respectively, and grouping across these two axes indicated morphological distinction between Lake Michigan and littoral DRM lake fish (Figure 2.3). Profundal fish generally grouped intermediately between Lake Michigan and littoral fish, with more overlap with Lake Michigan. DFA showed significant differences in Mahalanobis distance between all habitat pairs (Table 2). Cross-validation correctly identified >79% of images in pairwise comparisons.

2.3.3 Environmental isotope signature

Ambient water δ^2H_w and $\delta^{18}O_w$ measured across habitats displayed an approximate linear relationship (Figure 2.4). DRM lake δ^2H_w and $\delta^{18}O_w$ values ranged from -78 to -63‰ and -11 to -7‰, respectively. Isotopic values increased from north to south, except for Portage Lake, which fell between Lake Macatawa and Lake Michigan values, and was less distinct from Lake Michigan δ^2H_w and $\delta^{18}O_w$ values than other DRM lakes. In general, DRM lake values differ from previously published Lake Michigan δ^2H_w (-44‰) and $\delta^{18}O_w$ (-5.83‰) values (Jasechko et al. 2014).

2.3.4 Otolith

Otolith core isotope ratios, $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$, varied by habitat (Figure 2.5). In general, $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values of yellow perch collected in DRM lake littoral habitats were relatively low and highly distinct ($p \leq 0.005$) from $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values of yellow perch from Lake Michigan. Similar to ambient water isotopes, $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values of yellow perch from the littoral zone of Portage Lake grouped closer to Lake Michigan isotope values than did those from other DRM lakes.

In contrast to littoral-caught individuals, $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values of fish collected in profundal zones of DRM lakes were either similar to fish from Lake Michigan or DRM lakes. In particular, $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values of fish collected from profundal zones in the fall tended to be similar to Lake Michigan values. Differences between Lake Charlevoix profundal $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values and Lake Michigan values were highly significant. Pentwater and Muskegon lakes profundal $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values were similar to either Lake Michigan or littoral DRM lake values. Differences between Pentwater and Muskegon lakes profundal $\delta^{13}C_{oto}$ values and Lake Michigan $\delta^{13}C_{oto}$ values were highly significant. Lake Macatawa profundal $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values were similar to values from Lake Michigan. Regarding within-DRM lake comparisons, all

differences in $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values were highly significant between littoral and profundal habitats for Lake Charlevoix, Pentwater Lake and Muskegon Lake (Figure 2.5).

2.3.5 Muscle

$\delta^{13}C_{muscle}$, $\delta^{15}N_{muscle}$, $\delta^{2}H_{muscle}$ and $\delta^{18}O_{muscle}$ indicated variable recent habitat use patterns (Figures 2.6, 2.7). Yellow perch collected in Lake Michigan generally displayed relatively high $\delta^{13}C_{muscle}$, $\delta^{2}H_{muscle}$ and $\delta^{18}O_{muscle}$ values, but often low $\delta^{15}N_{muscle}$ values. Isotope ratios of yellow perch collected in littoral zones of DRM lakes were highly distinct from those of Lake Michigan fish, except for fish from Portage Lake ($\delta^{15}N_{muscle}$: W=168, p=0.967) and Pentwater Lake ($\delta^{15}N_{muscle}$: W=124, p=0.244). In Lake Macatawa, $\delta^{15}N_{muscle}$ values of littoral-collected DRM yellow perch were very high, with values between 15-25‰. The $\delta^{2}H_{muscle}$ stable isotope value for one fish from Lake Michigan was out of the expected range ($\delta^{2}H_{muscle}$ = -283‰), so all data for the individual were removed from biplots and statistical analyses.

Similar to otolith core isotope ratios, muscle isotope ratios of yellow perch collected in profundal zones of DRM lakes displayed greater variability than analogous values from yellow perch collected in littoral zones. All stable isotope values for fish collected in profundal zones were significantly different than fish collected in Lake Michigan, except for $\delta^{15}N_{muscle}$ in Pentwater Lake (W=127, p=0.234). Profundal-caught fish generally displayed higher $\delta^{13}C_{muscle}$, $\delta^{2}H_{muscle}$, $\delta^{18}O_{muscle,}$ and $\delta^{15}N_{muscle}$ values compared to fish collected in littoral zones of DRM lakes, except for $\delta^{15}N_{muscle}$ values in Pentwater and Muskegon lakes. For within-lake comparisons, all differences in stable isotope ratios were highly significant between littoral and profundal habitats, except for Pentwater Lake $\delta^{13}C_{muscle}$ and $\delta^{15}N_{muscle}$ (Figures 2.6, 2.7).

2.3.6 Individual otolith – muscle relationships

Biplots of otolith and muscle stable isotope values of yellow perch collected in the profundal zones of DRM lakes demonstrated agreement between isotopic values of natal origin and recent habitat use (Figure 2.8). Individuals that had otolith isotope values indicative of Lake Michigan origin generally had muscle isotope values that reflected recent time spent in Lake Michigan. Similarly, individuals that had otolith isotope values indicative of a DRM lake origin had muscle isotope values that reflected recent time spent in a DRM lake. Spearman rank correlation tests yielded significant, positive correlations between otolith and muscle stable isotope values of profundal-caught yellow perch in Muskegon Lake.

2.4 Discussion

Morphometric and stable isotope analyses supported genetic evidence (Chorak et al. 2019) of distinct resident populations of yellow perch in eastern Lake Michigan and littoral zones of DRM lakes. However, there was less consistency in the distinction between yellow perch collected in profundal zones of DRM lakes and the other two habitat types. Some yellow perch collected in profundal zones of DRM lakes during fall appear to have spent early and recent life in Lake Michigan, while others seem to have spent early and recent life in DRM lakes. Furthermore, across-habitat variation patterns of morphology and isotope ratios differed among sampling locations. Collectively, these results suggest complex and highly variable habitat use by yellow perch in nearshore Lake Michigan and connected habitats.

Like genetic analyses, morphometrics distinguished yellow perch between Lake Michigan and littoral DRM lake habitats, while there was less morphological separation between Lake Michigan and profundal-caught fish. DFA indicated significant morphological differences between all pairwise comparisons. Furthermore, morphological differences between littoral and

profundal fish did not differ in the same way in each DRM lake. For example, littoral fish in Lake Charlevoix and Pentwater Lake were deeper-bodied than profundal fish, but in Muskegon Lake the opposite was true. The inconsistent morphological variation among sites may be attributed to influence of local factors, like prey availability and habitat structure (Svanbäck and Eklöv 2002; Olsson and Eklöv 2005). We must also note different storage methods of Lake Michigan and DRM lake fish. Freezing of Lake Michigan fish prior to photographing likely impacted the overall body shape and warrants caution when interpreting results (Berbel-Filho et al. 2013; Kočovský 2016).

The ability to distinguish habitat types, and ultimately habitat use of yellow perch, was dependent on environmental differences in stable isotope ratios. Isotopic values of DRM lakes not only differed from Lake Michigan values, but also varied among sites. This variation may be due to differences among DRM lakes, such as surface area, average depth, catchment size, average retention time, and water source (Chubb and Liston 1986; Rutherford et al. 2013; Steinman et al. 2016). The interface between the nearshore zone of large lakes and tributaries creates complex patterns in production and distribution of biotic communities (Larson et al. 2013b). DRM lakes often have higher temperatures and greater phytoplankton and zooplankton densities than large lakes, like Lake Michigan (Höök et al. 2007; Janetski et al. 2013). Carbon and nitrogen stable isotopes, specifically of primary producers, in the lake differ from tributaries because of biogeochemical processes (Vander Zanden and Rasmussen 1999; Ngochera and Bootsma 2011). Photosynthesis by aquatic autotrophs (e.g., algae) typically increases baseline $\delta^{13}C$ values compared to allochthonous inputs (Kelly 2000). This pattern was demonstrated consistently in this study with lower $\delta^{13}C_{muscle}$ values of DRM lake yellow perch compared to $\delta^{13}C_{muscle}$ values of Lake Michigan fish. While $\delta^{15}N$ values are influenced by biogeochemical processes (e.g., N uptake, nitrification, denitrification, and degradation of organic matter; Mariotti et al. 1981; Brandes and

Devol 1997), the baseline isotopic composition of lacustrine nitrogen is primarily driven by external nitrogen loading (Ostrom et al. 1998; Teranes and Bernasconi 2000). Residence time is also known to influence $\delta^{13}C$ values of DIC because of equilibration with atmospheric CO_2 (Zeigler and Whitledge 2011). Lower water temperatures in Lake Michigan may lower metabolic rates and affect the amount respiratory carbon contributed to otoliths, increasing the $\delta^{13}C_{oto}$ values of Lake Michigan yellow perch compared to DRM lake fish (Whitledge 2009).

$\delta^{2}H$ and $\delta^{18}O$ stable isotope values of ambient water within DRM lakes were lower than Lake Michigan values. High $\delta^{2}H_{w}$ and $\delta^{18}O_{w}$ values in Lake Michigan were expected because the preferential evaporation of the lighter isotopes has a larger effect on the isotope budget of the longer-residing Lake Michigan water (Gat et al. 1994; Jasechko et al. 2014). Dufour et al. (2005) recorded similar isotope values with relatively low $\delta^{18}O_{w}$ values in Lake Charlevoix (-9.1‰) and Muskegon Lake (-8.6‰), although Lake Macatawa had a higher value (-6.2‰). $\delta^{18}O_{w}$ values also were lower in the Muskegon (-8.73‰), St. Joseph (-7.76‰) and Trail Creek (-6.83‰) rivers compared to Lake Michigan, as reported by Stein (2018). Differences in $\delta^{18}O_{w}$ and $\delta^{2}H_{w}$ values among sites may be due to variation in surface area (range 1.70 to 17.05 km^2), which is known to affect fractionation associated with evaporation (Whitledge et al. 2006), or differences in the isotope ratios of precipitation within the watersheds (e.g., Bowen et al. 2012). Differences between studies in tributary ambient water isotope values could be related to annual and seasonal variation (Figure 2.4; Walther and Thorrold 2009). Nonetheless, the consistent distinction between Lake Michigan and DRM lake environmental isotope values provided a basis to examine across-habitat patterns in otolith and muscle isotopic values.

Stable isotope analyses of otoliths and muscle yielded similar results, showing a distinction between Lake Michigan and littoral DRM lake yellow perch, but more variable isotopic patterns

for profundal DRM lake fish. Profundal-caught fish grouping with littoral fish are likely residents of the DRM lake and may have moved to deeper water in the fall. Fall, profundal-caught fish with stable isotope values similar to fish collected in Lake Michigan support the idea of yellow perch migration from Lake Michigan proper to overwinter in the DRM lake.

Although there were general patterns in both otolith core and muscle isotope values, some observations deviated from these general patterns. Otolith core and muscle isotope values of yellow perch caught in the littoral zone of Portage Lake overlapped with values of Lake Michigan fish. This may reflect similar water chemistry between Portage Lake and Lake Michigan. Portage Lake has a surface area of approximately 8.5 km^2, reaches depths up to 18 m, is fed by 12 groundwater-fed tributaries and connects to Lake Michigan with a relatively short channel (Seites 2009). Water samples collected from multiple years (2015, 2018) suggest δ^2H and $\delta^{18}O$ values in Portage Lake are more similar to Lake Michigan values than other DRM lake values, likely a result of water exchange with Lake Michigan. As another example, littoral-collected fish in Lake Macatawa had higher $\delta^{15}N_{muscle}$ values. Lake Macatawa is a hypereutrophic lake that receives large amounts of agricultural and urban runoff, which are often enriched in ^{15}N (Larson et al. 2013a; Hassett and Steinman 2016). Thus, high input of nutrients enriched in ^{15}N from runoff is likely reflected in muscle $\delta^{15}N$ values (Larson et al. 2013a).

Correlation of otolith and muscle isotope values for individual DRM lake profundal-collected fish indicated that some adult fish that spent early and recent life in Lake Michigan migrate into DRM lakes in the fall. In total, over half the profundal-collected fish from Pentwater and Muskegon lakes have stable isotope values that overlap with Lake Michigan values. Not only do these profundal-caught DRM lake fish seemingly have Lake Michigan natal origins, but they appear to have spent time recently foraging in Lake Michigan. Schoen et al. (2016) proposed a

similar life history in which lakes Michigan and Huron yellow perch migrate annually to wetland habitats to spawn. In addition, yellow perch along the west shoreline of southern Lake Michigan were documented to have high spawning site fidelity (Glover et al. 2008). Although little evidence supports the migration of Lake Michigan yellow perch into DRM lakes to spawn, fish may be searching for more favorable resources within DRM lakes prior to spawning. It is unclear if these movements into DRM lakes represent a single event by individual, or if they are migrating between Lake Michigan and DRM lakes each year.

Recent genetic analyses suggest three habitat-use patterns for yellow perch in eastern Lake Michigan: Lake Michigan residents, DRM lake residents, and Lake Michigan fish that move into the profundal zone of DRM lakes (Chorak et al. 2019). These results were supported by stable isotope analyses of otolith cores and muscle tissue from the present study. The mechanism driving these movement patterns is unclear. Prey densities are often higher in DRM lakes than nearshore Lake Michigan (Höök et al. 2007) and would offer better forage opportunities for Lake Michigan migrants. DRM lakes also experience hypolimnetic hypoxia in the summer (Biddanda et al. 2018; Chorak et al. 2019), which may prevent yellow perch from residing in the profundal zone year-round (Altenritter et al. 2013; Weinke and Biddanda 2018).

Elucidation of yellow perch habitat occupancy may have important implications for fisheries management and assessment plans. Harvest estimates via creel surveys intended to differentially index distinct populations may be inappropriate if fish migrate between Lake Michigan proper and DRM lakes. For instance, roughly three-quarters and all of the fall-profundal-collected fish in Pentwater and Muskegon lakes, respectively, grouped with Lake Michigan fish with regard to otolith core isotope values. By that logic, roughly three-quarters or all the yellow perch caught by anglers in the profundal zones of Pentwater or Muskegon lakes during fall may

be Lake Michigan fish. Such harvest could represent unrecognized losses from the Lake Michigan yellow perch population and exacerbate seasonal fishing mortality.

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Table 2.1 Site, habitat, season of collection, and number of yellow perch (*n*) included in each analysis (morphometrics, otolith stable isotope, and muscle stable isotope. Seasons represented include: summer (August-September) and fall (October-December).

Site	**Habitat**	**Season**	**Morphometrics (*n*)**	**Otolith SI (*n*)**	**Muscle SI (*n*)**
Lake Michigan	Nearshore	Summer	74	19	34
Charlevoix	Littoral	Summer	42	9	25
	Profundal	Summer/ Fall	29	9	25
Portage	Littoral	Summer/ Fall	77	10	10
Pentwater	Littoral	Summer	64	10	10
	Profundal	Summer/ Fall	61	9	10
Muskegon	Littoral	Summer/ Fall	89	10	25
	Profundal	Summer/ Fall	38	9	25
Macatawa	Littoral	Summer/ Fall	-	2	10
	Profundal	Fall	-	5	-

Table 2.2 Discriminant function analysis results of pairwise comparisons within sites and between habitats. Number of images for each habitat (*n*), Mahalanobis distance (MD), and the percent of images correctly classified by cross-validation (%). Significant differences in MD are denoted by *.

Site	Pair (*n*)	MD	% correctly classified
Charlevoix	Lake Michigan (34) Littoral DRM (42)	8.04*	100 100
	Lake Michigan (34) Profundal DRM (29)	5.67*	88.2 79.3
	Littoral DRM (42) Profundal DRM (29)	6.93*	95.2 93.1
Portage	Lake Michigan (40) Littoral DRM (77)	6.27*	95.0 98.7
Pentwater	Littoral DRM (64) Profundal DRM (61)	5.34*	92.1 84.8
Muskegon	Littoral DRM (89) Profundal DRM (38)	4.91*	97.8 89.7

Figure 2.1. Eastern Lake Michigan and drowned river mouth (DRM) lake sample sites. Blue circle denotes Lake Michigan site.

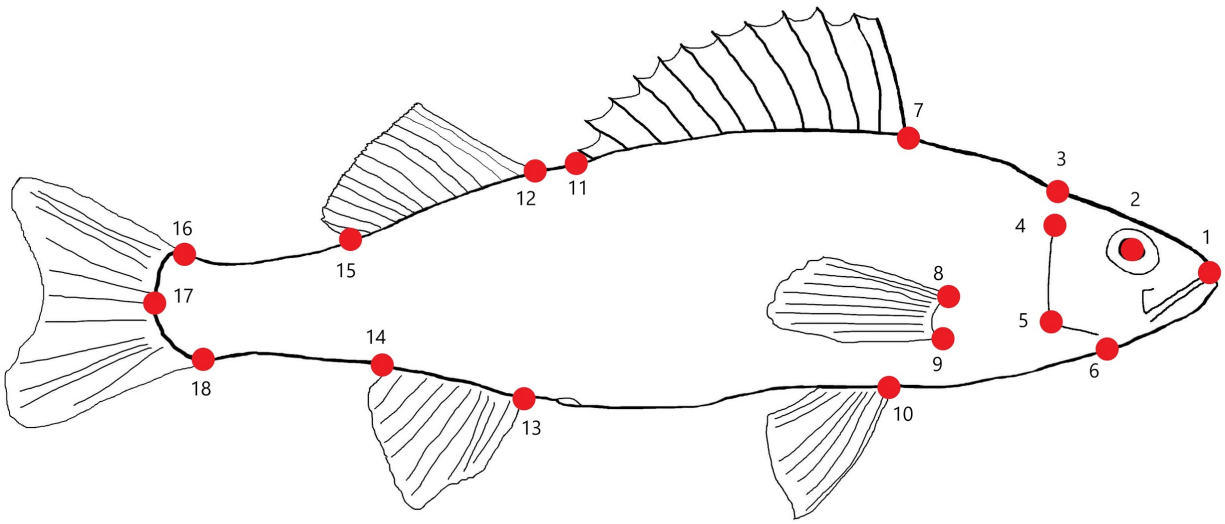

Figure 2.2. Eighteen digital landmarks placed on yellow perch images for morphometric analysis. Image credit: Tim Malinich.

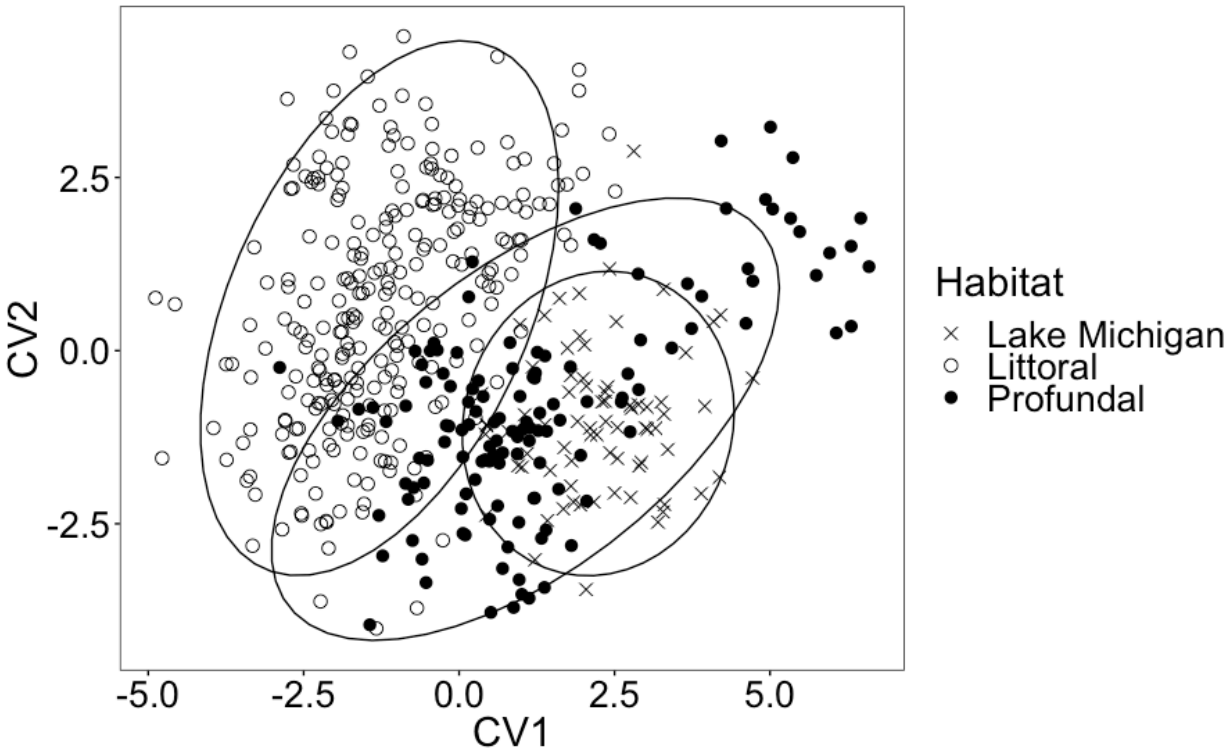

Figure 2.3. Canonical variate analysis results demonstrate morphological variation among habitats – Lake Michigan (x), littoral DRM lake (open circle), profundal DRM lake (filled circle). CV1 and CV2 represent 43.4% and 27.1% of variation, respectively.

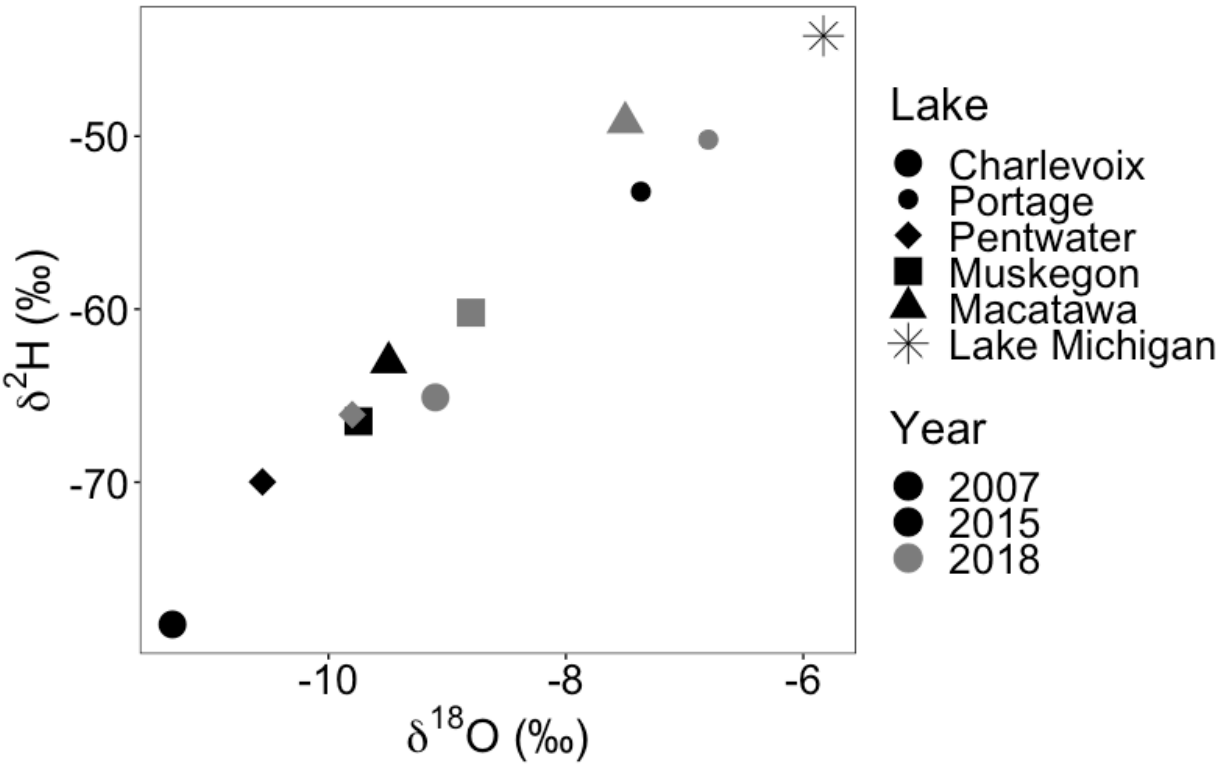

Figure 2.4. Oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) isotope ratios of ambient water for five DRM lakes and Lake Michigan. Site denoted by symbol and year denoted by color. Mean 2007 Lake Michigan value from Jasechko et al. (2014).

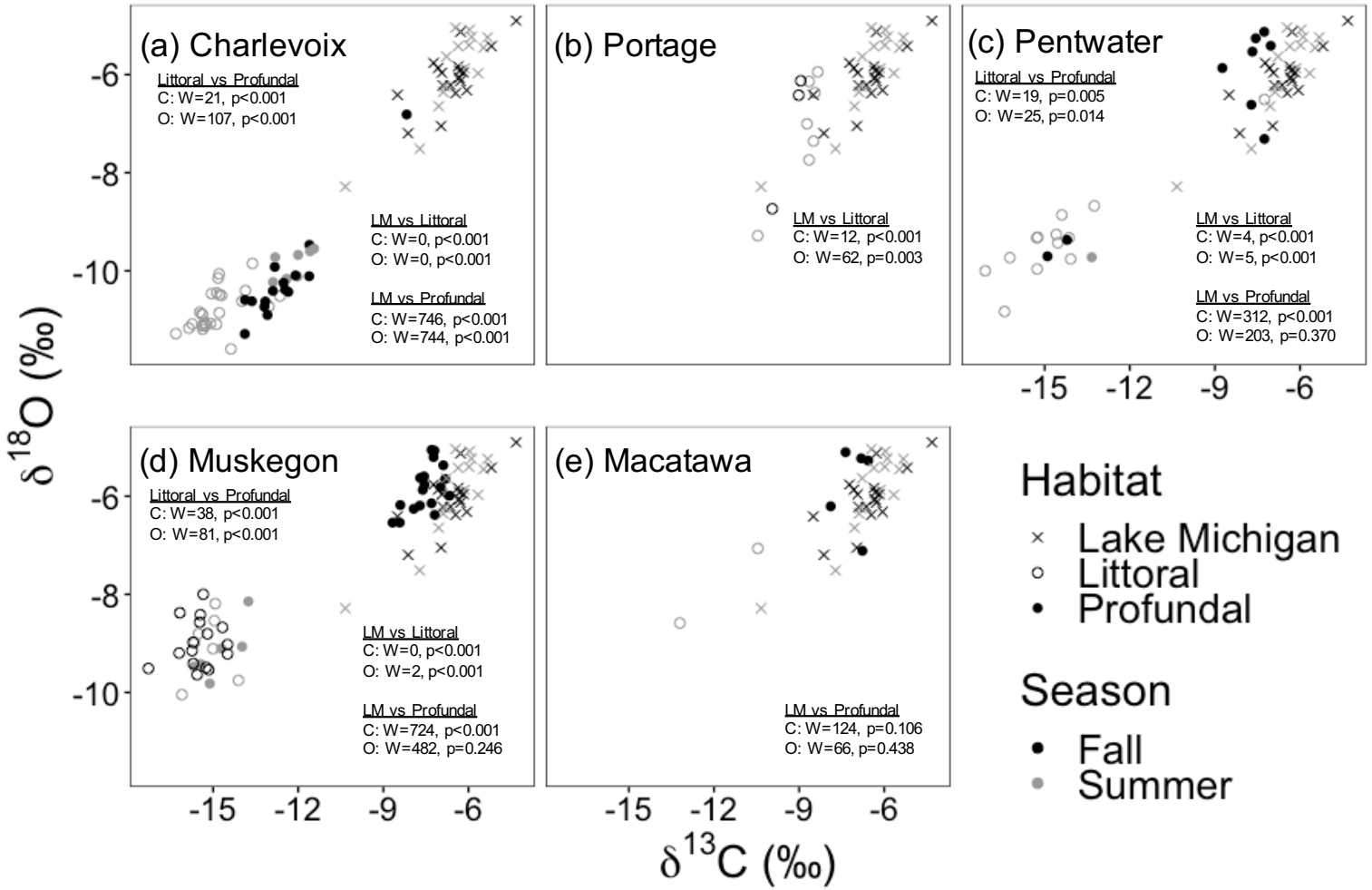

Figure 2.5. Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope ratios of yellow perch otolith cores by site. Sites: (a) Charlevoix, (b) Portage, (c) Pentwater, (d) Muskegon, (e) Macatawa. Habitat denoted by symbol: Lake Michigan (x), littoral DRM lake (open circle), profundal DRM lake (filled circle). Season denoted by color: fall (black), summer (gray). Results of Mann-Whitney tests printed in each panel.

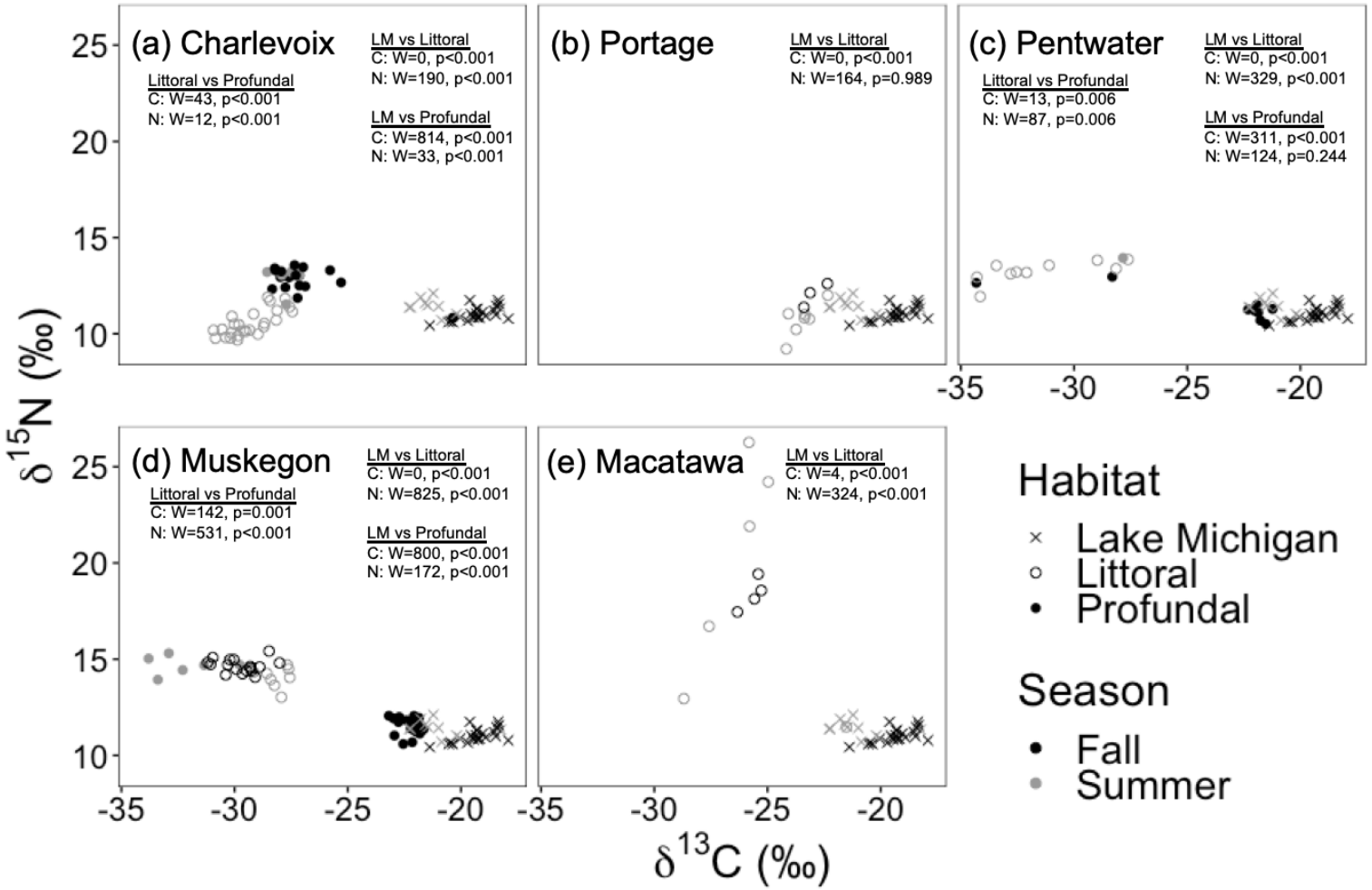

Figure 2.6. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of yellow perch muscle samples by site. Sites: (a) Charlevoix, (b) Portage, (c) Pentwater, (d) Muskegon, (e) Macatawa. Habitat denoted by symbol: Lake Michigan (x), littoral DRM lake (open circle), profundal DRM lake (filled circle). Season denoted by color: fall (black), summer (gray). Results of Mann-Whitney tests printed in each panel.

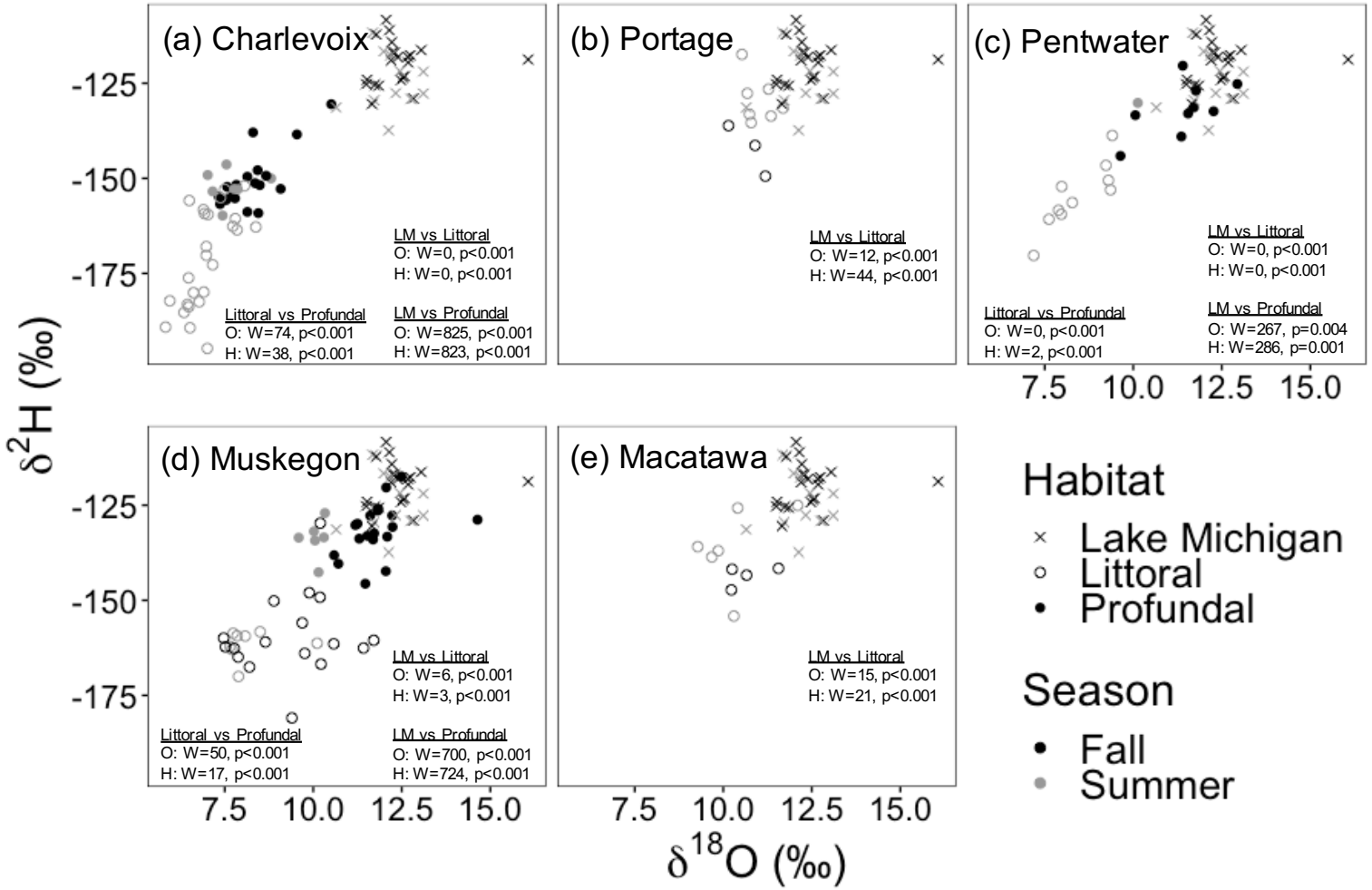

Figure 2.7. Oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) isotope ratios of yellow perch muscle samples by site. Sites (a) Charlevoix, (b) Portage, (c) Pentwater, (d) Muskegon, (e) Macatawa. Habitat denoted by symbol: Lake Michigan (x), littoral DRM lake (open circle), profundal DRM lake (filled circle). Season denoted by color: fall (black), summer (gray). Results of Mann-Whitney tests printed in each panel.

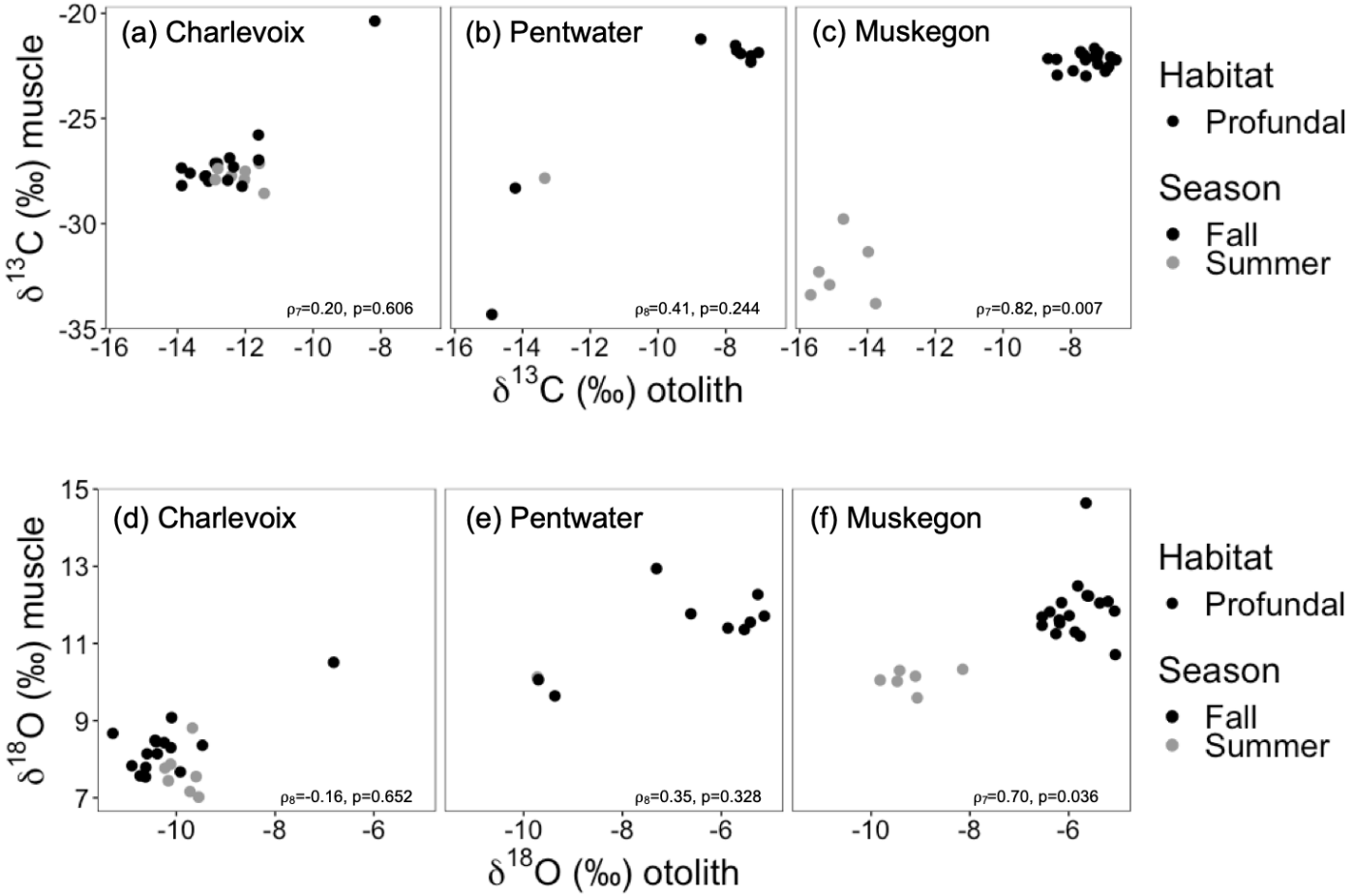

Figure 2.8. Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope ratios of profundal-collected yellow perch otolith and muscle samples by site. Sites (a,d) Charlevoix, (b,e) Pentwater, (c,f) Muskegon. Season denoted by color: fall (black), summer (gray). Results of Spearman's rank correlation tests printed in each panel.

CHAPTER 3. SPATIO-TEMPORAL VARITION OF STABLE ISOTOPES RATIOS AND MORPHOLOGY OF AGE-0 YELLOW PERCH *PERCA FLAVESCENS* IN SAGINAW BAY, LAKE HURON

3.1 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 have shown that treatment of conspecifics as homogenous groups is inappropriate and intrapopulation variation is widespread (Bolnick et al. 2003). Differences in ecological attributes (e.g., prey preferences and foraging strategies, activity and susceptibility to predation) may strongly influence population dynamics (Araújo et al. 2011). These differences occur in a wide range of taxa (Bolnick et al. 2003), with fish being one of the most studied taxonomic groups (Araújo et al. 2011).

Resource use and energy pathways in aquatic systems can be understood through the examination of trophic niches of fishes. Fish trophic niches 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, diet of age-0 largemouth bass *Micropterus salmoides* varied spatially and were influenced by local (e.g., vegetation, prey abundance) characteristics (Middaugh et al. 2013). Diets of Eurasian perch *Perca fluviatilis* in a small Swedish lake varied between littoral and pelagic habitat types (Svanbäck and 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 production pathways in the east (Happel et al. 2015; Foley et al. 2017).

Roswell et al. (2013) observed interindividual diet variation of age-0 yellow perch in Saginaw Bay, Lake Huron in 2009 and 2010. Not only was spatial diet variation evident (likely related to prey availability), but individuals also differed in their relative specialization on either zooplankton or benthic prey (Figure 3.1). Though available prey densities shifted from more zooplankters in 2009 to more benthic invertebrates in 2010, patterns of spatial diet variation remained (Roswell et al. 2013). Despite variation in diet item composition, it is unclear if these differences are consistent among individuals. 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.

Several other measures of trophic reliance, such as stable isotopes and fatty acids, reflect resource use on a longer timescale. In contrast to stomach content analyses, which provide information on ingested prey, stable isotope ratios of soft tissues are a measure of assimilated diet (Peterson and Fry 1987). Isotopic turnover rates vary among species and year classes, but provide dietary information on a scale of weeks to months as opposed to days (Weidel et al. 2011). Since

isotopic values are predictably transferred from diet to consumer (Budge et al. 2008), stable isotope ratios in soft tissues, like carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), are commonly used to study foraging ecology (Post 2002). $\delta^{13}C$ values of soft tissues in part reflect sources of primary production (i.e., carbon source) assimilated by a consumer (DeNiro and Epstein 1978; Peterson and Fry 1987; Post 2002). While $\delta^{15}N$ values of soft tissues are often used to estimate trophic position (Deniro and Epstein 1980; Post 2002), they also can reflect nitrogen sources and relative abundance. For example, agricultural ^{15}N, which has a distinct isotopic value, was found to be strongly influential on $\delta^{15}N$ values of aquatic consumers in receiving water bodies (Larson et al. 2013a). Thus, in large lakes, spatial differences (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 are thought to influence the body form of a fish (Skulason and Smith 1995; Svanbäck and Eklöv 2003). Morphological variation is well documented in Eurasian perch *Perca fluviatil*is and serves as an ideal example of the influence of habitat and resource use on morphology (Svanbäck and Eklöv 2002, 2003; Hjelm and Johansson 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 et al. 2001; Svanbäck and Eklöv 2002, 2003). In addition, perch in littoral habitats often exhibit mouths directed downwards, opposite the

terminal or upturned mouths of perch in pelagic habitats (Svanbäck and Eklöv 2002). Prolonged utilization of resources in a specific area, may be reflected by these long-term diet indicators.

Beyond spatial differences, temporal patterns (e.g., seasonal, annual) may also contribute to differences in consumer stable isotope values and morphology. Variation in $\delta^{13}C$ values are attributed to phytoplankton growth and species distribution, and the resulting CO_2 concentration in surface waters (Cifuentes et al. 1988; Bernasconi et al. 1997; Hodell and Schelske 1998). $\delta^{15}N$ values are influenced by N uptake, nitrification, denitrification, and degradation of organic matter (Mariotti et al. 1981; Brandes and Devol 1997; Teranes and Bernasconi 2000). Lacustrine nitrogen isotopic composition is predominantly driven by external nitrogen loading (Ostrom et al. 1998; Teranes and Bernasconi 2000). Autochthonous primary production is often higher in the summer, resulting in increased $\delta^{13}C$ values; conversely, increased relative contribution of allochthonous inputs in winter increase $\delta^{15}N$ values (e.g., Lehmann et al., 2004). Because Saginaw Bay is subject to fluctuations in allochthonous input and primary productivity, stable isotope composition of consumers may vary temporally. Seasonal shifts in prey availability (e.g., Roswell et al., 2013) may influence morphological variation as well. Seasonal changes in prey consumption (e.g., Hrycik et al., 2018), due to availability or preference, could favor specific foraging strategies and body shapes.

Yellow perch, a congener of Eurasian 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 (Fielder and Thomas 2006) and may be partially attributed to low growth rates, and thus, diet. Roswell et al. (2013) observed intrapopulation variation of yellow perch stomach contents across sampling sites in Saginaw Bay. However, as this measure only served as a short-term diet indicator, the consistency of these individual spatial diet differences is

uncertain. We employed two long-term diet and habitat-use indicators, stable isotopes of soft tissue and morphology, to reexamine age-0 yellow perch collected in 2009 and 2010 and elucidate the consistency of spatiotemporal variation of their diets. 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 annual variation in both indicators because of a shift in relative densities of prey (zooplankton to benthic invertebrates) between 2009 and 2010 (Roswell et al. 2013).

3.2 Methods

3.2.1 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 (Figure 3.2). Detailed methods can be found in (Roswell et al. 2013, 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}. We performed 1-5 tows per site-date, with 1-3 site-dates per year. We collected all sites' samples within a 3-day period for each sampling event. After collection, we placed fish in coolers with ice, then stored at -20°C on shore. In the laboratory, we thawed, weighed and measured fish for total length.

3.2.2 Morphology

After thawing the 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 on the images using tpsDig2w64 (Figure 3.3). We analyzed fish

images with MorphoJ, a program that employs geometric morphometrics to discriminate among images (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 et al. 2013). We regressed Procrustes coordinates against individual centroid size to account for allometry and used the regression residuals for all subsequent analyses (Klingenberg 2011).

3.2.3 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 IRMS. Tissue samples had a consistently low C:N ratio (mean 1.9±0.17) and we did not intend to use isotope ratio values to estimate contributions of different prey types, so we did not perform a mathematical lipid correction on values (Post et al. 2007). Isotope ratios were measured against Vienna Pee Dee beleminite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$). Soft tissue isotopic analysis occurred at the Cornell University Stable Isotope Laboratory. We report stable isotope ratios as delta (δ) values, or per mil (‰) = $((R_{sample}/R_{standard})-1)\ x10^3$.

3.2.4 Statistical analyses

We visualized morphological patterns among sites with canonical variate analysis (CVA) and shape differences between site pairs with discriminant function analysis (DFA). Due the complexity of morphometric data, we performed multiple multivariate tests to compare agreement of results and increase confidence in our interpretation. We visualized differences between years and months (see Appendix Figure A1), but anticipated greater morphological variation among sites due to diet differences (Figure 3.1). In MorphoJ, we created wireframe plots associated with DFA results to describe morphological variation. Upon visual inspection of the data, we observed large

site differences and subsequently performed a permutational multivariate analysis of variance (perMANOVA) with 10,000 permutations on regression residuals to examine morphological variation among individuals. Due to the absence of data from SB-14 in September 2010 (Table 1), we performed three separate perMANOVAs, each with a one factor excluded (i.e., one test with only SB-2 and SB-10 data, a second test with only 2009 data, a third test with only August data).

We visualized stable isotope data with biplots of $\delta^{13}C$ vs $\delta^{15}N$. Initial visualization of the data showed strong site differences for $\delta^{15}N$ and temporal differences for $\delta^{13}C$, so we performed univariate tests to examine the isotopes individually. Due to the absence of data from SB-14 in September 2010, we tested the effect of month on carbon and nitrogen isotope values with the intention of grouping months within years. An analysis of covariance (ANCOVA) with length as a covariate yielded a significant month effect on $\delta^{13}C$ values (Appendix Table A1). Therefore, similar to the morphology analyses, we performed three ANCOVAs and excluded separate factors from each analysis (i.e., one test with only SB-2 and SB-10 data, a second test with only 2009 data, a third test with only August data). All statistical analyses were performed in R (R Core Team 2019).

3.3 Results

3.3.1 Fish collection

We collected 150 age-0 yellow perch total (morphology, n = 150; stable isotopes, n = 80; Table 3.1). However, no fish were collected in September of 2010 at SB-14. Yellow perch total length ranged from 41-75 mm (average = 57.4 mm).

3.3.2 Morphology

Visualization of CVA results displayed morphological similarity between fish from SB-2 and SB-14, with less overlap from SB-10 fish (Figure 3.5). CV1 and CV2 displayed 78.6% and 21.4% of the morphological variation, respectively. 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 3.6). The perMANOVA without SB-14 was the only test that yielded significant results; both site ($R^2_{1,110}$=0.03, p=0.008) and year ($R^2_{1,110}$=0.03, p=0.024) were significant. Results of the other perMANOVAs are presented in Appendix Table A2.

3.3.3 Stable isotopes

Biplots of soft tissue isotope values showed enriched $\delta^{13}C$ values in 2010 and a depletion of $\delta^{15}N$ values at sites further from the Saginaw River input (Figure 3.4). Though $\delta^{13}C$ values were significantly influenced by site, year and month and $\delta^{15}N$ values were significantly influenced by site across all analyses (Table 3.2), 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 interaction effect with site ($F_{1,62}$=10.98, p=0.002) and year ($F_{1,62}$=13.97, p<0.001) on $\delta^{13}C$ values. When September was removed, length also had a significant effect ($F_{1,35}$=6.48, p=0.016) on $\delta^{13}C$ values. When only including 2009, month also had a significant effect ($F_{1,40}$=8.31, p=0.006) on $\delta^{15}N$ values. The analysis without September had an interaction effect between year and length ($F_{1,34}$=12.98, p=0.001).

3.4 Discussion

Long-term habitat-use, foraging and diet indicators, stable isotopes and morphology, displayed intrapopulation variation of young-of-year yellow perch in Saginaw Bay. As expected, spatial variation was evident in both stable isotope values and morphology. While both isotopes 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 unexpected, however, was the annual variation of soft tissue $\delta^{13}C$ values.

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 a bay-wide shift in available prey densities, from more zooplankters in 2009 to more benthic macroinvertebrates in 2010, these general stomach content patterns remained consistent (Roswell et al. 2013). The same spatial differences were reflected by stable isotopes and morphology, with yellow perch collected at SB-10 separating out from the other two sites. These consistent spatial patterns suggest that fish likely remain and forage in the same location where captured.

Diet variation of yellow perch may be influenced by differences between benthic and pelagic habitats. In freshwater environments, $\delta^{13}C$ values can be used to differentiate between littoral and pelagic production because primary producers in the littoral zone (e.g., algae, detritus) are typically enriched in ^{13}C compared to producers in the pelagic zone (e.g., phytoplankton; France, 1995). Soft tissue $\delta^{13}C$ values in the present study did not reflect this pattern. Yellow perch with benthivorous diets (i.e., SB-10) were slightly depleted in ^{13}C compared to fish with pelagic diets (i.e., SB-2 and SB-14; Figure 3.4). However, as the bay-wide density of available prey items

shifted from more zooplankton to more benthic invertebrates between 2009 and 2010 (Roswell et al. 2013), $\delta^{13}C$ values for all sites enriched. The lack of spatial agreement between expected $\delta^{13}C$ values based on stomach contents versus observed $\delta^{13}C$ values of soft tissues could reflect differences between ingested and assimilated diet items (e.g., Happel et al., 2015).

While not necessarily reflective of benthic or pelagic habitat differences, sites closer to Saginaw River had higher $\delta^{15}N$ values. Enriched $\delta^{15}N$ values are often a result of increased contribution and influence of allochthonous input (Lehmann et al. 2004b). In addition, tributaries containing agricultural or urban runoff are typically enriched in ^{15}N (Larson et al. 2013a). Considering the southeastern position of SB-2 and SB-14 and the general counter-clockwise flow of the Saginaw River plume (Stow and Höök 2013), observed spatial patterns of age-0 yellow perch $\delta^{15}N$ values are consistent with this pattern.

Morphological variation of fish, and in particular congeneric Eurasian perch, between benthic and pelagic habitats is well documented (e.g., Hjelm and Johansson, 2003; Svanbäck and Eklöv, 2003, 2002). Yellow perch with benthivorous diets (i.e., SB-10) were deeper-bodied, which is consistent for fish foraging on the bottom. In contrast, yellow perch with 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.

A potential driver of annual differences in prey densities and diet variation is annual discharge into Saginaw Bay and water current patterns within the 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 flows counter-clockwise (Stow and Höök 2013). Total phosphorus and chlorophyll *a* are higher in the river plume and have a stronger effect on the southeast side of inner Saginaw Bay, where sites SB-2 and SB-14 are located. In addition, 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). Annual differences in internal and external nutrient loading, as well as allochthonous inputs, could favor the differential production of benthic invertebrates and zooplankters. Though estimated total phosphorus loading from the Saginaw River decreased from 2009 to 2010, total phosphorus concentrations in the inner bay remained relatively stable (Stow and Höök 2013). Chlorophyll *a* concentrations, however, slightly increased between 2009 and 2010. Furthermore, primary production may have been influenced by variable water clarity, and thus light penetration, caused by variable discharge or resuspended sediments (Hawley et al. 2014; Turschak et al. 2018).

Stable isotope values have been used to distinguish between allochthonous and autochthonous inputs (Kling et al. 1992; France and Peters 1997). For example, Lehmann et al. (2004) observed seasonal and annual variation in isotopic composition in Lake Lugano, a large eutrophic lake on the border of Switzerland and Italy. Increased primary productivity and phytoplankton biomass in summer was associated with enriched $\delta^{13}C$ values of surface water particulate organic carbon and dissolved inorganic carbon; carbon isotope values subsequently decreased in winter with lower primary productivity. In contrast, $\delta^{15}N$ values of particulate organic nitrogen increased in the winter, indicating increased contribution of refractory or allochthonous input (Lehmann et al. 2004b).

In this study, yellow perch soft tissue $\delta^{13}C$ values enriched approximately 2‰ from 2009 to 2010. Unlike the clear seasonal patterns of $\delta^{13}C$ values (e.g., Lehmann et al., 2004b), annual patterns are not necessarily as straightforward. Available prey densities in Saginaw Bay shifted from more zooplankters in 2009 to more benthic invertebrates in 2010 (Roswell et al. 2013), and diets consisting of a greater proportion of benthic invertebrates typically have relatively enriched $\delta^{13}C$ values (Post 2002). However, this shift was not strongly reflected in stomach content of young yellow perch (Roswell et al. 2013). $\delta^{13}C$ 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). Greater chlorophyll *a* concentrations in 2010 (Stow and Höök 2013) could be related to increased autochthonous production, which typically results in enriched $\delta^{13}C$ values (Post 2002). In short, while the increased availability of benthic prey may be a proximate driver of 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.

Overall, age-0 yellow perch foraging patterns displayed consistent spatial intrapopulation variation. General agreement of long-term foraging indicators (i.e., stable isotopes and morphology) with stomach content analysis supports the position that local conditions strongly influence prey consumption of young yellow perch (Roswell et al. 2013). Despite enriched soft tissue $\delta^{13}C$ values in 2010, spatial patterns for isotopic values and morphology remained consistent and provided further evidence of local habitat influence. 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 production pathways, suggesting that annual variation in dominant production pathways may alter the yield of yellow perch at each location.

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Table 3.1 Yellow perch collection overview with site, year, month, and day-of-year (DOY). Abundances (*n*) for stable isotope (SI) and morphological (Morpho) analyses.

Site	Year	Month	DOY	SI (*n*)	Morpho (*n*)
SB-2	2009	August	216, 217, 222	7	9
		September	244, 245	14	24
	2010	August	222, 223	8	19
		September	266	6	29
SB-10	2009	August	216, 217, 222	4	4
		September	244, 245	5	6
	2010	August	222, 223	6	10
		September	266	9	10
SB-14	2009	August	216, 217, 222	9	12
		September	244, 245	6	7
	2010	August	222, 223	6	9
		September	266	0	0

Table 3.2 ANCOVA results for 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. Significant results ($p<0.05$) in bold.

			Site	Year	Month	Length	Site:Month	Year:Month	Year:Length
a)	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	
	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)	C	F	4.98		31.78	0.94			
		p	**0.012**	--	**<0.001**	0.339	--	--	--
		df	2, 40		1, 40	1, 40			
	N	F	11.80		8.31	0.36			
		p	**<0.001**	--	**0.006**	0.552	--	--	--
		df	2, 40		1, 40	1, 40			
c)	C	F	2.12	183.49		6.478			
		p	0.136	**<0.001**	--	**0.016**	--	--	--
		df	2, 35	1, 35		1, 35			
	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

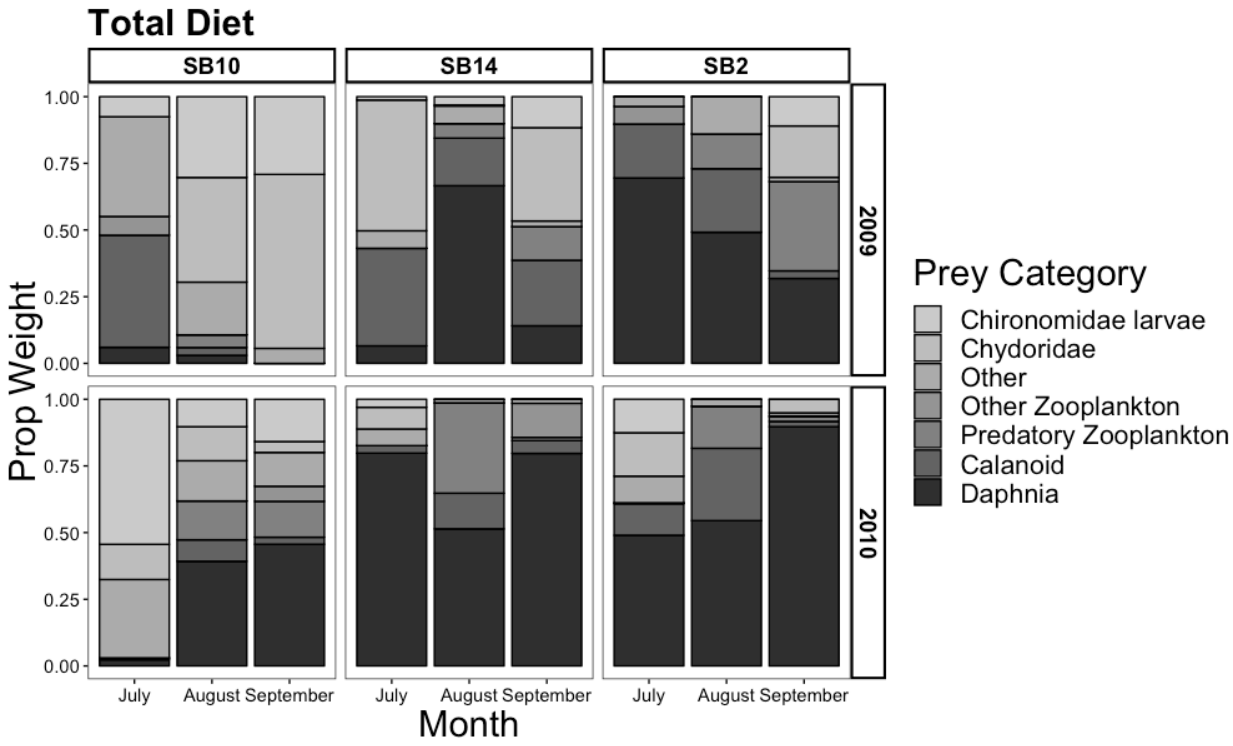


Figure 3.1. Yellow perch stomach contents displayed by site, year, and month. Prey categories include: calanoid, chironomidae larvae, chydoridae, *Daphnia*, other, other zooplankton, and predatory zooplankton. Data adapted from (Roswell et al. 2013).

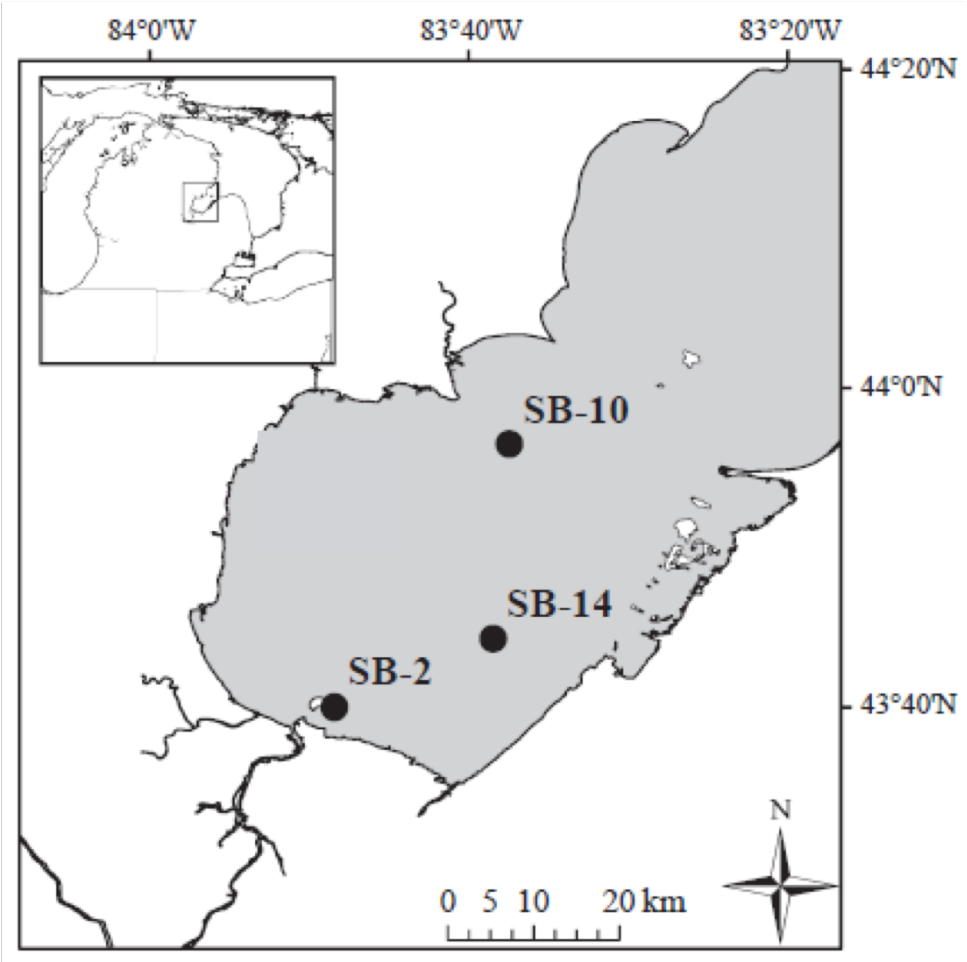


Figure 3.2. Sampling sites in Saginaw Bay, Lake Huron. Figure adapted from (Roswell et al. 2013).

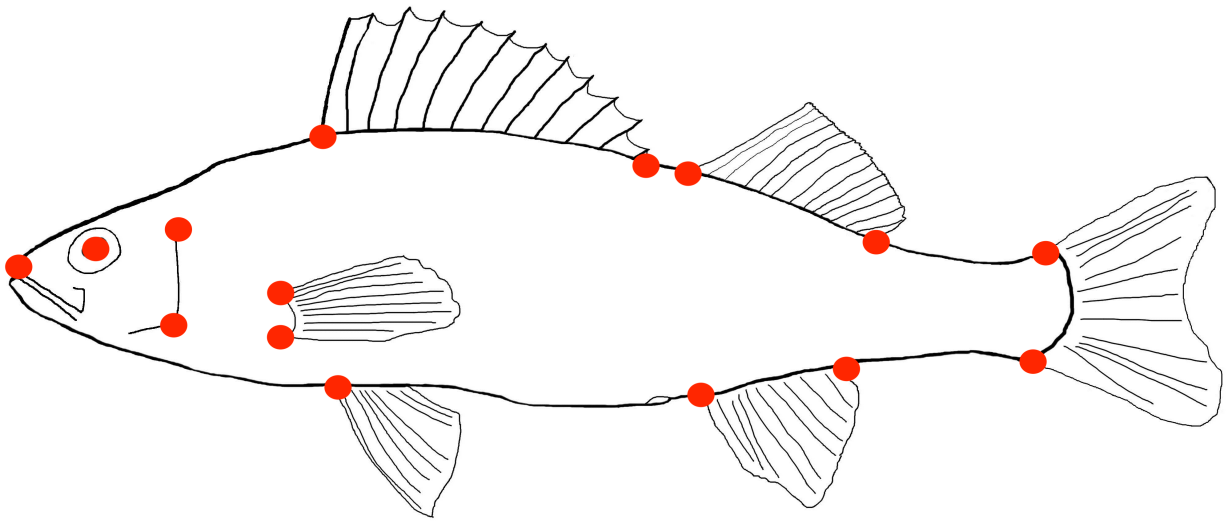


Figure 3.3. Landmark locations on image of yellow perch for geometric morphometrics. Image credit: Tim Malinich.

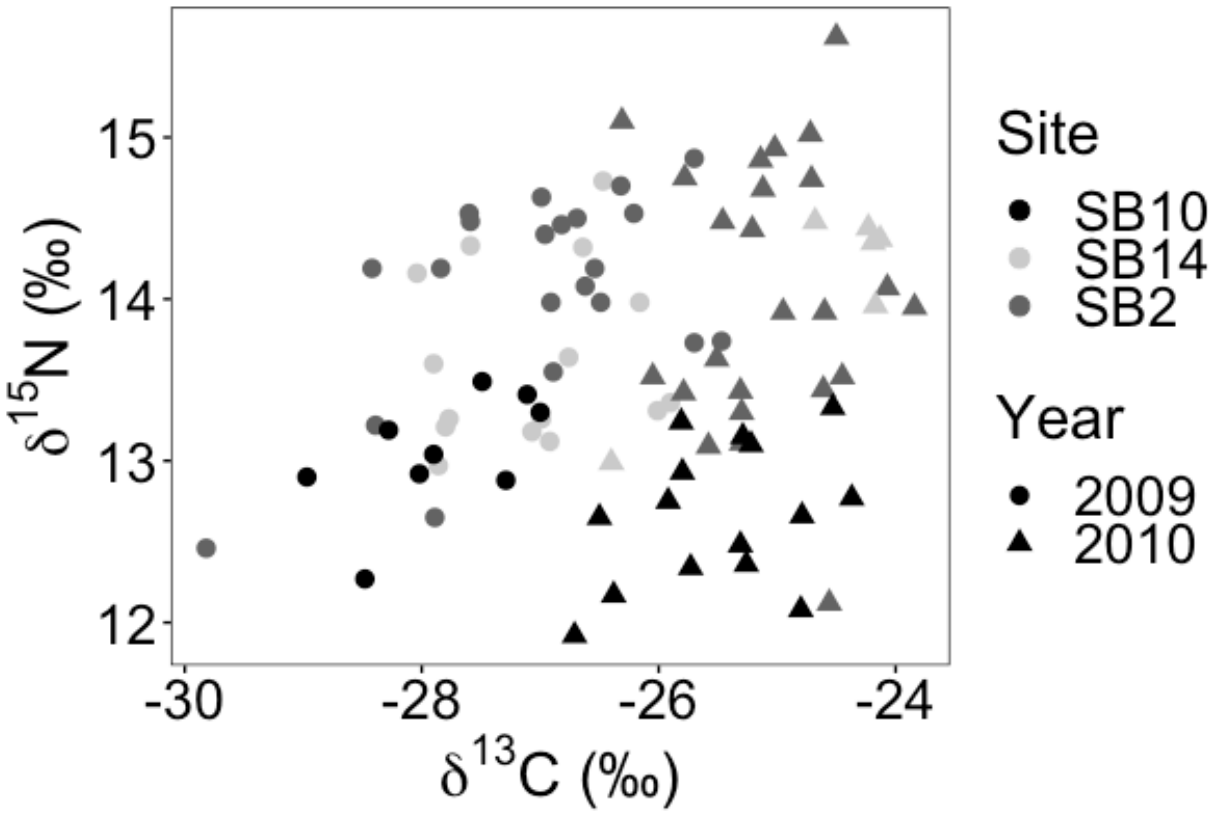


Figure 3.4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of yellow perch soft tissues. Site denoted by color and year denoted by symbol.

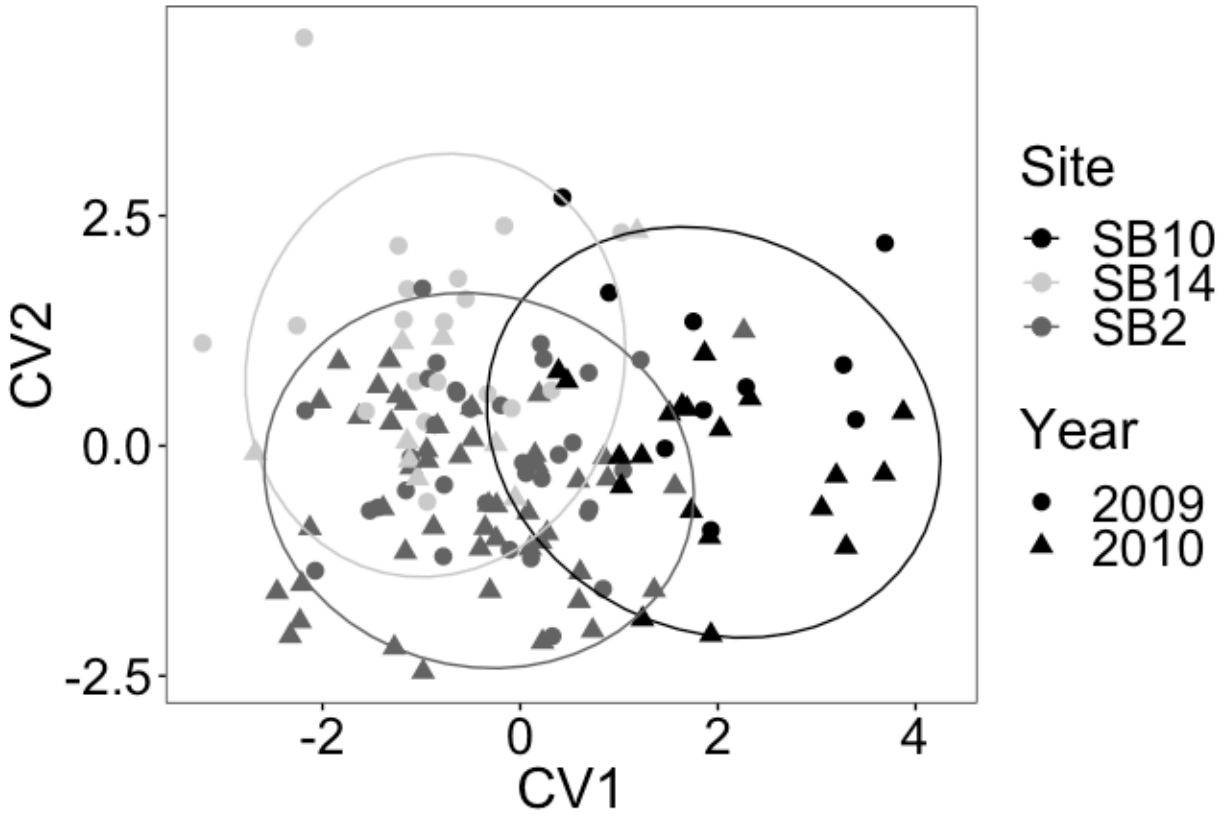
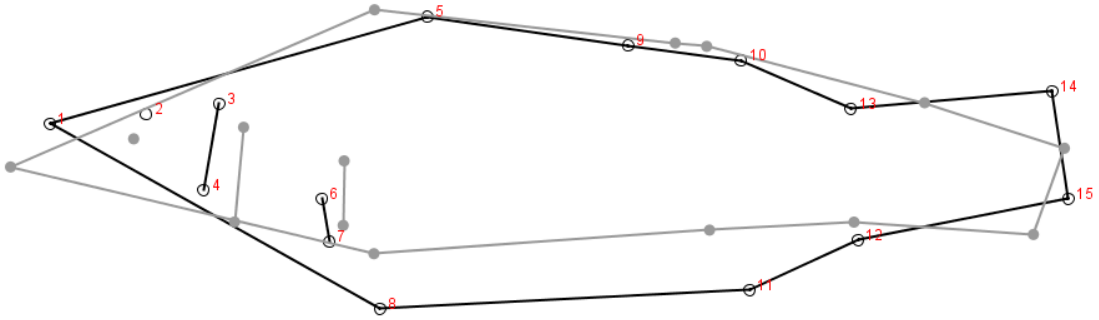
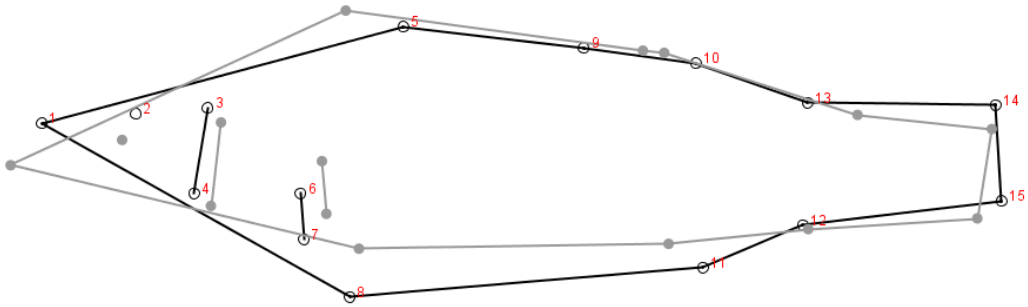


Figure 3.5. Canonical variate analysis (CVA) results demonstrate morphological variation among sites. Site denoted by color and year denoted by symbol. CV1 and CV2 represent 78.64% and 21.36% of variation, respectively.

(a) SB-10 (black) vs SB-14 (gray)



(b) SB-10 (black) vs SB-2 (gray)



(c) SB-14 (black) vs SB-2 (gray)

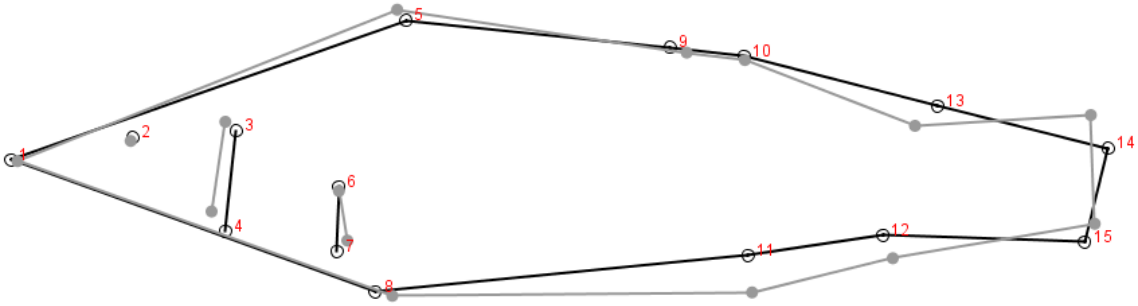


Figure 3.6. Wireframe plots from discriminant function analysis (DFA) displaying shape differences in average shape between site pairs. Sites denoted by color.

APPENDIX

Appendix Table 1. ANCOVA results from testing month significance on carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values. Significant results ($p<0.05$) in bold.

Site	Year			Month	Length	Month:length
SB-2	2009	C	F	**21.41**	1.58	0.00
			p	**<0.001**	0.225	0.989
			df	**1,17**	1,17	1,17
		N	F	**4.31**	0.43	1.70
			p	**0.053**	0.522	0.210
			df	**1,17**	1,17	1,17
	2010	C	F	**9.79**	0.00	0.143
			p	**0.005**	0.959	0.709
			df	**1,20**	1,20	1,20
		N	F	0.33	3.31	0.46
			p	0.572	0.084	0.505
			df	1,20	1,20	1,20
SB-10	2009	C	F	**13.60**	0.59	1.65
			p	**0.014**	0.478	0.256
			df	**1,5**	1,5	1,5
		N	F	2.23	1.37	0.25
			p	0.196	0.295	0.636
			df	1,5	1,5	1,5
	2010	C	F	2.72	1.44	0.161
			p	0.127	0.255	0.696
			df	1,11	1,11	1,11

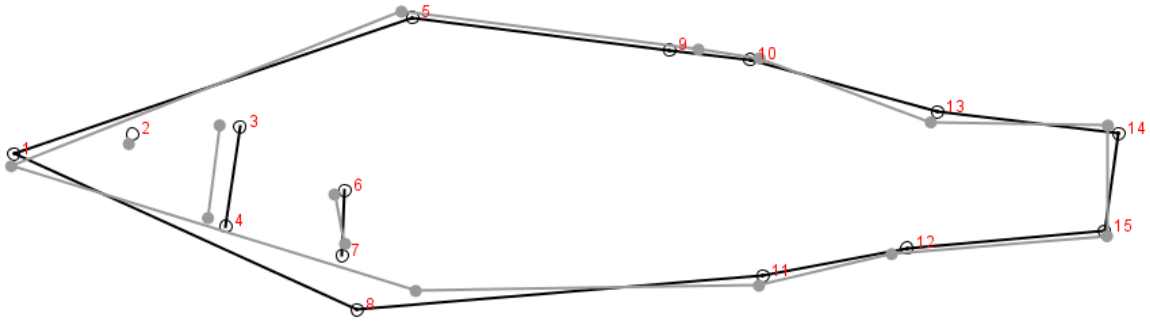
Appendix Table 1 continued

			F	0.02	0.31	1.79
		N	p	0.902	0.591	0.208
			df	1,11	1,11	1,11
SB-14	2009	C	F	4.03	0.66	0.21
			p	0.070	0.434	0.660
			df	1,11	1,11	1,11
		N	F	2.48	2.52	1.02
			p	0.143	0.141	0.334
			df	1,11	1,11	1,11

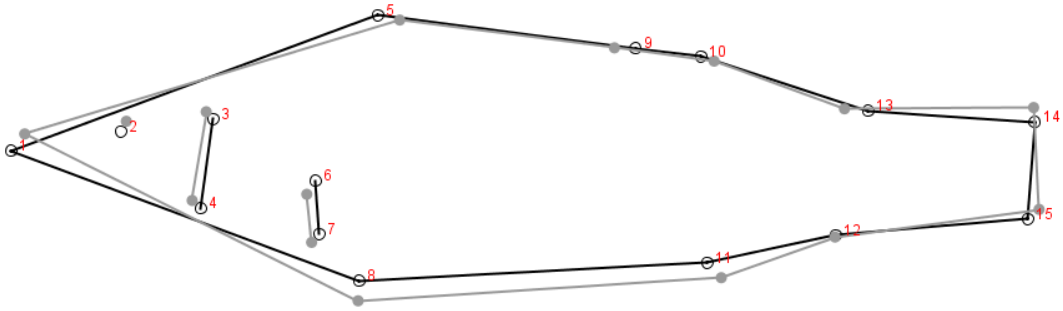
Appendix Table 2. perMANOVA results for morphometric analyses. Results from three separate analyses: a) excluding SB-14, b) excluding 2010, and c) excluding September. Significant results ($p<0.05$) in bold.

		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	--

(a) 2009 (black) vs 2010 (gray)



(b) August (black) vs September (gray)



Appendix Figure 1. Wireframe plots from discriminant function analysis (DFA) displaying shape differences in average shape between (a) years and (b) months. Year and month denoted by color.