ANALYZING LIFE HISTORY CHARACTERISTICS OF LAKE ERIE FISHES: MIGRATION AND PHILOPATRY

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ABSTRACT

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Migration and philopatry are important components of the life history strategies of many fish species. Migration trajectories and the extent of philopatry of native fish species in western Lake Erie were explored using naturally occurring trace elemental markers in fish earbones (otoliths). Some naturally occurring trace elements such as strontium and barium are incorporated in otoliths such that otolith chemistry reflects water chemistry. Therefore, fish movements between water masses with different chemistries can be inferred by changes in trace element otolith chemistry. To investigate the potential for using otolith chemistry to identify fish migrations in western Lake Erie, a controlled field enclosure experiment was conducted to identify site-specific otolith chemistry signatures. Juvenile yellow perch *(Perca flavescens)* were placed in field enclosures at multiple locations in the western basin of Lake Erie. Following the experimental trial, site-specific otolith chemistry signatures were assessed using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS). Results of this study indicate that the site-specific otolith chemistry signature from enclosures located in the Sandusky Bay and likely the Maumee Bay were unique from all other enclosure sites. Furthermore, site-specific otolith chemistry signatures from the offshore regions of western Lake Erie did not differ. A synoptic survey of trace elemental water chemistry supported the trends observed in otolith chemistry.

The unique site-specific otolith chemistry signature of Sandusky Bay provided a unique opportunity to assess the extent of philopatry of white bass *(Morone chrysops)*. This native fish species undergoes spawning migrations into the Sandusky Bay and River from mixed offshore populations in western Lake Erie. Therefore, if spawning white bass collected in the Sandusky River are philopatric, then otolith chemistry will reflect the characteristic Sandusky River otolith signature. Results of this study suggest that 73% of the white bass population was philopatric to the Sandusky River spawning site, suggesting that the overall population may exist as multiple spawning subpopulations linked by non-philopatric individuals. This is the first observation of philopatry in a naturally reproducing, iteroparous fish species in the Great Lakes.

Dedicated to my patient and understanding wife.

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INTRODUCTION

Migration, or the periodic movement of individuals in a population between separated habitats, is fundamentally linked to the evolution of life history strategies and serves to genetically link subpopulations (Northcote 1978, Dodson 1997). The distance moved by an organism is used to distinguish between migrations and other types of movement patterns such that migration are large compared to an individual's home range (Dingle and Drake 2007). Often, understanding migration and its role in species persistence is explored using a cost-benefit framework to estimate the trade-offs to an individual undergoing a migration under the assumption that the benefits of migrating must, on average, exceed the costs to be favored by natural selection (Northcote 1978, Wootton 1990, Dodson 1997, Brönmark et al. 2008). In fish, quantification of migrations across different spatio-temporal scales and environments (e.g., marine, freshwater, estuarine) have led to numerous hypotheses on the relationships between migration and life history (Lucas and Baras 2001, Wells et al. 2003, Roberts et al. 2008, Rooker et al. 2008). Generally, migrations occur in response to environmental tolerances (e.g., water temperature), predator avoidance, intra- or inter- specific competition, and obtaining prey or reproductive resources (Wootton 1990, Dodson 1997). However, in many cases, knowledge of migration trajectories are coarse and inferred from observations of fish aggregations at specific time periods, such as during spawning events or at seasonal refugia.

Philopatry is a specific type of migration in which an individual returns to their natal site for reproduction (Pearce 2007). In fish, high mortality of early life stage individuals is common and philopatric behavior may improve survival by returning to known and "proven" spawning habitats (Wootton 1990, Pearce 2007). This behavior is well studied in the anadromous Pacific salmonids, and in these species, homing rates to the natal site often exceed 95% for reproductive

adults (Quinn and Fresh 1984). Depending on the extent of philopatry in a population, this behavior can facilitate linkages between subpopulations that result in the formation of metapopulation complexes, or facilitate the formation of genetically distinct subpopulations in systems lacking geographical barriers (Thorrold et al. 2001, Webster et al. 2002).

In Lake Erie, the white bass *(Morone chrysops)* is a naturally reproducing, native fish species with a life history strategy that includes high fecundity, broadcast spawning, and no parental care (Kohler et al. 1994, Smith et al. 1996, Salek et al. 2001). Fertilized eggs adhere to substrate until hatching when larval fish are dispersed from the natal location via water currents (Guy et al. 2002). This species is extensively exploited, and harvest data suggest that it undergoes seasonal spawning migrations to tributaries and nearshore reef-complexes in western Lake Erie from large offshore populations in Lake Erie (Ohio Division of Wildlife 2008). However, the relationship between life history and the potamodromous migrations of white bass is not well known. Furthermore, although the basic ecology of white bass has been investigated in Lake Erie, relatively little is known about the role of migration in structuring the population, habitat selection, or abiotic/biotic resource acquisition (Hartman 1998, Madenjian et al. 2000)

This dissertation deals with investigating migration and philopatry of white bass in the western basin of Lake Erie. Specifically, I have 1) used a field-enclosure approach to evaluate the potential for otolith chemistry to track seasonal migration of white bass in western Lake Erie and 2) determined the degree of white bass philopatry to an important spawning site in western Lake Erie.

Note: Each chapter has been written in publication format with tables and figures indexed by chapter (rather than numbered continuously throughout the dissertation). As such,

each chapter can stand alone, however this has resulted in overlap of some information, especially for site and methodological descriptions.

SUMMARY OF RESULTS

Testing the utility of otolith chemistry signatures for assessing migration patterns and habitat use by fishes in western Lake Erie.

The use of naturally occurring otolith chemical tags as a tool for inferring fish migrations, movement, and population dynamics has recently gained popularity in the scientific community (e.g., Campana et al. 2007). This technique is based on the principal that naturally occurring trace elements in water are represented in the chemistry of the otolith. Therefore, by analyzing otoliths, changes in trace metal chemistry can be used to resolve fish migrations, provided migrations are between water masses with different trace metal chemistries. In western Lake Erie, there are three main tributaries that supply water to the system and, through mixing of water masses, can potentially influence otolith chemistry. Given the difficulty in determining if changes in otolith chemistry are the result of fish migrations or water mass mixing in wild-caught fish, an experimental field-enclosure approach was used to determine site-specific otolith chemistry in juvenile yellow perch *(Perca flavescens)* (juvenile white bass were unavailable) at eight locations in western Lake Erie in June, 2005. Site-specific otolith chemistry was unique at the enclosure location near the mouth of the Sandusky River and likely unique at the enclosure located near the mouth of the Maumee River. Site-specific otolith chemistry quantified at all other enclosure locations located in the offshore regions of western Lake Erie did not differ. Given the relationship between water and otolith chemistry, a synoptic sampling survey of water chemistry was conducted on multiple dates during summer, 2006. Results of this sampling effort confirmed the patterns observed in otolith chemistry in the enclosure experiment and suggested

that the largest tributary (Detroit River) strongly dominated water and otolith chemistry in the offshore regions of western Lake Erie. Furthermore, results of this study suggested that trace elemental otolith chemistry will not be useful for resolving fish migrations occurring in the offshore regions of western Lake Erie; however, spawning migrations to the Sandusky and likely the Maumee River tributaries (e.g., white bass, walleye (*Sander vitreus)*) result in a distinct otolith chemistry natural tag that may be used to identify natal origins or inhabitation of these tributaries.

Philopatry by white bass (*Morone chrysops*): evidence of metapopulation structure in Lake Erie using otolith chemistry

Using the distinct otolith chemistry signature of the Sandusky River, the extent of philopatry by white bass to the Sandusky River system in Lake Erie was determined. In the summer of 2003, YOY white bass were collected from the three major spawning regions in western Lake Erie, including the Sandusky and Maumee bays and offshore Lake Erie. From these collections, baseline otolith chemistry signatures at the spawning locations were quantified. In the spring of 2006 and 2007, spawning age-3 (2006) and age-4 (2007) (2003 cohort) white bass were collected from the Sandusky River spawning location, and subsequently, core region otolith chemistry was quantified. A statistical linear discriminant function model developed from YOY white bass otolith chemistry was used to identify philopatric spawning adult fish individuals based on the otolith chemistry of adult white bass. Results of this analysis suggest that the majority (73%) of white bass are philopatric and return to their natal site for spawning. Furthermore, the extent of philopatry did not vary significantly by age (i.e., age-3 versus age-4) or fish sex, although a trend towards less philopatry by older fish (age-4) was observed. Given the magnitude of vagrancy by spawning white bass to the Sandusky River and the lack of

physical barriers between spawning locations, it is unlikely that genetically distinct spawning populations have evolved. As well, the overall white bass population likely exists as a metapopulation with vagrant individuals linking subpopulations. To my knowledge, this is the first definitive investigation of philopatry in an iteroparous, naturally reproducing fish species in Lake Erie.

CHAPTER I

Testing the utility of otolith chemistry signatures for assessing migration patterns and habitat use by fishes in western Lake Erie.

ABSTRACT

Migration is an important component in the ecology of many fish species, yet it is poorly understood for many Great Lakes fishes because of the difficulty in tracking fish migrations in large aquatic systems using standard fish marking and tracking techniques. However, the incorporation of naturally occurring waterborne trace elements into fish otoliths may provide a natural tag that resolves fish migrations in the Great Lakes. To evaluate the potential for otolith chemistry tags to resolve fish migrations in Lake Erie, we conducted complementary studies to quantify site-specific otolith chemistry in the western basin of Lake Erie and spatial and temporal variation in water chemistry. Using juvenile yellow perch (~30mm TL) placed in enclosures for a 21-day time period in summer 2005, we quantified site-specific otolith chemistry signatures (Ca, Sr, Ba, Mg, Pb, Mn) at eight locations in western Lake Erie. Additionally, temporal trends in trace element water chemistry (Sr, Ba, Mg, Pb, Ca) were quantified from 23 locations in western Lake Erie on five dates in summer/fall, 2006. Site-specific otolith chemistry signatures for fish enclosed in Sandusky Bay were significantly different from fish at all other enclosure sites, including sites near Maumee Bay, but otolith chemistry at no other locations were different from each other. Water chemistry differed between the Maumee and Sandusky Bays and Lake Erie and was temporally variable, but these differences only occurred near the mouths of the Sandusky and Maumee Rivers where the river water mixed with Lake Erie. Given that the

Sandusky and Maumee Bay regions are important spawning locations, otolith chemistry may be a useful natural tag for understanding migrations of fishes (e.g., walleye and white bass) that use these regions, but the uniformity of water chemistry in the offshore regions in the western basin of Lake Erie make it difficult to track broad scale migrations using elemental chemistry signatures in otoliths.

INTRODUCTION

Understanding migrations and movement patterns of fish can be critical for understanding the ecology, life history strategy, and habitat use of a species. Many fish species undergo extensive migrations that may allow them to avoid predators, reproduce in optimal habitats, or maximize foraging potential (Wootton 1990). As well, the scale of migrations may change as a function of fish age and ontogenetic state. At the population level, migrations may connect subpopulations and are necessary for the development of metapopulation complexes (Webster et al. 2002, Rubenstein and Hobson 2004).

Seasonal migrations are well documented in some fish species, especially the freshwater-marine migrations of anadromous salmon (Dittman and Quinn 1996). However, much less is known about migrations in freshwater systems like the Great Lakes. This lack of information results from the inherent difficulty in tracking fish movements over time and space. A standard technique for investigating fish migrations includes mark/recapture approaches. Studies using these techniques are limited because of the logistical difficulties of tagging sufficient numbers of fish to ensure recapture of tagged individuals, and thus adequately infer migration trajectories (Guy et al. 1996). In addition, it is difficult to mark small fish or early life stage individuals; therefore, information concerning migrations of early life-stage individuals or small species is often unavailable using traditional tagging methods, although technological advances and

miniaturization of tags (i.e., coded wire tags, PIT tags) have enabled researchers to successfully conduct mark/recapture studies on progressively younger juvenile and smaller bodied fish species. Regardless of the technological advances, these techniques are best suited for small, confined populations that require relatively few marked individuals or hatchery-based fisheries in which large numbers of individuals may be easily obtained for marking. Obtaining a sufficient number of individuals for marking in large, naturally reproducing populations is often difficult or impossible.

Another technique for investigating fish migrations in large systems involves natural tags in fish otoliths. Some trace metals found naturally in water (e.g., Sr, Ba, Mg, Mn) are incorporated into otoliths as fish grow to produce a natural, location-specific, time-resolved "elemental tag" (Elsdon and Gillanders 2003, Walther and Thorrold 2006). Because otoliths grow incrementally around a central point (primordium) throughout the life of the fish, if fish move and inhabit locations with different water chemistry, then differences in otolith trace element chemistry signatures may be used to infer movement patterns throughout the life of the fish (Campana and Neilson 1985, Campana and Thorrold 2001, Campana et al. 2007). Otolith chemistry techniques have been used to investigate a wide range of population level processes in marine, estuarine, or anadromous fish species at large spatial scales (Campana et al. 1999, Warner et al. 2005, Elsdon and Gillanders 2006). Owing to the large differences in water chemistry between freshwater and marine systems, otolith chemistry is especially effective for investigating anadromous migrations (Secor 1992). Only recently have these techniques been used to investigate population level processes in freshwater systems that are characterized by subtle differences in water chemistry at biologically relevant spatial scales (Wells et al. 2003).

In the spatially and temporally dynamic western basin of Lake Erie, limited tagging and harvest data suggest that several economically important fish species (e.g., walleye *Sander vitreus*, white bass *Morone chrysops*) undergo spawning migrations of up to several hundred kilometers to nearshore reef complexes and tributaries (Ohio Division of Wildlife 2007). The role of these migrations on species persistence, population, and community interaction are not well understood. As such, understanding the role of migrations in this system is necessary for conserving biodiversity and managing exploitation.

Because fish and water masses move dynamically, we conducted a field experiment in the summer of 2005 to quantify site-specific otolith chemistry signatures in western Lake Erie. Juvenile yellow perch (*Perca flavescens*) were placed in enclosures in western Lake Erie and were allowed to incorporate a site-specific otolith elemental signature. Locations were chosen for their proximity to known important spawning tributaries and reef complexes in western Lake Erie, as well as to span the lake areas with the likely greatest differences in water chemistry (i.e., because of different source waters). Spatial heterogeneity in otolith chemistry signatures at these locations was quantified to develop a database of site-specific otolith chemistry signatures that could then be used to identify locations fish inhabit during migrations. In addition to the experiment, to address the temporal component of water chemistry differences in western Lake Erie, we conducted a synoptic survey of trace elemental water chemistry at multiple sites in western Lake Erie. These data were used to evaluate temporal and spatial variability of water masses in western Lake Erie and the potential influence on otolith chemistry.

MATERIALS AND METHODS

Juvenile yellow perch (~30mmTL) were obtained from the Ohio Division of Wildlife St. Mary Fish Hatchery in June, 2005. Fish were removed from hatchery ponds and transported to

temperature-controlled 530-liter Living Stream (Frigid Units, Inc. ®) tanks at Bowling Green State University. These holding tanks contained the local water which is naturally high in Sr concentration (~3300 $\mu g \cdot L^{-1}$; ~2.5 times higher than the highest concentration found in Lake Erie). As a result, a distinctive Sr peak was incorporated into the otolith providing a means to easily distinguish fish/otolith growth in the lab from growth during the lake enclosure experiment. Fish were maintained in the lab for at least 10 days at 15°C water temperature before being placed into field enclosures. During this holding period, fish were fed a diet of assorted zooplankton collected from a local pond using multiple tows of a plankton net.

Eight experimental sites for enclosures were selected in the western basin of Lake Erie; however two sites near the Detroit River and two sites near the Lake Erie islands were combined to increase within site sample sizes (Figure 1). In both cases, combined sites were separated by less than 10 km. Sites were chosen near the inputs of the three major tributaries (i.e., Detroit River, Sandusky River, Maumee River) in the western basin to obtain source chemical signatures in otoliths, as well as throughout the central region of the western basin. With the exception of the Sandusky and Maumee bay locations, all enclosures were placed in water depths of >6 meters; the Maumee and Sandusky bay enclosures were in water depths of ~1-2 meters. At each site, we placed 10 separate enclosures, each containing two juvenile yellow perch (20 fish per site). Because fish were not fed artificially throughout the experiment, enclosures consisted of plastic ~20-L cylindrical containers covered with ~2-mm nylon mesh to allow prey to enter. These enclosures were constructed entirely of plastic components to eliminate possible metals contamination of fish otoliths. Enclosures were attached to iron anchors using nylon rope and suspended approximately 1-m from the lake bottom (0.5-m in Sandusky Bay) by attaching a buoyant float to the enclosure opposite the anchor. By suspending the enclosure in the water

column, fish were less likely to be impacted by siltation or anoxic conditions in the water column. Prior to deployment of enclosures, 10 fish from the lab population were removed to estimate initial fish length and weight at the beginning of the enclosure trial. This approach was chosen to eliminate the stress associated with measuring each fish in the field. Fish growth data were used to validate that site-specific otolith chemistry signatures were obtained in the enclosures. In addition, water temperature was recorded in the enclosures using automated thermographs set to measure water temperature hourly (Dallas Semiconductor I-Button-model #DS1921).

Because of the spatial distances among sites and weather conditions, fish were placed in enclosures over the 14-day period from June 8-20 2005 and retrieved over the 10-day period from July 1-11, 2005. At the conclusion of the experiment, fish were removed from enclosures, euthanized in the field, and stored on ice for transport to the lab where they were frozen at -10°C until otoliths were removed. Preparation of otoliths for microchemical analysis were adapted from procedures outlined in Secor et al. (1991). Briefly, otoliths were removed, washed to remove organic residue with hydrogen perioxide (3%) and embedded in Petropoxy 154™ (Burnham) epoxy. Once embedded, otoliths were sectioned transversely using a wafering saw with a diamond tipped blade into ~400-µm sections that included the otolith core. Otoliths were wet polished on both sides using 3M® aluminum oxide sandpaper and lapping film (particle size: 20µm, 10µm, 6µm, 2µm) until the core region was atthe otolith surface, as determined using a light microscope, and total otolith section was ~200µm thick. Once the otolith core was exposed, any remaining polishing defects on the otolith surface were removed by final polishing with a power buffing wheel and 0.5-µm aluminum oxide slurry. After all otoliths were polished, multiple otoliths were mounted onto standard petrographic slides using Crystal Bond® heat

activated adhesive (~15-20 otoliths/slide). Completed slides were then placed in acid-washed Petri dishes containing Milli-Q ultrapure water, ultrasonicated for 5 minutes, triple-rinsed with Milli-Q water, and allowed to dry. Otoliths were stored in a covered Petri dish until analysis.

Laser Ablation-Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS) was used to analyze otolith trace elemental concentrations and all analyses were conducted at the Great Lakes Institute for Environmental Research (University of Windsor, ON). The LA-ICPMS system consisted of a Continuum Surelight I Nd:YAG laser (wavelength: 266nm, maximum power = 40 mJ, pulse rate = 20 Hz) linked to a Thermo-Elemental X7 ICPMS operating in peak-jumping mode (isotope dwell time: 10ms, carrier gas: Ar). The laser (~25-µm laser spot size) was used to remove otolith material for analysis along a continuous transect (5.0-5.7 µm/sec travel rate) parallel to the longest growth axis of the otolith at each end of the otolith (1-traverse/otolith end; 2-traverses/otolith).

The LA-ICPMS sampling protocol provided background-subtracted, drift-corrected trace elemental otolith concentrations (Longerich et al. 1996, Hand et al. 2008). Briefly, the analysis protocol consisted of sampling a carrier gas blank for 60 seconds before each analysis. In addition, replicate analyses of a reference standard (National Institute of Standards and Technology 610 glass) were collected before and after each group of ~16-30 otoliths. This protocol enabled otolith elemental concentrations to be estimated and corrected for instrument drift. Additionally, elemental concentrations were calculated for otoliths using ^{44}Ca as an internal standard set equal to the theoretical concentration of calcium in calcium carbonate (400432 $\mu g\ Ca \cdot g^{-1}\ CaCO_3$). Multiple isotopes (n=16) were quantified in this study, but only ^{25}Mg, ^{43}Ca, ^{44}Ca, ^{55}Mn, ^{86}Sr, ^{88}Sr, ^{137}Ba, ^{138}Ba, and ^{208}Pb met the criteria for inclusion in the statistical analyses. For an isotope to be included in the statistical analyses, 100% of the samples

had to be >LOD (LOD = limit of detection) for the isotope (see Hand et al. 2008) and the CV(%) calculated for the NIST standards for all runs had to be less than 3.0% to ensure precise and accurate quantification of otolith trace elemental concentrations. In the case of Sr and Ba, more than one isotope was analyzed; however, only ^{88}Sr and ^{138}Ba were used to estimate elemental concentrations and in statistical analyses. All data processing and calculations of detection limits were completed off-line using a Microsoft Excel spreadsheet macro (Yang 2003) based on algorithms developed by Longerich et al. (1996).

Yellow perch otoliths do not grow evenly around the otolith core and one edge of the otolith has greater accretion than the other edge (as measured from otolith core to otolith edge, parallel to the major growth axis); therefore, only transects encompassing the edge of the otolith with greater accretion were used in all analyses. Site-specific trace elemental concentrations were estimated by calculating mean concentrations for all elements from the final 10 readings at the edge of the otolith. Given the traverse rate of the laser and the time interval necessary to record elemental concentrations for all isotopes quantified (204ms), the laser traversed ~9µm in 10 readings. For a ~25 micron laser beam width, this corresponds to the outer ~34 microns of the otolith material.

All fish were combined upon collection and treated as independent measures. Statistical tests for differences in site-specific otolith chemistry were conducted using elemental concentrations in parts-per-million (μg element $\cdot g^{-1} CaCO_3$). For graphical interpretation of multielemental otolith chemistry, normalized residuals were calculated by subtracting the grand mean (calculated for each quantified element across all sites) from each individual elemental concentration. Residuals were normalized by dividing each residual by the largest absolute value of the residuals such that all residual values were between -1 and 1.

Initial inspection of normal quantile plots suggested data were not normally distributed; therefore, a non-parametric multiresponse permutation procedure (MRPP) using an Euclidean distance function was used for multivariate and univariate analyses (Mielke and Berry 2001a). This procedure does not require data to be normally distributed and compares average within-group (i.e., location) Euclidean distance (observed δ) to the average distance (expected δ) of all other permutations of the dataset (Mielke and Berry 2001b, McCune and Grace 2002). The null hypothesis of no difference among sites was rejected when the probability of obtaining the observed δ was low; that is, within-site distance differences were less than predicted if there were no site differences (based on the frequency distribution of expected δ calculated from the permutations of the original dataset). Because of the large number of permutations possible in the dataset, a Pearson type III distribution was used to approximate the frequency distribution of expected δ (McCune and Grace 2002). Site-specific differences in multivariate otolith chemistry signatures were evaluated using separate MRPP analyses with Hommel's sequential Bonferroni correction to control type I error inflation (overall $\alpha = 0.05$; sequential Bonferroni $\alpha = 0.008$; Hommel 1988). In addition, single variable MRPP analyses were used to evaluate the importance of each element to the overall multivariate site-specific otolith chemistry signature (Slauson 1988). All permutation analyses were conducted using PC-Ord software (McCune and Mefford 2006).

To determine the potential role of spatial and temporal water chemistry variability on otolith chemistry in Lake Erie, surface water samples were collected on five sampling dates in 2006 (16-June, 4-July, 19-July, 18-August, and 26-October) and analyzed for trace elemental concentrations at 23 locations throughout western Lake Erie (one water sample per date and location). Water sample collection sites were chosen in an effort to quantify the spatial and

temporal heterogeneity of the three main tributaries (Detroit River, Sandusky River, and Maumee River) in addition to quantifying the effects of these tributaries on the water chemistry of western Lake Erie. Therefore, water collection sites were located in transects extending away from the mouths of the tributaries in Sandusky Bay, (n=2 sites) Maumee Bay, (n=4 sites) and the mouth of the Detroit River (n=1 site) (Figure 2). Mid-basin water chemistry dynamics were quantified at multiple sites (n=12) and nearshore water chemistry was quantified using a north-south transect of sample locations (n=4 sites) extending from the nearshore region (Figure 2). Given that this nearshore region contains biologically important shallow reef complexes used as spawning locations, the transect was used to quantify the potential for site-specific otolith chemistry signatures along the southern shore of Lake Erie as a result of water masses originating from the Maumee River.

Water samples (80-ml) were collected using disposable syringes and filtered through 0.45-µm Whatman cellulose-acetate disposable syringe filters in the field. Samples were stored on ice in acid-washed 100-ml polyethylene Nalgene bottles for transport. In the laboratory, water samples were acidified to form a 2% acid-water sample solution (v:v) using high-purity analytical grade nitric acid and were then refrigerated (4°C) until analysis (Eaton and Franson 2005). Trace element analyses were conducted at Bowling Green State University using a Thermo Elemental iCap 6500 Inductively Coupled Plasma - Optical Emission Spectrometer (ICP-OES) interfaced with a CETAC autosampler (ASX-520). Five trace elements were analyzed (Ba, Ca, Mn, Mg, Sr) using an externally calibrated instrumental operating protocol with a radial plasma - sample induction configuration (Opfer 2008). Three repeat estimations for each trace element concentration were calculated for each sample and the mean was used for statistical analyses. Instrument drift was monitored by analyzing quality control samples of

known concentrations after every 10 unknown samples. For an analytical run to pass quality control, all QC samples had to be within ± 10% of known values. Mean method detection limits (MDL) for Ba, Ca, Mg, Mn, and Sr were 0.0188 (SE = 0.0047), 0.0993 (SE = 0.0385), 0.8701 (SE = 0.0118), 0.0446 (SE = 0.0166), and 0.0192 (SE = 0.0031) (units: $mg \cdot L^{-1}$), respectively. All QC samples were within ±10% of known values and all unknown samples were above MDL for all trace elements except Mn; as a result, Mn was not included in final analyses.

Nonmetric Multidimensional Scaling (NMDS) techniques were used to explore multivariate relationships in water chemistry from water samples collected in 2006 (i.e., one NMDS analysis- all dates combined). NMDS is an iterative optimization distance-based ordination technique used to extract and display patterns in multidimensional data in fewer dimensions. The procedure minimizes stress (non-fit of model) by iteratively finding the best position of data within the lowest number of dimensions (McCune and Grace 2002). Unlike principal component analysis, NMDS does not assume linear relationships among variables while preserving spatial relationships among samples. All NMDS analyses were conducted using PC-ORD software in "autopilot" mode using Euclidean distances (Kruskal 1964a, b, McCune and Mefford 2006). Prior to NMDS analyses, data were standardized to the same scale to remove the effects of the different absolute ranges and magnitudes of variables on analyses $[(x - \mu)/sd]$ (Dorval et al. 2005). The appropriate number of dimensions to summarize patterns in the data was determined by calculating a series of preliminary solutions (runs) using the water chemistry dataset. A run consisted of randomly assigning starting configurations for each datapoint and calculating stress (model fit) for each of 1-6 dimensions. Given that stress is a measure of monotonicity between the original multivariate space and distance in the proposed ordination space (reduced dimensionality), low stress values suggest the original multivariate

space is well represented by the simplified ordination space. A plot of mean stress versus the number of dimensions suggested that two dimensions sufficiently represented the dataset and the inclusion of additional dimensions resulted only in marginal improvement. Following determination of the optimal number of dimensions, the best solution was calculated by iteratively adjusting data points in two dimensions to minimize stress. The final solution was found when instability (standard deviation in stress over the preceding 10 iterations) was less than 1×10^{-6}. The instability criterion was met in 79 iterations (final instability = 1×10^{-6}; final stress = 3.0095).

RESULTS

Spatial pattern in otolith chemistry

Multivariate otolith chemistry signatures were significantly different among enclosure sites (MRPP, $T=-13.08$, $p<0.0001$, effect size $= 0.44$; Table 1, 2; Figure 1). Low survivorship of fish at the Maumee Bay enclosure location, (Location 1- Figure 1; Table 1) prevented including this site in statistical analyses. The multivariate otolith chemistry signature for Sandusky Bay (Location 3 in Figure 1) was significantly different from all other enclosure locations in the western basin of Lake Erie. Otolith chemistry signatures from enclosure sites characterizing mid-basin western Lake Erie (Locations 4, 5) were not significantly different from sites located near the mouth of the Detroit River (Location 6) or in proximity to Maumee Bay (Location 2; Figure 1). Individually, Mg, Mn, and Sr were significantly different ($\alpha < 0.05$) among enclosure sites; however, the differences in Sr and Mn were the dominant factors in multivariate site-specific otolith chemistry (effect size A = 0.44 and 0.37 for Sr and Mn, respectively; Table 2). Mg was significantly different among enclosure sites; however, the low effect size for this element (A = 0.055) indicates that the magnitude of differences in Mg among

enclosure locations were small (Table 2, Figure 1). Elemental Ba and Pb did not differ among enclosure locations, although Ba differences were marginally significant ($\alpha = 0.056$) (Table 2).

Surface water chemistry, 2006

Overall, the 2-dimensional NMDS ordination plot represents 99% of the variation in surface water chemistry with the first and second dimensions representing 78% and 21% of the variation in the dataset, respectively. Dimension 1 represents Ca, Mg, and Sr and dimension 2 represents Ba. Surface water chemistry of western Lake Erie was spatially and temporally heterogeneous across the 5-sampling time periods in 2006 (Figures 2, 3). The [trace elemental] chemistry of the Sandusky Bay water was characterized by relatively high concentrations of Ca, Mg, and Sr and low concentrations of Ba, whereas the nearshore north-south transect sites, offshore (midbasin sites), and Detroit River site had relatively low concentrations of all elements (Figures 2, 3). Mean concentrations of Sr in the Sandusky Bay water samples were approximately 2 and 10 times greater than samples collected at the mouths of the Maumee and Detroit Rivers, respectively. The Maumee River water had similar concentrations of Ca and Mg when compared to the Sandusky Bay sites, but differed from the Sandusky Bay because of moderate concentrations of Sr and high Ba concentrations (Figures 2, 3). Ba concentrations averaged across all sample dates were highest in the Maumee River mouth and were approximately double the concentrations measured in the Detroit and Sandusky Rivers.

A large scale, basin-wide shift in Ba concentrations was observed in June and July, 2006. A substantial increase in Ba concentrations (~20%) at offshore mid-basin sites, nearshore north-south transect sites, and Maumee River locations was observed on 16-June 2006 (Figures 3A and B). The mechanism behind the increased Ba concentrations recorded on 16-June is unknown;

however, the consistent increase across the western basin of Lake Erie indicates a basin-wide phenomenon.

Spatial relationships of water chemistry among sites within sample collection dates were similar. The surface water chemistry of sites located in the Maumee River mouth and Sandusky Bay grouped together in NMDS plots and were clearly distinguishable from each other and all other nearshore and offshore midbasin sites within each sample date (Figures 2, 3). Trace element water chemistry quantified at the mouth of the Detroit River was similar to the nearshore north-south transect sites and all offshore, midbasin sites (Figures 2, 3). Thus, during this June to October sampling period, the Maumee River water mass was diluted sufficiently by the Detroit River water mass that no measurable influence of Maumee River water chemistry was detectable at the nearshore reef complexes located in this southern region of Lake Erie. Furthermore, fish inhabiting this region would likely not obtain a site-specific otolith chemistry signature that varies from the Detroit River or the offshore regions of Lake Erie during this period. The magnitude of the differences in water chemistry among sites varied temporally, but was less pronounced during the 18-August sample collection date (Figure 2, 3). Given that the Detroit River drains the upper Great Lakes and discharge rates are not strongly influenced by precipitation in the Lake Erie watershed, the trend towards uniform water chemistry in the western basin observed in August is likely the result of low river discharges from the Maumee and Sandusky Rivers.

Water inputs from the Maumee and Sandusky rivers resulted in only minor regions in western Lake Erie with mixed trace elemental chemistry (Figures 2, 3). The locations of these mixing regions varied temporally but were always located within or at the mouth of the bays (Figure 2, 3). These regions were characterized by diluted Maumee and Sandusky River water

chemistry signatures owing to the lower concentrations of Ca, Mg, and Sr in the Detroit River water mass (Figures 2, 3).

DISCUSSION

Fish otoliths grew at all sites and thus generated measurable elemental otolith chemistry signatures, and, at the Sandusky Bay enclosure location in western Lake Erie, the signature was unique. Although otolith chemistry techniques have been used previously to discriminate spawning stocks of fish in Lake Erie, these studies focused on collections of larval and juvenile fish near spawning locations (Hedges 2002, Bartnik et al. 2005, Ludsin et al. 2006). These studies generally corroborate our study and suggest that fish resident in the Sandusky River have distinct otolith chemistry signatures.

Water chemistry in western Lake Erie confirmed the site-specific otolith chemistry from the enclosure experiment. As with otolith chemistry, trace elements in the water chemistry revealed significant spatial heterogeneity, predominately near the Maumee, and Sandusky river mouths. Given the importance of water chemistry on regulating otolith chemistry, determining spatial and temporal variability of water mass trace element chemistry is essential to address fish movements based on changes in otolith chemistry. Observed differences in water chemistry can be explained by the proportion of water contributed by the three major tributaries in western Lake Erie and the composition of the bedrock underlying the tributaries watersheds. The largest tributary, the Detroit River, contributes approximately 80-95% of the water entering Lake Erie, while all other tributaries (including the Maumee and Sandusky Rivers) combined account for less than 18% of the water (Ragotzkie 1974, Croley et al. 1999). Our study confirms that the Detroit River strongly influences the water and otolith chemistry signatures in the western basin of Lake Erie. Furthermore, the bedrock characteristics of the watersheds that feed the Detroit,

Maumee and Sandusky Rivers explain differences in tributary water chemistry. The Detroit River contributes water originating in the upper Great Lakes and includes major areas that are located in the Canadian Shield underlain by Precambrian age granite gneisses and greenstones, whereas the Sandusky and Maumee Rivers watersheds are located in regions dominated by much younger (Silurian to Devonian- age) carbonate bedrock formations (Ragotzkie 1974, Coogan 1996). These bedrock formations have substantive differences in major and trace elemental concentrations and are likely the mechanisms behind the observed differences in trace elemental water chemistry.

Site-specific otolith chemistry signatures differed from the Detroit River only at the Sandusky Bay enclosure site in 2005, despite the strong differences observed in water chemistry in the Maumee River in 2006. The breakdown of the water-otolith chemistry relationship at the Maumee Bay enclosure location (Locations 1 and 2) in 2005 is likely the result of insufficient water discharge from the Maumee River during the enclosure trial to influence the water and otolith chemistry at the enclosure locations. On average, daily water discharge rates recorded by the USGS for the Maumee River (Waterville, OH recording station; http://nwis.waterdata.usgs.gov/nwis) during the enclosure trial were 56% lower than the median historical (1939-2005) discharge rates for the same dates. During periods of low discharge by the Maumee River, it is likely that the Detroit River water overwhelmed and diluted the distinct water chemistry signature near the mouth of the Maumee River such that otolith chemistry from fish in the enclosures located near the mouth of Maumee Bay (Locations 1 and 2, Figure 1) were indistinguishable from individuals located in offshore regions of Lake Erie. Similarly, seasonal patterns in river discharge may influence site-specific otolith chemistry signatures in western Lake Erie. Peak river discharges in the Maumee and Sandusky Rivers typically occur in March

and April and decline rapidly through September (USGS National Water Information System- http://nwis.waterdata.usgs.gov/nwis). Therefore, the potential influence of these tributaries on Lake Erie water chemistry are likely strongest during periods of high discharge (e.g., March/ April). Given that the Detroit River discharge varies little seasonally (U.S. Army Corps of Engineers- http://www.lre.usace.army.mil/greatlakes), fish species that undergo migrations into Maumee or Sandusky bays during periods of high flow may obtain a distinguishable site-specific otolith chemistry mark from inhabiting these systems whereas a similar migration to the same locations during a period with lower discharge (e.g., late summer) may not be distinguished by the otolith chemistry. Furthermore, analysis of water samples collected in 2006 indicates that water chemistry at the mouth of Maumee Bay (i.e., enclosure location 2) is a "mixing region" and often indistinguishable from the offshore regions of Lake Erie, especially during the summer when river input is low. Temporal analysis of western basin Lake Erie indicates that water chemistry varies across relatively short time periods, likely a result of changes in meteorological conditions (i.e., river discharge, wind/wave conditions) influencing water mass movements and mixing. Additionally, the hydraulic residence time of the western basin of Lake Erie is approximately 47 days, suggesting that the influence of the Sandusky and Maumee rivers on the water chemistry of the western basin of Lake Erie may be rapidly diluted and removed from the system (Horne and Goldman 1994). Therefore, in most of western Lake Erie, a fish residing in one location will experience new water masses throughout the growing season, but only in regions closely associated with the Sandusky and Maumee tributaries will water chemistry (and thus otolith chemistry) will be potentially unique. In western Lake Erie, the potential for a "mixed" otolith signature is especially likely in the regions that are often influenced by multiple water masses (mixing regions). Although strong differences between tributary water chemistry

were detected for all sample dates, absolute concentrations of trace elements in the water varied at the seasonal scale (June vs. October). Therefore, frequent validation of otolith chemistry signatures is necessary to identify the site-specific otolith chemistry signature at the time of the study.

Numerous studies have suggested that there is a predictable relationship between water and otolith chemistry (Bath et al. 2000, Milton and Chenery 2001, Wells et al. 2003). Similarly, water Sr and Ba have been identified as the majority source of otolith Sr (>80%) and Ba (>90%) in both marine and freshwater species (Farrell and Campana 1996, Walther and Thorrold 2006). As such, the site-specific differences in otolith chemistry recorded in this study were likely the result of differences in water chemistry. In addition to water chemistry, environmental factors such as water temperature have been identified as potentially regulating otolith chemistry (Bath et al. 2000, Elsdon and Gillanders 2002). In this study, mean water temperatures across all enclosure sites varied relatively little (<5°C) and as such, it is unlikely that temperature differences played a substantive role in the observed patterns in otolith chemistry.

The combination of water mass movements and fish movements can complicate interpretation of fish movements using otolith chemistry. Additionally, teasing apart fish migrations from shifts in water mass recorded in otolith chemistry may be further complicated by the duration of time necessary for otoliths to incorporate a new otolith signature. Recent studies suggest that the residence time necessary for otolith chemistry to completely equilibrate to a new level is on the order of weeks, not days (Elsdon and Gillanders 2005). Therefore, daily variation in water chemistry owing to changes in meteorological conditions may not be distinguishable in otolith chemistry and the otolith chemistry may represent the mean water chemistry conditions.

Otolith chemistry is a valid natural tag for identifying fish movements and residence in the biologically important Sandusky and Maumee Bay/River systems. Several exploited fish species (i.e., walleye, white bass) undertake spawning migrations into the Maumee and Sandusky Bay/River systems, and our results suggest that otolith chemistry may be used to potentially understand the role and importance of these tributary habitats in fish production, spawning success, and survival. Likewise, otolith chemistry may be useful for understanding the dynamics among migratory and resident contingents of some fish in Lake Erie. However, the overwhelming influence of the Detroit River on the water chemistry prevents the fine-scale differences in water chemistry necessary for tracking migrations of fish in the midbasin or nearshore regions of western Lake Erie. Furthermore, this study demonstrates the advantages of using an experimental approach for investigating the water-otolith chemistry relationship in large, heterogeneous systems and as such, the enclosure approach may be easily adapted to other large freshwater systems and fish species characterized by multiple tributary inputs such as in the Colorado River system or the upper Great Lakes.

CHAPTER II

Philopatry by white bass (*Morone chrysops*): evidence of metapopulation structure in Lake Erie using otolith chemistry

ABSTRACT

Although philopatry is well studied in anadromous salmon, few studies have investigated philopatry in large, freshwater systems. In western Lake Erie, white bass *(Morone chrysops)* undergo seasonal spawning migrations from the open-water regions of Lake Erie to nearshore reef complexes and tributaries. We used naturally occurring differences in otolith strontium concentrations among major spawning locations to determine the extent of philopatry to the Sandusky River spawning location. The majority of individuals were philopatric (73%), and there were no statistically significant differences in the extent of philopatry by sex or age of spawning, although a trend for decreasing philopatry with increased age of fish was observed. The three primary spawning locations in Lake Erie are within 80 kilometers of each other and there are no physical barriers among them. Given the proportion of vagrant individuals we found spawning in the Sandusky River, it is unlikely that Lake Erie white bass spawning populations are genetically distinct. Further, the white bass population in Lake Erie appears to be structured as a metapopulation with non-philopatric individuals linking spawning populations.

INTRODUCTION

Philopatry, the return of individuals to natal sites for reproduction, is an important mechanism for regulating population structure, dynamics, and persistence by isolating populations, determining colonization rates, and limiting dispersal (Clobert et al. 2001, Mora and

Sale 2002). The influence of philopatry on population level processes is largely dependent on the extent of philopatry in a population and can range from no between-population interactions (strict philopatry) and to complete population mixing (no philopatry-panmixia). Strict philopatry effectively isolates populations, and, in systems lacking geographical barriers, is necessary for the development of genetically distinct subpopulations. In these systems, management practices are often focused on conserving genetic diversity, such as with salmon of the Pacific Northwest (Hanski and Gaggiotti 2004). However, most systems contain both philopatric and vagrant (non-philopatric) contingents, and thus, populations are structured as metapopulations with multiple subpopulations (stocks) connected by dispersing (vagrant) individuals. Metapopulations often lack genetic structure among subpopulations given that relatively few vagrant individuals are required to eliminate genetic differences (Waples 1998). Therefore, in systems with weak philopatry, management practices to conserve subpopulations for the purpose of putative genetic distinctness may not be necessary; however, population assessment at the subpopulation level (e.g., by spawning location) provides fishery biologists with information on local dynamics and thus the opportunity to manage specific stocks within the fishery.

Most studies of philopatry have focused on the anadromous migrations of salmonid fishes or oceanodromous migrations of marine fish species (Dittman and Quinn 1996, Mora and Sale 2002, Campana et al. 2007). Less is known about potamodromous migrations of fish species in large freshwater systems such as the Great Lakes or the role of these migrations in structuring populations. As in marine systems, implementing standard mark/recapture techniques to estimate migrations and philopatry is difficult, given that these studies require large numbers of individuals to be marked for sufficient recapture success (Guy et al. 1996). Techniques such as wire-coded tags can potentially work well to mark large numbers of stocked fish (e.g.,

salmonids, Adlerstein et al. 2007), but for stocking of small fish (larvae and early juveniles) and for naturally reproducing populations, few techniques are available. In systems like Lake Erie, standard genetic techniques for investigating philopatry are limited due to the lack of geographical barriers necessary to establish genetic differences among subpopulations at the within-lake scale. Thus, for assessing philopatry and mixed stock structure of naturally reproducing potadromous fishes in large systems, new techniques are needed, such as elemental analysis of otoliths.

Some trace metals found naturally in water (e.g., Sr, Ba, Mg, Mn) are incorporated into otoliths to produce a natural, location-specific, time resolved "elemental tag" (Elsdon and Gillanders 2003, Walther and Thorrold 2006). Because otoliths grow incrementally around a central point (primordium) throughout the life of the fish, if fish move and inhabit locations with different water chemistry, differences in otolith trace element chemistry signatures can be used to infer movement patterns throughout the life of the fish (Campana and Neilson 1985, Campana and Thorrold 2001). Similarly, if water chemistry at spawning or nursery areas are different, this information may be incorporated into the core region of otoliths of young fish and provide a natal signature for stock discrimination in adults. Otolith chemistry techniques have been used to investigate a wide range of population level processes in marine, estuarine, and anadromous fishes at large spatial scales. Owing to the large differences in water chemistry between freshwater and marine systems, otolith chemistry is especially effective for investigating anadromous migrations. However, fewer studies have utilized otolith chemistry techniques to investigate population level processes in freshwater systems that are often characterized by subtle differences in water chemistry (but see Wells et al. 2003, Crook and Gillanders 2006, Elsdon and Gillanders 2006).

We employed naturally occurring elemental tags in the otolith to investigate philopatry and dispersal in the Lake Erie white bass *(Morone chrysops)* population. The white bass is an economically important sport and commercial fish that undergoes spring spawning migration from offshore regions to nearshore reef complexes and tributaries in western Lake Erie (Goodyear et al. 1982). In this study, the extent of philopatry of adult white bass to the Sandusky River spawning site was determined using otolith chemistry. The Sandusky River/Bay system is an important spawning site and has distinctly different water chemistry, especially its strontium chemistry, compared to other important spawning sites in western Lake Erie. As such, the Sandusky River system results in a stable and unique otolith chemical signature for fish inhabiting this region (Hedges 2002, Getz 2003, Bartnik et al. 2005, Ludsin et al. 2006), and afforded a unique opportunity to definitively investigate philopatry in a large population of naturally reproducing fish in the Great Lakes. In addition to investigating philopatry, we also evaluated if philopatry is a function of fish age or sex, with the expectation that first-spawning white bass (generally age-3) would exhibit greater philopatry than older fish as has been found for salmonids (Quinn and Fresh 1984, Unwin and Quinn 1993).

METHODS

To evaluate philopatry, location-specific otolith chemistry signatures were determined for the major spawning regions in western Lake Erie using young-of-year (YOY) white bass. YOY white bass were collected from the Sandusky and Maumee bays as well as the central region of western Lake Erie in 2003 (Figure 1). The natal origin of spawning age-3 (2006) and age-4 (2007) adult fish collected from the Sandusky River was determined using the location-specific otolith chemistry signatures developed from YOY fish. This use of YOY and adult fish from

only the 2003 year-class eliminated potential classification errors to natal origin resulting from potential annual variation in otolith chemistry signatures.

YOY white bass were collected in the open lake as part of the standard Ohio Department of Natural Resources' YOY survey using bottom otter trawls (Ohio Division of Wildlife 2004), while bay sites were sampled with similar gear as part of another study on white bass (Bales 2005). At all sites, collected YOY fish were immediately placed on ice for transport to the lab where they were frozen until otoliths were removed. YOY fish were collected at several locations within the Sandusky and Maumee Bays and the open water region of Lake Erie (Figure 1).

Spawning adult white bass were collected at night in the Sandusky River (Fremont, Ohio) in April-May 2006 (age-3) and 2007 (age-4) (Table 1, Figure 1). All spawning fish were collected using a boat-mounted electrofishing system, employing standard operating procedures (Reynolds 1996). Following collection, fish were placed on ice, transported to the lab where they were frozen until otoliths were removed. Fish sex was determined by examining gonads at the time of otolith removal.

Procedures for preparation of otoliths for microchemical analysis were adapted from Secor (1991). In both adult and juvenile fish, otoliths were removed and placed in dilute hydrogen peroxide (3% V: V) to remove any adhering organic residue. Once clean, otoliths were embedded in Petropoxy 154 (Burnham) and subsequently sectioned in the transverse plane using a low speed diamond tipped wafer saw (South Bay Technology Inc., model 650)(~450µm thick otolith sections). Otoliths were wet polished on both sides using 3M silicon carbide sandpaper and 3M lapping film (particle size: 20µm, 10µm, 6µm, 2µm) to a thickness of ~200µm, such that the otolith core was exposed as determined by a light microscope. Final

preparation of the otolith included using a polishing wheel and 0.5-µm aluminum oxide slurry to remove surface imperfections and improve optical clarity. Once all otoliths were polished, they were mounted on standard petroscopic microscope slides (~16 otoliths per slide) using Crystalbond™ #509 adhesive. Prior to analysis, otoliths were decontaminated by triple-rinsing each slide with Milli-Q™ (Millipore) ultrapure water followed by sonicating for 5 minutes in Milli-Q™ water. This cleaning and decontamination sequence was conducted twice. Slides were then covered and allowed to air dry overnight. Once dry, slides were stored in clean Petri dishes until analysis. Fish age at capture was determined by enumerating annual growth increments on otoliths prepared for trace element analysis.

Laser ablation-inductively coupled plasma mass spectrometry (LA-ICPMS) was used to analyze otolith trace elemental concentrations and all analyses were conducted at the Great Lakes Institute for Environmental Research (University of Windsor, ON). The LA-ICPMS equipment used to analyze otoliths from the YOY fish and age-3 adult fish consisted of a Continuum Surelight I Nd:YAG laser operating at 266nm wavelength (Laser flashlamp power: 1.16 kV, pulse rate: 20 Hz, pulse width: 4-6 ns, ~25 µm laser crater size) linked to a Thermo-Elemental X7 quadrupole ICPMS operating in low resolution, peak-jumping mode (isotope dwell time: 10ms, carrier gas: Ar). Laser ablation occurred within a sample chamber located on a computer controlled stage (X-Y-Z direction) of an Olympus BX-51 light microscope. [See Crowe et al. (2003) for an in-depth discussion of sampling system]. A similar LA-ICPMS instrument configuration was used to analyze the age-4 adult fish; however, because of system upgrades, the laser source consisted of a Quantronix Integra C femtosecond laser operating at a 100Hz pulse rate producing 0.05-mjoules/pulse at the sample, with a resulting laser crater size of ~25-µm. All otoliths were analyzed for multiple isotopes including ^{25}Mg, ^{43}Ca, ^{44}Ca, ^{55}Mn, ^{66}Zn,

^{86}Sr, ^{88}Sr, ^{120}Sn,^{137}Ba, ^{138}Ba, and ^{208}Pb, using continuous linear ablation transects (traverse rate: ~5µm·sec^{-1}). However, initial inspection of otolith chemistry data indicated that Sr concentrations effectively discriminated the Sandusky River/Bay from the Maumee and offshore Lake Erie spawning locations and the inclusion of additional trace elements in the analyses did not improve discrimination of fish collected from the Maumee River/Bay system from offshore Lake Erie. Therefore, only the ^{88}Sr isotope was used to estimate otolith Sr concentrations and subsequently used in analysis of white bass philopatry. Furthermore, all otoliths analyzed in this project had Sr concentrations well above the mean instrument detection limit (0.148 µg Sr · g^{-1} otolith; standard error = 0.0155 µg Sr · g^{-1} otolith).

The LA-ICPMS sampling protocol consisted of collecting background counts for 60 seconds prior to analysis of otolith or reference material. Replicate analyses of a certified standard reference glass (National Institute of Standards and Technology 610) were conducted before and after each group of ~16 otoliths and were used to determine otolith elemental concentrations and correct for instrument drift. To correct for variation in the mass of material sampled among analyses, calcium was used as an internal standard and was set equal to the theoretical concentration of calcium in calcium carbonate (400432 µg Ca · g^{-1} $CaCO_3$). All data processing and calculations of detection limits were completed off-line using a Microsoft Excel spreadsheet macro (Yang 2003) based on algorithms developed by Longerich et al. (1996).

Given that white bass typically spawn during May and dispersal is primarily through advection at the larval or early juvenile life stages, fish collected in Sandusky Bay and Lake Erie in July, 2003 were assumed to have originated in the same locale as collected. YOY white bass were collected in September, 2003 in Maumee Bay as larger individuals, and were not assumed to have originated at the same location as collection (Table 1). As a result, different methods

were used to establish YOY otolith elemental signatures for fish collected in Sandusky Bay and Lake Erie versus Maumee Bay. Ablation transects of otoliths from YOY white bass collected in July, 2003 (Lake Erie and Sandusky Bay) and spawning adults consisted of a 200-µm transect, parallel to the longest otolith growth axis, beginning within ~25-µm of the otolith core, extending through the otolith core region towards the outside edge of the otolith. The core region was distinguished by increased Mn concentrations and confirmed by visual inspection of the transect trajectory using a transmitted light microscope (Brophy et al. 2004, Ruttenberg et al. 2005). In all fish collected in July, 2003, otolith chemistry did not vary between the otolith core region and otolith edge. Analysis of YOY white bass otoliths collected in September, 2003 consisted of a 50-µm transect along the longest growth axis, located at the otolith edge. Given the sequential growth of otoliths, this region consisted of new otolith material and, as such, is considered to represent the signature of the collection site (i.e., Maumee Bay). Furthermore, initial comparisons of elemental Sr concentrations from the otolith edge and core regions of these fish suggested that these fish may have underwent migrations because the otolith core (natal signature) did not match the collection location. The edge otolith chemistry signature from fish collected in September 2003 was assessed by comparing the edge otolith signatures with core-region chemistry from YOY white bass collected in June 2005 from the Maumee River mouth.

The extent of white bass philopatry to the Sandusky River spawning location was analyzed using a combination of univariate statistical methods. Single-factor analysis of variance (ANOVA) was combined with Tukey post-hoc comparisons to evaluate differences in mean Sr concentrations among YOY white bass collection locations. To ensure statistical tests were unbiased, graphical residual analyses were used to evaluate the distribution and variance of the data, as well as identify potential statistical outliers (i.e., when the standardized residual =

[residual ⁄ √ MSE] was >|3|; Dean and Voss 1999). Initial analysis of ANOVA model residuals of YOY otolith chemistry signatures indicated variances were unequal across sites and positively correlated with mean otolith chemistry; therefore otolith Sr concentrations were $\log_{10}$ transformed and all statistical tests were conducted using transformed data (Dean and Voss 1999). Transformed data met assumptions of normality (assessed using a normal probability plot), and equal variances (Dean and Voss 1999).

A linear discriminant function analysis using YOY white bass otolith Sr concentrations was used to determine if otolith chemistry differed sufficiently among spawning locations to classify individuals to their collection site. Classification accuracy was assessed by using the developed model to reclassify the individuals of known natal origin (YOY white bass) using a jackknife procedure, assuming equal prior probabilities for all groups (SAS Institute Inc. 2007). Cohen's kappa statistic was used to evaluate the chance-corrected percentage of agreement between actual and predicted group classification using the results from the jackknife procedure. This statistic ranges between 0% and 100% with 0 indicating the DFA model results in no improvement over chance and 100% indicating perfect agreement between actual and predicted group membership (Titus et al. 1984, White and Ruttenberg 2006). The discriminant function model was then used to classify spawning adult white bass to probable natal site based on otolith Sr concentrations. Following classification of adult individuals to natal site, the relationship between fish age and sex on homing propensity (philopatric or vagrant) was analyzed using a contingency table analysis. The log-likelihood G-test statistic was used to test for mutual independence among all variables (Zar 1999).

RESULTS

Otolith Sr concentrations varied significantly among collection sites for YOY white bass ($F=249.5$, d.f.=2,48, $P < 0.0001$) with Tukey post-hoc tests indicating statistical differences ($P<0.05$) for all pairwise comparisons (Maumee Bay- 2003, Maumee River- 2005, Sandusky Bay, Lake Erie, Figure 2). Otolith Sr concentrations were significantly higher in YOY white bass collected in Sandusky Bay compared to all other sites and years (Table 1; Figure 2). A small, yet statistically significant ($\alpha = 0.05$) difference in otolith Sr concentration was found when comparing individuals collected from Maumee Bay in 2003 and the Maumee River in 2005, and was primarily driven by 4 individuals with low otolith Sr concentrations collected in 2003 (Figure 2). Although these results may represent interannual shifts in otolith elemental concentrations (Campana et al. 1999, Ludsin et al. 2006) the four individuals driving the relationship may have been recent immigrants from another Lake Erie location, such that their otoliths did not represent otolith chemistry at the collection location. Although this specific result points to the importance of obtaining reliable reference samples, the goal of this project was to evaluate philopatry of white bass to the Sandusky River spawning region and these data suggest the Sandusky River Sr signature is unique.

Results of the discriminant function analysis using YOY white bass otolith Sr suggests otolith chemistry can be used to distinguish individuals originating from the Sandusky Bay. Although all squared Mahalanobis distances were significantly different from zero ($P<0.05$) for all pairwise comparisons (LDFA; Lake Erie-Maumee Bay, $p=0.0084$; Lake Erie-Sandusky Bay, $p<0.0001$; Maumee Bay-Sandusky Bay, $p<0.0001$), jackknifed reclassification accuracy of YOY white bass to their collection location was lower for the Lake Erie and Maumee Bay sites (78%

and 67%, respectively) but high (100%) for individuals collected from the Sandusky Bay site. Cohen's kappa statistic was 76%, with 95% confidence intervals ranging from 61% to 91%. Overall, the statistical model discriminates significantly better than expected by chance alone. Although there was some misclassification between the Maumee Bay and Lake Erie sites, the goal of the study was to estimate philopatry of adult white bass to the Sandusky River spawning site. Thus, individuals classified as originating from the Maumee Bay or Lake Erie sites were not distinguished and all were classified as vagrant individuals originating from an unknown location outside of Sandusky Bay. Cross-validated reclassification accuracy of YOY white bass to the Sandusky Bay site did not change when suspected Maumee Bay immigrants were removed from the analysis (i.e., 2003 Maumee Bay, n=4 lowest Sr concentrations, see Figure 2), and thus these fish were included in the discriminant function model. Fish collected from the Maumee River in 2005 were not included in the model. Linear discriminant function analysis derives the probability that each case is a member of each potential classification group (i.e., posterior probability) based on the measured dependent variables. The posterior probability of group membership for the Sandusky Bay YOY white bass was greater than 0.9 for all individuals. In sum, the discriminant function model developed using YOY white bass accurately identifies individuals originating from Sandusky Bay using otolith Sr concentrations.

Adult individuals classified by the discriminant function model as originating from the Sandusky River had high Sr concentrations compared to individuals classified as vagrants (Figure 2). Specifically, philopatric age-3 and age-4 individuals had mean Sr concentrations of 3580 µg Sr · g^{-1} otolith (1 SE = 104) and 3494 µg Sr · g^{-1} otolith (1 SE = 72), respectively. Estimates of mean otolith Sr concentration for vagrant white bass were 884 µg Sr · g^{-1} otolith (1 SE = 93) for age-3 individuals and 894 µg Sr · g^{-1} otolith (1 SE = 63) for age-4 individuals. The

probability of group membership (posterior probability) for age-3 philopatric individuals was greater than 0.95 for all but two individuals, which had probabilities of 0.70 and 0.81. All age-4 fish classified as originating from the Sandusky River had probabilities of group membership = 1. Given the high posterior probabilities (>0.70) of individuals classified to the Sandusky River spawning site and high reclassification success of juvenile white bass used to parameterize the linear discriminant model, otolith Sr concentrations accurately identifies fish originating from the Sandusky River.

Clearly, white bass are philopatric to the Sandusky River spawning region (Table 3). However, 27% of the age-3 and age-4 white bass spawning in the Sandusky River had Sr otolith core region concentrations that differed from the highly detectable Sr concentrations of the Sandusky Bay (Table 3). Thus, these individuals were spawned elsewhere but subsequently reproduced in the Sandusky River. Results of a contingency analysis to evaluate the relationship between fish age, sex, and homing behavior indicated there was insufficient evidence to conclude homing behavior was sex or age-biased (omnibus loglinear G-test, df=4, G=6.19, p=0.18). That is, rates of philopatry were similar between male and female white bass and individuals collected spawning as age-3 or age-4 (Table 3).

DISCUSSION

Approximately 73% of white bass are philopatric to the Sandusky River spawning site. To our knowledge, no other study has evaluated philopatry or investigated the population genetics of white bass in Lake Erie. In this study, estimates of philopatry in white bass are comparable to estimates of philopatry for other species in other locations. For example, using otolith chemistry, Thorrold et. al. (2001) estimated rates of philopatry to be between 60-81% for weakfish *(Cynoscion regalis)* collected at multiple spawning locations along the east coast of

North America. Estimates of philopatry for anadromous Pacific salmonids *(Oncorhynchus sp.)* to their natal site in coastal tributaries using mark/recapture techniques vary by species, location, and age, but generally range between 80% and 100% (Quinn and Fresh 1984, Quinn et al. 1991, Labelle 1992, Unwin and Quinn 1993). Mounting evidence from multiple techniques suggests philopatry is common, but not strict, in many marine and freshwater fish species (Patterson et al. 2004, Strange and Stepien 2007).

In this study, otolith Sr concentration accurately discriminated YOY white bass originating in the Sandusky River/Bay system. In a recent study designed to evaluate analytical techniques, otolith Sr concentrations from larval walleye collected from Sandusky and Maumee Bays were lower than measured in this study, although in both studies, the highest otolith Sr concentrations were measured in fish collected from Sandusky Bay (Ludsin et al. 2006). Differences in site-specific otolith chemistry among fish species may be the result of different physiological parameters (i.e., different ontogenetic stages- larval vs. juvenile; Bath et al. 2000, Brophy et al. 2004), species differences (Hamer and Jenkins 2007), interannual variability in water chemistry (Campana 1999), or a combination of these factors. Therefore, frequent validation of baseline site-specific otolith chemistry is needed when drawing conclusions from these studies.

The physiological adaptations and mechanisms used for successful natal homing by anadromous salmon to their natal site suggests multiple navigational tools may be used, including an internal magnetic compass while in the pelagic ocean environment and olfactory cues for navigating the riverine system to the natal site (Dittman and Quinn 1996). As well, social transmissions or tradition may influence philopatry (Nevitt and Dittman 1998). However, the mechanisms used by white bass for natal homing are unknown.

In this study, classification errors and the resulting biases in estimates of philopatry could potentially have resulted if adult white bass collected from the Sandusky River originated from an unknown and unsampled spawning region with the same otolith chemistry signatures. However, the high Sr concentrations observed in white bass otoliths from fish collected in the Sandusky River/Bay system is consistent across several fish species, including walleye *(Sander vitreus)* and yellow perch*(Perca flavescens)*, and in all cases, high otolith concentrations of Sr uniquely identify fish inhabiting the Sandusky River/Bay system from all other locations sampled in western and central Lake Erie (Hedges 2002, Getz 2003, Bartnik et al. 2005, Ludsin et al. 2006). Indeed, water chemistry analyses of Sr concentrations (units: µg Sr · L water^{-1}) and Sr/Ca ratios (units: mmole Sr · mole Ca^{-1}) collected on Februrary 7, 2006 from the Sandusky, Maumee, and Detroit Rivers near the mouths (<25 km from mouth) corroborate the unique otolith signature of the Sandusky River. Mean Sr/Ca ratios of replicate water samples and all post-hoc pairwise comparisons were significantly different (1 factor ANOVA, d.f.=2,3, F= 425.30, P<0.0002; Tukey's HSD, α <0.05). In these comparisons, Sr concentrations (µg Sr · L water^{-1}) were 517 (SE = 1.5), 351 (SE = 1.4), and 168 (SE = 8.6), corresponding to Sr/Ca ratios (mmole Sr · mole Ca^{-1}) of 6.06 (SE = 0.003), 3.15 (SE = 0.051), 2.37 (SE = 0.155), for the Sandusky, Maumee, and Detroit Rivers, respectively. Furthermore, water samples collected and quantified for Sr and Sr/Ca ratios in the Maumee and Sandusky Bays near the river mouth (<10 km from river mouth) during the white bass spawning period (water samples collected May 17, 24, and 31 and June12 in 2006) further confirmed the robust differences in water Sr concentrations and Sr/Ca ratios when comparing the Sandusky and Maumee systems. In these Water samples, Sr concentrations in Sandusky Bay ranged between 1111 and 1637 µg Sr · L water^{-1}, (mean across dates: 1366 µg Sr · L water1) while corresponding Sr/Ca ratios ranged

between 8.6 and 11.6 mmole Sr · mole Ca^{-1} (mean across dates: 10.4 mmole Sr · mole Ca^{-1}). In Maumee Bay, Sr concentrations ranged between 359 and 868 µg Sr · L $water^{-1}$, (mean across dates: 553 µg Sr · L $water^{-1}$) corresponding to Sr/Ca ratios ranging between 2.7 and 5.3 mmole Sr · mole Ca^{-1} (mean across dates: 3.55 mmole Sr · mole Ca^{-1}). Although both Sr concentrations and Sr/Ca ratios varied through time in these systems, likely because of meteorological events (i.e., river discharge, wind action), water Sr concentrations or Sr/Ca ratios in the Sandusky Bay never overlapped with Sr concentrations or Sr/Ca ratios in the Maumee Bay. These data support the distinct otolith Sr signature observed in the Sandusky River/Bay system. In addition, major spawning areas for white bass in Lake Erie are well known and consist of the Sandusky River, Maumee River, and reef complexes in western Lake Erie (Goodyear et al. 1982). As a result of the unique otolith tag originating from the Sandusky Bay/River system and the importance of the Sandusky, Maumee, and reef spawning locations, it is unlikely that fish were incorrectly classified as originating from the Sandusky system.

Using LDFA, classification results closely followed the natural break in the otolith Sr concentrations and estimates of the probability of group memberships for philopatric individuals was greater than 0.95 for all fish collected (2006 and 2007), except two spawning fish collected at age-3 with the lowest otolith Sr concentrations (Figure 2). These fish may represent individuals that were spawned near the Sandusky Bay-Lake Erie interface and were receiving a mix of Sandusky River and Lake Erie water during the larval and early juvenile time period. Although anecdotal evidence suggests some white bass spawning does occur at the mouth of the Sandusky Bay (i.e., on breakwalls), the lakebed substrate is characterized by silt, marl, and clay and is not optimal spawning habitat (i.e., cobble and persistent water currents).

Although sex-biased dispersal by non-philopatric, vagrant individuals is common in many animal species, especially birds and mammals, (Greenwood 1980, Ruusila et al. 2001) patterns of fish dispersal (vagrancy) have received less attention and are often contradictory for the same or related species (Hutchings and Gerber 2002, Bekkevold et al. 2004, Fraser et al. 2004). In general, polygamous, promiscuous animals tend to be characterized by male-biased dispersal and various hypotheses have been used to explain patterns of sex-biased dispersal including inbreeding avoidance, competition for mates by related individuals of the same sex (local mate competition), and competition for breeding resources among related individuals (local resource competition) (Hamilton 1967, Clarke 1978, Dobson 1982, Pusey 1987). Although the white bass mating system is an example of a polygamous mating system (Salek et al. 2001), we did not find evidence of sex-biased vagrancy. In a review of 24 published research articles that investigated sex-biased philopatry in various fish mating systems, only 50% of the studies found evidence of sex-biased dispersal (Consuegra and de Leániz 2007). In addition, only two of the 24 studies assessed fish species that reproduce using a polygamous, externally fertilized mating system with broadcast spawning and neither study found evidence for sex-biased dispersal (Consuegra and de Leániz 2007). Although not strong evidence, these studies support the pattern that we found.

In our study, there also was no statistical evidence for age-biased homing behavior; however, there was a trend towards greater vagrancy in age-4 individuals compared to age-3 individuals (Table 3). To our knowledge, no other studies have investigated age-biased homing in an iteroparous fish, such as white bass. However, estimates of age-related homing behavior of semelparous salmonid species suggest straying rates increase for older spawning individuals and may result from older fish “forgetting” the natal environmental cues necessary for successful

homing (Quinn and Fresh 1984, Unwin and Quinn 1993). Similarly, the trend towards greater vagrancy in older white bass straying may be explained by biotic factors such as "forgetting" natal cues used for successful homing or could represent temporal shifts in site-specific abiotic cues used for homing (i.e., variable water chemistry).

In conclusion, this study highlights the potential of otolith chemistry techniques to address population level questions across relatively small spatial scales (10's of kms) in freshwater fisheries, provided that there are sufficient differences in water chemistry. Furthermore, this study suggests that the majority of Lake Erie white bass spawning in the Sandusky River were philopatric, although sufficient vagrancy between spawning populations has likely prevented the formation of genetically distinct subpopulations. Furthermore, it is likely that the overall white bass population in Lake Erie may exist as a metapopulation with vagrant individuals linking spawning populations. Managers may need to adopt metapopulation management practices such as enacting population-specific management strategies to limit exploitation of specific fish populations now that they have the tools to discriminate subpopulations.

With the ability to identify spawning stocks, fishery biologists now have the potential to assess panmixia of these stocks throughout Lake Erie. Given that Lake Erie is managed by five government agencies and the fishery is exploited differently by commercial and sport fishery interests, it would be useful to know where the different spawning stocks migrate and the extent to which they mix. Understanding the degree of philopatry also helps fishery managers to assess changes in fish abundance at spawning sites. For example, vagrancy could lead to the assessment that spawning stocks at a site are not declining or that the rate of decline is not substantive. By tracking origin specific individuals, better and more timely stock assessment can

be conducted. This approach may also be applicable to other important species like walleye *(Sander vitreus)* that use the same spawning regions in Lake Erie.

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TABLES

Chapter I

Table 1. Mean otolith trace elemental concentrations (by site) quantified using LA-ICPMS from yellow perch otoliths reared in enclosures in western Lake Erie in 2005. See Figure 1 for enclosure locations. Values in brackets ([ ]) are mean LOD (limits of detection), for all otoliths analyzed. All elemental concentrations and LOD values are reported in $\mu g_{element} * g^{-1}_{CaCO3}$ (parts-per-million). N = number of fish analyzed. SE = standard error.

Location	N	Mg (SE) [1.9±0.1]	Mn (SE) [0.3±0.02]	Sr (SE) [0.2±0.01]	Ba (SE) [0.05±0.003]	Pb (SE) [0.03±0.003]
1	1	37.64	1.46	1115.74	14.89	1.48
2	15	26.58 (4.65)	1.03 (0.08)	1081.46 (66.29)	9.55 (0.44)	1.16 (0.33)
3	11	52.24 (13.03)	5.68 (0.84)	2204.69 (69.13)	12.13 (1.10)	1.01 (0.28)
4	11	59.29 (11.35)	1.25 (0.23)	1210.92 (39.78)	10.81 (0.83)	0.68 (0.13)
5	16	33.39 (4.85)	1.91 (0.28)	1282.70 (51.05)	12.03 (0.61)	1.53 (0.49)
6	10	36.57 (6.95)	2.43 (0.32)	1275.45 (115.18)	11.45 (0.89)	1.62 (0.48)

Table 2. Results of Multiresponse Permutation Procedure (MRPP) to statistically test for differences in multivariate and univariate (separate analyses) otolith chemistry signatures (units: $\mu g_{element} * g^{-1}_{CaCO3}$) among enclosure sites in western Lake Erie. (see text for test details). Rows denote response variable or variables included in models (all elements = Mg, Mn, Sr, Ba, Pb). Observed δ and expected δ are the mean weighted within-group distances for the original and permutated data, respectively. T = test statistic calculated using a Pearson type III distribution to estimate the distribution of δ (using variance and skewness of permutated data). A = effect size (within-group homogeneity compared to random expectation $[1 - (observed\ \delta / expected\ \delta)]$. Range: $0 \leq A \leq 1$. If A=0, then within-site heterogeneity is equal to the expectation by chance and if A=1, all values are the same within a site but different among sites.

Response variables [element]	observed δ	δ under null hypothesis: expected δ	δ under null hypothesis: variance	δ under null hypothesis: skewness	T	p	A
all elements	280.05	496.95	173.58	-1.13	-16.46	<0.0001	0.44
Mg	27.75	29.36	0.58	-1.11	-2.11	0.038	0.055
Mn	1.28	2.02	0.0028	-1.12	-13.97	<0.0001	0.37
Sr	274.65	493.04	176.75	-1.12	-16.43	<0.0001	0.44
Ba	3.00	3.15	0.0068	-1.08	-1.81	0.056	0.047
Pb	1.28	1.27	0.0009	-1.07	0.42	0.61	0.00

TABLES

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Table 1. Characteristics of juvenile white bass collected from Lake Erie for philopatry study. For all sites, except the fish collected from the Maumee Bay, otolith core region Sr concentrations (±1 SE) were measured using LA-ICPMS traverses of a 200-µm region near the otolith core. Because of their size and multiple potential origins, characteristic otolith Sr concentrations of the Maumee Bay were quantified using a 50- µm traverse at the otolith edge.

Collection site	Date (month/year)	Mean total length mm (SE)	N	Otolith Sr concentration µg $Sr \cdot g^{-1}$ otolith (SE)
Sandusky Bay	7/2003	42.3 (3.8)	21	4002.8 (175.9)
Maumee Bay	9/2003	97.8 (4.7)	12	1005.5 (101.4)
Lake Erie	7/2003	29.5 (0.54)	18	730.7 (23.6)
Maumee River	6/2005	30.5 (0.69)	10	1419.0 (60.2)

Table 2. Jackknifed reclassification of YOY white bass to collection site (known) using otolith Sr concentrations. Read across table. Data presented are the collection location and the number of fish (percent) assigned to a location using the discriminant function developed from otolith Sr concentrations. Misclassified individuals were not assigned to the correct collection site using the discriminant function.

	Classified as:			
Collection site	Lake Erie	Maumee	Sandusky	Misclassified
Lake Erie	14 (77.8)	4 (22.2)	0 (0.0)	4 (22.2)
Maumee Bay	4 (33.3)	8 (66.7)	0 (0.0)	4 (33.3)
Sandusky Bay	0 (0.0)	0 (0.0)	21 (100.0)	0 (0.0)

Table 3. Results of linear discriminant function analysis of white bass from the 2003 year class. Fish were collected while spawning in the Sandusky River in Fremont, Ohio as age-3 and age-4 individuals in 2006 and 2007, respectively. Table denotes the number and (percentage by age and sex) of individuals collected that were classified as originating from the Sandusky River (philopatric) or outside of the Sandusky River (vagrant) using LDFA parameterized from 2003 YOY white bass collected from 3 important spawning locations in the western basin of Lake Erie.

	Philopatric		Vagrant	
Age	Male	Female	Male	Female
3	29 (80.6)	18 (85.7)	7 (19.4)	3 (14.3)
4	33 (62.3)	19 (73.1)	20 (37.7)	7 (26.9)
overall	99 (72.8)		37 (27.2)	

FIGURES

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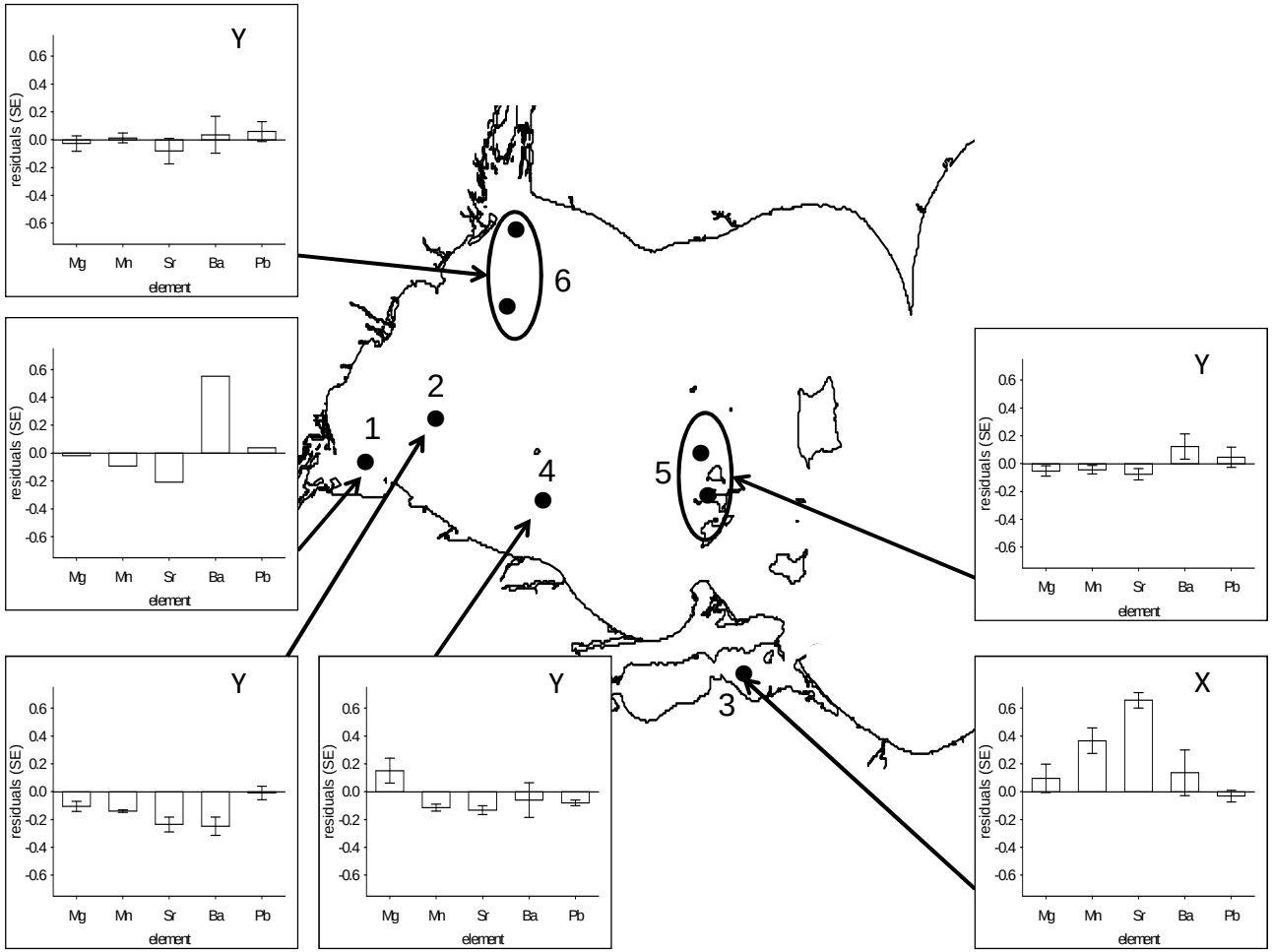

Figure 1. Multivariate site-specific otolith chemistry signatures quantified from six enclosure locations in western Lake Erie. Arrows denote enclosure location in western Lake Erie. Circles denote combined sites for analyses. Graphs represent (values normalized -1 to 1 for display purposes) trace element residuals. Residuals were calculated by subtracting the grand mean (calculated from all enclosures for each element individually) from individual element. Letters in top right corner of graph panes represent multivariate post-hoc multiple comparisons using sequential Bonferroni correction (overall $\alpha = 0.05$). Statistical analyses were conducted on element concentration data.

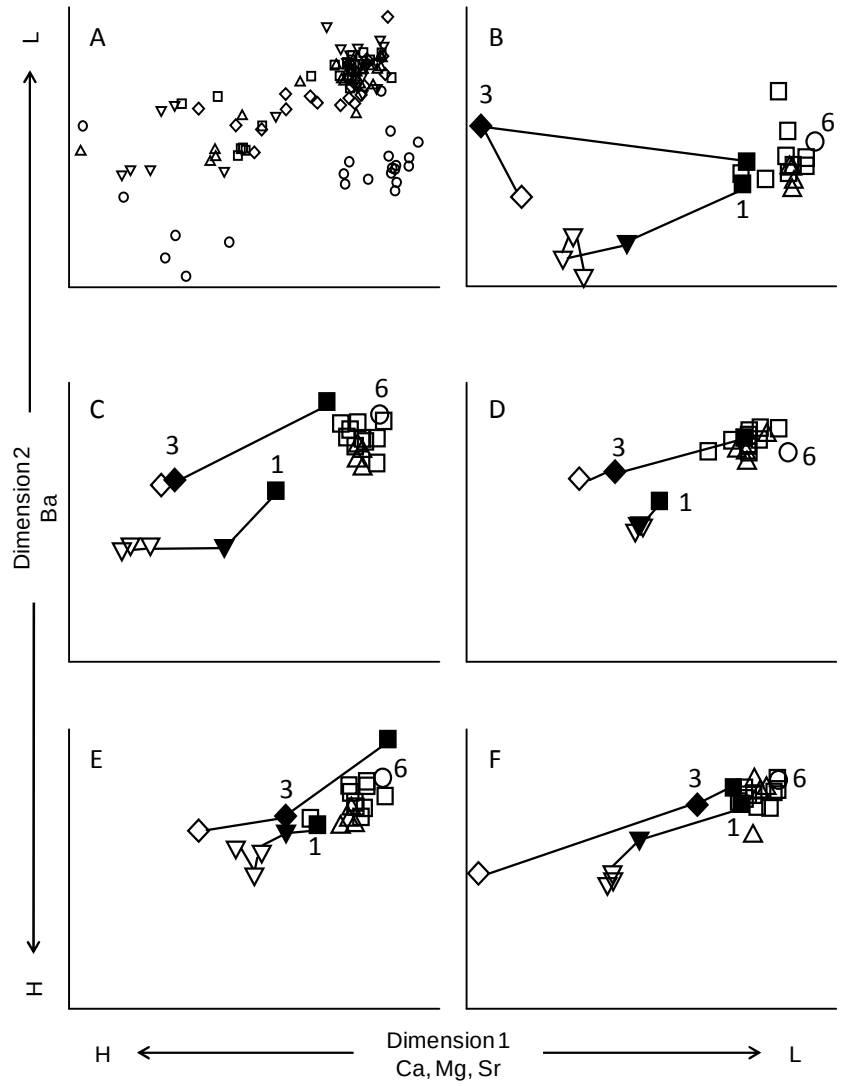

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination graphs of trace elemental water chemistry (Sr, Ba, Mg, Ca) collected from 23 sites in western Lake Erie on 5 dates in 2006. Axis scaling is the same for all graphs. Axis labels denote dominant dependent variables (Ba, Ca, Mg, Sr) represented by ordination axes and the correlation between ordination axes and dependent variables. High (H) and low (L) denote direction of correlations between water chemistry and axes. Lines connect sample transects beginning at sample sites closest to the Sandusky and Maumee River mouths and ending at the Lake Erie-tributary mixing regions. Numbers identify enclosure sites and approximate locations in proximity to Maumee, Sandusky, and Detroit rivers from 2005 cage enclosure experiment. A: NMDS ordination data grouped by sample collection date (○ = 16-June 2006, ▽ = 4-July 2006, □ = 19-July 2006, ◇ = 18-August 2006, △ = 26-October 2006). B - F: NMDS ordination data grouped by site within a sample date (B = 16-June 2006, C = 4-July 2006, D = 19-July 2006, E = 18- August 2006, F = 26-October 2006). See Figure 2 for sample locations. Note: One sample is missing from 16 June 2006, collected at an offshore Lake Erie site

FIGURES

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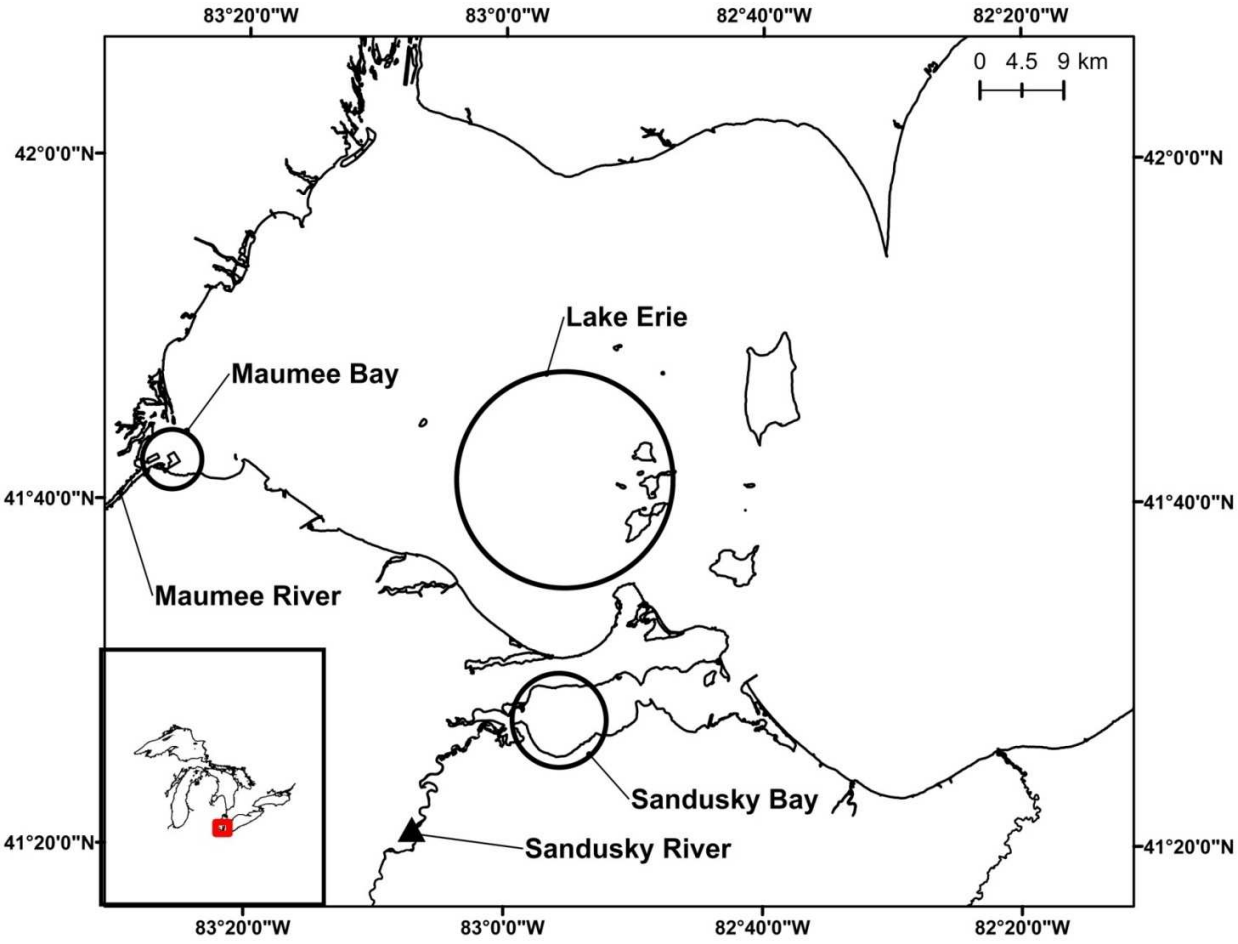

Figure 1. Circles denote juvenile YOY white bass collection locations in 2003. Fish were collected at multiple sites within circles were combined. Juvenile YOY white bass were collected from one location at the mouth of the Maumee River in 2005. Filled triangle denotes collection location of spawning age-3 and age-4 white bass in 2006 and 2007.

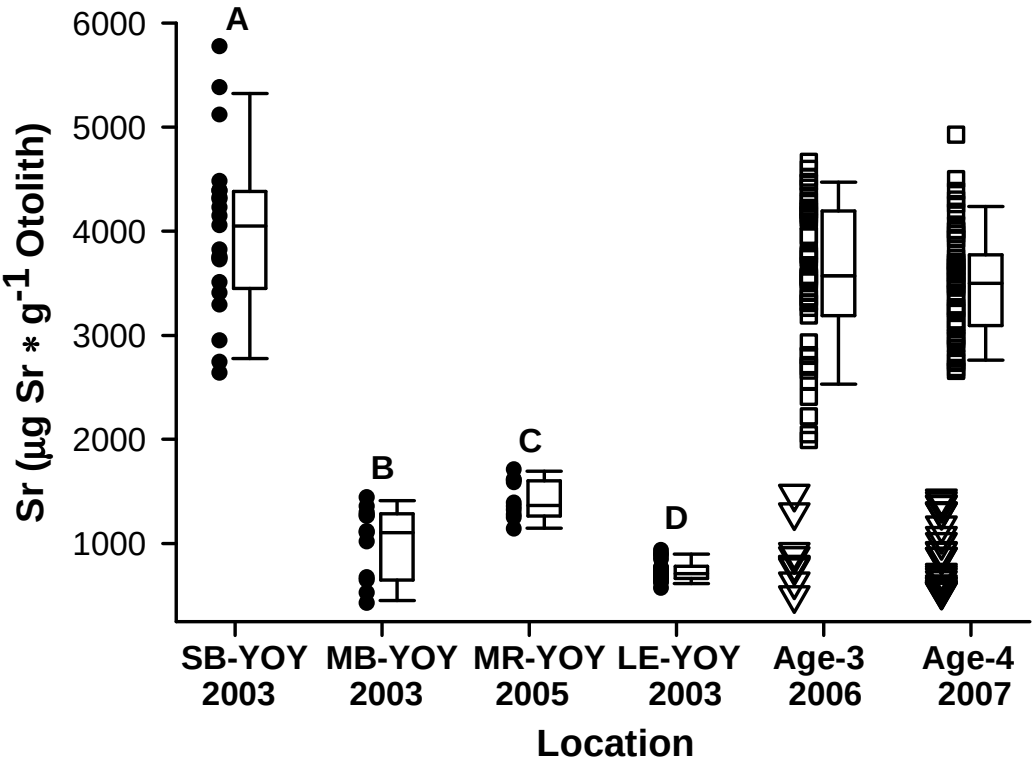

Figure 2. Otolith Sr concentrations (µg Sr · g^{-1} otolith) from YOY white bass collected from three locations in western Lake Erie in 2003 and one location in 2005. SB= Sandusky Bay, MB= Maumee Bay, MR= Maumee River, LE= Lake Erie. Adult fish were collected while spawning from one site in the Sandusky River in 2006 (Age-3) and 2007 (Age-4). Whiskers of box-plots denote 10^{th} and 90^{th} percentiles, boxes denote 75^{th} and 25^{th} percentiles, solid line within box represents the median values. Letters above data denote post-hoc (Tukey's HSD; $\alpha = 0.05$) statistical differences in otolith Sr concentrations for YOY white bass collected in 2003 and 2005 (same letters are not statistically different). Filled circles represent otolith Sr concentrations for individual YOY white bass, open squares represent otolith Sr concentrations for spawning adults classified as philopatric by LDFA, and open triangles denote vagrant individuals as classified using LDF.

APPENDIX

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Appendix

Table A1. Mean (across dates) and standard error for elemental water chemistry concentrations from surface water samples collected on five dates (2006) in western Lake Erie. Latitude and longitude coordinates for collection locations are in decimal degree format. All concentration values are in micrograms element per liter of water (ppb). See Figure 3 for sample locations. SE = standard error. Note: Samples were analyzed for Mn, but concentrations for all samples were below LOD.

site	Latitude	Longitude	Ca	(SE)	Mg	(SE)	Sr	(SE)	Ba	(SE)
1	41.61 N	83.09 W	32012	(565)	9617	(241)	209	(10)	163	(20)
2	41.62 N	83.09 W	31910	(431)	9374	(154)	170	(9)	155	(20)
3	41.64 N	83.09 W	32314	(491)	9200	(202)	149	(8)	155	(17)
4	41.68 N	83.09 W	32084	(1285)	9185	(359)	135	(13)	155	(17)
5	41.77 N	83.09 W	29970	(225)	8742	(208)	117	(8)	149	(17)
6	41.70 N	83.47 W	57054	(2418)	15986	(1100)	569	(60)	174	(20)
7	41.70 N	83.46 W	56946	(2609)	15946	(1218)	570	(66)	171	(11)
8	41.70 N	83.45 W	57442	(3602)	16068	(1283)	582	(74)	171	(15)
9	41.71 N	83.43 W	49518	(2878)	14552	(771)	489	(37)	172	(18)
10	41.74 N	83.38 W	39712	(2435)	11664	(614)	321	(48)	160	(15)
11	41.79 N	83.28 W	34930	(1069)	10352	(522)	207	(29)	149	(19)
12	41.84 N	83.17 W	27544	(568)	7963	(99)	89	(4)	106	(19)
13	42.00 N	83.14 W	26960	(202)	7941	(78)	82	(2)	141	(17)
14	41.62 N	82.86 W	32176	(602)	9062	(114)	142	(7)	145	(17)
15	41.71 N	82.86 W	31628	(504)	8856	(127)	133	(10)	143	(13)
16	41.78 N	82.92 W	29044	(319)	8456	(167)	102	(5)	131	(6)
17	41.49 N	82.82 W	51226	(3466)	15176	(1224)	991	(66)	154	(8)
18	41.62 N	82.72 W	45094	(2760)	13958	(1598)	698	(137)	130	(1)
19	41.50 N	82.66 W	32254	(2229)	9125	(659)	183	(27)	127	(21)
20	41.53 N	82.60 W	32626	(457)	8976	(121)	130	(5)	147	(19)
21	41.45 N	82.62 W	33876	(1236)	9409	(540)	182	(26)	143	(18)
22	41.58 N	82.75 W	33000	(596)	9223	(209)	160	(15)	145	(20)
23	41.67 N	82.75 W	32344	(468)	9005	(141)	152	(12)	142	(21)