Early life history of Lake Michigan alewives (*Alosa pseudoharengus*) inferred from intra-otolith stable isotope ratios

Elise Dufour, William P. Patterson, Tomas O. Höök, and Edward S. Rutherford

Abstract: We apply a robotic micromilling technique to the sampling of young-of-the-year (YOY) and 1+ otoliths from alewives (*Alosa pseudoharengus*) captured in different habitat types of Lake Michigan during 2001–2003. $\delta^{18}O$ values of otolith cores of YOY alewives from Muskegon Lake (a sheltered, drowned river mouth lake connected to Lake Michigan), Muskegon Channel (which connects Muskegon Lake to Lake Michigan), and Lake Michigan proper are compared with $\delta^{18}O$ values of ambient water from different potential early life habitats. Otolith core $\delta^{18}O$ values used in conjunction with $\delta^{13}C$ values serve as good discriminators of nursery areas. The majority of YOY alewives captured in Muskegon Lake emerge and grow in this habitat, whereas the majority of YOY alewives captured in Lake Michigan emerge and grow in Lake Michigan. In addition, early-life movements of alewives between the two lakes are documented but limited. Even if drowned river mouth lakes are more favorable for alewife growth and survival, their contribution to the Lake Michigan population could be limited because all of the 1+ alewives were individuals that spent their early life in Lake Michigan. The application of high-resolution isotope analysis of small otoliths of forage fish for fish population dynamics studies appears promising.

Résumé : Nous avons appliqué un système automatisé de microfraisage à l'échantillonnage d'otolithes de gaspareaux (*Alosa pseudoharengus*) jeunes de l'année et 1+ pêchés dans différents types d'habitats du Lac Michigan durant la période 2001–2003. Nous avons comparé les valeurs de $\delta^{18}O$ des centres des otolithes de jeunes de l'année pêchés dans le lac Muskegon, dans le Muskegon Channel (qui relie le lac Muskegon au lac Michigan) et dans le lac Michigan aux valeurs de $\delta^{18}O$ de l'eau environnementale prélevée dans différentes zones potentielles de grossissement des alevins. Les valeurs de $\delta^{18}O$ des centres des otolithes utilisées conjointement aux valeurs de $\delta^{13}C$ des otolithes permettent de discriminer les lieux de grossissement potentiels. La majorité des jeunes de l'année capturés dans le lac Muskegon est originaire de ce lac et y a grandi, alors que la majorité des jeunes de l'année capturés dans le lac Michigan est originaire de ce dernier. Même si des changements d'habitats des alevins entre le lac Muskegon et le lac Michigan sont détectés, ils demeurent limités. Enfin, les gaspareaux 1+ capturés dans le lac Michigan étaient des individus ayant passé leur première saison de croissance dans ce lac. Bien que les conditions d'habitat apparaissent plus favorables à la croissance et à la survie des gaspareaux dans le lac Muskegon, leur contribution à la population du lac Michigan pourrait donc n'être que limitée. Le microfraisage s'avère adapté à l'étude des otolithes de petite taille, et cette technique apparaît très prometteuse pour documenter la dynamique des populations des espèces fourrage.

Introduction

The alewife (*Alosa pseudoharengus*) population is currently a critical component of Laurentian Great Lakes ecosystems, providing the forage base for a diverse salmonine predator community that supports valuable sport and commercial fishing. Simultaneously, alewives are capable of restructuring zooplankton communities and suppressing native planktivores. Since its invasion during the 1940s the alewife population in Lake Michigan has fluctuated dramatically

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owing to variable recruitment and predation by salmonines (Jude and Tesar 1985; Madenjian et al. 2002, 2005). A better understanding of alewife recruitment processes should aid in the management of the entire ecosystem. During the spring and summer, alewives migrate inshore to spawn in a variety of habitat types (e.g., drowned river mouth lakes, harbors, embayments, tributaries, and nearshore coastal areas of Lake Michigan proper). Because certain sheltered habitat types (e.g., drowned river mouth lakes, harbors, and embayments) are productive and relatively warm, they have been hypothesized to be more favorable for early-life alewife growth compared with exposed shorelines. Therefore, young-of-the-year (YOY) individuals hatched in such habitats may contribute significantly to alewife year classes.

Dramatic improvements have been made in the range of techniques used in the study of spatial behavior of fishes in natural environments, including population genetics, parasite loads, mark–recapture and hydroacoustic studies, and more recently microchemistry of otolith carbonate (Campana 1999; Lucas and Baras 2000). Teleost otoliths are accretionary calcium carbonate structures usually in the form of aragonite laid down on an organic matrix (Carlström 1963; Degens et al. 1969). The use of otolith chemistry as a record of fish life history is based on three key properties. First, otoliths begin to form near the time of hatching and grow throughout the entire life of a fish, displaying a regular series of growth increments (Campana and Nielson 1985). Second, they remain metabolically inert (i.e., aragonite is not reworked once deposited). Third, elements deposited onto the growing otolith reflect the physical, chemical, and biological environments experienced by individual fish (e.g., Campana 1999). $\delta^{18}O$ values of otolith aragonite ($\delta^{18}O_{oto}$) reflect $\delta^{18}O$ values of the ambient water ($\delta^{18}O_w$), as modified by ambient temperature (Kalish 1991; Patterson et al. 1993; Thorrold et al. 1997). In contrast with oxygen, carbon isotopes in otolith aragonite ($\delta^{13}C_{oto}$) are deposited in isotopic disequilibrium with the ambient water (e.g., Iacumin et al. 1992) because 20%–30% of the carbon in otolith is derived from metabolic processes (Tohse and Mugiya 2002; Høie et al. 2003; Wurster and Patterson 2003). However, otoliths can still record geographic differences in $\delta^{13}C$ of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) (Thorrold et al. 1997; Weidman and Millner 2000). Therefore, geographic variation in isotope ratios of the environment can be used as an indicator of home range, natal origin, nursery habitat, and spatial distribution of a fish stock or species (e.g., Northcote et al. 1992; Campana 1999).

We hypothesized that the differences in physical, chemical, and biological conditions in different Lake Michigan habitat types would lead to significant variations in $\delta^{18}O_w$ and $\delta^{13}C_{DIC}$, which should translate into $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ variations in alewife otoliths. Because we want to reconstruct alewife early life, a technique that enables the recovery of $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values at the otolith core is needed. New developments in robotic microsampling and mass spectrometry techniques (Wurster et al. 1999) have been combined with the chronological record of growth increments to provide unprecedented high-resolution environmental and biological records from stable isotope values. Analysis of pen-reared Atlantic cod (*Gadus morhua*) otoliths by Høie et al. (2004*a*) demonstrated that only high-resolution sampling (at an intra-seasonal scale) could accurately extract the true temperature range experienced by fish. This methodology has been successfully applied toward the reconstruction of thermal histories of modern and archaeological fishes (Patterson 1998; Wurster et al. 2005). However, stable isotope profiles of otoliths at an intra-seasonal scale have not been specifically applied toward studies of spatial behavior or to YOY otoliths.

This study represents the first attempt to apply high-resolution sampling of small otoliths from forage fish to the study of early life history. We analyzed cores of YOY alewives captured during the fall of 2002 in Muskegon Lake (a sheltered, drowned river mouth lake connected to Lake Michigan) and compared them with cores of YOY and yearling alewives from other Lake Michigan habitat types captured during 2001–2003. The objectives of this study were to (*i*) evaluate whether $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ of cores can discriminate nursery areas of YOY alewives in Lake Michigan, (*ii*) document the occurrence and frequency of movement between habitats by alewives during their first season of growth, and (*iii*) infer the relative contributions of alewife recruits from the different habitat types.

Material and methods

Water and fish collection

Seventy-three water samples (30–500 mL) were collected and stored in Nalgene™ bottles for $\delta^{18}O_w$ analysis (Table 1). During 2002, geographic and depth variation in $\delta^{18}O_w$ was evaluated by collecting water in Lake Michigan (off Sturgeon Bay and near Muskegon Lake) and in three drowned river mouth lakes adjacent to Lake Michigan (Muskegon Lake, Pigeon Lake, and Manistee Lake) (Fig. 1). To assess both spatial and temporal variability, water samples were also collected in various habitats during 2003 (although no YOY born this year were isotopically analyzed).

From mid-May to November of 2001 and 2002, we compared physical and biological conditions in various drowned river mouth lakes and a nearshore coastal zone of Lake Michigan and simultaneously collected age-0 alewives from these habitats (Fig. 1). We focused our sampling on Muskegon Lake, an inland, drowned river mouth lake located along the east shoreline of Lake Michigan, the adjacent nearshore area of Lake Michigan, and Muskegon Channel (which connects Muskegon Lake to Lake Michigan). YOY alewives were captured in these habitats with bottom and midwater trawls. We also obtained YOY alewives collected by the US Geological Survey Great Lakes Science Center at one location in Lake Michigan (near Sturgeon Bay) using bottom trawls. To infer the nursery areas of these YOY alewives, we analyzed otoliths from specimens collected during September–November 2002. We completed our sampling of the 2002 year class by collecting overwintering yearling alewives in the adjacent nearshore area of Lake Michigan. Fish were captured using bottom trawls during June 2003.

For comparison, we also analyzed alewives belonging to the 2001 year class. We selected YOY that we collected in October in the nearshore area of Lake Michigan adjacent to Lake Muskegon as well as YOY that were collected in October in two locations of Lake Michigan (near Saugatuck and

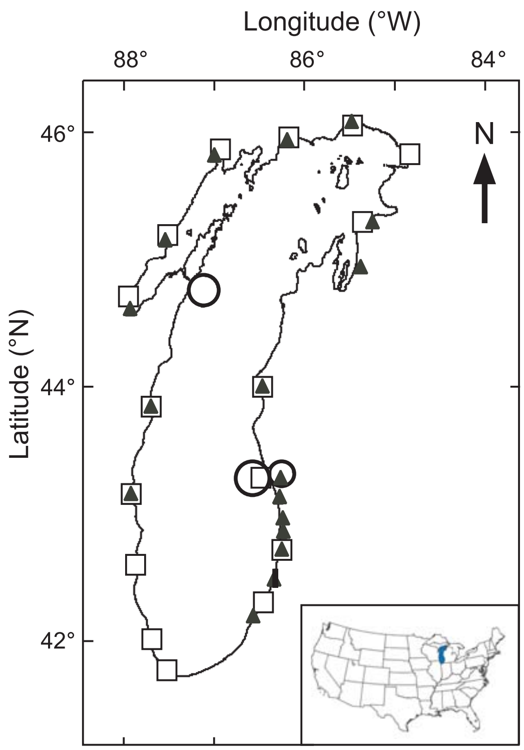
Table 1. $\delta^{18}O_w$ values (Vienna Standard Mean Ocean Water) collected in 2002 and 2003 in Muskegon Lake and other drowned river mouth lakes, as well as tributaries and different sites of Lake Michigan.

		$\delta^{18}O_w$ (‰) (depth (m))	
Site	Date of collection	Value(s)	Mean
Muskegon Lake			–8.6
Downstream area	9 July 2002	–8.9 (1), –8.8 (6)	
	15 July 2002	–8.7 (1), –8.7 (5)	
	27 Aug. 2002	–8.3 (1)	
	10 Sept. 2002	–8.2 (1), –8.2 (10)	
	24 Sept. 2002	–8.6 (1), –8.2 (8)	
	22 Oct. 2002	–8.2 (1)	
	18 Nov. 2002	–8.5 (2)	
	10 Oct. 2003	–8.7 (1)	
Upstream area	23 July 2002	–8.6 (2), –8.7 (5)	
	7 Aug. 2002	–8.6 (1), –8.6 (4)	
Lake Michigan, nearshore area adjacent to Muskegon Lake			–6.0
25–50 m depth contour	24 June 2002	–6.2 (1), –6.2 (15)	
	15 July 2002	–6.1 (1), –5.8 (10)	
	24 July 2002	–5.8 (1), –6.1 (10)	
	7 Aug. 2002	–5.9 (1), –5.9 (10)	
5–25 m depth contour	8 July 2002	–6.0 (1), –6.2 (10)	
	27 Aug. 2002	–5.9 (1), –5.9 (10)	
	9 Sept. 2002	–5.6 (1), –5.8 (17)	
	24 Sept. 2002	–6.1 (1), –6.2 (25)	
	22 Oct. 2002	–6.1 (1), –6.0 (37)	
	18 Nov. 2002	–5.8 (1)	
	10 Oct. 2003	–6.2 (1)	
Lake Michigan			
Sturgeon Bay	Oct. 2002	–6.3 (1)	
Hagar Park	10 Oct. 2003	–6.4 (1)	
Saugatuck (Oval Beach)	10 Oct. 2003	–6.3 (1)	
Ludington	10 Oct. 2003	–6.3 (1)	
Fisherman's Island State Park	2 Nov. 2003	–6.3 (1)	
Buffinton Harbor	11 Nov. 2003	–6.0 (1)	
Chicago	11 Nov. 2003	–5.9 (1)	
Zion	11 Nov. 2003	–6.1 (1)	
Milwaukee (McKinley Park)	11 Nov. 2003	–6.4 (1)	
Sheboygan	11 Nov. 2003	–6.2 (1)	
Green Bay	11 Nov. 2003	–6.5 (1)	
Menominee	11 Nov. 2003	–7.6 (1)	
Bay de Noc (Gladstone)	11 Nov. 2003	–7.3 (1)	
Manistique	11 Nov. 2003	–7.5 (1)	
Nanbinway	11 Nov. 2003	–7.0 (1)	
Point La Barbe	11 Nov. 2003	–6.8 (1)	
Manistee Lake			–10.9
South	9 July 2002	–11.1 (1)	
	23 July 2002	–10.9 (1)	
	13 Aug. 2002	–10.8 (1)	
Pigeon Lake			–7.3
Upper	30 July 2002	–7.3 (1)	
Lower	30 July 2002	–6.2 (1)	
Port Sheldon	10 Oct. 2003	–8.5 (1)	
Others			
Black River (South Haven)	10 Oct. 2003	–7.2 (1)	
Charlevoix Lake (south of Charlevoix)	2 Nov. 2003	–9.1 (1)	
Elk Lake (near Kewadin)	2 Nov. 2003	–9.5 (1)	
Escanaba River (Gladstone)	11 Nov. 2003	–11.0 (1)	
Fox River (Green Bay)	11 Nov. 2003	–6.8 (1)	
Kalamazoo River (Saugatuck)	10 Oct. 2003	–9.0 (1)	

Table 1 (*concluded*).

Site	Date of collection	$\delta^{18}O_w$ (‰) (depth (m))	
		Value(s)	Mean
Lake Macatawa (Holland)	10 Oct. 2003	–6.2 (1)	
Manistique River (Manistique)	11 Nov. 2003	–11.5 (1)	
Menominee River (Marinette)	11 Nov. 2003	–10.6 (1)	
Millecoquins River (US-2)	11 Nov. 2003	–11.5 (1)	
Milwaukee River (Milwaukee)	11 Nov. 2003	–7.8 (1)	
Pere Marquette Lake (Ludington)	10 Oct. 2003	–10.5 (1)	
Sheboygan River (Sheboygan)	11 Nov. 2003	–8.1 (1)	
Spring Lake (Grand Haven)	10 Oct. 2003	–8.7 (1)	
St. Joseph River (St. Joseph)	10 Oct. 2003	–8.0 (1)	

Fig. 1. Map of Lake Michigan with the location of water and alewife (*Alosa pseudoharengus*) YOY and 1+ individuals collection. Squares, water collected from Lake Michigan; triangles, water collected from drowned river mouth lakes or tributaries; circles, alewife collection sites.

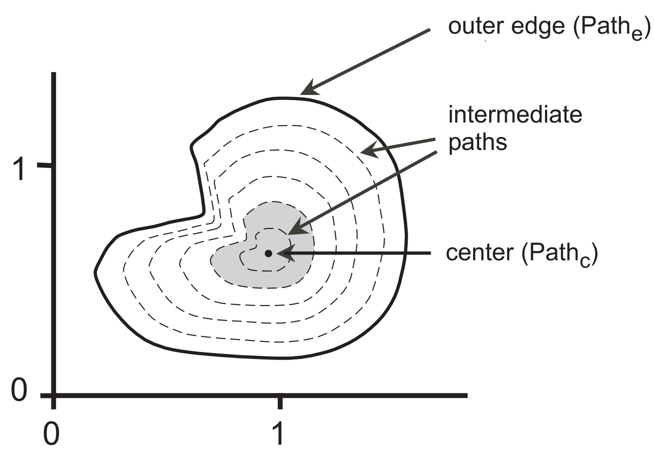


Sturgeon Bay) by the US Geological Survey Great Lakes Science Center (Fig. 1). We also selected yearlings that we collected in the same nearshore area of Lake Michigan and in Muskegon Channel in April and May 2002.

Otolith preparation and micromilling

YOY alewives were stored frozen in the field and transferred to the laboratory. At least three specimens from each location were selected for sagittal otolith removal and were dissected using fine probes. We used the computer-controlled apparatus described by Wurster et al. (1999) for micromilling YOY alewife otoliths. We adapted the sampling procedure to address several technical difficulties, including the small size and fragility of specimens. Originally,

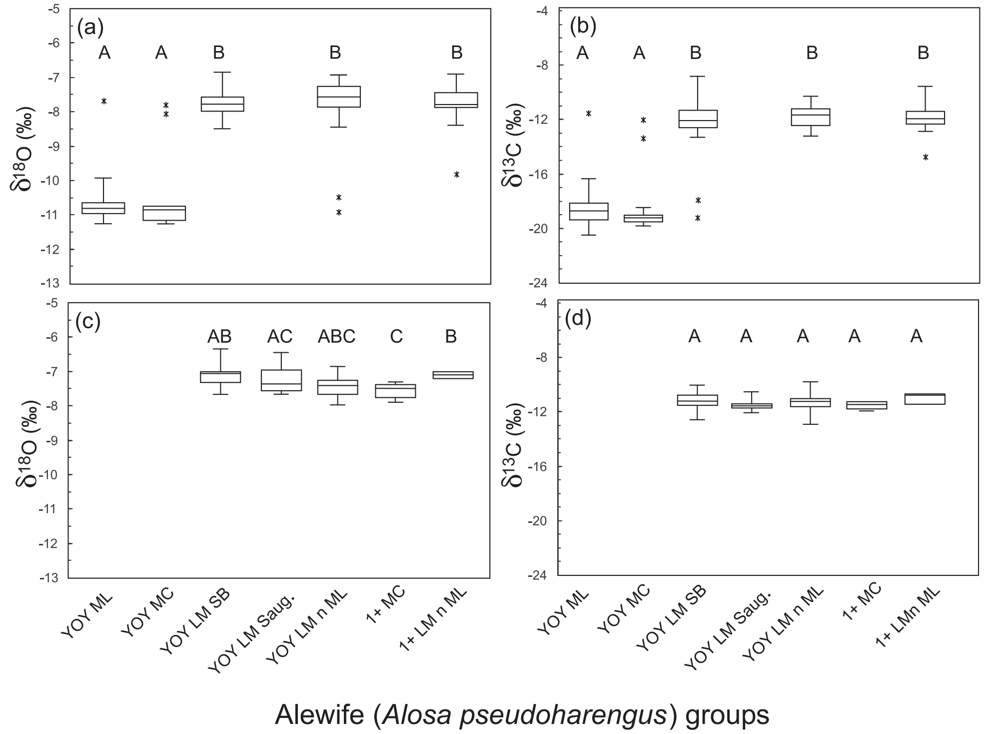
Fig. 2. Microsampling of an alewife (*Alosa pseudoharengus*) otolith using a robotic micromilling apparatus. The center ($Path_c$) and the outer edge ($Path_e$) were digitized as two series of three-dimensional coordinates and interpolated using a cubic spline. Five intermediate sampling paths (IP) (broken lines) were then calculated. The core (shaded) represents the early life of the fish and was obtained by combining the powder collected during the milling of $Path_c$ with that of the two following IPs. The core represents the early life of a fish, whose isotope ratios were used to infer origin and potential habitat switch.



otoliths were directly glued onto glass slides for polishing and micromilling, but a number of them fractured during this process. Therefore, otoliths were subsequently placed in a plastic mold positioned on their inner side and embedded in an epoxy resin (Epofix Struers^{TM}). The resin was allowed to harden overnight at room temperature and then at 50 °C for an additional hour. Individual hardened blocks were removed and carefully polished by hand until growth bands and the nucleus of each otolith were revealed. Resin blocks were then cleaned in deionized water, dried, and glued onto glass slides.

Specimens were attached to a three-dimensional micropositioning stage under a fixed high-precision dental drill. For each specimen, the center ($Path_c$) and the outer edge ($Path_e$) were digitized in real time as two series of three-dimensional coordinates and interpolated using a cubic spline (Fig. 2). Subsequently, from four to nine intermediate sampling paths were calculated between $Path_c$ and $Path_e$. Core samples consisted of a mixture of the powder from

Fig. 3. Comparison of the core isotope ratios (‰; Vienna Pee Dee Belemnite) of alewife (*Alosa pseudoharengus*) groups (YOY and 1+ groups) captured in different habitats of Lake Michigan in (*a* and *b*) 2002 and (*c* and *d*) 2001. The upper and lower parts of the box represent 75% and 25% of the scores, respectively. The horizontal line inside the box represents the median. The end of the whiskers represents the largest and smallest values that are not outliers. Stars represent outliers. Different letters indicate significantly different values (Mann–Whitney, $p < 0.001$). ML, Muskegon Lake; MC, Muskegon Channel; LM SB, Lake Michigan offshore of Sturgeon Bay; LM Saug., Lake Michigan offshore of Saugatuck; LM n ML, Lake Michigan near Muskegon Lake.



$Path_c$ with that of the following two to four intermediate paths (Fig. 2). The theoretical mass of core samples, calculated by estimated powder volume and density, was ~10–25 μg.

Isotope analysis of water and otoliths

$\delta^{18}O_w$ values were determined using a continuous-flow pyrolysis technique. Aliquots of 1 μL of water were injected into a Finnigan MAT ThermoChemical Elemental Analyzer (TC/EA) via a GC PAL® autosampler. The resulting CO was analyzed with a ThermoFinnigan DeltaPlus XL via a ConFloIII interface. Values are reported in standard per mil notation relative to Vienna Standard Mean Ocean Water (VSMOW). Accuracy and precision were checked through the repetitive analysis of internal laboratory standards. Sample precision was determined to be ±0.3‰.

Otolith subsamples were stored in stainless steel cups and roasted in vacuo for 1 h at 200 °C. Stable oxygen and carbon isotope ratios were determined using a Finnigan MAT 252 (Department of Geology, Syracuse University, Syracuse, New York) or MAT 253 (Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan) directly coupled to a KIEL-III automated carbonate preparation device. The mass spectrometers were optimized to process CO_2 samples evolved from very small carbonate samples (>10–15 μg) of otolith cores. The mass of samples was ascertained by comparing the amount of CO_2 generated after reacting with phosphoric acid with that of precisely weighed NBS-19 standard samples. All measurements are reported in the standard delta notation (per mil, ‰) relative to the Vienna Pee Dee Belemnite standard. Accuracy and precision were checked by routine analysis of the NBS-19 standard and was determined to be ±0.1‰.

Results

The $\delta^{18}O_w$ values in which YOY alewives reside were determined for use as an indicator of retrospective habitat. $\delta^{18}O_w$ values range from –11.5‰ to –5.8‰ (Table 1). Multiple analyses of Muskegon Lake and the nearshore area of Lake Michigan adjacent to Muskegon Lake during the growing season of 2002 and between 2002 and 2003 exhibit no significant variation in $\delta^{18}O_w$ with depth or time of collection (Table 1). However, a significant spatial variability was observed. For example, drowned river mouths have lower $\delta^{18}O_w$ values than Lake Michigan, while large embayments like Green Bay have values similar to Lake Michigan (Table 1). This general pattern is not exhibited by habitats such as Lake Macatawa and Pigeon Lake, which present relatively high $\delta^{18}O_w$ values, whereas in Lake Michigan near Menominee and Manistique, $\delta^{18}O_w$ values are relatively low (Table 1).

A total of 207 valid $\delta^{18}O$ values and 215 valid $\delta^{13}C$ core values were obtained for 256 YOY and yearling alewife otoliths, demonstrating that high-resolution sampling can be applied to small otoliths of a forage fish species (Fig. 3). In 2002, $\delta^{18}O$ and $\delta^{13}C$ values for YOY ranged from –11.2‰ to –6.9‰ and from –20.9‰ to –9.0‰, respectively (Figs. 3*a* and 3*b*). A nonparametric Mann–Whitney test was used to compare fish groups because not all of them present a normal distribution. There were no significant differences in $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values between YOY groups captured in Lake Muskegon and Muskegon Channel or among YOY groups captured from different locations in Lake Michigan (Mann–Whitney, $p < 0.001$) (Figs. 3*a* and 3*b*). On the contrary, otoliths from both Muskegon Lake and Muskegon Channel fish groups had significantly lower $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ compared with alewives captured in Lake Michigan. In 2001, YOY $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values ranged from –8.0‰ to –6.4‰ and from –12.9‰ to –10.0‰, respectively (Figs. 3*c* and 3*d*). There was no significant difference among fish groups (Mann–Whitney, $p < 0.001$) (Figs. 3*c* and 3*d*).

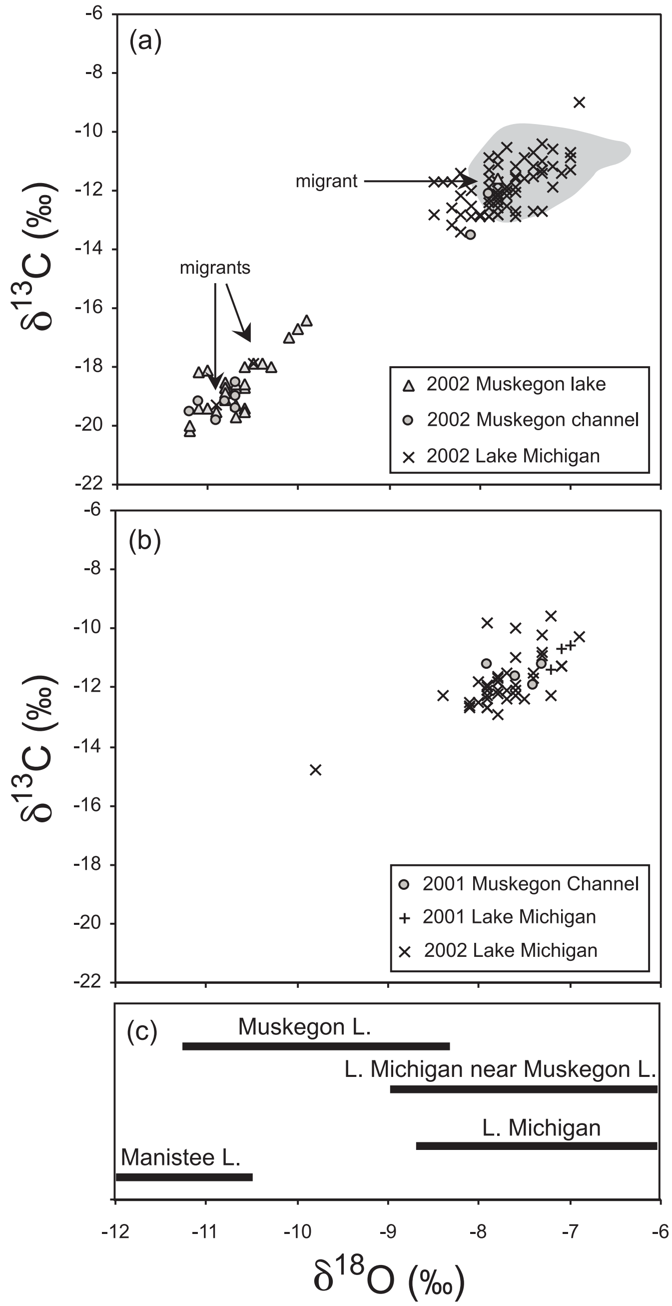
In addition to geographic differences, isotope variability was observed within YOY fish groups. Four groups contained outlier individuals in 2002 (Figs. 3*a* and 3*b*). One individual captured in Muskegon Lake and two individuals from Muskegon Channel exhibited values similar to those of Lake Michigan. Two individuals captured in the nearshore area of Lake Michigan exhibited values similar to those of Muskegon Lake. There were no outliers for fish born in 2001 (Figs. 3*c* and 3*d*). Statistical tests remained unchanged whether or not the outlier values were included.

$\delta^{18}O$ and $\delta^{13}C$ values for yearlings born in 2002 ranged from –9.8‰ to –6.9‰ and from –14.8‰ to –9.6‰, respectively (Figs. 3*a* and 3*b*). One 1+ individual captured in the nearshore area of Lake Michigan exhibited a lower $\delta^{18}O_{oto}$ value than the rest of the group (Fig. 3*a*). $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values for yearlings born in 2001 ranged from –7.9‰ to –7.0‰ and from –11.9‰ to –10.6‰, respectively (Figs. 3*c* and 3*d*). The 1+ alewives from Muskegon Channel and the nearshore habitat of Lake Michigan fish are significantly different for $\delta^{18}O_{oto}$ values but not for $\delta^{13}C_{oto}$ values (Mann–Whitney, $p < 0.001$) (Figs. 3*c* and 3*d*).

Discussion

To evaluate whether variation of $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values of otolith cores of alewives from different habitats of Lake Michigan can be attributed to different geographic origins, we characterized the isotope values of probable habitats. The few values available in the literature confirm the general pattern of variation in $\delta^{18}O_w$ among Lake Michigan habitat types. We observed a $\delta^{18}O_w$ value of –6.4‰ for a sample that we collected at Grand Traverse Bay in 1998, while during the early 1950s, Epstein and Mayeda (1953) measured a $\delta^{18}O_w$ value of –6.1‰ at an undisclosed Lake Michigan location. $\delta^{18}O_w$ values of tributaries of Lake Michigan analyzed by Coplen and Kendall (2000) displayed a range from approximately –12‰ to approximately –8‰. Although we documented spatial variation, we did not observe significant temporal variation in $\delta^{18}O_w$ within habitats over the growing season of YOY. This is to be expected given the size and the residence time of the habitats. Therefore, mean $\delta^{18}O_w$ values observed during 2002–2003 (–8.6‰ for Muskegon Lake, –6.0‰ for the nearshore area of Lake Michigan adjacent to Muskegon Lake, –6.3‰ for Lake Michigan, and –10.9‰ for Manistee Lake) are likely indicative of oxygen isotope signatures within these habitats during recent years (Table 1).

Fig. 4. (*a*) Plot of $\delta^{18}O$ and $\delta^{13}C$ values (‰; Vienna Pee Dee Belemnite) of YOY alewife (*Alosa pseudoharengus*) otolith cores collected during the fall of 2002 in different habitats of Lake Michigan. The range of $\delta^{18}O$ and $\delta^{13}C$ values of otolith cores of YOY alewives collected in 2001 is indicated by the shaded area. (*b*) Plot of $\delta^{18}O$ and $\delta^{13}C$ values (‰; Vienna Pee Dee Belemnite) of otolith cores of 1+ alewives from the 2001 and 2002 year classes collected in 2002 and 2003. (*c*) Estimation of potential ranges of $\delta^{18}O_{oto}$ values of otoliths crystallized in different origins calculated using measured $\delta^{18}O_w$ values and the equation of Patterson et al. (1993) and assuming potential temperature ranges experienced by fish in these habitats.



$\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values of otolith cores of YOY alewives captured in Muskegon Lake during 2002 were compared with values from alewives captured in other habitat types in 2001 and 2002. We observe a clear distinction between $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values of alewives collected from Muskegon Lake and those from Lake Michigan (Figs. 3 and 4). $\delta^{18}O_{oto}$ values are a function of ambient $\delta^{18}O_{w}$ values and temperature (e.g., Patterson et al. 1993; Thorrold et al. 1997). Therefore, we can predict the potential range of $\delta^{18}O_{oto}$ values of aragonite crystallized within each habitat using an aragonite temperature–fractionation relationship and mean $\delta^{18}O_{w}$ habitat values and assuming potential temperature ranges experienced by fish in these habitats (Fig. 4*c*). Multiple otolith-specific temperature–fractionation relationships have been developed from fish growing in well-constrained natural and laboratory environments (e.g., Patterson et al. 1993; Thorrold et al. 1997; Høie et al. 2004*b*). Although these relationships have slopes that are statistically indistinguishable from each other and from the inorganic aragonite temperature–fractionation relationship of Kim and O'Neil (1997), the intercepts differ significantly (Campana 1999; Thorrold and Hare 2002). We used the equation of Patterson et al. (1993) because it was specifically developed for freshwater fishes in natural systems, whereas the other equations were generated for marine fish. Additionally, the other equations have been noted to generate temperatures that may be 4 °C off the true temperatures of freshwater fishes raised in the laboratory and captured from well-constrained natural environments. A broad potential temperature range from +16 °C to +30 °C was estimated based on field temperature measurements (T.O. Höök, unpublished data) and laboratory experiments (Edsall 1970). Comparison between predicted and measured $\delta^{18}O_{oto}$ values suggests that YOY alewives captured in Muskegon Lake could have theoretically emerged in various drowned river mouth lakes including Muskegon Lake but not in Pigeon Lake or the majority of Lake Michigan sites (Fig. 4*a*). We were not able to measure the $\delta^{13}C_{DIC}$ values of the different habitats, but significant differences between drowned river mouth lakes and Lake Michigan are expected. The DIC originates from the atmosphere or the mineralization of organic matter, which have significantly different $\delta^{13}C$ values. The relative contribution of the two end members depends on lake size and is reflected by the positive relationship between $\delta^{13}C$ values of planktivorous fish tissues, including otoliths, and the size of the lake surface (Dufour 1999; Perga and Gerdeaux 2004). Drowned river mouth lakes such as Muskegon Lake have a smaller surface area compared with Lake Michigan (Muskegon Lake surface area is ~0.03% that of Lake Michigan) and thus should exhibit lower $\delta^{13}C_{DIC}$ values. Therefore, low $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values of cores of YOY alewives captured in Muskegon Lake during the fall of 2002 are consistent with an early life spent in a small sheltered habitat, most likely Muskegon Lake.

Based on $\delta^{18}O_{oto}$ values, individuals captured in Lake Michigan during the fall of 2002 could have emerged in various habitats, including Muskegon Lake (Fig. 4*a*). Theoretically, it is not possible to unequivocally assign these fish to a precise origin because Lake Michigan itself contains, or is connected to, numerous habitats that could potentially exhibit large differences, and we did not measure $\delta^{18}O_{w}$ values within all of these habitats. However, the clear segregation between most alewives from Lake Michigan habitats and those of Muskegon Lake suggests different environmental conditions experienced during early life (Fig. 4*a*). Moreover, the combination of relatively high $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values exhibited by most individuals captured in Lake Michigan is characteristic of open large lake habitats rather than drowned river mouth lakes or tributaries. Therefore, it is likely that the majority of YOY alewives captured in our lake-wide and nearshore study areas grew in Lake Michigan.

Although a large majority of surviving YOY captured during the fall of 2002 in Muskegon Lake grew in Muskegon Lake, we did find evidence of alewives moving between this drowned river mouth lake and Lake Michigan. One alewife captured in Muskegon Lake exhibited a value compatible with an early life spent in Lake Michigan (Fig. 4*a*). Individuals collected in Muskegon Channel had isotope values that suggest an early life in Muskegon Lake or Lake Michigan (Fig. 4*a*). In addition, movements of individual alewives into Lake Michigan are suggested by isotope values of two YOY alewives captured in Lake Michigan during the fall of 2002, which present values compatible with early growth in a small sheltered habitat (Fig. 4*a*). Even though it is not possible to unequivocally ascribe an origin to all fish because not all potential habitat origins have been characterized, these two alewives likely emerged and grew in a drowned river mouth (such as Muskegon Lake) or tributary and then moved to the Lake Michigan nearshore habitat. The presence of migrant specimens from drowned river mouth lakes within the Lake Michigan groups was not suggested for 2001 because no YOY individuals exhibited relatively low $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values (Fig. 4*b*). Alewife habitat switches described by $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ core values are consistent with field observations that suggest that larvae and juveniles born in Lake Muskegon could be transported through advection or active swimming during early stages of development in Lake Michigan (T.O. Höök, unpublished data).

During the summers of 2001 and 2002, Muskegon Lake and other drowned river mouth lakes of Lake Michigan had warmer waters and greater densities of small-bodied zooplankton than Lake Michigan (T.O. Höök, unpublished data). Because these conditions are favorable for faster larval and juvenile growth rates than exposed shorelines of lakes, drowned river mouth lakes should yield a disproportionate (relative to their volume) number of recruits to the year class.

Similarly to YOY captured in the fall of 2002, a large majority of yearlings captured in the nearshore study area in the spring of 2003 were individuals that spent their early life in Lake Michigan (Fig. 4*b*). Only one individual exhibiting an intermediate $\delta^{18}O_{oto}$ value is likely to have spent at least part of early life in a different habitat, whereas no 1+ alewives captured in Muskegon Channel in 2002 exhibited values typical of an early life in Muskegon Lake (Fig. 4*b*). Therefore, all of the 2001 year-class fish and the majority of the 2002 year-class individuals likely emerged and grew in Lake Michigan (Figs. 4*a* and 4*b*). Alewife habitat switches occur between drowned river mouth lakes and Lake Michigan itself during the first season of growth, but individuals originating from drowned river mouth lakes constitute a small fraction of the Lake Michigan population. This could be due to the fact that nearshore and lake-wide habitats of Lake Michigan are significantly more voluminous and would ultimately generate significantly more recruits than drowned river mouth lakes.

Because individuals of rapidly growing species such as alewife are small, susceptible to dispersive processes, and experience high mortality rates, they are difficult to study by conventional approaches such as mark–recapture studies. Therefore, studies of natural tags such as stable isotope ratios of soft tissues or elemental composition and stable isotope ratios of otoliths represent an alternative. However, only accretionary structures such as otoliths permit recognition a posteriori of habitats occupied throughout the entire life of a fish. Contrary to elemental analysis of otoliths (e.g., Patterson et al. 2004), application of $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values to fine-scale temporal studies of YOY dynamics has been extremely limited (Thorrold et al. 2001). Most otolith isotope studies used whole crushed otoliths (e.g., Ayvazian et al. 2004) or have recovered relatively low temporal resolution data, resulting in isotope values that integrate the first 6–12 months of a fish's life (e.g., Gao et al. 2001). Such temporal resolution limits potential applications to the early life history of fish.

Our study of alewife otoliths demonstrates that high-resolution sampling can be applied successfully to evaluate the life history of small forage fish otoliths. This technique presents a tremendous opportunity for increasing the temporal resolution of spatial behavior pattern studies. Ultimately, information pertaining to migration and habitat preferences should contribute to the understanding of temporal dynamics and recruitment variability of fish populations.

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