THE DYNAMICS OF LARVAL FISH DEMOGRAPHICS IN NEARSHORE SOUTHERN LAKE MICHIGAN

A THESIS SUBMITTED TO THE GRADUATE SCHOOL IN PARTIAL
FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
MASTER OF SCIENCE

BY

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BALL STATE UNIVERSITY

MUNCIE, INDIANA

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ABSTRACT

THESIS: The Dynamics of Larval Fish Demographics in Nearshore Southern Lake Michigan
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Nearshore larval fishes were collected with an oblique trawl tow during day and night from mid-May to August 2010 and 2011 in the Indiana waters of Lake Michigan to determine diel differences in the distribution, depth, and abundance of larval fishes. Alewife, spottail shiner, yellow perch and round goby were the prevailing larval species. Alewives dominated the catch and were in highest abundance near East Chicago. In general, night catch rates were greater when compared to day catch rates, suggesting a diurnal difference in trawl susceptibility. Stratified larval trawling was subsequently conducted during June and July 2011 to detect whether diurnal vertical migration existed, potentially affecting day and night catch rates. Vertical migration was not detected in the stratified larval sampling, eliminating it as a factor in higher nighttime catch rates. Further, the most common fish, alewife, was measured (TL) to determine whether size was a factor in trawl avoidance and to provide information regarding trawl selectivity. Night trawls yielded larger size classes of alewife, potentially explaining higher nighttime catch rates. These data suggests a size bias of our larval trawl exists when comparing day and night samples, as well as the limited efficiency of our trawl to catch larger larval size classes.

INTRODUCTION

Defining larval fish demographics provides the foundation for understanding early life history characteristics, such as year-class strength, predation mechanisms, spawning characteristics, and genetic structures (Robichaud-LeBlanc et al. 1996; Ruzzante et al. 1996; Sammons and Bettoli 1998; Bremigan et al. 2003). Early assessment can be advantageous for making a variety of management decisions when compared to fishes obtained at the juvenile or adult stage (Anderson et al. 1998). Unfortunately, the ability to accurately assess larval populations is often difficult due to system-specific factors such as tidal and coastal currents, river drift, and flooding events (Fore and Baxter 1972; Gale and Mohr 1978; Harvey 1987; Höök et al. 2006). Accordingly, it is beneficial to understand how these factors affect larval fish catch rate variability prior to embarking on a sampling scheme in an effort to collect a representative sample.

To address this variability, studies have focused on identifying factors of larval sampling that may influence efficiency (Thayer et al. 1983; Pepin and Shears 1997; Petrakis et al. 2001). One of the well-known factors is diel (i.e., day-night) variability in larval catch abundances (Gehrke 1992; McGurk 1992; Yousif 2003). The most common diel pattern is to have increased catches of larval fishes at night when compared to day (Muth and Schmulbach 1984; Brander and Thompson 1989; Petrakis et al. 2001). These results have been attributed to light-mediated behavioral reactions of larvae (Araujo-Lima et al. 2001). Even at early development stages when eyesight is not fully developed, larval fishes are able to detect and respond to changing levels of light intensity (Blaxter 1968; Job and Bellwood 2000).

Light-mediated behavioral reactions of larval fish, such as vertical migration and trawl avoidance, are a common research topic and are well-established in aquatic science (Loesch et al. 1982; McGurk 1992; Hensler and Jude 2007). These reactions have the potential to affect the susceptibility to trawl capture, thus altering overall larval density estimates. Thus, understanding how diel larval trawling affects the catch abundances of different species is mandatory to accurately assess larval fish assemblages.

The purpose of this study was threefold. First, we wanted to determine the temporal, spatial, and diel properties of larval fish in nearshore southern Lake Michigan. We hypothesized that larval fish densities would be uniform across sampling locations and densities would increase with time to peak abundance, then gradually decrease, yet be higher at night when compared to day. Second, we wanted to determine whether size-selective trawl avoidance was occurring, with larger size classes of larval fish being collected at night. We hypothesized that trawl avoidance by larvae was size specific with larger fish being better able to detect the trawl during the daytime and avoid capture, resulting in greater nighttime catch rates of larger larval fish. Third, we would determine whether the vertical distribution of larval fish changes diurnally, potentially as a result of vertical migration that may affect susceptibility to trawl capture and overall larval fish densities. We hypothesized that larval fish have a non-random vertical distribution in this system that changes diurnally. The results of this study describe the demographics of the larval fish community in southern Lake Michigan and may further explain variability in catch rates of larval fishes in this system.

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CHAPTER 1: Spatial, temporal, and diel evaluations of the nearshore larval fish assemblage in the Indiana waters of Lake Michigan in 2010 and 2011

Abstract- Nearshore larval fishes were collected with an oblique trawl tow during day and night from mid-May to August 2010 and 2011 in the Indiana waters of Lake Michigan to determine temporal, spatial and diel variability in abundance of larval fishes. Three sampling frames were used for this study; Michigan City (east), Burns Harbor (central), and East Chicago (west). These frames, each with twelve individual sites, were sampled using an oblique trawl at three different depth contours (2-4 m, 6-8 m, and 10-12 m) during both night and day. Alewife, yellow perch, spottail shiner, and round goby were the prevailing larval species, with 95% of the total catch being alewife. Most of these alewives were caught near East Chicago. After the initial catch near mid-May, larval catches gradually increased to peak abundance in late-June and decreased to nearly zero fish in August. In general, larval catch rates were higher at night when compared to day, suggesting a diel difference in trawl capture susceptibility. The results of this study have identified the current demographics of the larval fish community in the nearshore Indiana waters of Lake Michigan, as well as provide information to improve the efficiency of larval fish sampling in this system.

INTRODUCTION

Defining larval fish demographics provides the foundation for understanding early life history characteristics, such as year-class strength, predation mechanisms, spawning characteristics, and genetic structures (Robichaud-LeBlanc et al. 1996; Ruzzante et al. 1996; Sammons and Bettoli 1998; Bremigan et al. 2003). Early assessment can be advantageous for making a variety of management decisions when compared to fishes obtained at the juvenile or adult stage (Anderson et al. 1998). Unfortunately, the ability to accurately assess larval populations is often difficult due to system-specific factors such as tidal and coastal currents, river drift, and flooding events (Fore and Baxter 1972; Gale and Mohr 1978; Harvey 1987; Höök et al. 2006). Accordingly, it is beneficial to understand how these factors bias larval fish catch prior to embarking on a sampling scheme in an effort to collect a representative sample.

Larval fishes exhibit patchy horizontal and vertical dispersion patterns that can make catch rates variable (Wiebe and Holland 1968; Mackas et al. 1985; Munk 1988). As a result, larval fish samples can potentially show biased, inaccurate abundance estimates unless sampling protocols, including sufficient sample sizes and numbers are employed (Cyr et al. 1992). Spatial distribution can also be affected by habitat features, such as spawning areas within the ecosystem, which are often specific to localized spawning structure. For example, Robillard and Marsden (2001) proposed that the distribution of spawning yellow perch *Perca flavescens* along the southwest shoreline of Lake Michigan was nonrandom, with fish associating with specific substrate types. Thus, the spatial distribution of larval fishes may identify with or be linked to spawning areas within a water body (Sabatés 1990). Unfortunately, defining the connection between spawning areas and larval drift in bodies of water, such as Lake Michigan, may be limited due to the large size of the lake (Höök et al. 2006).

Temporal variation in larval fish abundance can vary within and among sampling years due to environmental constraints. Within a sampling season, the window of time that shallow-spawning species of larval fishes are present near spawning sites is often narrow and dependent on factors such as hatch dates and water movements (Dettmers et al. 2005; Beletsky et al. 2007). This timeframe may be even shorter in some systems, such as Lake Michigan, where larval swimming speed cannot overcome the coastal water movement from currents or winds, promoting larval drift away from natal areas (Houde 1969; Höök et al. 2006). Among sampling years, abundances of larval fish are highly variable and often unpredictable (Karjalainen et al. 2000). This inter-annual abundance variability is often caused by variation in environmental factors such as temperature, wind, and water levels (Clady 1976; Allen and Barker 1990; Killgore and Baker 1996). As a result of temporal variation in abundance, accurately assessing larval fish populations is difficult (Cyr et al. 1992) and increases the need to better understand optimal sampling timeframes.

Larval fishes are known to respond behaviorally to changes in light intensity (Batty 1987; Puvanendran and Brown 1998), generally through vertical migration (Levy 1990; Gehrke 1992; Scheuerell and Schindler 2003; Hensler and Jude 2007). The positioning of fishes in the water column can affect their susceptibility to trawl capture (Petrakis et al. 2001), potentially biasing abundance estimation. Further, diel variation in light will influence catch rates, as larval fishes may be better able to detect and avoid a trawl during daylight (McGurk 1992). Trawl avoidance and the extent of its effects on catch rates may depend on a number of factors, such as trawl size, trawling speed, larval species and larval length (Heath and Dunn 1990; Pepin and Shears 1997; Itaya et al. 2007). These factors collectively increase larval fish catch rates at night when compared to day (Fore and Baxter 1972; Loesch et al. 1982; Morse 1989).

The objectives of this study were to determine the spatial, temporal, and diel properties of larval fishes in the Indiana waters of Lake Michigan from May to August, 2010 and 2011. We hypothesized that larval abundance would have a non-random spatial distribution among the Indiana nearshore waters and expected to observe a unimodal temporal distribution of larval fish density. Finally, we hypothesized that larval catch rates would be higher at night when compared to day. The results of this study identify the demographics of the larval fish community in the nearshore Indiana waters of Lake Michigan, as well as provide direction and methodology when considering larval sampling in this system.

METHODS

Study area- Lake Michigan is one of the five Great Lakes of North America and covers a surface area of about 58,000 km^2. The mean depth of the lake is about 100 m and the maximum depth reaches 265 m. Sampling for this study took place within the Indiana waters of southern Lake Michigan. These waters are relatively shallow (< 20 m) and are comprised of homogeneous sandy substrates (Janssen et al. 2005).

Collection of larval fishes- Larval fishes were collected from mid-May to August 2010 and 2011 using a stratified random sampling design (Hansen et al. 2007) in the Indiana portion of Lake Michigan. These waters were divided into three strata, one near Michigan City, Burns Harbor, and East Chicago (Figure 1). Each strata was comprised of 12 individual sampling units (locations) which were distributed at distances of one km and oriented along the shoreline. A single sample location from each strata was randomly selected on each sampling date using a random number generator. Sampling was conducted twice per week, except the first and last weeks of each sampling season when only one sample was collected. Fish were captured using a Tucker trawl with a 1 m^2effective mouth area fitted with 350 micrometer (µm) mesh to ensure collection of small, newly hatched larvae (O'Gorman 1984). The trawl was obliquely towed for 10 min (bottom to surface) behind the boat at a speed of 2.5-3.0 knots (Thayer et al. 1983). Three depth contours were sampled (2-4 m, 6-8 m, 10-12 m) to ensure coverage in all nearshore waters. Lastly, samples were collected both day and night for each sample date. Daytime samples were collected between 0800 and 2000 hours, while nighttime samples were collected between 2200 and 0400 within the same 24 hour period. Thus, 18 samples were collected each sampling date (three locations X three depth contours X two diel periods) unless shoreline development, such as break walls, inhibited collection at the shallowest depth. Each sample was preserved immediately after collection in a 10% formalin-lake water solution (Murphy and Willis 1996). In the laboratory, fish were picked from the sample debris, enumerated, and identified to species using Auer (1982). Larval density was indexed by catch per unit effort (CPUE), which was represented as number of larvae captured per cubic meter of water sampled.

Statistical analysis- We used a factorial analysis of variance (ANOVA) (SPSS 17.0) to determine whether differences in alewife *Alosa pseudoharengus* catch rates (CPUE) were influenced by location, year, depth, diel period, or their interactions. We chose a factorial ANOVA because it allows consideration of the effect of multiple independent variables in the same study. A Tukey's Honestly Significant Difference (HSD) post hoc analysis was used to determine which locations produced significantly different alewife densities.

Diel differences in larval catch rates (CPUE) of yellow perch, spottail shiner *Notropis hudsonius*, and round goby *Neogobius melanostomus* were assessed using a paired *t*-test (SPSS 17.0). For each species, paired differences in larval abundance between day and night samples determined whether these differences were non-random (LeBlanc 2004). Sample pairs that had zero values for both day and night were excluded from the analysis. Further statistical analyses of yellow perch, spottail shiner and round goby were limited by the low abundance and high variability of these fishes in the catch.

We used a Kolmogorov-Smirnov two-sample test (K-S test) (SPSS 17.0) to determine whether the larval catch frequency distributions for each species differed between 2010 and 2011. This test allowed us to determine whether the two frequency distributions were of the same shape (Marascuilo and McSweeney 1977). For all statistical analysis, $\alpha = 0.05$.

RESULTS

A total of 16,498 larval fishes was collected in southern Lake Michigan during 2010 and 2011 (Table 1). The catch primarily consisted of four species: alewife (95%), yellow perch (2%), spottail shiner (2%), and round goby (1%). Other species collected in small densities (< 0.001% overall) were rainbow smelt *Osmerus mordax*, gizzard shad *Dorosoma cepedianum*, burbot *Lota lota*, and centrarchids from the genus *Lepomis* that were not identifiable to species level. Catch per unit effort (fish/m^3) ranged from 0 to 0.94 for alewife, 0 to 0.03 for yellow perch, 0 to 0.06 for spottail shiner, and 0 to 0.04 for round goby.

In both 2010 and 2011, larval alewife, spottail shiner, and round goby were first caught in the second week of May, increasing to peak abundance the first week in July and decreasing to near zero in August (Figure 2). No differences were found for the time of peak abundance between 2010 and 2011 for these three species (K-S test, $Z = 0.97$, $N = 484$, $P = 0.30$, $Z = 0.63$, $N = 484$, $P = 0.82$, $Z = 0.38$, $N = 484$, $P = 0.99$; respectively). The catch frequency distributions for larval yellow perch abundance, which peaked in early June (Figure 2) were significantly different between 2010 and 2011 (K-S test, $Z = 2.1$, $N = 484$, $P < 0.01$).

Alewife catch rates differed significantly among locations, between years, and in the location x year interaction (Table 2). East Chicago produced more alewives than any other sampling location (Table 2). East Chicago had larval alewife abundances 43% greater than Michigan City and 47% greater than Burns Harbor. The significant interaction revealed that the effects of year on alewife abundance were different among locations, particularly Michigan City and Burns Harbor (Figure 3). However, East Chicago produced significantly more alewives than any other location, regardless of year (Figure 3).

Spottail shiner and round goby abundances were significantly higher at night when compared to day (Table 3). Although approximately 50% more yellow perch were caught at night, catch rates were only marginally significant (Table 3).

DISCUSSION

Our study revealed that larval fishes in this system exhibit species specific variability in spatial, temporal, and diel abundance. The spatial analysis showed that alewives had greater abundances at East Chicago than any other sampling location. This finding supports our hypothesis of non-random larval distribution. We were able to determine temporal variability in larval abundance by sampling sufficiently early in the season to catch the first spawning fish of these species (Wells and House 1974; Brazo et al. 1975), and continuing larval collections until the sampling gear no longer recruited to the fish or they were transported offshore (Dettmers et al. 2005; Höök 2006), which resulted in a unimodal time distribution for each larval fish species. However, only yellow perch had different temporal catch distributions between sampling years. We also experienced greater catch rates at night when compared to day, but the extent of this diel variation was species dependent.

The four most abundant larval fishes were alewife, yellow perch, spottail shiner, and round goby. These findings were similar to Jude et al. (1981) who found alewife, spottail shiner and yellow perch to be the most abundant larval species in nearshore Lake Michigan. At the time of this 1981 survey, round goby had not yet been naturalized to the Great Lakes (Jude et al. 1992). These four species were expected in the larval catch, as they mimic the recent and dominant nearshore adult fish species collected in these waters (Forsythe and Lauer 2010) and spawn during the spring in shallow water (< 6 m; Perrone et al. 1983; Mansfield 1984; Jude et al. 1992; Leslie and Timmons 1992). The high proportion of larval alewives in our catch has been reported in similar studies on the Great Lakes (Nash and Geffen 1991, Warner et al. 2012). Alewives have made their impact in the Great Lakes, in part, because of their high fecundity and strong interspecific competition (Norden 1967; Tisa and Ney 1991). As a result, the alewife is the most prevalent fish species in Lake Michigan, making up a large proportion of its fish biomass (Madenjian et al. 2012).

The spatial distribution of larval alewife abundance was non-random among the three sampling locations and was consistently greater near East Chicago, but this increase in larval alewife catch rates at this location may not necessarily be explained by localized favorable spawning substrate. The southwest portion of Lake Michigan, especially near Illinois, exhibits increased rocky spawning substrate (Robillard and Marsden 2001). However, alewives typically spawn on sand or gravel substrates (Nigro and Ney 1982), which are common throughout the southern basin of Lake Michigan (Shroyer and McComish 1998). Larval drift may be influential in determining larval fish spatial distributions (Höök et al. 2006). However, the increased alewife density near East Chicago was likely not influenced by drift, since this trend did not exist for the other larval species that are also at the mercy of current. Also, the increased alewife abundance was not a matter of a few large outlying sample sizes, as East Chicago out-produced both other sampling locations about 68% of the time. Thus, the increased larval alewife abundance near East Chicago discovered in this study may not be explained by these components and requires further attention.

We observed a unimodal temporal distribution in abundance for each species in 2010 and 2011. After peak abundance, larval catches decreased to near zero in August, which we suspected was the result of offshore movement of larval fishes in the late summer (Höök et al. 2006). Similar temporal patterns in nearshore larval fish abundance have been identified by Jude et al. (1981). Catch frequency distributions for alewife, spottail shiner, and round goby did not differ between 2010 and 2011, indicating that annual variance in the temporal pattern we experienced is probably minimal. Yellow perch catch frequency distributions differed likely because of differences in density levels at peak abundance between 2010 and 2011, rather than timing of peak abundance (Figure 2).

Although year-class strength was not indexed in this study, many studies have correlated larval abundance with year-class strength in fishes (Rijnsdorp et al. 1985; Johnston et al. 1995; Sammons and Bettoli 1998). Warner et al. (2012) found that 2010 produced the largest alewife year-class in Lake Michigan since 2001. Considering this finding, correlating our results of higher larval alewife abundance in 2010 than in 2011 with year-class strength may be a plausible connection.

We experienced a trend of higher larval fish catch rates at night when compared to day; however, the extent of this diel variation was not the same for all species. Nighttime catches of spottail shiner and round goby totaled over 200 for each species, while daytime catches were approximately an order of magnitude lower ($N = 25$ and 5, respectively). Conversely, diel differences in alewife abundance were statistically insignificant and only marginally significant for yellow perch. This interspecific variability may reveal physical or behavioral characteristics of each species that influence day and night trawl catch susceptibility (Petrakis et al. 2001). Even though the day and night differences were insignificant for alewife and only marginally significant for yellow perch, the trend of greater night catch rates for both species may have biological significance worth further interpretation. Our results suggest that trawling at night may be more efficient than during the daytime because greater sample sizes increase precision of abundance estimates and reduce sampling effort (Cyr et al. 1992). Although many explanations of higher abundances of larval fish at night may exist, we have two hypotheses for this phenomenon.

Our first hypothesis is that diel vertical migration may affect the susceptibility of larval fish to trawl capture. The widely accepted pattern in diel vertical migration is for organisms to rise in the water column at night and remain near the bottom during the day (Lampert 1989; Hensler and Jude 2007). If this phenomenon is occurring in nearshore southern Lake Michigan, larval fish may be less susceptible to oblique trawl capture during the day as the immediate bottom is not effectively sampled. Conversely, if larval fish are rising at night and are suspended throughout the water column, they may be more susceptible to our oblique trawl (Hjellvik et al. 2004). Ultimately, this may result in higher nighttime catch rates similar to those found in our study.

Our additional hypothesis is that larger larval fish are being captured only at night as a result of size-selective trawl avoidance. Larger larval fish may be better able to detect the trawl during the day (Michalsen et al. 1996), promoting early detection and enhanced escape capabilities (Bailey 1984) when compared to smaller larvae. Thus, this differential, size selective catch of larval fish may only materialize at night when larger fish are less likely to detect the trawl, ultimately influencing catch vulnerability.

The results of this study provide direction and methodology that may improve efficiency of larval sampling in Lake Michigan and other bodies of water, essential to the management and research of fish populations. Our results suggest that larval sampling at night may increase overall catch rates, potentially decreasing sampling effort to reach sample sizes large enough for robust statistical treatment. Further, sampling near the time of peak larval abundance indicated in this study may also benefit efficiency. We have also identified the current demographics of the larval fish assemblage in nearshore southern Lake Michigan in 2010 and 2011, which may be used when considering year-class strength or temporal trends in larval abundance.

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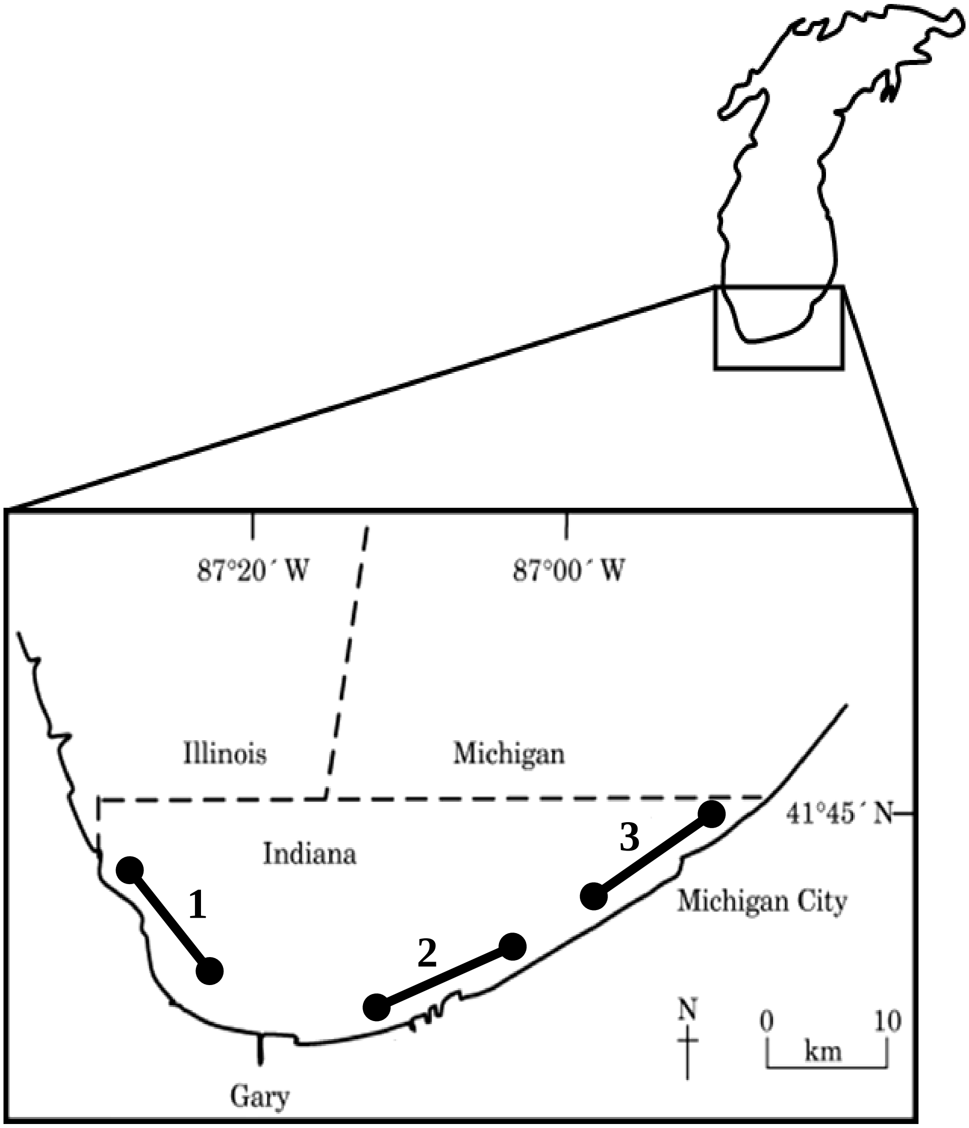

Figure 1. Approximate locations of 2010 and 2011 larval sampling zones East Chicago (1), Burns Harbor (2), and Michigan City Harbor (3) in the Indiana waters of southern Lake Michigan.

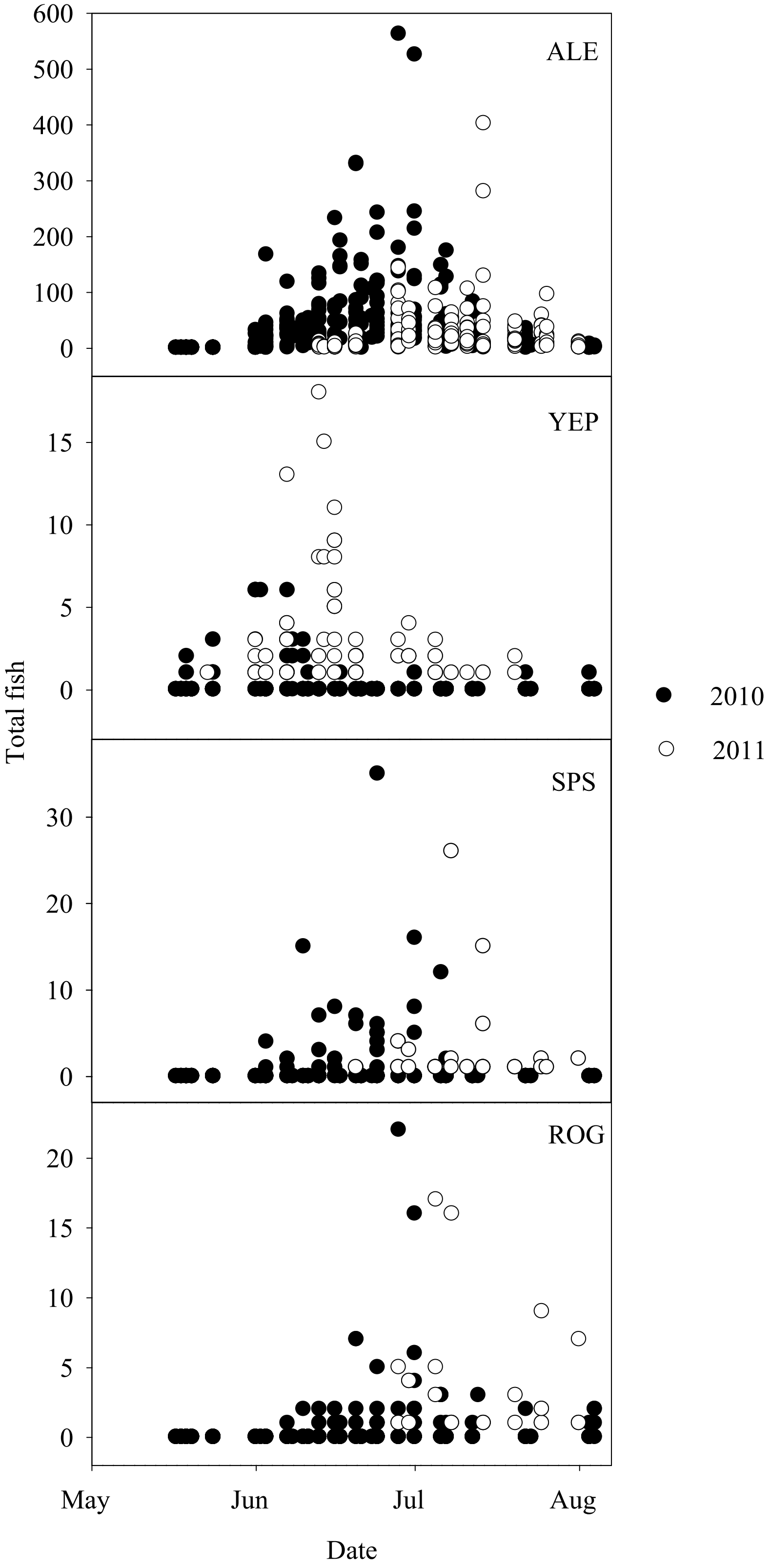

Figure 2. Larval fish catches from mid-May to August 2010 and 2011 in the Indiana waters of Lake Michigan (ALE = alewife, YEP = yellow perch, SPS = spottail shiner, ROG = round goby).

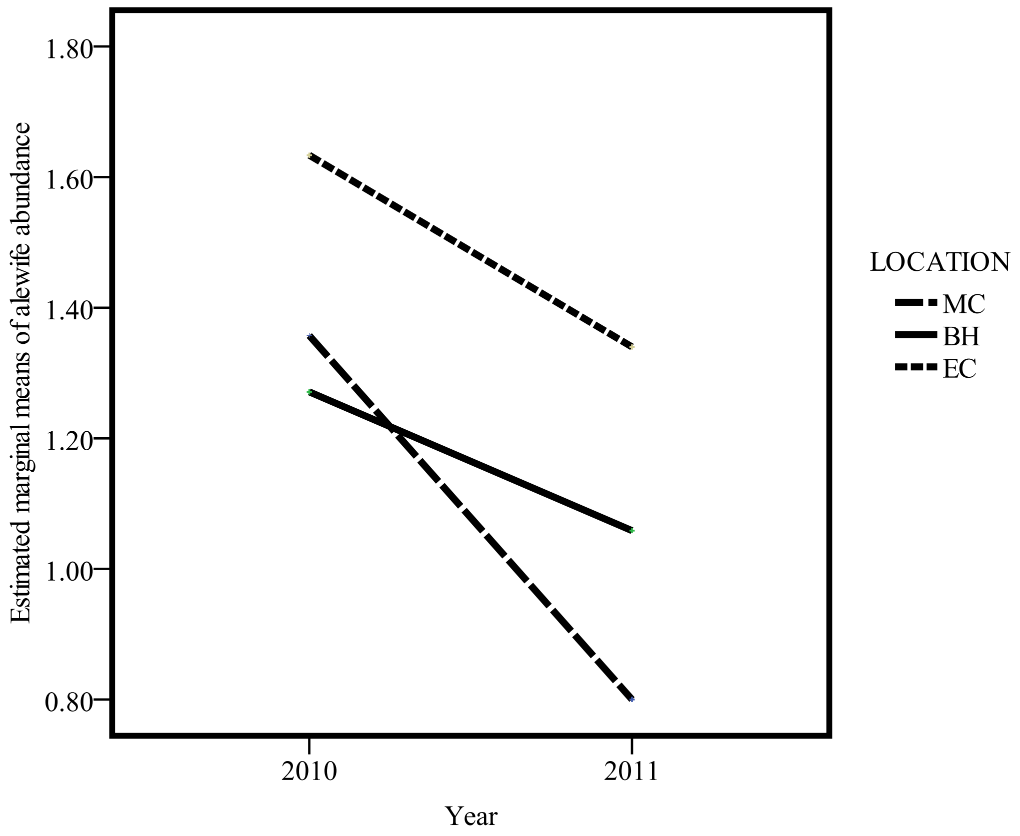

Figure 3. Profile plot showing the effects of the factorial ANOVA interaction between location and year on larval alewife abundance in the Indiana waters of Lake Michigan. Locations are abbreviated as the following: MC = Michigan City, BH = Burns Harbor, EC = East Chicago.

Table 1. Total catch for each larval species (ALE = alewife, YEP = yellow perch, SPS = spottail shiner, ROG = round goby, and Other = rainbow smelt, gizzard shad, burbot, and centrarchids) caught during 2010 and 2011 in the Indiana waters of Lake Michigan.

	Number of larval fishes		
Species	2010	2011	Total
ALE	11,500	4,213	15,713
YEP	77	218	295
SPS	170	78	248
ROG	122	90	212
Other	15	15	30

Table 2. Results of the factorial ANOVA to determine whether differences in alewife catch rates were influenced by various factors. Only univariate and statistically significant interactions are reported. Tukey's HSD post hoc analysis shows *P*-values among the sampling locations (MC = Michigan City, BH = Burns Harbor, EC = East Chicago).

Source	df	F	*P*
Depth	2	0.82	0.44
Location	2	11.60	<0.01
Diel Period	1	0.75	0.39
Year	1	24.93	<0.01
Location * Year	2	4.19	0.02
Tukey's HSD post hoc analysis	Location	MC	BH
	BH	0.61	
	EC	<0.01	<0.01

Table 3. Mean CPUE (±SE) of yellow perch (YEP), spottail shiner (SPS), and round goby (ROG) caught in the Indiana waters of Lake Michigan during 2010 and 2011. A paired *t*-test was used to determine whether differences in larval catch abundances between day and night were significant at α = 0.05 for each species.

		Mean CPUE [fish / 100 m³] (± SE)			
Species	N	Day	Night	*t*	*P* (two-tailed)
YEP	82	0.239 (0.031)	0.360 (0.066)	1.6	0.06
SPS	52	0.080 (0.033)	0.715 (0.153)	3.6	<0.01
ROG	65	0.013 (0.007)	0.531 (0.088)	5	<0.01

CHAPTER 2: Factors affecting diel variability in larval fish abundance in the nearshore waters of southern Lake Michigan in 2010 and 2011

Abstract- To examine potential factors influencing diel variability in larval fish catch rates, stratified larval trawling was conducted in southern Lake Michigan during June and July 2011 to detect whether diel vertical migration existed, potentially affecting trawl susceptibility. Vertical migration was not detected in the stratified larval sampling, eliminating it as a factor in higher nighttime catch rates. Further, the most common fish, alewife, was measured (total length) to determine whether size was a factor in trawl avoidance and to provide information regarding trawl selectivity. Night trawls produced larger size classes of alewife, potentially explaining higher nighttime catch rates. These data suggested a size bias of our larval trawl exists when comparing day and night samples, as well as the limited efficiency of our trawl to catch larger larval size classes. The results of these studies provide ecological insight to the larval fish community in nearshore Indiana waters of Lake Michigan, as well as providing direction and methodology when considering larval sampling in Lake Michigan and other bodies of water.

INTRODUCTION

Larval fish sampling can be an effective and reliable method of estimating year-class strength and other components of early life history in fishes (Matthews 1984; Sammons and Bettoli 1998; Partridge and DeVries 1999). However, due to the patchy temporal and spatial distribution of larval fishes, sampling for these organisms often shows highly variable catches (Wiebe and Holland 1968; Mackas et al. 1985; Maynou et al. 2006), which may be a biased representation of fish abundance. To address this variability, studies have focused on identifying factors of larval sampling that may influence efficiency (Thayer et al. 1983; Pepin and Shears 1997; Petrakis et al. 2001). One of the well-known factors is diel (i.e., day-night) variability in larval catch abundances (Gehrke 1992; McGurk 1992; Yousif 2003), and the most common pattern is increased catches of larval fishes at night when compared to day (Muth and Schmulbach 1984; Brander and Thompson 1989; Petrakis et al. 2001). These results have been attributed to light-mediated behavioral reactions of larvae (Araujo-Lima et al. 2001). Even at early development stages when eyesight is not fully developed, larval fishes are able to detect and respond to changing levels of light intensity (Blaxter 1968; Job and Bellwood 2000).

Two hypotheses have been proposed to elucidate diel variability in larval abundance as a result of these light-mediated behavioral reactions. The first is trawl avoidance where fish actively evade capture, typically by visually detecting the approaching gear and fleeing (Blaxter 1968; McGurk 1992). Light-mediated trawl avoidance during daytime has a negative effect on larval fish catch rates (Brander and

Thompson 1989; McGurk 1992; Ryer and Olla 2000). As a result, larval catch rates are often higher in night trawls when compared to those conducted during the day (Loesch et al. 1982). The second hypothesis on trawl avoidance is related to and dependent upon larval fish size (Heath and Dunn 1990). As larvae increase in size and continue development of swimming ability, trawl avoidance capabilities increase (Wardle 1977).

Sampling gear and methods can have substantial impacts on larval catch. Because swimming speeds are limited in larval fishes (Houde 1969), trawl avoidance is negatively related to trawl size (Itaya et al. 2007). Presumably, an increasing mouth dimension and associated sampling area decreases the ability of larval fishes to avoid capture (Itaya et al. 2007). Catch rates have also been positively correlated with trawl towing speed, likely related to larval swimming speed (Thayer et al. 1983). Munk (1988) found that increased trawl speeds resulted in lower catch rates, likely the result of backwash expelling larvae out of the net. Thus, an optimum speed will provide the most efficient trawl tow, balancing the target organism's abilities with the recruitment limitations of the gear.

Diel vertical migration, or the phenomenon of larval fishes moving vertically throughout the water column as a response to changes in light intensity, may also influence catch rates, particularly if the sampling does not account for this behavior. The most common pattern of diel vertical migration is for larval fishes to migrate toward the water surface at night and remain near the bottom during the day (Lampert 1989; Hensler and Jude 2007). Although vertical migration is not fully understood, accepted explanations for diel vertical migration of larval fishes are feeding, anti-predation, thermal energetics, and ultraviolet light exposure (Brewer and Kleppel 1986; Speekmann et al. 2000; Scheuerell and Schindler 2003; Donner and Eckmann 2011).

Vertical distribution of fishes in the water column may be the single most influential factor in catch variance by sampling gear (Parrish et al. 1964). Because of vertical migration, the catch rates of larval fishes can be confounded with the type of sampling gear deployed (Thayer et al. 1983). For example, when using a midwater trawl, larval fishes may be less susceptible to trawl capture during daylight if they are near the bottom, as opposed to nighttime collections where the fish may be suspended throughout the water column or near the surface. Alternatively, a benthic sampler may yield lower catches at night when fish are suspended (Loesch et al. 1982). In addition to sampling gear, the type of system (i.e. river, lake, estuary) sampled can influence the presence and degree of diel vertical migration in larval fishes. Downstream river current, upwelling events, and tidal drift affect larval dispersal in various ways and can influence catch abundances (Heufelder et al. 1982; Pavlov 1994; Kimmerer et al. 1998). Consequently, these system effects must be fully understood when studying potential diel vertical migration of larval fishes in order to accurately determine population demographics.

The purpose of this study was twofold. First, we determined whether size-selective trawl avoidance occurs by alewife *Alosa pseudoharengus* in two related, but distinctly different habitats: southern Lake Michigan and Muskegon Lake (Michigan). We hypothesized that trawl avoidance by larvae was size specific with larger fish being better able to detect the trawl during the daytime and avoid capture, resulting in greater nighttime catch rates of larger alewives. Second, we determined whether the vertical distribution of larval fish in southern Lake Michigan changed between night and day, which may represent potential diel vertical migration. We hypothesized that larval fish had a non-random vertical distribution in this system that changed diurnally. The results of this study may further explain variability in catch rates of larval fishes in this system.

METHODS

Study Areas – Lake Michigan is one of the five Great Lakes of North America and covers a surface area of 57,850 km². The mean depth of the lake is 99 m and the maximum depth reaches 265 m (Truemper and Lauer 2005). Sampling for this study took place within the Indiana waters of southern Lake Michigan, which are bordered to the north by Illinois and Michigan jurisdiction. These waters are relatively shallow (< 20 m) and are comprised of homogeneous sandy substrates (Janssen et al. 2005). Muskegon Lake (Muskegon County, Michigan) is a drowned river mouth lake connected to eastern Lake Michigan by the Muskegon River. The lake has a surface area of 16.8 km², a mean depth of 7.1 m, and a maximum depth of about 25 m (Carter et al. 2006, Höök et al. 2007). Substrate is composed primarily of sandy substrate with small cobble (Diana 2006). Dufour et al. (2005) found that young alewives migrate through a navigation channel that connects Lake Michigan and Muskegon Lake, a distance of approximately 1 km.

Larval Trawl Avoidance - Larval alewives were collected mid-May to late October 2001 and mid-May to late August 2002 in nearshore eastern Lake Michigan and Muskegon Lake. Sampling was conducted using a random survey design to characterize two habitat types, from which four sampling stations were randomly selected for each sampling week. Habitat typing was based on physical and biotic habitat factors, details of which can be found in Höök (2005). Fish were collected weekly during mid-May through July and biweekly during August through October with 5 minute oblique trawl tows (near bottom to surface) at 1-2 knots during day and night. Sampling gear included a 60 cm diameter bongo sampler with paired 335 and 500 µm mesh nets, which was used through August, after which a 2 m^2 Tucker trawl sampler with 700 µm mesh was used to collect larger size classes of alewife. Larval alewives were preserved in 90% ethanol and identified in the laboratory using Auer (1982) and Wallus and Kay (1990). Since few samples were collected in this earlier study, datasets from 2001 and 2002 were combined for further analysis. Thirty larval alewives were randomly selected from each sample and were measured for total length (TL) using a dissecting microscope and camera with Optimus image analysis software. When fewer than 30 alewives were collected in any single tow, all alewives were measured. To adjust for shrinkage that may have occurred in the preservation process, TL was multiplied by 1.1 (Höök et al. 2007). Details of sampling and measurement procedures are found in Höök (2005) and Höök et al. (2007).

Larval alewives were also collected from mid-May to August 2010 and 2011 using a stratified random sampling design (Hansen et al. 2007). The Indiana shoreline of Lake Michigan was divided into three sampling frames, one each near Michigan City, Burns Harbor, and East Chicago (Figure 1). Each of these frames was comprised of 12 individual sampling units which were distributed at distances of one km and oriented parallel to the shoreline. A single unit from each of the three sampling frames was randomly selected on each sampling date using a random number generator. Sampling was conducted twice per week, except the first and last weeks of each sampling season when only one sample was collected. Fish were captured using a Tucker trawl with a

1 m^2 effective mouth area with 350 μm mesh to ensure collection of small, newly hatched larvae (O'Gorman 1983). The trawl was obliquely towed for 10 min (near bottom to surface) behind the boat at a speed of 2.5-3.0 knots (Thayer et al. 1983) parallel to shore. Three depth contours were sampled (2-4 m, 6-8 m, 10-12 m) to ensure coverage in all nearshore waters. Lastly, samples were collected both day and night for each sample date. Daytime samples were collected between 0800 and 2000 hours, while nighttime samples were collected between 2200 and 0400 within the same 24 hour period. Thus, 18 samples were collected each sampling date (three locations X three depth contours X two daily time periods) unless shoreline development, such as break walls, inhibited collection at the shallowest depth. Each sample was preserved immediately after collection in a 10% formalin-lake water solution (Murphy and Willis 1996) and returned to the laboratory where each larval fish was picked from the sample debris, enumerated, and identified to species using Auer (1982). Fifty larval alewives were randomly selected from each sample and were photographed under a dissecting microscope at 2X magnification using a PAXcam 3 ® digital microscope camera. From these photographs TL was measured to 0.1 mm using SigmaScan Pro 5 by calibrating pixel size at 2X magnification and converting pixels to mm. When fewer than 50 alewives were collected in any single tow, all alewives were measured. To adjust for shrinkage that may have occurred in the preservation process, total length was multiplied by 1.1 (Höök et al. 2007). All larval alewives were grouped into 1-mm length bins.

Diel Stratified Sampling- Diel stratified sampling was conducted twice per week during June and July 2011 in southern Lake Michigan near Michigan City, IN (Figure 1, zone 3). A single unit (location) was randomly selected on each sampling date using a random number generator. Fish were collected using a Tucker trawl with a 1 m^2 effective mouth area and 350 μm mesh for 10 min trawl tows in 12 m of water. Three separate strata layers were used for the collections [surface (0-1 m), mid-water (6-7 m), and bottom (11-12 m)] during day and night at a speed of 2.5-3.0 knots (Thayer et al. 1983). Daytime samples were collected between 0800 and 2000 hours, while nighttime samples were collected between 2200 and 0400 within the same 24 hour period. Each sample was preserved immediately after collection in a 10% formalin-lake water solution (Murphy and Willis 1996) and returned to the laboratory where each larval fish was picked from the sample debris, enumerated, and identified to species using Auer (1982).

Statistical Analysis- For the size-selective trawl avoidance data, alewife length distributions comparing day and night were analyzed using a Kolmogorov-Smirnov (K-S) two-sample test (Siegel 1956). This test determined whether lengths of alewife caught during the day were significantly different from the lengths of those caught at night.

The stratified samples identifying diel vertical distribution were analyzed using a two-way analysis of variance (ANOVA) to test the effects of the diel period, the strata layer, and their interaction on larval abundance. To meet the normality assumption, the dependent variable, larval abundance, was natural-log transformed. For all tests, $\alpha = 0.05$.

RESULTS

Throughout the size-selective trawl avoidance study, a total of 9,642 alewives was measured from 2001 and 2002 ($N = 319$), 2010 ($N = 6{,}331$), and 2011 ($N = 2{,}992$). Alewife lengths ranged from 2 to 33 mm TL, with a mode of 5 mm in 2001-02 and 4 mm in 2010 and 2011 (Figure 3). Length distributions differed between day and night samples in 2001-02 ($Z = 1.819$, $N = 319$, $P = 0.003$) and 2011 ($Z = 1.576$, $N = 2{,}992$, $P = 0.014$), but not 2010 ($Z = 0.919$, $N = 6{,}331$, $P = 0.367$). Alewife ≤ 17 mm TL were collected in similar abundances between day and night, but alewife > 17 mm TL were only caught at night (Figure 2).

Diel stratified sampling caught a total of 556 larval fishes in southern Lake Michigan in June and July 2011. The catch consisted of four species: alewife, yellow perch *Perca flavescens*, spottail shiner *Notropis hudsonius*, and round goby *Neogobius melanostomus*. The overall species composition was 81% alewife and 17% yellow perch, while spottail shiner and round goby split the remaining 2%. The number of larval fishes collected was not significantly different diurnally (df = 1, $F = 0.002$, $P = 0.964$), among the strata layers (df = 2, $F = 1.312$, $P = 0.276$), and the interaction was not significant (df = 2, $F = 0.019$, $P = 0.982$). Although statistically insignificant, the trend in mean number of larvae in surface trawls was higher than bottom trawls during both day and night (Figure 3).

DISCUSSION

Our first objective identified that size-selective trawl avoidance by alewives was occurring diurnally in the Indiana waters of Lake Michigan and is in agreement with others (Castonguay and McCleave 1987; Heath and Dunn 1990; McGurk 1992) that have identified reasons contributing to larval catch variability. Larval avoidance capabilities are often determined by identifying a specific length that the fish is able to swim sufficiently fast to escape the trawl (Heath and Dunn 1990). Our study revealed that, when using 1 and 2 m^2 Tucker trawls and a 60 cm diameter bongo sampler, smaller alewives (< 17 mm TL) were collected in similar abundances between day and night, but larger alewives (> 17 mm TL) were only caught at night. Additionally, 16 post-larval alewives (43-71 mm TL) were collected in the 1 and 2 m^2 Tucker trawls, but all were taken at night. Heath and Dunn (1990) showed related findings with larval herring catch rates being similar between day and night up to 25 mm, whereas at night larger larvae were captured. These data agree also with Glass and Wardle (1989) that described that when the trawl is not detected visually, larger fishes are caught, contributing to variability in day and night larval catch rates.

All fish sampling gears are biased and typically do not recruit to all sizes of fish (Gulland 1980). The specific length at which larval fish are able to avoid the trawl is often dependent on the trawl mouth size (Pepin and Shears 1997). We found alewife showed nighttime length distributions that were larger when using the 60 cm diameter bongo sampler and 2 m^2 Tucker trawl (2001 and 2002) when compared to the 1 m^2 trawl (2010 and 2011), which is likely the result of a larger Tucker trawl (2 m^2) and bongo sampler being used. Itaya et al. (2007) found a positive relationship between the lengths of larval Japanese anchovy *Engraulis japonica* and trawl size, with catches up to 28 mm in 4 m^2 trawls, 44 mm in 12.3 m^2, and 60 mm in 16 m^2. Thus, this study had a similar pattern of increased larval length with larger trawl size as found in our study, albeit with different larval species. An alternative explanation for larger catch distributions in the

2001-02 data than the 2010 and 2011 data may be related to the extended sampling season, which continued until late-August in 2001 and late-October in 2002, as sampling later into the growing season may have produced larger size classes (Höök et al. 2007). However, the 1 m^2 Tucker trawl quit sampling even the larger alewives at night later in the summer (early August), suggesting they may no longer be present.

Although diel vertical migration is well established in larval fishes (Loesch et al. 1982; Brewer and Kleppel 1986; Job and Bellwood 2000; Donner and Eckmann 2011), our data did not identify a vertical migrational pattern between day and night in southern Lake Michigan. Variability in larval fish abundance is often explained by the tendency of larval fish to rise in the water column at night, which is the most common pattern observed (Gehrke 1992; Hensler and Jude 2007). This trend may increase nighttime susceptibility to surface and midwater trawl capture when compared to day, when larval fishes remain near the bottom. Our failure to illustrate this pattern may be the result of the southern Lake Michigan hydrodynamics, thermal refuge, sample size, sampling depth, or sampling gear.

The hydrodynamics of southern Lake Michigan involve complex current patterns that are highly influenced by wind and bottom topography (Jude et al. 1981). The relatively shallow basin of southern Lake Michigan is subject to frequent upwelling events produced by prevailing southwestern winds as a result of Ekman transport (Mortimer 2004). These upwellings and current dynamics caused by wind and earth spin (Mortimer 2004) do not allow larval fish to actively position themselves throughout the water column on a continuing basis (Höök et al. 2006). As a result, larval fish are at the mercy of current drift and often remain near the surface of the water (O'Gorman 1983;

Nash and Geffen 1991). This pattern may explain the trend we found for increasing abundance near the surface for both day and night collections.

The slight increase in larval fish abundance toward the surface may have also been influenced by thermal refuge. Although these nearshore waters typically have weak thermal stratification until late-July, water temperatures are always higher near the surface than near the bottom (Höök et al. 2006; K. Rounds, unpublished data). Considering this, larval fishes may seek thermal refuge in warmer waters near the surface. Brandt (1980) showed that young-of-the-year alewives in Lake Michigan were always in highest abundance in the warmest water available, which was near the surface in his study. In a controlled laboratory experiment, Olla and Davis (1990) determined that larval walleye pollock *Theragra chalcogramma* migrated up and away from colder benthic water temperatures to avoid physiological torpidity. Thus, vertical migration of larval fishes in southern Lake Michigan may be influenced by thermoregulatory dynamics.

Our efforts failed to describe non-random vertical distribution of larval fish at the 12 m depth contour. Whether this result accurately described larval distributions or the sampling lacked the statistical robustness to discern differences is unknown. Sampling depth can be an important consideration when detecting vertical migration in larval fishes. Brewer and Kleppel (1986) tested for diel vertical migration in nearshore larval northern anchovy *Engraulis mordax* and white croaker *Genyonemus lineatus* at three separate contours (8 m, 22 m, and 30 m) and found that abundance was highest at the 22 m depth contour, but this trend was species specific and was highly influenced by a few large samples. Hensler and Jude (2007) conducted surface trawl tows over two depth contours (3 and 6 m) to investigate diel vertical migration of larval round goby in nearshore Lake Michigan but found no difference in abundance between these two depth contours. Considering these other findings, it is unlikely that including additional depth contours in our study, either deeper or shallower, would have affected our outcome.

Sampling gear and methodology can have profound effects on the interpretation of abundance results (Colton et al. 1980; Cada and Loar 1982). During our stratified sampling to detect diel vertical migration, the Tucker trawl was deployed deep enough below the boat to sample one meter off the bottom during the bottom strata tow. This was to avoid hanging the net on potential hazards, such as boulders, and to avoid collections of heavy clay and sand. As a result, it is possible that the immediate bottom was not efficiently sampled and the trawl passed over benthic larvae. Hensler and Jude (2007) used a benthic larval sled that was able to more efficiently sample the immediate bottom in an effort to study diel vertical migration in round goby. However, their benthic sled tows produced few larval round goby ($N = 3$) compared to surface tows conducted with a separate net ($N = 208$). Thus, even for benthic species like round goby, water currents or the bottom environment in this system may keep fish suspended and off the bottom during the larval stage. If so, the inability of our trawl to effectively sample the immediate bottom was likely not a confounding factor in our results.

This study concluded that diel variability in catch rates of larval fishes from nearshore southern Lake Michigan may not be explained by vertical migration, but rather by size-selective trawl avoidance specific to the size of the trawl mouth opening. We suggest that fisheries managers and researchers should know and understand gear bias for larval collections. Although we did not evaluate mesh size of the trawl, there has been some indication that mesh size will also affect larval catch, particularly when towing speeds create backwash (O'Gorman 1984). We found no difference of catch abundance comparing day and night catches for varying size trawls, but trawling at night will capture larger fish, regardless of trawl size. We described recruitment of alewife to a commonly used trawl, which should provide a template for other fishes, both in Lake Michigan and elsewhere. However, across the board size-selective trawl inferences for different species cannot be directly assumed, but rather, determined on a species by species basis.

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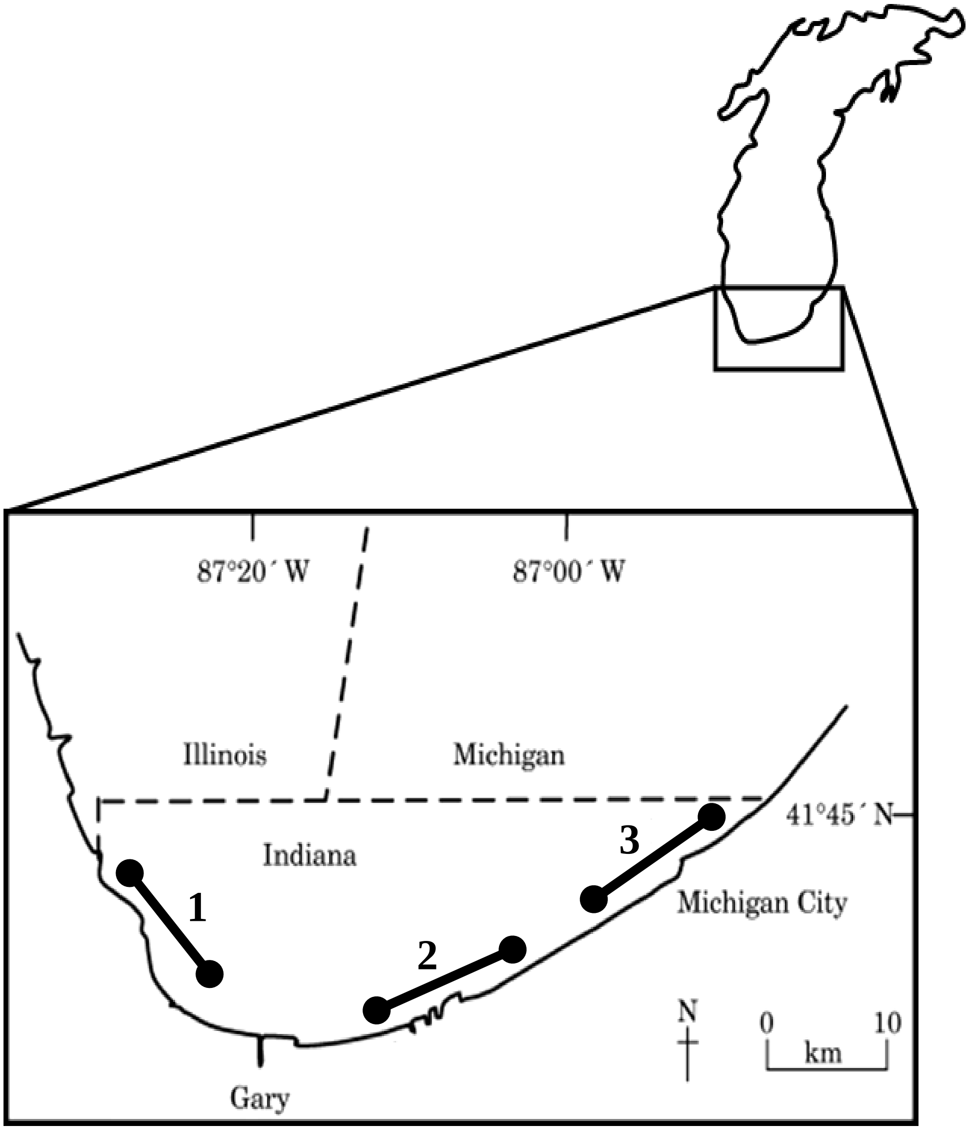

Figure 1. Approximate locations of 2010 and 2011 larval sampling zones East Chicago (1), Burns Harbor (2), and Michigan City Harbor (3) in the Indiana waters of southern Lake Michigan. Diel stratified sampling in 2011 was conducted at Michigan City (3).

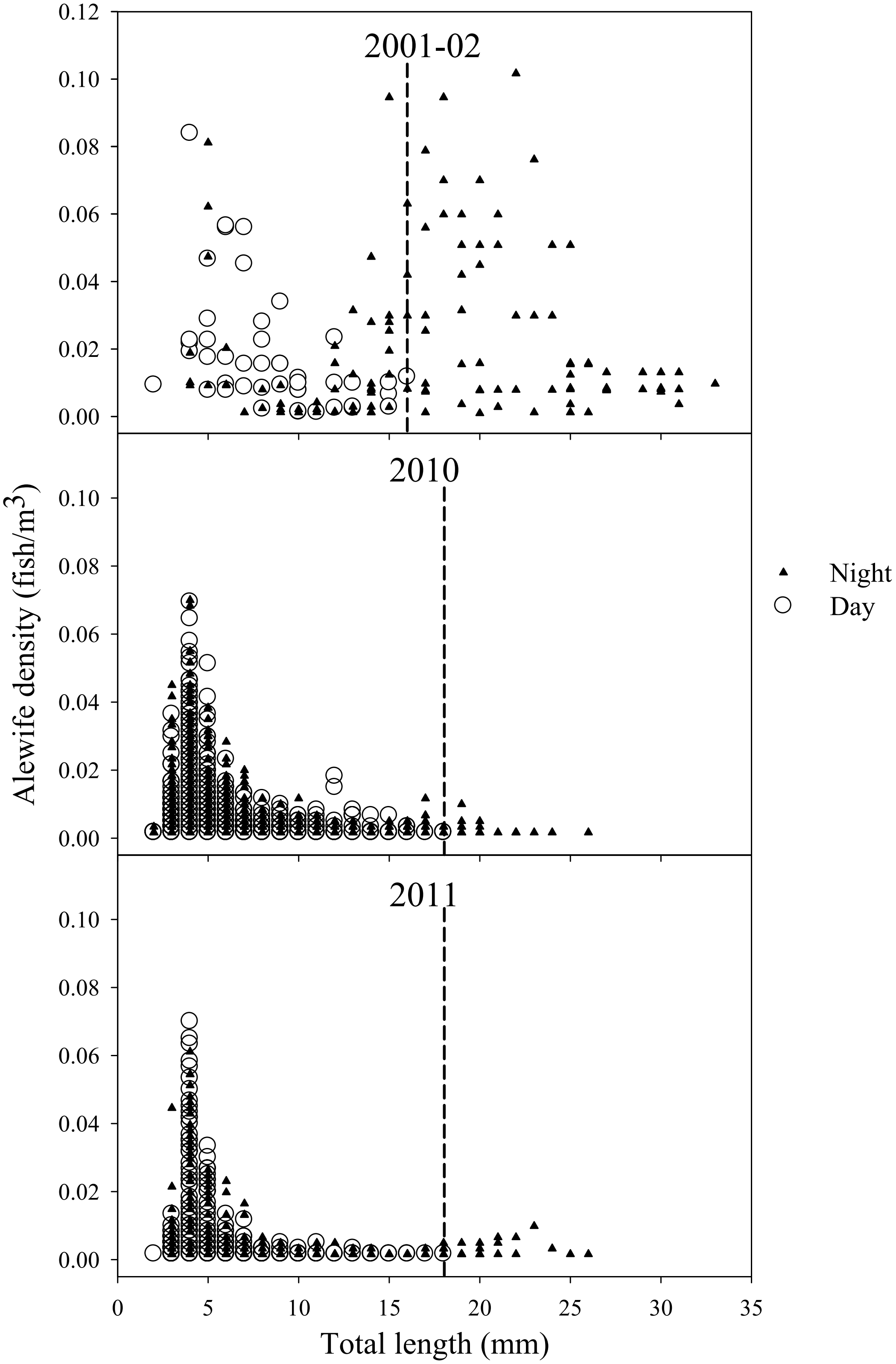

Figure 2. Length distributions of larval alewife collected day and night during 2001 and 2002 (top panel), 2010 (middle panel), and 2011 (bottom panel) from lakes Michigan and Muskegon. The vertical dashed lines represent the cutoff length for day samples. Lengths are total length measurements in 1 mm bins.

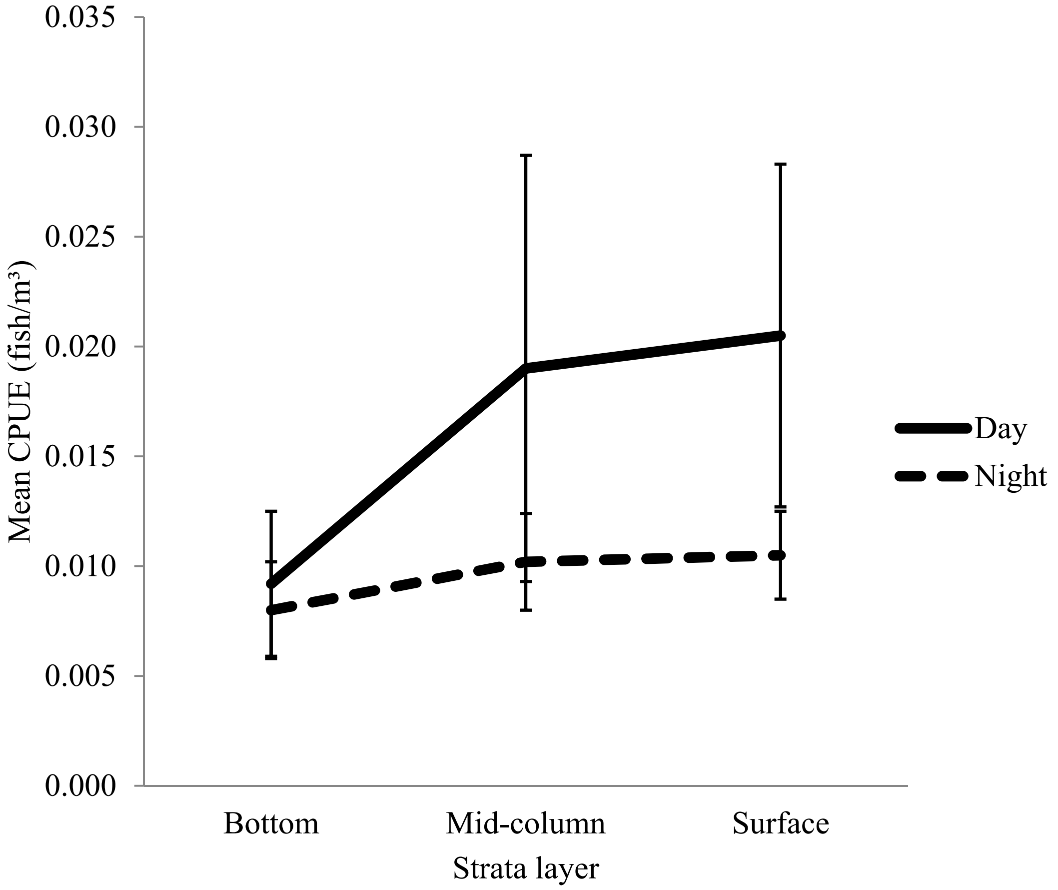

Figure 3. Mean CPUE of larval fish (with standard error bars) caught during day and night at each strata layer during 2011 in the Indiana waters of Lake Michigan.