Status and condition of *Mysis diluviana* in Lakes Michigan and Huron, 2007-2008

by

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Table of Contents

Page

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List of Tables

Page

List of Figures

Page

Abstract

The opossum shrimp (*Mysis diluviana*) is an important part of Great Lakes ecosystems, but its role may be changing as invasive species alter the lower food web. I investigated the new role of *Mysis* in food webs in Lakes Michigan and Huron in spring and summer 2007-08, with a focus on describing and comparing the abundance and condition of *Mysis* in the two lakes. I also investigated the importance of *Mysis* in late summer/early fall diets of pelagic forage fishes from both lakes. *Mysis* abundance and population characteristics were determined by counting and measuring samples taken from vertical tows in the two lakes. *Mysis* condition was assessed by analyzing total lipid content and fatty acid profiles of samples of *Mysis* collected from the study areas. Fishes for diet studies were obtained using midwater trawls performed during acoustic surveys. *Mysis* were more abundant in Lake Michigan than in Lake Huron, and comparisons with past studies suggested that densities might have declined in Lake Huron over time. Population dynamics revealed that *Mysis* had similar reproductive patterns in the two lakes, with some recruitment occurring year-round, but gravid female *Mysis* in Lake Huron were smaller than in Lake Michigan and had smaller brood sizes. Large bloaters (*Coregonus hoyi*) and rainbow smelt (*Osmerus mordax*) were the most effective pelagic predators of *Mysis* in 2007 and 2008, but in general, occurrence of *Mysis* in fish diets was low. On average, *Mysis* in Lake Huron had lower total lipids and elevated concentrations of the fatty acid docosahexaenoic acid (DHA) in comparison with Lake Michigan mysids, particularly in spring, suggesting that they may have experienced food limitation in Lake Huron. These data suggest that declines in phytoplankton and zooplankton production in Lake Huron in recent years, linked to dreissenid mussel expansion, are resulting in starvation of *Mysis* during at least part of the year.

Introduction

Since European colonization, the Laurentian Great Lakes have been defined by rapid environmental change. Past anthropogenic impacts on the Great Lakes were often direct and measurable, such as the presence of contaminants in fish and eutrophication due to phosphorus enrichment. Solutions to these issues were clear, although not always easy to implement. Recently, however, human impacts have become more indirect and solutions are even more elusive. Invasive species, introduced via shipping canals and ballast water, have dramatically altered aquatic food webs in the Great Lakes, making them "severely impaired" in all four lower Lakes (EPA and Environment Canada 2007). Perhaps most dramatic has been the collapse in populations of the once-dominant benthic amphipod *Diporeia*, which has been linked to the spread of invasive dreissenid mussels (quagga, *Dreissena bugensis* and zebra, *D. polymorpha*) (Nalepa et al. 1998, Nalepa et al. 2007). Non-indigenous species introductions have rapidly and dramatically altered phytoplankton, zooplankton, benthos, and fish communities in Lake Michigan (Madenjian et al. 2002). Primary production in Lake Michigan and Lake Huron has declined drastically in the last 5 years, likely due to dreissenid mussel filtering (Barbiero et al. 2009a, Fahnenstiel et al. 2010, Mida et al. 2010). In Lake Huron, changes in the lower food web have led to decreased condition of salmonines, requiring reductions in stocking and resulting in the loss of an important recreational fishery (Michigan Dept. of Nat. Res. 2005). This begs the question: will Lake Michigan soon follow the pattern observed in Lake Huron? Will changes in the lower food web jeopardize the economically important Lake Michigan salmonine fishery as well?

To begin to investigate these questions, many unanswered questions in the understanding of Great Lakes food webs must be addressed. Linkages between trophic levels must be elucidated, and the status of important species must be monitored. One such species is the opossum shrimp, *Mysis diluviana* (formerly *Mysis relicta*, hereafter *Mysis*), which along with *Diporeia* is known to be an important prey item for numerous species of fish, both benthic and pelagic (Wells and Beeton 1963, Crowder et al. 1981, Crowder and Crawford 1984, Kraft and Kitchell 1986, Kitchell et al. 2000). *Mysis* is an opportunistic omnivore that feeds on phytoplankton and zooplankton in both the benthic and pelagic regions of lakes (Grossnickle 1982), making it important to energy and nutrient exchanges between these two zones. *Mysis* has been shown to have substantial impacts on food webs both as a native species (Kitchell et al. 2000, Gal et al. 2006) and as an introduced species (Chess and Stanford 1998, Chess and Stanford 1999). Thus, *Mysis* may be a linchpin in recent food web responses to external drivers such as invasive species. Additionally, the importance of *Mysis* as a prey item may have increased as food webs respond to the loss of the formerly dominant *Diporeia.* In Lake Ontario, fishes such as juvenile lake trout (*Salvelinus namaycush*), alewives (*Alosa pseudoharengus*), and rainbow smelt (*Osmerus mordax*) shifted their ranges deeper following the *Diporeia* collapse, increasing predation pressure on *Mysis* (O'Gorman et al. 2000). Predation pressure on *Mysis* from lake whitefish (*Coregonus clupeaformis*) (Owens and Dittman 2003) and the invasive round goby (*Neogobius melanostomus*) (Walsh et al. 2008) has also increased in Lake Ontario. In southern Lake Michigan, contribution of *Mysis* to lake whitefish diets increased following the *Diporeia* decline, and whitefish condition declined with the loss of their preferred prey (Pothoven et al. 2001). Predation on *Mysis* by bloaters (*Coregonus hoyi*) and slimy sculpin (*Cottus cognatus*) also increased in southern Lake Michigan in response to the *Diporeia* decline

(Hondorp et al. 2005). In Lake Huron, the contribution of *Mysis* to deepwater sculpin (*Myoxocephalus thompsoni*) diets increased as the contribution of *Diporeia* decreased (O'Brien et al. 2009).

Despite its demonstrated importance to Great Lakes food webs, *Mysis* has been poorly studied in Lake Huron, and recent studies in Lake Michigan are limited in spatial extent (Pothoven et al. 2010). The goal of this study was to establish a baseline understanding of the status and condition of *Mysis* populations in lakes Michigan and Huron to provide insight into the role *Mysis* may play in changing Great Lakes food webs. Including both lakes permits comparisons between a system with a severely impaired food web (Lake Huron) and a system that remains more stable (Lake Michigan).

Specifically, this study had three objectives. The first was to describe the abundance and population characteristics of *Mysis* in Lakes Michigan and Huron, and to compare these data with past research to evaluate long-term changes in *Mysis* populations. Data for abundance and population characteristics came from *Mysis* samples collected in spring and summer 2007 and 2008 as part of the U.S. EPA's Great Lakes National Program Office's (GLNPO) monitoring program. The second objective was to examine the diets of pelagic prey fish in both lakes to quantify predation pressure faced by *Mysis* and to understand *Mysis*-fish interactions in pelagic food webs. Fish for these analyses were obtained using midwater trawls during the United States Geological Survey – Great Lakes Science Center's (USGS-GLSC) annual acoustic surveys. The final objective of this study was to assess *Mysis* condition to examine whether recent declines in primary production are having important bottom-up effects on *Mysis*. Ideally, bottom-up effects on *Mysis* populations would be studied through direct analysis of *Mysis* diets, or more indirectly through stable isotope analysis. For the purposes of this study, however, *Mysis* total lipids (TL) and fatty acid (FA) composition were used as proxies for food quality and availability. Information on TL can indicate whether invertebrates are food-limited and near the minimum level necessary for reproduction (Hill et al. 1992, Cavaletto et al. 1996). Fatty acid profiles can provide even more detail, as they represent the diet of an organism integrated over a longer time than the snapshot provided by direct diet analysis (Napolitano 1999). Further, certain fatty acids, called essential fatty acids (EFAs), are of particular importance to fish (Arts 1999) and respond in a predictable manner to starvation (Schlechtreim et al. 2008). Analyses in this study focused on these EFAs, especially docosahexaenoic acid (DHA), because *Mysis* experiencing starvation consistently contain elevated levels of this fatty acid (Schlechtreim et al. 2008). Results from this study should help managers understand changes in the food webs of Lakes Huron and Michigan, and to predict changes that may occur in Lake Michigan if it follows Lake Huron’s example.

Methods

Field collection of *Mysis*

Mysis samples were collected from lakes Michigan and Huron in spring and summer 2007 and 2008 during EPA-GLNPO monitoring cruises aboard the R/V Lake Guardian (Figs. 1 and 2, Table 1). Generally, spring cruises were in April during isothermal conditions, and summer cruises were in August when the water column was fully stratified. Temperature and conductivity profiles at each station were recorded with a Seabird STE-911 CTD (conductivity, temperature, depth) multi-sensor unit. Station depths were generally deeper in Lake Michigan than in Lake Huron (Table 1).

Mysis vertical tows were taken only at night, at least 1 hr after sunset and no later than 1 hr before sunrise. Although the research vessel operated 24 hours a day, with some stations sampled during daylight, only those stations reached at night were sampled for *Mysis*. Prior to arrival at a Mysis station, all external ship lights were extinguished and technicians used infrared flashlights on deck to avoid mimicking sunlight and causing *Mysis* to descend in the water column. Tows were taken with a 1 m x 1 m square net, which extended 2 m to a cod end container. The top two-thirds of the net was made of 1 mm bar mesh Nitex, and the bottom one-third of 250 µm Nitex. The mouth of the net was sent to 2-4 m above bottom, depending on conditions. It was raised to the surface at a speed of 0.5 $m \cdot s^{-1}$ and washed down to ensure collection of any *Mysis* that were clinging to the net. Samples were transferred to 500 mL or 1 L Nalgene bottles, where *Mysis* were anesthetized immediately with carbonated water and preserved in 10% sugar-buffered formaldehyde solution. Two replicate tows per station were preserved in this way in both 2007 and 2008. In 2008, a third tow, taken at each station for lipid analysis, was anesthetized as described above, then individuals were blotted dry, sorted into three categories according to sex and maturity level (males, females, and juveniles), placed in plastic vials, and immediately frozen in liquid nitrogen. Deep-freezing ensured lipids did not degrade or leach before samples arrived at the laboratory for analysis.

Mysis samples for lipid analysis were also collected during USGS-GLSC acoustic surveys in late summer and early fall of 2008, in Lake Huron aboard the R/V Grayling and in Lake Michigan aboard the R/V Sturgeon. Sampling took place at 13 stations in Lake Michigan (Fig. 1, Table 1) and eight stations in Lake Huron, with three of the Lake Huron stations occurring in Georgian Bay (Fig. 2, Table 1). Tows were performed as described above; however, samples for lipid analysis from these third tows were stored onboard the ship in a -80°C freezer.

Laboratory analysis

In the laboratory, formaldeyhde-preserved *Mysis* were rinsed and transferred to an enamel pan. Individual animals were counted and measured, and adults (defined as length > 10 mm, Pothoven et al. 2004) were sexed. Total length was defined as the length from the tip of the rostrum to the end of the last abdominal segment. All measurements were performed on photographs of about 20 *Mysis* at a time using a Moticam 1000 1.3M-pixel camera and Motic Images Plus 2.0 imaging software (Motic 2007). Length was measured to the nearest 0.1 mm. Brood sizes were determined for gravid females, and type of brood (eggs or larvae) was recorded. Females in samples with larvae or eggs found free-floating were noted as possibly having expelled part of their broods during sampling. For abundance determination, *Mysis* heads that had become separated from bodies were counted as one individual; these individuals were not measured or sexed.

Lipid and fatty acid analyses were conducted at the USGS-GLSC. Samples were held at -80°C until processing. Fatty acids were extracted according to Folch et al. (1957), using chloroform:methanol (2:1 v:v) containing 0.025% butylated hydroxytoluene (BHT) as an antioxidant. Solvents were evaporated under nitrogen gas and the percent lipid was determined gravimetrically. A minimum wet weight of 0.10 g of tissue was necessary for accurate extraction, so generally three to five adult mysids from an individual station were pooled into a single sample. In some cases, only juvenile mysids were pooled into one sample, usually requiring 40-50 individuals to reach the minimum weight needed for extraction. When sample sizes were especially small, male, female, and juvenile mysids were combined. This resulted in three different sample types for lipid and fatty acid analyses: adults only, juveniles only, and mixed. Sex and length of individual *Mysis* were not determined prior to fatty acid extraction. Preliminary statistical tests determined that lipids and fatty acids of samples containing only juveniles and samples containing a mix of juveniles and adults did not differ significantly, so these two types were pooled in subsequent statistical analyses.

Fatty acid methyl esters (FAMEs) preparation followed Metcalfe and Schmitz (1961). Thirty-five separate FAMEs, including C19:0 as an internal standard, were quantified by a gas chromatograph-mass spectrometer (GC/MS) using an Agilent GC/MS system (HP 6890 GC and HP 5973 MS) with a Supelco® Omegawax™ 320 column and helium as the carrier gas. Injector temperature was 250°C. Oven temperature programming was per Rinchard et al. (2007). Mass spectrometer source temperature was 230°C. Positive identification of FAMEs was made by comparing retention times of standards prepared by Nu-Chek-Prep, Inc. and Supelco®; and with known spectrographic patterns of FAMEs as determined by William W. Christie at the Scottish

Crop Research Institute (and MRS Lipid Analysis Unit), Invergowrie, Dundee (DD2 5DA), Scotland (www.lipidlibrary.co.uk).

Total lipids (TLs) were measured as percentage of *Mysis* wet weight or %WW. Total lipids are typically reported as percentage of dry weight (%DW). Thus, I converted the wet weight of each sample to dry weight using the equation developed for *Mysis* by Chipps (1997):

$$DW = \left(\frac{WW}{1.14}\right)^{1.37}$$

I then calculated %TL for each sample using the dry weights, and these values are reported and compared to data from the literature.

Individual FAMEs are reported as percentage of total FAMEs detected. Weight (in mg) of separate FAMEs in each sample was determined during analysis, making it possible for fatty acid to TL ratios for each sample to be calculated gravimetrically using weights of individual FAs and TL weight.

Fish diet analysis

Diet analysis was performed on three species of pelagic prey fish: bloaters, rainbow smelt and alewives. These fish were chosen because they comprise a majority of the pelagic prey fish community in both lakes (Bunnell et al. 2006, Warner et al. 2009). Fish for diet analysis were collected in midwater trawls performed during USGS-GLSC and Michigan Department of Natural Resources (DNR) acoustic surveys of both lakes in 2007 and 2008 (Figs. 1 and 2, Table 1), using methods outlined in Warner et al. (2008) and Warner et al. (2009). Lake Michigan surveys were in August and Lake Huron surveys were in September in both years. Fish were frozen aboard the vessels and transported to the lab for storage. Fish were thawed only when ready to be processed, and once thawed had their total length measured to the nearest 1 mm and wet weight recorded to the nearest 0.1 g. Fish stomachs were excised and preserved in glass vials with 70% ethanol.

Fish of each species were divided into three size categories based upon length-frequency histograms. Categories were as follows: bloaters: 0-90 mm, 90-150 mm, >150 mm; rainbow smelt: 0-60 mm, 60-120 mm, >120 mm; and alewives: 0-90 mm, 90-130 mm, >130 mm. Hereafter, these size categories are referred to as small, medium, and large. Up to five non-empty stomachs from each size category from each species were sub sampled at random for every site and analyzed for stomach contents (overall N=376). To expedite diet analyses, only *Mysis* remains, when present, were identified and counted. Other contents were reserved for future analysis. Whole *Mysis*, individual eyes, and individual statocysts (clear, hard, round structures in the telson) were counted. The highest obtained count between eyes and statocysts was divided by two (after adding one to any odd numbers), and this number was added to the count of whole *Mysis* to obtain a total. Percent occurrence (%O) was used to analyze the importance of *Mysis* in prey fish diets and was calculated by dividing the number of stomachs containing evidence of *Mysis* by the total number of stomachs processed for a particular species and size class. Abundance of *Mysis* in diets was also used as a metric in analyses.

When possible, size of *Mysis* in stomachs was determined by measuring the antennal scale (exopodite of the second antenna) length and converting to total length using the equation from Sell (1982), derived from Grossnickle and Beeton (1979):

Total body length (mm) = 6.18*[antennal scale length (mm)] + 0.50.

Total length in Grossnickle and Beeton (1979) was measured from the tip of the rostrum to the apices of the telson, whereas total length in this study (hereafter referred to as standard length) was defined as the length from the tip of the rostrum to the end of the last abdominal segment. A linear regression was performed to convert *Mysis* standard length to Grossnickle and Beeton's (1979) definition of total length. From the EPA's spring and summer 2008 cruises in both Lake Michigan and Lake Huron, 44 adult and 108 juvenile *Mysis* had their standard and total lengths measured, and a linear regression was performed to relate both length measurements (Figure 3). The resulting equation (R^2=0.97) is as follows:

Mysis total length (mm) = 1.2653*[*Mysis* standard length (mm)] – 0.223.

This equation was used to convert the antennal scale measurements to standard lengths that are comparable to the rest of the measurements in this study.

Data analysis

Generally, data on *Mysis* abundance, length, total lipids, FAMEs, and %O in fish diets were pooled according to lake basin. In other words, data from all stations within a particular basin were averaged to obtain basin-wide means. This was necessary due to low sample sizes. Lake Michigan was divided into a southern basin (SLM) and a northern basin (NLM) based on a line drawn west from the town of Ludington on the eastern shore. Lake Huron was split into northern (NLH) and southern (SLH) basins based on a line drawn east from the town of Oscoda at the northwest end of Saginaw Bay. Lake Huron's two embayments, Georgian Bay (LHGB) and the North Channel (LHNC), were analyzed as separate basins.

Data were compared among basins within a lake using independent samples Student's t-tests or one-way ANOVAs, with results reported as (t, p) or (F, p), respectively. Where assumptions of tests were not met, the equivalent non-parametric tests, Mann-Whitney U (U,p) and Kruskal-Wallis H (χ^2, p), respectively, were used. Data were log transformed when necessary. When no significant differences were detected among basins, those basins were pooled. In some cases, either when sample sizes were very low or when no significant differences among basins were detected, all data from a lake were pooled to obtain lake-wide means. Data were compared between the two lakes, or within a lake across seasons or years, using independent samples t-tests or the equivalent non-parametric test where necessary. Linear regressions were used to analyze the relationships between some variables; data were log transformed when necessary to meet the assumptions of linear regression. Predictive Analytics SoftWare (PASW) Statistics 17.0 software was used for all statistical analyses (SPSS Inc. 2009, Chicago, IL). A significance level of $\alpha = 0.05$ was used in all tests; for nonparametric Mann-Whitney U tests, exact significance is reported.

Results

Mysis abundance and population characteristics

Abundance: During spring and summer 2007 and 2008 mean *Mysis* abundance (number·m^{-2}) was generally higher in Lake Michigan than in Lake Huron, and basin-wide mean abundances were higher in summer than in spring in both lakes (Fig. 3, Table 2). While lake-wide abundances in Lake Michigan were consistently higher than in Lake Huron, these differences were not always significant. In spring 2007, Lake Michigan mean abundance was significantly higher than Lake Huron mean abundance (U, $p=0.008$), but Michigan and Huron lake-wide means were not significantly different in spring 2008 (U, $p=0.533$). In summer 2007 mean abundance in Lake Michigan was higher than in Lake Huron, but this difference was not significant (U, $p=0.085$); the Lake Michigan mean in summer 2008 was significantly higher than the Lake Huron mean (U, $p<0.001$). Although some interannual variability in *Mysis* abundance was observed, lake-wide means in both lakes did not differ significantly within either season across years, and there was no consistent pattern from 2007 to 2008 (Fig. 3, Table 2).

Population composition: Juvenile *Mysis* (those <10 mm) generally dominated the population, especially in summer, comprising 40 to 71% of the catch in spring and 65 to 88% of the catch in summer in Lakes Michigan and Huron (Table 3). In Lake Michigan's two basins, adult females generally made up a larger portion of the population than adult males. Proportion of males was higher than that of females in only one case, in Lake Michigan's southern basin in spring 2007; however, 20% of adults in this sample were not sexed so relative proportions are unreliable (Table 3). There was no consistent pattern in male-female ratios in Lake Huron, although proportion of females tended to be higher in the northern basin and proportion of males higher in the southern basin

In Lake Michigan in spring (pooling 2007 and 2008 samples), 16% of females had broods; in Lake Huron the proportion was 21%. Proportions of females with broods were lower in summer; no gravid females were encountered in Lake Huron summer samples, and only 6% of females had broods in Lake Michigan. Mean length of gravid females in spring in Lake Michigan was larger than in Lake Huron, with averages of 14.7 and 14.0 mm, respectively, but this difference was not significant (U, p=0.148). Of the two brood types – eggs and larvae – larvae were more common in Lake Michigan in spring, comprising 67% of broods. In Lake Huron in spring and in Lake Michigan in summer, 50% of broods consisted of larvae. Average brood size (number of eggs or larvae) was 17.5 (SD 3.6) in Lake Michigan in spring, significantly larger than the average size of 12.3 (SD 3.8) in Lake Huron in spring (U, p=0.022). Mean brood size of gravid mysids was 16.0 (SD 4.6) in Lake Michigan in summer.

Mysis size: *Mysis* length distributions (Figs. 4 and 5) show modes (representing individual cohorts) generally occurring at around 5 and 10 mm in spring and at around 5 and 15 mm in summer. Presence of juveniles between 2 and 5 mm in August indicates that some recruitment took place in summer, although the largest influx of juveniles to the population appears to occur in spring. Generally, adult females were larger than adult males, except in southern Lake Huron in summers 2007 and 2008 (Fig. 6, Table 4). On a lake-wide mean basis, males in Lake Michigan were larger than males in Lake Huron during all periods except spring 2007. Females were also generally larger in Lake Michigan, except in spring 2007 (Table 4). Juvenile mysids (<10 mm) were usually larger in Lake Michigan as well, with spring 2008 the exception. Mean length of adults consistently increased from spring to summer, representing growth, whereas mean size of juveniles tended to decrease between the two seasons, likely reflecting timing of recruitment of new cohorts.

Factors influencing Mysis abundance: Pearson correlations and linear regressions were used to explore relationships between *Mysis* abundance and several other variables. Using data from both years and both seasons, *Mysis* abundance in Lake Michigan increased significantly with increasing station depth (b=1.91, R^2=0.72, $p<0.001$) (Fig. 7a). While abundance in Lake Huron appears to show an increasing trend with increasing station depth (Fig. 7b), the relationship was not clearly linear. Depth and *Mysis* abundance in Lake Huron were significantly correlated, but station depth explained a much lower amount of the variation in abundance than in Lake Michigan (r=0.50, p=0.006; Lake Michigan: r=0.85, $p<0.001$). Pooling data from both lakes, there was no significant correlation between *Mysis* abundance and total lipids (r= -0.08, p=0.739).

Pelagic prey fish diet analyses

Fish characteristics: A subsample of alewives, rainbow smelt, and bloaters collected from midwater trawls in Lakes Michigan and Huron in late summer and early fall 2007-08 had their diets processed for *Mysis* remains. On average, bloaters collected from Lake Michigan were similar in size to those collected from Lake Huron (Fig. 8), with averages of 108 mm (SD 65) and 103 mm (SD 41), respectively. Bloaters were more abundant in the catches from Lake Huron than from Lake Michigan (Table 5). Alewives were larger in Lake Michigan (Fig. 9), with a mean size of 107 mm (SD 44); mean length in Lake Huron was 45 mm (SD 5). Alewives were more abundant in catches from Lake Michigan (Table 5). Rainbow smelt tended to be larger in Lake Huron than in Lake Michigan (Fig. 10), with mean sizes of 94 mm (SD 30) and 45 mm (SD

26), respectively. More rainbow smelt were analyzed from Lake Huron than from Lake Michigan (Table 5).

Frequency of occurrence (%O) of Mysis in diets: Lake-wide total %O of *Mysis* for a given size category of fish ranged from 0 to 77%, with the maximum found in bloaters larger than 150 mm from Lake Michigan in 2008. Frequency of occurrence for fish size categories in individual basins was as high as 100% (Table 5). Large bloaters were consistently effective *Mysis* predators in both lakes, with generally higher %O of *Mysis* than the other two species studied. Alewives had consistently low %O of *Mysis* in diets (Table 5), with a maximum of only 20% for large (>130 mm) alewives observed in northern Lake Michigan in 2007. In 2008, %O for all alewives was 0% in both lakes. Rainbow smelt appeared to be more effective predators of *Mysis* in Lake Huron than in Lake Michigan. No rainbow smelt were caught in trawls in Lake Michigan in 2007, but of 14 processed from that lake in 2008, none contained *Mysis*.

Number and size of Mysis consumed: Number of *Mysis* in alewife diets in Lake Michigan in 2007 was low, ranging from zero to eight. No bloater stomachs collected from Lake Michigan in 2007 contained *Mysis*. In 2007, numbers of *Mysis* consumed by fish in Lake Huron were relatively high, with maximums of 79 for rainbow smelt and 68 for bloaters. In Lake Huron in 2008, number of mysids in diets was lower, with a maximum of only eight for rainbow smelt. No bloater or alewife stomachs collected from Lake Huron in 2008 contained *Mysis*. The number of mysids consumed by bloaters from Lake Michigan in 2008 ranged from zero to 48.

Number of *Mysis* in stomachs showed a significant positive relationship with fish length (b=0.01, R^2=0.17, p=0.001) (Fig. 11). In Lake Huron in 2007, large bloaters and large rainbow smelt consumed *Mysis* in similar numbers; differences were insignificant (t, p=0.904), with means of 9.2 (SD 17.2) and 10.1 (SD 24.0), respectively. Large bloaters in Lake Michigan on average consumed 14.9 (SD 17.8) *Mysis*, which was not significantly different from the mean of 9.2 (SD 17.2) *Mysis* per fish consumed by large bloaters in Lake Huron (t, p=0.385).

Mean length of *Mysis* consumed also increased significantly with increasing fish length (b=0.01, R^2=0.03, p=0.006) (Fig. 12). In Lake Huron in September 2007, bloaters on average preyed upon significantly larger *Mysis* than rainbow smelt (U, p<0.001), with mean lengths of mysids in diets of 9.0 mm (SD 3.0) and 7.4 mm (SD 1.9), respectively. Mean size of *Mysis* consumed by large bloaters in Lake Michigan was 9.5 mm (SD 2.2), which was not significantly different from the mean *Mysis* size of 9.0 (SD 3.0) eaten by Lake Huron fish (t, p=0.402).

Lipid and fatty acid analyses

Spring Total lipids: *Mysis* sample sizes were low in both lakes in spring 2008 (Table 6), so samples of all types from all basins within a lake were pooled for statistical analyses. Total lipid as % of wet weight (%TL) of *Mysis* from Lake Michigan was higher than *Mysis* from Lake Huron, but this difference was not significant (U, p=0.333).

Summer total lipids: Sample sizes were generally higher in summer than in spring (Tables 7 and 8). Total lipids of adult mysids in Lake Michigan were consistently higher than in Lake Huron. The mean %TL of adult mysids from northern Lake Michigan was significantly higher than that of Lake Huron mysids (U, p<0.001) (Fig. 13). Northern Lake Michigan’s mean %TL was not significantly different from southern Lake Michigan’s mean (U, exact sig.=0.152, asymptotic sig.=0.047). Total lipids in southern Lake Michigan and Lake Huron mysids did not differ significantly (U=39.0, p=0.176).

As with adult *Mysis*, samples containing juvenile mysids from Lake Michigan had significantly higher mean %TL than from Lake Huron, with means of 17.3% and 10.7%, respectively (t, p=0.033) (Fig. 14, Table 8).

Seasonal change in total lipids: Because of small sample sizes in spring, data from all sample types and all basins within each lake were pooled for analyses of seasonal changes. Mean lake-wide %TL in Lake Michigan in spring was not significantly different from the summer mean of 22.2% (SD 8.4) (t, p=0.530). Total lipids from Lake Huron also did not change significantly from the spring mean to the summer mean of 13.5% (SD 4.8) (U, p=0.338) (Fig. 15).

Spring % Docosahexaenoic acid (%DHA): Amount of the fatty acid DHA is expressed as percentage of total fatty acids. Due to low sample sizes in spring, as explained previously, all sample types and lake basins were pooled. In Lake Michigan, mean %DHA was lower than in Lake Huron (Table 6), a difference that was barely insignificant (U=0.0, exact sig.=0.056, asymp. sig.=0.040).

Summer %DHA: In Lake Michigan, mean %DHA in adult mysids from the southern basin was significantly higher than the northern basin mean (U, p=0.038) (Table 7). Thus, the two basins of Lake Michigan were analyzed separately in subsequent comparisons with Lake Huron. Significant differences in %DHA of adult mysids were also observed among the basins of Lake Huron (χ^2, p=0.003). Post-hoc comparisons revealed that the mean %DHA in Georgian Bay samples was not significantly different from the North Basin mean (U, p=0.368), but that the southern basin mean was significantly lower than both the northern basin (U, p=0.004) and Georgian Bay (U, p=0.003). Thus, in comparisons with Lake Michigan, samples from northern

Lake Huron and Georgian Bay were pooled (LHN/GB), but southern Lake Huron was kept separate.

Significant differences were found in %DHA of adult mysids between the two lakes (Fig. 16). Mean proportions of DHA in NLM, SLM, and SLH were significantly lower than the northern Lake Huron/Georgian Bay mean of 13.3% (SD 2.7) (U, respectively: $p<0.001$; $p=0.032$; $p<0.001$). Percent DHA in SLH did not differ significantly from SLM (U, $p=0.371$) or NLM ($U=42.0$, $p=0.387$).

Mean %DHA of juvenile mysids in southern Lake Michigan was not significantly different from the northern basin mean (U, $p=0.667$), so the two basins were pooled. Percent DHA in juvenile mysids from the three basins of Lake Huron showed no significant differences (χ^2, $p=0.053$), so the three basins were pooled. The Lake Michigan overall juvenile *Mysis* mean %DHA of 12.0 (SD 4.5) was significantly lower than the Lake Huron mean of 15.6% (SD 3.5) ($U=24.0$, $p=0.017$).

Seasonal change in %DHA: Because of low sample sizes in spring from both lakes, data from all sample types and basins were pooled within each season for seasonal comparisons. In Lake Michigan, no significant change in %DHA was detected in *Mysis* collected during spring (11.1%) and summer (10.5%) ($U=84.0$, $p=0.780$) (Fig. 17). For Lake Huron *Mysis*, however, the average spring %DHA of 25.8% was significantly higher than the summer mean of 13.1% (SD 3.4) ($U=0.0$, $p=0.003$).

Other essential fatty acids (EFAs), spring: When data from all sample types and lake basins were pooled to obtain spring means (Table 6), no significant differences were detected in other EFAs between the two lakes, although some differences were almost significant. In Lake Michigan mysids, the mean proportion of linoleic acid methyl ester (LIN) was not significantly different than the Lake Huron mean (U, p=0.889). The EFA α-linolenic acid (ALA) was not detected in some *Mysis* from Lake Michigan and was low when detected; ALA was not detected in any Lake Huron samples. In Lake Michigan *Mysis*, mean proportion of arachidonic acid methyl ester (ARA) was barely insignificantly lower than the Lake Huron mean (U, exact sig.=0.056, asymp. sig.=0.040). Lake Huron *Mysis* also had higher percentage eicosapentaenoic acid (EPA) than Lake Michigan *Mysis*; however, the difference was not significant (U, exact sig.=0.056, asymp. sig.=0.040).

Other EFAs, summer: All summer means and comparisons used samples of adult mysids only (Table 7). This approach was used because the analyzed EFAs were chosen for their importance to fish, and larger *Mysis* appeared to be targeted by effective pelagic fish predators. Data from separate basins were pooled in the same way as in the %DHA analyses.

Significant differences in %LIN in *Mysis* were detected among the four basins (χ^2, p=0.035) (Fig. 18a). Mean %LIN was highest in northern Lake Huron/Georgian Bay, with a mean of 6.5% (SD 3.7), which was significantly higher than *Mysis* from NLM (U, p=0.011). The SLM mean %LIN was significantly higher than the northern basin mean (U, p=0.005). %LIN of adult mysids in SLH did not differ significantly from any of the other basins.

There was also a significant difference in %ALA among lake basins (χ^2, p=0.005), with consistently higher values in Lake Michigan (Fig. 18b). All basins contained some *Mysis* samples in which this EFA was not detected. Mean %ALA in southern and northern Lake Michigan did not differ significantly (U, p=0.661). Both were significantly higher than the northern Lake Huron/Georgian Bay mean of 0.8% (SD 1.3) (U, LMS: p=0.011; LMN: p=0.011). Mean %ALA in both Lake Michigan basins was also significantly higher than the SLH mean (U, LMS: p=0.028; LMN: p=0.043). Mean %ALA of adult mysids in the two basins of Lake Huron did not differ significantly (U, p=0.776).

Significant differences in %ARA of adult mysids were detected among the four basins (χ^2, p<0.001) with a pattern similar to that of LIN (Fig. 18c). The proportion of ARA was highest in NLH/GB with a mean of 5.7% (SD 1.0), which as significantly higher than the means from the other three basins (U, SLM: p=0.019; NLM: p<0.001; SLH: p<0.001). Mean %ARA in SLM was not significantly different from the SLH mean (U, p=0.206). Lowest mean %ARA was observed in northern Lake Michigan and was significantly lower than means for *Mysis* from all other basins (U, LMS: p=0.001; LHN/GB: see above; LHS: p=0.001).

Finally, %EPA in samples of adult mysids also differed significantly among lake basins (χ^2, p=0.001) and values were lowest in Lake Michigan, the opposite of what was observed with %ALA (Fig. 18d). Mean %EPA of northern and southern Lake Michigan mysids were not significantly different (U, p=0.069), but the NLM mean was significantly lower than both the NLH/GB mean of 17.5% (SD 1.8) (U, p<0.001) and the SLH mean (U, p=0.001). Percent EPA in southern Lake Michigan was also significantly lower than in NLH/GB (U, p=0.019), but was not significantly lower than SLH (U, p=0.099). Mean %EPA in Lake Huron's two basins did not differ significantly (U, p=0.517).

Fatty acid:total lipid ratio: Basin- and lake-wide mean ratios of fatty acids to total lipids (by weight) in mysids were calculated for each season and sample type (Tables 6-8). No significant difference in population-wide (i.e., all sample types pooled) summer ratios among basins was detected (χ^2, p=0.28), so basins within each lake were pooled to obtain lake-wide means for both spring and summer (Fig. 19). The FA:TL ratio in Lake Michigan mysids did not change significantly from spring to summer (U, p=0.450). In Lake Huron, on the other hand, the

FA:TL ratio in mysids increased significantly from spring to summer (U, $p<0.005$). The mean spring ratio in Lake Huron was marginally insignificantly lower than the mean spring ratio in Lake Michigan *Mysis* (U, exact sig.=0.056, asymp. sig.=0.040), and the ratios did not differ significantly in summer (U, $p=0.069$).

EFAs vs. Total Lipids: To further explore the relationship between EFAs and %TL in adult mysids in summer, linear regressions between total lipids and the percent composition of EFAs were performed (Table 9, Fig. 20). Only samples from summer were used in these analyses because of larger sample sizes; only adult *Mysis* samples were used because many of the samples containing juveniles were composed of a mix of adults and juveniles, potentially obscuring results. In addition, fish diet analyses showed that larger (adult) mysids are more important in fish diets. Samples in which a particular EFA was not detected were not used in regressions for that EFA.

In both lakes, %DHA decreased significantly with increasing %TL (Fig. 20a). The correlation was stronger in Lake Michigan than in Lake Huron (Table 9). Percent EPA also decreased significantly with increasing %TL in Lake Michigan, but there was no significant relationship in Lake Huron (Fig. 20e). The only other significant regression was between %ALA and %TL in Lake Michigan, with %ALA increasing with increasing %TL (Fig. 20c). Overall, %ARA showed a decreasing trend with increasing %TL (Fig. 20d), but this relationship was not significant in either lake. After removing two outliers from Lake Huron, %LIN still did not have a significant relationship with %TL in either lake (Fig. 20b).

Discussion

Mysis abundance and population characteristics

Mysis abundance was generally higher at Lake Michigan stations than at Lake Huron stations, a pattern apparent from past studies (Beeton 1960, Carpenter et al. 1974, Morgan and Beeton 1978, Grossnickle and Morgan 1979) and likely stemming from differences in productivity and suitable habitat between the two lakes. Densities in Lake Michigan have historically varied widely, but values observed in this study are generally similar to values from the 1970s (Morgan and Beeton 1978, Grossnickle and Morgan 1979), the 1980s (Lehman et al. 1990) and the mid-1990s and 2000 (Pothoven et al. 2000, Pothoven et al. 2004). Summer *Mysis* densities observed at offshore stations in this study were higher than those at a single offshore (110 m) station in southern Lake Michigan sampled by Pothoven et al. (2010) in 2007-08. Pothoven et al. (2010) concluded that *Mysis* abundance had declined at their offshore station between the late 1990s and 2007-08. Thus, it remains unclear whether *Mysis* abundance in Lake Michigan has remained stable or declined in recent years. Data on past *Mysis* abundance in Lake Huron is sparse, but mean *Mysis* densities in April and August 1971 (Carpenter et al. 1974) were similar to mean densities in 2007-2008. Comparisons between this study and work done in the 1950s (Beeton 1960) and 1970s (Carpenter et al. 1974) suggest that maximum densities in Lake Huron have declined. However, maximum density is dependent on the number of samples taken during a study, and thus may not be a good measure of comparison.

In Lake Michigan, there was a strong linear relationship between station depth and *Mysis* density, with the highest densities occurring at the deepest, farthest offshore stations. This pattern has been noted in Lake Michigan in the past (McDonald et al. 1990, Pothoven et al. 2000, Pothoven et al. 2004) and is consistent with the life history of *Mysis* since they prefer deep, cold waters (1-6 °C) (Balcer et al. 1984). In Lake Huron, however, station depth and *Mysis* density were not as strongly correlated and there was no significant linear trend. Past observations in Lake Huron showed a pattern similar to what I observed in Lake Michigan (Carpenter et al. 1974). Further exploration of the relationship between *Mysis* abundance and other environmental variables would be required to understand the mechanisms controlling *Mysis* density, but it appears there are important limiting factors other than depth in Lake Huron.

Females tended to outnumber males in Lake Michigan in this study, which has been observed in Lake Michigan *Mysis* populations in the past (Pothoven et al. 2000, Pothoven et al. 2004), whereas Lake Huron sex ratios did not show a consistent pattern. Past research in Lake Michigan indicates that juveniles dominated the population (Pothoven et al. 2000, Pothoven et al. 2004), as I observed for both lakes in this study. Analysis of growth rates from these data is not possible given the limited temporal sampling of this study, but length-frequency histograms suggest cohorts (4-5 mm) were recruited into the population during spring and late summer in both lakes, with larger cohorts in spring. Pothoven et al. (2000) also observed influxes of juveniles into the population in spring and late summer in Lake Michigan. This pattern of recruitment suggests that most reproduction occurs in late winter or early spring, but that some takes place year-round. Mean size of females with broods at offshore stations in southern Lake Michigan in the 1990s was 16.0 mm (Pothoven et al. 2000), slightly larger than the mean of 14.9 mm observed in this study. Proportion of females with broods in Lake Michigan in this study was similar to that in Pothoven et al.’s studies in southern Lake Michigan (2000, 2004, 2010), as were brood sizes. In general, population dynamics and reproductive characteristics of offshore *Mysis* populations in Lake Michigan appear to have changed little over the past decade.

Unfortunately, historical data on *Mysis* population and reproductive characteristics in Lake Huron is lacking, so trends over time cannot be assessed. Comparing Lake Huron to Lake Michigan, however, reveals some interesting differences. Population structures are similar, but mean size of females with broods and average brood size were both smaller in Lake Huron than in Lake Michigan. In general, both adult and juvenile *Mysis* in Lake Michigan were larger than those in Lake Huron. It seems that *Mysis* in Lake Huron may reach sexual maturity earlier than those in Lake Michigan and that they may not have as much energy to allocate to growth and reproduction. However, population dynamics and reproductive characteristics of *Mysis* populations in the Great Lakes vary widely due to various environmental factors (Balcer et al. 1984), so it is difficult to determine what may be causing these differences. Beeton and Gannon (1991) found that *Mysis* brood size was correlated with lake productivity, so the differences observed in this study may result from higher overall productivity in Lake Michigan.

Pelagic prey fish diets

Frequency of occurrence of *Mysis* in diets was generally low, with only a few size groups having a %O greater than 20%. Large bloaters were the only group with consistently high %O of *Mysis*. Wells and Beeton (1963) found that 59% of large bloaters in Lake Michigan contained mysids, and since frequencies of occurrence for large bloaters in this study were higher, it is possible that consumption of *Mysis* by individual bloaters has increased. Frequency of occurrence of *Mysis* in alewife diets was especially low. Walsh et al. (2008) noted similarly low %O of *Mysis* in alewives from Lake Ontario in 1995, 2002, 2003, and 2005, but found a high mean frequency of occurrence of 88% in rainbow smelt. Percent occurrence of *Mysis* in rainbow smelt diets in this study was much lower, with the maximum lake-wide mean only 42%

(for small rainbow smelt in Lake Huron in 2007), although %O was 100% in northern Lake Huron in 2008.

Overall, results from this study suggest that *Mysis* were not a substantial part of the diets of alewives, bloaters, or rainbow smelt in late summer/early fall 2007 or 2008 in Lakes Michigan and Huron. While it is possible that fish could be exerting considerable predation pressure on *Mysis* during other times of year, pelagic prey fish biomass in both lakes has declined so dramatically in recent years (Bunnell et al. 2006, Riley et al. 2008, Warner et al. 2009) that it is unlikely that predation is causing excessive mortality. Large bloaters were the only group with relatively high %O of *Mysis* in diets, but bloater abundance is currently very low (Riley et al. 2008), so any predation pressure exerted by bloaters is likely minor. The lack of substantial predation pressure suggests that top-down factors are unlikely to be important in controlling *Mysis* abundance and distribution.

Total lipids and DHA

Patterns in %TL and %DHA suggest that *Mysis* in Lake Michigan were in better condition than those in Lake Huron, which we may expect given that Lake Huron is historically less productive than Lake Michigan (Schelske et al. 2006). However, there is some indication that Lake Huron *Mysis* may be experiencing starvation. In Lake Huron in spring 2008, a mean %TL of 9.8% and a mean %DHA of 25.8% were observed. Schlechtriem et al. (2008) collected *Mysis* from Lake Ontario in April, exposed them to 6 weeks of fasting in the lab, and then measured their %TL and FA composition. They found that total lipids in starving *Mysis* dropped below 14% dry weight and that %DHA was elevated above 25%. Thus, observations from this study indicate possible starvation of mysids in spring in northern Lake Huron, at least on average. Because of the low sample size from Lake Huron in spring (three replicates from a single station, HU37), it is impossible to say with any certainty that mysids in Lake Huron are starving in spring. Due to spatial variation in *Mysis* populations and in the distribution of their food resources, these samples may not be indicative of the lake as a whole, or even the entire northern basin. In addition, conversion from wet weight to dry weight using the Chipps (1997) equation results in estimates of lipids as %DW that may not be directly comparable to Schlechtriem et al.'s (2008) data. However, %DHA is directly comparable to Schlectriem et al.'s (2008) data and lends support to the conclusion that *Mysis* at station HU37 are experiencing starvation in spring. In Lake Michigan in spring, mean %TL was well above the starvation threshold, and mean %DHA was well below it. Thus, there is no indication that *Mysis* in Lake Michigan were experiencing food limitation to the degree observed in Lake Huron. Lipid content of *Mysis* in Lake Michigan as measured in this study was lower than the mean of about 27% in Lake Michigan in April 1984 (Gardner et al. 1985), but that value is relative to ash-free dry weight (AFDW) and is thus expected to be higher. Based on this limited historical data, *Mysis* in Lake Michigan in spring appear to be in similar condition as populations in the 1980s.

Total lipids in both lakes increased from spring to summer, a pattern that has been observed in Lake Michigan in the past and that probably reflects increasingly available, high-quality food (Gardner et al. 1985). Although *Mysis* in Lake Michigan had consistently higher %TL and consistently lower %DHA than those in Lake Huron, none of the basin-wide means fit Shlechtriem et al.'s (2008) criteria for starvation in summer, so it appears that *Mysis* in both lakes experienced sufficient food resources in summer 2008. However, mean %TL of adult mysids in Lake Huron was 14.8%, close to the threshold level of 14%, suggesting that food resources were scarcer than in Lake Michigan. As observed in spring, mean %TL of *Mysis* in

Lake Michigan in summer 2008 was lower than means observed in summer 1984 (Gardner et al. 1985), but values from the 1980s are skewed high (because they were measured relative to AFDW), and differences were not large. Mean %DHA decreased in both lakes from spring to summer, with a drastic drop in Lake Huron, further indicating increased food availability in summer.

Schlechtriem et al.'s (2008) threshold levels represent starvation after 42 days, but sub-threshold levels are potentially also important to *Mysis* populations. For example, %TL in Shlechtriem et al.'s (2008) study dropped below 20% and %DHA surpassed 22% after 14 days of starvation. Several individual samples from both lakes were at or very close to those threshold levels, even in summer, suggesting that some *Mysis* may be experiencing periods of starvation year-round.

Other essential fatty acids

As was observed with %DHA, %ARA and %EPA tended to decrease with increasing %TL. Schlechtriem et al. (2008) also noted elevated ARA at low lipid contents, but they report a positive relationship between %EPA and %TL, although this relationship was not always significant. The current study suggests a positive relationship between %ALA and %TL, which was also observed by Schlechtriem et al. (2008). No relationship was apparent between %LIN and %TL; Schlechtriem et al. (2008) found a significant positive relationship between the two. Clearly, the response of EFAs to changes in total lipids is complex and likely varies from individual to individual and among populations of *Mysis*. Fatty acid profiles not only respond to quantity or quality of food, but also reflect the type of food in the diet (e.g., diatoms tend to be rich in EPA, zooplankters tend to be rich in ARA) (Schlechtriem et al. 2008), so spatial and temporal variation in phytoplankton and zooplankton populations will result in differences in *Mysis* FA profiles.

Because numerous variables affect fatty acids, it is difficult to interpret spatial differences in their composition. However, DHA and ARA are consistently conserved during fasting, with this pattern observed both in this study on *Mysis* from Lakes Michigan and Huron and in Schlechtriem et al.'s (2008) study on *Mysis* from Lake Ontario, so these FAs may be more reliable metrics of condition. The explanation for this phenomenon is that while storage lipids (primarily triglycerides) are used or depleted during starvation, membrane lipids tend to remain stable and thus will compose an increasing portion of total fatty acids under starvation conditions (Shlechtriem et al. 2008). Since these membrane lipids are rich in ARA and DHA, it follows that *Mysis* experiencing starvation will have increased proportions of these two EFAs. For adult mysids in summer in this study, %ARA was higher in southern Lake Michigan and northern Lake Huron/Georgian Bay than in the other basins. This is the same pattern as %DHA and suggests that *Mysis* in southern Lake Michigan and northern Lake Huron/Georgian Bay are in poorer condition than those in northern Lake Michigan and southern Lake Huron. Other EFAs, while less reliable as indicators of condition, show a different pattern. %ALA was higher in both Lake Michigan basins than in Lake Huron, and %EPA was lower in both Lake Michigan basins than in Lake Huron. The relationships between ALA and EPA and %TL support the hypothesis that *Mysis* in Lake Huron are in poorer condition than *Mysis* in Lake Michigan. Clearly, the factors determining fatty acid profiles in *Mysis* are complex, and we can do no better than speculate as to what spatial differences may mean.

In general, however, it is clear that *Mysis* in Lake Huron in 2008 were in poorer condition than *Mysis* in Lake Michigan, particularly in spring. This is supported by consistently higher

%TL and lower %DHA in Lake Michigan in both seasons and for both adult and juvenile *Mysis*, and by patterns in EFAs that respond directly to changes in %TL. The fatty acid: total lipid ratio was lowest in Lake Huron in spring, further supporting this finding. This ratio tends to be higher in animals with large amounts of storage lipids (Olsen 1999). Thus, the relatively low FA:TL ratio in spring samples from Lake Huron suggests that these *Mysis* had depleted their storage lipid reserves over winter and early spring. Further supporting the finding that *Mysis* in Lake Huron in spring 2008 were starving are the aforementioned differences in reproductive characteristics. Gravid females from Lake Huron were smaller than and had smaller brood sizes than gravid females from Lake Michigan, suggesting that stored lipid energy that would normally be allocated to growth and reproduction was used instead for survival and maintenance.

General discussion/integration

As discussed above, predation pressure on *Mysis* appears to be low, and prey fish biomass has declined drastically in both lakes. Increases in other food sources for pelagic prey fish may also be relieving predation pressure on *Mysis*. Abundance of the large copepod *Limnocalanus macrurus* has increased in Lake Michigan in the past decade, representing another food source for fish (Barbiero et al. 2009b). In Lake Ontario, the introduction of *Bythotrephes longimanus* and *Cercopagis pengoi* appears to be relieving predation pressure on *Mysis* (Walsh et al. 2008); this could be happening in lakes Michigan and Huron as well. Indeed, although food items other than *Mysis* were not counted or measured as part of the diet analyses in this study, qualitative observations suggest that the most common food items in diets of all species were *Bythotrephes* and large copepods.

This release from predation pressure due to declines in fish populations and increases in other viable prey items should result in increasing *Mysis* abundance. However, results of this and other studies show that *Mysis* abundance has remained steady or declined in Lake Michigan and may have declined in Lake Huron. It thus appears that top-down effects of predation on *Mysis* play a limited role in controlling their current abundance, and that bottom-up factors may be of primary importance. Results of the TL and FA analyses support this hypothesis. As discussed above, condition of *Mysis* in Lake Huron in spring suggests that parts of the population may be struggling to recover from overwinter starvation. *Mysis* in Lake Huron also appear to be in worse condition than those in Lake Michigan, even though density is lower in Huron. These results suggest that *Mysis* in Lake Huron are experiencing food limitation during at least part of the year.

There are several possible causes for the apparent food limitation of Lake Huron *Mysis* populations. If intraspecific competition among *Mysis* was important, we would expect to see worse *Mysis* condition where abundance is higher. As evidenced by the regression between *Mysis* abundance and %TL, higher *Mysis* densities do not appear correlated with deteriorated condition. Further, pelagic fish biomass in northern Lake Huron and Georgian Bay is much higher than in the southern basin (Warner et al. 2009), which should result in fewer *Mysis* that are in better condition in the north. However, *Mysis* in this region appear to be in the poorest condition of any basin (which is discussed in further detail below). Thus, density-dependent factors seem unlikely to be responsible for food limitation.

Competition with other large zooplankton species could also contribute to food limitation in *Mysis*. Diets of both *Limnocalanus* and *Bythotrephes* overlap with *Mysis* (Warren 1985, Branstrator and Lehman 1991, Lehman 1991) and these species have recently increased in abundance (Barbiero et al. 2009a, Barbiero et al. 2009b), which could increase competition for already-limited food resources and further stress *Mysis* populations.

The most likely explanation for decreased condition in *Mysis* is a decline in the availability of phytoplankton and zooplankton food resources due to the oligotrophication of open-water regions of the Great Lakes. Anthropogenic phosphorus loadings have decreased over the past several decades, resulting in a gradual decline in total phosphorus levels in the pelagic zones in Lake Michigan (Barbiero et al. 2002, Mida et al. 2010) and Lake Huron (Beeton et al. 1999, Barbiero et al. 2009a). Declines in offshore phosphorus concentrations have likely contributed to reduced primary production, although the long-term response of offshore production in Lake Michigan has been mixed (Johengen et al. 1994, Mida et al. 2010). In contrast, declines in offshore primary production in the past 5 to 10 years have been abrupt and dramatic. Beginning in about 2004, Barbiero et al. (2009b) noted increasingly deeper Secchi depths in Lake Michigan. Spring phytoplankton production in the southern basin of Lake Michigan in 2007-2008, inferred from chlorophyll *a* concentrations, was significantly lower than production in the 1980s and 1990s (Fahnenstiel et al. 2010, Mida et al. 2010). Reductions in phytoplankton biomass were especially dramatic for diatoms that typically bloom early in the spring; this peak in production has recently all but disappeared and its timing has shifted to later in the spring (Fahnenstiel et al. 2010). Silica dynamics in the southern basin of Lake Michigan shifted beginning in about 2004 and currently resemble ultra-oligotrophic Lake Superior (Mida et al. 2010). Silica dynamics also changed abruptly in Lake Huron in 2003 (Barbiero et al. 2009b), suggesting that production by the formerly diatom-dominant phytoplankton community (Barbiero and Tuchman 2001) decreased dramatically. These abrupt changes have been linked to the invasion and spread of dreissenid mussels, in particular the deeper-colonizing quagga mussel.

The recovery of some zooplankton species from food limitation is highly dependent on the type of algae available during the restoration period, and it is for this reason that zooplankton populations tend to synchronize peak population densities with densities of high-quality, lipid-rich foods (Arts 1999). If this concept also applies to *Mysis*, which experience deficiency of quality food in winter (Schlechtriem et al. 2008) and rely on the spring diatom bloom as an important food source (Gardner et al. 1985), then it is not surprising that changes in the timing and magnitude of phytoplankton productivity in the spring may be preventing their recovery from starvation.

Changes in zooplankton biomass and community composition resulting from oligotrophication are likely affecting *Mysis* as well. Zooplankton biomass, particularly that of cladocerans such as *Daphnia*, a preferred food of *Mysis* (Balcer et al. 1984), decreased in Lake Michigan beginning in the early 2000s, and the large copepod *Limnocalanus macrurus* became dominant (Barbiero et al. 2009b). In Lake Huron, drastic declines in populations of cladocerans began in 2003, especially in the northern basin, and unprecedented declines of cyclopoid copepods were documented in 2005 (Barbiero et al. 2009a). *Mysis* are omnivorous and zooplankton can contribute substantially to their diets, particularly when phytoplankton abundance is low (Grossnickle 1982). Thus, while starvation of *Mysis* in spring is likely due to decreased diatom production, poor condition in summer may be linked to reduced zooplankton populations. Increases in the abundance of *Limnocalanus* likely do not represent a new food source for *Mysis* because their ability to successfully capture *Limnocalanus* is limited (Grossnickle 1982).

Since phytoplankton and zooplankton production has decreased in both lakes, we might expect to see poor condition of *Mysis* in Michigan as well. Relative to Lake Huron, however, *Mysis* in Lake Michigan appear to be in better condition, and it is difficult to determine whether or not %TL has decreased over time in Lake Michigan mysids. It is possible that decreases in production have not been severe enough to affect *Mysis* in Lake Michigan. However, Lake Michigan is historically more productive than Lake Huron, and the colonization and spread of dreissenid mussels occurred later in Lake Michigan (Nalepa et al. 2001), so food limitation for *Mysis* may become a problem in Lake Michigan as changes progress in the next several years. Indeed, spatial variation in some measures of *Mysis* condition suggests that Lake Michigan may not be far behind Lake Huron. For example, in terms of total lipids of *Mysis*, the southern basin of Lake Michigan seems to be more similar to the northern basin of Huron and Georgian Bay than it is to northern Lake Michigan. It is somewhat surprising that *Mysis* in the shallower, historically more productive southern basin of Lake Michigan should experience these changes in condition more severely than those in the deeper, less-productive northern basin. As discussed above, recent dramatic reductions in primary production in Michigan's southern basin have been attributed to the filtering activities of quagga mussels, which have in the last 2-3 years begun to increase in abundance in offshore waters (Nalepa et al. 2009). Since the southern basin of Lake Michigan is shallower than the northern basin, quagga mussels may have been able to expand across larger areas of the basin more rapidly, affecting more of the lake and causing more severe drops in production. We may expect similar changes in productivity, and thus *Mysis* condition, to occur in the northern basin of Lake Michigan as quagga mussels spread to deeper waters. Adult mysids' %DHA in southern Lake Michigan was also lower than in northern Lake Michigan, further supporting the above argument. However, factors influencing fatty acid composition and %TL are complex, so it is difficult to determine whether *Mysis* in southern Lake Michigan are truly in worse condition than those in the northern basin.

Caveats and limitations

The most critical limitation to this study is sample size. Particularly in spring, sample sizes for lipid and fatty acid analyses were very low. *Mysis* appear to be at or near starvation thresholds in spring in northern Lake Huron, but these data come from only one station and a limited number of samples. In some cases, data from different sample types (adults, juveniles, and mixed) and even separate lake basins had to be pooled to obtain large enough sample sizes for statistical analyses. Pooling data results in generalized means that may be helpful in identifying patterns, but it does not accurately reflect variation within *Mysis* populations or across space.

In addition to being spatially limited, *Mysis* sampling in this study was temporally limited. These data are only snapshots of the *Mysis* population in April and August, and it is difficult to determine the mechanisms underlying observed differences. *Mysis* life histories vary from lake to lake, depending on factors like temperature and depth (Balcer et al. 1984, Adare and Lasenby 1994), with *Mysis* in Lake Huron likely living longer than those in Lake Michigan do. Timing and frequency of reproduction also vary among populations of *Mysis* (Balcer et al. 1984). Thus, it is possible that differences in lipids and fatty acids between the two lakes are at least partially explained by variations in the reproductive status of the animals. With monthly or even weekly sampling for lipids and fatty acids, researchers could gain a more detailed understanding of changes in *Mysis* condition as different life histories progress. These data could provide further evidence for starvation and could prove or disprove the hypothesis that the disappearance of the spring diatom bloom is preventing *Mysis* from recovery after winter food limitation.

These data span only two years, and interannual variability in condition may be substantial. There is currently no long-term monitoring program in place for *Mysis*, and data are particularly sparse in Lake Huron. Further work should expand sampling both spatially and temporally to obtain a more reliable understanding of the current condition of *Mysis* populations and to monitor long-term trends. In addition, an ideal long-term monitoring program would sample the same stations consistently across seasons and years. This study was limited by the nature of the EPA-GLNPO monitoring surveys; as discussed in methods, *Mysis* were only sampled at night during 24 hr ship operations, so *Mysis* sampling stations were chosen by chance instead of study design.

A final caveat stemming from sampling design is the difference in timing of USGS lipid sampling in the two lakes. Lake Michigan was sampled in mid- to late August in 2008, and Lake Huron was sampled in late September. Temperature and changes in lake physical structure between these periods could result in dramatic differences in the availability of food, so comparisons in *Mysis* condition between the two lakes may not be accurate. We would expect food to be less available later in the season, when Lake Huron was sampled, and thus for lipids in these samples to be biased low. However, EPA sampled *Mysis* in Lake Huron in August, closer to the timing of USGS sampling in Lake Michigan. Mean %TL of EPA samples from August was 14%, and mean %TL of USGS samples from late September was 13%, so it does not appear that *Mysis* condition changed substantially from August to September in Lake Huron in 2008.

General limitations are also imposed by the methods used to determine %TL and FA profiles. Female *Mysis* tend to have higher %TL than males, and sex was not determined prior to lipid analyses. In addition, reproductive status (gravid vs. not gravid) was not recorded, a factor which could also confound lipid analyses. Looking at overall population composition in 2008, proportion of females in the population tended to be higher in Lake Michigan than in Lake Huron, which could bias %TL of Lake Michigan samples high. Proportion of females with broods in the overall population was higher in Lake Huron, however. While sample composition could be affecting differences in %TL between the two lakes, differences were still dramatic enough that the effect is likely unimportant. In addition, fatty acid analyses support the conclusion drawn from lipid analyses that *Mysis* in Lake Huron are in poorer condition than those in Lake Michigan. Another possible limitation inherent in the %TL determination method is the amount of tissue necessary for analysis. To maintain large enough sample sizes, it was necessary to use weights close to 0.1 g of tissue, putting analyses very close to the detection limit of the instruments. This could introduce errors and variation in the data. In the future, it is recommended that numerous *Mysis* tows be performed at each station of interest to obtain a sufficient amount of tissue for each sample (e.g., a minimum of 1 g of tissue or 30-40 adult *Mysis* for each replicate).

Data on %TL were converted from %WW to %DW to facilitate comparisons with historical data. The equation used was developed for *Mysis* in Lake Pend Oreille, ID (Chipps 1997), which may have a different wet weight/dry weight relationship than Great Lakes *Mysis*. Thus, it is possible that some error was introduced in converting values for comparisons with past data, and this problem could be remedied by developing a WW/DW relationship specific to Great Lakes mysids.

In line with this study’s objectives, only diets of pelagic prey fish were analyzed. However, to understand fully the top-down impacts on *Mysis* populations from predation, it would be necessary to analyze diets of all potentially important predators. Benthic fish such as sculpins and burbot that are not collected in midwater trawls are known to prey on *Mysis* (Balcer et al. 1984, Kraft and Kitchell 1986) and may exert substantial predation pressure. However, biomass of most benthic fishes, with the exception of slimy sculpins, has also declined drastically in recent years (Bunnell et al. 2006, Riley et al. 2008, O'Brien et al. 2009), so it is likely that predation pressure from these fishes has decreased as well. Additionally, expanding diet analyses across seasons would give a better understanding of the relationship between *Mysis* and their predators. It is possible that predation pressure is higher during times of year not sampled for this study. However, Hondorp et al. (2005) observed that consumption of *Mysis* by pelagic planktivores was highest in southern Lake Michigan in the fall, so it is possible that these data do represent the highest predation pressure experienced by *Mysis* throughout the year.

Implications and future work

While limited sampling constrains conclusions that can be drawn from this research, these data suggest that some *Mysis* in Lake Huron may be experiencing food limitation during at least part of the year. Despite declines in pelagic and benthic prey fish densities, *Mysis* populations in lakes Michigan and Huron have not increased, but rather have remained steady or even declined in some areas. It appears that bottom-up factors are currently limiting populations of *Mysis*, supporting the hypothesis that the oligotrophication of Lake Huron may have been responsible for the crash in top predator populations. *Mysis* populations in Lake Michigan appear to be in better condition than those in Lake Huron, but differences between Michigan's north and south basins suggest that the lake may be following the trajectory of Lake Huron. It is clear from studies of primary production and nutrient dynamics that Lake Michigan is experiencing oligotrophication, just as Lake Huron did, so a subsequent collapse in the lower food web is possible. Managers need to be aware of these recent, dramatic changes in the lower food web, and may need to adjust stocking of predators accordingly. It is recommended that populations of *Mysis*, and other components of the lower food web such as zooplankton, be intensively studied both seasonally and annually in order to monitor changes. Lipid and fatty acid analyses may be particularly useful in identifying populations that are experiencing starvation, but efforts should be made to increase sample sizes to obtain adequate amounts of tissue. Finally, the number of monitoring stations needs to be increased in order to better understand differences in the condition of spatially distinct populations.

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Table 1. Characteristics of stations at which *Mysis* and fish were sampled in lakes Michigan and Huron, 2007-2008. Agency abbreviations: USGS = United States Geological Survey - Great Lakes Science Center, EPA = U.S. Environmental Protection Agency – Great Lakes National Program Office. Sample type abbreviations: M = Mysis abundance/lengths; L = *Mysis* lipids/fatty acids; F = midwater trawl for prey fish diets. ID numbers coordinate with Figures 1 and 2.

ID	Station Name/Serial	Agency	Date(s) sampled	Sample type(s)	Station depth (m)
1	1063	USGS	12-Aug-2008	F	249
2	1095	USGS	22-Aug-2007	F	135
3	1094	USGS	22-Aug-2007	F	240
4	1062	USGS	11-Aug-2008	F	318
5	MI11	EPA	2-Aug-2007	M	122
‘	‘	‘	14-Apr-2008	M,L	‘
6	1093	USGS	22-Aug-2007	F	315
7	1061	USGS	11-Aug-2008	F	333
8	105	USGS	4-Nov-2008	F,L	90
9	MIFE	EPA	15-Apr-2008	M,L	64
10	108	USGS	5-Nov-2008	L	115
11	MI18M	EPA	1-Apr-2007	M	156
‘	‘	‘	1-Aug-2008	M	‘
12	MI17	EPA	1-Aug-2008	M	102
13	1089	USGS	15-Aug-2007	F	112.5
14	1090	USGS	21-Aug-2007	F	375
15	MI23	EPA	1-Apr-2007	M	85
16	1065	USGS	13-Aug-2008	F	188
17	1064	USGS	12-Aug-2008	F	334
18	1066	USGS	13-Aug-2008	F	71
19	97	USGS	1-Nov-2008	L	60
20	1092	USGS	22-Aug-2007	F	203
21	90	USGS	31-Oct-2008	L	105
22	MI27M	EPA	2-Aug-2008	M	101
23	1067	USGS	13-Aug-2008	F	169
24	82	USGS	17-Oct-2008	L	80
25	81	USGS	17-Oct-2008	F	55
26	1086	USGS	15-Aug-2007	F	165
27	1087	USGS	15-Aug-2007	F	281
28	80	USGS	16-Oct-2008	F	30
29	88	USGS	25-Oct-2008	L	130
30	MI34	EPA	3-Aug-2007	M	156
31	78	USGS	16-Oct-2008	L	150
32	1069	USGS	18-Aug-2008	F	73
33	74	USGS	16-Oct-2008	L	150
34	MI41M	EPA	2-Apr-2007	M	258
‘	‘	‘	18-Apr-2008	M,L	‘
35	70	USGS	12-Oct-2008	L	210
36	62	USGS	11-Oct-2008	F	40
37	67	USGS	11-Oct-2008	L	150
38	66	USGS	11-Oct-2008	L	150
39	61	USGS	9-Oct-2008	L	55
40	59	USGS	9-Oct-2008	L	55
41	1072	USGS	20-Aug-2008	F	305
42	1071	USGS	20-Aug-2008	F	188
43	1073	USGS	21-Aug-2008	F	323
44	1070	USGS	20-Aug-2008	F	314
45	1075	USGS	25-Aug-2008	F	333
46	1074	USGS	25-Aug-2008	F	151
47	57	USGS	9-Oct-2008	F	20
48	182	USGS	1-Oct-2008	F	35
49	470	USGS	6-Oct-2007	F	55
50	462	USGS	7-Oct-2007	F	40

51	HU61	EPA	3-Apr-2007	M	117
52	175	USGS	29-Sep-2008	F	31
53	173	USGS	29-Sep-2008	F	40
54	456	USGS	5-Oct-2007	F	28
55	453	USGS	5-Oct-2007	F	23
56	109	USGS	5-Nov-2008	F	53
57	111	USGS	20-Sep-2008	L	82
58	451	USGS	5-Oct-2007	F	36
59	446	USGS	5-Oct-2007	F	50
60	169	USGS	29-Sep-2008	F	45
61	441	USGS	4-Oct-2007	F	50
62	365	USGS	21-Sep-2007	F	88
63	153	USGS	26-Sep-2008	F	96
64	165	USGS	28-Sep-2008	L	82
65	439	USGS	4-Oct-2007	F	105
66	HUFE	EPA	5-Aug-2008	M,L	111
67	148	USGS	25-Sep-2008	L	66
68	420	USGS	30-Sep-2007	F	77
69	147	USGS	25-Sep-2008	F	64
70	157	USGS	26-Sep-2008	L	108
71	433	USGS	4-Oct-2007	F	55
72	428	USGS	3-Oct-2007	F	75
73	373	USGS	22-Sep-2007	F	104
74	414	USGS	29-Sep-2007	F	51
75	422	USGS	30-Sep-2007	F	63
76	HU97b	EPA	6-Aug-2008	M	40
77	119	USGS	21-Sep-2008	F	71
78	160	USGS	27-Sep-2008	F	61
79	120	USGS	21-Sep-2008	L	74
80	161	USGS	27-Sep-2008	L	96
81	385	USGS	23-Sep-2007	F	73
82	HU37	EPA	20-Apr-2008	M,L	70
83	HU38	EPA	3-Apr-2007	M,L	136
84	HU32	EPA	4-Apr-2007	M	81
85	125	USGS	22-Sep-2008	F	67
86	HU95b	EPA	7-Aug-2008	M,L	65
87	141	USGS	23-Sep-2008	L	77
88	387	USGS	23-Sep-2008	F	54
89	HU27	EPA	14-Apr-2007	M	53
‘	‘	‘	7-Aug-2008	M,L	‘
90	HU45M	EPA	5-Aug-2008	M,L	95
91	132	USGS	22-Sep-2008	F	61
92	394	USGS	24-Sep-2007	F	67
93	399	USGS	24-Sep-2007	F	61
94	138	USGS	23-Sep-2008	F	70
95	401	USGS	26-Sep-2007	F	47
96	139	USGS	23-Sep-2008	F	48
97	HU09	EPA	7-Aug-2007	M	56
98	HU06	EPA	6-Aug-2007	M	48
99	407	USGS	27-Sep-2007	F	30
154	154	USGS	26-Sep-2008	L	114

Table 2. Mean *Mysis* abundance (number·m^{-2}) in the north and south basins of Lake Michigan and Lake Huron determined from nighttime vertical tows in spring and summer 2007-2008. Sampling was performed during EPA surveys. Standard deviations (SD) and sample size (n) are also given. Generally, two duplicate tows were performed at each station, so n is not always equivalent to the number of stations sampled. NA = basin not sampled.

		Basin/Lake																	
		Lake Michigan South			Lake Michigan North			**Σ Lake Michigan**			Lake Huron North			Lake Huron South			**Σ Lake Huron**		
Year	Season	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
2007	Spring	62.0	31.1	2	245.0	1.4	2	153.5	107.2	4	19.7	16.2	6	6.0	2.8	2	16.3	15.1	8
	Summer	180.0	46.2	3		NA		180.0	46.2	3	100.0	106.7	4	19.8	17.2	4	59.4	83.0	8
2008	Spring	26.3	25.1	6	386.5	109.6	2	116.4	173.1	8	19.5	10.6	2		NA		19.5	10.6	2
	Summer	159.8	29.2	6		NA		159.8	29.2	6	29.0	31.3	4	47.8	34.7	6	40.3	33.0	10

Table 3. *Mysis* catch compositions (as % of total mysids collected) in the north and south basins of Lake Michigan and Lake Huron determind from nighttime vertical tows in spring and summer 2007-2008. Replicates and stations within a basin were pooled. Sampling was performed during EPA surveys. N = total number of *Mysis*. NA = basin not sampled.

			Basin/Lake					
Year	Season	*Mysis* Type	Lake Michigan South	Lake Michigan North	**Σ Lake Michigan**	Lake Huron North	Lake Huron South	**Σ Lake Huron**
2007	Spring	Adult Females	0.6	30.3	**12.6**	19.1	20.0	**19.2**
		Adult Males	11.5	8.2	**10.1**	15.7	40.0	**17.6**
		Adults (sex undet.)	19.6	-	**11.6**	-	-	**-**
		Juveniles	68.4	61.5	**65.6**	65.2	40.0	**63.2**
		N	357	244	**601**	115	10	**125**
	Summer	Adult Females	10.9	NA	**10.9**	9	4.7	**8.3**
		Adult Males	7.6		**7.6**	10	7.0	**9.8**
		Juveniles	81.2		**81.2**	81	88.4	**81.9**
		N	357		**357**	211	43	**254**
2008	Spring	Adult Females	27.9	21.5	**23.0**	14.3	NA	**14.3**
		Adult Males	7.5	17.5	**15.1**	14.3		**14.3**
		Juveniles	64.6	61.1	**61.9**	71.4		**71.4**
		N	147	475	**622**	28		**28**
	Summer	Adult Females	16.4	NA	**16.4**	19.2	10.0	**13.1**
		Adult Males	11.3		**11.3**	15.4	14.3	**14.6**
		Juveniles	72.3		**72.3**	65.4	75.7	**72.3**
		N	799		**799**	104	210	**314**

Table 4. Mean *Mysis* lengths (mm) in the north and south basins of Lake Michigan and Lake Huron determined from nighttime vertical tows in spring and summer 2007-2008. Sampling was performed during EPA surveys. Standard deviations (SD) and sample size (n) are also given. Replicate tows were performed at most stations, so n is not equivalent to the number of stations sampled. Male and female *Mysis* types include adults (>10 mm) only. NA = basin not sampled.

			Basin/Lake																	
			Lake Michigan South			Lake Michigan North			**Σ Lake Michigan**			Lake Huron North			Lake Huron South			**Σ Lake Huron**		
Year	Season	*Mysis* Type	Mean	SD	n	Mean	SD	n	**Mean**	**SD**	**n**	Mean	SD	n	Mean	SD	n	**Mean**	**SD**	**n**
2007	Spring	Females	14.0	2.8	2	12.5	1.8	74	**12.5**	**1.8**	**76**	13.0	2.2	22	13.9	0.0	2	**13.1**	**2.1**	**24**
		Males	10.7	1.0	41	12.4	0.9	20	**11.3**	**1.2**	**61**	12.0	1.3	18	12.4	0.5	4	**12.0**	**1.2**	**22**
		ΣAdults	11.2	1.4	107	12.5	1.7	94	**11.8**	**1.7**	**207**	12.6	1.9	40	12.9	0.9	6	**12.6**	**1.8**	**46**
		Juveniles	5.9	2.6	244	7.3	2.8	150	**6.4**	**2.7**	**394**	5.5	2.5	75	3.8	0.2	4	**5.4**	**2.5**	**79**
	Summer	Females	14.5	1.9	39				**14.5**	**1.9**	**39**	14.7	1.8	19	11.3	1.2	2	**14.4**	**2.0**	**21**
		Males	13.3	1.8	27				**13.3**	**1.8**	**27**	13.1	1.1	22	12.3	1.3	3	**13.0**	**1.2**	**25**
		ΣAdults	14.0	2.0	66		NA		**14.0**	**2.0**	**66**	13.8	1.7	41	11.9	1.2	5	**13.6**	**1.7**	**46**
		Juveniles	5.8	1.9	290				**5.8**	**1.9**	**290**	5.2	1.3	170	5.6	2.1	38	**5.3**	**1.5**	**208**
2008	Spring	Females	13.8	2.4	41	12.0	1.8	102	**12.6**	**2.1**	**143**	11.0	0.5	4				**11.0**	**0.5**	**4**
		Males	11.5	1.1	11	11.1	0.7	83	**11.2**	**0.7**	**94**	10.9	0.5	4				**10.9**	**0.5**	**4**
		ΣAdults	13.3	2.4	52	11.6	1.5	185	**12.0**	**1.9**	**237**	11.0	0.4	8		NA		**11.0**	**0.4**	**8**
		Juveniles	5.4	2.1	95	6.8	2.4	290	**6.4**	**2.4**	**385**	7.6	1.9	20				**7.6**	**1.9**	**20**
	Summer	Females	14.9	2.1	131				**14.9**	**2.1**	**131**	14.1	1.9	20	12.9	1.8	21	**13.5**	**1.9**	**41**
		Males	13.5	1.9	90				**13.5**	**1.9**	**90**	13.9	0.9	16	12.7	1.8	30	**13.1**	**1.6**	**46**
		ΣAdults	14.4	2.1	221		NA		**14.4**	**2.1**	**221**	14.0	1.5	36	12.8	1.8	51	**13.3**	**1.8**	**87**
		Juveniles	6.0	1.8	578				**6.0**	**1.8**	**578**	5.4	1.5	68	5.7	1.8	159	**5.6**	**1.7**	**227**

Table 5. Percent occurrences (%O) of *Mysis* in pelagic fish diets by species, size category, lake basin, and year. Percent occurence was calculated as number of stomachs containing *Mysis* divided by total number of stomachs processed. Sample sizes (number of stomachs processed) are in parentheses. Basin abbreviations are as follows: Lake Michigan south (LMS), Lake Michigan north (LMN), total Lake Michigan (∑LM), Lake Huron Georgian Bay (LHGB), Lake Huron North Channel (LHNC), Lake Huron north (LHN), Lake Huron south (LHS), and total Lake Huron (∑LH). NA = none collected.

		Bloater (*Coregonus hoyi*)				Alewife (*Alosa pseudoharengus*)				Rainbow Smelt (*Osmerus mordax*)			
Year	Basin	< 90mm	90-150mm	> 150mm	Total	< 90mm	90-130mm	> 130mm	Total	< 60mm	60-120mm	> 120mm	Total
2007	LMS	0.0 (13)	NA	NA	0.0 (13)	0.0 (10)	0.0 (4)	0.0 (7)	0.0 (21)	NA			
	LMN	NA	NA	NA	NA	NA	0.0 (5)	20.0 (5)	10.0 (10)				
	Σ LM	0.0 (13)	NA	NA	0.0 (13)	0.0 (10)	0.0 (9)	8.3 (12)	3.2 (31)				
	LHGB	6.3 (16)	5.0 (20)	66.7 (9)	17.8 (45)	NA				18.2 (11)	62.5 (16)	0.0 (3)	40.0 (30)
	LHNC	0.0 (1)	NA	0.0 (3)	0.0 (4)					0.0 (3)	0.0 (4)	0.0 (5)	0.0 (12)
	LHN	0.0 (7)	40.0 (15)	100.0 (4)	38.5 (26)					NA	50.0 (4)	100.0 (4)	75.0 (8)
	LHS	0.0 (9)	7.1 (14)	100.0 (1)	8.3 (24)					50.0 (2)	14.3 (7)	0.0 (2)	18.2 (11)
	Σ LH	3.0 (33)	16.3 (49)	64.7 (17)	20.2 (99)					18.8 (16)	41.9 (31)	28.6 (14)	32.8 (61)
2008	LMS	16.7 (6)	0.0 (9)	71.4 (7)	27.3 (22)	0.0 (5)	NA	0.0 (5)	0.0 (10)	NA	0.0 (1)	NA	0.0 (1)
	LMN	0.0 (3)	75.0 (4)	83.3 (6)	61.5 (13)	0.0 (11)	0.0 (17)	0.0 (12)	0.0 (40)	0.0 (12)	0.0 (1)	NA	0.0 (13)
	Σ LM	11.1 (9)	23.1 (13)	76.9 (13)	40.0 (35)	0.0 (16)	0.0 (17)	0.0 (17)	0.0 (50)	0.0 (12)	0.0 (2)	NA	0.0 (14)
	LHGB	0.0 (7)	NA	NA	0.0 (7)	NA	NA	NA	NA	NA	11.1 (9)	0.0 (1)	10.0 (10)
	LHNC	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0 (5)	0.0 (2)	0.0 (7)
	LHN	0.0 (10)	0.0 (2)	NA	0.0 (12)	0.0 (5)	NA	NA	0.0 (5)	NA	100.0 (4)	100.0 (1)	100.0 (5)
	LHS	0.0 (11)	NA	NA	0.0 (11)	0.0 (5)	NA	NA	0.0 (5)	0.0 (4)	0.0 (6)	0.0 (1)	0.0 (11)
	Σ LH	0.0 (28)	0.0 (2)	NA	0.0 (30)	0.0 (10)	NA	NA	0.0 (10)	0.0 (4)	20.8 (24)	20.0 (5)	18.2 (33)

Table 6. Summaries of spring means of total lipids (as % wet weight) and fatty acid methyl esters (FAMEs) (as % of total FAMEs detected) for Lakes Michigan and Huron. All basins within a lake were pooled and sample types (adults only, juveniles only, and mixed) were combined. Standard deviations are in parentheses. n = sample size. nd = not detected. Three-letter abbreviations are given for the five essential fatty acids of interest in this study.

	Lake	
Parameter	Michigan (n=7)	Huron (n=2)
Total lipids	19.9 (9.3)	9.8 (5.8)
FAMEs		
Saturated		
12:0	0.2 (0.04)	0.1 (0.04)
14:0	3.2 (1.2)	1.2 (0.3)
15:0	0.4 (0.1)	0.3 (0.1)
16:0	15.2 (1.0)	16.4 (2.1)
17:0	nd	nd
18:0	1.2 (0.2)	1.8 (0.2)
23:0	nd	nd
Σ Saturated	20.2 (2.0)	19.7 (2.7)
Monounsaturated		
14:1	nd	nd
16:1*n*-9	nd	nd
16:1*n*-7	12.9 (7.5)	1.2 (0.6)
17:1	nd	nd
18:1*n*-9	13.6 (3.3)	13.1 (0.2)
18:1*n*-7	4.0 (0.8)	3.8 (0.1)
20:1	0.2 (0.3)	nd
20:1*n*-9	1.0 (0.3)	0.9 (0.1)
22:1	nd	nd
22:1*n*-9	nd	nd
Σ Monounsaturated	31.7 (5.4)	19.0 (0.5)
Polyunsaturated		
18:2*n*-6 (LIN)	8.0 (7.7)	4.0 (1.2)
18:2 – 11,14	0.1 (0.1)	nd
18:3*n*-3 (ALA)	0.6 (1.0)	nd
18:4*n*-3	3.0 (1.6)	nd
20:2*n*-6	1.0 (0.3)	1.4 (0.1)
20:3*n*-6	nd	nd
20:4*n*-6 (ARA)	3.0 (1.6)	5.6 (0.6)
20:3*n*-3	0.7 (0.4)	nd
20:4*n*-3	1.3 (0.5)	nd
20:5*n*-3 (EPA)	17.8 (3.2)	23.5 (0.7)
22:4*n*-6	nd	nd
22:5*n*-6	1.2 (0.4)	1.0 (1.4)
22:5*n*-3	0.3 (0.3)	nd
22:6*n*-3 (DHA)	11.1 (4.1)	25.8 (1.6)
Σ Polyunsaturated	48.1 (6.9)	61.3 (3.2)
Σ *n*-3	34.9 (7.2)	49.4 (2.3)
Σ *n*-6	13.2 (7.0)	11.9 (0.9)
Σ *n*-3/ Σ *n*-6	3.3 (1.5)	4.1 (0.1)

Table 7. Summaries of summer mean total lipids (as % wet weight) and fatty acid methyl esters (FAMEs) (as % of total FAMEs detected) for adult *Mysis* in lakes Michigan and Huron. Standard deviations are in parentheses. n = sample size. nd = not detected. Three-letter abbreviations are given for the five essential fatty acids of interest in this study. Basin abbreviations are as follows: Lake Michigan south (LMS), Lake Michigan north (LMN), total Lake Michigan (∑LM), Lake Huron Georgian Bay (LHGB), Lake Huron North Channel (LHNC), Lake Huron north (LHN), Lake Huron south (LHS), and total Lake Huron (∑LH).

	Basin/Lake						
	LMS (n=5)	LMN (n=11)	**Σ LM**	LHGB (n=6)	LHN (n=10)	LHS (n=10)	**Σ LH**
Total lipids	20.0 (7.8)	27.7 (5.7)	**25.3 (7.2)**	12.9 (2.9)	14.6 (4.1)	16.1 (4.2)	**14.8 (4.0)**
FAMEs							
Saturated							
12:0	0.3 (0.04)	0.3 (0.1)	**0.3 (0.1)**	0.2 (0.1)	0.3 (0.1)	0.3 (0.1)	**0.3 (0.1)**
14:0	4.7 (0.6)	5.1 (0.6)	**5.0 (0.6)**	3.0 (0.7)	5.0 (0.9)	4.5 (1.0)	**4.2 (1.0)**
15:0	0.5 (0.1)	0.5 (0.02)	**0.5 (0.03)**	0.4 (0.1)	0.5 (0.1)	0.4 (0.02)	**0.4 (0.1)**
16:0	15.4 (0.9)	15.1 (1.0)	**15.2 (0.9)**	15.4 (1.1)	15.6 (1.1)	16.3 (0.7)	**15.8 (1.0)**
17:0	nd	nd	**nd**	nd	nd	nd	**nd**
18:0	1.2 (0.1)	1.1 (0.2)	**1.2 (0.2)**	1.3 (0.2)	1.4 (0.2)	1.2 (0.2)	**1.3 (0.2)**
23:0	nd	nd	**nd**	nd	nd	nd	**nd**
Σ Saturated	22.1 (1.4)	22.1 (1.5)	**22.1 (1.5)**	20.3 (1.7)	21.9 (1.1)	23.3 (1.3)	**22.0 (1.7)**
Monounsaturated							
14:1	nd	nd	**nd**	nd	nd	nd	**nd**
16:1*n*-9	nd	nd	**nd**	nd	nd	nd	**nd**
16:1*n*-7	8.2 (1.0)	15.6 (3.3)	**13.3 (4.5)**	5.7 (1.8)	6.5 (1.7)	11.5 (1.8)	**8.2 (3.1)**
17:1	nd	nd	**nd**	nd	nd	nd	**nd**
18:1*n*-9	15.2 (1.2)	13.5 (0.6)	**14.0 (1.1)**	18.3 (2.5)	15.4 (1.3)	13.8 (1.4)	**15.4 (2.4)**
18:1*n*-7	4.6 (0.2)	4.3 (0.3)	**4.4 (0.3)**	4.3 (0.1)	4.5 (0.6)	4.2 (0.9)	**4.3 (0.7)**
20:1	nd	0.3 (0.4)	**0.2 (0.4)**	nd	0.1 (0.2)	0.04 (0.1)	**0.1 (0.2)**
20:1*n*-9	1.2 (0.2)	1.2 (0.2)	**1.2. (0.2)**	1.4 (0.4)	1.3 (0.2)	1.2 (0.3)	**1.3 (0.3)**
22:1	nd	nd	**nd**	nd	nd	nd	**nd**
22:1*n*-9	nd	nd	**nd**	nd	nd	nd	**nd**
Σ Monounsaturated	29.1 (1.0)	34.9 (3.3)	**33.1 (3.9)**	29.7 (2.9)	27.7 (2.6)	30.7 (2.3)	**20.3 (2.8)**
Polyunsaturated							
18:2*n*-6 (LIN)	5.8 (0.6)	4.3 (0.8)	**4.8 (1.0)**	8.4 (5.8)	5.4 (0.9)	5.0 (1.6)	**5.9 (3.1)**
18:2 – 11,14	nd	0.01 (0.03)	**0.01 (0.02)**	nd	nd	0.2 (0.3)	**0.1 (0.2)**
18:3*n*-3 (ALA)	3.0 (1.7)	2.6 (1.8)	**2.7 (1.8)**	nd	1.3 (1.4)	1.0 (1.3)	**0.9 (1.3)**
18:4*n*-3	3.6 (0.3)	4.0 (0.5)	**3.8 (0.5)**	1.5 (0.6)	2.7 (0.6)	3.1 (0.9)	**2.6 (1.0)**
20:2*n*-6	1.2 (0.1)	1.0 (0.2)	**1.1 (0.2)**	0.9 (0.3)	1.0 (0.1)	0.8 (0.1)	**0.9 (0.2)**
20:3*n*-6	nd	0.01 (0.03)	**0.01 (0.03)**	nd	<0.001	0.02 (0.05)	**0.01 (0.03)**
20:4*n*-6 (ARA)	4.5 (0.6)	2.6 (0.6)	**3.2 (1.1)**	6.0 (1.0)	5.5 (0.9)	3.9 (0.9)	**5.0 (1.3)**
20:3*n*-3	0.7 (0.2)	0.8 (0.2)	**0.8 (0.2)**	nd	0.5 (0.1)	0.3 (0.1)	**0.3 (0.2)**
20:4*n*-3	1.2 (0.2)	1.5 (0.2)	**1.4 (0.3)**	0.6 (0.4)	1.1 (0.1)	0.9 (0.2)	**0.9 (0.3)**
20:5*n*-3 (EPA)	16.0 (0.8)	15.0 (1.2)	**15.3 (1.1)**	16.2 (2.2)	18.3 (1.1)	19.1 (3.2)	**18.1 (2.5)**
22:4*n*-6	nd	0.03 (0.1)	**0.02 (0.1)**	nd	nd	nd	**nd**
22:5*n*-6	2.0 (0.2)	1.5 (0.3)	**1.6 (0.4)**	1.8 (0.5)	1.7 (0.1)	1.5 (0.5)	**1.7 (0.4)**
22:5*n*-3	0.4 (0.3)	0.5 (0.3)	**0.5 (0.3)**	0.1 (0.1)	0.4 (0.2)	0.4 (0.3)	**0.3 (0.3)**
22:6*n*-3 (DHA)	10.4 (1.0)	9.1 (1.2)	**9.5 (1.3)**	14.6 (3.5)	12.6 (1.9)	9.9 (1.2)	**12.0 (2.3)**
Σ Polyunsaturated	48.8 (2.2)	43.0 (3.4)	**44.8 (4.1)**	50.0 (4.0)	50.4 (2.6)	46.0 (2.1)	**48.6 (3.4)**
Σ *n*-3	35.3 (2.3)	33.5 (2.1)	**34.1 (2.3)**	32.9 (5.3)	36.9 (2.4)	34.7 (1.2)	**35.1 (3.2)**
Σ *n*-6	13.5 (1.3)	9.5 (1.6)	**10. (2.4)**	17.1 (4.8)	13.6 (1.1)	11.2 (2.1)	**13.5 (3.4)**
Σ *n*-3/ Σ *n*-6	2.7 (0.4)	3.6 (0.5)	**3.3 (0.6)**	2.1 (0.7)	2.7 (0.3)	3.2 (0.7)	**2.8 (0.7)**

Table 8. Summaries of summer mean total lipids (as % wet weight) and fatty acid methyl esters (FAMEs) (as % of total FAMEs detected) for samples containing juvenile *Mysis* in lakes Michigan and Huron. Standard deviations are in parentheses. n = sample size. nd = not detected. Three-letter abbreviations are given for the five essential fatty acids of interest in this study. Basin abbreviations are as follows: Lake Michigan south (LMS), Lake Michigan north (LMN), total Lake Michigan (∑LM), Lake Huron Georgian Bay (LHGB), Lake Huron North Channel (LHNC), Lake Huron north (LHN), Lake Huron south (LHS), and total Lake Huron (∑LH).

	Basin/Lake						
	LMS (n=3)	LMN (n=7)	**Σ LM**	LHGB (n=3)	LHN (n=5)	LHS (n=4)	**Σ LH**
Total lipids	11.0 (3.5)	19.9 (8.1)	**17.3 (8.1)**	7.7 (2.2)	10.7 (3.1)	13.1 (8.4)	**10.7 (5.3)**
FAMEs							
Saturated							
12:0	0.3 (0.003)	0.3 (0.1)	**0.3 (0.1)**	0.2 (0.1)	0.3 (0.1)	0.3 (0.1)	**0.3 (0.1)**
14:0	5.2 (0.5)	4.5 (1.2)	**4.7 (1.1)**	3.1 (0.6)	3.7 (0.6)	4.3 (0.7)	**3.7 (0.8)**
15:0	0.3 (0.3)	0.4 (0.04)	**0.4 (0.1)**	0.4 (0.04)	0.4 (0.1)	0.5 (0.03)	**0.4 (0.1)**
16:0	15.1 (0.1)	15.0 (1.3)	**15.1 (1.1)**	16.2 (0.9)	16.5 (1.6)	17.4 (1.8)	**16.7 (1.5)**
17:0	nd	nd	**nd**	nd	nd	nd	**nd**
18:0	1.2 (0.1)	1.2 (0.2)	**1.2 (0.2)**	1.3 (0.2)	1.6 (0.2)	1.4 (0.2)	**1.4 (0.2)**
23:0	nd	nd	**nd**	nd	nd	nd	**nd**
Σ Saturated	22.1 (0.2)	21.4 (1.8)	**21.6 (1.5)**	21.2 (1.4)	22.5 (1.8)	23.9 (2.6)	**15.6 (3.5)**
Monounsaturated							
14:1	nd	nd	**nd**	nd	nd	nd	**nd**
16:1*n*-9	nd	nd	**nd**	nd	nd	nd	**nd**
16:1*n*-7	10.0 (2.5)	12.4 (5.1)	**11.7 (4.5)**	4.9 (1.3)	5.6 (2.1)	10.8 (2.2)	**7.1 (3.2)**
17:1	nd	nd	**nd**	nd	nd	nd	**nd**
18:1*n*-9	14.3 (0.4)	13.7 (1.1)	**13.9 (1.1)**	15.3 (1.6)	13.4 (1.3)	13.6 (2.2)	**14.0 (1.8)**
18:1*n*-7	4.3 (0.1)	4.2 (0.3)	**4.2 (0.2)**	4.2 (0.1)	4.0 (0.8)	4.4 (0.9)	**4.2 90.7)**
20:1	nd	0.1 (0.3)	**0.1 (0.2)**	nd	nd	nd	**nd**
20:1*n*-9	1.2 (0.2)	1.0 (0.5)	**1.1 (0.4)**	1.3 (0.3)	1.1 (0.3)	1.0 (0.7)	**1.1 (0.4)**
22:1	nd	nd	**nd**	nd	nd	nd	**nd**
22:1*n*-9	nd	nd	**nd**	nd	nd	nd	**nd**
Σ Monounsaturated	29. 8 (2.1)	31.4 (4.3)	**30.9 (3.8)**	25.7 (3.3)	24.1 (1.9)	29.7 (1.7)	**26.3 (3.2)**
Polyunsaturated							
18:2*n*-6 (LIN)	5.6 (0.6)	4.3 (1.2)	**4.7 (1.2)**	4.6 (0.6)	4.5 (0.5)	6.4 (5.5)	**5.1 (3.1)**
18:2 – 11,14	nd	nd	**nd**	nd	nd	0.03 (0.1)	**0.01 (0.04)**
18:3*n*-3 (ALA)	4.2 (1.2)	2.1 (2.3)	**2.8 (2.2)**	nd	0.5 (1.2)	0.4 (0.9)	**0.4 (0.9)**
18:4*n*-3	4.0 (1.0)	3.6 (1.4)	**3.7 (1.2)**	1.4 (0.4)	2.2 (0.5)	1.9 (0.2)	**1.9 (0.5)**
20:2*n*-6	1.1 (0.1)	1.0 (0.1)	**1.0 (0.1)**	0.9 (0.01)	0.9 (0.1)	0.6 (0.5)	**0.8 (0.3)**
20:3*n*-6	nd	nd	**nd**	nd	nd	nd	**nd**
20:4*n*-6 (ARA)	4.2 (0.2)	3.0 (0.7)	**3.4 (0.8)**	7.0 (1.0)	5.9 (1.2)	3.5 (1.0)	**5.3 (1.7)**
20:3*n*-3	0.6 (0.1)	0.6 (90.3)	**0.6 (0.2)**	nd	0.3 (0.2)	0.2 (0.2)	**0.2 (0.2)**
20:4*n*-3	1.0 (0.2)	1.1 (0.5)	**1.1 (0.5)**	1.0 (0.2)	1.0 (0.2)	0.5 (0.4)	**0.8 (0.3)**
20:5*n*-3 (EPA)	15.1 (1.1)	17.1 (2.6)	**16.5 (2.4)**	17.7 (1.4)	19.0 (1.1)	19.4 (5.7)	**18.8 (3.2)**
22:4*n*-6	nd	0.02 (0.1)	**0.02 (0.1)**	nd	nd	nd	**nd**
22:5*n*-6	2.0 (0.5)	1.4 (0.7)	**1.5 (0.7)**	2.3 (0.2)	2.2 (0.6)	1.0 (0.8)	**1.8 (0.8)**
22:5*n*-3	0.2 (0.3)	0.3 (0.3)	**0.3 (0.3)**	nd	0.2 (0.3)	0.3 (0.2)	**0.2 (0.3)**
22:6*n*-3 (DHA)	10.2 (0.6)	12.8 (5.3)	**12.0 (4.5)**	18.3 (1.5)	16.9 (3.0)	11.9 (2.1)	**15.6 (3.5)**
Σ Polyunsaturated	48.1 (2.0)	47.2 (5.2)	**47.5 (4.3)**	53.1 (4.5)	53.5 (3.2)	46.4 (2.1)	**51.0 (4.5)**
Σ *n*-3	35.2 (1.0)	37.5 (5.2)	**36.8 (4.4)**	38.4 (3.0)	40.1 (2.4)	34.9 (6.1)	**37.9 (4.4)**
Σ *n*-6	12.9 (1.0)	9.6 (2.1)	**10.6 (2.4)**	14.8 (1.6)	13.4 (2.1)	11.5 (4.3)	**13.1 (3.0)**
Σ *n*-3/ Σ *n*-6	2.8 (0.2)	4.1 (1.2)	**3.7 (1.2)**	2.6 (0.1)	3.1 (0.6)	3.5 (1.7)	**3.1 (1.0)**

Table 9. Results of linear regressions with *Mysis* total lipids (as percent of wet weight) as the explanatory variable and various essential fatty acids as the response variables. Regressions were performed using only data from adult *Mysis* collected in summer 2008. Fatty acids analyzed include 18:2[n-6] (linoleic acid, LIN), 18:3 [n-3] (α-linolenic acid, ALA), 20:4[n-6] (arachidonic acid, ARA), 20:4 [n-3] (eicosapentaenoic acid, EPA), and 22:6[n-3] (docosahexaenoic acid, DHA). p-values denoted with an asterisk (*) are significant at the α=0.05 level.

	Lake Michigan			Lake Huron		
Fatty acid	B	R^2	p-value	B	R^2	p-value
LIN	-0.03	0.06	0.373	0.04	0.01	0.608
ALA	0.07	0.39	0.030*	-0.06	0.34	0.101
ARA	-0.07	0.25	0.051	-0.09	0.08	0.151
EPA	-0.10	0.41	0.008*	0.06	0.01	0.636
DHA	-0.14	0.58	0.001*	-0.30	0.18	0.031*

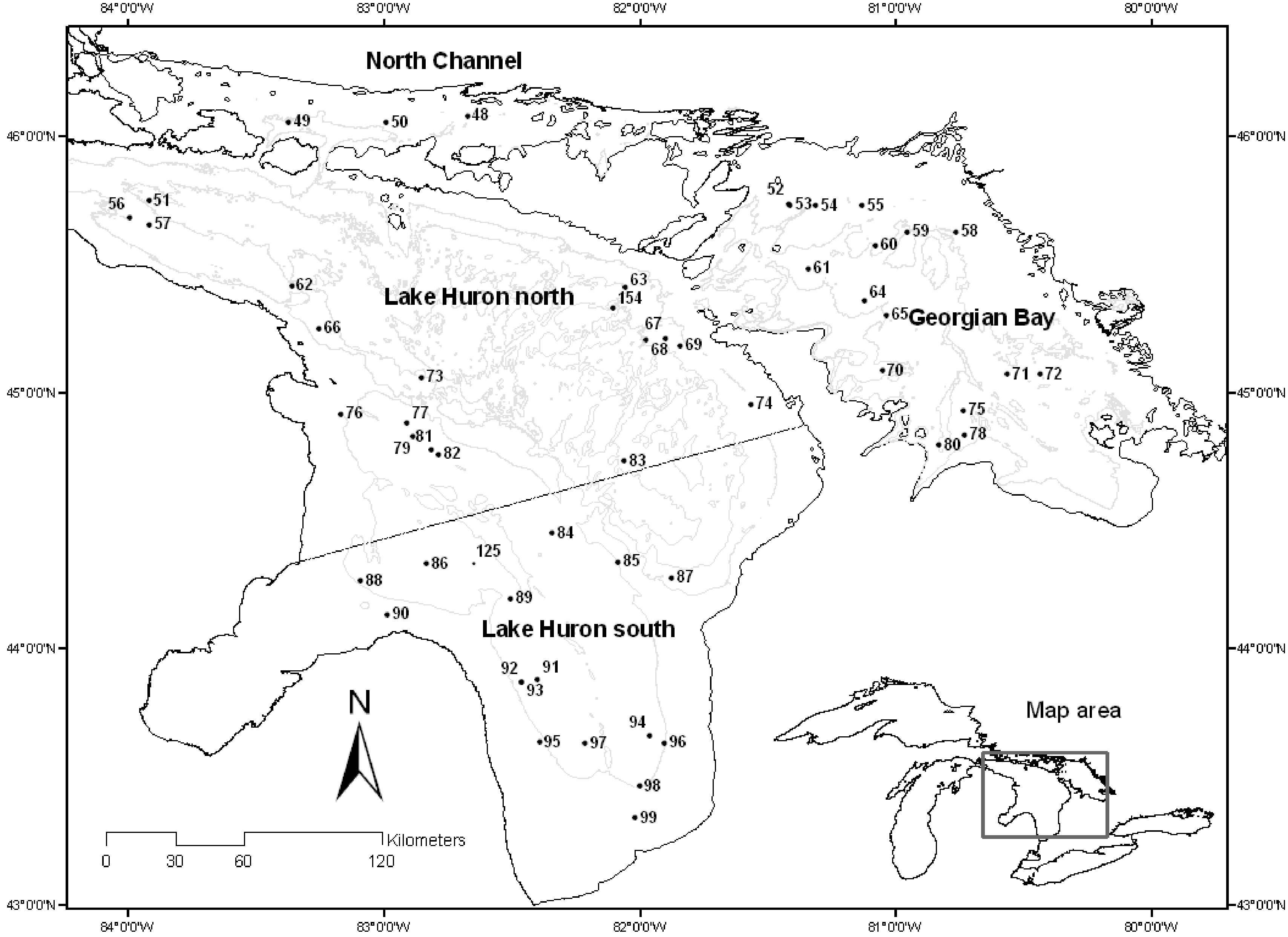

Figure 1. Map showing station locations of Mysis and fish sampling in Lake Huron. Depth contours are every 50 m and begin at 50 m. See Table 1 for additional station information.

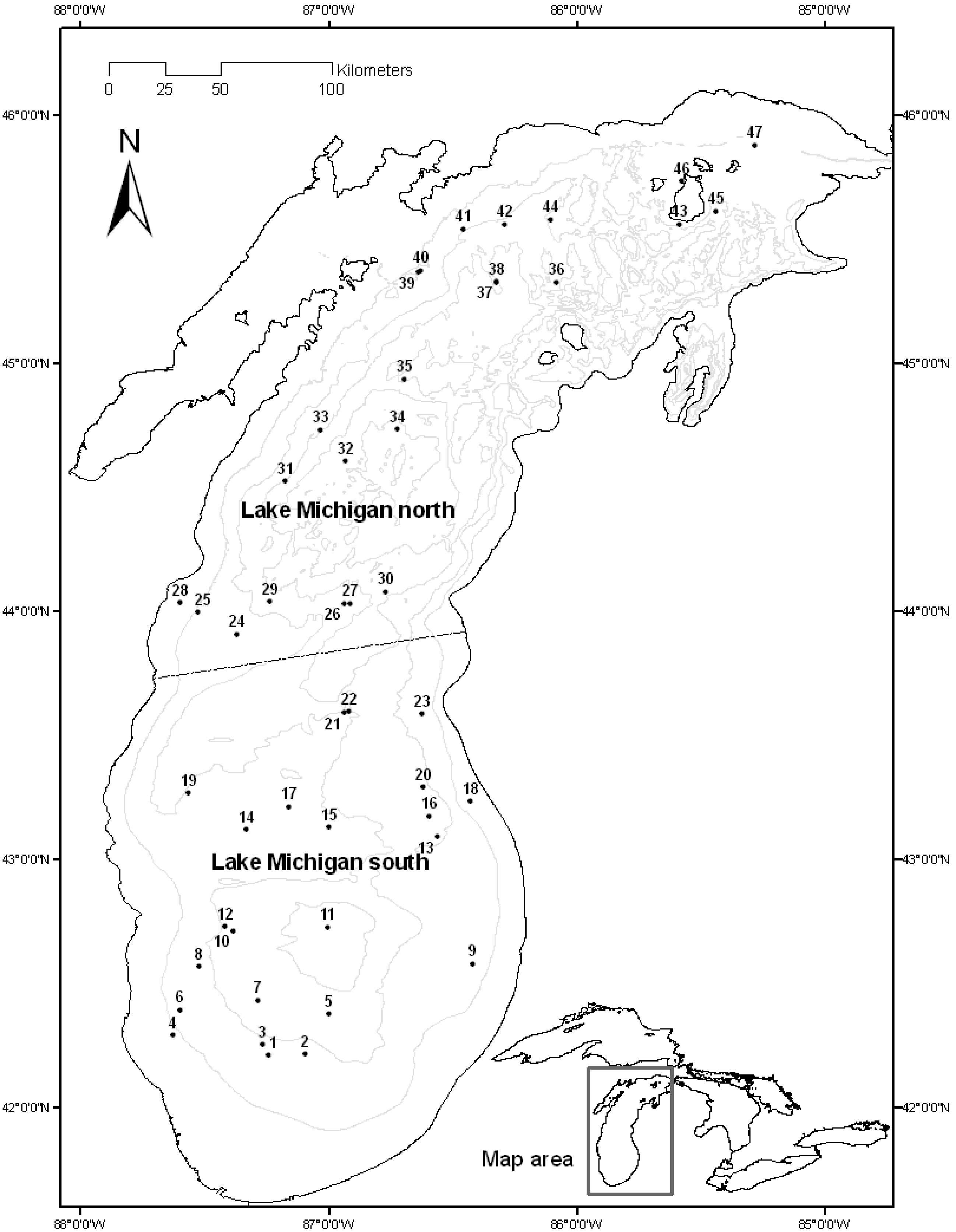

Figure 2. Map showing station locations of Mysis and fish sampling in Lake Michigan. Depth contours are every 50 m and begin at 50 m. See Table 1 for additional station information.

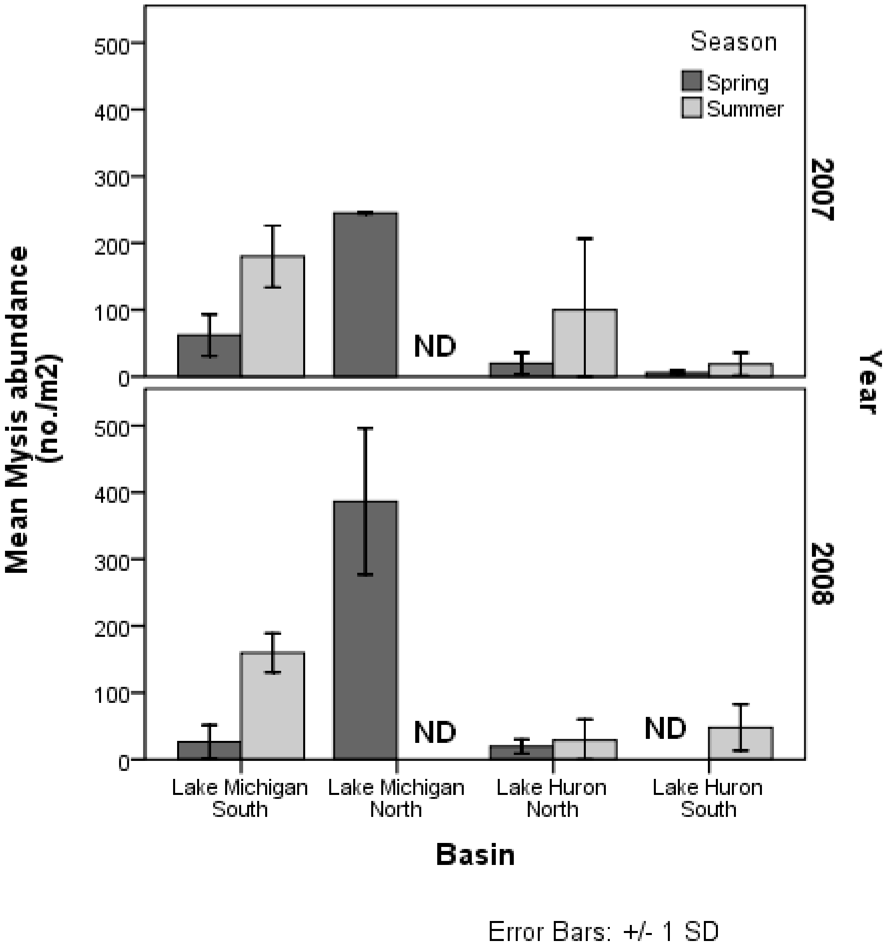

Figure 3. Mean *Mysis* areal density (number·m^{-2}) in lakes Michigan and Huron from nighttime vertical tows in spring and summer 2007 and 2008. ND: no data.

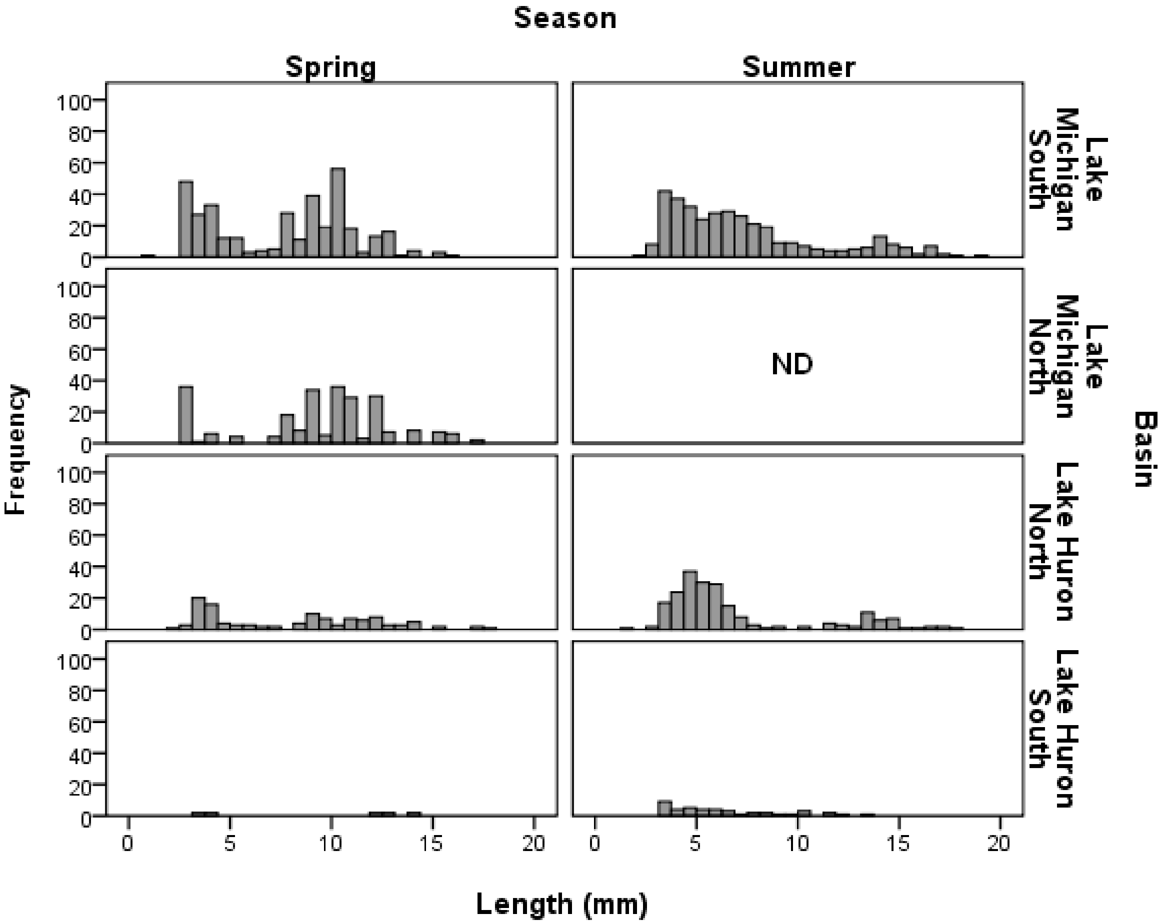

Figure 4. Length-frequency histograms of all *Mysis* collected during nighttime vertical tows, spring and summer 2007, in lakes Michigan and Huron. ND: no data.

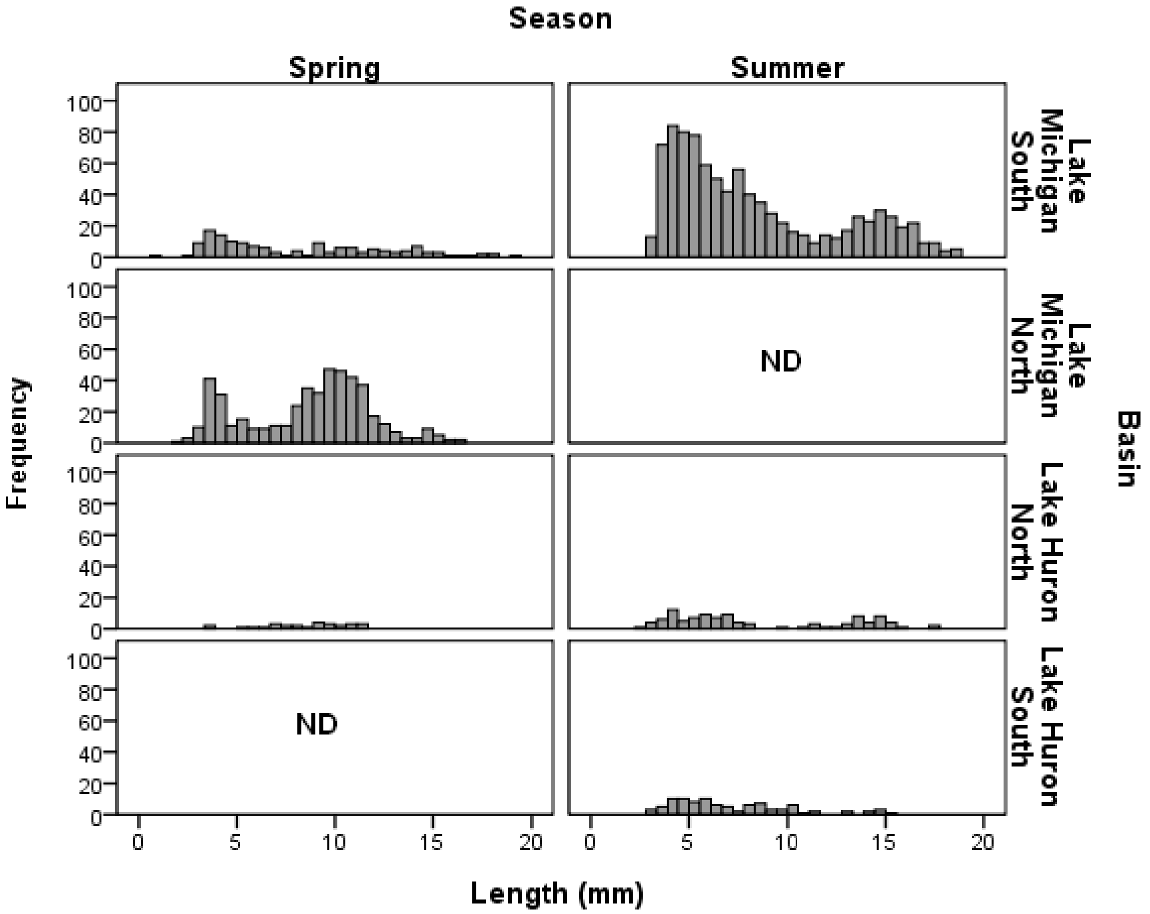

Figure 5. Length-frequency histograms of all *Mysis* collected during nighttime vertical tows, spring and summer 2008, in lakes Michigan and Huron. ND: no data.

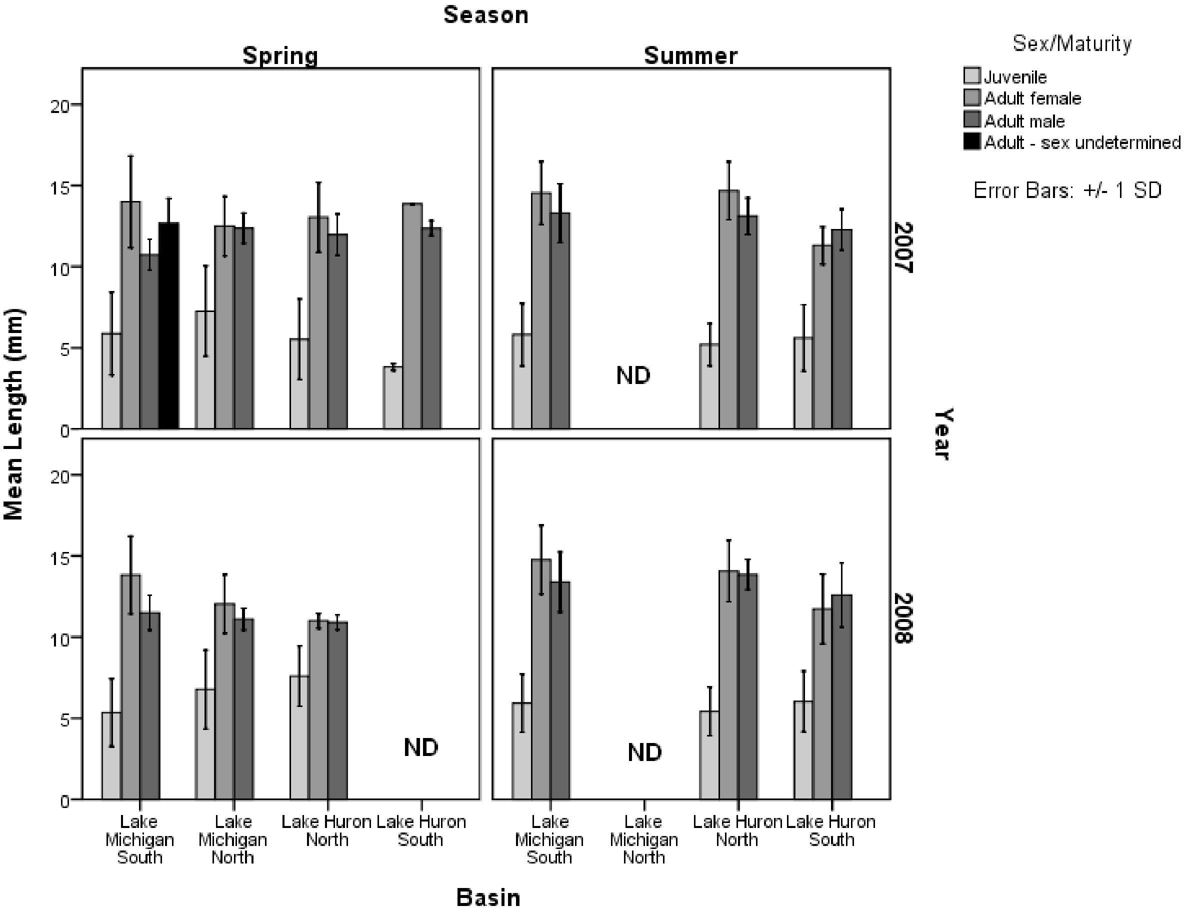

Figure 6. Mean lengths (mm) of adult male, adult female, and juvenile (<10 mm) *Mysis* collected during nighttime vertical tows, spring and summer 2007 and 2008, in lakes Michigan and Huron. Errors bars are ± 1 SD. In southern Lake Michigan in spring 2007, some adults did not have their sexes recorded and are designated by “sex undetermined.” In all other basins during all other periods, all adults were sexed. ND: no data.

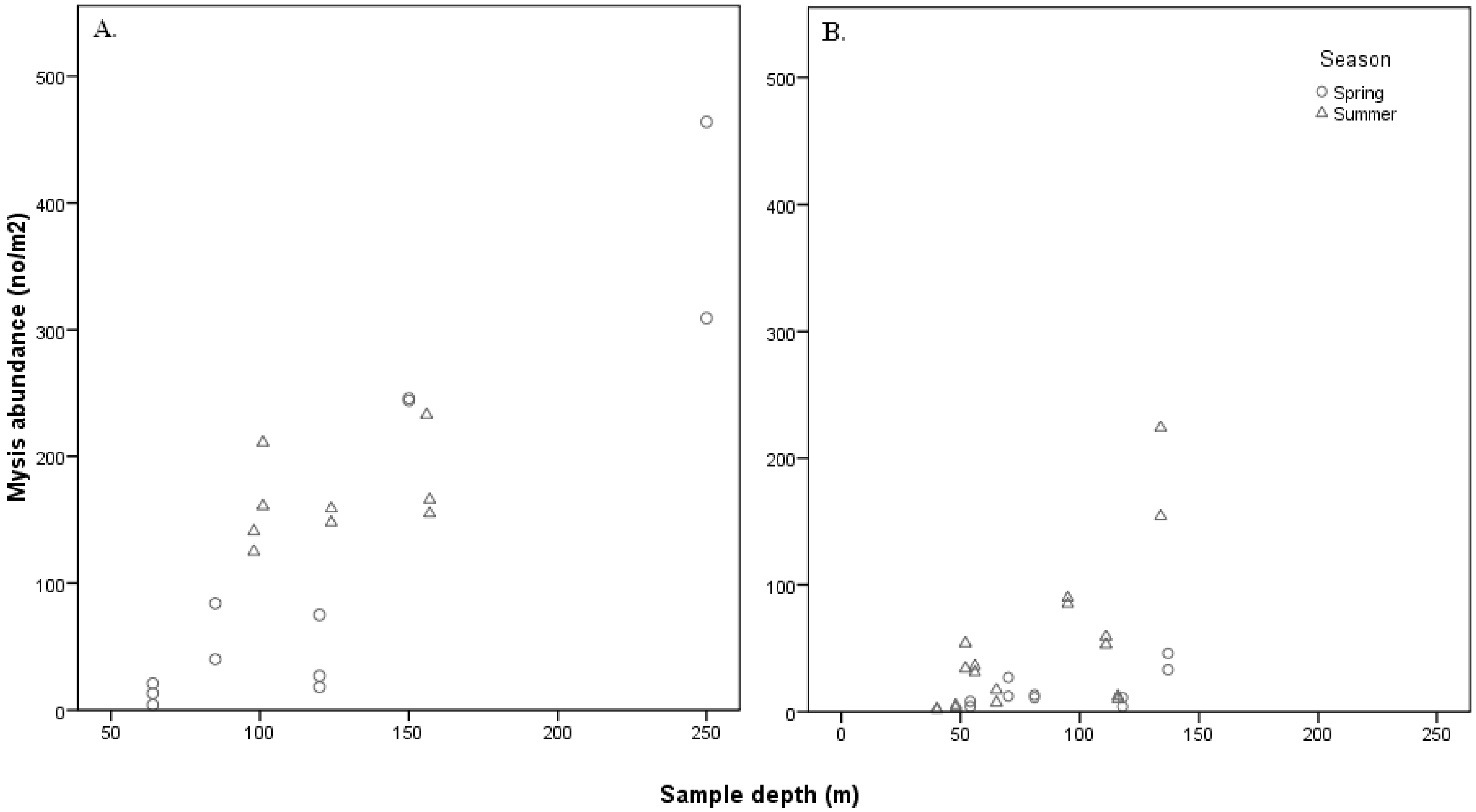

Figure 7. *Mysis* areal density (no·m^{-2}) as a function of station depth (m) in a) Lake Michigan and b) Lake Huron in spring and summer 2007 and 2008. *Mysis* were collected using nighttime vertical tows.

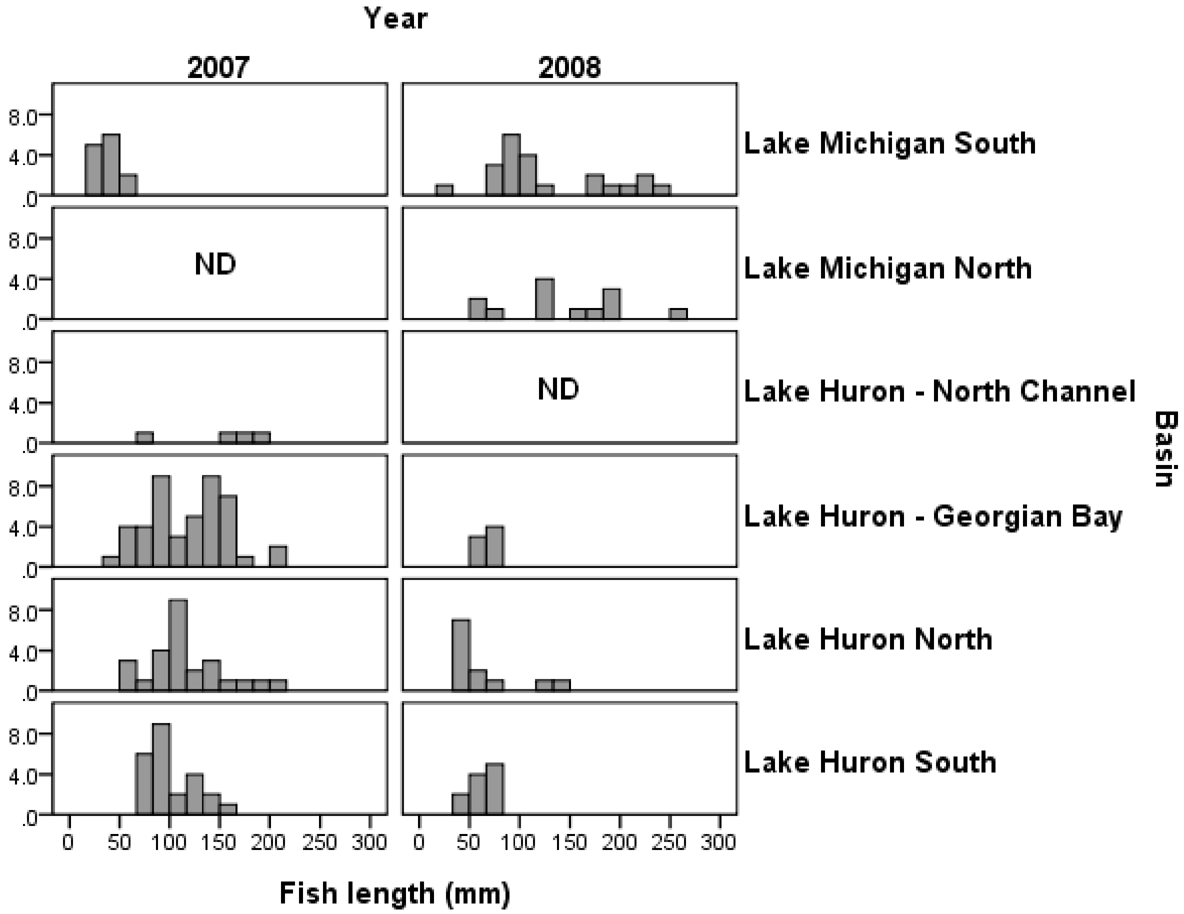

Figure 8. Length frequencies of bloaters (*Coregonus hoyi*) processed for diets. Fish were collected with midwater trawls in lakes Michigan and Huron in late summer/early fall of 2007 and 2008. ND: no data.

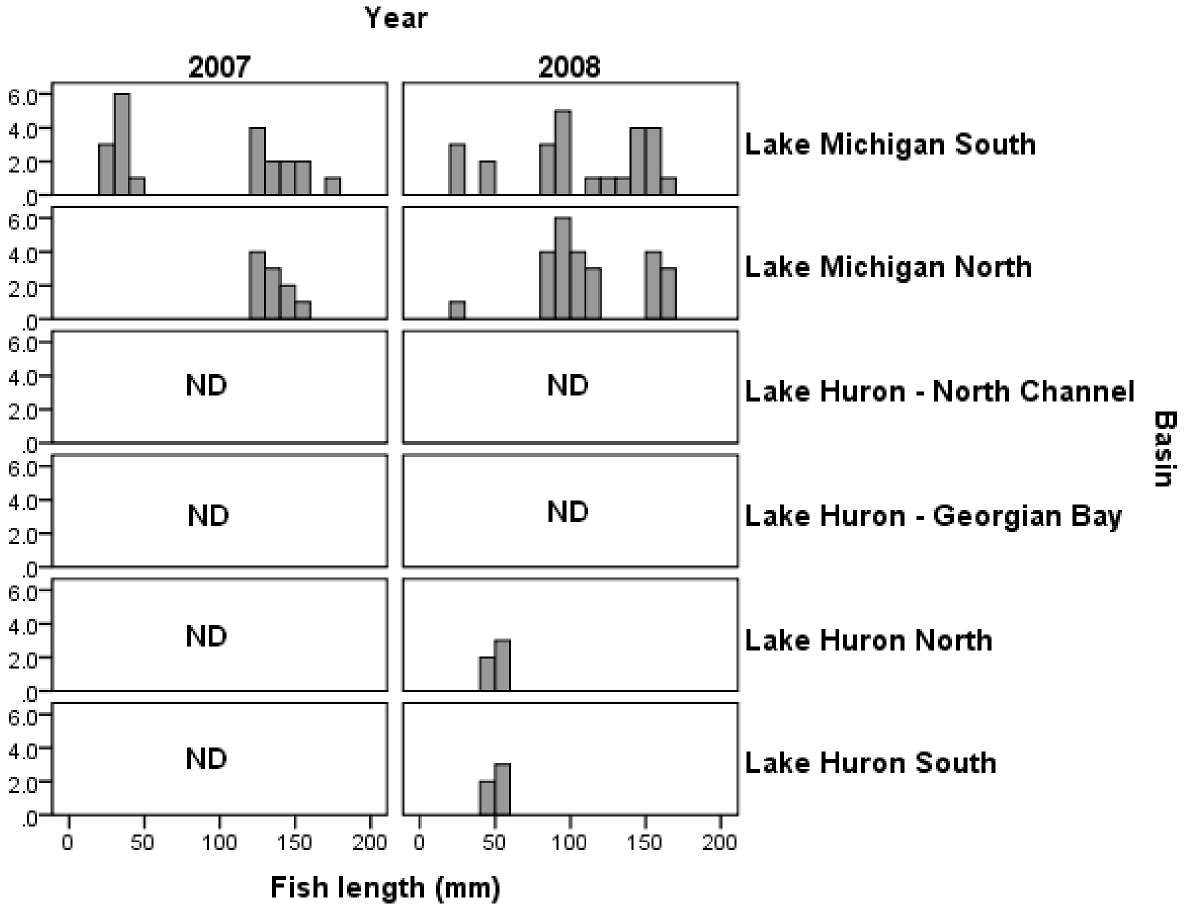

Figure 9. Length frequencies of alewives (*Alosa pseudoharengus*) processed for diets. Fish were collected with midwater trawls in lakes Michigan and Huron in late summer/early fall of 2007 and 2008. ND: no data.

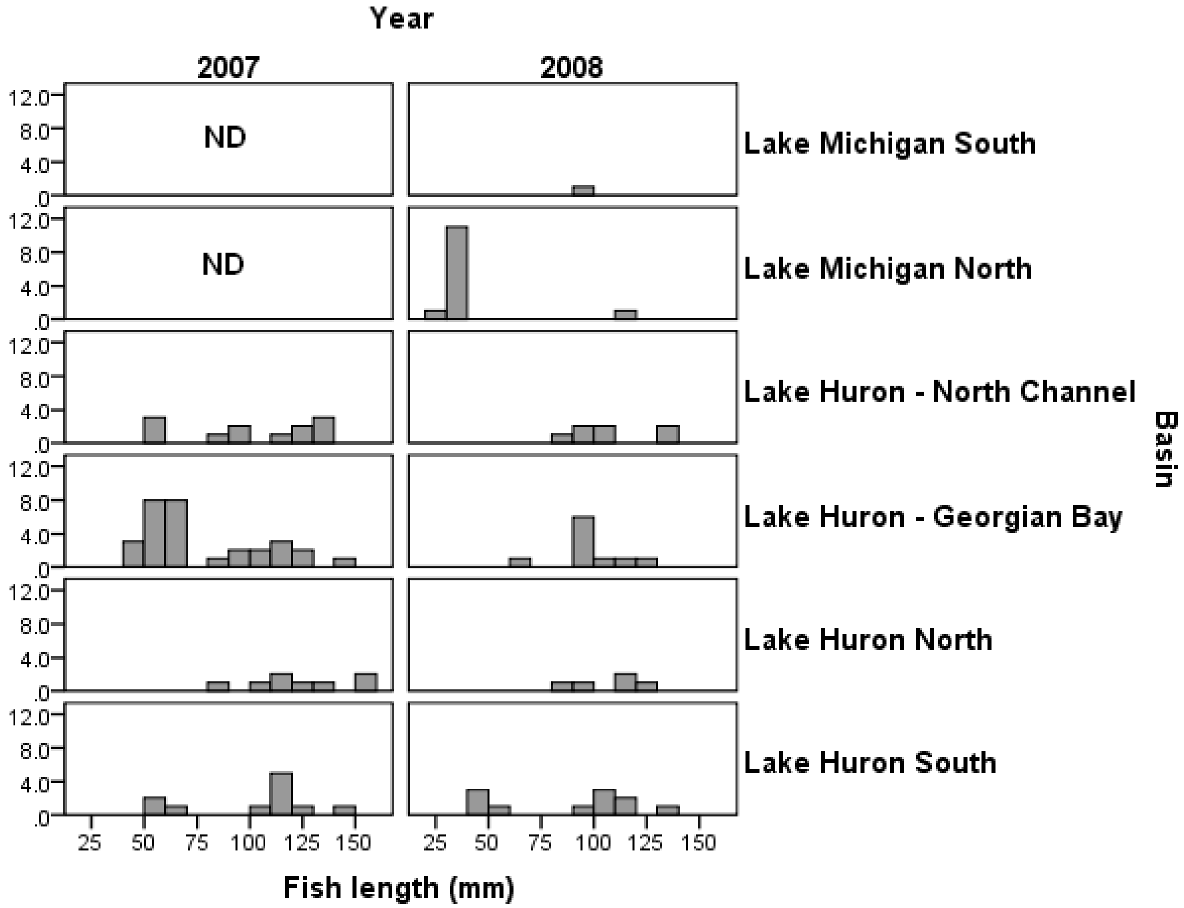

Figure 10. Length frequencies of rainbow smelt (*Osmerus mordax*) processed for diets. Fish were collected with midwater trawls in lakes Michigan and Huron in late summer/early fall of 2007 and 2008. ND: no data.

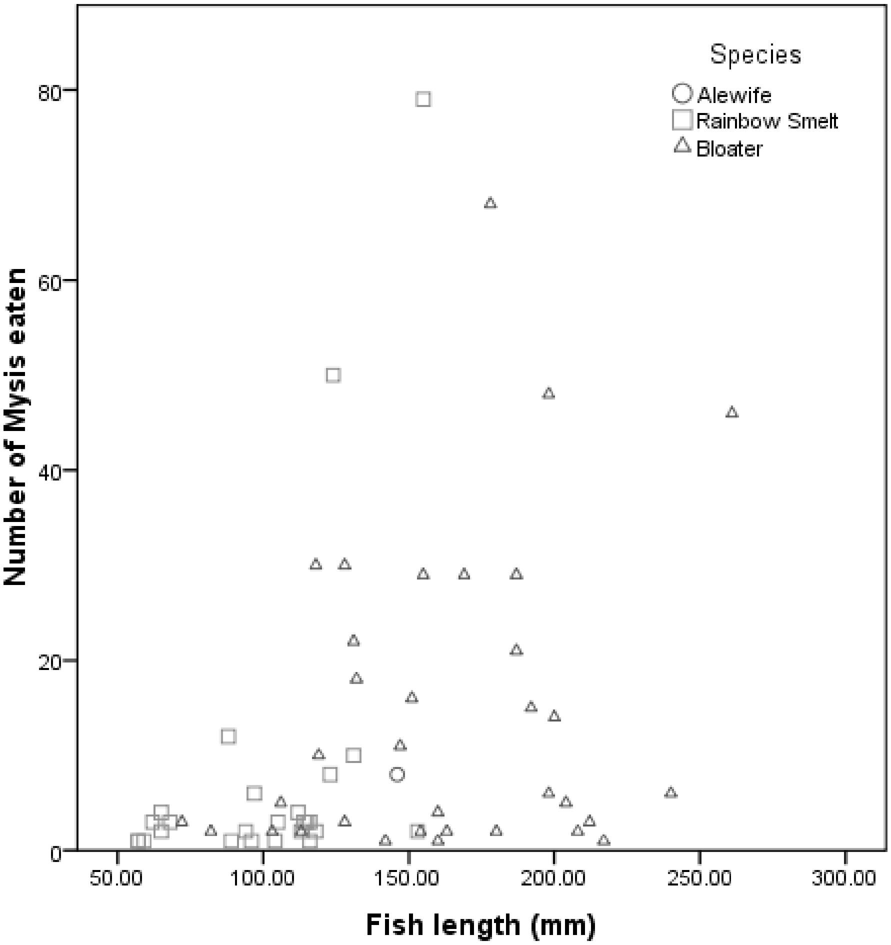

Figure 11. Number of *Mysis* occurring in pelagic prey fish diets (alewives *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, and bloaters *Coregonus hoyi*) as a function of fish total length (mm). Fish were collected in midwater trawls in lakes Michigan and Huron in late summer/early fall 2007 and 2008.

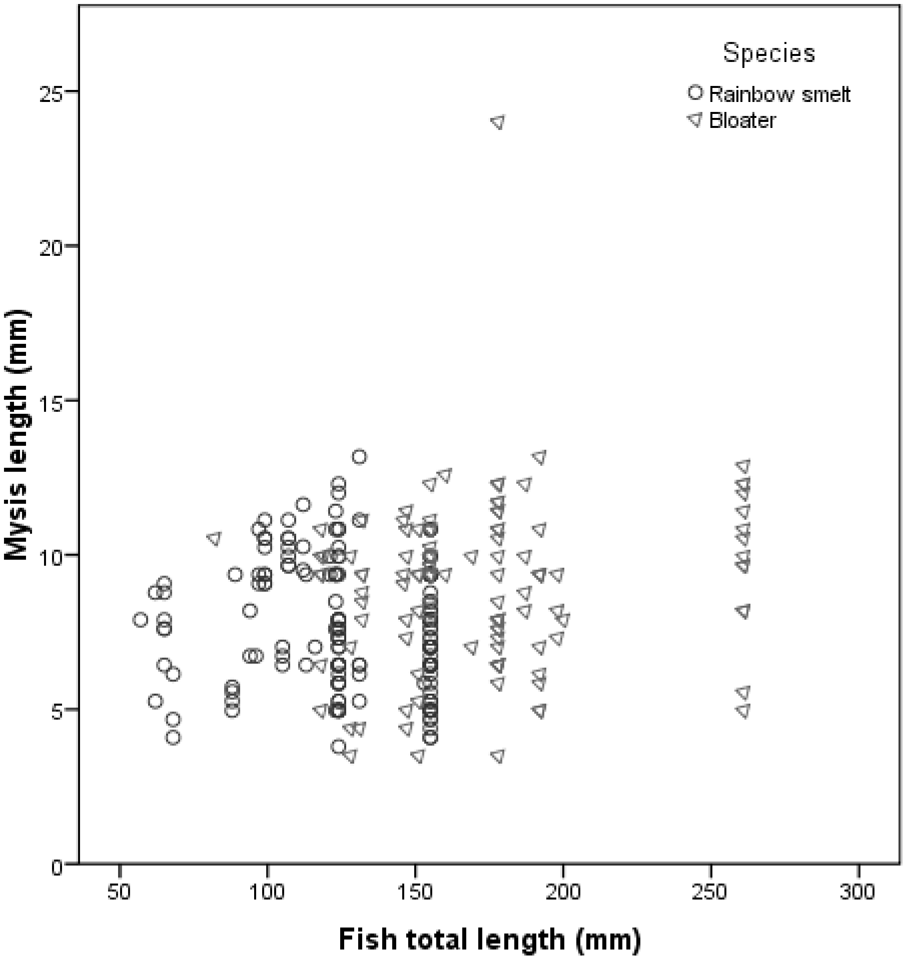

Figure 12. Mean length (mm) of *Mysis* occurring in pelagic prey fish diets (alewives *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, and bloaters *Coregonus hoyi*) as a function of fish total length (mm). No measurable *Mysis* remains were found in alewife (*Alosa pseudoharengus*) diets. Fish were collected in midwater trawls in lakes Michigan and Huron in late summer/early fall 2007 and 2008.

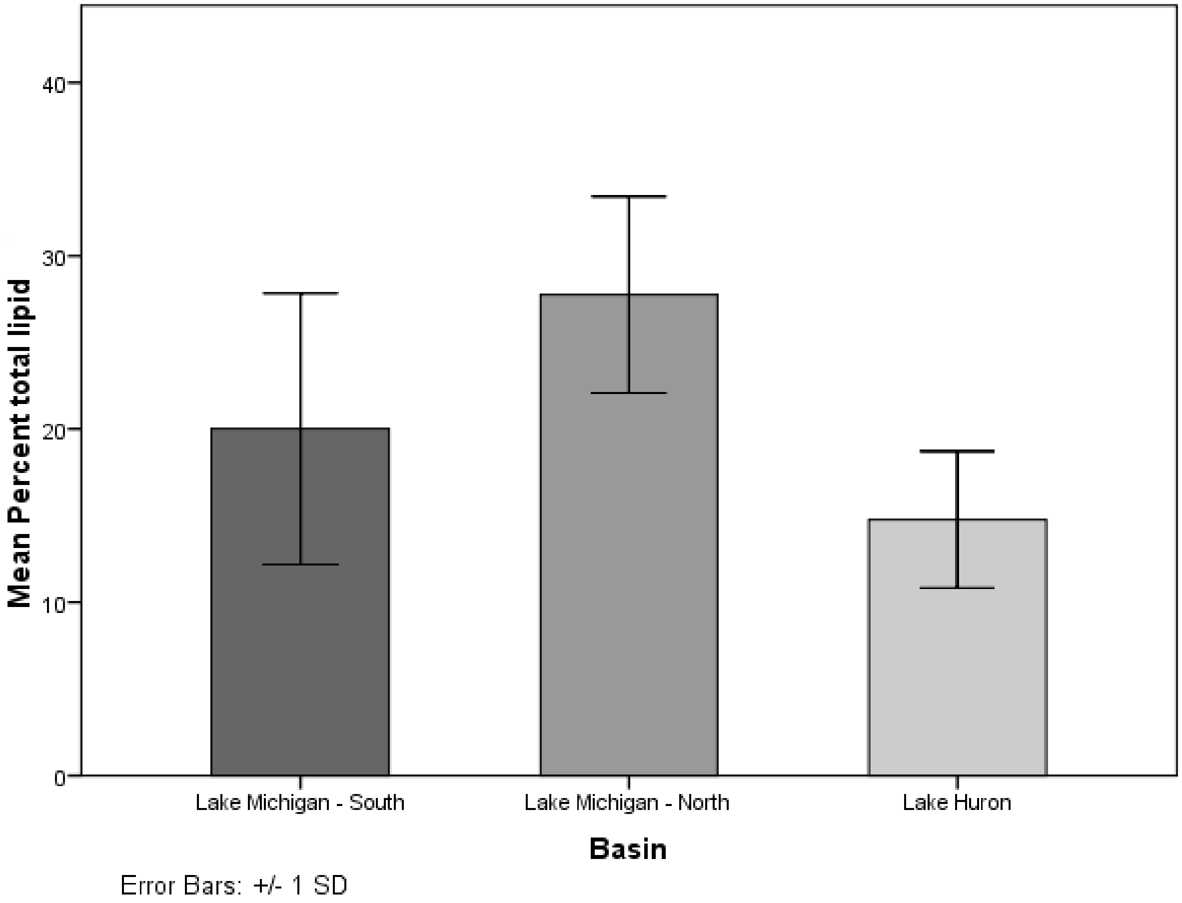

Figure 13. Mean total lipids (as percentage of wet weight of tissue) of adult *Mysis* in Lakes Michigan and Huron, August 2008. *Mysis* were collected using nighttime vertical tows.

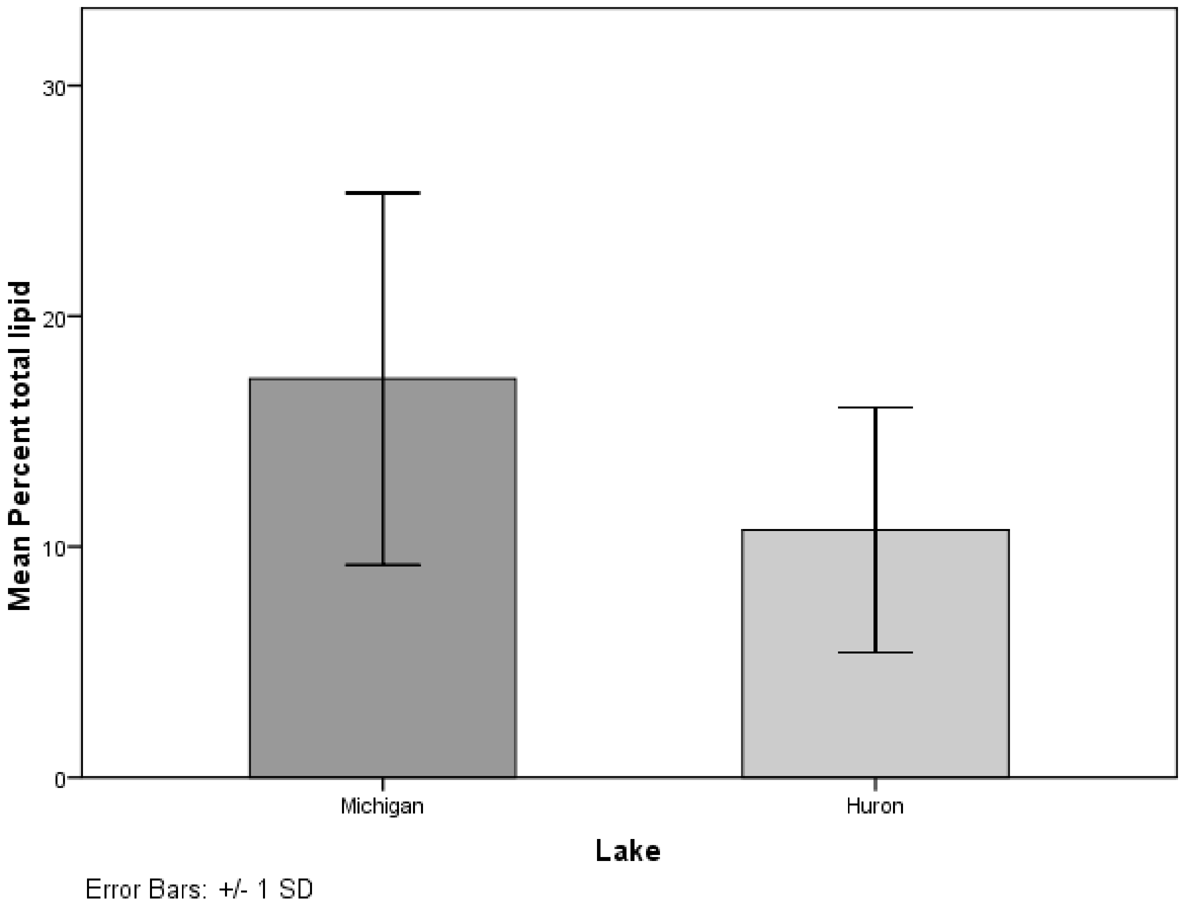

Figure 14. Mean total lipids (as percentage of wet weight of tissue) of samples containing juvenile *Mysis* (composed of all juveniles or mixed juveniles/adults) collected from Lakes Michigan and Huron, August 2008. *Mysis* were collected using nighttime vertical tows.

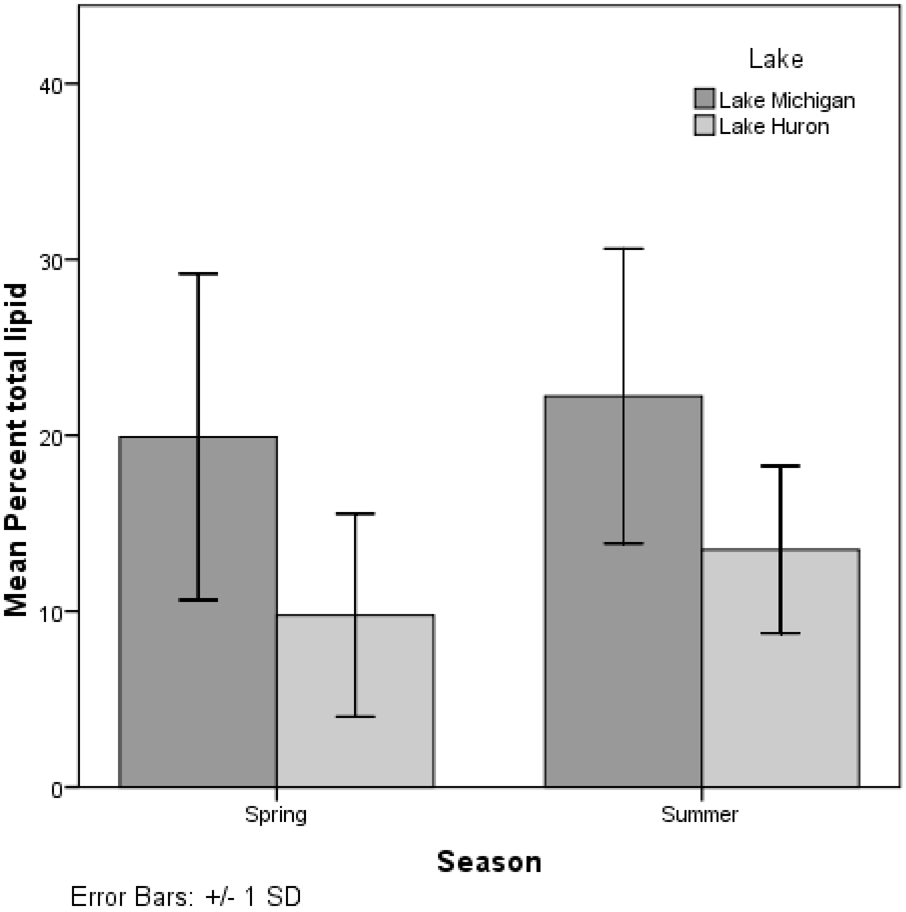

Figure 15. Seasonal change in total lipids (as percentage of wet weight) of all *Mysis* in lakes Michigan and Huron, 2008. *Mysis* were collected using nighttime vertical tows.

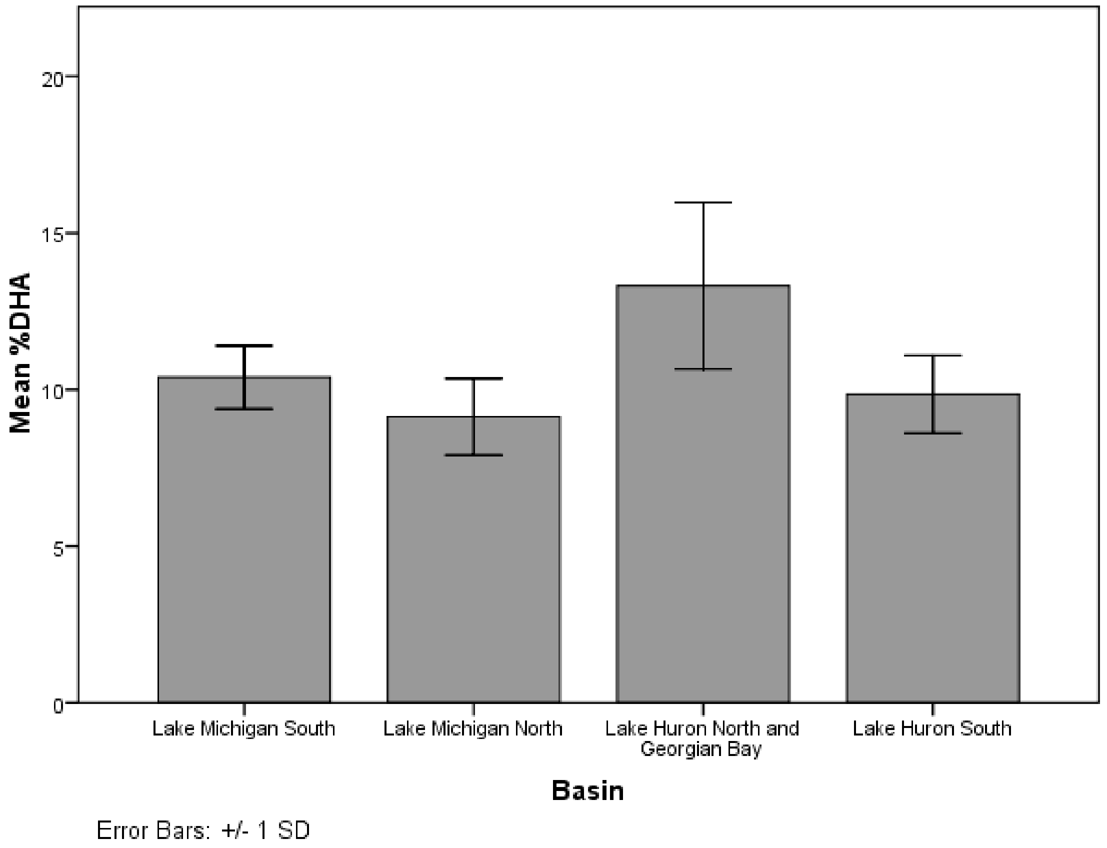

Figure 16. Relative proportion of the fatty acid docosahexaenoic acid methyl ester (DHA) (22:6*n*-3), expressed as proportion of total fatty acids detected, in adult *Mysis* from Lakes Michigan and Huron in summer 2008. *Mysis* were collected with nighttime vertical tows.

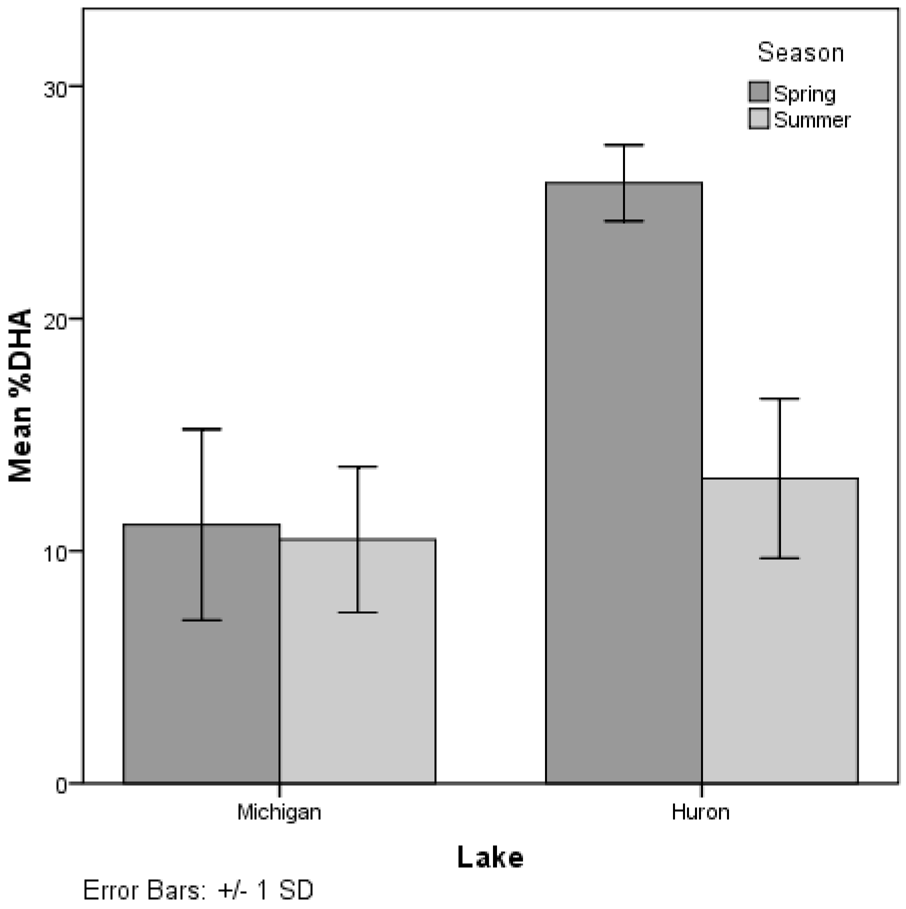

Figure 17. Seasonal change in relative proportion of the fatty acid docosahexaenoic acid methyl ester (DHA) (22:6*n*-3), expressed as proportion of total fatty acids detected, in *Mysis* from Lakes Michigan and Huron in 2008. *Mysis* were collected with nighttime vertical tows.

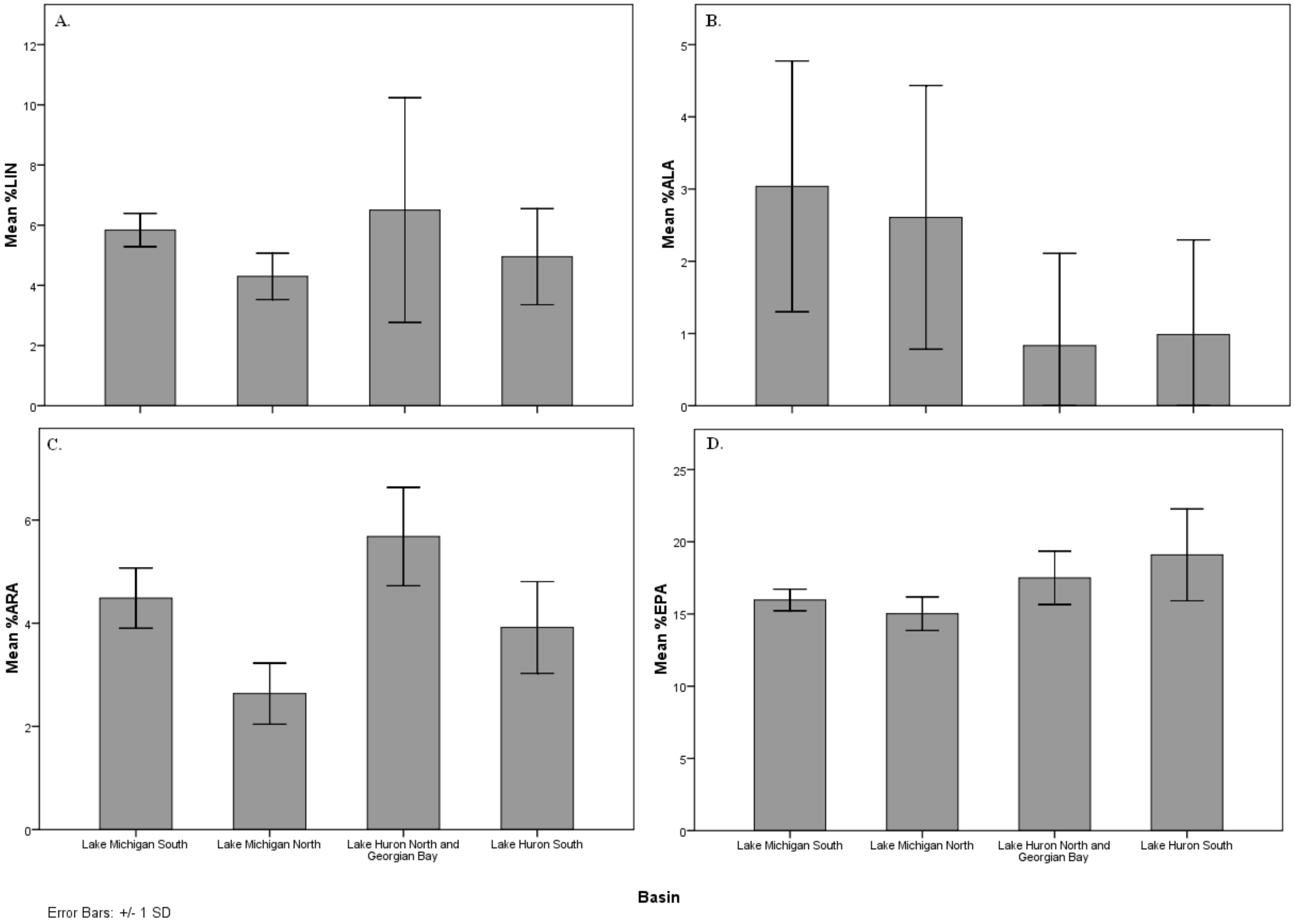

Figure 18. Relative proportions (as percentage of total fatty acids detected) of a) linoleic acid methyl ester (18:2*n*-6) (LIN); b) α-linolenic acid (18:3*n*-3) (ALA); c) arachidonic acid methyl ester (20:4*n*-6) (ARA); and d) eicosapentaenoic acid (20:5*n*-3) (EPA). Data are from adult *Mysis* collected using nighttime vertical tows in summer 2008.

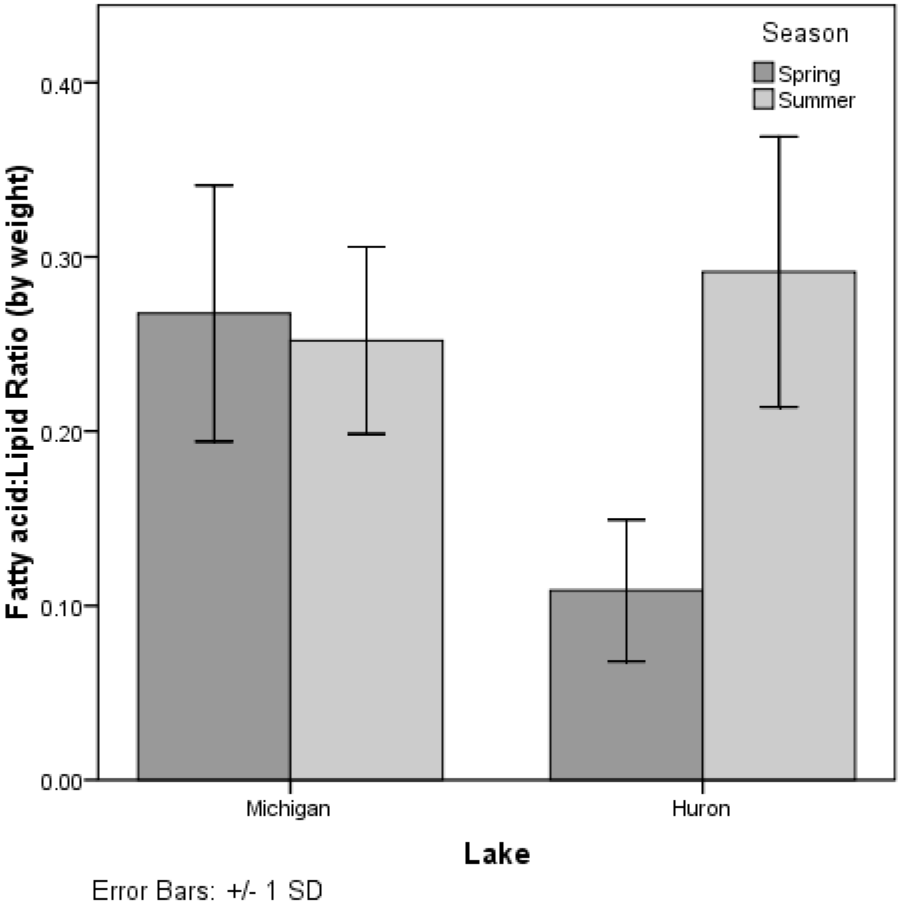

Figure 19. Seasonal change in fatty acid to total lipid ratios (by weight) for *Mysis* in lakes Michigan and Huron in 2008. *Mysis* were collected with nighttime vertical net tows.

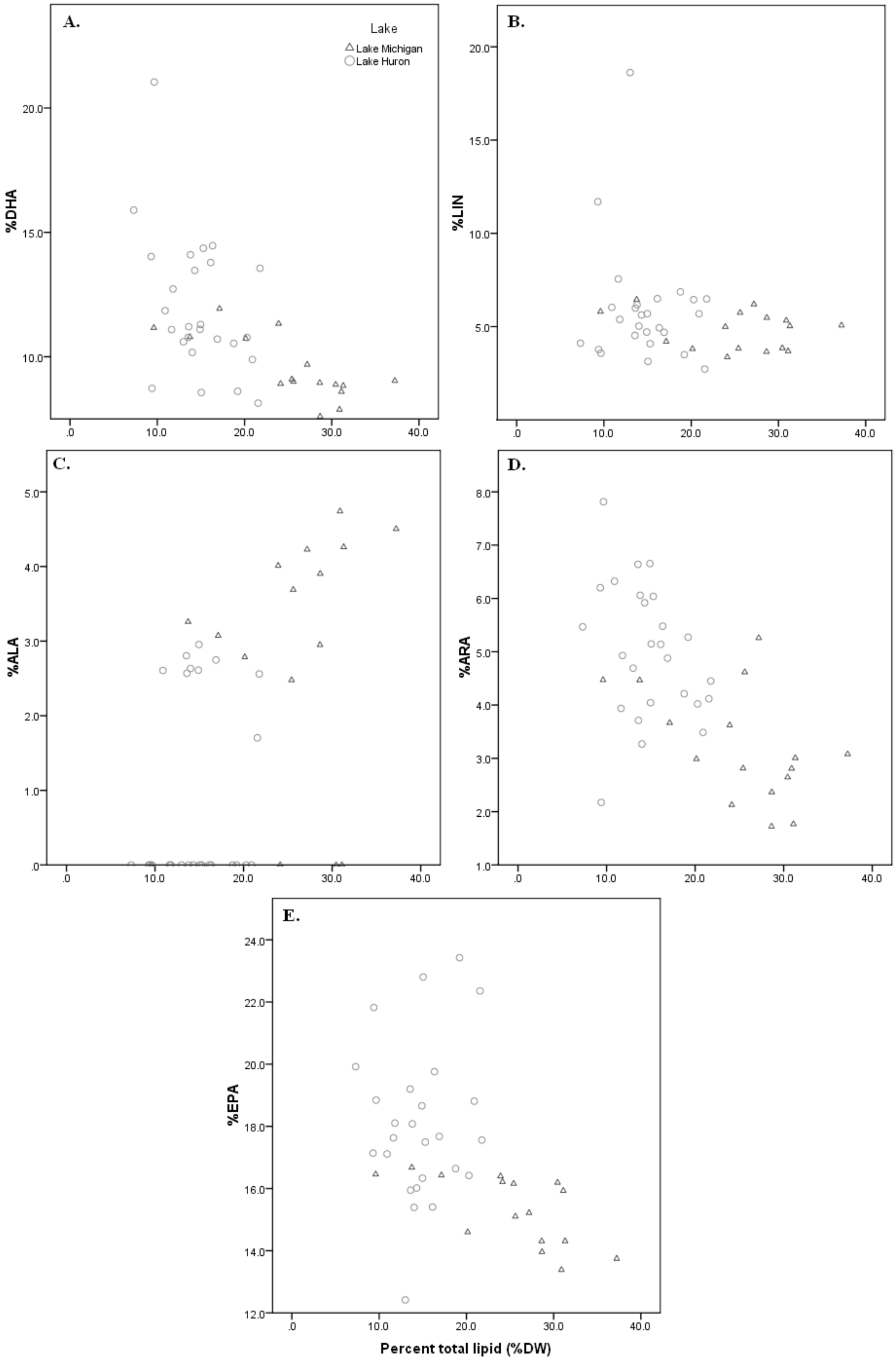

Figure 20. Linear regressions with relative proportions of various fatty acids (as percentage of total fatty acids detected) as the response variables and total lipids (as percentage of wet weight) as the explanatory variable: a) linoleic acid methyl ester (18:2*n*-6) (LIN); b) α-linolenic acid (18:3*n*-3) (ALA); c) arachidonic acid methyl ester (20:4*n*-6) (ARA); and d) eicosapentaenoic acid (20:5*n*-3) (EPA). Data are from adult *Mysis* collected using nighttime vertical tows in summer 2008. Circles represent data from Lake Huron, squares from Lake Michigan.