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Temporal trends in *Mysis relicta* abundance, production, and life-history characteristics in southeastern Lake Michigan

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ABSTRACT

The density and life history characteristics of *Mysis relicta* were evaluated at a 110-m and 45-m station in southeast Lake Michigan during spring, summer, and fall for two time periods, 1995–2002 and 2007–2008. *Mysis* were more abundant during 1995–2002 than 2007–2008 for all seasons and depths, with average declines across seasons of 81% at 45 m and 70% at 110 m. Offshore densities of *Mysis* in 2007–2008 were similar to published densities within the same region during 1985–1989, but under differing ecosystem conditions (e.g. higher fish biomass and primary production in the 1980 s). Growth averaged 0.032 ± 0.002 mm/day in both 1995–2002 and 2007–2008, and the proportion of females with broods (overall 7%) did not differ between time periods. Mean brood size adjusted for length did not differ between 1995–2002 (17 ± 0.6) and 2007–2008 (15 ± 1.3). The mean length of reproductive females was higher in 2007–2008 (17 ± 0.2) than during 1995–2002 (16 ± 0.1). New recruits (≤ 4 mm) were collected during each season for each time period, but were lower in abundance in 2007–2008 than in 1995–2002. During spring, there was a significant relationship between offshore water column chlorophyll concentration and *Mysis* recruit abundance, but not during summer/fall. Declining spring chlorophyll levels may be altering food availability for small mysids in spring, and the decline of the benthic macroinvertebrate *Diporeia* may be increasing fish predation pressure on *Mysis* despite declining planktivore abundance.

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Introduction

The opossum shrimp *Mysis relicta* (hereafter *Mysis*) is a large, benthic-pelagic crustacean that plays a key role in the food-web dynamics of the Laurentian Great Lakes including Lake Michigan. Due to their well documented diel vertical migrations and broad diets, *Mysis* play a key role in the transfer of energy from phytoplankton to fish and between the benthic and pelagic food webs (Nordin et al., 2008; Johannsson et al., 2001). As a predator, *Mysis* can exert considerable predation pressure on phytoplankton (Bowers and Grossnickle, 1978) and zooplankton communities (Nero and Sprules, 1986; Johannsson et al., 1994; Gal et al., 2006). In turn, *Mysis* provide a high-energy food source for many planktivorous and benthivorous fishes (Wells, 1980; Hondorp et al., 2005).

Although they have the ability to move vertically within the water column and eat a wide variety of prey, the intermediate position of

Mysis in the food web as both a predator and as a prey imposes both bottom-up and top-down forces on their populations. The importance of bottom-up control is evidenced by the variation in mysid brood sizes, growth, and age-at-maturity across gradients of system primary productivity (Morgan, 1980; Beeton and Gannon, 1991). As *Mysis* grow, they typically shift from herbivory to zooplanktivory, so changes in one component of the food-web may disproportionately affect certain life stages (Lasenby and Landgford, 1973; Branstrator et al., 2000). Herbivory by *Mysis* in Lake Michigan in the past may have occurred over an extended period of ontogeny due to abundance of large diatoms in spring and the deep chlorophyll layer in the summer (Bowers and Grossnickle, 1978; Branstrator et al., 2000). Changes in the zooplankton community or invasions by invertebrate predators, such as *Bythotrephes* can alter *Mysis* diets (Cooper and Goldman, 1980; Nordin et al., 2008). Therefore, recent changes in the primary producer and zooplankton communities (Fahnenstiel et al., 2010, H. Vanderploeg, personal communication) certainly have the potential to alter *Mysis* production in Lake Michigan.

Mysis, along with *Diporeia*, have historically been among the most important food items for most forage and commercial fish in Lake Michigan (Ward, 1896; Wells, 1980; Rand et al., 1995). Following drastic declines of *Diporeia* in Lake Michigan in the late 1990s, the importance of *Mysis* as a food resource increased for many fish species

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(Hondorp et al., 2005; Pothoven and Madenjian, 2008). For example, annual consumption of *Mysis* by the average alewife doubled following *Diporeia* declines (Pothoven and Madenjian, 2008). Changes in fish community structure can also impact *Mysis* populations (McDonald et al., 1990). Although fish biomass within Lake Michigan is currently low (Bunnell et al., 2009), predation may still be an important factor structuring *Mysis* populations given the low abundance of alternative large prey such as *Diporeia* within the lake.

In light of the ongoing changes in the lower food-web, this study evaluates *Mysis* life history including abundance, size, reproductive characteristics, and production in southeast Lake Michigan. Understanding the status of *Mysis* relative to these changes is critical for understanding energy flow within the Lake Michigan ecosystem.

Methods

Mysis were collected from southeastern Lake Michigan at a 110-m station (hereafter referred to as offshore), and from a 40- or 45-m station (hereafter referred to as nearshore), during 1995–2002 (excluding 1997; nearshore only in 2001) and 2007–2008. The nearshore and offshore stations were located approximately 10 and 20 km off Muskegon, Michigan, respectively. For most years, collections were scheduled monthly during March–December at each station, but some sample periods were missed because of adverse weather or logistical constraints. Only limited sampling was conducted in 2002. Two to four replicate samples were collected with a 1-m diameter plankton net (1000- μ m mesh; 1:3 mouth-to-length ratio) towed vertically from 1 to 3 m above bottom to the surface at speeds of approximately 0.5 m/s. Mysids were anesthetized with carbonated water and preserved with sugar-buffered formaldehyde to form a final 3% solution. All samples were taken at least 1-h after sunset or 1-h prior to sunrise.

A Seabird Conductivity-Temperature-Depth (CTD) profiler was cast at each station when *Mysis* were collected. In conjunction with an associated study on primary production at the offshore site, discrete water samples were collected with a Niskin bottle to collect samples to determine chlorophyll levels (see Fahnenstiel et al., 2010). Weighted, mean water-column chlorophyll concentrations were determined to provide a measure of offshore productivity.

In the laboratory all mysids were counted, and body length, sex, and eggs-per-female were recorded for 100 randomly selected individuals in 1995 and for all individuals in subsequent years. Body length (standard length, SL) was measured from the tip of rostrum to the base of the telson. Total length (TL; rostrum to the cleft in the telson) was also measured for a subsample of individuals to develop a regression between SL and TL. Sex was only determined for animals longer than 10-mm because sex for most smaller individuals was undistinguishable. Brood size for females larger than 10 mm was determined as the number of eggs or embryos present.

To examine trends in abundance, areal density of *Mysis* was calculated to facilitate comparisons across depths and with previous studies. *Mysis* densities for replicate tows at a site for a given date were averaged to produce a single estimate of *Mysis* abundance for that date and site. *Mysis* abundances were placed into seasonal categories based on surface water temperature. Seasons were delineated as spring (isothermal to early stratified, surface temperatures < 15 °C), summer (stratified period with surface water temperatures > 15 °C), and fall (late stratified period with surface temperatures < 15 °C). *Mysis* were further categorized into two time periods, 1995–2002 and 2007–2008. These time periods were based on the temporal break in data collection over time. The two time periods also represent pre and post proliferation of quagga mussels *Dreissena bugensis* in the region which would incorporate any subsequent impacts on primary production (Nalepa et al., 2009). Finally, the time periods represent a period with stable or gradually declining *Diporeia* numbers and a period with very low numbers

(Nalepa et al., 2009). ANOVA was used to evaluate trends in *Mysis* abundance using depth zone, season, and time period as factors. All abundance data were transformed ($\log_e(\text{catch} + 1)$) prior to analysis to better meet the assumptions of ANOVA.

We used Menzie's (1980) size-frequency method to calculate secondary production of *Mysis*, a method that has previously been used for Lake Michigan (Sell, 1982). Annual production is expressed as

$$P = \sum_{j=1}^i (N_j - N_{j+1}) \times (W_j W_{j+1})^{1/2} \quad (1)$$

where P is annual production ($\text{mg}/\text{m}^2/\text{year}$) and N_j is number of individuals that developed into a particular size category (j) during the year. Size categories were based on 1-mm intervals for 3 to 22 mm following Sell (1982). W_j is the mean weight of an individual (mg , dry weight) in the j th size category, $(W_j W_{j+1})^{1/2}$ is the geometric mean between two adjacent size categories, i is the number of size categories (19). W was determined using the length-to-dry mass equation presented in Sell (1982). This equation is based on total length (TL), so we developed a SL to TL correction for our length measurements. The number of individuals that develop into a size category (N_j) is expressed as

$$N_j = i \bar{n}_j \times P_e / P_a \times 365 / \text{CPI} \quad (2)$$

Where i is the number of size categories, \bar{n}_j is the average density of all animals in the size category j , P_e is the proportion of time estimated spent in a size category and P_a is the actual proportion of time spent in a size category. We assumed P_e/P_a to be 1. CPI is the cohort production interval, or life span, which we assumed to be 19 months (570 days) as in Sell (1982). Growth was assumed constant across all sizes and over the course of the year.

To evaluate growth, lengths of most populated size classes (1-mm intervals) of a cohort (mode and two adjacent size classes) were averaged to calculate mean cohort length (Johannsson, 1992). For cohorts that could be followed within a year over at least 4 months, the mean cohort length was plotted against day of year, and regression used to determine average daily growth. Growth was compared across time periods using a t -test.

The proportion of females with broods was compared between time periods using chi-square analysis. Brood size (eggs plus embryos) was compared between the two time periods using ANCOVA, because brood sizes may vary with female length (Johannsson, 1995). The mean length of adult female *Mysis* was evaluated using ANOVA with depth zones, seasons, and time periods as factors. Further, female *Mysis* were categorized as small (10–15 mm) or large (> 15 mm) (Branstrator et al., 2000) and the proportion of females that were reproductive in each size class between time periods was compared using chi-square analysis. Abundance of new recruits (≤ 4 mm) was evaluated using ANOVA with depth zones, seasons, and time periods as factors.

The relationship between monthly abundance of recruits (≤ 4 mm) offshore and monthly mean water column chlorophyll concentration for the spring or summer/fall period was evaluated using linear regression. All analyses were done using SYSTAT 10 and P values of 0.05 were considered significant.

Results

Over time periods 1995–2002 and 2007–2008, *Mysis* abundance varied with depth zone ($F=62.15$, $df=1,102$, $P<0.001$), season ($F=4.54$, $df=2,102$, $P=0.012$), and time period ($F=49.94$, $df=1,102$, $P<0.001$) (Fig. 1). No interaction terms were significant. *Mysis* were more abundant at the offshore site than at the nearshore site. Seasonally, densities were generally highest in summer. *Mysis* were more abundant during 1995–2002 than during 2007–2008.

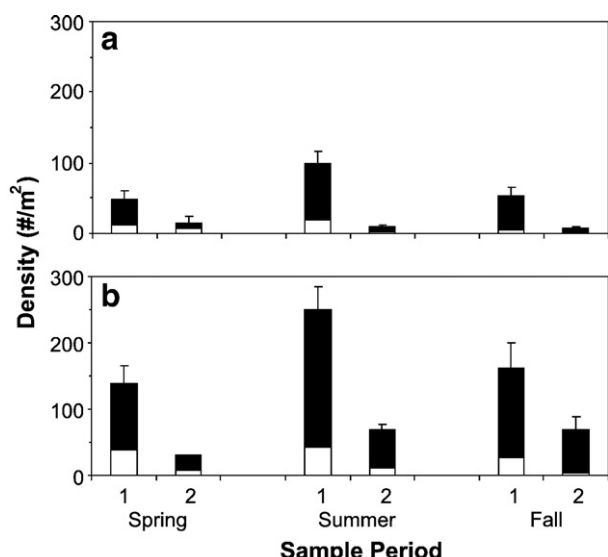


Fig. 1. Mean density (± 1 SE) of *Mysis relicta* at a nearshore (40–45 m) (panel a) and an offshore (110 m) station (panel b) during spring, summer and fall during two time periods (1) 1995–2002 and (2) 2007–2008. Open bar represents new recruits (≤ 4 mm) and shaded bar represents all larger individuals.

Total length (TL) was strongly correlated with SL ($R^2=0.99$, $n=106$, size range of mysids 4–20 mm SL), and was described by the equation: TL (mm) = $1.1261 \times \text{SL (mm)} + 0.1353$. Secondary production of *Mysis* declined over the period 1995–2008 (Fig. 2). Production was always higher offshore than nearshore. Production was highest in 1995–1998 at both depths, and declined at both sites in 1999 and 2000, and declined further in 2007 and 2008. In 2007 and 2008, production at the offshore site was similar or lower than that at the nearshore site in 1995–1998, and production at the nearshore site in 2007–2008 was almost negligible.

Growth did not differ between the two time periods for cohorts that could be followed, averaging 0.032 ± 0.002 mm/day in both 1995–2000 ($n=12$ cohorts) and in 2007–2008 ($n=4$ cohorts) ($t=0.08$, $df=14$, $P=0.93$).

The overall proportion of females that were reproductive (i.e., with broods) did not differ between the 1995–2002 (6.9%, $n=267$ total females) and 2007–2008 (8.2%, $n=48$ total females) periods ($\chi^2=1.18$, $df=1$, $P=0.27$). The proportion of females with broods also did not differ between time periods within any particular season ($\chi^2 < 2.66$, $df=1$, $P > 0.10$) (Fig. 3). Although reproductive females were found over the entire course of the year, the overall proportion of females with broods was highest in the spring (13%) and fall (9%) compared to the summer (3%). Adjusted brood size did not differ between 1995–2002 (17.4 ± 0.56 , 1 SE) and 2007–2008 (15.0 ± 1.26) time periods (ANCOVA, $F=3.01$, $df=1,312$, $P=0.08$). The mean length of reproductive females was higher in 2007–2008 (17.0 ± 0.25 mm) than during 1995–2002

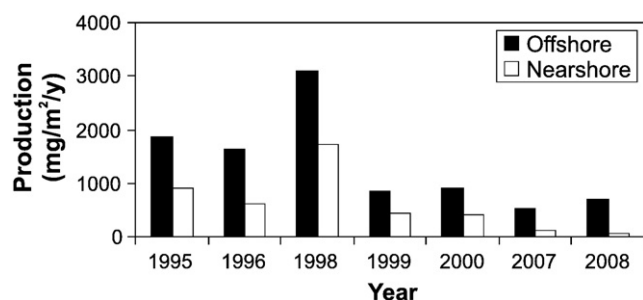


Fig. 2. Secondary production (dry weight) of *Mysis relicta* based on size frequency methods at a nearshore (open) and an offshore (shaded) station located off Muskegon, MI during 1995–2008.

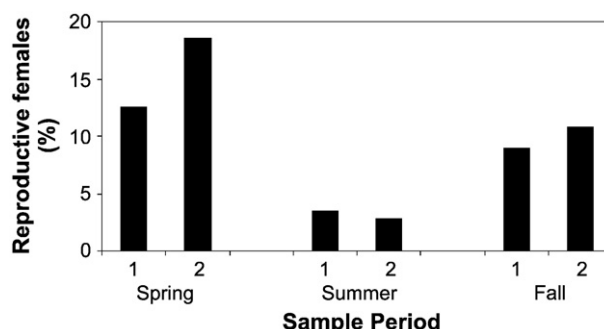


Fig. 3. Percentage of adult female *Mysis relicta* (≥ 10 mm) with broods during spring, summer, and fall during two time periods (1) 1995–2002 and (2) 2007–2008.

(15.8 ± 0.12 mm) ($F=15.14$, $df=1,313$, $P < 0.01$). The proportion of females < 15 mm with broods was 35% in 1995–2002 and 10% in 2007–2008, and differed between time periods ($\chi^2=11.60$, $df=1$, $P=0.001$).

The abundance of *Mysis* new recruits (≤ 4 mm) varied by depth zone ($F=31.62$, $df=1,102$, $P < 0.001$), season ($F=10.74$, $df=2,102$, $P < 0.001$), and time period ($F=24.76$, $df=1,102$, $P < 0.001$) (Fig. 1). Small mysids were collected all year during each time period, but were lower in abundance in 2007–2008 than in 1995–2002. During spring, there was a significant relationship between offshore water column chlorophyll concentration and *Mysis* recruit abundance ($P < 0.01$, $R^2=0.46$, $n=21$), but not during summer/fall period ($P=0.53$, $R^2=0.02$, $n=27$) (Fig. 4).

Discussion

Over time, *Mysis* numbers in southeast Lake Michigan appear to vary widely (Lehman et al., 1990; McDonald et al., 1990; Pothoven et al., 2000; this study). Although no data exist for our exact sites prior to 1995, a study was conducted at a 100-m deep site off Grand Haven, Michigan located 20 km southwest of our 110-m site (Lehman et al., 1990). Paired collections from each site during 2000 and 2002 suggest that *Mysis* abundance at the two sites were equivalent (paired t -test, $P > 0.05$). Based on pair-wise comparisons, abundance during the 1995–2002 time period was different from that during both 1985–1989 and 2007–2008 (Bonferroni multiple comparison test, $P < 0.05$), but there was no difference between the 1985–1989 and 2007–2008 periods.

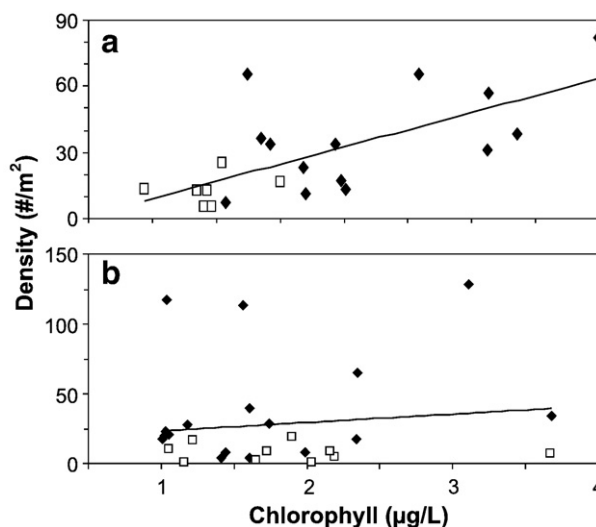


Fig. 4. Mean number of *Mysis relicta* new recruits (≤ 4 mm) as a function of mean water column chlorophyll levels during spring period (panel a) and summer/fall period (panel b). Filled symbols represent 1995–2002, open symbols represent 2007–2008.

A dramatic suppression of *Mysis* abundance in Lake Michigan between the late 1970s and late 1980s was attributed to increasing planktivory, particularly by a resurgent population of the benthivorous bloater *Coregonus hoyi* (McDonald et al., 1990; Rand et al., 1995). In the mid 1990s *Mysis* abundance in southeast Lake Michigan apparently rebounded as bloater numbers steadily declined (Szalai et al., 2003). By 2007–2008 however, *Mysis* numbers declined back to 1985–1989 levels (Lehman et al., 1990) despite relatively low bloater and overall planktivore biomass within Lake Michigan (Bunnell et al., 2009).

Despite low planktivore abundance in 2007–2008, fish predation still could be influencing *Mysis* abundance in Lake Michigan. As *Diporeia* declined at shallower depths (< 90 m) during the late 1990s (Nalepa et al., 2009), importance of *Mysis* as a prey item was increasing for some fish species such as bloater and slimy sculpin *Cottus cognatus* (Hondorp et al., 2005). In addition, alewife, which often select *Mysis* (Pothoven and Vanderploeg, 2004) doubled their consumption of *Mysis* on an individual-fish basis following *Diporeia* declines (Pothoven and Madenjian, 2008). Deepwater sculpin, an obligate benthivore, appears to have shifted toward a diet consisting almost entirely of *Mysis* after *Diporeia* declined to near negligible levels in our sampling region (S. Pothoven, unpublished data). So, it is possible that even with low abundances, fish could still impact *Mysis* as the importance and/or consumption of this prey increases for many fish species.

In addition to fish predation, trophic conditions can regulate *Mysis* production. For example, variation in *Mysis* growth and reproductive characteristics has been linked to differences in system productivity (Morgan, 1980; Beeton and Gannon, 1991). The recent dramatic decline in spring primary production relative to the 1980s and 1990s (Fahnenstiel et al., 2010) could have implications for *Mysis* production. Abundance of small *Mysis* (≤ 4 mm) appeared to be weakly but significantly linked to chlorophyll levels during spring but not during the summer/fall period. The relationship between chlorophyll and *Mysis* recruits was similar when only the 1995–2002 were included as well (ANCOVA, $P=0.78$), suggesting that the link between spring chlorophyll and *Mysis* recruits was important even in the past and not due simply to lower adult *Mysis* abundance during the latter time period.

Unlike larger *Mysis*, which are capable of eating prey such as zooplankton, small *Mysis* are generally herbivores (Lasenby and Landford, 1973; Branstrator et al., 2000). In San Francisco Bay Estuary, California, the invasion of the Asian clam *Potamocorbula amurensis* was implicated in declines of the mysid *Neomysis mercedis*, presumably through competition for phytoplankton that limited young mysid survival (Kimmerer and Orsi, 1996; Orsi and Mecum, 1996). Although growth rates based on mysid length did not change between the 1995–2002 and the 2007–2008 periods in southeastern Lake Michigan, these growth rates were calculated over March–December and do not necessarily reflect the overwinter through spring growth that would be most impacted by the loss of the spring phytoplankton bloom. Data on RNA/DNA ratios or lipid content could provide more insight into whether mysids, especially small mysids, are actually food limited during certain periods of the year such as the spring (Schlechtriem et al., 2008a,b).

For adult *Mysis* metrics examined that have been linked to trophic conditions (brood size, proportion of females that are reproductive overall and seasonally, and size distribution of reproductive females), the only changes noted between 1995–2002 and 2007–2008 was a decrease in the proportion of small females with broods during the latter time period. This suggests a potential increase in age to maturation that corresponded to the observed increase in mean length of females with broods.

In San Francisco Bay Estuary, declines in chlorophyll were not associated with any changes in *N. mercedis* brood size, although the apparent number of cohorts within a year decreased as did the overall

abundance of neonates (Orsi and Mecum, 1996). In our study, reproduction appeared to continue year-round over the entire course of the study based on the presence of reproductive females and small (≤ 4 mm) *Mysis*, but abundance of small *Mysis* within any given season was reduced in 2007–2008 relative to 1995–2002. Orsi and Mecum (1996) suggested that reduced chlorophyll levels might not impact larger mysids to the same degree as the smaller mysids that are more herbivorous. However, in Lake Michigan, an abundance of large diatoms in spring and other filamentous algae in the deep chlorophyll layer during summer historically provided adults with an important food source as well (Bowers and Grossnickle, 1978; Grossnickle, 1979; Branstrator et al., 2000). In the Baltic Sea, *M. relicta* switched from omnivory during winter when food was limited to herbivory following the spring phytoplankton bloom of diatoms and dinoflagellates (Lehtiniemi et al., 2009). Therefore, loss of the spring phytoplankton bloom may expand predation by adult mysids on other prey such as copepods or nauplii (Johannsson et al., 2001; Lehtiniemi et al., 2009).

Although growth and reproductive characteristics did not appear to be affected by the recent decline in spring primary production, we do not know whether this change in system productivity led to declines in *Mysis* condition. The spring bloom has been associated with seasonal increases in lipid content in the benthic amphipod *Diporeia* in Lake Michigan, and possibly with *Mysis* as well (Gardner et al., 1985). In Conception Bay, Newfoundland, a period of rapid lipid accumulation and release of neonates of *Mysis mixta* coincided with the spring phytoplankton bloom (Richoux et al., 2004, 2005). A seasonal change in *Mysis* energy content could indicate that food resources are limited at times during the year (Gardner et al., 1985), which could be further exacerbated by the loss of the spring phytoplankton bloom.

Our sampling took place along a single transect, but owing to monthly sampling, was designed to capture the temporal variation indicative of mysid life history dynamics. Mysids can vary spatially on both large and relatively small scales (Pothoven et al., 2004), so we cannot state for certain how representative our results are of the lake at larger spatial scales. However, previous work suggests that our sites are generally representative of sites of the same depth within the southern basin and almost certainly, the southeastern region of the lake (Pothoven et al., 2004; Hondorp et al., 2005). Regional differences in currents, fish abundance, productivity, and *Diporeia* abundance could affect larger-scale variability of *Mysis* population characteristics and abundance in the lake as a whole (Pothoven et al., 2004). Also, it should be pointed out that our work was done in the 45 to 110 m depth zone, and given that *Mysis* abundance increases with depth and fish abundance likely decreases (Johannsson, 1995; Pothoven et al., 2000), *Mysis* may be more abundant in deeper areas of the lake and basin. The maximum depth of the southern basin is approximately 160 m. It is unclear whether these deepest areas could provide a reservoir of *Mysis* that is redistributed into the shallower areas during winter (Johannsson, 1995).

Changes in *Mysis* production can ultimately affect fish production. *Mysis* production in 1995–1998 was similar to that reported for the 1970s (Sell, 1982). However, production appeared to have declined in 1999–2000 and continued to be low into 2007–2008. Recent work indicates that alewife condition and growth have declined in Lake Michigan and despite doubling their consumption of *Mysis*, individual fish total consumption still declined on average 31%, possibly because *Mysis* production is inadequate to fully compensate for the loss of prey such as *Diporeia* even at low fish abundances (Madenjian et al., 2003, 2006; Pothoven and Madenjian, 2008). Changes in alewife condition or abundance ultimately impact stocked salmonine populations that prey upon them (Madenjian et al., 2006). Nobriga and Feyrer (2008) found that fish production in the San Francisco Estuary was lower following declines in mysid shrimp in part because the system had been highly impacted by invasives, decreasing a fish's ability to fully compensate for changes in its prey community.

The offshore ecosystem in Lake Michigan is clearly in a state of dramatic change (Fahnenstiel et al., 2010). The future of *Mysis* production within the lake is uncertain. Some current parameters in the system suggest the potential for increased *Mysis* production, including absence of changes for *Mysis* reproductive characteristics and declining forage–fish numbers. Other changes including declining spring primary production, altered phytoplankton community composition, and absence of other large bodied crustacean prey (i.e. *Diporeia*) suggest that *Mysis* production may be suppressed in the future. *Mysis* is a key species within the Lake Michigan ecosystem and future work should pursue an understanding of the ongoing and future dynamics of *Mysis* within Lake Michigan and the mechanisms that control their populations.

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