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Lake-wide, annual status of the *Mysis diluviana* population in Lake Michigan in 2015

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Abstract

Mysis diluviana is one of the most abundant zooplankter by biomass in the Laurentian Great Lakes of North America, a predator of other zooplankton and an important prey for fishes. Studies of long-term trends in Lake Michigan have shown 2005-2016 densities to be 50-80% lower than 1990s densities, but these observations have been based on annual monitoring that is either spatially or seasonally limited. We combined Lake Michigan *Mysis* data from three annual programs and the 2015 Cooperative Science and Monitoring Initiative to achieve broad spatial coverage during spring, summer, and fall of 2015 and broad depth coverage during spring 2016. Lake-wide, annual density and biomass were 82 (SE: 10) *Mysis*/m^2 and 200 (SE: 36) mg dry mass/m^2. Density and biomass estimates were highest offshore, generally higher in the north basin, and seasonally highest in summer. Annual lake-wide averages for depths > 30 m were better captured by seasonally-extensive annual programs than spatially-extensive annual programs, although spring sampling may bias annual values low. *Mysis* cohorts grew 0.026 mm/d (age-0) and 0.007 to 0.027 mm/d (age-1). Annual mortality was 81-98%. Reproduction was fall-spring and seasonal lake-wide estimates ranged from 0.6 – 19.1 % females brooding, 13 – 20 embryos/brood, and 3 – 46 embryos/m^2. Annual production (423 mg dry mass/m^2/yr, SE: 31) was lower than all but one previous estimate from lakes Michigan, Huron, and Ontario. While *Mysis* tend to persist, low *Mysis* production may be a concern for prey fishes that feed on *Mysis*.

Keywords

production; growth; basin; spatial; life history; Cooperative Science and Monitoring Initiative (CSMI)

Introduction

Mysis diluviana (hereafter, "*Mysis*") is an ecologically important native species in the Laurentian Great Lakes of North America (hereafter, "Great Lakes") (Johannsson et al., 2003). *Mysis* is a key food source for fishes in the Great Lakes, especially native deep water taxa (Gamble et al., 2011; Pothoven et al., 2000b), and the role of *Mysis* as prey may have increased after amphipod *Diporeia* populations declined (Bunnell et al., 2015; Hondorp et al., 2005; Turschak and Bootsma, 2015). *Mysis* is an omnivore that feeds on zooplankton as well as phytoplankton and detritus, and *Mysis* is potentially important as a competitor of planktivorous fish in the Great Lakes (Gal et al., 2006; O'Malley et al., 2017; O'Malley and Bunnell, 2014). In addition, *Mysis* performs extensive diel vertical migrations determined largely by vertical structure of the light and temperature environment in the pelagic zone (Beeton, 1960; Boscarino et al., 2010, 2009), although some animals may remain on the bottom during the night (O'Malley and Stockwell, 2019; Shea and Makarewicz, 1989; Stockwell et al., 2020). *Mysis* plays a key role in linking benthic and pelagic habitats in the Great Lakes as it is the only 'migratory macroinvertebrate' present in those lakes (Patwa et al., 2007; Stockwell et al., 2014). Thus, monitoring *Mysis* populations is important for understanding Great Lakes ecosystems.

Lake Michigan has perhaps the longest record of assessing *Mysis* populations in the Great Lakes, with population studies conducted as early as 1954 (Beeton, 1960; Beeton and Gannon, 1991; Sell, 1982) and continuing through the 1960s (McWilliam, 1970), the 1970s and 1980s (Grossnickle and Morgan, 1979; Lehman et al., 1990; McDonald et al., 1990; Morgan and Beeton, 1978), and the 1990s and early 2000s (Hondorp et al., 2001; Pothoven et al., 2000a, 2004). For the past 13-15 years, *Mysis* have been sampled annually from Lake Michigan as part of three distinct, complementary, annual monitoring programs run by: 1) the US Geological Survey's (USGS) Great Lakes Science Center (GLSC) and the Michigan Department of Natural Resources (MI DNR) since 2005 (Bunnell et al., 2018; Warner et al., 2010), 2) the US Environmental Protection Agency's (EPA) Great Lakes National Program Office (GLNPO) since 2006 (Jude et al., 2018), and 3) the National Oceanic and Atmospheric Administration's (NOAA) Great Lakes Environmental Research Laboratory (GLERL) since 2007 (Pothoven and Vanderploeg, 2017; Pothoven et al., 2010). These annual programs have reported density and biomass since 2006 and 2007 to be 50-80% lower than estimates in the 1990s, (Bunnell et al., 2018; Jude et al., 2018; Pothoven and Vanderploeg, 2017). These studies also indicate that from 2005 to 2016, density and biomass of *Mysis* in Lake Michigan did not change or may have declined slightly (Bunnell et al., 2018; Jude et al., 2018). In addition, these studies have reported size structures, growth rates, reproductive effort, and annual mortality (Jude et al., 2018; Pothoven and Vanderploeg, 2017) although they did not report production as the last *Mysis* production estimates reported for Lake Michigan were for 2007, 2008 and 2009-2011 and were based on a single transect (Pothoven et al., 2010; Pothoven and Bunnell, 2016). However, each of these annual programs is limited in either space or time, with the USGS program only sampling in August but throughout the lake at different bottom depths, the EPA program sampling in spring and summer but at few sites and mostly in deep water, and the NOAA program sampling throughout the season but only at one 45-m station and one 110-m station close to Muskegon, MI. We do not know how well each program may be indictive of lake-wide annual averages.

Horizontal spatial distributions of *Mysis* density in Lake Michigan are primarily related to bottom depth as commonly observed in other lakes (Carpenter et al., 1974; Jude et al., 2018;

Pothoven et al., 2004; Reynolds and DeGraeve, 1972). However, other factors may affect horizontal distributions, including horizontal migration or advection by currents (Johannsson, 1995; Morgan and Threlkeld, 1982; Pothoven et al., 2004). In Lake Michigan, basin morphology and prevailing currents are different in the north and south basin and along the eastern and western nearshore regions (Beletsky et al., 1999; Beletsky and Schwab, 2001), which can lead to thermal, bio-optical, and biological habitat differences important for *Mysis* (e.g., Bunnell et al., 2018). Thus, north and south basins or east and west sides of Lake Michigan could have substantial differences in *Mysis* density and biomass which could impact inferences about lake-wide density and biomass from spatially limited sampling. In addition, such spatial differences may vary by season.

In 2015, collaborations among several agencies around Lake Michigan through the Cooperative Science and Monitoring Initiative (CSMI) allowed for a more comprehensive assessment of the *Mysis* population in both space and time. In this study, we present these data and ask four questions about *Mysis* populations in Lake Michigan. 1) Do *Mysis* density and biomass vary spatially in addition to the known effect of depth? Here we explore the importance of the potential spatial variables: lake basin (north and south) and lake side (east and west). 2) What are the 2015 lake-wide estimates of density, biomass, and population stage structure at seasonal and annual temporal scales, and how similar are these estimates to those from each of the annual programs in 2015? 3) Using this complete seasonal coverage, what are 2015 lake-wide annual estimates of growth rate, fecundity, and mortality, and how similar are they to estimates from the NOAA annual program for 2007-2015? 4) What is the 2015 lake-wide estimate of annual production of *Mysis* in Lake Michigan, and how does it compare with other available estimates of *Mysis* production in the Great Lakes?

Methods

Field collections and sample processing

Sampling for *Mysis* in 2015 in Lake Michigan was conducted by the USGS R/V *Sturgeon*, the EPA R/V *Lake Guardian*, and the NOAA R/V *Laurentian* (Table 1a). Samples collected in spring 2016 by NOAA and EPA were included in this study to achieve a full year of coverage (April 2015 – April 2016). Each sampling program collected 1-3 samples (Table 1b) per station-visit (hereafter, "visit"), for a total of 272 samples in 136 visits (Table 1a). The combined efforts of the three sampling programs resulted in good spatial coverage during spring 2015 (sampled April 14 – June 1), summer 2015 (sampled July 6 – August 25), and fall 2015 (sampled September 1 – November 3), poor spatial coverage during winter 2015 (sampled December 7), and moderate spatial coverage during spring 2016 (sampled March 27 – April 28) (Fig. 1).

The USGS conducted two different sampling programs in Lake Michigan in 2015. One program was the annual lake-wide summer hydroacoustic survey in collaboration with the MI DNR on August 12 – 25, during which USGS scientists collected *Mysis* samples along nearshore-offshore acoustic transects at bottom depths ranging from 33 m to 232 m. A second USGS program was specific to the CSMI-year and consisted of spring (May), summer (July), and fall (October) surveys. During each of these surveys, USGS scientists collected *Mysis* at eight nearshore-offshore transects around Lake Michigan (Frankfurt, Ludington, Saugatuck, St. Joseph, Waukegan, Racine, Manitowoc, and Sturgeon Bay). Each transect included a nearshore, a mid-depth, and an offshore station, located at 18 m, 46 m, and 91-110 m. NOAA scientists collected *Mysis* at the mid-depth and offshore (45-m and 100-m) stations of their standard monthly monitoring transect offshore of Muskegon, MI in south-east Lake Michigan. The EPA conducted two different sampling programs in Lake Michigan in 2015. One program was the annual biological monitoring conducted by GLNPO. These surveys were designed to assess offshore areas of the Great Lakes and not nearshore habitats (Barbiero et al., 2018a). Scientists from the EPA and the Cornell Biological Field Station collected *Mysis* at stations visited at night. Depths of EPA GLNPO stations sampled for *Mysis* during spring 2015, summer 2015, and spring 2016 ranged from 90 m to 190 m (except for one 40-m site sampled in August 2015). The second EPA program during 2015 was designed to support the 2015 CSMI field year in Lake Michigan. These surveys included the four south-basin USGS transects in Lake Michigan (with nearshore, mid-depth, and offshore stations, sampled at depths of 17-23 m, 46-52 m, and 88-107 m).

All three agencies employed similar gear and methods in field and lab, including vertical tows with 1-m diameter net opening, 250-1000 μm mesh, 2-3 m long plankton nets towed from 3-5 m above the bottom to the surface and retrieved at a speed of 0.5 m/s (Table 1b). Differences in *Mysis* catches using different mesh sizes (333-μm vs 1000-μm) or net opening diameters (0.5-m vs 1-m) have been found to be not significant (Chipps and Bennett, 1996; Silver et al., 2016), and we assumed the nets used by different agencies to have equivalent catchabilities. All *Mysis* sampling was conducted at night between 1 hr after sunset and 1 hr before sunrise under red-light-only deck conditions. *Mysis* samples were preserved in either 70-95% ethanol or 6-10% formalin (2-4 % formaldehyde solution) (Table 1b). Samples were processed by the collecting agency (USGS and NOAA) or Cornell University (EPA collections). All *Mysis* in all samples were counted. When broken *Mysis* individuals were present, heads (but not bodies) were included in the total counts.

Data on individual *Mysis* including length, sex, and (for brooding females) brood count (embryos/brood), were obtained for each sample for either all individuals or for a representative subsample of individuals. Scientists from NOAA obtained length, sex, and brood count data for all individual *Mysis* in the entire sample for each sample collected. Cornell scientists obtained length, sex, and brood count data for all individual brooding female *Mysis* (primarily isolated in the field), and for all non-brooding *Mysis* if there were 100 or fewer non-brooding *Mysis* in the sample for each sample collected as part of the EPA programs. If more than 100 non-brooding *Mysis* were present in an EPA sample, a random subsample of 100 non-brooding individuals was measured and sexed; details in the EPA standard operating procedure LG408 (U.S. EPA, 2019). USGS scientists recorded length, sex, and brood count data for all individual *Mysis* if there were 100 or fewer individuals in the sample, or they obtained these data for a random subsample using a simple randomizing procedure described in EPA (2019) of 100 individuals if there were more than 100 in the sample.

All three agencies used the same methods to obtain individual *Mysis* data. Lengths of individual *Mysis* were measured as standard length (from tip of rostrum to end of abdomen) to the nearest 0.1 mm. *Mysis* $<$ 10 mm length were classified as juveniles (Holda et al., 2019; Pothoven et al., 2004). For this study, *Mysis* $\geq$ 10 mm length were classified as males when the third and fourth pleopods exhibited bifurcation and elongation and as females when the third and fourth pleopods were undifferentiated (typically confirmed by presence of brood lamellae). Standard length of *Mysis* for which we only had heads was neither estimated nor measured (e.g., antennal scales) and thus not included in size distributions. Individual dry mass, was calculated with the regression equation: $\ln(g) = -12.27 + 2.72 \ln(L)$ (Johannsson et al., 2011), where L is the distance in mm from the tip of the rostrum to the end of the abdomen. All values of mass that we report in this paper are based on this regression and are therefore dry mass values (rather than wet mass values).

From these individual and sample data, we estimated sample and visit averages. Mean individual mass was calculated for each sample. Total sample mass was calculated as the total count of animals in the sample multiplied by the average individual mass (in mg). Density (*Mysis*/m^2) and biomass (mg/m^2) were calculated by dividing sample total count and total sample mass by the area of the net opening (0.785 m^2 for all surveys), assuming 100% filtering efficiency. (A net-filtering efficiency of 100% was also assumed by the EPA, NOAA, and USGS annual monitoring programs to which we principally compare our results; Jude et al., 2018; Pothoven and Vanderploeg, 2017; Warner et al., 2010). When more than one sample was collected during the same visit, that visit's density and biomass were calculated by averaging values of replicate samples.

Seasonal, depth zone, and regional mean estimates

We grouped visits into the following five seasons: spring 2015 (sampled April 14 – June 1), summer 2015 (sampled July 6 – August 18), fall 2015 (sampled September 1 – November 3), winter 2015 (sampled December 7), and spring 2016 (sampled March 27 to April 28). We grouped sampling into these seasons to achieve lake-wide spatial coverage during each season (except for winter 2015). Although we expect higher density and smaller animals at the beginning than the end of each season period, we did not correct for the timing of a visit within each defined season. Note that while we report density, biomass, size-frequency, and fecundity data from winter 2015 collections, these data were not used in calculations of annual averages nor annual rates due to low sample size (*n* = 2). Estimates of *Mysis* density, biomass, and production (below) for the other four seasons were scaled up to annual estimates using weighted means and standard errors, with weights based on the number of days represented by each sampling period (see Table 2).

For seasons when spatial coverage of sampling included multiple depths (20-100 m) in all four quadrants of the lake, we compared models of horizontal distributions using the corrected Akaike information criterion (AICc) scores of candidate analysis of variance (ANOVA) models (Burnham and Anderson, 2004). We then chose a model that had a delta AICc of ≤ 2 by which to group visit estimates of *Mysis* density and biomass into areal zones. All candidate ANOVA models of horizontal distribution of density or biomass included at least three depth zones (< 30 m, 30-70 m, and > 70 m), and some divided the last depth zone into two zones (70-130 m and > 130 m). We chose these particular depth zones to reflect the original survey designs. Other predictors analyzed included: 1) lake side (east vs. west), which was applied only for depth zones < 70 m; 2) lake basin (north vs. south, divided at 43.65° N) applied to all depth zones; 3) lake basin but only applied to the offshore (> 70 m) depth zone(s); and 4) combinations of all three potential spatial predictors (depth, lake side, and lake basin). After selecting a spatial zone model for each season, we grouped visit estimates of *Mysis* density and biomass into those zones and obtained zonal means and standard errors. Then, we calculated lake-wide estimates from these zonal means and standard errors using zonal lake-areas as weighting factors. Note that we did not test for lake basin or lake side effects in winter 2015 or spring 2016 due to limited spatial coverage in those seasons, and we therefore based lake-wide estimates for those two seasons on samples from the 30-70 m depth zone and the > 70 m depth zone (we assumed 0 *Mysis* were present in the < 30 m zone where no samples were taken).

In addition to estimating the lake-wide annual density and biomass of *Mysis* in Lake Michigan during 2015 based on the comprehensive CSMI dataset (which included the three annual surveys described above), we directly compared these comprehensive CSMI estimates with those of each of the three annual programs. For the USGS GLSC and MI DNR summer acoustic survey, we calculated lake-wide estimates of mean density and biomass directly from estimates for each station visited (Bunnell et al., 2018, Fig.7). For the EPA annual monitoring surveys, we first calculated the mean areal density and biomass for April and August and then the mean of those two sampling periods (Jude et al., 2018, Fig 1). For the NOAA GLERL monthly Muskegon transect survey, we calculated monthly density and biomass estimates as a weighed mean of the 45-m and 110-m station estimates (weights = 0.274 and 0.726, respectively), stations weights previously used to obtain lake-wide estimates of *Mysis* from that transect (Pothoven and Bunnell, 2016). Then, we calculated annual density and biomass estimates from these monthly estimates (see Pothoven and Vanderploeg, 2017, Fig. 1b, 1d, 2b, and 2d; and Bunnell et al., 2018 Fig. 7). Because none of the annual programs sampled < 30 m, we compared each program's estimate (calculated as described in this paragraph) to a CSMI estimate excluding the < 30 m zone. While we report standard errors for each estimate, we do not report statistical significance of differences because the estimates are not independent. Instead, we report percent differences between the comprehensive CSMI and annual program estimates and discuss possible causes for differences between programs.

At each spatial and temporal scale for which we estimated *Mysis* biomass (zonal and lake-wide, seasonal and annual), we compared *Mysis* biomass with pelagic crustacean zooplankton biomass based on data from all three agencies acquired at the same spatial and temporal strata as *Mysis* data. Zooplankton biomass was estimated from samples collected using standard 153-µm mesh, vertical plankton nets towed to the surface from 100 m or (for sites < 100 m) from 2 m above the bottom (Barbiero et al., 2019; Bunnell et al., 2018; Pothoven and Vanderploeg, 2019).

We assumed whole water column zooplankton samples to be similar both day and night, and so we included biomass data from zooplankton samples regardless of the time of day of collection. We report zone-specific zooplankton biomass values and the percentage of zooplankton and *Mysis* biomass. .

Cohort analysis

Mysis live 1.5 to 2.5 years in the Great Lakes, so we expected to see at least two cohorts at any one time. We constructed lake-wide 1-mm size-frequency distributions (x ≤ standard length < x + 1) scaled to lake-wide density for each season using zone-area-weighting methods described above in methods above. To obtain estimates of cohort-specific parameters, we fitted Gaussian mixture models to the *Mysis* length distribution for each visit using the function *Mclust* in the *mclust* package for R (Scrucca et al., 2016). The advantage of the *Mclust* function is that it takes a vector of data values (measured lengths in mm in our case), and uses a maximum-likelihood approach to both fit Gaussian mixture models (including our needed mean cohort size estimates), and classify each input data value into one of the resulting mixture model components. Standard error estimates for the model parameters (standard errors of mean cohort size estimates in our case) were obtained with the bootstrap function *MclustBootstrap*. These functions required the input of the actual measured length values for each visit, rather than the relative size-frequency distribution. Thus, for each input to the *Mclust* function, we pooled all length measurements of *Mysis* collected during a single visit, regardless of any subsampling in any samples (one to three samples per visit).

While fitting our Gaussian mixture models with *Mclust*, we restricted fitting options in three ways: 1) we required each mixture model to include at least two or three components at times of the year when at least two or three cohorts should be present; 2) we required each mixture model to include no more than four components; 3) we required all components within each mixture model to have equal variance; and 4) if any two component means in a resulting model's fit were within 3 mm of each other, we re-fit that mixture model to its data with one less component, thus merging these two. The requirement for equal variance was necessary to reduce a high degree of overlap and to encourage the detection of large-length, small-density cohort components of the overall distributions. In addition, we only fit mixture models for visits with 10 or more individual length measurements.

Life history rates

We obtained estimates of cohort growth rate in mm/d by weighted linear regression of *Mclust* mean cohort length estimates as a function of visit date. We used the squared inverse of bootstrapped standard errors for each mean length estimate as the weighting factor in the linear regression. In addition, because *Mysis* growth is typically faster in summer and slower in winter in Lake Michigan (Pothoven et al., 2000a; Pothoven and Vanderploeg, 2017), we fit piecewise linear models for 2014 and 2015 cohorts with change-points provided by the function *segmented* in the package *segmented* for R (Muggeo, 2008). We used AICc to compare simple and piecewise regressions.

For each visit, we used *Mclust* classifications of each individual *Mysis* into one of the four cohorts to obtain estimates of the total density in each cohort and also the density in each demographic (juvenile, male, non-brooding female, brooding female) within each cohort. We used these visit estimates to obtain seasonal lake-wide estimates of cohort density and of cohort-demographic density. We used these values to calculate the percentage of the total lake-wide *Mysis* density in each season which was made up by each cohort, and the percentage of each cohort's lake-wide density which was made up by each demographic, using the techniques described in *Sample and visit calculations* section above.

We modeled brood counts of brooding females with analysis of covariance (ANCOVA), including candidate terms for the covariate brooding female length, the factor season, the factor collecting agency nested under season (due to differences introduced by EPA separation of brooding females in individual bullet tubes with embryos prior to preservation), and their interaction terms. We first excluded brooding females with brood counts of less than five from our model fit, as these were likely brooding females that did lose embryos during sampling (Morgan, 1980). We used a Tukey highly significant difference post-hoc test to identify significant pairwise differences in factor levels. For each season, we also estimated mean length and mean brood count for all brooding females with five or more embryos. In addition, we estimated mean brooding female density and mean embryo density for each season.

Cohort mortality rates were obtained by estimating the slope of natural log-transformed lake-wide, seasonal cohort density estimates as a function of mean sampling dates (see Table 2). We estimated 95% confidence intervals for cohort mortality rates by a bootstrapping approach in which seasonal cohort densities were picked randomly from normal distributions with mean = mean cohort density, and standard deviation = standard error of seasonal cohort density. *Mysis* tend to be underestimated by vertical net hauls in spring, and this is thought to be due to a higher proportion of *Mysis* remaining benthic at night during spring (Johannsson et al., 2003). Therefore, we did not include spring in our mortality estimate, using cohort densities only from summer 2015 and fall 2015. However, because the nocturnal benthic proportion of *Mysis* might be similar each spring, we also estimated annual mortality for spring 2015 to spring 2016, excluding summer 2015 and fall 2015 densities. We did not estimate mortality for the 2013 and the 2016 cohorts.

We estimated production by the Hynes-Menzie size-frequency method, which is the method most commonly applied to Great Lakes *Mysis* populations (Holda et al., 2019; Johannsson, 1995, 1992; Pothoven et al., 2010; Pothoven and Bunnell, 2016; Sell, 1982). Here we present an equivalent but relatively simple formulation similar to that used by Sell (1982):

$$P = \sum_{\mathrm{j=1}}^{\mathrm{m}} (N_{\mathrm{j+1}} - N_{\mathrm{j}}) \cdot (W_{\mathrm{j}} W_{\mathrm{j+1}})^{1/2} \qquad (1)$$

$$\text{and } N_{\mathrm{j}} = \bar{n}_{\mathrm{j}} / D_{\mathrm{j}} \cdot 365 \qquad (2)$$

where m = number of size categories, N_j = an estimate of the number of *M. diluviana* that grew into size category j within a year, W_j = mean mass of *M. diluviana* in category j (calculated as the geometric mean of mass at the upper and lower bounds of size category j), $\bar{n}_j$ = mean number of *M. diluviana* in category j over the course of a year, and D_j = an estimate of the mean number of days spent in in size category j by all *Mysis* passing through size category j during the study year. We estimated $\bar{n}_j$ for each size category as described for total density in the *Seasonal, depth zone, and regional mean estimates* subsection of the methods. We estimated D_j as 1/growth rate we estimated for *Mysis* individuals in size category j. As in previous applications to *Mysis* production estimates in Lake Ontario (Holda et al., 2019; Johannsson et al., 1995), N_j values that were underestimated due to sparse overwinter sampling or partial migration in springtime were excluded from Hynes-Menzie size-frequency summation, and W_j values adjusted accordingly. We estimated variance in production according to Krueger and Martin (1980) as applied to this formulation (see also: Holda et al., 2019), and calculated the P/B ratio for Lake Michigan *Mysis* population during 2015-16 by dividing production (mg/m$^{2/}$yr) by mean annual biomass (mg/m^2).

We obtained 95% CIs for our P/B estimate computed using a simulated distribution of P/B based on randomly paired values from the distributions of annual lake-wide biomass and annual production (assuming normal distributions).

Results

Horizontal distributions of density and biomass

Horizontal distributions of *Mysis* density and biomass in Lake Michigan during spring, summer, and fall 2015 were strongly related to bottom depth, and lake basin was also important in offshore (> 70 m) waters (Table 3). In contrast, lake side did not improve model performance after accounting for depth zone and lake basin which were more explanatory of our data (Table 3). Bottom depth was included in all candidate ANOVA models, and all candidate models (including models in which zones were based only on depth) were significant at the $p < 5.0 \times 10^{-4}$ level or lower (Table 3), except for the fall 2015 model based on the full combination of depth zone, lake basin, and lake side ($p \leq 0.01$). The addition of a fourth depth zone gave the lowest AICc for biomass in summer 2015, and also produced models supported by the data (ΔAICc < 2) for densities in spring and summer 2015. Therefore, we report density and biomass for three depth zones for spring and fall 2015, and four depth zones for summer 2015 (Table 4). Lake basin (north vs south) was also important in predicting density and biomass in offshore (> 70 m) waters of the lake, as shown by the lower AICc values of models including that predictor in spring and summer, and the low ΔAICc of that model in fall 2015 for density and biomass (ΔAICc = 1.9 and 2.9, respectively, Table 3). Thus, given significant model fits and AICc support, we report separate density and biomass estimates for north and south basins for offshore (> 70 m) depth zone(s) during spring, summer, and fall 2015 (Table 4). Lake side (east vs west) was not important, and our model fits were not improved by addition of a lake-side effect on Lake Michigan *Mysis* density or biomass (Table 3). Therefore, we do not report different density and biomass for different lake sides (Table 4).

Density and biomass estimates

During all seasons, *Mysis* density and biomass were higher and were a greater percentage of total crustacean zooplankton biomass in offshore waters (> 70 m) than in shallow nearshore (< 30 m) and mid-depth (30-70 m) waters (Table 4). Sampling of the nearshore zone (< 30 m) was performed exclusively by CSMI-specific surveys, and these samplings confirmed the minimal contribution to *Mysis* density and biomass from such shallow water depths (Table 4). In addition, for spring 2015 and summer 2015, the *Mysis* population biomass and total crustacean zooplankton biomass were higher in the north basin offshore water than in the south basin offshore water (Table 4), but *Mysis* were a greater percentage of total crustacean zooplankton biomass in the south basin offshore water than in the north basin offshore water (Table 4). The highest *Mysis* biomass in spring, summer, and fall 2015 was observed in the north basin near Sturgeon Bay and Manitowoc transects at depths of about 100 m (Fig. 1). This was associated with the highest observed densities of age-1+ *Mysis* at those stations during each of these three seasons.

Estimates of lake-wide density and biomass of the *Mysis* population peaked during summer 2015, with low values during spring 2015 and spring 2016 (Table 4). The annual lake-wide *Mysis* density and biomass estimates for 2015-16 were 81 *Mysis*/m^2 (SE: 10/m^2) and 200 mg/m^2 (SE: 36 mg/m^2) (Table 4). These estimates included shallow water areas and were therefore ~25% lower than estimates based on > 30 m depths (Table 5). Comparisons of our CSMI estimate based on depths > 30 m with the three annual survey's 2015 data showed that the USGS annual program yielded 85% higher densities and 67% higher biomass, the NOAA annual program yielded 18% lower density and 1% lower biomass, and the EPA annual program yielded 20% higher density and 24% lower biomass (Table 5). Note that the > 30 m CSMI estimate was based on a combined effort of 105 station visits, while annual programs in 2015 were based on just 10-18 station visits each (Table 5). The average proportion of total crustacean zooplankton that was *Mysis* ranged from 11 to 13% during the four sampling periods in which we estimated it, and our estimate of annual lake-wide percentage of total crustacean zooplankton biomass that was *Mysis* was 12% (Table 4).

Cohorts and life history rates

Based on the combined effort of all sampling programs, four distinct *Mysis* cohorts were identified between spring 2015 to spring 2016, each released in 2013, 2014, 2015, and 2016. At any one time, two or three coexisting cohorts could be identified in the size distributions (Fig. 2). The 2013 cohort remained through spring 2015 and summer 2015, the 2014 and 2015 cohorts were present in all seasons, and the 2016 cohort appeared in spring 2016 (Fig. 2). We only estimated growth rates for the 2014 and 2015 cohorts, which were present in all four seasons (Fig. 3). The 2014 *Mysis* cohort grew fast from spring 2015 to summer 2015 (0.027 mm/d, SE: 0.005 mm/d) and slower from summer 2015 to spring 2016 (0.007 mm/d, SE: 0.003 mm/d) (Fig. 3). This 80% reduction of growth rate after July was captured by the piecewise linear model (df = 89, $r^2 = 0.56$), which fit the data better than the simple linear model (ΔAICc = 13.1). Estimated growth rate of the 2015 *Mysis* cohort in terms of mean cohort length was affected by the continued release of small *Mysis* through early June. From April to June, 2015, the segmented regression estimated no growth in the mean cohort length (-0.001 mm/d, SE: 0.011 mm/d); but starting in June 2015, the estimated growth rate of the 2015 cohort was positive and remained constant through spring 2016 (0.026 mm/d, SE: 0.001 mm/d) (Fig. 3). These different growth rates prior to- and after- June were well described by the piecewise linear model (df = 96, r = 0.82), but could not be detected by the simple linear model, which had a ΔAICc of 24.4.

Mysis during the first two years of life had a 50:50 sex ratio (measured for *Mysis* >10mm), but the majority of *Mysis* individuals remaining in a cohort by the second spring were female (85% females in the 2014 cohort in spring 2016, 77% females in the 2013 cohort in spring 2015) (Table 6). Brooding female *Mysis* were present in each season, and 15% (2014 cohort) or 50% (2015 cohort) of female *Mysis* in their second spring were brooding (Table 6). The total percentage of females that were brooding in each season ranged from 0.6 % in summer 2015 to 19.1 % in spring 2016 (Table 6). The average length of brooding females ranged from 14.9 mm in spring 2015 to 17.4 mm in fall 2015 (Table 6). Mean brood size ranged from 12.7 embryos/brood in spring 2015 to 19.8 embryos/brood in fall 2015 (Table 6). Density of brooding females ranged from 0.2/m^2 in summer 2015 to 2.5/m^2 in spring 2016 and density of embryos ranged from 2.7/m^2 in summer 2015 to 46.2/m^2 in spring 2016 (Table 6).

Of 186 brooding females, 17 had less than five embryos and were excluded from further analyses. Because collecting agency and the interaction of length and season were not significant predictors ($p = 0.25$ and $p = 0.15$, respectively), we removed them from the final model. The number of embryos in the brood pouch increased with female length (slope of 1.7 embryos/mm, $p \ll 0.001$, $F = 96.4$, $df = 1, 163$), and brooding females carried about five fewer embryos in spring and summer 2015 than in winter 2015 and spring 2016 ($p \leq 0.02$, Tukey highly significant difference test) (Fig. 4). No other differences among seasons were significant.

The 2014 *Mysis* cohort had a daily instantaneous mortality rate of 0.011/d (95% CI: 3.3×10^{-3} – 0.032) when estimated between summer 2015 and fall 2015 and a mortality rate of $5.4 \times 10^{-}$

^{3}/d (95% CI: 3.6 x 10^{-3} – 0.010) when estimated between spring 2015 and spring 2016 (Fig. 5). Compounded for an entire year, these instantaneous rates represent annual mortalities of 86-98%. The 2015 *Mysis* cohort had a mortality rate of 4.6 x 10^{-3}/d (95% CI: 2.2 x 10^{-3} – 0.016) when estimated between summer 2015 and fall 2015 (Fig. 5) (81% annual mortality). We could not estimate the 2015 *Mysis* cohort mortality rate from spring 2015 to spring 2016 because the 2015 cohort was still recruiting to the population through summer 2015. Lake-wide annual *Mysis* production in Lake Michigan for 2015-16 was estimated to be 0.423 g/m^2/yr (SE: 0.031) resulting in an annual lake-wide *Mysis* P/B of 2.12/yr (95% CI's: 1.51 – 3.34).

Discussion

Mysis is an important component of the Lake Michigan food web as both a predator on zooplankton and as prey for dominant fish species (Pothoven et al. 2004, Bunnell et al. 2018, Eshenroder et al., 1999). Concerns about decreased forage fish production and how oligotrophication may affect fisheries (Bunnell et al. 2018), the decline in another important, native, large crustacean (*Diporeia*, Burlakova et al., 2018), and the continued high abundance of invasive dreissenid mussels affecting spring diatom blooms (Vanderploeg et al., 2010; Barbiero et al., 2018b) have resulted in increased concerns about declines in *Mysis* populations. Even so, current estimates are limited either in space or in time. This study is only the second lake-wide, year-round population assessment of *Mysis* in Lake Michigan; the other such study was conducted in 2000 (Pothoven et al., 2004). This analysis was possible due to collaborations among several agencies during the CSMI year 2015 that resulted in coverage of most of the lake in spring, summer and fall seasons. *Mysis* is clearly an important component of the Lake

Michigan food web as 12% (annual average) of the zooplankton biomass consisted of *Mysis* in 2015-16, similar to long-term estimates by Jude et al. (2018) for Lake Michigan in 2006-2016.

Spatial and seasonal patterns in density and biomass.

As expected, *Mysis* density and biomass were lowest in the shallowest zone and highest in the deepest zone(s). This is a common observation in *Mysis* populations in the Great Lakes (Johansson 1995; Jude et al. 2018), and is likely a light avoidance response as *Mysis* needs to find sufficiently dark daytime refuges to minimize fish predation (Johannsson et al. 2003; Boscarino et al. 2010). However, lake basin was also significant as there was horizontal spatial structure in *Mysis* density and biomass that was independent of bottom depth, with more *Mysis* in the north basin than in the south basin, at least in spring and summer 2015. During 2015, we found the highest biomass and density in the north basin at 90-120 m deep stations, depths also present in the south basin. Similarly, Lehman et al. (1990) observed higher densities of *Mysis* in the north half than in the south half of Lake Michigan during 1985-89. In contrast, Pothoven et al. (2004) did not detect a basin difference when comparing same-depth stations sampled during 2000, and they suggested the findings of Lehman et al. (1990) were due to deeper water sampled in the north basin than in the south basin in that study. While this may have been true for the Lehman et al. (1990) study, we found that the north basin had higher density and biomass than the south basin in 2015 also when comparing the same depth zones (e.g., 70-130 m zone, Table 4). This suggests a difference in north and south basin *Mysis* densities independent of the more important depth effect.

Seasonal patterns we observed were similar to those observed by Jude et al. (2018) and Pothoven and Vanderploeg (2017). Multi-year averages of offshore density and biomass in both studies were lowest in spring months (range: 30 – 100 *Mysis*/m^2, 50 – 220 mg/m^2), highest in summer months (range: 70 – 150 *Mysis*/m^2, 250 – 475 mg/m^2), and at in-between levels in fall months (range: 40 – 100 *Mysis*/m^2, 200 – 425 mg/m^2). *Mysis* juveniles primarily recruit to the population in the late spring to early summer and typically live up to 2.5 years after release. This seasonal recruitment and a two-year life span create the observed seasonal pattern of high density and biomass in summer and low density and biomass in spring in Lake Michigan and other Great Lakes (Jude et al., 2018).

Comparisons with current annual surveys.

Our comparisons of density and biomass obtained by the agencies collaborating through the CSMI program indicate that the seasonally intensive program with limited spatial extent (NOAA) resulted in average annual values most similar to the complete CSMI data set (Table 5). Thus, it appears more important to cover spring, summer and fall seasons than to obtain broad spatial coverage. Apparently the two NOAA stations at Muskegon, MI were representative of the larger lake, at least in 2015. The EPA survey, although sampling only in spring and summer (and thereby having lower biomass), was also similar to the complete CSMI data set. However, it is important to also sample some intermediate depths (30-70 m) as density and biomass at these depths are substantially lower than in deeper water (by ~ 75%) and these depths represent about 20% of the lake surface area. Depths shallower than 30 m may be assumed to have no *Mysis*. Averages based on sampling of other depths will be most representative of lake-wide annual averages if sampling is conducted throughout the year.

The USGS-MI DNR annual survey was the most spatially extensive and included the deepest sampling of the lake (up to 230 m) and was therefore critical for us to assess differences among lake basins and depth zones. The USGS-MI DNR survey provided the highest estimate of density and biomass in 2015 (Table 5), while the NOAA survey provided the lowest (Table 5).

This difference was typical of these surveys during overlapping years (2007-2015) presented in figure seven of Bunnell et al. (2018) (NOAA range: 35 – 115 *Mysis*/m^2, USGS-MI DNR range: 50 – 120 *Mysis*/m^2). Because sampling by USGS-MI DNR was only done during the season with the highest density and biomass (and included the deepest stations sampled), this survey was the least similar to the annual averages obtained by the CSMI data set. Note however, that spring data may have under-estimated *Mysis* density and biomass, perhaps due to limited vertical migration in the spring (Johannsson et al., 2003). If so, annual averages that included spring sampling (like the CSMI, the NOAA and the EPA data sets) would have under-estimated true annual values (perhaps especially if they also did not sample the deepest waters). Thus, the true lake-wide annual mean density was likely somewhere between our CSMI 2015 estimate and our summer/fall estimates. The true value of *Mysis* density also depends on the proportion of *Mysis* remaining on the bottom at night (partial migration, Johannsson et al., 2003; O'Malley et al., 2019) which would be a subset of the population which is not sampled by the vertical net hauls used here and on how that proportion varies seasonally. To date, the benthic component of *Mysis* ecology has received comparatively little attention (Stockwell et al., 2020).

Life history rates

Our estimates of lake-wide life history rates in 2015 were very similar to those reported by Jude et al. (2018) for 2006-2016 and by Pothoven and Vanderploeg (2017) for 2007-2015. Similar to these two studies, we observed two primary cohorts, with a small third cohort present in the spring. Both our age-0 spring-fall growth rate (0.026 mm/d) and our spring-summer age-1 growth rates (0.027 mm/d) were almost identical to Pothoven and Vanderploeg's (2017) estimates for 2007-2015 (0.027 mm/d for both cohorts). Our estimated sex ratio was also consistent at a little more than 50% females, similar to the 50-60% females for years 2007-2015 reported by Pothoven and Vanderploeg (2017). Pothoven and Vanderploeg (2017) found percent females brooding to be highest in spring at about 20% and lowest in summer at about 5%, similar to our findings of 15% (spring 2015) and 19% (spring 2016) brooding in the spring and ~1 % brooding in the summer. Lake-wide annual mean length of brooding females was 15.9 mm, compared with 16.3 mm near Muskegon during 2007-2015 (Pothoven and Vanderploeg, 2017). Lake-wide annual mean brood size of brooding females was 16.2 embryos/brood, compared with 17.9 embryos/brood near Muskegon during 2007-2015 (Pothoven and Vanderploeg, 2017). Density of embryos was lowest in summer and higher in spring and fall in both our 2015 CSMI estimate and the Muskegon estimates for 2007-2015, but our spring 2015 estimates were higher than our fall 2015 estimates, which was reversed for Muskegon during 2007-2015 (Pothoven and Vanderploeg, 2017). Our estimates of annual mortality rates for Lake Michigan *Mysis* during 2015 were 81% for age-0 and 86-98% for age-1 *Mysis*, which are comparable to mortality rates of 67% for age-0 and 95% for age-1 at the Muskegon transect, 2007-2015 (Pothoven and Vanderploeg, 2017). Thus, our seasonal lake-wide life history rates calculated from the more extensive CSMI data set (which do include NOAA data from 2015) closely matched those produced by the NOAA program transect sampling near Muskegon, MI.

We observed two unusual patterns in the seasonal growth rates of the 2015-16 *Mysis* population. First, growth rate of age-1 *Mysis* changed mid-summer to a very slow rate of 0.006 mm/d and continued at that rate through winter. This is the lowest growth rate reported for an age-1 *Mysis* cohort in Lake Michigan, including overwinter rates (Morgan and Beeton, 1978; Pothoven et al., 2000a; Pothoven and Vanderploeg, 2017) and similar to the low winter growth rate (0.004 mm/d) reported for age-0 *Mysis* for the 2013-15 winters (Pothoven and Vanderploeg 2017). On the other hand, our estimate of over winter age-0 growth in 2015-16 was much higher

(0.026 mm/d). This suggests that the 2015-16 fall and winter conditions in Lake Michigan were more conducive to higher juvenile *Mysis* growth rates than the previous two winters in which temperatures were extremely low (Pothoven and Vanderploeg, 2017). We also note that we observed higher mean number of embryos/brood and a much higher embryo density in spring 2016 than in spring 2015, which both suggest better energetic conditions were present in winter of 2015-16 than in winter of 2014-15. While winter temperature may be important, the availability of plankton prey may also play a role as it does in the spring (Pothoven et al., 2010). Hampton et al. (2017) suggested that under-the-ice diatoms and zooplankton can be relatively abundant in temperate lakes and may be more important for annual production than previously thought. Whatever the cause, an overwinter *Mysis* growth rate of 0.026 mm/d results in an additional 0.5-0.7 mm of overwinter growth compared with the average rate observed since the 1980s of 0.020 mm/d (Pothoven et al., 2000; Pothoven and Vanderploeg, 2017), and means the range of overwinter growth observed for Lake Michigan *Mysis* (0.004 to 0.026 mm/d) now represents a possible difference in total overwinter growth of 2-2.5 mm. Therefore, our results both affirm that overwinter conditions and *Mysis* growth rates can be variable and also indicate that this variability may be important for the *Mysis* population.

We observed annual production of 0.42 g/m^2/yr for the Lake Michigan *Mysis* population in 2015. Except for one estimate for 1970-71 (0.25 g/m^2/yr), our estimate for 2015 was lower than all other Lake Michigan *Mysis* production estimates based on the Hynes-Menzie size-frequency method, including the most recent estimates from 2007-2011 (Table 7). In addition, available *Mysis* production estimates for lakes Huron and Ontario (select years during 1970 to 2013) were all higher than our estimate for Lake Michigan in 2015. This finding of low *Mysis* production in Lake Michigan in 2015 is not surprising given previous observations of density, biomass, and reproductive effort of *Mysis* in Lake Michigan being lower in the 2000s and 2010s as compared with the 1980s and 1990s (Bunnell et al., 2018; Jude et al., 2018; Pothoven et al., 2010; Pothoven and Vanderploeg, 2017). In addition, it supports the suggestion based on the Muskegon transect that production of Lake Michigan *Mysis* is declining over a longer time scale (Pothoven et al., 2010; Pothoven and Bunnell, 2016). Although *Mysis* will probably persist as forage for prey fishes in Lake Michigan, they may not be able to support levels of prey fish populations observed in the 1980s and 1990s at such low levels of annual *Mysis* production (Bunnell et al., 2018; Madenjian et al., 2015).

Finally, we caution against any assumption that *Mysis* densities have remained at similar levels to those observed in 2015. Published *Mysis* densities in Lake Michigan since 2015 indicate lower offshore, summer densities in 2016 (Jude et al., 2018), and lower lake-wide, summer densities in 2017-2018 (U.S. Geological Survey, 2019). No published data are available for 2019 or later. Therefore, until an updated analysis of long-term trends with inclusion of recent years since 2016 is published, we must consider that *Mysis* densities in Lake Michigan may have been lower in 2016-2019 than we observed here during 2015.

Conclusions

In summary, the effort associated with the CSMI year combined with annual monitoring efforts provided us with a sufficiently comprehensive data set to estimate lake-wide seasonal parameters of the *Mysis* population in Lake Michigan during 2015-16. Our results indicate that: (1) *Mysis* density and biomass are strongly related to depth in Lake Michigan in all regions and during all seasons, (2) offshore density and biomass of *Mysis* were higher in the north basin of Lake Michigan in 2015 though we are uncertain if this is a persistent phenomenon, (3) our lake-wide estimates of annual *Mysis* density and biomass lie between those observed lake-wide by

USGS and EPA in select seasons and those observed monthly by NOAA in the southeast, (4) lake-wide growth rates, reproductive effort, and mortality in 2015 were similar to estimates for 2007-2015 from SE Lake Michigan, (5) winter conditions were more conducive to juvenile *Mysis* growth in warmer winter of 2015-16 than in cold winter of 2014-15, and (6) *Mysis* production in 2015 was lower than in 2007-2011, and may be on a downward trend.

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Table 1. Monthly sampling coverage by survey program and survey methodology differences among programs. a) Monthly number of station visits at which *Mysis* were sampled in Lake Michigan from April 2015 to April 2016, by agency. The spring 2015 season includes the April, May, and June visits, the summer season includes the July and August visits, the fall 2015 season includes the September, October, and November visits, the winter season includes the December visits, and the spring 2016 season includes the March 2016 and April 2016 visits. b) Methodological differences in sample collection and preservation between survey programs (EPA = US Environmental Protection Agency, CSMI = Cooperative Science and Monitoring Initiative, GLNPO = Great Lakes National Program Office, NOAA = National Oceanic and Atmospheric Administration, USGS = US Geological Survey).

a)

	Number of Visits				
	EPA CSMI	EPA GLNPO	NOAA	USGS Annual and CSMI	Total
April 2015	0	6	2	10	18
May 2015	7	0	2	14	23
June 2015	0	0	2	0	2
July 2015	9	0	2	24	35
August 2015	0	4	2	12	18
September 2015	6	0	2	0	8
October 2015	0	0	2	13	15
November 2015	0	0	2	5	7
December 2015	0	0	2	0	2
March 2016	0	4	2	0	6
April 2016	0	0	2	0	2
Total	22	14	22	78	136

b)

	EPA CSMI	EPA GLNPO	NOAA	USGS Annual and CSMI
		Net Specs		
Opening	Circular	Circular	Circular	Circular
Diameter	1 m	1 m	1 m	1 m
Length	2 m	2 m	3 m	3 m
Upper Mesh	500 µm	500 µm	1000 µm	1000 µm
Lower Mesh	250 µm	250 µm	1000 µm	1000 µm
Cod End	250 µm	250 µm	1000 µm	1000 µm
		Additional Methods Details		
Reps/Visit	1	2	3	2
Preservation	EtOH	Formaldehyde	Formaldehyde	EtOH

Table 2. Range of dates sampled, mean visit date, represented dates, number of days, and weighting factors for each of the four seasons used for annual weighted mean and standard error estimates of density and biomass of *Mysis* in Lake Michigan in 2015. Mean visit date is based on the temporal distribution of visit dates within each season. Dates represented are based on location of mean visit dates relative to each other. Number of days is the sum of dates represented. Weights are equal to the number of days/365. (see similar approach used for Lake Ontario in Holda et al., 2019 and described in detail in Holda, 2017). Annual weighted means and standard errors were calculated based on seasonal means and standard errors with these seasonal weights.

Season	Dates Sampled	Mean Visit Date	Dates Represented	No. Days	Weights
Spring 2015	Apr 14 – Jun 1	May 4	Apr 14 – Jun 14	62	0.170
Summer 2015	Jul 6 – Aug 25	Jul 26	Jun 15 – Aug 31	78	0.214
Fall 2015	Sep 1 – Nov 3	Oct 12	Sep 01 – Jan 7	129	0.353
Spring 2016	Mar 27 – Apr 28	Apr 4	Jan 8 – Apr 13	96	0.263

Table 3. Table of ΔAICc (corrected Akaike Information Criterion) values for spatial zone models of *Mysis* in Lake Michigan in 2015. Models with ΔAICc values up to 7.00 are included in this table (Burnham and Anderson, 2004). All models presented in this table had $p < 0.001$. Underlined models for each season were used to calculate lake-wide averages (see Table 4). Note there was no sampling in the "> 130 m" zone in fall, and thus four depth zone models were not an option in that season.

Density					Biomass				
Zone Divisions	k	ΔAICc	F-stat	df	Zone Divisions	k	ΔAICc	F-stat	df
Spring 2015									
3 Depths, Basins >70	5	0.00	20.1	3, 39	3 Depths, Basins >70	5	0.00	18.6	3, 39
3 Depths	4	0.76	28.3	2, 40	3 Depths	4	1.38	24.4	2, 40
4 Depths	5	1.81	19.5	3, 39	4 Depths	5	3.88	15.9	3, 39
3 Depths, Basins	7	5.33	12.0	5, 37	3 Depths, Basins	7	5.11	10.8	5, 37
3 Depths, Sides	6	6.01	13.5	4, 38	3 Depths, Sides	6	6.64	11.6	4, 38
Summer 2015									
3 Depths, Basins >70	5	0.00	56.3	3, 49	4 Depths, Basins >70	7	0.00	27.3	5, 47
4 Depths, Basins >70	7	1.30	35.6	5, 47	3 Depths, Basins >70	5	3.22	38.1	3, 49
3 Depths, Basins	7	3.60	33.7	5, 47	4 Depths, Basins	9	3.70	19.6	7, 45
3 Depths, Basins	9	5.26	25.4	7, 45	3 Depths, Basins	7	6.74	22.9	5, 47
Fall 2015									
3 Depths	4	0.00	6.09	2, 27	3 Depths	4	0.00	18.6	2, 27
3 Depths, Basins >70	5	1.91	13.4	3, 26	3 Depths, Basins >70	5	2.86	11.9	3, 26
3 Depths, Sides	6	5.63	9.3	4, 25	3 Depths, Sides	6	6.03	8.6	4, 25
3 Depths, Basins	7	6.98	8.0	5, 24	3 Depths, Basins	7	8.46	7.0	5, 24

Table 4. Density (No. *Mysis*/m^2) and biomass (mg/m^2) of *Mysis* in 2015-16 by season and depth, with standard errors (in parentheses) and ranges. N refers to the number of visits where *Mysis* samples were collected. Zp Bms is biomass of other crustacean zooplankton in mg/m^2 and % *Mysis* is the percentage of total crustacean biomass represented by *Mysis*. Note that italicized rows and values represent weighted averages taken across multiple depth zones (> 70 m zones or all depth zones) in a single season, while bold rows and values represent weighted annual averages taken across all seasons (excluding winter). Cells with double dashes ("--") indicate values are not available due to limited number or lack of samples. Note that winter 2015 values include only the Muskegon 45-m and 110-m stations.

Depth Zone	N	Density	Range	Biomass	Range	Zp Bms	% *Mysis*
			Spring 2015				
< 30	11	1.1 (0.8)	0 - 9	1.4 (1.3)	0 - 14	218	0.6
30 – 70	12	10 (3)	2 -34	31 (9)	0.6 - 94	675	4.4
> 70 South	13	72 (9)	38 - 136	185 (19)	88 - 271	1106	14.3
> 70 North	7	98 (25)	8 - 211	267 (76)	40 - 673	1600	14.3
> 70		*84 (9)*		*224 (27)*		*1353*	14.2
Lake-wide		*49 (7)*		*130 (22)*		*931*	12.3
			Summer 2015				
< 30	12	3 (2)	0 - 24	2 (1.2)	0 - 15	417	0.5
30 – 70	13	60 (15)	6 - 206	163 (46)	2 - 557	1047	13.5
70-130 South	15	144 (12)	20 - 209	288 (26)	25 - 405	1649	14.9
70-130 North	6	262 (41)	130 - 364	480 (58)	276 - 720	2463	16.3
> 130 South	2	211 (1)	210 – 213	519 (21)	497 – 540	1852	21.9
> 130 North	5	290 (30)	196 - 341	539 (34)	417 - 595	5460	9.0
> 70		*221 (13)*		*464 (21)*		*1915*	19.5
Lake-wide		*134 (8)*		*287 (14)*		*1956*	12.8
			Fall 2015				
< 30	10	1.1 (0.7)	0 - 6	0.6 (0.4)	0 – 4	581	0.1
30 – 70	13	32 (14)	0 - 177	72 (28)	0 - 323	1716	4.0
> 70 South	5	151 (15)	108 - 192	364 (56)	189 - 483	1859	16.4
> 70 North	2	114 (100)	14 - 215	384 (358)	26 - 742	2789	12.1
> 70		*134 (34)*		*373 (122)*		*2325*	13.8
Lake-wide		*79 (28)*		*220 (99)*		*1761*	11.1

Winter 2015							
30 – 70	1	17	--	64	--	--	--
> 70	1	115	--	451	--	--	--
Spring 2016							
0 – 30	0	0	--	0	--	--	--
30 – 70	2	19 (3)	17 - 22	75 (16)	59 - 90	708	9.6
> 70	6	105 (9)	72 - 129	243 (37)	91 - 340	1751	12.2
Lake-wide		*61 (5)*		*148 (21)*		*1101*	11.9
Annual							
0 – 30		**1 (1)**	**0 – 3**	**1 (0)**	**0 - 2**	**334**	0.3
30 – 70		**31 (6)**	**10 - 60**	**85 (15)**	**31 – 163**	**1137**	7.0
> 70		**136 (13)**	**84 - 221**	**333 (45)**	**224 – 464**	**1929**	14.7
Lake-wide		**81 (10)**	**49 - 134**	**200 (36)**	**130 - 287**	**1499**	11.8

Table 5. Mean annual density and biomass estimates for comprehensive CSMI data set (excluding <30-m data) and annual programs ± standard errors, with percent difference compared to the CSMI 2015-16 estimate for waters > 30 m. Rather than report 0% difference when comparing CSMI 2015-16 >30m estimates to themselves, we have put double dashes ("--") to indicate this would not be a meaningful value in this context.

Program	# Visits	Density	% Diff	Biomass	% Diff
CSMI 2015-16 >30m	105	108 ± 10	--	268 ± 33	--
USGS – MI DNR 2015	12	200 ± 26	+85%	447 ± 47	+67%
EPA 2015	10	129 ± 70	+20%	205 ± 96	-24%
NOAA 2015	18	88 ± 13	-18%	264 ±32	-1%

Table 6. Seasonal 2015-16 lake-wide, area-weighted age structure and demographic data. Values presented include: 1) the percentage of the total *Mysis* population during each season which was made up by each cohort, 2) the percentage of *Mysis* in each cohort during each season which was made up by: juveniles (< 10 mm), males, non-brooding or spent females (NB females), and brooding females, 3) the mean length and lake-wide density of brooding females in each season, and 4) the mean number per brood and lake-wide density of embryos in each season. Estimates for winter were not included as all *Mysis* in winter were categorized as 2015 cohort, when many were certainly of the 2014 cohort. Cells with double dashes ("--") indicate values for a specific cohort that could not be computed because the cohort was not present in that time period.

	Spring	Summer	Fall	Spring 2016
Percentage of Total *Mysis* Population				
2013 Cohort	10.1	0.7	0.0	0.0
2014 Cohort	44.6	38.4	28.4	8.1
2015 Cohort	45.3	60.9	71.6	40.0
2016 Cohort	0.0	0.0	0.0	51.9
Percentage of 2013 Cohort				
Juveniles	0.0	0.0	--	--
Males	23.5	24.4	--	--
NB Females	64.5	75.6	--	--
Brooding Females	12.0	0.0	--	--
Percentage of 2014 Cohort				
Juveniles	27.4	1.9	0.9	0.0
Males	36.6	35.7	47.6	14.8
NB Females	30.6	61.9	46.2	38.4
Brooding Females	5.4	0.4	5.2	46.8
Percentage of 2015 Cohort				
Juveniles	100.0	98.3	82.7	18.8
Males	0.0	0.5	6.2	44.9
NB Females	0.0	1.3	11.2	35.6
Brooding Females	0.0	0.0	0.0	0.7
Percentage of 2016 Cohort				
Juveniles	--	--	--	100.0
Males	--	--	--	0.0
NB Females	--	--	--	0.0
Brooding Females	--	--	--	0.0
Percentage of all Females				
Non-Brooding	94.8	99.4	93.5	80.9
Brooding	15.2	0.6	6.5	19.1

	Brooding Females			
Mean Length (mm)	14.9	15.6	17.4	15.5
Density (#/m^2)	1.8	0.2	1.2	2.5
	Embryos			
Mean #/Brood	12.7	14.0	19.8	18.5
Density (#/m^2)	22.3	2.7	23.2	46.2

Table 7. All available Hynes-Menzie size-frequency *Mysis* production ($g/m^2/yr$) estimates in the Great Lakes, with P/B (/yr) and literature references. Cells for with double dashes ("--") were P/B values that could not be calculated because published biomass estimates were unavailable at the appropriate spatial and temporal scale for comparison to the production estimates.

Lake	Year(s)	Region	Prod (SE)	P/B	Reference
Michigan	2015-16	Lake-wide	0.42 (0.03)	2.1	*This study*
Michigan	2009-11	45-110 m	0.78 (-)	--	Pothoven and Bunnell, 2016
Michigan	2007-08	45-110 m	0.48 (0.06)	--	Pothoven et al., 2010
Michigan	1999-00	45-110 m	0.76 (0.02)	--	Pothoven et al., 2010
Michigan	1995-98	45-110 m	1.91 (0.42)	--	Pothoven et al., 2010
Michigan	1975-76	115 m	1.7 (-)[a, b]	3.3	Sell, 1982
Michigan	1975-76	50 m	3.20 (-)	2.9	Sell, 1982
Michigan	1970-71	45-75 m	0.25 (-)[a, b]	2.2	Sell, 1982
Michigan	1954	75 m	2.5 (-)[a]	2.9	Sell, 1982
Huron	1971	90-210 m	1.5 (-)[b]	2.8	Sell, 1982
Ontario	2013	Lake-wide	0.85 (0.03)	2.7	Holda et al., 2019
Ontario	1984-95	125 m	3.4 (0.27)	--	Johannsson et al., 2003
Ontario	1990	Lake-wide	2.2 (0.23)	3.2	Johannsson, 1995
Ontario	1986	50 – 150 m	2.6 (0.24)	--	Johannsson, 1992

[a] Estimates based on data collected with horizontal tow or benthic sled

[b] Estimates based on data collected at least partly during the day

Figure captions

Figure 1. *Mysis* sampling locations and areal biomass estimates in Lake Michigan 2015-2016 by season: spring 2015 (April 14 – June 1), summer 2015 (July 6 – August 18), fall 2015 (September 1 – November 3), and spring 2016 (March 27 to April 28). The horizontal axes are decimal degrees longitude, and the vertical axes are decimal degrees latitude. The dashed line represents the north-south basin distinction at 43.65° N. The grey lines represent the 30-m, 70-m, and 130-m isobaths. USGS and NOAA transect names are marked in the spring 2015 panel (Bay = Sturgeon Bay, Man = Manitowoc, Rac = Racine, Wau = Waukegan, Jos = St. Joseph, Sau = Saugatuck, Mus = Muskegon, Lud = Ludington, and Fra = Frankfurt). Biomass estimates are represented by area of bubbles at each site. Each visit location is indicated with a (+) sign, which is overlaid with a biomass-scaled circle; (+) signs are visible on the plot when overlaid biomass circles are absent ($mg/m^2 = 0$) or small enough ($< 150\ mg/m^2$) not to eclipse (+) signs.

Figure 2 *(color version)*. Lake-wide seasonal size-frequency plots scaled to lake-wide seasonal densities for all five seasons: spring 2015 (April 14 – June 10), summer 2015 (June 11 – August 30), fall 2015 (August 31 – January 7), winter (December 7), and spring 2016 (January 8 – April 13). Lengths in mm from tip of rostrum to end of abdomen; bins are ($x \leq$ length $< x+1$). Shading represents different life stages: juvenile (<10 mm) in brown, male in blue, non-brooding female in pink, brooding female in purple (see legend on figure). Each stage, when present, is stacked in this order from bottom to top. Spent females were rare and binned with non-brooding. All panels have the same scale for the Y axis, but note that 3-4 -mm *Mysis* in spring 2016 had a density of 20 (higher than the figure bounds).

Figure 2 *(grayscale version)*. Lake-wide seasonal size-frequency plots scaled to lake-wide seasonal densities for all five seasons: spring 2015 (April 14 – June 10), summer 2015 (June 11 – August 30), fall 2015 (August 31 – January 7), winter (December 7), and spring 2016 (January 8 – April 13). Lengths in mm from tip of rostrum to end of abdomen; bins are (x ≤ length < x+1). Shading represents different life stages: juvenile (<10 mm) in dark gray, male in white, non-brooding female in light gray, brooding female in black (see legend on figure). Each stage, when present, is stacked in this order from bottom to top. Spent females were rare and binned with non-brooding. All panels have the same scale for the Y axis, but note that 3-4 -mm *Mysis* in spring 2016 had a density of 20 (higher than the figure bounds).

Figure 3 *(color version)*. Cohort length (mean ± SEM) from each *Mclust* Gaussian mixture model component fit on each station visit plotted versus visit date. Point color and style indicate the *Mysis* cohort: green diamond, 2013; blue triangle, 2014; mustard circle, 2015; black square, 2015 (Mean ± 1 SEM). Solid lines represent piecewise linear growth rate regressions by cohort, with regressions weighted by $(1/SE)^2$ for each point. Dashed error bars around regression lines represent 95% confidence intervals of the regression lines.

Figure 3 *(grayscale version)*. Cohort length (mean ± 1 SEM) from each *Mclust* Gaussian mixture model component fit on each station visit plotted versus visit date. Point shading and style indicate the *Mysis* cohort: grey diamond, 2013; dark grey triangle, 2014; grey circle, 2015; black square, 2015. Solid lines represent piecewise linear growth rate regressions by cohort, with regressions weighted by $(1/SE)^2$ for each point. Dashed error bars around regression lines represent 95% confidence intervals of the regression lines.

Figure 4 *(color version)*. Individual brooding female embryo count as a function of individual brooding female length (as defined in Fig. 2) and season of collection (seasons defined in Fig. 1). Lines represent the best-fit ANCOVA model with a single term for the covariate ‘length’ and additive terms for the factor ‘season.’ Point styles and point and line colors represent season (see data legend on the figure). Brooding females with less than five embryos/brood were excluded from the analysis (see open points and x and + signs in left column of legend). Color-shaded areas bordered by dotted lines represent 95% confidence intervals of the regression lines.

Figure 4 *(grayscale version)*. Individual brooding female embryo count as a function of individual brooding female length (as defined in Fig. 2) and season of collection (seasons defined in Fig. 1). Each point represents one individual brooding female, and lines represent the best-fit ANCOVA model with a single term for the covariate ‘length’ and additive terms for the factor ‘season.’ Point styles and point and line shadings represent season (see data legend on the figure). Brooding females with less than five embryos/brood were excluded from the analysis (see open points and x and + signs in left column of legend). Shaded areas and areas bordered by narrow lines represent 95% confidence intervals of the regression lines.

Figure 5 *(color version)*. Seasonal lake-wide cohort density (Mean ± 1 SEM) plotted against seasonal mean sampling date for spring 2015, summer 2015, fall 2015, and spring 2016 (seasons defined in Fig. 1). Point color and style indicate the *Mysis* cohort: green diamond, 2013; blue triangle, 2014; mustard circle, 2015; black square, 2015. Lines are derived from the slope of ln(cohort density) versus date for either summer 2015 – fall 2015 or spring 2015 – spring 2016.

Dotted lines represent bootstrapped 95% confidence intervals of slope estimates. Equation for plotted lines as follows: [Embryos/brood] = 1.7 * [Brooding female Length (mm)] + [Seasonal Intercept], where the Seasonal-Intercepts were -12.9 for spring 2015, -12.8 for summer 2015, -10.1 for fall 2015, -7.0 for winter, and -8.2 for spring 2016.

Figure 5 *(grayscale version)*. Seasonal lake-wide cohort density (Mean ± 1 SEM) plotted against seasonal mean sampling date for spring 2015, summer 2015, fall 2015, and spring 2016 (seasons defined in Fig. 1). Point shading and style indicate the *Mysis* cohort: grey diamond, 2013; dark grey triangle, 2014; grey circle, 2015; black square, 2015. Lines are derived from the slope of ln(cohort density) versus date for either summer 2015 – fall 2015 or spring 2015 – spring 2016. Dotted lines represent bootstrapped 95% confidence intervals of slope estimates. Equation for plotted lines as follows: [Embryos/brood] = 1.7 * [Brooding female Length (mm)] + [Seasonal Intercept], where the Seasonal-Intercepts were -12.9 for spring 2015, -12.8 for summer 2015, -10.1 for fall 2015, -7.0 for winter, and -8.2 for spring 2016.