Densities, diets, and growth rates of larval Alewife and Bloater in a changing Lake Michigan ecosystem

Suggested Running Head: Larval densities, diets, and growth rates in Lake Michigan

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Abstract

Variability in abiotic and biotic factors during larval stages have profound impacts on fish recruitment. In Lake Michigan, where the composition of lower trophic levels have undergone considerable changes in the past decade, managers are concerned that fish recruitment could be negatively affected. We hypothesized that spatial variation in Lake Michigan larval fish density and growth can be explained by various environmental predictor variables. In July 2015, we sampled larval fish and zooplankton at 24 sites (distributed among eight transects) around Lake Michigan. We measured larval fish densities and estimated growth rates and diets of the two most abundant species: Alewife *Alosa pseudoharengus* and Bloater *Coregonus hoyi* (prey fish that represented 89% and 4% of total catch, respectively). Larval Alewife densities at a given site ranged from 0 to 42.57 per 100 m^3, but no explanatory variables explained the variation. Alewife mean growth rate equaled 0.50 mm/d, and fish age and zooplankton density best explained growth variation across sites. Larval Bloater densities ranged from 0 to 1.16 per 100 m^3, and mean growth rate equaled 0.21 mm/d. Across all sites, 67% of larval Alewife stomachs were empty, whereas only 16% of Bloater stomachs were empty. Our study reported larval fish growth rates that were at least 40% slower than those reported in previous decades for both Alewife and Bloater. Worsening prey environment for pelagic larvae such as Alewife and Bloater during the era of abundant dreissenid mussels could reduce the probability of strong year-classes, which in turn may affect growth and survival of recreationally important salmonine predators.

Introduction

Fish recruitment dynamics within the Laurentian Great Lakes are exceedingly complex and more closely resemble those in large marine systems than traditional, lentic freshwater environments (Janssen et al. 2014; Ludsin et al. 2014; Pritt et al. 2014). Disentangling potential mechanisms underlying the growth and survival of larval fish is important because subtle variability in abiotic and biotic factors during larval stages may exert tenfold effects on fish recruitment (Houde and Hoyt 1987; Houde 1989). For example, the Hjort-Cushing hypothesis asserts that the success of a year class is determined by the availability of food resources during crucial periods of larvae development (i.e. following yolk-sac absorption), and therefore matches or mismatches in timings of plankton production can have significant recruitment implications (Hjort 1914; Cushing 1990). Several of the Laurentian Great Lakes (e.g., Lake Michigan, Huron, Ontario) have undergone changes in lower trophic levels since the proliferation of nonindigenous dreissenid mussels in the early 2000s, including declines in the spring phytoplankton bloom (Vanderploeg et al. 2010; Rowe et al. 2015) and changes in the densities and community composition of zooplankton (Barbiero et al. 2009, 2012, 2014; Pothoven and Fahnenstiel 2015) which, in turn, could influence the growth and availability of prey during critical larval periods.

Lake Michigan is illustrative of one of the Laurentian Great Lakes that has undergone dramatic structural ecosystem changes over the past several decades as a result of declining nutrient inputs, reduction of ice cover, proliferation of nonindigenous species, and large stocking efforts to restore piscivores (Madenjian et al. 2002, 2015; Wang et al. 2012). One key fish management concern is declining biomass of planktivorous prey fish species, such as Alewife *Alosa pseudoharengus*, Bloater *Coregonus hoyi*, and Rainbow Smelt *Osmerus mordax*, that support a multi-million-dollar recreational fishery for Chinook Salmon *Oncorhynchus*

tshawytscha, Coho Salmon *Oncorhynchus kisutch*, Lake Trout *Salvelinus namaycush*, Steelhead *Oncorhynchus mykiss*, and Brown Trout *Salmo Trutta* (Thayer and Loftus 2012). Two complementary lakewide surveys (i.e., bottom trawl and hydroacoustics with midwater trawl) reveal biomass of prey fishes in 2010-2017 to be ≤ 88% of the biomass estimated in the 1990s (Madenjian et al. 2018; Warner et al. 2018). Predation on juvenile and adult planktivorous fish is one important driver underlying this declining trend, especially for Alewife (Madenjian et al. 2005; Tsehaye et al. 2014). Another untested, yet hypothesized, mechanism is declining recruitment emanating from reduced larval growth and survival as a result of reduced availability of zooplankton prey (see Bunnell et al. 2018). In ecosystems such as Lake Michigan that are experiencing oligotrophication simultaneous with high levels of predator stocking, both top-down and bottom-up regulation can be operating and influencing intermediate trophic levels, such as the prey fish community (Bunnell et al. 2014; Kao et al. 2017).

Larval fish studies in the Laurentian Great Lakes have been intermittent and spanned decades. Comparisons of these studies can reveal how changes in lower trophic levels could be affecting larval fish dynamics. Seminal Lake Michigan studies by Wells (1966), Rice et al. (1987a) and Nash and Geffen (1991) provide insights into the community composition and densities of pelagic larval fish during the 1960s through 1980s, prior to the proliferation of Ponto-Caspian invaders that have significantly altered the lake, such as dreissenid mussels, water fleas, and Round Gobies *Neogobius melanostomus*. These studies describe a nearshore larval fish community dominated by Alewife and Rainbow Smelt, whereas the offshore community was dominated by Bloater and Deepwater Sculpin *Myoxocephalus thompsonii* (Rice 1987a; Nash and Geffen 1991). Among these earlier studies, only Rice et al. (1987a) used otoliths to estimate growth and survival of larval fish, and they concluded Bloater were feeding at near optimal rates.

In the 2000s, studies reported the densities and growth rates of larval Alewife (e.g., Höök et al. 2007; Weber et al. 2015; Withers et al. 2015) and Yellow Perch *Perca flavscens* (e.g., Dettmers et al. 2005; Weber et al. 2011) at different locations around Lake Michigan. Diets reported from these studies were not consistent with larvae feeding at optimal levels, given that 79-87% of Alewife larvae, for example, had empty stomachs (Withers et al. 2015). Furthermore, these studies were designed to evaluate how larval growth rate varied spatially within a region of the lake. Given putative spatial variation in temperature and zooplankton density, it should not be surprising that Alewife growth rates varied across sites in Illinois waters (Weber et al. 2015) and Michigan waters, including drowned-rivermouths that are connected to Lake Michigan (Höök et al. 2007).

Across a diversity of ecosystems, temperature, densities of zooplankton prey and larval competitors have been identified as important variables to explain larval fish growth rates. In marine ecosystems, Landaeta et al. (2015) documented faster growth of a larval Pearlsides *Maurolicus parvipinnis* in warmer, more productive areas of the South Pacific, and Meekan et al. (2003) found that temperature better explained variation in growth of Neon Damselfish *Pomacentrus coelestis* than chlorophyll or zooplankton abundance on an Australian reef. Furthermore, Pepin (1991) argued that temperature regulates the vital rates of all early life stages of marine fishes. In riverine systems, growth rates of larval American Shad *Alosa sapidissima* were also positively correlated with zooplankton densities and water temperatures (Crecco and Savoy 1985). Across Midwest reservoirs, temperature explained variation in larval growth of *Pomoxis* spp., *Lepomis* spp., and American Gizzard Shad *Dorosoma cepedianum* (Claramunt and Wahl 2000), and biomass of zooplankton prey explained 64% of the variation in growth of first-feeding *Pomoxis* spp.larvae (Bunnell et al. 2003).

In our study, we sought to describe larval fish dynamics in July 2015 at 24 sites broadly distributed around Lake Michigan that we expected to differ in prey densities given their variable proximity to rivermouths with different nutrient loading. We measured larval fish densities and estimated instantaneous growth rates and diets of the two most abundant species: Alewife and Bloater. We hypothesized that larval growth rates would be higher at sites with higher indices of primary and secondary zooplankton production, which contribute to greater prey resources for the larvae. A secondary objective was to compare larval growth rates and densities in 2015 to those estimated in the 1980s and 2000s, with the hypothesis that larval growth rates would be higher in the previous years when the zooplankton community might have been more favorable to higher consumption by larval fish through greater densities and prey overlap.

Methods

Field sampling

Twenty-four sites throughout Lake Michigan (Figure 1) were sampled for water temperature, chlorophyll *a* (herein CHL), zooplankton, and larval fish from July 8-27, 2015 during nighttime hours. The sites were organized across eight transects, each with three unique depths (18 m, 46 m, and 91 or 110 m). Moving clockwise around the lake, these transects included Frankfort, MI (offshore of the drowned river mouth Arcadia Lake fed by Bowen's Creek); Ludington, MI (offshore of the Pere Marquette River); Saugatuck (offshore of the Kalamazoo River), MI; St. Joseph, MI (offshore of the St. Joseph River); Waukegan, IL (offshore of the Waukegan River); Racine, WI (offshore of the Root River); Manitowoc, WI (offshore of the Manitowoc River); Sturgeon Bay, WI (connecting Green Bay). The distance between two adjacent sites within a transect ranged from 5.0 km (between 18 m and 46 m off of Frankfort) to 31.9. km (between 46 m and 110 m off of Saugatuck).

At each of the 24 sites, a profile of the water column temperature and fluorescence was measured with a Seabird bathythermograph. The data collected were bin averaged in 1 m intervals. After observing the profile, we used a Niskin bottle to collect discrete water samples at up to three vertical depths to sample a range of fluorescence values to compare extracted CHL concentrations to fluorescence values. For each of two replicates per depth, 500-900 mL of water were immediately filtered through a 47 mm Whatman glass fiber filter. Filters were then placed in a Falcon tube wrapped with foil and frozen at –80 °C aboard the USGS R/V Sturgeon for later CHL analysis.

Zooplankton were sampled from vertical, whole-water column tows using a conical, 0.5-m diameter, 2-m length, 153-µm mesh net retrieved at a speed of 0.5 m/s. The net was equipped with a calibrated flowmeter to estimate volume of water sampled. After the samples were rinsed into the cod end, the cod end was bathed in a bucket of water and the animals were narcotized with CO_2 from antacid before being preserved in 5% sugar buffered formalin.

Larval fish were sampled with a circular, 1-m diameter, 500-µm mesh ichthyoplankton (IP) net towed at 4.2 km/h. A calibrated flowmeter was placed in the mouth of the net to calculate volume sampled. On the bottom of the net, we mounted a mensuration sensor (Netmind) that provided real-time estimates of net depth when paired with a hydrophone towed behind the vessel. At each site, both a surface and “oblique” IP tow were conducted. The surface tows were typically 10 min in duration and were fished off the starboard side of the vessel to avoid wash from the vessel propeller. The oblique tows were fished behind the vessel and sampled several different discrete layers (4-5 min per layer) from the metalimnion through epilimnion. At 18 m bottom depth, oblique tows were typically 10 min in total and fished at ~ 10 m and 7 m layers. At 46 m bottom depth, oblique tows were typically 12 min total and fished at

~ 30 m, 20 m, and 10 m layers. At the most offshore depth (i.e., 91 or 110 m bottom depth), oblique tows were typically 16 min total and fished at 40 m, 30 m, 20 m, and 10 m layers. At the end of each IP tow type, the net was rinsed from the outside to concentrate larvae in the cod end, which were promptly preserved in 95% ethanol.

Laboratory processing

In the laboratory, CHL was extracted in a dark room with 90% buffered acetone using the modified fluorometric technique from EPA method 445.0 (Arar and Collins 1997). In addition, filters went through a freeze-thaw cycle to break cell walls prior to extraction instead of grinding filters. Fluorescence values were estimated with a fluorometer (Turner Trilogy) that was calibrated with commercial standards to calculate CHL concentrations (µg/L). Replicates were averaged to determine mean concentrations at specific vertical depths at each site.

To process zooplankton, the samples were first stained with Phloxine B to improve identification of animals. The entire sample was then inspected for "clumps" of large predatory cladocerans (i.e., *Bythotrephes longimanus* or *Cercopagis pengoi*) that could affect subsampling; when "clumps" were found, they were removed for later processing (after ensuring smaller crustacean zooplankton were not attached). The remaining "clump-free" zooplankton sample was then diluted with reverse-osmosis water to between 30-750 mL, with the goal of obtaining a solution with about 200 crustacean zooplankters per mL. The sample was mixed by moving a glass rod in a figure-8 pattern, and a 1-mL aliquot was removed with a Hensen-Stempel pipette. All individual crustacean zooplankton from the sub-sample were identified to the highest taxonomic resolution possible (see below) and counted under a dissecting microscope. Copepod nauplii, dreissenid veligers, and rotifers were not counted because of the large mesh size of the

zooplankton net. All adults were identified to species (except for *Bosmina* spp.), and copepodites (immature copepods) were identified to genus in a few instances (i.e., *Mesocyclops*, *Tropocyclops*, *Limnocalanus*, *Epischura*, *Senecella*) but were otherwise identified as cyclopoid or calanoid copepodites. If 200 crustacean zooplankters were counted in the first 1-mL subsample, no additional aliquots were processed. Otherwise, aliquots were removed in 1-mL increments and processed until at least 200 individuals (total) were identified and counted. The entire sample (including any "clumps" that were previously removed) was then processed to identify and count predatory cladocerans, noting the instar for *Bythotrephes* and *Cercopagis*. For all taxa, the first 20 individuals encountered were measured using an ocular micrometer. We measured cladocerans from either the top of their head or the front of their rostrum to the base of the caudal spine or the distalmost part of their carapace. *Bythotrephes* was measured from the proximal end of its spine to the base of the 'S-curve' of the spine (Berg and Garton 1988). Body length of *Cercopagis* was measured (Grigorovich et al. 2000). We measured copepods from the anterior-most part of cephalosome to the distal end of the caudal ramus.

Larval fish in the IP samples were removed while using an overhead magnifier light. Ninety-nine percent of larval fish were identified to species level using Auer (1982). The remaining larvae unable to be identified were excluded from subsequent analyses. We measured total length of all larval fish to the nearest 0.01 mm using a dissecting microscope and ImagePro software and corrected these lengths for 10% shrinkage after preservation in 95% ethanol (Foley et al. 2010). Alewife and Bloater were the most abundant species, and therefore subsequent age and diet analyses focused only on these two species.

A subset of up to 30 Alewife and Bloater from each IP tow were randomly selected for age examination. In total, ages from 464 Alewife larvae and 72 Bloater larvae were estimated

using sagittal otoliths. Daily rings on larval otoliths were counted following a protocol adapted from Höök et al. (2007). Using a dissecting scope, sagittal otoliths were removed from each larva and mounted on glass slides with super glue. Daily growth rings were counted using a Nikon Eclipse 80i microscope at 400-1200x magnification. Two individuals (DEE, LAT) read the otoliths independently on separate dates. If the difference between the readings was less than 10% (occurred for 63% of Alewife otoliths and 69% of Bloater otoliths), the mean of the two readings was used to estimate total number of rings. If the difference was greater than or equal to 10%, each reader conducted a second set of independent readings. For 28% of Alewife otoliths and 24% of Bloater otoliths, the mean of the second read was used because the difference was less than 10%. Otherwise, a third reader (DJW) performed an independent reading, and the median of the final three independent counts was used as the total number of daily growth rings (9% and 7% of Alewife and Bloater otoliths, respectively).

Diets of larval fish were examined to evaluate whether any evidence of daytime feeding could still be detected with nighttime collected larvae. From each IP sample, 10 larvae per species were randomly selected for diet evaluation. Stomachs were excised and opened with a scalpel or fine-tip scissors, and the contents were examined under a dissecting microscope. If at least 3 of 10 larvae had countable stomach contents, then up to 30 individuals per fish species were processed. Otherwise, no more individuals were examined from that sample. Diet items found in the stomachs were classified as copepod nauplii, calanoid or cyclopoid copepodite, *Leptodiaptomus minutus*, *L. ashlandi*, *L. sicilis*, *Epischura lacustris*, *Bosmina* spp., unidentified copepods (could be adult or copepodites), *Polyphemus pediculus*, *Bythotrephes longimanus*, *Leptodora kindtii*, dreissenid veliger, *Keratella* spp., or *Conochilus* spp.

For different zooplankton species within the stomachs, different body parts were used to identify and count individuals to prevent double-counting. For copepods, the fifth legs and urosome needed to be present to count and identify to species level. The urosome was used to identify and count calanoid and cyclopoid copepodites. To avoid double counting copepods, cephalosomes were counted separate from caudal rami and subtracted from each other. Any extra cephalosomes after subtracting the caudal rami were counted as an unknown copepod. In cases where there was only a part (or parts) of the copepod (e.g., metasome) present and the cephalosome and urosome were absent, it was counted as a single unknown copepod. To qualify as a countable cladoceran, the head and rostrum needed to be present for *Bosmina* spp., the eye and part of body for *Polyphemus pediculus*, the body or tail spine with some body tissue attached for *Bythotrephes longimanus*, and the tail spine for *Leptodora kindtii*. Dreissenid veliger shells needed to be present, but inside tissue did not need to exist to be countable. Rotifers were identified based on intact organisms. The proportion of empty stomachs was estimated for each species at each site. For non-empty stomachs, the proportion (by count) of each diet category was calculated for each fish and averaged across all non-empty individuals to provide a snapshot of the important prey items.

To determine what sizes of sampled zooplankton could theoretically be available to larvae, we measured the mouth gape on a subset of larval Alewife. A small probe was inserted into the mouth of the fish, and the dorsoventral gape was measured to the nearest 0.01 mm using ImagePro software. Gape was measured on up to 10 larvae from each of five different size classes: 5-10 mm, 11-15 mm, 16-20 mm, 21-25 mm, 26-30 mm for a total of 45 fish.

Statistical modeling

Linear regression was used to determine a relationship between mean *in situ* CHL and corresponding fluorescence value (*FL*) (at the same vertical depth) from the Seabird bathythermograph, pooled across all sites and depths: CHL = (*FL* ×0.0883) – 0.0854, $r^2 = 0.78$, $P < 0.0001$. This enabled us to estimate CHL at 1-m increments within the water column at each site.

Larval densities for each fish species at each site were calculated by summing the total number of larvae caught in each tow (i.e., surface and oblique) and dividing by the total volume sampled across the tows. The age (A, in days) of an individual fish was estimated as the number of sagittal daily growth rings counted plus 2 for Alewife (Essig and Cole 1986) or plus 3 for Bloater (Rice et al. 1985). Individual instantaneous growth rate (G, in mm/d) was estimated as $G = (L_c – L_h/A)$, where L_c equals the corrected length at capture (in mm) and L_h equals the length at hatch (in mm). We assumed L_h equaled 3.5 mm for Alewife (Auer 1982) and 9.75 mm for Bloater (Rice et al. 1985).

We sought to explain spatial variation in larval Alewife and Bloater mean density and growth with several environmental predictor variables: temperature, CHL, and zooplankton density. Because the age and size distribution of larvae differed across sites and the larval growth rate increased with age, we also included age as a growth predictor variable in addition to the variables above. For each sampling site, the mean larval age (days) and growth rate were calculated from all individuals collected in both the surface and oblique tows. Our growth analyses were limited to those sites where at least three larval ages were determined ($n = 15$ and $n = 8$ for Alewife and Bloater, respectively). Our attempt to conduct growth analyses for Bloater failed owing to insufficient sample size.

To characterize temperature, we used different methods for the two species. For Alewife that were caught primarily in the surface tows (see Results), we estimated the temperature experienced over their lifetime, rather than simply the water temperature measured on the day of collection. However, we had to assume that where larvae were captured was representative of where larvae spent their lifetime. We used daily estimates of lake surface temperature at each sampling site using a blended *in situ* and remotely sensed 1-km resolution dataset produced by NASA's Jet Propulsion Laboratory Regional Ocean Modeling System (Chao et al. 2009). These daily lake surface temperatures were cross checked with hourly buoy temperature data from the nearest Lake Michigan buoy maintained by the NOAA National Data Buoy Center. For each larva with an estimated age, daily lake surface temperatures were averaged from estimated hatch date to sampling date at each site. For Bloater, which were primarily captured in oblique tows (see Results), we were unable to utilize lake surface temperatures. Instead we calculated the mean temperature from our fishing depths as measured on the date of sampling with a CTD.

For CHL and zooplankton density, we were only able to estimate the variables on the night of collection. The estimated CHL was averaged from the surface to the maximum fishing depth at each transect-depth. For zooplankton, the mean numeric density of prey was calculated to estimate prey small enough to be eaten by gape-limited Alewife larvae. Schael et al. (1991) documented the importance of gape limitation for prey selectivity and determined that gape size in larval fish predicted the upper limits of prey sizes. Our gape-limited zooplankton densities for Alewife remove potential bias by eliminating individuals larger than the gape size. The gape versus Alewife total length regression revealed a linear relationship: Gape = $0.067\times TL_c - 0.187$ ($r^2 = 0.71$, $P < 0.0001$). For each site, the mean gape of the larvae was estimated based on their mean length. Mean gapes ranged from 0.31-1.17 mm across sites with a grand average equal to

0.57 mm. For each zooplankton taxon at a given site, the proportion of lengths that were less than or equal to the mean gape was estimated, and the areal density (#/m^2) was reduced proportionally. The densities of each taxa were then summed. For bloater, gape measurements were not made, in part because the minimum size of Bloater was relatively large (10.2 mm versus 4.8 mm for Alewife), and we expected minimal gape limitation based on the large diet items we encountered. Hence, zooplankton prey density for the Bloater density model included all potential zooplankton prey. For both species, we recognize our estimates of available zooplankton are biased low owing to the absence of nauplii, rotifer, and veliger counts because of the zooplankton net mesh size.

We used generalized additive models (GAM) in the statistical program R with the package mgcv (i.e., mixed GAM Computational Vehicle, Wood 2006; 2008) to explore spatial variation in larval Alewife density and growth and larval Bloater density. GAMs function as generalized linear models with linear predictors involving a sum of smooth functions (s) of covariates (Wood 2006). Gam.check was used to optimize smoothness selection (k) and identify any potential issues with model fitting (Wood 2006). With the R package MuMin (Multi-Model Inference), we used Akaike information criterion corrected for small sample size (AICc) to identify the most parsimonious model(s) (Anderson and Burnham 2002; Burnham and Anderson 2004). To confirm that our sites exhibited no spatial autocorrelation in larval densities or growth, despite the transect design, we calculated correlograms within R package ncf (Spatial Covariance Functions; Bjornstad 2018). For each response variable, we evaluated the spatial distribution of GAM residuals and whether any pattern emerged between the correlation and distance class.

For both density models, we included sites where 0 larvae were sampled. Our full model for Alewife density included temperature, gape limited zooplankton densities, and CHL as predictor variables: Density ~ s(Temp, k=4) + s(logZooplankton, k=4) + s(logCHL, k=4). CHL and Zooplankton were log10 transformed to improve the normality of these predictor variables. For Alewife sites where no larvae were sampled, we estimated temperature and zooplankton densities based on relevant Alewife data from the closest non-zero density site. Our full model for Bloater density included temperature, zooplankton densities, and CHL as predictor variables: Density ~ s(Temp, k=4) + s(logZooplankton, k=4) + s(logCHL, k=4).

Our full model to explain variation in Alewife growth included the same predictor variables as for density, but we removed CHL, added Alewife density (Density) and mean Alewife age (Age), and weighted the data based on the number of larvae that were used to estimate the mean growth rate at each site: Growth ~ s(logDensity, k=3) + s(Temperature, k=3) + s(logZooplankton, k=3) + s(Age, k=4), weights=n. Alewife density and zooplankton density were log10 transformed to improve normality. Alewife density was added to account for potential density dependent control of growth, and age was added to account for potential changes in growth rate associated with ontogeny. We removed CHL because of model overfitting concerns (from too many predictors) and because we assumed zooplankton could characterize site productivity in relation to growth rates.

Results

In the vertical strata where IP were sampled, CHL ranged from 0.49 to 1.56 µg/L, while temperature ranged from 14.9 to 18.3°C. Zooplankton density in the whole water column ranged from 1,509.6 to 131,395.4 individuals/m^2. A total of 2,047 larval fish were captured in surface

and oblique tows and identified to species. Eighty-nine percent of larvae were identified as Alewife (n=1,813), 4% as Bloater (n=83), and the remaining proportion was comprised of Burbot *Lota lota* (n=62), Yellow Perch (n=50), Deepwater Sculpin (n=27), Slimy Sculpin *Cottus cognatus* (n=11), and Common Carp *Cyprinus carpio* (n=1). Alewife larvae were relatively evenly distributed across bottom depths (526 at 18 m, 653 at 46 m, and 634 at ≥91 m), but 1,650 of the total 1,813 (91%) were collected from surface tows. In contrast to Alewife, 74 of the 83 Bloater larvae (89%) were collected at the farthest offshore sites (≥91 m bottom depth), only 8 were captured at 46 m, and 1 at 18 m; 67 of the larvae (81%) were captured in oblique tows. Burbot were captured most commonly at ≥91 m bottom depth (36 individuals, versus 21 at 46 m and 5 at 18 m) and in oblique tows (54 of 62 total larvae, 87%). Finally, Yellow Perch larvae were captured most frequently at 18 m bottom depth (35 of 50, versus 13 at 46 m and 2 at ≥91 m) and in surface tows 45 of 50 total larvae (90%).

Larval Alewife densities at a given site ranged from 0 to 42.57 per 100 m^3 (Table 1, Figure 2). Densities exceeded 10 per 100 m^3 at four sites in southern Lake Michigan: 46 m at St. Joseph, 18 m at St. Joseph, 91 m at Waukegan, and 18 m at Saugatuck (Table 1). At the northernmost sites, no larvae were collected at Sturgeon Bay, and only 1 larva was collected at Frankfort. An information-theoretic approach to explain larval Alewife density revealed the highest ranked model included only the intercept (Table 2), and the residuals exhibited no spatial autocorrelation. Three other models also had ΔAICc <2, each with only one explanatory variable of either temperature, zooplankton, or CHL. But variation explained was relatively low, with only 14% of the deviance explained in the full model.

Across all larval Alewife that were processed for age (n = 464), mean growth rate equaled 0.50 mm/d (SE, 0.01). Growth rates varied across sites (Table 1, Figure 2), and Alewife

larvae from St. Joseph grew the fastest (0.56 mm/d across all depths). Mean age (24 days) and size (17.0 mm) were also greatest for Alewife from St. Joseph. Alewife larvae from Manitowoc also grew at a relatively fast rate (0.51 mm/d, with mean age and length = 12 days, 9.6 mm, respectively) but were only collected at the deepest depth (Table 1). Waukegan (0.48 mm/d, 10 days, 8.2 mm) and Racine (0.46 mm/d, 12 days, 9.0 mm) larval Alewife growth rates were also relatively fast. Alewife larvae from Ludington sites had the slowest mean growth rate (0.37 mm/d, 12 days, 8.1 mm).

Using an information-theoretic approach to explain mean growth rates of Alewife larvae across the sites, our full growth model explained 92.7% of the deviance. One model outperformed all the others, and it included both age and zooplankton density as predictors (Table 3). Of the models with ΔAICc <6, 2 out of 3 included age, and 2 out of 3 included zooplankton density, which further reinforces their importance as explanatory variables (Table 3). Furthermore, larval Alewife growth had a positive linear relationship with zooplankton density (Figure 3a). The relationship between Alewife age and growth was non-linear showing a negative correlation with young larvae (<15 days) and a positive correlation with old larvae (>20 days) (Figure 3b). For the best performing model, the residuals exhibited no spatial autocorrelation.

Sixty-seven percent of larval Alewife stomachs (n = 313) were empty, although considerable variation was observed across sites (Table 1). Among the 12 sites that had at least 10 diets analyzed, only two sites had less than 50% of larvae with empty stomachs, and both of those sites were offshore: 110 m at Saugatuck and 91 m at Waukegan (Table 1). Among the Alewife stomachs that were not empty, the taxa with the highest mean proportion were dreissenid veligers (39.2%), unidentifiable copepods (27.8%), cyclopoid copepodites (13.3%),

and calanoid copepodites (5.5%; see Supplementary Table 1). In addition to veligers having the highest mean proportion within a diet, they were also observed in 56% of the Alewife stomachs that were not empty.

Bloater larvae were collected at 13 sites across all eight ports, and their densities were generally lower than those estimated for Alewife. Two exceptions were more northerly ports (Ludington and Sturgeon Bay), where densities for Bloater were comparable to or higher than those for larval Alewife. The highest Bloater density was 1.16 per 100 m^3 at 110 m at Saugatuck (Table 1). Similar to the Alewife density model, the highest ranked model included only the intercept (Table 4), and the residuals exhibited no spatial autocorrelation. The explanatory power of the full model was very low (8.19% of the deviance explained), and all of the model weights were small. Across all larval Bloater that were aged (n = 72), mean growth rate equaled 0.21 mm/d (SE, 0.01). The fastest mean growth rates (0.27 mm/d) occurred on the western side of the lake: 91 m at Waukegan, 91 m at Racine, 110 m at Manitowoc. The slowest mean growth rates were 0.17 mm/d at 110 m at both Ludington and St. Joseph.

Only 16% of larval Bloater stomachs (n = 81) were empty. Most of the Bloater diets that were processed came from only three sites (Table 1), which ranged from only 0-29% empty (Table 1). Among the stomachs that were not empty, the taxa with the highest mean proportion were unidentifiable copepods (51.3%), cyclopoid copepodites (28.1%), dreissenid veligers (9.2%), and calanoid copepodites (4.5%; see Supplementary Table 1). Unidentified copepods were found in 91% of the stomachs, whereas the most common Alewife prey, dreissenid veligers, only occurred in 35% of Bloater stomachs.

Discussion

409 Our hypothesis that larval Alewife densities and growth rates would be higher at sites
410 with higher primary and secondary production was partially supported. Zooplankton density was
411 included among the best models to explain larval Alewife growth rates, and the relationship was
412 positive, as predicted. Conversely, variation in larval Alewife and Bloater densities were not
413 explained by any of our predictor variables, including CHL and zooplankton densities. Our
414 secondary objective was to compare larval growth rates in 2015 to those from previous decades,
415 given that some time series surveys of zooplankton have revealed declining trends since the
416 1980s or 1990s (Dettmers et al. 2003; Madenjian et al. 2015; Bunnell et al. 2018).
417 We found evidence for reduced growth rates for both Alewife and Bloater. Weber et al.
418 (2015) reported mean larval Alewife growth rates as 0.81 mm/d (SE, 0.08) in 2005 and 1.11
419 mm/d (SE, 0.11) in 2006 offshore of Waukegan, IL. At approximately this same location in
420 2015, we estimated mean larval Alewife growth rates as 0.49 mm/d (SE, 0.02), which was a 47%
421 decline. From 1989 to 1992, Alewife larvae collected in southeastern Lake Michigan had growth
422 rates of 0.8–0.9 mm/d (D. Jude, unpublished data as cited by Höök et al. 2007), and Höök et al.
423 (2007) reported 0.89 mm/d (SE, 0.06) and 0.84 mm/d (SE, 0.06) growth rates near Muskegon,
424 MI in 2001 and 2002, respectively. Although our sampling sites did not include Muskegon, the
425 average growth rate from our two southeastern sites (Saugatuck and St. Joseph) was 0.52 mm/d
426 (SE, 0.01), which was approximately a 35-42% decline from 1989-1992 and a 40% decline from
427 2001-2002. A similar growth reduction was noted for Bloater larvae in Lake Michigan. Rice et
428 al. (1987a) reported larval growth rates averaging 0.50 mm/d (SE, 0.01) in 1982 and 0.45 mm/d
429 (SE, 0.01) in 1983 northeast of Racine, WI (digitized data from Figure 6 in Rice et al. 1987a). In
430 2015, Bloater larvae were relatively rare among our samples, and we caught only 17 individuals
431 offshore of Racine with an average growth rate of 0.27 mm/d (SE, 0.02), which was a 43%

decline from the early 1980s. When all Bloater larvae (N=72) from Lake Michigan in 2015 were pooled, the average growth rate was even slower: 0.21 mm/d (SE, 0.01). When comparing these two species in our study, mean Alewife growth rate was more than twice that of Bloater, which is consistent with faster mean larval growth by Alewife when comparing previous studies. One possible explanation for faster Alewife growth is a warmer thermal environment for Alewife given that 91% of Alewife were captured in the warmer epilimnion, whereas 81% of Bloater were captured by oblique tows in colder, sub surface waters.

Alewife hatch dates across our sampling sites showed a bimodal distribution distinguishing eastern vs. western Lake Michigan (Figure 4). Alewife from eastern Lake Michigan hatched earlier with a peak on June 24th, while those from western Lake Michigan hatched later with a peak on July 12th. The nearshore water temperature estimated on the modal hatch date were all between 15 and 19°C (Table 5), which corresponds to the temperature range of 15 to 22°C at which previous studies have documented peak Alewife hatching in Lake Michigan (Weber et al. 2015). Future research could seek to determine whether the earlier hatching on the eastern coastline is a consistent pattern. In general, the western coastline may be cooler, on average, owing to its higher frequency of upwelling events given the prevailing wind patterns (Plattner et al. 2006).

Comparisons of our 2015 larval densities to previous Lake Michigan studies indicate similar Alewife densities and lower Bloater densities. For Alewife, we can make comparisons in the southern basin between daytime estimates from previous studies and nighttime estimates in our study, recalling that 91% of Alewife larvae caught in 2015 were in surface tows. As larvae catchability has been shown to increase during nighttime (Martin et al. 2011), we cannot rule out methodological differences when our larval density estimates are higher. In the southeastern

nearshore, larval Alewife densities in July 1983 at the surface ranged from 3.3 larvae per 100 m^3 off of Grand Haven, MI (Nash and Geffen 1991) to 200 larvae per 100 m^3 (SE, 90) in the summer of 2002 off of Muskegon, MI (Höök et al. 2007). The average of our 2015 estimates from the two southeastern sites was 32.1 larvae per 100 m^3 (SE, 9.2). At Waukegan (in southwestern Lake Michigan), peak Alewife densities in the summers of 2005-2006 were 0.3-2.1 larvae per 100 m^3 in the nearshore (surface only) and 4.0-16.0 larvae per 100 m^3 in the offshore (tucker trawl in midwater plus neuston net in surface, Weber et al. 2015). In 2015, our nearshore (i.e., 0.3 larvae per 100 m^3, surface only) and offshore (i.e., 15.4 larvae per 100 m^3, oblique and surface combined) Alewife densities were within the range observed by Weber et al. (2015).

For Bloater, we can compare our July 2015 study to one in July 1983 in southeastern Lake Michigan that sampled larvae during the daytime at the surface with a neuston net, as well as the epi-, meta-, and hypolimnion with a tucker trawl at five sites off of Grand Haven, MI (Nash and Geffen 1991). To compare our estimates from oblique tows (where we caught 81% of bloater larvae in 2015) to Nash and Geffen (1991), we averaged their densities from the metalimnion and epilimnion layers. Every comparison between 2015 and 1983 revealed significantly lower densities in 2015. In surface tows, we only caught Bloater larvae at the 46 m and 110 m sites at our southeastern locations, but our non-zero densities (i.e., 0.17 and 0.87 larvae per 100 m^3, respectively) were orders of magnitude lower than the 1983 densities (i.e., 34.9 and 1,551.9 larvae per 100m^3 at the 50 m and 100 m site, respectively). Bloater densities at every other 1983 sampling site ranged 0 – 1,551 larvae per 100 m^3. Larval Bloater densities were undoubtedly higher in the 1980s than in 2015, whereas Alewife densities were comparable between 1983 and 2015. However, larval densities typically exhibit high interannual variability.

Further research is needed to see if our results are a single-year event or are indicative of a larger decline in productivity for Bloater.

Our finding that larval growth increased with relatively greater densities of zooplankton is consistent with a broad range of studies, but our inability to detect a temperature effect on growth was surprising and should not be excluded as a hypothesis in future research. The shape of the nonlinear relationship between Alewife age and growth (Figure 3b) was unexpected; a more common nonlinear relationship between age and length is sigmoidal or logistic (Quist et al. 2012). One potential explanation for the initial growth decline that we observed is that young larvae were gape limited following yolk-sack absorption and had fewer prey resources available for consumption thus reducing growth rates.

Spatial variation in larval Alewife growth rates in 2015 was explained by zooplankton prey densities, and larval growth rates (on average) were at least 40% lower in 2015 than in previous years. One unequivocal change in Lake Michigan since the late 1990s has been declining primary production in spring, owing to declining nutrient inputs and increasing herbivory by nonindigenous dreissenid mussels (Fahnenstiel et al. 2010; Rowe et al. 2015; Warner and Lesht 2015). Even though declining secondary production (such as zooplankton) might be expected given declining primary production, the evidence for this pattern is equivocal and only partially supports the hypothesis that reduced larval Alewife and Bloater growth rates in 2015 were the result of declining prey availability (see Bunnell et al. 2018).

In addition to reduced total zooplankton prey densities, reduced vertical overlap with zooplankton prey could be contributing to reduced larval growth rates in 2015 relative to previous decades. Many zooplankton species have been documented to migrate to deeper, darker, and colder waters in the hypolimnion to avoid predation from *Bythotrephes longimanus*,

a large predatory cladoceran (Pangle and Peacor 2006; Bourdeau et al. 2011, 2015). In addition, the irruption of quagga mussels since 2004 has increased water clarity and depth of the euphotic zone by 5 m (Yousef et al. 2017), which could be inducing zooplankton to migrate to deeper waters to reduce exposure to ultraviolet radiation (Leech and Williamson 2001) or reduce vulnerability to visual predators.

We have circumstantial evidence that fish larvae sampled deeper in the water column at night have more feeding opportunities than those in the top meter of water. More than 80% of Bloater larvae were sampled in our oblique tows, which fished down to 40 m of water in the offshore, to 35 m of water in the intermediate site, and 10 m of water in the nearshore. Only 16% of Bloater larvae had empty stomachs. Conversely, more than 90% of Alewife larvae were caught in the surface tow at night, and 67% of all Alewife larvae had empty stomachs. We do not think this discrepancy was due to time of sampling because, on average, oblique tows were conducted one hour later in the night than surface tows, and those later-collected larvae might be expected to have more of their prey digested, given that feeding is highest during the day (Boeuf and Le Bail 1999). Nonetheless, our high percentage of empty stomachs for Alewife larvae corroborate earlier findings from daytime collections during the 2000s: 66-87% empty in 2001-2002 (Höök et al. 2007) and 79-87% in 2010-2011 (Withers et al. 2015). Decreasing spatial overlap between zooplankton prey and larval Alewife could explain high empty stomach rates.

It is important to examine not just the presence/absence of food in larval fish stomachs, but also the relative quality of the prey items. For example, the most common prey item in larval Alewife diets was dreissenid mussel veligers, a similar result to what Withers et al. (2015) reported in their 2010-2011 sampling of southeast Lake Michigan. Veliger densities are not well monitored in the Great Lakes, but it is logical to conclude that their densities have increased

concomitant with increasing densities of dreissenid mussels in Lake Michigan (Nalepa et al. 2009). The short- or long-term consequences of relying on veligers for larval fish nutrition is not well understood. For example, how well can larval fish digest veligers or what is their energy density relative to comparably sized copepod nauplii or large rotifers? Studies on the consumption of adult dressenid mussels by adult fishes have been linked to decreased growth rates (Pothoven and Madenjian 2008). Alternatively, Withers et al. (2015) speculated that veligers could represent an abundant prey source for larval fish that may help offset lower availability of other prey. Veligers may be important for larval growth, and we acknowledge that if they are an important nutritional source, our growth analysis should be revisited so that density of prey can include both veligers and copepod nauplii.

Larvae that are not feeding could be vulnerable to starvation, especially larvae that hatch out at small sizes (Miller et al. 1988). First-feeding Alewife between 3-5 mm in size (Auer 1982) may be particularly vulnerable to starvation during this critical period, especially when one considers the higher percentage of empty stomachs that our study and others have observed. A laboratory study documented that under ideal water temperatures (15°C), unfed larval Alewife survived an average of 7.6 days after hatch (Edsall 1970). Whereas, another lab study showed that 50% of Bloater larvae survived without food for up to 25 days after hatch (Rice et al. 1987b), and a concurrent field study concluded starvation was not an important source of mortality (Rice et al. 1987a). However, if Bloater larvae are indeed growing 40% more slowly than they were in the 1980s, then some negative effects on survival are very possible. For example, slower growth rates and resultant smaller sizes can increase their vulnerability to predation (Crowder et al. 1987).

The role of currents in transporting larvae in the Great Lakes also has been hypothesized to play an important role in fish recruitment (Ludsin et al. 2014). Current-driven transport of ichthyoplankton in the Great Lakes has been documented for several species (e.g., Alewife, Yellow Perch, Cisco *Coregonus artedi*) and can influence their growth and survival by affecting their thermal and prey environment (Dettmers et al. 2005; Oyadomari and Auer 2008; Weber et al. 2011). Alewife spawn in the nearshore waters of Lake Michigan in mid-summer (Auer 1982). Similar to Weber et al. (2015), we observed advection of young Alewife larvae to offshore sampling stations: 21% of offshore larvae were aged 10 days or younger. Because Alewife larvae typically occupy the epilimnion (Martin et al. 2011, this study), wind-driven surface currents may be the primary mechanism (Weber et al. 2015) for advection of the larval fish. Heufelder et al. (1982) documented advection of Alewife larvae following upwelling events and hypothesized they increased mortality through thermal shock and/or movement into less favorable habitat. Future research that synthesizes physical current models with biological vital rates of fishes could improve the understanding of whether offshore transport has a net positive or negative effect on larval fish survival.

In conclusion, managers in Lake Michigan are increasingly concerned about the impact of declining primary production and changing zooplankton community on the production of prey fishes (Bunnell et al. 2018), and our study supported the hypothesis that growth rates of larval Alewife are limited by zooplankton prey density. Furthermore, our study reported larval fish growth rates in 2015 that were at least 40% slower than those reported in previous decades, for both Alewife and Bloater. Recognizing that fish recruitment is regulated by a suite of interacting abiotic and biotic factors (see Crowder et al. 1987; Letcher et al. 1996), slower larval growth, alone, is not sufficient to explain declining Alewife biomass in Lake Michigan (see Madenjian et

al. 2006; Collingsworth et al. 2014; Tsehaye et al. 2014). Nonetheless, we hypothesize that unless veligers represent a nutritional prey resource for larval fish, the dreissenid era will reduce the probability of strong year-classes emerging for pelagic larvae such as Alewife and Bloater when other conducive environmental variables might otherwise be present. To test this hypothesis, future larval fish monitoring that spans a broad spatial and temporal scale will need to be developed to evaluate possible linkages between larval growth, larval density, and year-class strength.

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Table 1: Summary of larval Alewife and Bloater densities, daily growth rates, and percent empty stomachs across 24 Lake Michigan sampling sites from July 8-27, 2015. N (in parentheses) represents the total number of stomachs analyzed for diets.

Transect name	Sampling Date	Depth (m)	Alewife Density (n/100 m^3)	Alewife Mean Growth rate (mm/d)	Alewife % empty stomachs (N)	Bloater Density (n/100m^3)	Bloater Mean Growth Rate (mm/d)	Bloater % empty stomachs (N)
Frankfort, MI	July 8	18	0	n/a	n/a	0	n/a	n/a
	July 8	46	0.09	n/a	100 (1)	0	n/a	n/a
	July 9	110	0	n/a	n/a	0.07	0.05	100 (1)
Ludington, MI	July 11	18	0.08	n/a	100 (1)	0	n/a	n/a
	July 11	46	0.21	0.41	67 (3)	0.21	0.18	33 (3)
	July 12	110	0.32	0.35	60 (5)	0.38	0.17	43 (7)
Saugatuck, MI	July 12	18	11.96	0.39	70 (40)	0	n/a	n/a
	July 13	46	3.24	0.45	78 (18)	0.06	0.24	0 (1)
	July 16	110	1.87	0.56	48 (31)	1.16	0.21	15 (20)
St Joseph, MI	July 18	18	25.93	0.51	90 (20)	0	n/a	n/a
	July 16	46	42.57	0.58	65 (34)	0.25	0.24	0 (2)
	July 19	110	8.85	0.58	86 (21)	0.83	0.17	29 (14)

Waukegan, IL	July 19	18	0.32	0.58	100 (3)	0	n/a	n/a
	July 20	46	2.84	0.44	90 (10)	0	n/a	n/a
	July 21	91	15.44	0.49	21 (38)	0.34	0.27	0 (6)
Racine, WI	July 22	18	1.50	0.48	82 (17)	0	n/a	n/a
	July 22	46	1.68	0.47	85 (26)	0	n/a	n/a
	July 23	91	6.23	0.44	60 (35)	1.12	0.27	0 (20)
Manitowoc, WI	July 25	18	0	n/a	n/a	0.08	0.20	0 (1)
	July 25	46	0	n/a	n/a	0	n/a	n/a
	July 24	110	3.55	0.51	100 (10)	0.17	0.27	0 (3)
Sturgeon Bay,	July 26	18	0	n/a	n/a	0	n/a	n/a
WI	July 26	46	0	n/a	n/a	0.07	0.09	0 (1)
	July 27	110	0	n/a	n/a	0.11	0.12	50 (2)

Table 2: Summary of Akaike's Information Criterion, corrected for small sample size (AICc), for Generalized Additive Models seeking to explain variation in larval Alewife density with site-specific water temperature (Temperature), CHL, and zooplankton density (Zooplankton) as explanatory variables. Models with ΔAICc < 6 are summarized, and "X" indicates the variable was included in the model. Weight is scaled from 0-1 and estimates the probability that a given model is actually the best, among all models considered.

Temperature	CHL	Zooplankton	df	logLik	AICc	ΔAICc	Weight
			2	-89.084	182.739	0.000	0.257
X			3	-88.056	183.311	0.572	0.193
		X	3	-87.734	183.333	0.594	0.191
	X		3	-88.445	184.091	1.352	0.131
X	X		4	-87.537	185.179	2.440	0.076
X		X	4	-87.566	185.286	2.546	0.072
	X	X	4	-87.707	185.615	2.877	0.061
X	X	X	5	-87.272	187.877	5.138	0.020

Table 3: Summary of Akaike's Information Criterion, corrected for small sample size (AICc), for Generalized Additive Models seeking to explain variation in mean larval Alewife growth rates with mean age (Age), site-specific zooplankton density (Zooplankton), alewife density (Density), and water temperature (Temperature) as explanatory variables. Only models with ΔAICc < 6 are summarized, and "X" indicates the variable was included in the model. Alewife density and temperature were not listed in the table because those variables were only included in models with ΔAICc > 6. Weight is scaled from 0-1 and estimates the probability that a given model is actually the best, among all models considered.

Age	Zooplankton	df	logLik	AICc	ΔAICc	Weight
X	X	5	35.015	-47.573	0.000	0.675
X		4	29.093	-45.485	2.089	0.238
	X	3	27.614	-43.489	4.085	0.088

Table 4: Summary of Akaike's Information Criterion, corrected for small sample size (AICc), for Generalized Additive Models seeking to explain variation in larval Bloater density with site-specific water temperature (Temperature), CHL, and zooplankton density (Zooplankton) as explanatory variables. Models with ΔAICc < 6 are summarized, and "X" indicates the variable was included in the model. Weight is scaled from 0-1 and estimates the probability that a given model is actually the best, among all models considered.

Temperature	CHL	Zooplankton	df	logLik	AICc	ΔAICc	Weight
			2	-7.988	20.548	0.000	0.427
		X	3	-7.587	22.375	1.826	0.171
X			3	-6.783	22.497	1.948	0.161
	X		3	-7.986	23.172	2.624	0.115
X		X	4	-6.954	25.014	4.465	0.045
	X	X	4	-7.530	25.165	4.616	0.042
X	X		4	-6.787	25.456	4.908	0.037

Table 5: Modal Alewife hatch date from eight Lake Michigan transects (pooling larvae captured across all depths) and corresponding water temperatures from nearshore (assuming all alewife hatch in this region). Note that we only sampled larvae once in July, so actual peak of hatching is unknown.

Port name	Modal hatch date	Temperature (°C)
Frankfort, MI	n/a	n/a
Ludington, MI	June 30	15.83
Saugatuck, MI	June 24	18.93
St. Joseph, MI	June 25	18.84
Waukegan, IL	July 12	17.22
Racine, WI	July 12	17.16
Manitowoc, WI	July 10-11, 13-14	15.56-18.50
Sturgeon Bay, WI	n/a	n/a

Figure legends

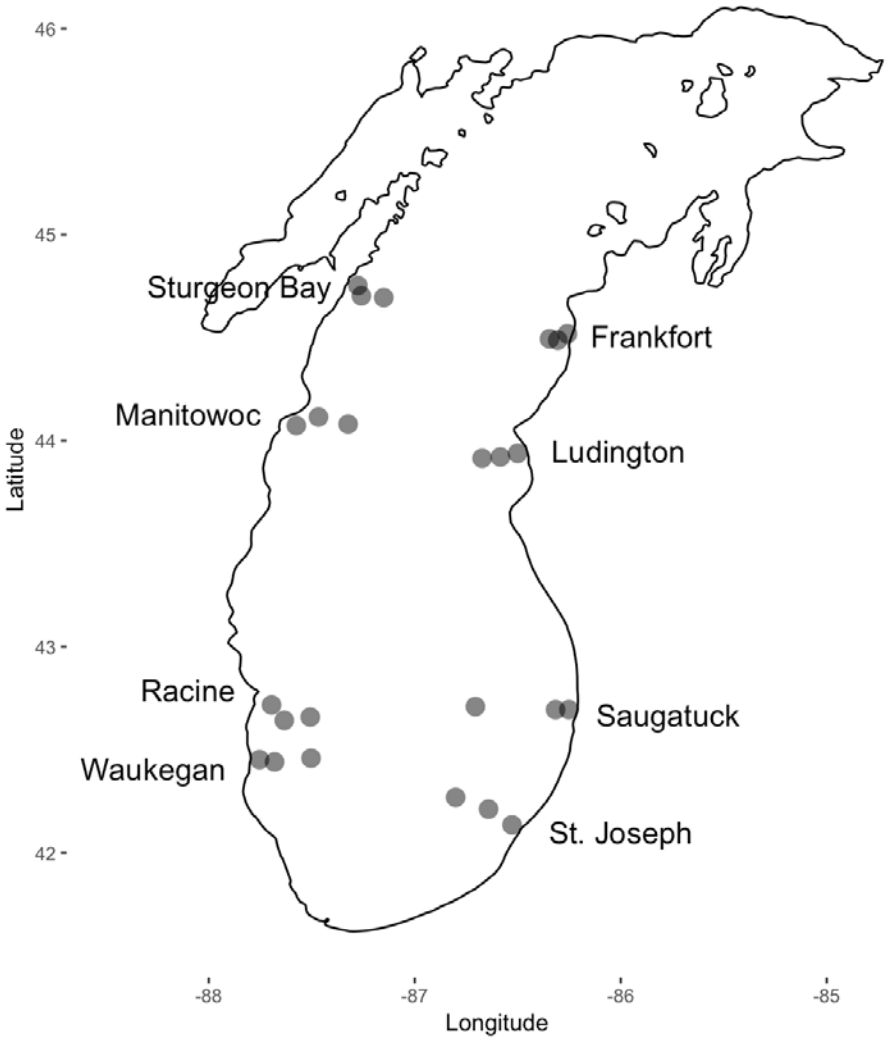

Figure 1: Location of sites where larval fish and associated environmental variables were sampled from July 8-27, 2015 in Lake Michigan.

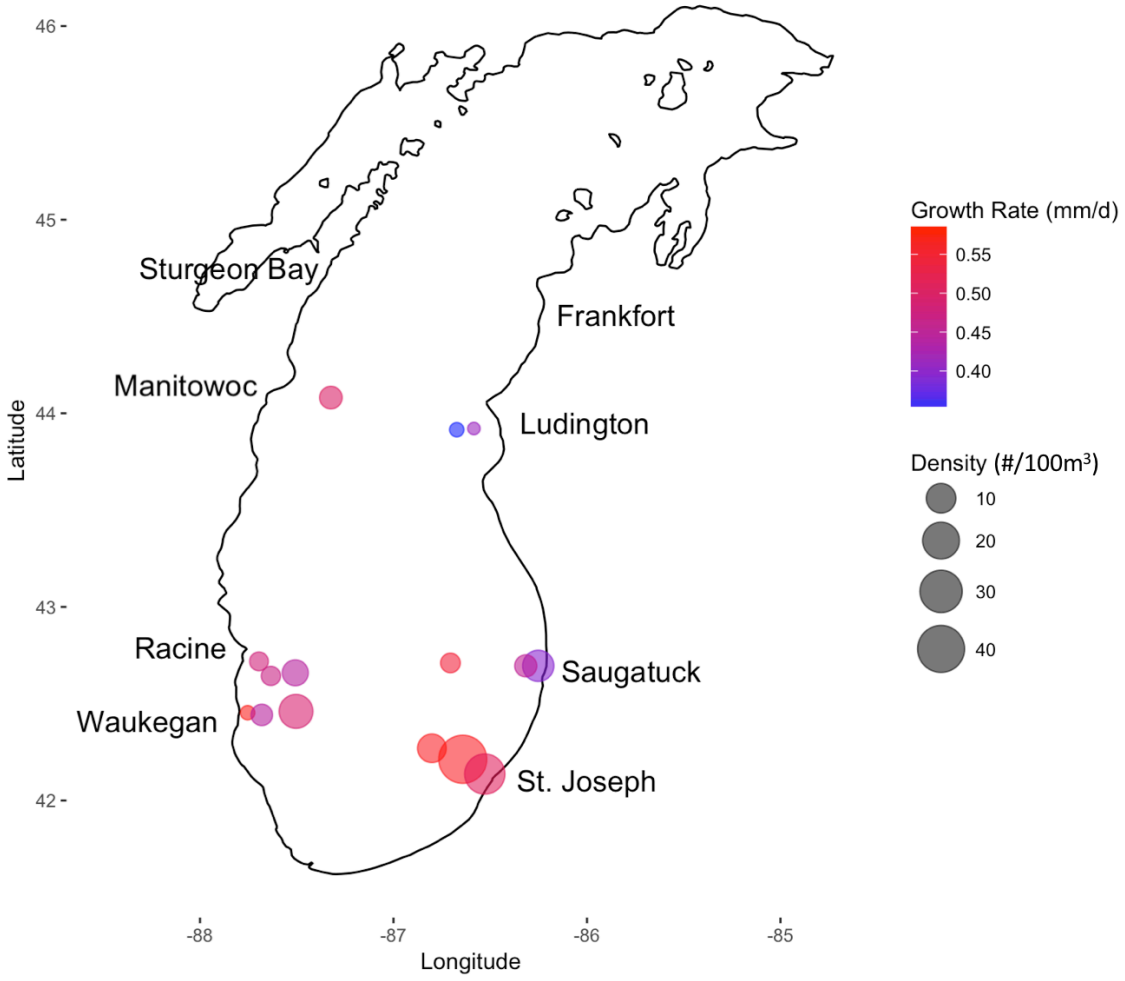

Figure 2: Larval Alewife average growth rates (circle color) and average densities (circle size) at each of our sampling locations from July 8-27, 2015 in Lake Michigan.

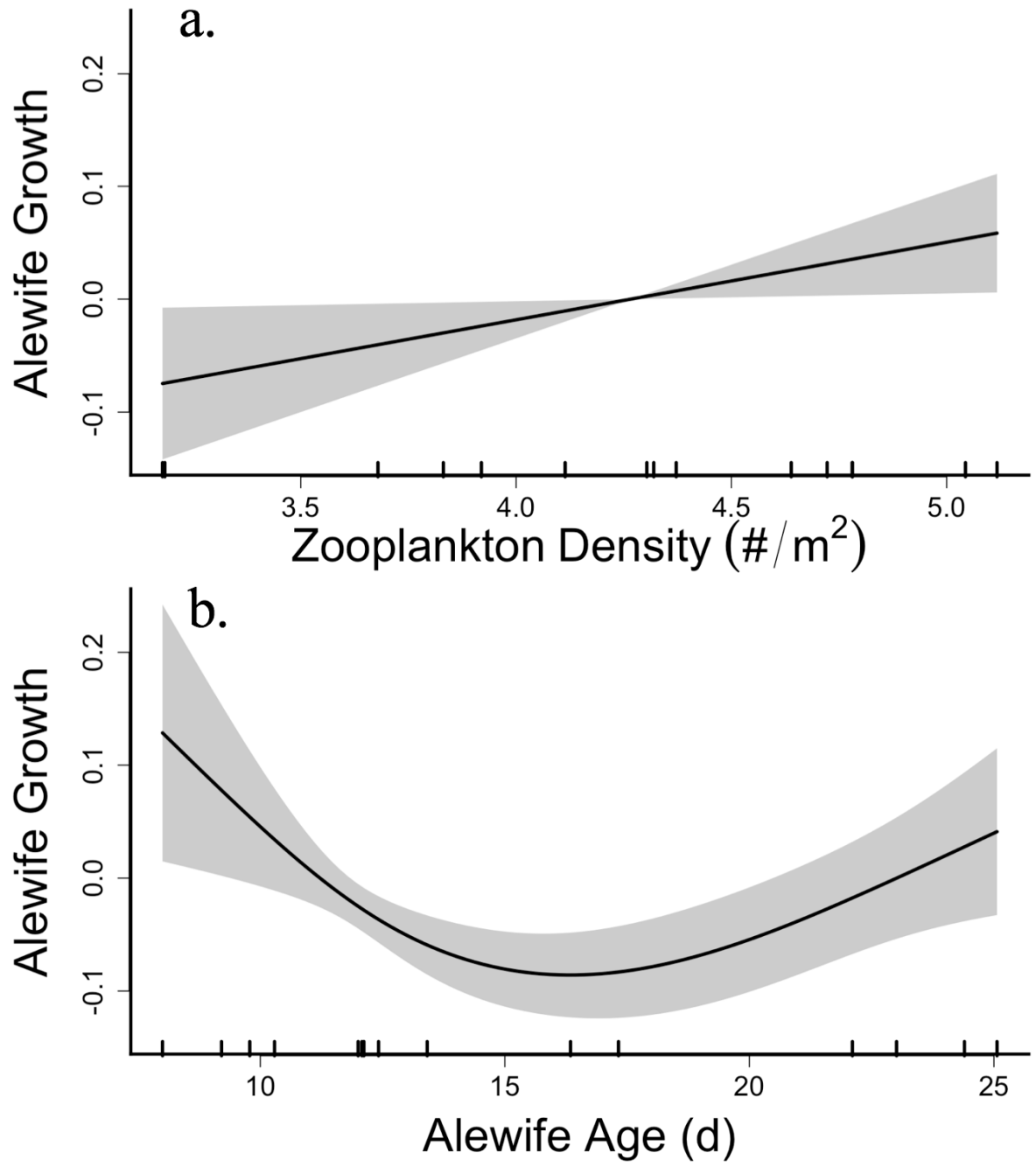

Figure 3: Predicted larval Alewife growth (mm/d) in Lake Michigan between July 8-27, 2015 as a function of log10 transformed zooplankton density (#/m^2, panel a) and Alewife age (days, panel b) using a generalized additive model. In each panel, the shaded area represents the 95% confidence interval. Dashes above the x-axis represent the distribution of data points.

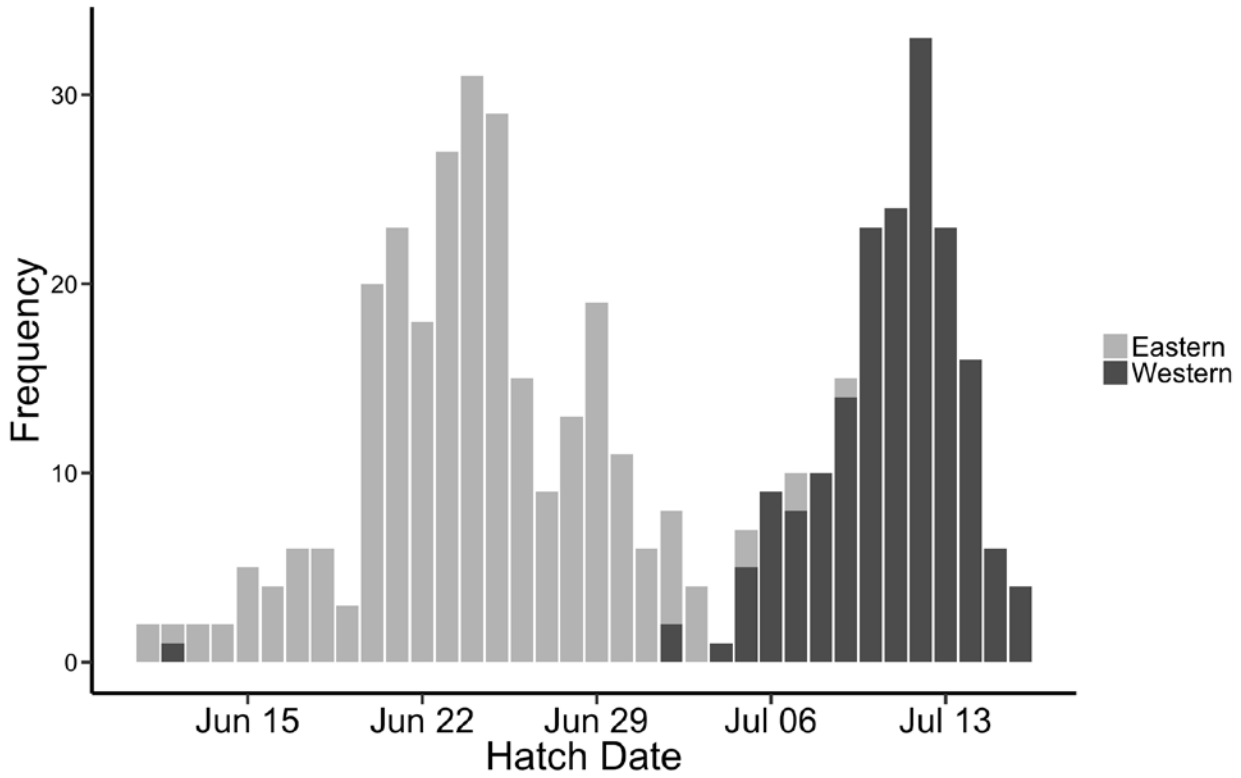

Figure 4: Frequency distribution of 2015 Alewife hatch date (day of capture – estimated age) for a subset of larvae randomly selected for otolith age processing. Frankfort, Ludington, Saugatuck, and St. Joseph were pooled under eastern Lake Michigan (gray), and Waukegan, Racine, Manitowoc, and Sturgeon Bay were pooled under western Lake Michigan (black).

Supplementary Table 1.

Mean diet percentage (by count) and frequency of occurrence for prey taxa identified in larval alewife (n=104, table A) and bloater (n = 68, table B) sampled in Lake Michigan across 24 sites between July 8-27, 2015. On average, larval Alewife were sampled at 0049 hours, whereas larval Bloater were sampled at 0154 hours.

Taxon	% in the diet	Frequency of occurrence
A) Alewife		
Dreissenid veliger	39.2	55.7
Unidentified copepod	27.8	47.1
Cyclopoid copepodite	13.3	24.0
Calanoid copepodite	5.5	9.6
Leptodiaptomus minutus	4.5	5.7
Bosmina spp.	3.2	3.8
Polyphemus pediculus	1.9	1.9
Diacyclops thomasi	1.9	1.9
Copepod nauplii	1.0	1.0
Conochilus spp.	0.7	1.0
Leptodiaptomus ashlandi	0.6	2.9
Leptodiaptomus sicilis	0.5	1.0
B) Bloater		
Unidentified copepod	51.3	91.1
Cyclopoid copepodite	28.1	44.1
Dreissenid veliger	9.2	35.3

Calanoid copepodite	4.5	25.0
Diacyclops thomasi	2.3	11.8
Bosmina spp.	2.1	16.2
Polyphemus pediculus	1.5	8.8
Leptodora kindtii	0.8	2.9
Leptodiaptomus minutus	0.2	2.9
Keratella spp.	0.1	1.5
Bythotrephes longimanus (1^{st} instar)	<0.01	1.5
Epischura lacustris	<0.01	1.5