NEARSHORE ZOOPLANKTON COMMUNITIES OF LAKE MICHIGAN AND IMPLICATIONS FOR INVASIBILITY BY ASIAN CARP

BY

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THESIS

Submitted in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources and Environmental Sciences in the Graduate College of the University of Illinois at Urbana-Champaign, 2017

Urbana, Illinois

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ABSTRACT

Recent, dramatic shifts have occurred within zooplankton community structure in Lake Michigan. Such changes could alter the ability of invasive species, such as Asian carp, to establish self-sustaining populations. Without knowledge of spatial characteristics of zooplankton communities, it is difficult to assess the potential for Asian carp establishment. We sought to better describe spatial heterogeneity of zooplankton community structure by surveying both large and small-bodied zooplankton at 25 nearshore embayment and open water locations around the lake for two years. With this geographically diverse dataset, we explored variation in zooplankton community structure and attempted to predict bighead and silver carp growth across large spatial scales. Our results indicate decreased total zooplankton biomass in nearshore open-water locations relative to embayments. Higher relative biomass of larger-bodied zooplankton was linked to embayments with higher primary production such as Green Bay and Michigan drowned river mouth lakes, while smaller-bodied zooplankton constituted the majority of biomass in open water and harbor locations with lower primary production. These biomass estimates, in turn, affected predicted Asian carp growth rates. Negative growth was predicted across most locations, with the exception of several drowned river mouth lakes along the Michigan coast and regions of Green Bay, Wisconsin. We suggest that recent declines in primary production related to establishment of quagga mussels throughout the basin and decreased nutrient loading in addition to increased prevalence of predatory zooplankton has led to a decrease in zooplankton biomass, shifted structure towards dominance by smaller-bodied taxa, and created a less hospitable environment for Asian carp survival through most nearshore regions of the lake.
ACKNOWLEDGEMENTS

The Illinois Department of Natural Resources funded this project; grants number IDNR RC09-13FWUIC and 375 IDNR 2013-06758. We would like to thank the technicians at the Lake Michigan Biological Station who assisted in collecting samples in Illinois and Wisconsin, the Forsythe lab at the University of Wisconsin- Green Bay for collecting the Green Bay samples, and the Ruetz lab at Grand Valley State University for collecting the Michigan samples. Special thanks to Kacie Jonasen, Rachel Moss, Rebecca Rogers, and Heather Sundstrom for assisting in zooplankton counting and identification. Diane Wudi and Jennifer Rimkus at LMBS provided administrative support.
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INTRODUCTION

Over the past several decades, significant shifts have occurred within the Lake Michigan planktonic food web (Madenjian et al., 2015; Vanderploeg et al., 2015). In particular, nutrient loading reductions compounded with the spread of invasive dreissenid mussels have resulted in bottom-up regulation of zooplankton populations and shifts towards dominance by species associated with lower levels of primary production (Barbiero and Warren, 2011; Bunnell et al., 2014; Driscoll et al., 2015). Additionally, the introduction of predatory cladocerans and increases in native, predatory copepod abundance are having top-down effects attributed to declines in taxa they preferentially prey upon, such as the historically important fish prey, *Daphnia spp.* (Barbiero et al., 2012, 2009; Engevold et al., 2015; Vanderploeg et al., 2012). Ultimately, fishes and invertebrates appear to have shifted consumption patterns from pelagic to alternative nearshore sources for energy subsidies, where primary production rates are higher (Brothers et al., 2016; Turschak et al., 2014).

This shift towards increased utilization of nearshore regions for energy subsidies has spurred interest in understanding zooplankton community structures found there and how they might affect fish recruitment. Despite this, zooplankton communities in sheltered nearshore locations are studied far less frequently than in open water regions and there is no available long-term dataset for nearshore zooplankton biomass (Madenjian et al., 2015). Additionally, environmental conditions and biological communities can vary drastically between harbors, river mouths, or nearshore waters and offshore locations, making it difficult to accurately estimate nearshore zooplankton community structure through extrapolation from offshore samples (Hall et al., 2003; Yurista et al., 2015). Excluding these regions from long-term surveys has made it
difficult to understand how recent shifts in zooplankton community dynamics might affect Lake Michigan’s food web.

Furthermore, gear related biases are a common issue due to the large range of zooplankton sizes in aquatic systems. Despite studies indicating that a significant portion of rotifer, veliger, and nauplii biomass can be missed if samples are filtered through mesh size > 20 μm, 64 μm has been the traditional standard mesh sized used in Great Lakes zooplankton assessments (Bottrell et al., 1976; Chick et al., 2010; Creque et al., 2017; Likens and Gilbert, 1970). The potential for underestimating zooplankton biomass and thus their contribution to higher trophic levels is a concern. Therefore, a sampling method referred to as the dual method has been developed where larger-bodied and smaller-bodied zooplankton are collected with different sampling gear to ensure more accurate collection of all taxa (Creque et al., 2017). Most significantly, a geographically diverse study of Lake Michigan’s nearshore zooplankton community has not been conducted using smaller mesh size sampling methods.

The lack of accurate nearshore zooplankton community documentation is particularly problematic when trying to predict the establishment risk of two well-known aquatic invasive species, silver carp (Hypophthalmichthys molitrix) and bighead carp (H. nobilis), collectively referred to here as Asian carp. While movement of Asian carp up the Illinois River is stymied by electric barriers, the possibility of their introduction, whether accidental or deliberate, to Lake Michigan or elsewhere in the Great Lakes basin is still of great concern (Pegg and Chick, 2001; Stokstad, 2010). These filter-feeders consume large amounts of zooplankton and phytoplankton and might alter Lake Michigan’s zooplankton structure, impacting native fish as has been seen in water bodies they have already invaded (Irons et al., 2007; Kolar et al., 2007; Sass et al., 2014). Additionally, Asian carp diets tend to be dominated by smaller organisms; bighead carp can filter
organisms 17-3,000 μm in length and silver carp can capture even smaller particles down to 4.5-10 μm (Cremer and Smitherman, 1980; Sampson et al., 2009; Xie, 1999). Dreissenid veligers and rotifers are common in alewife (Alosa pseudoharengus) and larval yellow perch (Perca flavescans) diets in Lake Michigan (Creque and Czesny, 2012; Fulford et al., 2006; Withers et al., 2015), but these fish are not as effective at filtering out such small organisms (Macneill and Brandt, 1990; Mills et al., 1995), potentially creating an exploitable niche for Asian carp and the potential for competition between larval fish, planktivorous fish, and Asian carp. Therefore, it is important to accurately estimate abundances of both large and small zooplankton taxa as researchers focus on predicting the potential impact of Asian carp in the Laurentian Great Lakes.

One method being used to predict bighead and silver carp establishment likelihood in uninvaded waters has been through bioenergetics modeling (Anderson et al., 2015; Cooke and Hill, 2010). Cooke and Hill (2010) summarized that limited plankton resources in open water regions would likely hinder bighead and silver carp establishment but that some regions of the lake could still support positive growth. This modeling exercise created a starting point, but there were several reasons we wished to revisit the Cooke and Hill (2010) bioenergetics model. First, the phytoplankton and zooplankton biomass values used for the Cooke and Hill (2010) model were sourced from samples collected in the early 2000’s- before the extensive shifts in the plankton community structure- and from limited locations in Lake Michigan. We wanted to update the model with current plankton biomasses and greatly increase the geographic sampling scope throughout the lake. Second, we wanted to focus on applying the model to nearshore regions. Because fish in the lake are increasingly relying on nearshore regions for energy subsidies, it seems likely that Asian carp would do the same. Nearshore regions are also more heavily used by boaters, making it important to understand where these fish, especially silver
carp, would likely establish due to their propensity to jump from the water when startled. Third, we believe the amount of zooplankton available for consumption has typically been underestimated through the gear related sampling biases mentioned earlier. Because Asian carp are especially suited to exploit smaller organisms, we wanted to employ a dual sampling approach to ensure accurate collection of both large and small-bodied zooplankton (Creque et al., 2017).

Our objectives for this study were three-fold:

1) Assess variation in micro- and macro-zooplankton communities among harbors, drowned river mouth lakes, and non-embayment nearshore locations around Lake Michigan,

2) Investigate whether using data from the dual sampling method substantially increases the estimated zooplankton biomass available to Asian carp, their predicted growth rates, and overall invasibility, and

3) Explore the potential for Asian carp to survive at sampled locations through bioenergetics modeling simulations.

We predicted zooplankton assemblages and subsequently Asian carp growth estimates would be higher when more accurate sampling methods were used, that zooplankton structure as well as predicted growth would vary among geographical regions, and that the heterogeneous nature of these nearshore regions would lead to different predicted bioenergetics outcomes within relatively small geographic scales.
METHODS

Sample Collection

We wanted to examine both specific habitat types (harbors, drowned river mouth lakes, and open water), and specific locations (e.g. Green Bay). Because these habitats were not distributed across all regions of the lake, we created six zones based on geography and habitat type. Wisconsin sampling locations included four Green Bay (GB), four harbor (WI-H), and two open water (WI-O); Illinois locations included four harbor (IL-H) and three open water (IL-O), and Michigan locations included eight drowned river mouth lakes (MI-DR) (Figure 1). Samples were collected from one to three sites at each location, with more sites at locations with a larger sampling area. Open water samples were collected at sites along a nearshore to offshore transect ranging in depth from 3 to 35 meters. Data from all sites at each open water location were averaged before final analyses, because we found no difference in zooplankton biomass with water depth (ANOVA F=0.19, df=2, p=0.82). Sites in other locations were positioned to cover a broad sampling area and were also averaged by location. We did this because environmental heterogeneity in nearshore regions as well as patchy distributions and high turnover rates characteristic of zooplankton populations can increase the variability encountered while sampling (Omori and Hamner, 1982). By taking samples from multiple sites at each location, we were able to account for variation within locations and better discern consistent differences among zones. Locations were sampled each month for two years, June through September 2013 and 2014, for a total of 453 paired micro and macrozooplankton samples.

We used a dual method approach to sample the entire zooplankton community. Macrozooplankton (copepods and cladocerans) were collected with a conical 64-μm mesh net vertical tow down to 0.5m off the bottom and steadily pulled through the water column (David et
Microzooplankton (rotifers, copepod nauplii, dreissenid mussel veligers) were collected with a 2.5 L capacity Van Dorn from each meter in the water column down to 0.5-1.0 m from the bottom (Creque et al., 2017; Likens and Gilbert, 1970). The collected water was filtered gently through a 20-μm mesh sieve and the aggregated organisms were rinsed into a sample bottle. Samples from both methods were narcotized with Alka-Seltzer tablets and fixed in a 4% sucrose-buffered formalin preservative with Rose Bengal stain to aid in identification.

**Sample Analysis**

Macrozooplankton samples were counted by examining three 5-mL subsamples from adjusted volumes under a dissecting microscope at 25x magnification with a Ward counting wheel. Copepods were identified to order and cladocerans to genus (*Daphnia* to spp.). Up to 30 measurements for each macrozooplankton taxa were taken from each sample using a digitizing tablet and ImageJ software (Rasband, W.S., Image J, U.S. National Institutes of Health, Bethesda, MD, USA, [http://imagej.nih.gov/ij/](http://imagej.nih.gov/ij/)).

Rotifers, copepod nauplii, and *Dreissena* veligers from microzooplankton samples were counted and identified from known-volume subsamples using a compound microscope at 100x magnification and 1-mL Sedgewick-Rafter counting cells. Subsamples were counted in their entirety and subsequent subsamples were enumerated until a minimum of 400 individuals were counted after a complete subsample. Rotifers were identified to genus when possible (Grothe and Grothe, 1977; Stemberger, 1979; Wallace and Snell, 2010). We obtained a mean total length for 30 individuals of each taxon using a 100x magnification microscope equipped with digital imaging software in ImageJ.
Dry weight biomass estimates (μg) were calculated for all measured organisms using appropriate length-weight regressions from various sources and averaged by taxa (Bottrell et al., 1976; Culver et al., 1985; Dumont et al., 1975; Sprung, 1993). A few rare taxa did not have formulas, in which case we used the average biomass of a similarly sized species.

Zooplankton community structure analysis

We used analysis of similarity (ANOSIM) to examine patterns in zooplankton community structure among zones, non-metric multidimensional scaling (nMDS) to visualize these patterns, and examined similarity percentages (SIMPER) to determine the taxa influencing patterns the most. We analyzed multivariate data using routines found in PRIMER-E v 6.1.16 multivariate software. Taxa comprising less than 0.001% of the total biomass were removed from community assemblage analysis to reduce the noise that taxa found in only a few samples might add (McCune and Grace, 2002). After comparing the effects of several transformations using dominance plots, a square root transformation was determined to be the best method for decreasing the influence of a few dominant taxa without removing all effects of abundance. A one-way ANOSIM was used to examine the effect of zone on community structure. Because we were examining a total of 15 pairwise comparisons, we applied a Bonferroni adjustment to a starting significance level of 0.05. With this correction, only p-values ≤ 0.003 are considered significant. When significant differences were found, we used the pairwise test statistic (R) to determine the degree to which the assemblages differed. An R value of 0 indicates complete similarity of community structure, whereas a value of 1 indicates completely different structure (Clarke and Gorley, 2006). When structure has a high degree of overlap, a negative R-value can sometimes be returned. Comparisons with R values ≤ 0.25 were considered to have species assemblages that overlap considerably whereas comparisons > 0.5 were considered highly
distinct (Creque and Czesny, 2012). A Bray-Curtis similarity matrix was used for ANOSIM and nMDS plots. Discriminating species contributing >10% to the observed dissimilarity in structure between zones as determined with SIMPER were layered on nMDS ordinations as bubble plots to display patterns in their biomass.

A mixed effects model was created in RStudio to examine the effect of location, zone, year, and month on total zooplankton biomass, accounting for heterogeneous zone variance (R Core Team, 2014). We did a post-hoc comparison for differences in total zooplankton biomass among zones using Tukey’s HSD.

**Bioenergetics parameter estimation**

Bioenergetics modeling for silver and bighead carp was done using Fish Bioenergetics 4.0 (Shiny by RStudio). The bioenergetics models for bighead and silver carp already provided most parameter input values, via Cooke and Hill (2010). The updated input components we provided were water temperature (°C), total consumption, and diet proportions.

Lake surface temperature (LST) was recorded in situ using a temperature meter (YSI Pro 20) for approximately 60 percent of samples. For samples were a temperature meter was not available, we estimated LST using satellite-derived data collected by the Moderate Resolution Imaging Spectrometer (MODIS) and provided by Michigan Tech Research Institute (MTRI) (www.greatlakesremotesensing.org). LST was derived from images taken during a night overpass at 250-meter resolution and collected at the 4 µm wavelength. These temperatures have a verified accuracy within 0.5 °C (www.greatlakesremotesensing.org). GPS coordinates logged during sample collection were pinpointed as 1 km² pixels on each map layer and the LST values for each sampling event were recorded. We used the GPS coordinates logged during sample collection to pinpoint the 1 km² pixels on each map layer and recorded the LST values for each
sampling event. Images were not recorded for every day and cloud cover often obscured
sampling sites, so the images were used from the closest date available. This was a
straightforward procedure for open water locations in GB, IL-O, and WI-O, because pixels were
almost always present at the sampling location, but the image resolution was not fine enough to
pick up water in harbors and drowned river mouths lakes. For such locations, we used values
from the closest pixel outside the harbor or river mouth.

Chlorophyll a levels were estimated using satellite images from the same MODIS data
source as LST data. MTRI offers lake-wide raster maps at a resolution of 1 km$^2$ of estimated
chlorophyll a biomass created using hydro-optical models, allowing us to pinpoint chlorophyll a
concentrations at each sampled location. As with LST, the resolution did not allow for
measurements in harbor and drowned river mouth lakes and values were recorded from the
closest possible location outside the embayment. Chlorophyll a estimates for such locations may
be conservative relative to actual levels within embayment, with the possible ramification of
conservative carp growth estimates. We converted chlorophyll a to wet mass following the
procedure in Cooke and Hill (2010) with a ratio of chlorophyll a to dry mass of 100, and a ratio
of wet to dry mass of 2.5. Zooplankton was also converted from dry to wet mass for analysis at a
ratio of 1:10. Parameters for predator energy density for bighead and silver carp (5442 J g$^{-1}$) were
obtained from Cooke & Hill (2010), as was zooplankton (2512 J g$^{-1}$) and phytoplankton (2460 J
g$^{-1}$) prey energy density. The model assumed non-swimming fish, with 100% assimilation
efficiency and filtration rates of 191 L d$^{-1}$ for 10 g fish and 9502 L d$^{-1}$ for 2400 g fish.

Bioenergetics modeling analysis

We first ran simulations to explore how more accurate estimates of microzooplankton
biomass affected Asian carp growth predictions. Creque et al. (2017) established relationships
between densities of various microzooplankton taxa collected with two sampling methods - the less accurate but more commonly used net-only approach and the more accurate dual method approach. These relationships can be used to convert densities of microzooplankton collected with the net-only approach to density estimates using the more accurate dual approach. Cooke and Hill (2010) used net-only microzooplankton densities for their model predictions, so to examine how using the dual approach sampling method could have impacted their zooplankton biomass estimates and predictions of Asian carp growth, we applied the relationships for rotifers, veligers, and nauplii from Creque et al. (2017) to the zooplankton biomass estimates used by Cooke and Hill (2010). We then re-ran their bioenergetics model with the altered biomass values to compare how predictions differed when biomasses obtained with the regressions were used.

We reran the bioenergetics model with these converted values to see how estimated Asian carp growth changed. We also used our 2013-2014 collected microzooplankton estimates from samples filtered through both the 63 μm mesh net and the 20 μm mesh to compare how biomass estimates from different sampling methods affected bioenergetics predictions. Statistically significant differences in total biomass gain/loss estimates among zones were determined using a one-way ANOVA with Bonferroni adjustment for multiple comparisons. We also reran the bioenergetics simulations for the six locations with the greatest zooplankton biomass, replacing the more accurate dual approach zooplankton biomass with net-only zooplankton biomass estimates to see how model results differed.

Finally, to explore how predicted growth varied geographically around Lake Michigan, we averaged zooplankton biomass, phytoplankton biomass, and temperature by zone to run the model. We then averaged the samples only by location and reran the model to see how changes
in spatial resolution affected predicted growth. Results were displayed using ERSI ArcGIS software.
RESULTS

Zooplankton community structure

In general, zooplankton biomass was higher in MI-DR and GB than in harbors and open water zones (Table 1). Specifically, cladocerans from the families Bosminidae, Daphnidae, and Cercopagidae followed this trend, as well as adult calanoid and cyclopoid copepods and copepod nauplii (Figure 2). Three rotifer genera - Asplanchna, Synchaeta, and Polyarthra - accounted for >75% of the average rotifer biomass in each zone. Of these taxa, Polyarthra was by far the dominant genus, accounting for at least 50% of rotifer biomass in all zones (Figure 3). Only Synchaeta had lower biomass in GB and MI-DR relative to harbors and open water zones.

Dreissenid mussel veligers also displayed different biomass patterns than most taxa, having highest biomass in IL-H and IL-O (Table 1).

We found substantial variation in zooplankton community structure among our zones. One-way ANOSIM of zooplankton community structure among zones revealed most comparisons to be significantly different, with the exception of MI-DR vs. GB, IL-H vs. WI-O, and WI-H vs. WI-O (Table 2). Of the significant comparisons, R statistics varied from 0.132 to 0.74, indicating a wide range in the degree of structure dissimilarity. SIMPER identified five taxa individually contributing >10% of the observed dissimilarity in structure among zones - Bosmina longirostris (hereafter referred to as Bosmina), copepod nauplii, adult cyclopoid copepods, Dreissena veligers, and the rotifer Polyarthra spp. (Figure 4). On average, these 5 taxa together accounted for 46% of the total observed dissimilarity between zones. Bosmina and adult cyclooids, both macrozooplankton, showed the highest biomass in GB and MI-DR and strong declines in all other zones. Copepod nauplii and Polyarthra spp. also had the highest biomass in GB and MI-DR, but their biomasses did not decrease to the same extent as Bosmina.
and cyclopoids in the open water and harbor zones. *Dreissena* veligers displayed biomass patterns distinct from the other four taxa, having the highest biomass in IL-O and IL-H and lowest biomass in MI-DR.

Total zooplankton dry biomass (microzooplankton plus macrozooplankton µg L\(^{-1}\)) differed significantly between zones (F=3.77, df=19, p=0.01), but there was no significant effect of month or year. Tukey contrasts by zone found significant differences in biomass between MI-DR vs. IL-O (p=0.02), MI-DR vs. WI-O (p=0.05) and MI-DR vs. WI-H (p=0.01). Total zooplankton biomass corresponded with levels of chlorophyll \(a\), both being higher in MI-DR and GB. In areas where total zooplankton biomass was higher, macrozooplankton comprised larger proportions of the biomass than microzooplankton (Figure 5).

**Bioenergetics modelling**

By applying microzooplankton regressions to the original zooplankton biomasses used in the Cooke & Hill (2010) bioenergetics model, we were able to estimate how total zooplankton biomass estimates might have differed had a more accurate sampling method been used. As expected, total zooplankton biomass increased anywhere from ~ 50 % to > 300 %. These increased zooplankton biomasses resulted in only modest decreases in the amount of Asian carp biomass lost compared to previous estimates in the nearshore dataset from Illinois, but biomass gain increased by almost 100% in Green Bay during the month of June (Table 3).

Our 2013-2014 collected zooplankton biomass estimates also varied depending on the sampling method used, with the more accurate estimates yielding significantly higher total zooplankton biomass across all zones (p<0.001) (Figure 6). This was especially true in open water locations, where microzooplankton made up a larger proportion of the zooplankton community. For the six locations where positive growth was predicted for 10 g or 2400g bighead
or silver carp using the dual approach, estimated growth decreased if only less accurate zooplankton biomass estimates were used (Table 4, Figure 7). In several instances, zooplankton biomass decreases from the less accurate method changed predicted Asian carp growth from positive to negative.

When we applied the more accurate zooplankton estimates across all zones, the resulted predicted biomass change for both bighead and silver carp was mostly positive for GB and MI-DR and negative for all other zones (Table 5, Figures 8-11). Within each zone, there was variation among locations. Specifically, in GB, growth decreased with increasing distance from the Fox River mouth. Within MI-DR locations, Macatawa had the greatest predicted percent biomass increase, followed by Spring Lake, Pentwater, and White Lake. All growth predictions for Asian carp in IL-H, WI-H, IL-O, and WI-O locations were negative. Silver carp growth reductions were lower than bighead carp in most locations. Additionally, growth predictions for 10 g silver and bighead carp were affected more strongly by changes in plankton concentrations than for 2400 g fish.
DISCUSSION

There were several main findings of this study. First, microzooplankton comprised a large proportion of total zooplankton biomass and made up the majority of biomass in all zones except MI-DR. Additionally, the use of more accurate sampling methods significantly increased estimated microzooplankton biomass, which in turn led to higher predicted Asian carp growth. Therefore, we recommend employing sampling methods to ensure more accurate microzooplankton collection when exploring zooplankton community structure and when estimating food available to fish able to exploit smaller organisms, such as Asian carp. Second, zooplankton biomass and community structure displayed a high degree of heterogeneity among locations. This makes generalizing findings to large regions difficult, but with a robust sampling design, we were able to identify broad patterns in zooplankton biomass and structure such as higher total biomass in GB and MI-DR and higher proportions of macrozooplankton in those zones. Finally, while our bioenergetics modelling exercises predicted negative growth for Asian carp in open water nearshore and harbor locations along the coast of Illinois and Wisconsin, certain locations in more productive regions such as GB and MI-DR predicted positive growth. We hope that by highlighting a method to identify areas where positive growth is predicted, managers can create effective strategies to pinpoint high-risk regions and quickly and effectively eradicate these fish, should they be introduced to the lake.

Zooplankton community structure

It was not unexpected that we found greater total zooplankton biomass in MI-DR and GB, as these zones had higher levels of primary production, but the distribution breakdown of different taxa among zones revealed interesting patterns. One of the most striking findings was the large contribution of microzooplankton to the overall zooplankton biomass in each zone.
Even at their lowest proportion in MI-DR, microzooplankton contributed on average 40% of total zooplankton biomass. The highest microzooplankton biomass percentage was in WI-H, where they contributed 83% of the biomass. This highlights the importance of obtaining the more accurate estimates of microzooplankton abundance (e.g., from the dual method) to better understand the makeup of the entire zooplankton community.

The dominance of smaller-bodied taxa in open water is consistent with findings from recent studies and could be due to indirect effects of reduced nutrient loading in open waters as well as the removal of organic matter by dreissenid mussels, reducing energy transfer from land to offshore zones (Hecky et al., 2004; Kelly et al., 2015). These findings have implications for fish recruitment. Larval fish are unable to overcome current velocities before sufficient fin development and rely on encountering prey patches (Beletsky et al., 2007; Höök et al., 2006). An overall reduction in zooplankton abundance and shift to smaller-bodied species may lower larval fish-zooplankton encounter rates in open waters and lead to higher mortality during early life stages (Dettmers et al., 2003). Higher plankton biomass and a greater proportion of large-bodied macrozooplankton in zones such as GB, MI-DR, and to some extent harbors may provide a greater quantity and higher quality food source for larval and juvenile fish and further increase the importance of these zones as nursery habitat (Weber et al., 2015).

Other observed patterns within various macrozooplankton and microzooplankton taxonomic groups were surprising. For example, the herbivorous cladocerans *Bosmina* and *Daphnia* spp. decreased in biomass more abruptly from MI-DR and GB to harbor and open water zones relative to declines in other taxa. Other studies have found herbivorous cladocerans to be generally superior competitors to rotifers for limited resources (Conde-Porcuna et al., 1994; Gilbert, 1985). Therefore, we would expect to see greater relative *Bosmina* and *Daphnia* spp.
biomass in zones such as IL-H, WI-H, IL-O and WI-O, where primary production is more limiting. The general disappearance of *Bosmina* and *Daphnia* spp. in less productive zones indicates factors such as increased predation pressure from predatory copepods and invasive cladocerans may be limiting *Bosmina* and *Daphnia* spp. biomass in open water regions of Lake Michigan (Vanderploeg et al., 2012). This in turn may be contributing to the shift in dominance towards small-bodied microzooplankton we observed in open water and harbor locations (Brooks and Dodson, 1965).

Observed biomasses of the invasive cladocerans *Bythotrephes longimanus* and *Cercopagis pengoi* in open water zones were lower than expected, as they have been documented at much higher biomasses than we recorded, some as high as 3 mg/m³ (Pothoven and Fahnenstiel, 2015; Vanderploeg et al., 2012; Witt et al., 2005). However, such studies typically found greater densities these two species further offshore and highest densities later in the year, beyond our sampling time frame.

The relatively high chydorid biomasses observed in IL-H warrant further study. Because chydorids are often associated with littoral or benthic habitats and occasionally occurring at high local abundances (Debastiani-Junior et al., 2016; Paterson, 1993; Tremel et al., 2000), we felt the high biomasses observed in IL-H samples were reasonable. The locations with high chydorid biomass were also areas with high aquatic vegetation presence (Pers. Observation). Plankton net tows were conducted to avoid collection of macrophytes, but disturbed plants in densely vegetated areas may have caused chydorids to leave the habitat. Increased water clarity attributed to dreissenid mussels and subsequent increases in submerged aquatic vegetation and benthic algae may be increasing the structural habitat available to chydorids and other littoral zooplankton (Turschak et al., 2014; Zhu et al., 2006). If water clarity remains high and promotes
submerged aquatic vegetation growth, chyordorid densities may increase around the lake.

Chyordorids have also been found in high abundance in stomach contents of nearshore fishes (Happel et al., 2015), indicating that the importance of chyordorids species in the food web may continue to grow as fish increase reliance on nearshore energy sources.

Observed biomass patterns for copepods suggest different factors may be impacting the three orders identified in our samples. Harpacticoida had highest biomasses in IL-H and WI-H. The prevalence of submerged aquatic vegetation in harbors, and in turn decaying plant matter, may increase Harpacticoid habitat and food availability, fitting with their life history characteristics of being predominately benthic detritus feeders (Hudson et al., 1998). Cyclopoids were another taxa identified by SIMPER as contributing to community structure differences among zones and had highest biomass in MI-DR and GB, but relatively unchanged biomass in open water and harbor zones. Calanoid biomass, on the other hand, actually increased in relative biomass in harbor and open water zones. Fish have been shown to prey preferentially upon cyclopoids relative to calanoids (Hurlbert and Mulla, 1981; Nassal et al., 1998), leading to several hypotheses, such as an increase in piscivorous predation pressure in open waters or that calanoids are better suited to forage at low plankton densities than cyclopoids. We did not identify calanoids to genus, but other studies have documented an increase in the calanoid copepods *Leptodiaptomus sicilis*, *Epishura lacustris*, and *Limnocalanus macrurus* in Lake Michigan post quagga-expansion (Barbiero et al., 2009; Vanderploeg et al., 2012), which may have contributed to the increase in calanoid dominance observed in open water zones. Copepod nauplii also contributed substantially to observed patterns in structure as identified with SIMPER. We would expect the ratio of adult nauplii to remain relatively constant among zones if predation pressure was the same for all zooplankton, but nauplii biomass did not decline to the
same extent as adult copepods in open water zones, supporting a shift towards heavy predation pressure on larger individuals in open water.

The six most abundant rotifer genera in our study—Asplanchna, Conochilus, Keratella, Polyarthra, Synchaeta and Trichocerca—were all found to vary in relative biomass by zone. Synchaeta made up a larger proportion of rotifer biomass in the zones with lower levels of chlorophyll a, supporting findings from other studies that some Synchaeta species are associated with oligotrophy (Stemberger, 1979). Conversely, Ascomorpha, Conochilus, Keratella, and Trichocerca appeared in greater proportions in GB and MI-DR, indicating they may be negatively impacted by lower primary production. Polyarthra did not appear to follow trends similar to other genera and was another taxa contributing greater than 10% to observed differences in zooplankton community structure. They constituted the highest rotifer biomass percentage in GB and IL-H but were found at significantly lower proportions in MI-DR, indicating they may not be affected by varying productivity levels to the same degree as other genera. These results are in contrast to Barbiero and Warren (2011), who recorded dramatic declines in Polyarthra dominance over the past several decades as the lake has shifted to a more oligotrophic state. Part of the difference in observed values may be due to differences in sampling methods. Barbiero and Warren (2011) used 64-μm conical mesh net for collection and Polyarthra has been found to be the rotifer genera underestimated to the greatest degree when using a mesh size larger than 20μm (Creque et al., 2017). This indicates that while Polyarthra abundances may be declining, they are still the dominant rotifer genus in the nearshore regions of the lake.

Veligers contributed up to 43% of the average zooplankton biomass across all zones and contributed greater than 10% to observed structural differences among zones, showing that they
are indeed a significant part of the zooplankton community. The zones with highest veliger biomass, IL-H and IL-O, were not the zones with the greatest total zooplankton or phytoplankton biomass, while the zone with greatest zooplankton biomass, MI-DR, had the lowest veliger biomass. Adult *Dreissena rostiformis bugensis* biomass is distributed relatively evenly throughout the open water nearshore regions in Lake Michigan (Nalepa et al., 2014), but environmental conditions in Michigan drowned river mouth lakes may not be as suitable to dreissenid establishment (Nelson et al., 2009). In the future, this may help locations in MI-DR retain relatively high levels of primary production and zooplankton biomass but would also provide enough plankton biomass to promote positive Asian carp growth.

**Bioenergetics modeling**

Applying regressions to the original Cooke and Hill (2010) zooplankton biomass estimates for nauplii, veligers, and rotifers allowed us to discover how more accurate biomass estimation could increase predicted Asian carp growth. We observed only a weak increase in predicted growth across both species and size classes for the southern basin, nearshore estimates, despite zooplankton biomass more than tripling for some months. On the other hand, in Green Bay, predicted growth increased by almost 100% in many cases. Before the expansion of quagga mussels, higher levels of phytoplankton and larger-bodied zooplankton likely made up a greater percentage of total plankton biomass (Fahnenstiel et al., 2010). Because of this, even large increases in microzooplankton biomass estimates did not greatly increase total plankton biomass in southern basin, nearshore waters, resulting in the modest predicted growth increases.

We also found higher total zooplankton biomass using more accurate estimates in all zones in the 2013-2014 dataset. As most zooplankton are currently collected in the Great Lakes with methods that inadequately sample microzooplankton, researchers need to be aware of how
drastically zooplankton biomass estimates can be affected by inaccurate methods. Accurately sampling smaller taxa may also become more important in the future, as our results confirm other surveys in Lake Michigan, which have observed a shift to smaller-bodied zooplankton. By re-running the bioenergetics models using zooplankton biomasses estimated from both sampling approaches, we saw how growth estimates would have been much lower had we not implemented an approach to obtain more accurate zooplankton estimates. The switch in some modeled silver carp growth rates from positive to negative when less accurate estimates were used highlights how sampling method might impact how systems are viewed and lead to management decisions based on inaccurate biomass assessments.

Our bioenergetics results by zone and location concur with the Cooke and Hill (2010) estimates in open water locations using data collected in 2003- there is likely not enough zooplankton and phytoplankton biomass to support Asian carp growth. Additionally, we found a decrease in predicted Asian carp growth in more productive regions such as Green Bay compared to predictions from 2000-2001 data, indicating the lake is becoming less conducive to carp establishment overall. On the other hand, we have identified several drowned river mouth lakes that could support Asian carp growth. These locations were not considered by other assessments and show how relatively small areas of the lake may play an important role in determining the impact of Asian carp. As a caveat, there are dozens of river mouths and harbors that we did not sample during this study. We also did not collect open water samples from the eastern side of the lake. Because nearshore regions have such high levels of variability, we cannot make conclusions as to whether Asian carp are predicted to survive in those areas. We recommend managers in those regions evaluate the risk of Asian carp establishment through smaller-scale studies to help with surveillance prioritization.
By averaging zooplankton and phytoplankton biomass by location and further averaging locations by zone, we found that much of the heterogeneity in model predictions was lost. For example, GB predictions showed a distinct growth gradient; Locations closer to the Fox River mouth (Benderville and Shoemaker Point) predicted positive growth, while locations further out in the bay (Sturgeon Bay and Fish Creek) predicted negative growth. When averaged to zone, the single predicted value tells nothing of how plankton biomass is distributed in this large bay. MI-DR locations displayed even greater heterogeneity in plankton biomass distribution. For example, Kalamazoo and Macatawa were the closest sampled locations to one another, but displayed the greatest disparity in predicted growth estimates, likely due to different environmental factors influencing the watershed they are connected to. Unfortunately, we were unable to explore correlations between environmental conditions and zooplankton community structure because we did not have equipment to collect in situ environmental measurements and nearshore locations including drowned river mouths and harbors are poorly represented in available Great Lakes geospatial datasets such as the Great Lakes Aquatic Habitat Framework (GLAHF). Improved coverage of these increasingly important nearshore habitats should be a priority for Great Lakes environmental monitoring and reporting.

In addition to zooplankton and phytoplankton, Asian carp can feed on other sources such as detritus and cyanobacteria (Kolar et al., 2007; Xie, 2003) and researchers are working on methods to accurately account for these potential sources in bioenergetics models (Anderson et al., in press.). In the interest of making reasonable comparisons to the original Cooke and Hill (2010) model, we used the same energetic parameters, but steps are also being taken to provide more accurate parameter values for modeling, such as species-specific bighead and silver carp energy density (Anderson et al., 2015). Our model also did not account for energetic costs.
associated with movement or energy lost to prey not entirely digested. As such, the model is likely to overestimate growth in many cases. Asian carp, however, are effective at selecting habitat with higher resource levels (Calkins et al., 2012), so by assuming fish are stationary, we are disregarding the potential for them to seek out areas that might promote positive growth. It has also been proposed that by reducing metabolic expenditures in colder water, it is possible Asian carp could retain positive growth at lower plankton densities. Despite this, plankton biomass is also generally much lower in cooler months due to suppression of the late winter production pulse in Lake Michigan by Dreissenid mussels (Kerfoot et al., 2008; Vanderploeg et al., 2012). Cooler water temperatures in northern regions of the lake may facilitate growth, but overall, the lack of plankton in most of the lake overpowers any potential growth benefit cooler water temperatures might provide.

Another proposed potential boon to Asian carp growth has been the offshore deep chlorophyll layer (DCL), which could provide a higher concentration of plankton and cooler temperatures than surface water (Bramburger and Reavie, 2016), and lower Asian carp’s required metabolic expenditures. Because Asian carp are effective at selecting habitat with higher resources levels, this makes understanding the distribution of plankton in Lake Michigan necessary when predicting where they are likely to establish. However, recent chlorophyll $a$ estimates at the deep chlorophyll maximum of Lake Michigan were $2.26 \pm 0.20$ mg chl a m$^{-3}$ in early summer and $2.52 \pm 0.21$ mg chlorophyll $a$ m$^{-2}$ in late summer (Pothoven and Fahnenstiel, 2013), equating to 0.57 and 0.63 mg L$^{-1}$ phytoplankton wet mass, respectively. These values are within the range of estimated phytoplankton biomass in many harbor and open water sites (0.17-0.84 mg L$^{-1}$), which all predicted negative growth. Therefore, it is unlikely that the DCL in Lake Michigan would provide a refuge to Asian carp.
OVERALL SUMMARY

We designed this study to explore Lake Michigan zooplankton community structure across geographically distinct and previously understudied nearshore zones to provide a unique, standardized assessment of Lake Michigan’s zooplankton communities and to explore how biological variation influences Asian carp establishment risk. Microzooplankton prevalence in all locations highlights their potential as a food source and the need to tailor sampling methods to ensure their accurate collection, especially when estimating food availability for planktivorous fish, such as Asian carp. Furthermore, the observed differences in zooplankton community structure among zones and corresponding bioenergetics predictions illustrate the heterogeneous nature of Lake Michigan. We recommend researchers consider adjusting study methods and scope to account for this heterogeneity, especially the increased energetic importance of nearshore zones. The observed levels of zooplankton and phytoplankton biomass could hinder Asian carp establishment throughout much of the lake, although more productive conditions persist in Green Bay, drowned river mouth lakes along the Michigan coast and to a lesser extent in harbors. These nearshore zones could play an important role in determining Asian Carp’s ability to persist in Lake Michigan. By providing insight into how energy allocation varies in this dynamic system, we hope to assist managers in assessing locations with high establishment risk to quickly detect and eradicate Asian carp, should they be introduced to Lake Michigan.
Fig. 1. Map of zooplankton sampling locations in harbors, bays, drowned river mouth lakes, and open waters of Lake Michigan, grouped by six sampling zones: circle- GB, open square- WI-O, closed square- WI-H, open triangle- IL-O, closed triangle- IL-H, diamond- MI-DR. 1 to 3 samples collected from each location monthly, June- September, 2013-2014.
Table 1. Mean dry biomass (μg L⁻¹) of rotifer (to genus), cladoceran (to family), copepod (to order), and veliger (to genus) from samples collected in Lake Michigan using the dual sampling approach. Numbers in parentheses show standard error of the mean.
Fig. 2. Mean dry biomass (μg L$^{-1}$) (top) and relative biomass (bottom) of most common macrozooplankton (cladoceran to family, copepod to order) for nearshore zones in Lake Michigan. Copepod nauplii are excluded (see Fig. 5). Values represent averages across year (2013-2014), month (June-September), and location.
Fig. 3. Mean dry biomass (μg L\(^{-1}\)) of most common rotifer genera (top) and percent biomass (bottom) in zones of Lake Michigan. Values represent averages across year (2013-2014), month (June-September), and location.
Table 2. One-way ANOSIM comparison results by zone for differences in zooplankton structure. The p-value for each comparison is shown in the top half and the R statistic is shown in the bottom half. Sample statistic (Global R): 0.311. Significance level of sample statistic: 0.001. Using Bonferroni correction for multiple comparisons, only p-values ≤ 0.003 are deemed significant (significant values are bold in table). Number of permutations: 999

<table>
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<th>R statistic</th>
<th>MI-DR</th>
<th>GB</th>
<th>IL-H</th>
<th>IL-O</th>
<th>WI-H</th>
<th>WI-O</th>
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Table 2. One-way ANOSIM comparison results by zone for differences in zooplankton structure. The p-value for each comparison is shown in the top half and the R statistic is shown in the bottom half. Sample statistic (Global R): 0.311. Significance level of sample statistic: 0.001. Using Bonferroni correction for multiple comparisons, only p-values ≤ 0.003 are deemed significant (significant values are bold in table). Number of permutations: 999
Fig. 4. (a) Patterns in zooplankton biomass for six zones in Lake Michigan during 2013-2014 demonstrated with a non-metric multi-dimensional scaling (nMDS) plot. Symbols closer together have greater similarity than those that are further apart. Bubble plots (b-f) of select taxa (b) *Bosmina longirostris*, (c) Cyclopoida, (d) copepod nauplii, (e) *Polyarthra* spp., and (f) *Dreissena* spp. veliger. Bubble size approximates the biomass at a given location on a scale of 0-100.
Fig. 5. Dry biomass (μg L$^{-1}$) of major taxa (top) and relative biomass (bottom) in zones of Lake Michigan. Average chlorophyll $a$ biomass (μg L$^{-1}$) estimated from satellite-derived images with standard error bars. Values represent averages across year (2013-2014), month (June-September), and location.
<table>
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<th>Location</th>
<th>Original or regression</th>
<th>Water temp. (C)</th>
<th>Phyto. wet mass (mg/L)</th>
<th>Zoop. wet mass (mg/L)</th>
<th>Predicted % biomass gain or loss over 30 days</th>
<th>10 g BC</th>
<th>10 g SC</th>
<th>2400 g BC</th>
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<td>+15</td>
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Table 3. Comparison of original bioenergetics results from Cooke and Hill (2010) nearshore Lake Michigan and Green Bay locations (original) versus regressions from Creque et. Al (2017) applied to microzooplankton values (regression). The regression equations convert microzooplankton densities collected with inadequate sampling methods to densities estimated with more accurate methods.
**Fig. 6.** Average dry zooplankton biomass (µg L\(^{-1}\)) using a dual sampling approach (light grey) versus a conical 63 µm mesh net (dark grey). Error bars represent 95% confidence intervals. Comparisons between biomass estimates are significant at p < 0.001 for all zones.
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<th>Zone</th>
<th>Location</th>
<th>Sampling method</th>
<th>Phyto. wet mass (mg/L)</th>
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<th>Predicted % biomass gain or loss over 30 days</th>
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<td>Net-only</td>
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**Table 4.** Comparison of predicted percent biomass gain or loss over 30 days using zooplankton values collected with the dual method (macrozooplankton from 63μm mesh net and microzooplankton from whole water samples filtered through 20μm mesh) versus zooplankton values estimated from the net-only method (microzooplankton and macrozooplankton collected with 63 μm mesh net).
Fig. 7. Comparison of predicted biomass gain or loss over 30 days for (a) bighead carp and (b) silver carp at four MI-DR locations, using microzooplankton biomass from zooplankton collected with 63 μm mesh net (white) versus microzooplankton biomass filtered through 20 μm mesh net (black) for 10 g fish (triangle) and 2400 g fish (circle).
Table 5. Projected growth of non-swimming juvenile (10 g) and adult (2400 g) bighead carp (BC) and Silver Carp (SC) consuming phytoplankton (Phyto.) and zooplankton (Zoop.) for 30 days in different locations of Lake Michigan. Bold values are zone means.
Fig. 8. Values represent average predicted percent biomass increase or decrease over 30 days at each location for 10 g bighead carp calculated using bioenergetics modelling, averaged June-September, 2013-2014. Circle size represents relative percent change, green circles represent positive growth, and red represent negative.
Fig. 9. Values represent average predicted percent biomass increase or decrease over 30 days at each location for 10 g silver carp calculated using bioenergetics modelling, averaged June-September, 2013-2014. Circle size represents relative percent change, green circles represent positive growth, and red represent negative.
Fig. 10. Values represent average predicted percent biomass increase or decrease over 30 days at each location for 2400 g bighead carp calculated using bioenergetics modelling, averaged June-September, 2013-2014. Circle size represents relative percent change, green circles represent positive growth, and red represent negative.
**Fig. 11.** Values represent average predicted percent biomass increase or decrease over 30 days at each location for 2400 g silver carp calculated using bioenergetics modelling, averaged June-September, 2013-2014. Circle size represents relative percent change, green circles represent positive growth, grey represent neutral growth, and red represent negative.
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