SPATIOTEMPORAL TRENDS AND RELATIONSHIPS IN THE ABUNDANCE, GROWTH, AND CONDITION OF COMMON NEARSHORE FISHES OF SOUTHWEST LAKE MICHIGAN

BY

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THESIS

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ABSTRACT

The Laurentian Great Lakes are large, diverse, and dynamic ecosystems whose biotic communities have undergone significant alteration over the last two centuries due to various effects of human habitation in the basin. Currently, the most noticeable effects are those wrought by numerous invasive species that have been brought to the region and established themselves in the food web. In southwestern Lake Michigan, the nearshore zone (<10m depth) is a diverse habitat with an array of benthic substrate types and thermal regimes. Common fish species in this region include a native omnivore, the yellow perch, which represents a valuable sport fishery; the round goby, an invasive omnivore; and the alewife, an invasive planktivore. The objective of this research was to explore spatiotemporal patterns in the abundance of fishes in the nearshore area of the Illinois waters of Lake Michigan as well as to assess the growth and condition of two of the most common species, the yellow perch and round goby. Finally, laboratory evaluations were done to improve upon otolith length back-calculation methods for future studies of round goby growth. Data were collected at three locations with contrasting habitat complexity. Age data were collected using otoliths of yellow perch and round goby, and Fulton’s condition factor was calculated for different age classes.

Yellow perch relative abundance was most variable annually whereas round goby and alewife abundances were variable spatially. Age-0 yellow perch abundance also showed a negative relationship with round goby abundance, possibly indicating that the smaller yellow perch are avoiding high densities of the more aggressive round goby. Round goby abundance was the highest at the location with the prevalence of rocky substrate, likely due to their preference for spawning habitat. Alewife abundance increased significantly from south to north sites.
For all yellow perch age classes studied, length-at-age varied annually while condition factor varied spatially. Yellow perch condition was the highest at the north location, where benthic substrate was dominated by sand and benthic invertebrate abundance was lowest. This unexpectedly high condition could be the result of reduced interaction with round goby enabling yellow perch more access to feeding on benthic prey. Round goby length-at-age was the greatest at the southern location, likely due to its warmer thermal regime.

A laboratory experiment was undertaken to measure the accuracy of back-calculation models for round goby otoliths. Live round gobies were measured then marked with oxytetracycline to create a fluorescent ring on their otoliths and given an individual tag for later identification. After spending three months in the lab, fish were culled and otoliths were removed, viewed under an epifluorescent microscope and back-calculated using the inserted mark as an annulus. Back-calculated lengths were most accurate when using the Fraser-Lee method on measurements made to the post-rostrum radius. Accuracy was significantly related to growth rate and based on previous research it was concluded that unusually fast or slow growth can both cause a decoupling of otolith and somatic growth, increasing back-calculation error.
ACKNOWLEDGEMENTS

I would like to thank past and present technicians and biologists of the Lake Michigan Biological Station who collected data and samples used in this project, especially Sara Thomas for all assisting me with all things related to the Nearshore Community Project. I would also like to especially thank Catherine Johnston, Kacie Jonasen, Mike Rucinski, and Heather Sundstrom for assistance in caring for round goby in the hatchery lab. Thanks to my committee, Dr. Sergiusz Czesny, Dr. David Wahl, and Dr. Cory Suski, for insight related to the design and analysis of my project. Special thanks as well to Corey DeBoom and Joshua Dub for extensive advice on study design and statistical analysis.
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CHAPTER I: PATTERNS IN ABUNDANCE OF THREE COMMON NEARSHORE FISH SPECIES IN SOUTHWEST LAKE MICHIGAN

Abstract:
The Laurentian Great Lakes are large dynamic aquatic ecosystems with a diversity of available habitats and associated fish communities. The increasing prevalence of invasive species has influenced habitat associations of native species and altered trophic relationships throughout the food webs. We sought to identify habitat and biotic relationships associated with common nearshore fish abundance at three locations within the Illinois waters of southwest Lake Michigan. We utilized small-mesh gillnets to assess the fish community from June to October, 2008-2012. For yellow perch (*Perca flavescens*), age-0 and age-1 abundance varied annually, with water depth and water temperature, whereas age-0 yellow perch also showed a negative relationship with round goby abundance. Round goby (*Neogobius melanostomus*), abundance differed across locations, likely due to varying benthic substrate. Alewife (*Alosa pseudoharengus*) abundance showed significant variation across locations, being most abundant at the most northerly site. Relationships between the relative abundance of nearshore fish species can likely be attributed to behavioral interactions and differences in habitat preferences. Understanding the diversity of fish communities in nearshore areas could have implications for management of sport fish populations and influence the decisions on protection of critical habitats.
Introduction

Spatial and temporal variability in Great Lakes fish communities have had implications for fisheries production (Bronte et al. 2003) and ecosystem functioning (Madenjian et al. 2002). Adding to the dynamic nature of these systems, invasive species, changes in productivity, and other perturbations have caused large scale alterations to many ecological processes (Fahnenstiel et al. 2010, Cuhel & Aguilar 2013). In Lake Michigan, decreases in system productivity have occurred due to the invasion of zebra and quagga mussels (Dreissena polymorpha and D. bugensis), which have localized nutrient concentrations in nearshore benthic areas, having significant impacts on overall fisheries production (Hecky et al. 2004, Warner & Lesht 2015). The effects of this increase in nearshore benthic nutrient cycling have had cascading impacts on the nearshore fish community and food web structure that have only recently been realized (Turschak et al 2014).

While many large-scale changes have been documented in the pelagic regions of Lake Michigan, the nearshore zone and its fish community have received comparatively less study, especially considering to its ecological importance (Vadeboncoeur et al. 2011). Increasing attention to the nearshore fish community variability, dynamics and interactions will be critical to understanding changing ecological process and properly managing the ecosystem (Seelbach et al. 2013). Given the diversity of nearshore habitats (Creque et al. 2010), it is necessary to look at nearshore ecology at the proper spatial scale in order to understand the influences of local factors affecting fish abundance (e.g. Goforth & Carman 2009).

The relationship that both native and invasive species have to local-scale physical and biotic conditions will likely determine how ecological processes play out across the ecosystem. The addition of round goby (Neogobius melanostomus) to the nearshore ecosystem has had
noticeable effects on the native fish community, including the extirpation of some benthic fishes (Janssen & Jude 2001, Lauer et al. 2004). There have also been observations that suggest round goby interact negatively with juvenile yellow perch, likely impacting the perch’s habitat and prey selection (Houghton & Janssen 2015). However, these interactions are taking place in an ecosystem with high levels of habitat variability that lead to heterogeneous distributions of fish (Janssen & Luebke 2004), further complicating our understanding of nearshore fish ecology. While behavioral interactions between yellow perch and round goby have been studied in a laboratory setting (Duncan et al. 2011), very little focus has been given to the relationship between the abundance of the two species in nearshore areas. In light of the increasing importance of nearshore fish ecology to the functioning of the Lake Michigan ecosystem, understanding these interactions and how they are mediated by habitat availability is crucial to predict and manage for the potential effects of invasive species and other changes to the ecosystem.

The influence of round goby and other invasive species, like the planktivorous alewife (Alosa pseudoharengus), has drastically altered the fish and invertebrate communities of nearshore Lake Michigan, potentially having dramatic impacts for native fishes (Lederer et al. 2008, Madenjian et al. 2008). Given the crucial role that both fish community interactions (Dopazo et al. 2008, Forsythe et al. 2012) and habitat (Ray & Corkum 2001, Janssen & Luebke 2004, Young et al. 2010) can play in the distribution, growth, and recruitment of individual species, we sought to understand the fine scale variation, dynamics, and relationships between the most common nearshore fishes in the Illinois waters of southwest Lake Michigan: yellow perch, round goby, and alewife. The objectives were to 1) understand the variation in the abundance of these three common fish species in three contrasting locations in nearshore Lake Michigan during summer
and fall for five years 2) identify effects of abiotic conditions (temperature, depth) on gillnet catch rate of nearshore fishes and 3) understand relationships between the abundances of the three species.

Methods

Study Sites

Sampling took place at three separate locations within the Illinois nearshore waters of Lake Michigan (Figure 1.1). Locations were selected based on contrasting habitat types, attempting to encompass the three distinct geologic zones within the region (Chrzastowski & Trask 1995). The North location is situated near Waukegan, IL and represents the Zion beach-ridge plain zone. It consists of fine sand substrate with a featureless shoreline and tends to have the coldest thermal regime. The Middle location represents the Lake Border Moraines bluff coast zone and is located near Highland Park, IL. It is the most structurally complex location, with substrates ranging from sand to boulders. The South location represents the Chicago/Calumet lake plain zone. This location is a mosaic of smaller substrates – sand, pebbles and intermittent cobble. It has a highly armored shoreline due its location near the city of Chicago and tends to be the warmest site, especially in the spring (Creque & Czesny 2009). Through a multivariate cluster analysis of Lake Michigan nearshore conditions, including temperature, conductivity, chlorophyll, and zooplankton measurements, these three locations were found to reside in three distinctly different regions (Yurista et al. 2015).

Field Sampling

Fish sampling was conducted from June to October 2008-2012 using micromesh gillnets consisting of 10m panels of 6, 8, 10, and 12mm mesh (bar measure). Sampling events were
attempted at each location twice per month; however this was commonly limited to fewer occasions due to weather restrictions. For each location (North, Middle and South), three transects were made perpendicular to shore and roughly 0.5 km apart. A “site” was designated as the intersection of each transect with depth contours of 3m, 5m, and 7.5m. For a given sampling event, one site from each depth was randomly selected for sampling. Nets were usually set for 2-4 hours. Individual gill net sets, representative of a site within a location on a given date, were considered the experimental unit. Bottom temperatures and secchi disk readings were recorded at each site on each sampling event.

For yellow perch, the net mesh sizes utilized in this study targeted younger fish (Doll et al. 2014), and the majority of fish caught in this study were age-0 and age-1. Because of the age-specific ecology of juvenile yellow perch (age-0 fish migrate to the nearshore zone in late summer and feed heavily on zooplankton, whereas age-1 perch feed more on benthic invertebrates (Creque & Czesny 2012)), fish were aged using sagittal otoliths to allow for cohort specific analysis of the factors influencing their abundance. When greater than 30 yellow perch were caught, up to an additional 30 were measured for total length (TL-mm) and the age structure was inferred from an age-length key. Additional fish were counted and released and the age structure of the measured catch was applied to the remaining fish to get an overall age structure for the catch.

Data Analysis

Gillnet catch per unit effort (# fish/hr) was used to index abundance of yellow perch (age-0 and age-1), round goby, and alewife. As typical for catch rate or count data, abundance data were highly non-normal with a high variance to mean relationship (Power & Moser 1999) and thus a generalized linear model was used for analysis (Irwin et al. 2013). This was done using
the `glm.nb` function in the MASS package in R, which runs a generalized linear model fitted to a negative binomial distribution (Venables & Ripley 2002, R Core Team 2013).

Separate multiple regression analyses were done for each of the following response variables: yellow perch age-0 abundance, yellow perch age-1 abundance, round goby abundance, and alewife abundance. The following explanatory variables were assessed using a multiple regression analysis: location (LOC), month (MO), year (YEAR), bottom temperature (TEMP), water depth (DEP), round goby abundance (RG), total yellow perch abundance (YP), and alewife abundance (ALE). Biotic variables were excluded from analyses of their own species (e.g. YP was not included as a variable in the model for yellow perch age-0 abundance). Bottom temperature was included in analyses to understand if there was variation in catch rates related to daily fish activity changes in response to temperature variation. The three spatiotemporal variables (LOC, MO, and YEAR) were categorical variables while the rest were continuous.

Prior to conducting regression analysis, pairwise Pearson’s correlations between all continuous explanatory variables were calculated to test for multicollinearity, which was not found to be present (see correlation matrix in Table 1.1). To understand spatial, monthly, and annual variation, a post-hoc Tukey test was conducted on comparisons of locations, months, and years when those factors were significant in the model.

The use of a single multiple regression model including all possible predictor variables for each response variables was warranted due to the lack of multicollinearity and because of the exploratory nature of the analysis. Refinement to remove unimportant variables and enhance model utility is necessary for making models with “predictive” ability, which was not a goal of this study thus making model selection or stepwise regression unnecessary in this analysis. Other methods, like hierarchical partitioning or PCAs, can be useful when creating large multiple
regressions with many predictor variables that may be correlated (Mac Nally 2000). Due to the lack of significant multicollinearity, this was also not necessary here.

Generalized linear models make it difficult to calculate traditional measures of model fit (Nakagawa & Schielzeth 2013). For this analysis, I used a likelihood-based estimate of $R^2$ referred to as the $R^2_M$ in which the “M” refers to the “geometric mean squared improvement per observation” used in the statistic (Menard 2000). The estimate of model fit was calculated as

$$R^2_M = 1 - \left( \frac{L_0}{L_\beta} \right)^{2/n}$$

where $L_0$ is the likelihood of the data given the null model, $L_\beta$ is the likelihood of the data given the model of interest, and $n$ is the overall sample size. In a study across multiple datasets using logistic regression, this statistic was found to correlate highly with a typical ordinary least squares $R^2$ (Menard 2000).

**Results**

**General Trends**

Across the five-year study period, a total of 303 gillnet set samples were collected. Mean bottom temperature across all years and sampling dates was 16.4˚C and ranged from 7.9 to 25.5˚C. Yellow perch CPUE averaged 6.1 fish/hr (range 0 – 122.2 fish/hr), alewife CPUE averaged 3.46 fish/hr (range 0 – 71.6 fish/hr), and round goby CPUE averaged 2.2 fish/hr (range 0 – 38.0 fish/hr). Proportional representation of alewife and round goby varied noticeably by location (Figure 1.2), whereas yellow perch overall were similarly distributed across the three locations. Round goby proportion of the catch was highest at the Middle location (30%) and lowest at the North location (3%).
Multiple Regression

Factors significant in the model for age-0 yellow perch abundance were month \((P = 0.01)\), year \((P < 0.0001)\), temperature \((P = 0.047)\), and round goby abundance \((P = 0.009)\). The estimate of overall model fit was \(R_M^2 = 0.32\) (Table 1.2). Temperature had a positive relationship with age-0 yellow perch abundance \((\beta = 0.16)\), whereas RG had a negative relationship \((\beta = -0.22)\); Figure 1.4).

Factors significant in the model for age-1 yellow perch abundance models were month \((P < 0.0001)\), year \((P < 0.0001)\; \text{Figure 1.3})\), and temperature \((P < 0.0001)\). There was a positive relationship with temperature \((\beta = 0.31)\). The estimate of overall model fit was \(R_M^2 = 0.26\) (Table 1.2).

Factors significant in the model for round goby abundance included location \((P < 0.0001)\), month \((P = 0.0004)\), year \((P = 0.003)\), depth \((P < 0.0001)\), temperature \((P = 0.0003)\), and yellow perch abundance \((P = 0.032)\). The relationships were positive with depth \((\beta = 0.59)\) and temperature \((\beta = 0.10)\) but negative with YP \((\beta = -0.02)\). Model fit for round goby was highest among abundance models for species in this study \((R_M^2 = 0.45)\). The Middle location had significantly higher round goby abundance than both the South \((P = 0.002; \text{Figure 1.5})\) and North locations \((P < 0.0001)\), while the South location was also greater than the North \((P < 0.0001)\).

Factors significant in the model for alewife abundance included location \((P < 0.0001)\), month \((P = 0.0004)\), year \((P = 0.006)\), and temperature \((P = 0.021)\). The relationship was slightly negative with temperature \((\beta = -0.07)\). Model fit for alewife was lowest among abundance models for species in this study \((R_M^2 = 0.17)\). The North location had significantly higher alewife abundance than both the Middle \((P = 0.0003; \text{Figure 1.6})\) and South \((P < 0.0001)\),
while the Middle location on average was greater than the South, approaching significance ($P = 0.09$).

**Discussion**

We found a negative relationship between relative abundance of age-0 yellow perch and round goby which, to our knowledge, now constitutes only the second time a result like this has been observed. Houghton and Janssen (2015) observed that the proportion of the sampled yellow perch on rocky sites (when paired rocky and sandy sites were assessed) had a negative relationship with round goby CPUE. It is well established that round gobies prefer rocky habitat for shelter and spawning substrate (Young *et al.* 2010) and it has been shown that age-0 yellow perch also prefer rocky habitat in southwest Lake Michigan (Janssen & Luebke 2004), which indicates that the two species should occupy similar habitats. One possible explanation for our observation is that the aggressive round goby could interfere with juvenile yellow perch access to their preferred habitat. Turschak *et al.* (2014) observed that, while much of the nearshore food web was becoming more benthic-oriented in Lake Michigan, age-0 yellow perch were actually feeding more pelagically since the invasion of round gobies, speculating that yellow perch were being excluded from their typical benthic prey. When comparing rocky and sandy locations, Happel *et al.* 2015 found age-0 yellow perch to feed on more benthic resources (e.g. Chironomid larvae) on sandy sites, concluding that this was possibly due to round goby presence on rocky sites. In Lake Erie, some diet overlap existed between round gobies and small (<95mm) yellow perch, but there was no effect of round goby presence on habitat selection by yellow perch in a laboratory environment (Duncan *et al.* 2011). However, to replicate Lake Erie conditions, habitat preference experiments done by Duncan *et al.* (2011) included sand, dreissenid beds, and
macrophytes. The presence of macrophytes could have provided a vertical refuge for yellow perch to avoid interaction with round goby but still be able to utilize structure for shelter. In southwestern Lake Michigan, macrophytes are much less common, potentially increasing competition for benthic (i.e. rocky) structure and prey between these two species to levels greater than observed in Lake Erie. Of all fish abundance relationships across species in our multiple regression analyses, the negative relationship between age-0 yellow perch and round goby was the strongest.

Other studies have documented relationships between juvenile yellow perch abundance and recruitment and the abundance of other fish species. In Lake Ontario, age-0 yellow perch abundance in the fall was negatively related to alewife abundance in the preceding spring (O’Gorman & Burnett 2001). In southern Lake Michigan, recruitment to age-2 was negatively related to the abundance of alewife and spottail shiner (Notropis hudsonicus) in the year of hatching (Shroyer & McComish 2000; Forsythe et al. 2012). Our study appears to be the first to find a significant negative relationship between age-0 yellow perch abundance and round goby abundance.

Spatial trends in round goby abundance conform to what would be expected based on previous studies. Round goby are a strictly benthic species, with a body morphology suited to living on the bottom and a diet consisting of mussels and a variety of other benthic invertebrates and thus prefer rocky habitat (Ray & Corkum 2001, Taraborelli et al. 2010, Kornis et al. 2012). When comparing among locations, round goby abundance increased with increasing benthic substrate particle size and complexity. The Middle location, with the highest density of boulders and cobble, had the highest abundance of round gobies, followed by the South location which is a mosaic of substrates from sand to cobble, and finally very few round gobies were collected at
the North location, which is almost entirely sandy. Selection for larger, rocky substrates by round goby has been commonly observed in the Great Lakes (Ray & Corkum 2001; Young et al. 2010). Habitat selection for rocky crevices provide spawning substrate (Janssen & Jude 2001) combined with avoidance of open, shelter-less habitat with higher predation risks (Belanger & Corkum 2003). Although there is currently no evidence in our study region that predation pressure is high enough to control the round goby population, there has been evidence that Lake Erie burbot (*Lota lota*), at high densities, could exert predatory control on round goby (Madenjian *et al.* 2011). The preference for rocky habitat could also be attributed to prey availability as benthic Chironomid densities were highest at rocky sites where round goby catch rates were highest (Kornis & Janssen 2011, Creque *et al.* 2009). As round goby have proliferated in Lake Michigan they have been incorporated as an important member of the food web. The drastic differences in goby abundance between the locations in this study has implications for food web modeling that incorporates goby as a prey source as their prevalence in the diets of predators could also vary significantly within small areas of the lake.

Alewife abundance was significantly greater at the North location than the Middle and South locations. Similarly, Hondorp *et al.* (2005) found that alewife abundances on the western shore of Lake Michigan were significantly greater at a cooler, northern site. In nearshore Lake Michigan, previous work has found a preference for rocky habitat by juvenile and adult alewifes, although possibly only coincident with feeding on midges in sporadic emergence events (Janssen & Luebke 2004; Kornis & Janssen 2011). Combined with these results, our findings may indicate that alewife tend to avoid either warm temperatures, low prey availability, or the gradually sloping bathymetry in extreme southern Lake Michigan, becoming more common as temperatures become cooler moving northward. Although our inclusion of bottom temperature
in models was intended to account for increasing activity at warmer temperatures, alewife catch rate showed a slight negative relationship with temperature, likely an artifact of their abundance being significantly greater at the northern, cooler location.

Depth and temperature were important factors influencing the catch rates of both yellow perch and round goby. Both variables were found to have similar positive relationships with the gillnet catch rates of yellow perch in Indiana waters of Lake Michigan (Rydell et al. 2010). The inclusion of bottom temperature in models for fish abundance in this study was intended to account for the effect of temperature fluctuations on fish activity (i.e. warmer temperatures would lead fish to be more active and thus more likely to encounter sampling gear). The expected pattern was realized for yellow perch and round goby; both being caught at a higher rate when it was warmer. However, alewife catches showed a negative relationship with temperature, potentially indicating an avoidance of warmer waters in southern Lake Michigan, in accordance with their greater abundance at the northernmost location.

Another fluctuating abiotic factor that can affect daily catch rates is water clarity. It could be assumed that lower visibility would lead to higher catch rates because fish are less likely to see monofilament gill nets before entanglement. Water clarity is often measured by secchi disk depth; unfortunately, due to the current oligotrophic state of Lake Michigan, secchi disk measurements were not a good index of water clarity because the values were often to the bottom. Rydell et al. (2010) observed no effect of secchi depth on yellow perch catch rate in gill nets, however they reported encountering similar issues of the secchi disk being visible on the bottom, even at depths greater than 10m. Future work utilizing a different metric of visibility to understand the effect of water clarity on catch rates would be beneficial, especially to understand how variation in visibility could affect different species. Other abiotic factors that were not
included in this study but have been found to relate to nearshore fish abundance or catch rate are anthropogenic shoreline factors (Goforth & Carmen 2009), direct measures of benthic substrate (Janssen & Luebke 2004), and wave height (Rydell et al. 2010).

One factor that may complicate interpretations of the relationship between species abundances is the contrasting behavior of our study species. Alewife are a strictly pelagic schooling fish, yellow perch can exhibit schooling behavior and be focused either pelagically or demersally depending on feeding stage, while round goby is a strictly benthic species that stay close to the bottom, making a single gear incapable of accurately describing the entire fish community (Fabrizio et al. 1997). In addition, fine scale habitat structure or other unknown abiotic factors may influence these species differently, impacting the manner and frequency that they encounter passive gear, such as gillnets. Due to schooling behavior, encounter rates of yellow perch and alewife are more likely to be highly variable (Krause et al. 2002) compared to round goby. Gill nets, however, are best in Lake Michigan to characterize the fish community over a diversity of habitats, including rocky areas in which benthic trawls would not be effective.

Spatial variability and contrasting habitat selection among nearshore fish species implies the need for cognizance of the diversity and distribution of benthic habitats when sampling to characterize the nearshore fish community. Within Lake Michigan, a mosaic of benthic substrates exists requiring consideration of habitats available when observing spatial variation of biotic parameters (Creque et al. 2010). Preference for rocky habitat by yellow perch suggests sampling only on soft substrates would lead to an underestimation of perch abundance (Janssen & Luebke 2004; Janssen et al. 2005). Similarly, based on our results, sampling on soft substrates would lead to an underestimation of the prevalence of round goby in the fish community whereas sampling only in the warmer southern Illinois waters of Lake Michigan may underestimate the
prevalence of alewife. Given the increasing appreciation for the ecological complexities of the coastal zone of Lake Michigan and the importance of these areas for fishery production, lake processes, and biotic community interactions, it is imperative to understand factors driving the spatial and temporal variability in fish distribution and abundance.
References


Table 1.1. Correlation matrix for continuous variables in model selection analysis for the abundance of nearshore fishes in southwest Lake Michigan 2008-2012.

<table>
<thead>
<tr>
<th></th>
<th>Yellow Perch Abundance</th>
<th>Alewife Abundance</th>
<th>Round Goby Abundance</th>
<th>Bottom Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water Depth</td>
<td>0.018</td>
<td>-0.034</td>
<td>0.344</td>
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<tr>
<td>Yellow Perch Abundance</td>
<td>-</td>
<td>-0.019</td>
<td>-0.031</td>
<td>0.319</td>
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<tr>
<td>Alewife Abundance</td>
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<td>-</td>
<td>-0.113</td>
<td>-0.149</td>
</tr>
<tr>
<td>Round Goby Abundance</td>
<td></td>
<td></td>
<td></td>
<td>0.110</td>
</tr>
<tr>
<td>Bottom Temperature</td>
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</table>
Table 1.2. Multiple regression results for models of the relative abundance (gillnet catch per unit effort) of age-0 and age-1 yellow perch (*Perca flavescens*), round goby (*Neogobius melanostomus*), and alewife (*Alosa pseudoharengus*) in the nearshore Illinois waters of Lake Michigan from 2008-2012.

<table>
<thead>
<tr>
<th>Model</th>
<th>$R^2_M$</th>
<th>Factor</th>
<th>$\beta$</th>
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<td>Location</td>
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<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
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<tr>
<td></td>
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<td>Depth</td>
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<tr>
<td></td>
<td></td>
<td>Temperature</td>
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<tr>
<td></td>
<td></td>
<td>Alewife</td>
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<td>Round Goby</td>
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<td>Age-1 Yellow Perch</td>
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<tr>
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<td>Month</td>
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<tr>
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<td></td>
<td>Year</td>
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<td></td>
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<td>Depth</td>
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<td>Temperature</td>
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Figure 1.1. Study site locations and dominant benthic substrate type in Illinois waters of southwestern Lake Michigan.
Figure 1.2. Proportion of gillnet catch from 2008-2012 represented by the main fish species (round goby *Neogobius melanostomus*, yellow perch *Perca flavescens*, alewife *Alosa pseudoharengus*, spottail shiner *Notropis hudsonius*, and rainbow smelt *Osmerus mordax*) and others in three distinct locations in the nearshore area of southwest Lake Michigan.
Figure 1.3. Monthly catch rates by year of age-0 and age-1 yellow perch (*Perca flavescens*) from 2008-2012 in southwest Lake Michigan. Error bars represent standard error.
Figure 1.4. Log scale relationship between the relative abundance of age-0 yellow perch (*Perca flavescens*) and round goby (*Neogobius melanostomus*) in southwest Lake Michigan. Individual points represent catch per unit effort of both species in a single gillnet sample.
Figure 1.5. Average monthly catch of round goby (*Neogobius melanostomus*) by the three locations in southwest Lake Michigan (North = black, Middle = light grey, South = dark grey) from 2008 to 2012. Error bars represent standard error.
Figure 1.6. Average annual catch rate of alewife (*Alosa pseudoharengus*) by the three locations in southwest Lake Michigan (North = black, Middle = light grey, South = dark grey) from 2008 to 2012. Error bars represent standard error.
CHAPTER II: SPATIOTEMPORAL VARIATION IN SIZE-AT-AGE AND CONDITION OF TWO COMMON NEARSHORE FISHES IN SOUTHWESTERN LAKE MICHIGAN FROM 2008-2012

Abstract:

The nearshore zone of Lake Michigan is a heterogeneous and dynamic region supporting popular recreational fisheries. The yellow perch (*Perca flavescens*) is a native omnivore that is a commonly sought sport fish, but whose population has been in decline for the last two decades due to a variety of factors. The round goby is a common benthivore that invaded the Great Lakes from the Ponto-Caspian region of eastern Europe and has reached high population densities in southwestern Lake Michigan. We sought to look at spatiotemporal variation in size-at-age and condition of yellow perch and round goby across three locations with contrasting habitat types in the nearshore zone of the Illinois waters of Lake Michigan. Understanding variation in fish growth and condition is necessary to identify population demographics and the effects of environmental conditions on fish production. There was significant annual variation in length-at-age for yellow perch, which can be important for juvenile survival. Condition in yellow perch varied spatially, being greatest at the northernmost location where round goby abundance was drastically lower compared to other sites.
Introduction

Fish growth and condition are influenced by a multitude of factors but generally are a reflection of habitat quality, prey availability, and physical conditions (DeVries & Frie 1996). In sport fish populations, age and growth information can influence management decisions such as harvest length, bag limits, and stocking needs. Population age and growth structure can also be utilized in bioenergetics and ecosystem modeling that can aid fishery management. For example, understanding of the influence of round goby (Neogobius melanostomus) presence in the food web of Lake Erie for predators like burbot (Lota lota), smallmouth bass (Micropterus salmoides), and yellow perch (Perca flavescens) helps fishery managers understand the importance of goby population density for sport fish production as well as the energetic connection they have provided between zebra mussels and higher level consumers (Johnson et al. 2005).

Fish growth and condition are closely related to prey availability, prey type, competition, and water temperature, and thus can be considered an indicator of changing food webs and aquatic communities (Hill & Magnuson 1990). In the Laurentian Great Lakes, these metrics have been used to identify higher trophic level effects of ecosystem changes caused by invasive species. For example, body condition and length-at-age of lake whitefish (Coregonus clupeaformis) changed significantly from the years before to the years after the arrival of zebra mussels in southeastern Lake Michigan, reflecting the decline of their main benthic prey source, Diporeia (Pothoven et al. 2001). While changes in prey source can affect fish growth and condition, they are also controlled to some degree by temperature regime (Hill & Magnuson 1990) and competition (Headley & Lauer 2008). As an example of the synergistic nature of these factors, age-0 perch body weight in inland lakes was directly related to zooplankton species
composition and biomass, but only after a certain cumulative temperature threshold was met (Mills et al. 1989). In large pelagic systems like Lake Michigan, documenting variability in fish growth and condition at multiple spatial and temporal scales is necessary to understand the effects of ecosystem change at all trophic levels.

While it is well established what ecosystem properties can affect fish growth and condition, the effect that small scale variability in these properties can have may often be underappreciated. Substantial variability exists in benthic habitat in southern Lake Michigan, creating a large diversity in benthic prey composition (Creque et al. 2010, Creque & Czesny 2010), which has been shown to affect fish diet (Hap pel et al. 2015). Nearshore substrate in this area varies widely from sand to large cobble and boulders, as well as mosaics of a range of substrate size. Juvenile perch, round goby, and other fishes have been observed to be present at varying densities across these habitat types (Janssen & Luebke 2004, Young et al. 2010), possibly in relation to prey availability.

Identifying the implications of this spatial variability in habitat on the growth and condition of nearshore fishes will be imperative to ensure that our understanding of ecosystem functioning takes into account the heterogeneous nature of nearshore ecology. For example, by identifying an area where reduced prey availability led to lower growth in juvenile lake trout (Salvelinus namaycush), Madenjian et al. (1998) recommended adjustments to stocking strategies for lake trout restoration in Lake Michigan. As discussed in Chapter 1, more attention is now being paid to the ecology of the nearshore area due to the large-scale shift in nutrients and energy into benthic pathways (Hecky et al. 2004, Turshak et al. 2014). In recent decades, fishery management in the Great Lakes has focused on maintaining a balance between pelagic predatory fish and planktivore biomass (Murry et al. 2010), but may now require a more holistic
view incorporating metrics of nearshore fishes that have an increasingly prominent role in ecosystem functioning (Seelbach et al. 2013, Bunnell et al. 2014).

Two important species to the nearshore benthic food web of southwest Lake Michigan are the yellow perch and round goby. Yellow perch are a native omnivore that have historically provided a productive sport and commercial fishery (Clapp & Dettmers 2004). Juvenile yellow perch (ages 0-3) tend to reside in nearshore areas and feed on benthic invertebrates and fish (Creque & Czesny 2012). Round goby have reached incredibly high densities in the last two decades since their original invasion, residing throughout the nearshore zone and feeding on Dreissenid mussels and other benthic invertebrates (Charlebois et al. 1997, Kornis et al. 2012). Their predation upon invasive mussels has created a new energy pathway in Lake Michigan by making those nutrients more available in the food web (Hecky et al. 2004). These two species play an integral role in the biotic community as predators, prey, and competitors thus making it necessary to understand the variability in their growth and condition as well as the factors that may influence them.

As the food web of Lake Michigan shifts to a more nearshore benthic focus, there is an increasing need to understand the ecology of diverse nearshore habitats and the changing fish communities that inhabit them. Just within the Illinois waters of the lake, there can be dramatic variation in benthic substrate, complexity, and thermal regime (Creque et al. 2010). Quantifying the variation in fish growth or abundance related to local-scale habitat variation has rarely been accomplished in large systems such as the Great Lakes (Danehy et al. 1991; Janssen et al. 2004). The objective of this study was to identify spatiotemporal trends in the size-at-age and condition of yellow perch and round goby in contrasting nearshore areas of southwestern Lake Michigan in
order to understand if there is local variability that could have implications for the effect of benthic habitat on fish growth.

**Methods**

*Study Sites*

Sampling took place in the Illinois nearshore waters of Lake Michigan at the three locations described in Chapter I.

*Field Sampling*

Fish were sampled using micromesh gill nets consisting of 10m panels of 6, 8, 10, and 12mm (bar measure) mesh. Sampling was conducted from June to October 2008-2012 and attempted to sample each location twice per month; however, weather restrictions on sampling commonly limited this to fewer occasions. For each location (North, Middle, and South), three transects were made perpendicular to shore and roughly 0.5 km apart. A “site” was designated at the intersection of each transect with the depth contours of 3m, 5m, and 7.5m. For a given sampling occasion, one site from each depth was randomly selected to be sampled. Nets were set for 2-4 hours generally spanning from late morning to early afternoon. Average length-at-age or condition-at-age of a given fish species from an individual gill net set, representative of a site within a location on a given date, were considered the experimental unit.

Subsamples of up to 30 fish of each species per sample were preserved in ethanol and their otoliths were removed for age analysis. Aging was done using whole or sectioned otoliths or otolith weight. Sectioning of yellow perch otoliths was done using a modified version of the methods of Secor et al. (1991). Yellow perch otoliths were mounted with the post-rostrum on the edge of a glass microscope slide with the transverse plane through the core perpendicular to
the edge using thermoplastic glue. The rostrum edge was sanded to the focus using 800-grit sandpaper, removed and reattached vertically from the face of the slide, and the post-rostrum edge was sanded until the annuli were clearly visible in the section. Sectioned otoliths were viewed under a compound microscope using transmitted light with a drop of mineral oil placed on the otolith to improve clarity and images were taken using a microscope mounted camera. For round goby, images of whole otoliths were taken under a dissecting scope. Ages were assigned by an experienced reader after reading each otolith twice, with separate viewings over two months apart. Unclear and difficult to read otoliths were removed from the analysis.

For yellow perch captured from July to September, fish were aged via weighing otoliths to the nearest 0.00001 g and then age was assigned using a predictive model created using 822 yellow perch otoliths from the same sampling locations. Using subsamples of these fish as a training data set and then testing predictions from a random forest model on the remaining fish, 95% of age classifications matched assigned ages from otolith section readings (Dub et al. 2013). The model utilized otolith mass, month, year, fish sex, fish total length, and location as factors to predict fish age, with otolith mass and month being the most important variables. The initial model was created using fish captured in August and September, for this study data were supplemented with fish from the month of July to increase temporal coverage.

Data Analysis

Analyses of covariance (ANCOVA) were used including the effects of year and location as categorical variables, and Julian date (day of the year) was included as a covariate to account for growth or change across the season. Analyses were run for the following response variables: yellow perch condition and length-at-age 0, 1 and 2, and round goby condition and length-at-age 2 and 3. The youngest round goby caught were age-1 and thus no analysis was done on that age.
as fish may not be fully recruited to the sampling gear. For round goby, sexual differences have been shown in length-at-age, with males being larger than females. These studies are in agreement that older gobies show sexual size dimorphism, however there have been contrasting results about whether younger goby (ages 1-3) show the same difference (Sokołowska & Fey 2011; Huo et al. 2014). A paired t-test was run comparing male and female length-at-age using average TL for any gillnet sample that contained at least one male and female of the same age to control for spatial and seasonal influences in growth. No significant difference was found between male and female round goby length-at-age from ages 1 to 3. (P = 0.54). Sexual size dimorphism is present in yellow perch, however not until fish are older than those analyzed in this study (Dub et al. 2013), thus sex was not included in models of yellow perch length-at-age. All model residuals were checked for normality and homogeneity of variance and found to meet the assumptions of ANOVA, except for analysis of age-1 yellow perch length. For this variable, a $y^{-1/2}$ transformation was found to bring the variable into compliance and was thus utilized for analysis. Least-squared means were then transformed back to understand realistic values. A Tukey post hoc test was utilized to test for significant differences between locations and years.

Results

Yellow perch ranged from 50mm to 213mm TL and age-0 to age-3 whereas round goby ranged from 43mm to 159mm TL and from age-1 to age-6. Gill net sets captured age-0 yellow perch (N = 67 sets, 1431 total fish), age-1 yellow perch (N = 121, 1236 total fish), age-2 round goby (N = 75, 451 total fish), and age-3 round goby (N = 60, 283 total fish).

Results of ANCOVAs for length-at-age and condition are presented in Tables 2.1 and 2.2, respectively. As expected, Julian date was a significant covariate in all tests of length-at-
age, indicating that it correctly represented growth across the year. Age-0 yellow perch length varied significantly by year ($F_{4,59} = 3.49, p = 0.0127$). There was a significant effect of location on age-0 yellow perch condition ($F_{2,59} = 8.33, P = 0.0006$). Fish caught in the North location had significantly greater condition than fish from the South location (Tukey HSD adjusted $P = 0.0009$) and the Middle location (adjusted $P = 0.017$; Figure 2.2).

Age-1 yellow perch length also showed significant annual variation ($F_{4,111} = 17.60, p < 0.0001$). There was a significant effect of location on age-1 yellow perch condition ($F_{2,111} = 10.2, p < 0.0001$). A Tukey’s HSD test found that age-1 yellow perch was significantly lower at the South location than the Middle location (adjusted $P = 0.008$), and the North location (adjusted $P = 0.00008$; Figure 2.2). Age-2 yellow perch length also showed significant annual variation ($F_{4,85} = 3.66, P = 0.008$). As with younger age classes, age-2 yellow perch condition showed significant spatial variation ($F_{2,82} = 3.18, p = 0.047$), however a post-hoc Tukey’s HSD test failed to identify any significant differences in pairwise comparisons of the three locations. Age-2 perch condition also showed annual variation ($F_{4,82} = 12.06, p < 0.0001$).

Round goby population size structure was similar between the Middle and South locations, but showed a prominence of large fish at the North location (Figure 2.3). Fish ranging from 50-80mm constituted 73% of the population at the Middle and 71% at the South location, but only 51% at the North, while fish ranging from 80-110mm only constituted 24% at the Middle and 26% at the South, but 46% of the population at the North location. Though the total number of fish at the North location (N=109) was large enough to analyze via length frequency histogram (Anderson & Neumann 1996), the experimental unit for analyses of length-at-age and condition was the individual gillnet pull rather than individual fish. This drastically reduced the
sample size from the North location to a point where it was of limited value and was thus removed from further analyses of spatial variation in round goby growth parameters.

Round goby age-2 length showed significant spatial variation ($F_{1,69} = 5.8, p = 0.018$), with fish at the South location being longer than those at the Middle location. Age-2 round goby condition showed significant variation across locations ($F_{1,68} = 5.8, p = 0.0188$), with the Middle location having significantly higher condition than the South location (Figure 2.5). Round goby length-at-age 3 and age-3 condition showed no significant variation by location or year.

**Discussion**

Within the small region of southwest Lake Michigan, we observed significant differences in age-0 yellow perch condition at three different locations with contrasting biotic and abiotic conditions. Condition factor for all ages of yellow perch was significantly greater at the North (sandy) location. Given the lack of benthic structure at the north site and the generally more diverse and abundant prey resources inhabiting larger benthic substrates, it was unexpected that yellow perch would be in greater condition in this habitat. Indeed, benthic invertebrate sampling in this region (North location) has shown the lowest densities of common prey species (e.g. larval Chironomids, Creque & Czesny, 2010). Despite potentially lower benthic invertebrate densities, age-0 yellow perch diets in Lake Michigan showed increased benthic reliance (mostly Chironomidae and Chydoridae) on sandy sites, with feeding more focused on zooplankton and fish at rocky sites (Happel et al. 2015). One possible explanation for this is that yellow perch are able to feed more effectively at the North (sandy) location due to a drastically lower abundance of round goby on sandy locations (Chapter I). If round gobies behaviorally interfere with yellow perch access to benthic prey, lower round goby density could give perch the ability to feed more
on Chironomids at this location (suggested by Happel et al. 2015 and Houghton & Janssen 2015), potentially resulting in greater condition. When behavioral interactions between the two species were observed in a laboratory setting, round goby presence did not cause a change in age-0 yellow perch habitat selection (Duncan et al. 2011). However, only round goby up to 67mm were used and it was concluded that a larger size range of round goby could still exert negative effects on yellow perch habitat selection. Duncan et al. (2011) also gave yellow perch the option of selecting macrophyte habitat, potentially giving them a vertical refuge from interaction with round goby that may not be present in habitats with low macrophyte abundance. It remains to be tested whether round goby will have a more negative effect on juvenile yellow perch in nearshore Lake Michigan, which is less productive and less structurally complex than Lake Erie.

We observed annual variation in yellow perch size-at-age and, though we do not have sufficiently comprehensive temperature data we suggest that annual variation in thermal regime is likely to affect growth. Length-at-age for both age-0 and age-1 yellow perch were greatest in 2012, which was characterized by record warm spring temperatures in the Great Lakes region. Annual variation in yellow perch age-0 growth has been commonly found across the Great Lakes ecosystems including Saginaw Bay, Lake Huron (Roswell et al. 2014), Lake Michigan (Fitzgerald et al. 2004), and Lake Ontario (O’Gorman & Burnett 2001). In northeastern Lake Ontario, annual variation in YOY perch growth was related to variation in YOY perch abundance, cumulative degree days (>13.5C), and total phosphorous (O’Gorman & Burnett 2001). Warmer temperatures in 2012 led to earlier spawning for yellow perch in nearby Indiana waters of Lake Michigan (Starzynski & Lauer 2015) potentially leading to earlier hatch dates and thus increased size later in the year when fish became demersal and returned to the nearshore.
Large-scale spatial variation in yellow perch length-at-age in Lake Michigan has been documented for adult fish, where age-3 to age-5 fish tended to be longer on the west shore (Wisconsin and Illinois waters) than on the east shore (Michigan and Indiana waters) (Horns 2001). Though it is important to understand regional variation in growth, comparing length-at-age more locally can help to identify factors that act on a smaller scale and are associated with juvenile yellow perch growth. Only one study has documented an effect of local-scale benthic habitat variation on yellow perch size-at-age. In nearshore Lake Ontario, back-calculated lengths of yellow perch at all age classes were greater at cobble/rubble sites than at nearby sandy sites (Danehy et al. 1991).

Although no spatial variation was found in length-at-age for yellow perch, Monthly variation in condition was not found in age-0 yellow perch, however it has been observed in Saginaw Bay, possibly due to the absence of an ontogenetic diet shift to benthic invertebrates in the fall (Roswell et al. 2014). Although no annual variation was found across 5 years, time period had a significant effect on yellow perch age-0 condition (Wr) in Saginaw Bay, Lake Huron from 1970-2011 (Staton et al. 2014). These variations in condition were attributed to food web shifts and possible density-dependent compensation. While these processes likely affect yellow perch growth in our study area, it is possible that their effects were outweighed by other factors influencing our data.

Few studies have examined age-1 yellow perch growth or condition. Research targeting YOY yellow perch is commonly used to understand influences on annual variation in recruitment to the juvenile stage, whereas assessments including adult fish normally use gears that exclude capture of age-1 fish due to large mesh sizes. The lack of attention to age-1 fish may be a mistake as it has been shown that year-class recruitment strength may be affected by
growth success that takes place after age-0 (Dub et al. 2014). Though age-0 growth in perch is commonly considered important for ontogenetic diet shift timing (Roswell et al. 2013) and overwinter survival (Heermann et al. 2009), there has been no evidence of size-selective mortality in the first winter for yellow perch in Lake Michigan (Fitzgerald et al. 2004; Dub et al. 2014). Size-selective mortality has, however, been found indicating that yellow perch less than <70mm at the beginning of age-1 generally did not survive to age-2 in southwest Lake Michigan (Dub et al. 2014).

The largest round goby caught in this study (159mm) represents the longest TL published for a round goby in its nonnative North American range (for a summary of global age-growth estimates of round goby, see Table 7 in Huo et al. 2014). Only two accounts of round goby reaching this size or larger (up to 165mm) have occurred in North America, however there is little detail associated with these reports (Charlebois et al. 1997). The oldest recorded age for round goby is 7 years, also found recently in Lake Michigan (Huo et al. 2014). Spatial variation was found in round goby size-structure with the North site showing a greater proportion of larger gobies (80-110mm) while the Middle and South locations retained the majority in the smaller size classes (50-80mm). One possible explanation for this difference in size structure is that the lack of benthic cover at the North location made small round goby more vulnerable to predation by smallmouth bass and adult yellow perch. Thus, round goby that survive to a length that is not vulnerable to predation are more prominent in the population. Because piscivores are often size-limited, they tend to prey upon smaller size-classes of available fish prey, leaving those that have outgrown vulnerability to predation to be more prominent in the size structure of the population (Tonn et al. 1992). Furthermore, it has been observed that round gobies are more susceptible to predation in habitats without shelter than those with shelter and that smaller fish are more
vulnerable (Belanger & Corkum 2003). Spatial variation in round goby size structure was present in the Bay of Quinte, Lake Ontario, where it was concluded that in the upper bay the size structure resembled that of an expanding population, while in the lower bay it resembled a stable population (Taraborelli et al. 2010).

Ours is the first study to document within-system spatial variability in round goby condition. Mean $K$ factor values were substantially lower (~60-90%) than previously reported in the Lake Erie (Thompson & Simon 2015) and the St. Lawrence River (Gendron et al. 2012). One explanation for this difference is the greater productivity of those systems leading to greater prey availability. A potentially more likely explanation for this is the effect of preservation on round goby weight. Our samples were preserved in 70% ethanol, which has been known to cause decrease in both length and mass of preserved fish. Although Thompson & Simon (2015) also preserved fish in ethanol, it is possible that they were not preserved for very long (fish in our study commonly remained in ethanol for > 1 yr) and did not experience as much desiccation, thus remaining in greater condition. Thus, conclusions made from estimates of fish condition here should be limited to spatiotemporal comparisons within this sampling regime to avoid bias stemming from contrasting preservation techniques. One possible complication in this study is the unknown extent to which juvenile yellow perch may move between locations. Site fidelity is high for round goby in the Great Lakes (Ray and Corkum 2001), however no study has quantified the movement of individual yellow perch following their settlement in nearshore areas. Because some differences have been observed between fish captured at different sites in terms of diet (Happel et al. 2015) and condition (this study) it is reasonable to believe that fish captured together in one location share a similar recent experience. However, our inability to fully describe the recent history of individual perch remains a limiting factor in this study.
In conclusion, although the nearshore area of Lake Michigan is generally considered a contiguous unit for the purposes of fish production, food web interactions, and nutrient processes, we showed spatial and temporal variation in the growth and condition of two common nearshore fish species. Size-structure of round goby varied noticeably across different habitats, indicating that production or predation upon them may vary due to benthic structure. We also found variation in condition among round goby, indicating that prey availability may be variable across habitats, further influencing round goby biomass. The importance of early growth for yellow perch has been noted in previous research, and the annual variation observed just over the short duration of this study could indicate the influence of varying environmental conditions. Circumstantial evidence from this and other studies could indicate that warmer spring temperatures may lead to earlier spawning by yellow perch and thus a longer growing season and larger sizes for juveniles. In addition to the potential effects that annual variability may have on growth, spatial variation in juvenile perch condition could influence winter survival as well. Significantly greater age-0 yellow perch condition at a sandier location, potentially related to increased benthic feeding, could indicate that interference by round goby (present at notably low densities at that location) is a potential limiting factor for juvenile perch feeding success. In combination, these results demonstrate the importance of biotic interactions in the nearshore area of Lake Michigan and stress the need for research into the synergistic effects of these interactions with dynamic abiotic conditions on fish production and food web ecology in the Great Lakes ecosystems.
References


Chapter II Tables and Figures

Table 2.1. Analysis of variance (ANOVA) results of spatiotemporal trends in length-at-age for yellow perch *Perca flavescens* (age-0, 1, and 2), and round goby *Neogobius melanostomus* (age-2 and 3) in southwest Lake Michigan, 2008-2012, bolded factors indicate significance at $\alpha = 0.05$.

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Table 2.2. Analysis of variance (ANOVA) results of spatiotemporal trends in condition for yellow perch *Perca flavescens* (age-0, 1 and 2), and round goby *Neogobius melanostomus* (age-2 and age-3) in southwest Lake Michigan, 2008-2012, bolded factors indicate significance at $\alpha = 0.05$.

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**Figure 2.1.** Least-squared means of size-at-age by year across the sampling season for age-0 (lower group) and age-1 (higher group) yellow perch *Perca flavescens* in southwest Lake Michigan, with error bars representing standard error. Note that prior to August, age-0 yellow perch have not yet settled into the nearshore area and were thus not vulnerable to our sampling.
**Figure 2.2.** Least-squared means of Fulton’s condition factor for three age classes of yellow perch *Perca flavescens* comparing the three sampling locations in nearshore southwest Lake Michigan. Error bars represent standard error and different letters denote significant differences from a post-hoc Tukey’s HSD test at $\alpha = 0.05$. 
**Figure 2.3.** Length-frequency histograms of round goby (*Neogobius melanostomus*) at three sampling locations in the nearshore Illinois waters of Lake Michigan. In the North (sandy) location, larger fish (80-110mm) constitute roughly 46% of the sample but only 25% at the Middle and South locations. The majority of the population (~70%) is in the 50-80mm range at the Middle and South locations, but only about 50% of the population at the North location.
**Figure 2.4.** Least-square means of length-at-age 2 of round goby (*Neogobius melanostomus*) across the sampling season at two locations in the nearshore Illinois waters of Lake Michigan. Error bars represent standard error.
**Figure 2.5.** Least-squared means of Fulton’s condition factor for age-2 round goby (*Neogobius melanostomus*) comparing two locations in nearshore Illinois waters of Lake Michigan across the sampling season. A post-hoc Tukey’s HSD test showed the Middle location to have significantly greater condition overall, while the star in the figure denotes significant differences among months.
CHAPTER III: USE OF OXYTETRACYCLINE MARKING OF ROUND GOBY (NEOGOBIUS MELANOSTOMUS) OTOLITHS TO COMPARE ACCURACY OF BACK-CALCULATION METHODS

Abstract

Understanding the factors influencing the invasion success of round goby (*Neogobius melanostomus*) is important to managing the dynamic food web of Lake Michigan. Growth is one aspect of fish biology commonly measured to identify ecological factors influencing the success of a species in a particular habitat. Past growth is often measured using back-calculation in order to compare varying influences over the lifetime of a fish. We compared the use of multiple otolith radii and back-calculation methods for round goby using artificial annuli created by immersion in an oxytetracycline (OTC) solution. Back-calculated length (BCL) was estimated using three otolith radii (rostrum, ventral, and post-rostrum) and two back-calculation methods (direct proportion, Fraser-Lee) and assessed for accuracy by direct comparison to the measured length at the time of OTC marking. In general, post-rostrum BCLs were the most accurate of the three radii and the Fraser-Lee method outperformed the direct proportion method. All but two BCLs (among all fish and radius x method combinations) underestimated length at marking. Growth rate was negatively correlated with the absolute value of percent error, indicating that faster growth leads to more accurate back-calculated lengths. Future work utilizing back-calculation to understand round goby growth should utilize a radius from the core to the post-rostrum point as well as the Fraser-Lee method with an appropriate biologic intercept in order to estimate the most accurate BCLs.
Introduction

The use of fish hard structures to understand age and growth is a common practice in fishery science. Back-calculation models are a valuable method because they can provide multiple growth data from a single sampling event and allow for the reconstruction of growth histories of individual fish. From this, information can be obtained about fish life history, population dynamics, and the effects of varying biotic and abiotic conditions on fish growth (DeVries & Frie 1996). Calcified structures such as scales, cleithra, vertebrae, and otoliths can serve these purposes to varying degrees based on the morphology and growth of the fish species in question. The application of back-calculation models can be useful to understand complicated life histories of fishes like the round goby (*Neogobius melanostomus*) which may have alternative forms and protracted spawning strategies. To date, only one study has utilized back-calculation on round goby otoliths to understand the growth histories of individual fish (Huo *et al.* 2014). Many questions remain about the ecology of round goby, including if different life history strategies (i.e. “parental” vs. “sneaker” males) show contrasting growth trajectories or if one is potentially an earlier life stage of the other (Kline-Brussee 2014). Understanding these aspects of round goby life history will be crucial to modeling and predicting their population dynamics and subsequent effect on the nearshore food web of Lake Michigan.

Because of their unusual otolith morphology (compared to more commonly studied sport and commercial fish species), it is necessary to ensure the accuracy of back-calculation measurements and the relationship between otolith growth and somatic growth for round goby. Utilizing back-calculation for a species based on untested assumptions can lead to an inaccurate understanding of their biology, making validation of back-calculation methods a necessity (Campana 1990). Back-calculation models rely on the assumption that there is a linear
relationship between hard part growth and somatic growth. Even though notable variation can exist in the accuracy of back-calculated lengths (BCL) based on the method and radius used (Klumb et al. 2001; Li et al. 2008) the performance of back-calculation models is rarely assessed. Validation requires either field mark-recapture (Howells et al. 1995) or laboratory study (Roemer & Oliveira 2007) in which the measured length at a previous point in time can be compared with the BCL estimate made using the interval on a structure corresponding to that time. The most certain way to accurately relate length measured at a previous point in time to the corresponding point in the radius of a hard structure is to induce an artificial mark that can be recognized later.

One of the main factors influencing the accuracy of back-calculation models, is the reality of the assumption of a consistent relationship between otolith growth and somatic growth. If there is a decoupling of these two rates, it will lead to error in back-calculated length estimates as the width of the intervals between annuli is not proportional to growth during the represented time frame. One potential factor influencing this relationship can be fish growth rate (Panfili & Tomás 2001) and thus it is critical to understand if exceptionally fast or slow growth in round goby will affect the relationship between body growth and otolith growth. This relationship has never been tested in round goby, though it has been assessed for other Gobiid species (Wilson et al. 2009, Shafer 2000). The utility of back-calculation models for understanding Gobiid life history is well established. For the endangered tidewater goby (Eucyclogobius newberryi), birth dates calculated through back-calculation showed a wide range of reproductive period lengths between populations and that populations with year-round reproductive activity showed greater genetic diversity than populations with short reproductive periods (Hellmair 2011). Also using back-calculation, Teichert et al (2012) were able to show that, although an amphidromous goby
species, *Cotylopus acutipinnis*, showed a very long spawning season, hatch dates peaked in two separate periods and that there may be selective mortality based on post-larval growth patterns.

The use of back-calculation to compare growth trajectories and size-at-age of round gobies of contrasting forms could help to shed light on several aspects of round goby ecology that would aid our understanding of their population biology. As it will be critical in order to utilize this tool in future research, the objective of this study was to test its accuracy of back-calculation for round goby sagittal otoliths, assess different methods, and validate the assumption that otolith growth and somatic growth show a consistent relationship. We implemented a fluorescent mark on the otoliths of live fish via immersion in a solution of OTC, followed by the measurement and individual marking of fish for comparison with future back-calculated lengths.

**Methods**

Round goby were captured via angling from Lake Michigan in Waukegan Harbor, Illinois, between May 30th and June 3rd, 2014, and immediately transported to the laboratory at the Lake Michigan Biological Station, Zion, Illinois. Due to early initial mortality after the first marking event, a second group of fish was captured June 30th, 2014. Fish were transferred to fiberglass raceways and given two weeks (first batch) or one week (second batch) to acclimate to the laboratory environment before marking.

The first batch of fish was marked on June 17th and 18th, and the second batch was marked on July 3rd, 2014. Round gobies were marked with immersion in a bath of oxytetracycline solution using Pennox® 343 soluble powder (oxytetracycline HCL, ~76% OTC) dissolved at 700 mg/L (recommended dosage for marking of fish hard parts). Due to the acidification caused by HCL in the compound, an equal mass of buffer (sodium phosphate,
dibasic, anhydrous buffer) was added to neutralize pH. Immersion was done in rubber storage
tubs with 25L of fresh water and nine or ten fish per tub. Oxygen was provided via an aeration
stone and shelter was provided in the form of ~4 inch sections of PVC pipe cut in half to form
half-cylinders. For the duration of the six-hour immersion, tubs were kept in a completely dark
room in order to minimize stress to fish. Pilot work had shown that this density of fish led to
minimal mortality.

Immediately after removal from the immersion bath, fish were lightly anesthetized using
immersion in a solution of MS-222 (concentration of 75 mg/L), measured for total length to the
nearest 0.01mm using dial calipers, and tagged. In order to identify and measure the growth of
individual fish, all round goby were given a standard sized (1.2mm x 2.7mm) visual implant
 alphanumeric tag (Northwest Marine Technology, Inc, Shaw Island, WA) with a unique letter-
number combination. Tags were inserted under the skin of the right cheek using a specialized
injector needle. Following tagging, fish were allowed to recover in a bucket of fresh water for
~5 minutes before being returned to the raceway for the duration of the experiment.

Initially, two temperature/feeding treatments were implemented in order to understand
the influence of variable growth rates on otolith growth and back-calculation measures. The two
treatments were conducted in two different raceways, with the fish divided between them. The
cooler raceway was held at constant Lake Michigan temperatures while the warmer raceway was
held 2-5°C above the natural temperature using heaters. Fish in the warmer treatment were fed
5% of their body weight per day of mysis shrimp from a commercial frozen fish food supplier
(JEHM Co, Inc. Aquatic Breeder Supplies), whereas fish in the cooler treatment were fed 3%.
Unfortunately, the colder treatment was subjected to unseasonably cold summer temperatures as
well as dramatic temperature fluctuations that led to higher mortality rates early in the
experiment. Thus, by the end of the experiment, sample size was low enough to warrant the combination of all fish into a single analysis. Also, within both treatments, growth among fishes was variable (-0.02 to 0.13 mm/day), indicating that food distribution may not have been uniform, potentially due to established hierarchy or other factors. Whatever the mechanism, inducing a wide range of growth rates was the goal and it was accomplished across the fish utilized in the study, rather than simply two groups (i.e. “fast growth” and “slow growth). Thus, growth (mm/day) was calculated for individual fish and included as a covariate in the analysis.

The experiment was concluded October 6th, 2014 by euthanizing all round goby with an overdose of MS-222. Fish were re-measured for total length, tag number was noted, and otoliths were removed and stored in plastic vials in an enclosed box to limit the photo-degradation of oxytetracycline. Otoliths were viewed whole under an epifluorescence microscope (Zeiss, West Germany) with a factory-installed exciter filter using a mercury vapor lamp light source for reflected light. Otoliths were imaged at 3.2x magnification using a Canon Rebel XTI digital camera affixed to the phototube with an adapter. Images were processed using ImageJ software (imagej.nih.gov) and measurements made in the software were converted to actual lengths using an image of a calibration slide.

Measurements were made on three radii that appeared most suitable for annuli reading, using the most prominent point on the rostrum, ventral, and post-rostrum edges (Figure 3.1). The OTC mark was treated as an annulus for back-calculation purposes. Two back-calculation methods were compared: the direct proportion (Dahl-Lea) and Fraser-Lee methods (DeVries and Frie 1996). The direct proportion (DP) method assumes there is a linear relationship between otolith radius length and body length and that the intercept of the relationship is at the origin. For the DP method, back-calculated length is given by:
\[ L_i = \frac{S_i}{S_c} L_c \]

where \( L_i \) = the back-calculated length of the fish at the time of the \( i^{\text{th}} \) increment formation, \( S_i \) = length of the radius of the hard part at increment \( i \), \( S_c \) = total hard part radius length at capture, and \( L_c \) = length of fish at capture.

The Fraser-Lee method (FL) also assumes a linear relationship between otolith radius length and body length, but that the intercept of the relationship is not at the origin. For the FL method, back-calculated length is given by:

\[ L_i = \frac{L_c - a}{S_c} S_i + a \]

where \( a \) is the intercept of the line created by regressing fish length on hard part radius. The \( a \) parameter was calculated for each radius using a regression made with total length and radius length measurements from all fish in the study.

Accuracy (per cent difference of predicted vs. measured length at marking) was calculated as:

\[ \% \text{ difference} = \frac{L_i - L_m}{L_m} \times 100 \]

where \( L_m \) = actual length at marking. Accuracy measurements were compared between the two back-calculation methods and three radii using a mixed-model ANCOVA, with growth rate (mm/day) included as a covariate to understand how growth rate affects back-calculation accuracy. Fish number was included as a random effect to control for the lack of independence among measurements made on the same individual. Differences among radii and methods were assessed using a post-hoc Tukey’s HSD test with a significance level set at \( \alpha = 0.05 \).
Results

Across the two marking events, a total of 78 fish were marked and tagged. At the end, a total of 44 fish (56%) retained their alphanumeric tags. Of the fish that retained their alphanumeric tags, and were thus able to be related to their measured length at marking, 21 fish (48%) had a discernable and measurable OTC mark. Measurements were made on these 21 fish but in a few instances, the OTC mark was not readable on certain radii. Using the two back-calculation methods for all readable radii gave a total sample size of 114 back-calculation measurements.

In general, back-calculation underestimated length at marking (mean percent error = -5.4%, range -18.5 to 1.4 %). Back-calculation error varied significantly among the three radii ($F_{2,92.25} = 16.08, P <0.0001$) but was marginally non-significant for method ($F_{1,89.52} = 3.7093, P = 0.057$, Figure 3.2). The post-rostrum radius had significantly lower back-calculation error (mean = -3.5% error) than the other two radii. Growth rate was a significant covariate ($P = 0.003$) with a positive coefficient (Figure 3.3). The overall model showed relatively good fit ($r^2 = 0.63$).

The relationship between otolith growth and somatic growth is considered the most important factor influencing the accuracy of back-calculation models. When comparing the strength of the relationship among the three radii selected, the post-rostrum showed the closest regression ($r^2 = 0.69$), while otolith growth and somatic growth were not as tightly coupled in the rostrum ($r^2 = 0.37$) and ventral ($r^2 = 0.33$) radii (Figure 3.4).

Discussion

The main concern for error in back-calculation is the potential for decoupling of somatic growth and otolith growth. Thus an otolith radius whose growth most closely relates to growth...
in total length will be most accurate. This study observed that faster somatic growth leads to more accurate BCLs in round goby. This is in contrast to the findings of Panfili & Tomás (2001), who showed BCL error increased with increasing growth rate. However, when considering the direction of BCL error, their results may, in fact, agree. Because most of the BCLs in this study were underestimated, the positive relationship between growth rate and % error led to BCLs becoming more accurate (i.e. $L_i - L_m$ becomes less negative). However, Panfili & Tomás (2001) found mostly overestimated BCLs, with error increasing as growth rate increased thus leading to % error becoming greater (i.e. $L_i - L_m$ becomes more positive). Thus in both cases the relationship of $L_i - L_m$ with growth rate has a positive slope. The authors conclude based on their results that the faster a fish grows, the further it is from the model. However, when combined with our results, we conclude that there is a continuum on which slower growth may make a back-calculation model underestimate past length, while faster growth results in overestimation. Thus, there may be a level of growth in which otolith growth and somatic growth are properly coupled, and thus back-calculation models meet their maximum accuracy. This is what would be expected if fast growth leads to body size growing faster than the otolith, in which case the measured increment on the otolith would make up a smaller proportion of the radius than what would truly represent growth since that mark, leading to an overestimation of the fish length at that mark when using back-calculation.

In purple-spotted gudgeon (*Mogurnda adspersa*) total length growth was influenced by both food and temperature, however otolith growth was only influenced by temperature, causing a decoupling (Starrs *et al.* 2013). In fringed flounder, a generally strong relationship existed between somatic growth rate and otolith increment growth, but it became decoupled at the high and low ends of the growth rate spectrum (Reichert *et al.* 2000). In this study, the coupling of
somatic growth and otolith growth varied across the three otolith radii that were measured. The post-rostrum radius had the most consistent relationship when compared to the other two radii, and this resulted in the post-rostrum providing the most accurate BCLs.

The back-calculation error rates for round goby (ranging from -18% to 1.4%) were within the range found in other studies, suggesting that using round goby sagittal otoliths for back-calculation is a viable method. Klumb et al. (2001) used multiple marking events and found that measurements made to the first mark tended to overestimate length-at-marking by 2-8%, but BCLS estimated for the second and third marks underestimated length-at-marking by a similar magnitude. Also using multiple marks, Li et al. (2008) found a similar trend in that older marks tended to show a greater overestimation but BCLS became more accurate with more recent marks, with errors ranging from -5% to 15%.

The comparison of different radii was done in order to identify the optimal radius for back-calculation accuracy in future studies. Due to the abnormal shape of otoliths in Gobiid fish, it would not be prudent to utilize results from studies of other species for this purpose. The superior accuracy of the post-rostrum is in contrast to Li et al. (2008) which found the dorsal and distal radii to be most accurate, while Klumb et al. (2001) found no radius to be consistently best. The dorsal and distal radii were not measured due to the morphology of round goby otoliths not providing a clearly prominent point in those areas on which to conduct measurements. Based on these results, future work incorporating back-calculation of lengths using round goby otoliths in whole-view should use measurements made to the most prominent point on the post-rostrum for maximum accuracy.

Prior studies using similar methodology have confirmed the superiority of the Fraser-Lee model. Klumb et al. (2001) found it to outperform the (more modern) Weisberg and Biological
intercept models. In juvenile bluefish (*Pomatomus saltatrix*), however, the direct proportion method was found to outperform the Fraser-Lee, scale proportion hypothesis, and body proportion hypothesis (Roemer & Oliveira 2007). The Fraser-Lee method on average outperformed the direct proportion method (at a level approaching significance, $P = 0.057$). Thus, it would be recommended to use the Fraser-Lee method when possible based on previous research and this study’s inability to prove another method superior.

The production of random lobes on the exterior of the otolith could occasionally influence back-calculation estimates. Li *et al.* (2008) found lobes at the periphery of Atlantic cod (*Gadhus morhua*) otoliths could create an 8-15% difference in otolith width. The error introduced by the presence of lobes led to the distal radius having the poorest relationship between otolith width and fish total length, however this radius still had the most accurate BCLs. The proportionality of the otolith radius growth to total length growth was maintained even with the variability caused by lobes. This could be supported by the different relationship between otolith growth and fish growth across the three radii in goby. Thus, it is possible that random lobes or other unusual growth processes are present less in the post-rostrum radius of round goby otoliths, causing it to be the most accurate radius of the three. Variability caused by “accessory primordia” (also known as secondary growth centers) which are known to be present in round goby otoliths (Sokołowska & Fey 2011), could potentially cause a similar effect in which growth in a particular radius is exaggerated over others.

In conclusion, we provide useful insight into the use of otoliths for back-calculating past length of round goby. Our results shed light on the impact of the decoupling of somatic growth and otolith growth on back-calculated length estimates. Though previous studies have concluded that faster somatic growth may lead to more inaccurate BCLs, we have shown that the opposite
can be true. At normal growth rates, back-calculation models may likely represent past length quite well. However, we believe that accuracy declines with both fast and slow growth rates. Because the main use of back-calculation models is to understand and compare past growth rates, future work should consider the effect that this variation can have in the very metric fishery biologists are attempting to measure.
References


Chapter III Figures

Figure 3.1. Round goby (*Neogobius melanostomus*) otolith showing three radii used for back-calculation measurements.
Figure 3.2. Comparison of the average percent error of back-calculated length from known length at marking using two back-calculation methods and three otolith radii in round goby (Neogobius melanostomus).
Figure 3.3. Relationship between round goby (*Neogobius melanostomus*) somatic growth rate and the accuracy (% error) of back-calculated lengths (BCL) using two back-calculation methods and three otolith radii (rostrum = grey triangle, ventral = black square, post-rostrum = open circle).
Figure 3.4. Regressions of otolith growth against total length growth for round goby (*Neogobius melanostomus*) using A.) the post-rostrum, B.) rostrum, and C.) ventral radii.

A. 

B. 

C. 

R² = 0.6926

R² = 0.3723

R² = 0.3341
CHAPTER IV: OVERALL CONCLUSION

The nearshore zone of Lake Michigan has come under increased scrutiny lately as it has come to light that the food web of the lake is shifting to one driven by production in nearshore benthic areas (Turschak et al. 2014). This has highlighted the need for managers and researchers to understand the dynamic nature of this ecosystem (Seelbach et al. 2013) as well as the biotic interactions taking place there, especially those among native and invasive species. The overall effect of the round goby is not known, as it has been shown to have both positive and negative effects on native fishes. However, the magnitude of its presence in the food web is impossible to ignore as it has reached very high densities in southwest Lake Michigan and thus comprises a sizeable portion of the biomass in the food web. Results discussed here may indicate that their abundance may be negatively related to the abundance and condition of age-0 yellow perch. Though currently not considered one of the potential factors in the poor recruitment of yellow perch, if round goby are interfering with their ability to access benthic prey resources at a critical early life stage, it could be contributing to the current yellow perch population decline.

These effects may be mitigated by the strict habitat requirements of round goby which came to light in this study. Significantly higher abundance of round goby in a rocky location compared to a sandy area likely indicates that their density is related to the availability of large, rocky substrate necessary for spawning and shelter. Within our study region yellow perch have shown no significant variation among locations in terms of abundance. However, annual variation is significant even over the short duration of this study indicating that more long-term data must be utilized to create models describing environmental effects on yellow perch recruitment (Redman et al. 2011).
Results in this study relating to the high variability in growth in these two nearshore fish species highlight the importance of understanding the effects of environmental variability on fish production. As stated before, the future overall impact of round goby on the food web of Lake Michigan is uncertain but, given their increasing inclusion in predator diets (Rush *et al.* 2012, Crane *et al.* 2015), it is likely that goby biomass will become an important factor in overall fishery production (Johnson *et al.* 2005). Thus, understanding the factors influencing round goby growth and condition will be necessary for the parameterization of future ecosystem modeling efforts (He *et al.* 2015). Results of the round goby age-growth analysis in Chapter II have shown that spatial variability can be significant in these parameters, while the efforts towards the verification of back-calculation procedures described in Chapter III have led the way for future studies to calculate accurate growth histories of individual round gobies, which will help researchers understand their life history as well as factors influencing their success.

Overall, the results of this research highlight the underappreciated variability inherent in the fish community of nearshore Lake Michigan, even at a local scale. Research into fish production and nearshore food web processes would benefit from more extensive and higher resolution data on the benthic substrate and habitat of this zone (Creque *et al.* 2010). Future study should take into account the diversity and complexity of these habitats when attempting to model and understand the complex and dynamic nature of this ecosystem.
References


