

Evidence for the importance of invasive *Dreissena* veligers as a novel prey item for larval fish

by

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ABSTRACT

The establishment of invasive dreissenid mussels in the Laurentian Great Lakes has had far reaching effects, from changes in the physical structure of habitat to changes in zooplankton community composition. Adult dreissenid mussels are believed to have indirectly contributed to reductions in prey fish growth by reducing densities of important prey items such as *Diporeia* and zooplankton. Through these effects, dreissenid mussels have altered the prey available to fish in the critical larval stages of their lives. However, the effects of larval dreissenid mussels (also called “veligers”) on fish are relatively unknown. There is potential for native and naturalized larval fish to take advantage of veligers as a novel prey item. To assess the importance of veligers in larval fish diets, we examined the stomach contents of larval burbot (*Lota lota*), rainbow smelt (*Osmerus mordax*), and *Coregonus spp.* consisting mainly of bloater (*Coregonus hoyi*) collected from Lake Huron in July of 2017. Preference for available environmental zooplankton prey items was evaluated using Vanderploeg and Scavia’s *E**. Results indicated that veligers were rarely selected by rainbow smelt or coregonines but were in some cases highly preferred by burbot. Further, the results of a mixed model analyzing the different factors that contribute to veliger preference indicated that small and medium sized larval burbot had more positive preference for veligers than larger larval burbot, indicating that veligers could be an important prey item while larvae are gape limited and unable to consume larger zooplankton. Thus, consideration of the ability of native fish species to adapt to and exploit abundant veliger prey is necessary for managers to fully understand the positive and negative impacts of dreissenid mussels on Great Lakes food webs.

INTRODUCTION

Invasive species and the negative effects they have on ecosystems are well studied. However, there is potential for native or naturalized species to exploit invasive species as prey items and potentially compensate for the well-documented negative consequences. Such occurrences are widespread and have been documented in numerous aquatic ecosystems. For example, in South America, invasive golden mussel (*Limnoperna fortunei*) veligers were found to be an important prey item in the larvae of 18 species of fish, with veligers being the dominant biomass ranging from 15-71% of larval diets examined (Boltovskoy & Correa, 2014; Paolucci et al., 2007). Consumption of invasive *Bythotrephes* by native cisco (*Coregonus artedii*) in Lake Superior and by naturalized alewife (*Alosa pseudoharengus*) in Lake Michigan was so extensive that it was hypothesized to seasonally regulate *Bythotrephes* abundance (Keeler et al. 2015). Round goby (*Neogobius melanostomus*), a species invasive to the Laurentian Great Lakes, has prominently appeared in the diets of native fishes. For example, round goby has been found to consist of 77% and 53% of adult burbot (*Lota lota*) diets by weight in Lake Huron and Lake Michigan, respectively (Hensler et al., 2007). In Lake Erie, growth rates of native smallmouth bass (*Micropterus dolomieu*) have increased due to the consumption of round gobies (Crane & Einhouse, 2016; Steinhart et al., 2004). Round goby has also become a dominant prey item in Lake Michigan lake trout (*Salvelinus namaycush*) diets, comprising 67% of diets by weight in the spring (Luo et al., 2019). Dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*), another set of species invasive to North America of Ponto-Caspian origins, have become features of native fish diets as well. Native larval American shad (*Alosa sapidissima*) in the Hudson River estuary were found to commonly consume invasive zebra mussel (*Dreissena polymorpha*)

veligers (Nack et al., 2015). Adult dreissenid mussels have also been found in the diets of adult fishes, such as freshwater drum (*Aplodinotus grunniens*) and yellow perch (*Perca flavescens*) in Lake Erie and lake whitefish (*Coregonus clupeaformis*) in Lakes Michigan, Huron, and Ontario (Hoyle et al., 1999; Morrison et al., 1997; Pothoven & Madenjian, 2008).

Since their discovery in Lake Erie in the 1980s (Carlton, 2008; Mills et al., 1993), invasive zebra and quagga mussels have become prolific within the Great Lakes and have had extensive impacts on abiotic processes. As ecosystem engineers, dreissenid mussels have significantly altered the benthic habitat they invade, affecting ecosystem processes such as oxygen availability, nutrient mineralization, and sedimentation as well as physically altering habitat by colonizing both hard and soft sediments and building reefs (Karatayev et al., 2002; Vanderploeg et al., 2002). Dreissenid mussels are also capable of increasing water clarity and thus may indirectly affect patterns of diel vertical migration in zooplankton as they must swim deeper to avoid predation and ultraviolet radiation (Alonso et al., 2004; Karatayev et al., 2002).

Beyond their effects on the abiotic environment, dreissenid mussels have also influenced multiple trophic levels in the Great Lakes. Along with declining phosphorus loads which resulted from the signing of the binational Great Lakes Water Quality Agreement in 1972, dreissenid mussels are thought to have contributed to the oligotrophication of some of the Laurentian Great Lakes (e.g., Lakes Michigan, Huron, Ontario) by consuming large portions of the spring phytoplankton bloom (Bunnell et al., 2014; Evans et al., 2011; Vanderploeg et al., 2010). Dreissenids may also contribute to alterations in the zooplankton community due to their ability to consume phytoplankton of a wide size range (which includes nano, pico, and microplankton) (Carrick et al., 2015). This generalized feeding strategy has led to the hypothesis that dreissenid mussels can outcompete native species of mesozooplankton that are restricted to feeding on specific types of phytoplankton (Jørgensen et al., 1984; Lavrentyev et al., 2014; Tang et al., 2014). Oligotrophication in these lakes has resulted in a zooplankton community dominated by calanoid copepods (Barbiero et al., 2009, 2012; Gannon & Stemberger, 1978). In addition to affecting zooplankton, dreissenid mussels are also hypothesized to have contributed to the decline of the native amphipod *Diporeia* (Vanderploeg et al., 2010). Both *Diporeia* and zooplankton are important prey for higher trophic levels, and their decline has consequences. The downward trend of *Diporeia* from the 1990s through the 2000s is consistent with declining prey fish growth in the Great Lakes, whereas reductions in zooplankton biomass may negatively affect the growth of planktivorous predators such as predatory zooplankton, planktivorous adult fish, and larval fish (Bunnell et al., 2018).

Prey fish populations in Lakes Superior, Michigan, and Huron have been declining since the 1990s through at least 2010, although this decline is not distributed equally amongst species (Bunnell et al., 2018; Gorman, 2019). Rainbow smelt (*Osmerus mordax*), one of the subjects of this study, has become a less dominant member of the prey fish community across the Great Lakes since the 2000s, and energy density of rainbow smelt in Lakes Huron and Erie are declining (Dai et al., 2019; Gorman, 2019). Bloater (*Coregonus hoyi*), another subject of this study, has recently replaced rainbow smelt and alewife in Lakes Michigan and Huron in terms of being a dominant prey species in the Great Lakes, although their recruitment is still in a precarious position. For example, larval bloater in Lake Michigan in 2015 were found to have growth rates 40% lower than reported in previous decades (Eppehimer et al., 2019). Meanwhile, cisco have experienced a resurgence in Lake Michigan beginning in the mid-2000s (Claramunt

et. al., 2019). Native predatory fish are not exempt from these population fluctuations either. United States Geological Survey (USGS) bottom trawl data shows that burbot populations have been declining in Lake Michigan-Huron and Lake Ontario from the late 1990s to at least 2004, with declines in Lake Erie also happening in the early 2000s (Stapanian et al., 2008). One potential explanation for the declining biomass of these fish species is reduced survival at the critical larval stage, as the zooplankton community has changed with ongoing oligotrophication.

One potential mechanism that contributes to declining larval survival is starvation. Species with relatively small larvae have been found to be disproportionately more likely to starve (Miller et al. 1988). Thus, larval rainbow smelt (length at hatch: 4.1-6.0 millimeters) and burbot (length at hatch: 3.9-5.0 millimeters), which have a smaller size at hatch, are at a greater risk of starvation than coregonines (bloater length at hatch: ~10 millimeters, cisco: 8.5-12.8 millimeters), which tend to have a larger size at hatch (Auer 1982). Thus, burbot and rainbow smelt may be more dependent on small zooplankton prey once they begin exogenous feeding.

Larval mussels (i.e., veligers) could serve as a supplemental prey item for larval fish. Despite the pervasive negative effects that dreissenid mussels have had on the Laurentian Great Lakes ecosystem, there is potential for larval fish to adapt and exploit veligers as a novel prey item given that they can be highly abundant within the Great Lakes in middle to late summer (Bowen et al., 2018; Kirkendall et al. 2021, Pothoven & Olds, 2020). Examples of Great Lakes larval fish eating veligers are numerous. One of the earliest observations of veligers in Great Lakes larval fish diets was when veligers were found to be common in the diets of larval alewife (Sprung, 1993). Early-feeding yellow perch in southeastern Lake Michigan have also been found with diets that mainly consisted of dreissenid veligers (Withers et al., 2015). In addition, while the importance of veligers in the diets of Great Lakes larval fish has not been a focus of many previous studies, some of these studies still report high numbers of veligers in larval fish diets. In a study of growth rates of Lake Michigan larval bloater and alewife, veligers were the most common diet item in larval alewife stomachs and the third most common in larval bloater stomachs (Eppheimer et al., 2019). Despite some evidence that veligers are being consumed by some larval fish species in the Great Lakes, scientists lack a comprehensive understanding of what species exploit veligers, the environmental conditions that lead to variation in exploitation, and under which conditions veligers are preferred. The objective of our study was to evaluate the importance of dreissenid veligers as novel prey items in the diets of three of the most common species of native or naturalized larval fish collected in July of 2017 in Lake Huron (i.e., burbot, rainbow smelt, and bloater) and to analyze what conditions create preference for veligers. By exploring these questions, we can learn which species have the potential to adapt to changing prey communities and may benefit from the presence of these novel prey items to avoid starvation.

MATERIALS & METHODS

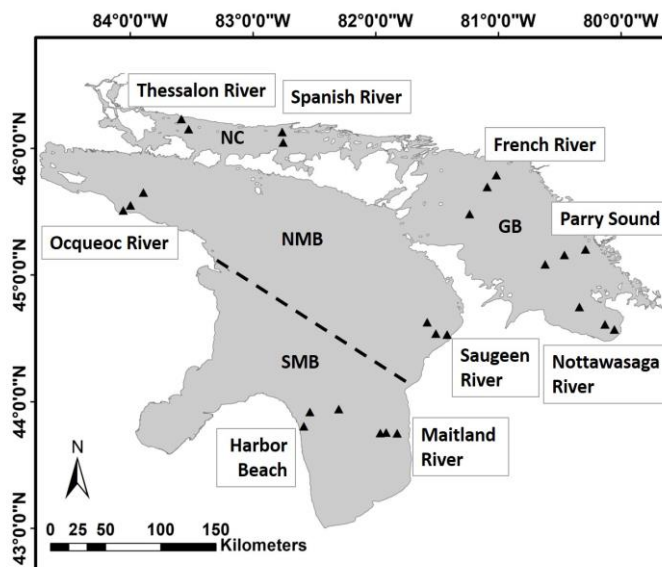


Figure 1: Map of sample sites ordered within transects along which sampling for the Cooperative Science and Monitoring Initiative occurred in the summer of 2017. Sampling locations are indicated by triangles. NMB=North Main Basin, SMB=South Main Basin, GB=Georgian Bay, NC=North Channel. Map by Patty Armenio.

Study Area:

Sampling was performed by USGS during the daytime at twenty-seven sites in Lake Huron from 6 July 2017 to 26 July 2017 as part of the Cooperative Science and Monitoring Initiative (Figure 1). These sites were organized within nine transects distributed across Lake Huron. The transects from North Channel extended outward from Thessalon River and Spanish River. In Georgian Bay, transects extended from French River, Parry Sound, and Nottawasaga River. The remaining four transects from the Main Basin were divided between North and South based on differences in bathymetry (Barbiero et al., 2009). In the North Main Basin, transects extended outward from Ocqueoc River and Saugeen River. In the South Main Basin, they extended from Harbor Beach and Maitland River. Sampling stations were placed at bottom depths of 18, 46, and either 68, 73, or 82 meters within each transect, depending on lake bathymetry. Samples were assigned serial numbers based on the type of sample, the port and depth they were taken at, and in the case of ichthyoplankton samples, if the sample was collected by surface or oblique tow.

Sampling locations were based on a study design intended to determine if nearby tributaries influenced the lower trophic level productivity in Lake Huron for at least the nearshore 18 meter stations. Thus, these transects are near rivers flowing into Lake Huron, except for Harbor Beach, which has no nearby river but is likely influenced by water flowing out of Saginaw Bay.

Field Sampling:

Environmental Data Collection

Temperature and fluorescence profiles were measured at each site using a Seabird bathythermograph to guide where samples for water quality analysis would be collected. Water samples were collected using a 1-liter Niskin bottle from the top, middle, and near-bottom of the profiles. In July, when the lake was stratified, top layer collections were taken 2 meters below the surface and bottom layer collections were taken 2 meters above the lake bottom. Middle layer collections were taken either at the depth where maximum fluorescence occurred (>2 times the baseline fluorescence) or, if no maximum fluorescence was observed, at the midpoint of the metalimnion. To directly measure chlorophyll *a* concentration, 1 liter of water was filtered through a 47-millimeter diameter Whatman GF/F filter under low vacuum pressure immediately after it was collected. The filter was then placed in a foil-wrapped vial and frozen at -80 degrees Celsius.

Environmental zooplankton collection

Using a 64-um closing mesh net, the same layers of water that were fished for ichthyoplankton were sampled for zooplankton. At 18-meter sites, samples were collected from 0-10 meters. At 46-meter sites, samples were collected from two layers, one layer from 0-20 meters and one layer from 20-35 meters. At 68-, 73-, or 82-meter sites, samples were collected in two layers, one layer from 0-20 meters and one layer from 20-40 meters. For a given sample, the beginning flowmeter numbers were recorded, and the net was lowered to the determined depth based on the site and brought back up to the top depth at a speed of 0.5 meters/second; if the top depth of the tow was 20 meters, rather than the surface, the net was closed by deploying a messenger at 24-meter bottom depth. The ending flowmeter numbers were recorded. The cod end was then placed in a bucket of water with half an effervescent tablet placed into the cod end of the net to narcotize the zooplankton. The contents of the cod end were rinsed into a labeled sample jar. 10% buffered formalin was added to the jar until the concentration measured 5%.

Ichthyoplankton:

Using a 1-meter by 2-meter neuston net, surface tows were collected off the side of the ship, towing the net through the top layer of the water column for 15 minutes. Using a 500-micrometer mesh, 1-meter diameter, circular ichthyoplankton net, oblique tows were collected off the stern of the ship. At 18-meter sites the net was towed for 5 minutes each at 10 and 7 meters deep. At 46-meter sites the net was towed for 2 minutes each at 35, 30, 25, 20, 15, 10, and 7 meters deep. At 68-, 73-, or 82-meter sites: net was towed for 2 minutes each at 40, 35, 30, 25, 20, 15, 10, and 7 meters deep.

The contents of the net were rinsed down to the cod end. As much of the water was removed as possible, and the sample was poured into a labeled jar and filled with 95% ethanol. All samples were checked within 48 hours to determine whether ethanol needed to be replaced to maximize preservation.

Laboratory Processing:

Environmental Zooplankton:

All environmental zooplankton samples were stained with phloxine B to ease identification. The whole sample was examined for “clumps” of large predatory cladocerans that could interfere

with subsampling methods. These “clumps” were checked to make sure that smaller zooplankton were not attached before being removed for later processing.

After removing the “clumps”, the sample was diluted with reverse osmosis water to reach an ideal concentration of 200 crustacean zooplankters per milliliter aliquot. After mixing the sample in a figure-8 pattern, a 1-milliliter aliquot was taken using a Hensen-Stemple pipette and transferred to a counting wheel. Using a dissecting microscope, all individuals except for dreissenid veligers, rotifers, and nauplii in this aliquot were identified and counted. Up to 20 individuals were measured for each taxa and sex was recorded for mature copepods. If 200 crustacean zooplankters were counted within the first 1-milliliter aliquot, no other aliquots were processed. If less than 200 zooplankters were counted, additional 1-milliliter aliquots were processed until at least 200 zooplankters had been counted.

All adult zooplankton were identified to species, except for *Bosmina* spp., and copepodites which were identified to genus only for *Limnocalanus*, *Senecella*, *Mesocyclops*, *Tropocyclops*, and *Epischura*. All other copepodites were identified simply as cyclopoid or calanoid copepodite. Copepod nauplii (except for *Senecella* nauplii), rotifers, and dreissenid veligers, were not counted as they are microzooplankton and are counted at a later stage during processing.

After at least 200 individual zooplankton were enumerated, the subsample was returned to the original sample. This sample was then diluted more using reverse osmosis water to reach a more ideal concentration of 200 microzooplankters per 1 milliliter aliquot before drawing a 1-milliliter aliquot using a Hensen-Stemple pipette. The aliquot was then placed in a Sedgewick-Rafter cell under a compound microscope to count microzooplankton. As with previous samples, 1 milliliter aliquots were taken until 200 individuals were counted. However, only nauplii and rotifers (identified to genus) contributed to the 200 count. Dreissenid veligers and Gymnosperm pollen were counted, but those counts did not contribute to the 200 microzooplankton threshold. Veligers were not broken down into *D. polymorpha* and *D. bugensis* by genetic analysis in this study. However, the Great Lakes of today are primarily dominated by *D. bugensis* and one may assume that most of the veligers are also *D. bugensis* (Burlakova et al., 2018).

Veligers and pollen were measured along the longest axis. Whether length, width, or both were measured for rotifers was dependent upon taxa according to the Environmental Protection Agency’s Standard Operating Procedure for Zooplankton Analysis (EPA, 2016). As with the crustacean zooplankton counts, the first 20 individuals counted for each group were measured.

After processing the microzooplankton and microzooplankton subsamples, a whole count was performed, which included the “clumps” of predatory zooplankton that might have previously been removed from the sample. All predatory cladocerans or mysids were enumerated during this step. A measurement was recorded for the first 20 individuals of each taxa. *Bythotrephes* and *Cercopagis* were counted and measured by instars. *Bythotrephes* were measured from the proximal end of the spine to the “S-curve” or its body length. Other zooplankters were measured from the top of the head or front of the rostrum to the base of the caudal spine or the most distant part of the carapace.

Ichthyoplankton:

For each serial, larval fish were identified to the lowest taxonomic level possible using Auer (1982). For burbot, rainbow smelt, and coregonines, up to the first 10 larvae of each taxa were selected for stomach dissection. If at least 30 percent of those 10 fish had identifiable stomach contents, then up to 30 fish per taxa from that serial were dissected.

Before a fish was dissected, total length and gape were measured using a camera microscope using Image Pro Premier version 9.1. Total length was measured from the head to the end of the fin. Gape was measured by inserting a minuten into the fish's mouth until it was open but not strained, and the measurement was taken from the top to bottom jaw. While total length measurements were taken for all fish, gape was taken for only a subset of them.

To process a larval fish diet, each fish was placed under a dissecting microscope in a dish of water. Using minutenens, the fillets of the fish were peeled away, and the gut was removed from the body. The stomach was then opened and scraped using minutenens to remove all organisms present in the fish's gut. These prey items were then identified and counted.

When counting, diet items were mostly identified to species, except for nauplii, rotifers, and veligers, and *Leptodiptomus* spp. One other exception to this rule is that all immature cyclopoid species were labeled 'cyclopoid copepodites' apart from *Mesocyclops* and *Tropocyclops* copepodites, which were identified to genus. Immature calanoids were identified to species when identifiable characteristics were present and identified as 'calanoid copepodites' when further definition was not possible.

There were specific requirements for counting different diet items. Fifth legs and urosomal segments needed to be present for copepod identification. Copepod heads and rami were counted individually. Copepod heads were identified as 'calanoid' or 'cyclopoid.' Rami were identified to genus if identifying features such as fifth legs or setae were present and identified to order if these characteristics were not present. After processing the sample, the number of rami was subtracted from the number of heads. Any leftover heads without rami counterparts were listed as unknown calanoid or cyclopoid copepods. Body parts without head, rami, or fifth legs were not counted to avoid double counting. Rotifers, dreissenid veligers, and nauplii were counted based on intact organisms.

When identifying cladocerans to genus, it was necessary for the post abdomen to be present. This rule had the following exceptions: For *Bosmina*, it was required that the rostrum be present. For *Bythotrephes*, tail spines had to be present and have some tissue attached to them. The eye and part of the body had to be present to count *Polyphemus*, and the tail spines were used when counting in absence of the body for *Leptodora*. For *Holopedium*, pairs of the large swimming antennae were counted in absence of the carapace.

The first 10 whole individuals of each taxa found in the diet were measured using the eyepiece of a dissecting microscope at five times magnification for nauplii, rotifers, and veligers and two times magnification for all other zooplankters. For cladocerans, the distance from the head to the caudal spine or the most distant part of the carapace was measured. For copepods, the distance from head to rami was measured. For nauplii, rotifers, and veligers, the body was measured along its longest axis. For *Bythotrephes*, the length of the spine was measured and the instar, if known, was recorded.

Chlorophyll

All water chemistry samples were analyzed at the EPA Great Lakes Toxicology and Ecology laboratory (see details in Kirkendall et al. 2021). Chlorophyll *a* was analyzed by fluorometry (TD-700 Turner Designs, Sunnyvale, CA, USA) after extraction using magnesium-saturated acetone (Welschmeyer, 1994).

Statistical Analysis

Comparing diet composition and electivity across three larval fish species

To look for evidence of size-based preference for veligers, we compared the size of veligers found in all larval fish diets to the size of available veligers in the environment using Welch's t-test. Welch's t-test was used to account for uneven sample size and non-normal distribution of data.

To determine the preferred prey items of burbot, rainbow smelt, and bloater, electivity, E^* (Vanderploeg & Scavia, 1979a, 1979b) was calculated for each larval fish using the following equation:

$$(1) E_i^* = [W_i - (1/n)]/[W_i + (1/n)],$$

where n is equal to the number of prey species present in the environment and i is the i^{th} prey taxon. W_i is derived from the following equation:

$$(2) \alpha_i = W_i = \frac{r_i/p_i}{\sum_i^n r_i/p_i},$$

where W_i and α_i are equivalent, r_i is the proportion of a given prey item i in the diet, and p_i is the proportion of prey item i in the environment. Proportions for diet prey items were calculated by dividing the number of a given prey item found in a fish's diet by the total number of all prey items in the diet in the same fish. Proportions for environmental prey items were calculated by dividing the density of a given environmental taxon found at one site by the total density of all environmental zooplankton at that same site. One issue we had to contend with was that, based on our collection methods, we did not know where in the water column the fish from deeper oblique tows came from and thus did not know what "layer" of zooplankton prey they were exposed to. In order to calculate environmental prey proportions that corresponded to fish collected in oblique tows at 46 meter and 68/73/82 meter sites, we used the average prey density based on what was collected in the two layers.

E^* was chosen, as opposed to other measures of selectivity, because it accounts for the uneven number of prey species encountered across samples which allows for meaningful comparisons between fish at different sites (Vanderploeg & Scavia 1979b). Given two fish that have the same W_i for a given prey item, the fish which encountered more possible prey items will have a higher E^* for the prey item in question. In addition, the range of E^* (-1 to 1) allows one to differentiate between avoidance (close to -1) and random (0) and preferential selection (close to 1). However, it is practically impossible to obtain an E^* value of 1, as this would require $r_i = 1$, $p_i = 0$, and n to be infinite (Lechowicz 1982).

Examining factors controlling burbot electivity

Of the three larval fish taxa that were dissected, only burbot had larger number of individuals that consumed veligers and thus was the only species examined to understand which factors may be controlling electivity for veligers. We first examined the relationship between larval size and electivity, prey size, and fish gape. In lakes, burbot begin their lives as passive drifters within the limnetic portion of the water column. As they grow, their swimming ability improves (McPhail & Paragamian, 2000). After the yolk sac is consumed, burbot will migrate to the surface to begin exogenous feeding. During this time, burbot may undergo weak diel migrations (Fischer 2003, Wang & Appenzeller 1998). Later, larval burbot will experience another habitat shift where they migrate to and settle in benthic habitats (Fischer 1999). We plotted the 95th percentile of prey lengths consumed by burbot based on their millimeter size class of total length and found a non-linear relationship between fish size and gape limitation (Figure 2A): fish less than 7 mm in length consumed prey smaller than their gape, fish between the lengths of 7 and 10 mm consumed larger prey with increasing fish size, and fish greater than 10 mm consumed a vast distribution of prey sizes unrelated to their length. Based on ontogenetic shifts in swimming ability and the relationship between maximum prey sizes and larval length, size classes for larval burbot were designated as: small: <7 mm, medium: 7-10 mm, large: >10 mm. We believe that these different stages reflect the biological and habitat changes burbot undergo in their early life history. Based on these divisions, there were 39 large, 98 medium, and 88 small larval burbot.

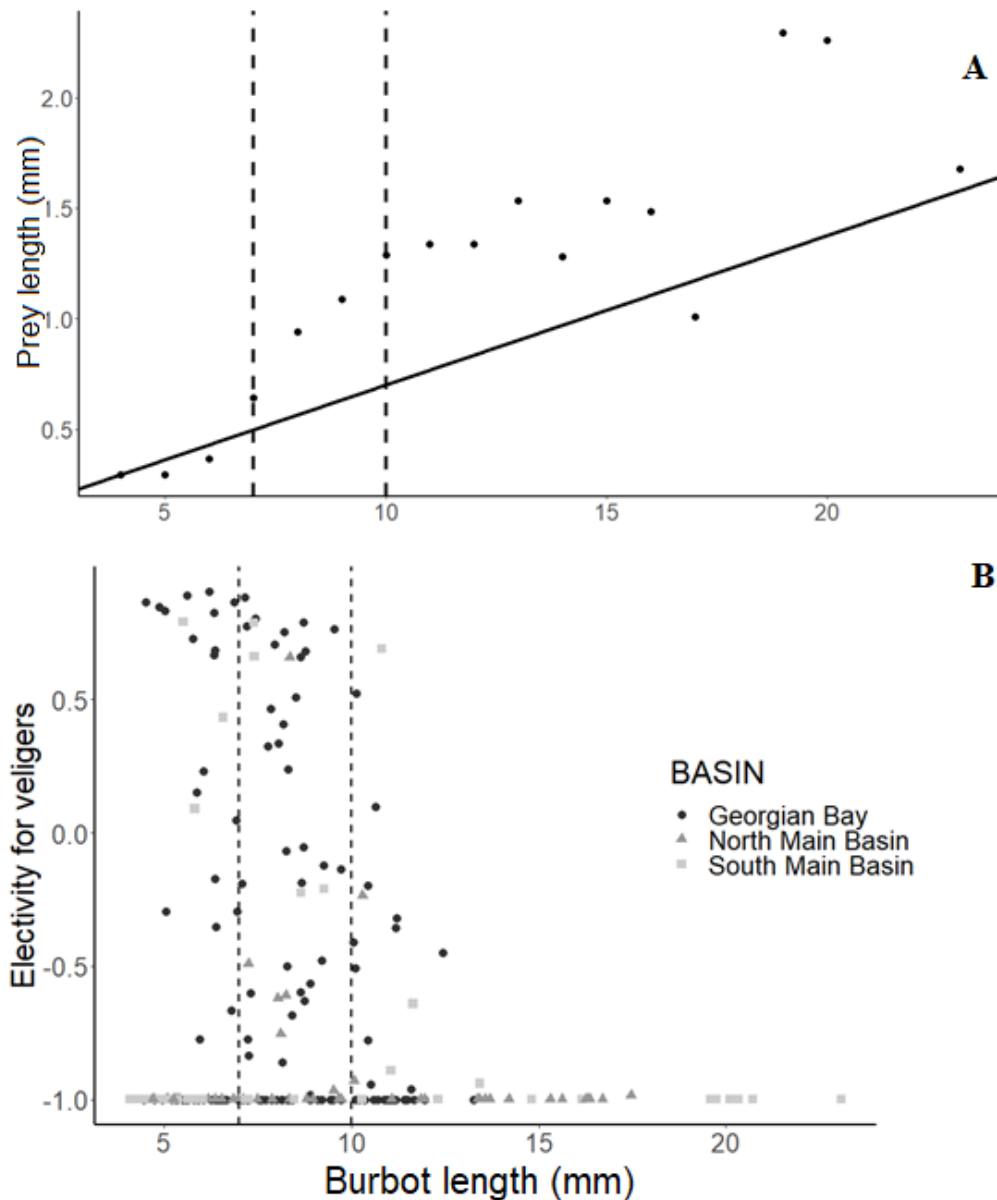


Figure 2: Illustrations of how burbot feeding varies with size. In both panels, dashed vertical lines represent the divisions ultimately decided to separate size classes at 7 and 10 millimeters, respectively. Panel A) illustrates how prey lengths consumed by burbot vary with total length. Solid line represents the length gape relationship estimated for larval burbot ($y=0.0676x+0.0241$). Solid points represent the 95th percentile for prey length for a given millimeter length class. Panel B) illustrates how estimated electivity for veligers changes with total length. Seventeen burbot with empty stomachs between 4 mm and 8 mm in length were excluded from this graph.

We fitted a mixed multivariate linear model to determine if there was any relationship between electivity and larval burbot size class, available prey size, and environmental characteristics including temperature, chlorophyll, and distance offshore. Average chlorophyll *a* down to fishing depth was included as a measure of productivity which may account for zooplankton prey present. Station depth accounted for how far offshore larvae were and the different potential prey

that may be available to them. Temperature was included due to its effects on fish consumption, growth, and basal metabolic rate. Fish have higher metabolisms at higher temperatures; thus, they must eat more as temperature warms. The average available zooplankton length for a given serial (excluding veligers) and average veliger length for a given serial were included in the model as separate parameters to account for the relative size of a veliger, which is often much smaller than the available alternative zooplankton prey. This model also included transect as a random effect to account for the potential spatial differences that could not be accounted for in our model. To avoid issues of differing scales in the data, a z-score transformation was applied to all continuous variables. Significance was determined using $\alpha = 0.05$.

When formulating these models, burbot collected from surface tows were excluded due to their small number (15 surface fish, 210 oblique fish) and due to their unequal error in measurement of environmental variables compared to burbot from oblique tows. For example, measurements of temperature for surface burbot were likely to be much more accurate than oblique burbot, because oblique burbot were taken from a much larger vertical range within the water column. Conversely, zooplankton were estimated from the same large vertical range that oblique burbot were collected over, but no zooplankton sample was taken from only the surface.

All aforementioned calculations, statistical comparisons and model fitting used R version 3.6.1 (R Core Team, 2019). The *lme4* package was used to fit the mixed multivariate linear model (Bates et al., 2015). The variance inflation factor (VIF) function in the package *car* was also used to look for collinearity among the fixed variables (Fox & Weisberg, 2019).

RESULTS

Larval Fish

Over the July sampling period, 383 larval burbot, 1270 larval rainbow smelt, and 107 larval coregonines were caught in Lake Huron. Genetic analysis performed on the coregonines collected estimated that greater than 95% of these coregonines were bloater, not cisco. Other species of larval fish caught during the July sampling period included 6 deepwater sculpin (*Myoxocephalus thompsonii*), 188 shiners (*Notropis* spp.), 401 round goby, and 7 yellow perch. The sites where larval fish were collected varied in terms of number of composition and abundance. Noticeably, only rainbow smelt were collected in the North Channel of Lake Huron (Tables S1 and S2). Of the fish that were dissected, 225 burbot, 46 rainbow smelt, 72 coregonines contained stomach contents. Of the 72 coregonines with stomach contents, 64 were identified as bloater, 4 were identified as cisco, and 4 were unable to be unidentified. Burbot ranged in total length from 4.09 mm to 23.08 mm, rainbow smelt ranged from 9.44 mm to 37.50 mm, and coregonines ranged from 8.36 mm to 31.00 mm. Burbot sported greater gape proportional to their length when compared to coregonines and rainbow smelt based on the slope of their length-gape relationship, although this difference was not tested for significance. Burbot also occupied a smaller size range compared to both rainbow smelt and coregonines and were more often shorter than rainbow smelt and coregonines (Figure S1).

Electivity

The most common prey item, in terms of diet proportion, was copepod nauplii for larval burbot and diatomid adults for larval rainbow smelt and coregonines. The most highly preferred prey

item based on the mean electivity for each species matched these respective prey items for burbot and rainbow smelt, while the most preferred prey item for coregonines were cyclopoid copepodites. Electivity calculations revealed that veligers were not a preferred prey item of rainbow smelt or coregonines (E^* was less than zero for all individuals of these species) but were preferred by several individual burbot larvae (Figure 3). Forty percent of burbot with stomach contents consumed veligers, with the number of veligers consumed ranging from 1 to 293. The mean electivity for veligers by burbot was -0.64, with a standard deviation of 0.60. For rainbow smelt and coregonines, instances of consumption of dreissenid veligers were less common. Less than 7% of rainbow smelt with stomach contents ate veligers (Figure 4), with no rainbow smelt having consumed more than 2 veligers. The mean electivity for veligers by rainbow smelt was -0.99, with a standard deviation of 0.04. For coregonines., 29% of those with stomach contents consumed veligers (Figure 5), none consuming greater than 7 veligers. The mean electivity for veligers by coregonines was -0.96, with a standard deviation of 0.24. Thus, rainbow smelt and coregonines were more likely to avoid veligers than burbot, whereas the tendency for burbot to elect veligers was more variable. In addition, the mean electivity for veligers by small burbot was -0.67, with a standard deviation of 0.64. For medium burbot, mean electivity was -0.5064 and standard deviation was 0.64. For large burbot, mean electivity was -0.94 and standard deviation was 0.18. Lower electivity for veligers means that large burbot avoided veligers more often than small or medium sized burbot, while the greater standard deviation in E^* by small and medium larvae shows that small and medium sized burbot had more varied instances of preference for veligers (Figure 7).

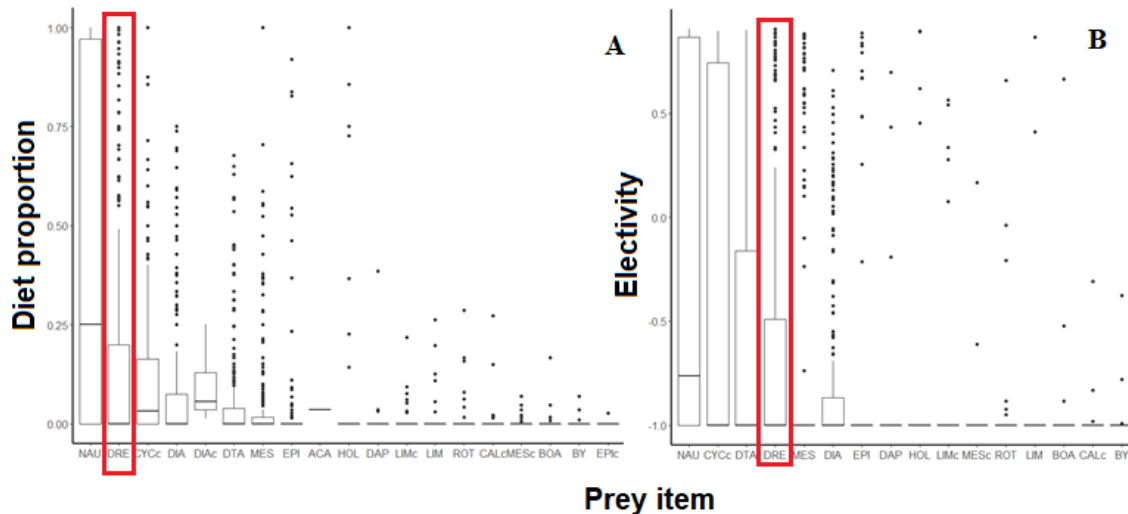


Figure 3: Diet summaries of all prey items for larval burbot sampled in Lake Huron in July of 2017. Panel A) depicts a box and whisker plot of estimated diet proportions. Panel B) depicts a box and whisker plot of estimated electivity (E^*). In both panels, the middle line of the box represents the median, while the top and bottom of the box represents the 25th and 75th percentiles respectively. Items with diet proportions equal to zero and electivity values equal to negative one were excluded. Dreissenid veligers (DRE) are outlined in red. Other prey abbreviations include NAU=copepod nauplii, CYCc=Cyclopoid copepodite, DIA=Diaptomid adult, DIAc=Diaptomid copepodite, DTA=*Diacyclops thomasi* adult, MES=*Mesocyclops edax* adult.

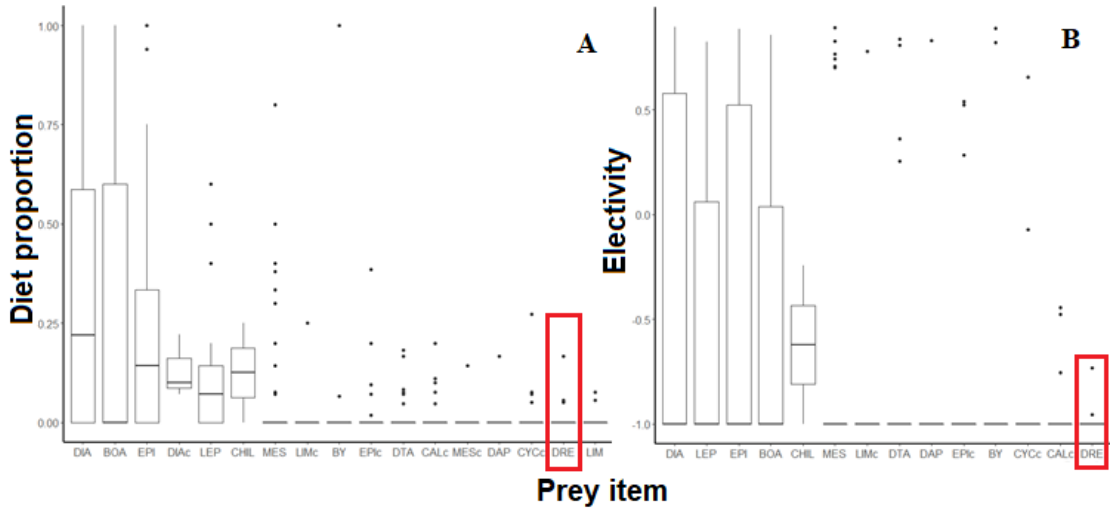


Figure 4: Diet summaries of all prey items for larval rainbow smelt sampled in Lake Huron in July of 2017. Panel A) depicts a box and whisker plot of estimated diet proportions. Panel B) depicts a box and whisker plot of estimated electivity (E^*). In both panels, the middle line of the box represents the median, while the top and bottom of the box represents the 25th and 75th percentiles respectively. Items with diet proportions equal to zero and electivity values equal to negative one were excluded. Dreissenid veligers (DRE) are outlined in red. DIA=Diaptomid adult, BOA=*Bosmina*, EPI=*Epischura lacustris* adult, DIAC=Diaptomid copepodite, LEP=*Leptodora kindtii*, CHIL=Chironomid larvae, DRE=Dreissenid veligers.

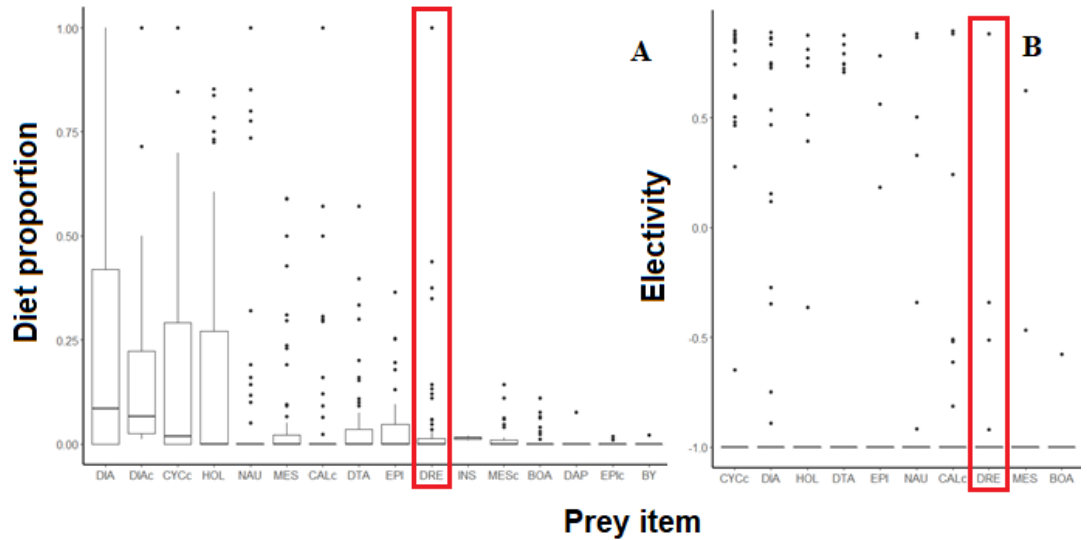


Figure 5: Diet summaries of all prey items for larval coregonines sampled in Lake Huron in July of 2017. Panel A) depicts a box and whisker plot of estimated diet proportions. Panel B) depicts a box and whisker plot of estimated electivity (E^*). In both panels, the middle line of the box represents the median, while the top and bottom of the box represents the 25th and 75th percentiles respectively. Items with diet proportions equal to zero and electivity values equal to negative one were excluded. Dreissenid veligers (DRE) are outlined in red. DIA=Diaptomid adult, DIAC=Diaptomid copepodite, CYCc=cyclopoid copepodite, HOL=*Holopedium gibberum*, NAU=copepod nauplii, DTA=*Diacyclops thomasi* adult, EPI=*Epischura lacustris* adult.

Veligers pooled from the diets of all three larval fish species were significantly larger than the veligers sampled in the environment for each basin ($P < 0.0001$ for all basins), except in the case of North Channel, where no fish were found to have veligers in their stomachs and thus the comparison could not be made (Table S3, Figure 6).

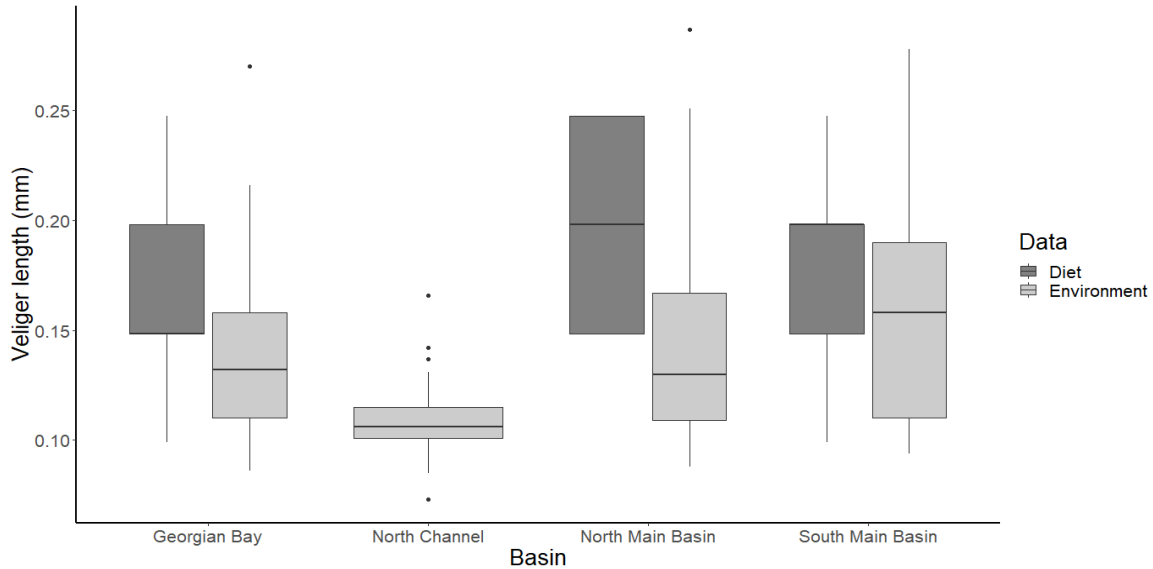


Figure 6. A box and whisker plot showing the lengths of veligers in the diets of larval fish and in the environment for each basin. Middle lines represent the median length of each group, while the box represents the 25th and 75th percentile. Further details can be found in Table S3.

The mixed model indicated that electivity for veligers varied by size class and average zooplankton length (of prey other than veligers) (Table 1). For fish in the large size class, in this case represented by the intercept, the estimated mean electivity for veligers was found to be significantly different from zero. For burbot of the medium size class, electivity for veligers was found to be different from the intercept and thus different from that of the large size class with estimated mean electivity for veligers being 0.31 greater than the large size class. The estimated mean for small larvae electivity for veligers was found to be not different ($p=0.08$) from the intercept. Electivity for veligers increased with increasing mean zooplankton size. Because the data were Z-score transformed, for every 1 standard deviation increase in the mean size of available zooplankton prey, electivity for veligers was predicted to increase by 0.21. None of the other environmental variables explained variation in larval burbot electivity for veligers. Collinearity was not a concern in the model (VIF less than 2.5 for all variables).

Table 1. Output of mixed model demonstrating how the variables of size class, temperature, station depth, chlorophyll a, mean zooplankton length and mean veliger length predicted electivity for veligers by larval burbot. (z) indicates that the variable underwent a z-score transformation. Symbols indicate level of significance for the t-statistic: *** = <0.001, ** = <0.01, * = <0.05, . = <0.1

Fixed Effects	Estimate	Standard Error	Pr(> t)	Significance
Intercept	-0.8341	0.0110	<0.0001	***
Size Class-Medium	0.3138	0.1214	0.0104	*
Size Class-Small	0.2166	0.1249	0.0845	.
Temperature (z)	0.0144	0.0570	0.8022	
Station Depth (z)	-0.0226	0.0637	0.7245	
Mean Chl a (z)	-0.0214	0.0534	0.6995	
Mean zooplankton length (z)	0.2092	0.0621	0.0147	*
Mean veliger length at serial (z)	-0.0640	0.0526	0.2443	

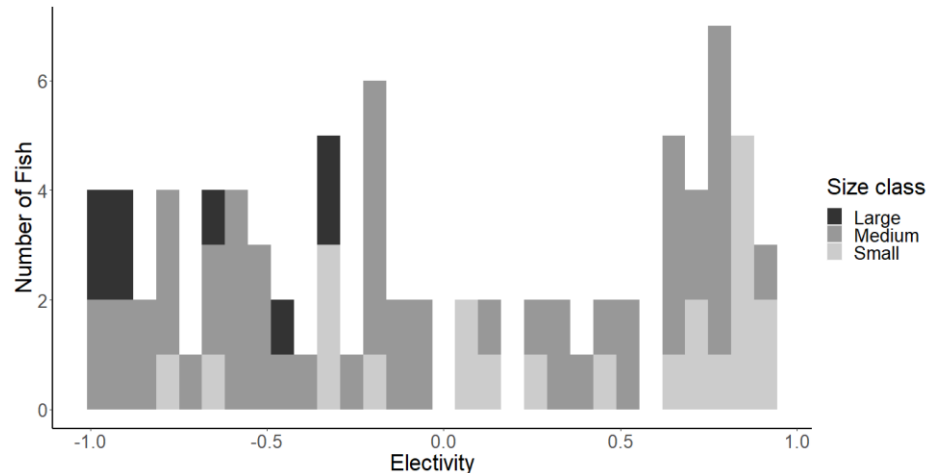


Figure 7: Distribution of electivity for veligers by small, medium, and large burbot collected in Lake Huron during July of 2017. Fish with electivity equal to -1 were excluded to aid in seeing the distribution of electivity values not equal to -1. This figure includes values close to -1 (-0.99, for example) which causes the figure to suggest the presence of electivity values equal to -1, but this is not the case.

DISCUSSION

Veligers were not a preferred prey item for larvae of rainbow smelt (mean E^* : -0.99) or coregonines (mean E : -0.97), and while larvae of burbot exhibit more variance in their electivity for veligers, they were still mostly not preferred (mean E^* : -0.64). Even though the observed electivity values do not indicate preference, it is important to remember that veligers were found to be the second most common diet item for burbot in terms of diet proportion. However, simple numeric dominance does not diminish electivity differences observed among species or size classes. Electivity for veligers was higher in small and medium size classes of burbot larvae, suggesting that gape limitation influences electivity. Meanwhile, interspecific differences in fish length at hatch and size at capture may have contributed to the different electivity for veligers exhibited by burbot, rainbow smelt, and coregonines. Finally, the temporal and local abundance of veligers may also have influenced electivity for veligers in the three species studied.

Small and medium sized burbot had higher electivity for veligers than their large sized counterparts, which had a mean electivity that indicated avoidance. Although the mean electivity values for small and medium larvae were less than zero, high variance in electivity was found. Large standard deviations, especially amongst the small and medium size class, indicate that larval burbot may be more flexible in terms of prey selection than has been previously reported (George et al., 2013). Although initially native predators may not exploit invasive prey as a resource, it is important to continuously monitor native predator-novel prey interactions as species can adapt to new prey items over time (Carlsson & Strayer, 2009). Thus, it is important to continue monitoring larval burbot diets into the future to understand how they are adapting to the presence of dreissenid mussel veligers.

Swimming ability, gape limitation, and the size distribution of zooplankton prey may explain why electivity for veligers was higher for burbot larvae < 10 millimeters. The mixed model revealed that as average zooplankton length increased electivity for veligers increased. This may

be due to smaller larval burbot being physically unable to engulf larger zooplankton prey. As a result, small larvae must rely on small prey items like veligers, while larger larvae may find small prey items less important as they grow larger and become less gape limited (Schael et al., 1991). In Lake Oneida, larval burbot were found to consume prey of increasing size as they grew, eating rotifers when small and moving on to copepod nauplii and later adult copepods and cladocerans as they grew larger (Ghan & Sprules, 1993). In a study of a fellow member of the *Gadidae* family, first feeding cod (*Gadus morhua*) larvae were found to consume protozoans while larger cod larvae could capture faster-swimming copepod nauplii (von Herbing & Gallagher, 2000). Numerous cases have found invasive *Limnoperna fortunei* veligers to be important features in the diets proto- and meso-larvae of native South American fishes while being less important for larger meta-larvae (Paolucci et al., 2007, 2010, 2015). Thus, future analyses of larval fish diets both inside and outside of the Great Lakes should take larvae size into consideration.

Burbot's small size at hatch may make them more vulnerable to starvation (Auer, 1982; Miller et al., 1988). This vulnerability may be further compounded by a limited amount of available small zooplankton prey, which can have further negative effects on foraging success for larval fish (Bremigan & Stein, 1994). A lack of appropriate prey is thought to be the most important factor when determining larval fish mortality (Gallagher et al. 1996). For small and medium sized larval burbot, veligers may alleviate constraints on feeding. The potential of veliger importance is not unprecedented; in the Paraguay and Parana rivers, golden mussel (*Limnoperna fortunei*) veligers, when widely available, were found to be capable of replacing the native cladoceran prey in the diets of younger larval fish (Paolucci et al., 2015). Burbot, as members of the cod family (*Gadidae*), in some ways have more in common with small marine larvae than the larger larvae of freshwater species in the Great Lakes. Thus, burbot recruitment may be heavily influenced by larval-stage dynamics (Houde, 1994). The declines in burbot populations in Lake Huron from the mid- to late- 1990s through at least 2004 have been attributed to declining recruitment (Stapanian et al., 2008). Although at what stage the recruitment bottleneck occurs in Lake Huron is unclear, evidence for a recruitment bottleneck at the pelagic larval stage and the age-1 juvenile stage has been found in Columbia Lake burbot (Taylor & Arndt, 2013). Changing trophic interactions in the critical larval stage caused by smaller larval burbot adapting to and consuming veligers could have positive implications for recruitment, and thus veliger-larvae interactions should be monitored further.

One potential contributor to the difference in electivity for veligers between the three species we analyzed is their size at capture. Based on the size data collected from fish that were dissected, the majority of coregonines and rainbow smelt that were collected were longer than burbot (Figure S1). Thus, we hypothesize that veligers may never be preferentially selected by coregonines due to their relatively large size at hatch, but we cannot make the same inference about rainbow smelt based on this study because so few small larvae were sampled. The difference in size between fish species that was observed may not only be due to the different lengths at which the fish hatch out (Auer 1982), but also the different times at which the three species of larvae emerge throughout the summer. Because this study took place in the month of July, it only offers a snapshot of larval fish and their available prey community. Rainbow smelt hatch in Lake Huron in May through July, depending on water temperature and location (O'Brien et al., 2012), but in this study we sampled very few recently hatched larval rainbow smelt in July. Some coregonine species (i.e., specifically lake whitefish and cisco) hatch in late

spring (Oyadomari & Auer 2008; Pothoven & Olds, 2020), but bloater reach peak hatching during mid-June (Wells, 1966). By examining larval fish diets over longer periods of time, researchers may be able to gain a greater understanding of how preference for dreissenid mussel veligers changes as fish grow and undergo changes in physiology and habitat. In addition, it is necessary to assess to what degree peaks in veliger density and larval hatchings overlap with each other to gain a better understanding of the importance of veligers in larval fish diets.

Temporal fluctuations of veliger availability may also have influenced their presence in the diets of the three larval taxa in question. In another study of veligers in larval fish diets, Nack et al. (2015) argued the importance of veligers to larval fish in the Hudson River estuary was dependent on the temporal overlap between larval fish and veligers. Using the same environmental zooplankton design that we used but including more months, Kirkendall et al. (2021) reported that veligers were relatively rare in April and May, and then peaked in June and July. Veliger density can, in part, determine the importance of veligers as prey items for larval fish. For example, when fed zooplankton communities enriched with *L. fortunei* veligers, *Prochilodus lineatus* proto- and meso- larvae consumed veligers almost exclusively, but when fed unaltered zooplankton communities only proto larvae consumed veligers (Paolucci et al., 2010). Thus, the fact that smaller burbot larvae overlapped with high veliger density may have played a role in burbot's somewhat higher electivity for veligers.

Larval fish (mainly burbot) were also found to consistently eat veligers of a larger mean size than the veligers available in their respective basins. Burbot, the smallest of the three species analyzed, were the most gape limited. For small burbot especially, the size of veligers in July may have influenced electivity for veligers. Kirkendall et al. (2021) found that veligers from Lake Huron in July of 2017 had the longest median length compared to veligers in other months. In addition, smaller burbot larvae have been found to consume the largest available prey that they can engulf (Ghan & Sprules, 1993). Due to their larger size, veligers in July may have appeared more preferable than they would in other months when they were smaller, further contributing to the comparably higher electivity for veligers seen in small and medium burbot. However, veliger length unlikely had much impact on electivity for veligers by rainbow smelt and coregonines which, as previously discussed, spanned a larger size range and were capable of consistently consuming larger prey.

Future research needs:

Potential competition between larval fish species is another factor that may contribute to electivity for veligers Rainbow smelt adults, for example, have been shown to competitively exclude other planktivorous species of fish (Willis & Magnuson, 2006). In addition, rainbow smelt larvae have also been described as possible direct competitors with larval burbot (George et al., 2013). Unfortunately, we were unable examine competitive effects due to the limited overlap between the species in the locations that were sampled. In the future, and under conditions where overlap occurs, we believe it would be valuable to assess how competition may influence the prey choices of larval fish with regards to their decision to exploit non-native prey items.

Our study highlights the importance of carefully examining the diets of larval fish for veligers, which are among the smallest of possible prey items. To gain a more accurate understanding of

larval fish diets in the Great Lakes, it will be important to take these non-native prey items into consideration in future studies. Due to their high number, veligers may be able to numerically replace other prey items, however, the extent to which dreissenid veligers provide quality nutrition to larval fish remains to be seen. As our understanding of the nutritional value of dreissenid veligers for fish grows, so will our understanding of the health of larval fish that consume this new prey source. In order to assess the validity of dreissenid veligers as a replacement for declining prey types, it is necessary to understand the caloric value that these larval mussels bring to larval fish diets, and if they offer any kind of dietary benefits.

CONCLUSION

In the management of aquatic ecosystems, large amounts of resources can be devoted to the removal and eradication of invasive species. However, for invasive species that become established and are more difficult to remove, it is important to recognize them as integrated parts of the ecosystem. While the negative effects of invasive species are well recognized, there is also potential for native species to adapt to their presence and even make use of them as a resource. In the case of veligers in Lake Huron, there is potential for burbot, a native fish declining in abundance, to exploit these larval mussels during the larval stage, potentially the most vulnerable period of their recruitment. Understanding these trophic interactions, especially at the critically understudied lower trophic levels, can give us a more holistic understanding of ecosystems when making decisions concerning invasive species management.

BIBLIOGRAPHY

- Alonso, C., Rocco, V., Barriga, J. P., Battini, M. Á., & Zagarese, H. (2004). Surface avoidance by freshwater zooplankton: Field evidence on the role of ultraviolet radiation. *Limnology and Oceanography*, 49(1), 225–232. <https://doi.org/10.4319/lo.2004.49.1.0225>
- Auer, N. A. (Ed.). (1982). Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage. *Great Lakes Fishery Commission*.
- Barbiero, R. P., Balcer, M., Rockwell, D. C., & Tuchman, M. L. (2009). Recent shifts in the crustacean zooplankton community of Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(5), 816–828.
- Barbiero, R. P., Lesht, B. M., & Warren, G. J. (2012). Convergence of trophic state and the lower food web in Lakes Huron, Michigan and Superior. *Journal of Great Lakes Research*, 38(2), 368–380. <https://doi.org/10.1016/j.jglr.2012.03.009>
- Bates, D., Mächler, M., Bolker, B., Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Boltovskoy, D., & Correa, N. (2014). Ecosystem impacts of the invasive bivalve *Limnoperna fortunei* (golden mussel) in South America. *Hydrobiologia*, 746(1), 81–95. <https://doi.org/10.1007/s10750-014-1882-9>

- Bowen, K. L., Conway, A. J., & Currie, W. J. (2018). Could dreissenid veligers be the lost biomass of invaded lakes? *Freshwater Science*, 37(2), 315-329. <https://doi.org/10.1086/697896>.
- Bremigan, M. T., & Stein, R. A. (1994). Gape-dependent larval foraging and zooplankton size: Implications for fish recruitment across systems. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(4), 913–922. <https://doi.org/10.1139/f94-090>
- Bunnell, D. B., Barbiero, R. P., Ludsin, S. A., Madenjian, C. P., Warren, G. J., Dolan, D. M., Brenden, T. O., Briland, R., Gorman, O. T., He, J. X., Johengen, T. H., Lantry, B. F., Lesht, B. M., Nalepa, T. F., Riley, S. C., Riseng, C. M., Treska, T. J., Tsehaye, I., Walsh, M. G., ... Weidel, B. C. (2014). Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *BioScience*, 64(1), 26–39. <https://doi.org/10.1093/biosci/bit001>
- Bunnell, D. B., Carrick, H. J., Madenjian, C. P., Rutherford, E. S., Vanderploeg, A., H., Barbiero, R. P., Hinchey-Malloy, E., Pothoven, S. A., Riseng, C. M., Claramunt, R. M., Bootsma, H. A., Elgin, A. K., Rowe, M. D., Sara M. Thomas, Turschak, B. A., Czesny, S., Pangle, K. L., & Warner, D. M. (2018). Are changes in lower trophic levels limiting prey-fish biomass and production in Lake Michigan? *Great Lakes Fishery Commission Miscellaneous Publication*, 2018–1, 41.
- Burlakova, L. E., Barbiero, R. P., Karatayev, A. Y., Daniel, S. E., Hinchey, E. K., & Warren, G. J. (2018). The benthic community of the Laurentian Great Lakes: analysis of spatial gradients and temporal trends from 1998 to 2014. *Journal of Great Lakes Research*, 44(4), 600–617. <https://doi.org/10.1016/j.jglr.2018.04.008>
- Carlsson, N. O. L., & Strayer, D. L. (2009). Intraspecific variation in the consumption of exotic prey - A mechanism that increases biotic resistance against invasive species? *Freshwater Biology*, 54(11), 2315–2319. <https://doi.org/10.1111/j.1365-2427.2009.02263.x>
- Carlton, J. T. (2008). The zebra mussel *Dreissena polymorpha* found in North America in 1986 and 1987. *Journal of Great Lakes Research*, 34(4), 770-773. [https://doi.org/10.1016/s0380-1330\(08\)71617-4](https://doi.org/10.1016/s0380-1330(08)71617-4)
- Carrick, H. J., Butts, E., Daniels, D., Fehringer, M., Frazier, C., Fahnenstiel, G. L., Pothoven, S., & Vanderploeg, H. A. (2015). Variation in the abundance of pico, nano, and microplankton in Lake Michigan: Historic and basin-wide comparisons. *Journal of Great Lakes Research*, 41, 66–74. <https://doi.org/10.1016/j.jglr.2015.09.009>
- Claramunt, R. M., Smith, J., Donner, K., Povolito, A., Herbert, M. E., Galarowicz, T., ... & Jonas, J. L. (2019). Resurgence of cisco (*Coregonus artedii*) in Lake Michigan. *Journal of Great Lakes Research*, 45(4), 821-829.
- Crane, D. P., & Einhouse, D. W. (2016). Changes in growth and diet of smallmouth bass following invasion of Lake Erie by the round goby. *Journal of Great Lakes Research*, 42(2), 405–412. <https://doi.org/10.1016/j.jglr.2015.12.005>
- Dai, Q., Bunnell, D. B., Diana, J. S., Pothoven, S. A., Eaton, L., O'Brien, T. P., & Kraus, R. T. (2019). Spatial patterns of rainbow smelt energetic condition in Lakes Huron and Erie in

- 2017: Evidence for Lake Huron resource limitation. *Journal of Great Lakes Research*.
<https://doi.org/10.1016/j.jglr.2019.06.001>
- De Meester, L., Dawidowicz, P., Van Gool, E., & Loose, C. J. (1999). Ecology and evolution of predator-induced behavior of zooplankton: Depth selection behavior and diel vertical migration, p. 160–176. In R. Tollrian and C. D. Harvell [eds.], *The ecology and evolution of inducible defenses*. Princeton Univ. Press.
- Eppheimer, D. E., Bunnell, D. B., Armenio, P. M., Warner, D. M., Eaton, L. A., Wells, D. J., & Rutherford, E. S. (2019). Densities, diets, and growth rates of larval alewife and bloater in a changing Lake Michigan ecosystem. *Transactions of the American Fisheries Society*, 148(4), 755-770. <https://doi.org/10.1002/tafs.10171>
- Evans, M. A., Fahnenstiel, G., & Scavia, D. (2011). Incidental oligotrophication of North American Great Lakes. *Environmental Science and Technology*, 45(8), 3297–3303. <https://doi.org/10.1021/es103892w>
- Fox, J. & Weisberg, S. (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Gallager S.M., von Herbing I., & Davis L., Alatalo, P. (1996) Yolk-sac cod larvae ingest microzooplankton exclusively from natural plankton assemblages on Georges Bank. In: *Proceedings of the 1996 Ocean Sciences Meeting*, San Diego, California.
- Gannon, J. E., & Stemberger, R. S. (1978). Zooplankton (especially crustaceans and rotifers) as indicators of water quality. *Transactions of the American Microscopical Society*, 16-35. <http://www.jstor.org/stable/3225681>
- George, E. M., Roseman, E. F., Davis, B. M., & O'Brien, T. P. (2013). Feeding ecology of pelagic larval burbot in Northern Lake Huron, Michigan. *Transactions of the American Fisheries Society*, 142(6), 1716–1723. <https://doi.org/10.1080/00028487.2013.788561>
- Ghan, D., & Sprules, W. G. (1993). Diet, prey selection, and growth of larval and juvenile burbot *Lota lota* (L.). *Journal of Fish Biology*, 42(1), 47–64. <https://doi.org/10.1111/j.1095-8649.1993.tb00305.x>
- Gorman, O. T. (2019). Prey fish communities of the Laurentian Great Lakes: A cross-basin overview of status and trends based on bottom trawl surveys, 1978-2016. *Aquatic Ecosystem Health & Management*, 22(3), 263-279. <https://doi.org/10.1080/14634988.2019.1674012>
- Hensler, S., He, J. X., & Jude, D. J. (2007). Burbot growth and diets in Lakes Michigan and Huron: an ongoing shift from native species to round gobies. *American Fisheries Society Symposium*, January.
- Houde, E. D. (1994). Differences between marine and freshwater fish larvae: implications for recruitment. *ICES Journal of Marine Science*, 51, 91–97.
- Hoyle, J. A., Schaner, T., Casselman, J. M., & Dermott, R. (1999). Changes in lake whitefish (*Coregonus clupeaformis*) stocks in eastern Lake Ontario following Dreissena mussel invasion. *Great Lakes Res. Rev*, 4, 5-10.

- Jørgensen, C., Kørboe, T., Møhlenberg, F., & Riisgård, H. (1984). Ciliary and mucus-net filter feeding, with special reference to fluid mechanical characteristics. *Marine Ecology Progress Series*, 15(3), 283–292. <https://doi.org/10.3354/meps015283>
- Karatayev, A. Y., Burlakova, L. E., & Padilla, D. K. (2002). Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. *Invasive Aquatic Species of Europe*, 433–434.
- Karatayev, A. Y., Burlakova, L. E., Mehler, K., Daniel, S. E., Elgin, A. K., & Nalepa, T. F. (2020). Lake Huron benthos survey cooperative science and monitoring initiative 2017. *Technical Report*. USEPA-GLRI GL00E02254.
- Kirkendall, D. S., Bunnell, D. B., Armenio, P. M., Eaton, L. A., Trebitz, A. & Watson, N. M. (2021). Spatial and temporal distributions of *Dreissena* spp. veligers in Lake Huron: does calcium limit settling success? *Journal of Great Lakes Research*. <https://doi.org/10.1016/j.jglr.2021.04.001>
- Lavrentyev, P. J., Vanderploeg, H. A., Franzé, G., Chacin, D. H., Liebig, J. R., & Johengen, T. H. (2014). Microzooplankton distribution, dynamics, and trophic interactions relative to phytoplankton and quagga mussels in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research*, 40(S1), 95–105. <https://doi.org/10.1016/j.jglr.2013.11.012>
- Luo, M. K., Madenjian, C. P., Diana, J. S., Kornis, M. S., & Bronte, C. R. (2019). Shifting diets of lake trout in Northeastern Lake Michigan. *North American Journal of Fisheries Management*, 39(4), 793–806. <https://doi.org/10.1002/nafm.10318>
- Miller, T. J., Crowder, L. B., Rice, J. A., & Marschall, E. A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*, 45(9), 1657–1670. <https://doi.org/10.1139/f88-197>
- Mills, E. L., Dermott, R. M., Roseman, E. F., Dustin, D., Mellina, E., Conn, D. B., & Spidle, A. P. (1993). Colonization, ecology, and population structure of the "Quagga" mussel (*Bivalvia: Dreissenidae*) in the lower Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(11), 2305–2314. <https://doi.org/10.1139/f93-255>
- Morrison, T. W., Lynch Jr, W. E., & Dabrowski, K. (1997). Predation on zebra mussels by freshwater drum and yellow perch in western Lake Erie. *Journal of Great Lakes Research*, 23(2), 177-189.
- Nack, C. C., Limburg, K. E., & Schmidt, R. E. (2015). Diet composition and feeding behavior of larval American shad, *Alosa sapidissima* (Wilson), after the introduction of the invasive zebra mussel, *Dreissena polymorpha* (Pallas), in the Hudson River estuary, NY. *Northeastern Naturalist*, 22(2), 437–450. <https://doi.org/10.1656/045.022.0216>
- O'Brien, T. P., Taylor, W. W., Briggs, A. S., & Roseman, E. F. (2012). Influence of water temperature on rainbow smelt spawning and early life history dynamics in St. Martin Bay, Lake Huron. *Journal of Great Lakes Research*, 38(4), 776–785. <https://doi.org/10.1016/j.jglr.2012.09.017>

- Oyadomari, J. K., & Auer, N. A. (2008). Transport and growth of larval cisco (*Coregonus artedi*) in the Keweenaw Current region of Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(7), 1447-1458. <https://doi.org/10.1139/F08-068>
- Paolucci, E. M., Almada, P., Cataldo, D. H., & Boltovskoy, D. (2015). Native fish larvae take advantage of introduced mussel larvae: field evidence of feeding preferences on veligers of the introduced freshwater bivalve *Limnoperna fortunei*. *Hydrobiologia*, 745(1), 211–224. <https://doi.org/10.1007/s10750-014-2108-x>
- Paolucci, E. M., Cataldo, D. H., & Boltovskoy, D. (2010). Prey selection by larvae of *Prochilodus lineatus* (Pisces: Curimatidae): Indigenous zooplankton versus veligers of the introduced bivalve *Limnoperna fortunei* (Bivalvia: Mitilidae). *Aquatic Ecology*, 44(1), 255–267. <https://doi.org/10.1007/s10452-009-9263-6>
- Paolucci, E. M., Cataldo, D. H., Fuentes, C. M., & Boltovskoy, D. (2007). Larvae of the invasive species *Limnoperna fortunei* (Bivalvia) in the diet of fish larvae in the Paraná River, Argentina. *Hydrobiologia*, 589(1), 219–233. <https://doi.org/10.1007/s10750-007-0734-2>
- Pothoven, S. A., & Madenjian, C. P. (2008). Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. *North American Journal of Fisheries Management*, 28(1), 308-320.
- Pothoven, S., & Olds, C. (2020). Spatial variation in feeding ecology of age-0 lake whitefish *Coregonus clupeaformis* in Lake Huron. *Journal of Freshwater Ecology*, 35(1), 349–366. <https://doi.org/10.1080/02705060.2020.1816228>
- R Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria. Retrieved from <https://www.R-project.org/>.
- Schael, D. M., Rudstam, L. G., & Post, J. R. (1991). Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 48(10), 1919-1925.
- Sprung, M. (1993). The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. IN: *Zebra Mussels: Biology, Impacts, and Control*. Lewis Publishers, Boca Raton, FL. 1993. p 39-53, 2 tab, 73 ref.
- Stapanian, M. A., Madenjian, C. P., Bronte, C. R., Ebener, M. P., Lantry, B. F., & Stockwell, J. D. (2008). Status of burbot populations in the Laurentian Great Lakes. *American Fisheries Society Symposium*, 59, 111–130.
- Steinhart, G. B., Stein, R. A., & Marschall, E. A. (2004). High growth rate of young-of-the-year smallmouth bass in Lake Erie: A result of the round goby invasion? *Journal of Great Lakes Research*, 30(3), 381–389. [https://doi.org/10.1016/S0380-1330\(04\)70355-X](https://doi.org/10.1016/S0380-1330(04)70355-X)
- Tang, H., Vanderploeg, H. A., Johengen, T. H., & Liebig, J. R. (2014). Quagga mussel (*Dreissena rostriformis bugensis*) selective feeding of phytoplankton in Saginaw Bay. *Journal of Great Lakes Research*, 40(S1), 83–94. <https://doi.org/10.1016/j.jglr.2013.11.011>

- Taylor, J. L., & Arndt, S. K. (2013). Variability in burbot cohort abundance at juvenile and adult stages in Columbia Lake, British Columbia. *Transactions of the American Fisheries Society*, *142*(6), 1705-1715.
- Vanderploeg, H. A., & Scavia, D. (1979a). Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecological Modelling*, *7*(2), 135–149.
[https://doi.org/10.1016/0304-3800\(79\)90004-8](https://doi.org/10.1016/0304-3800(79)90004-8)
- Vanderploeg, H. A., & Scavia, D. (1979b). Two electivity indices for feeding with special reference to zooplankton grazing. *Journal of the Fisheries Research Board of Canada*, *36*(4), 362–365. <https://doi.org/10.1139/f79-055>
- Vanderploeg, H. A. (1994). Zooplankton particle selection and feeding mechanisms. The biology of particles in aquatic systems, 205-234.
- Vanderploeg, H. A., Nalepa, T. F., Jude, D. J., Mills, E. L., Holeck, K. T., Liebig, J. R., Grigorovich, I. A., & Ojaveer, H. (2002). Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(7), 1209–1228. <https://doi.org/10.1139/f02-087>
- Vanderploeg, H. A., Liebig, J. R., Nalepa, T. F., Fahnenstiel, G. L., & Pothoven, S. A. (2010). Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. *Journal of Great Lakes Research*, *36*(SUPPL. 3), 50–59.
<https://doi.org/10.1016/j.jglr.2010.04.005>
- von Herbing, I. H., & Gallager, S. M. (2000). Foraging behavior in early Atlantic cod larvae (*Gadus morhua*) feeding on a protozoan (*Balanion* sp.) and a copepod nauplius (*Pseudodiaptomus* sp.). *Marine Biology*, *136*(3), 591–602.
<https://doi.org/10.1007/s002270050719>
- Wells, L. (1966). Seasonal and Depth Distribution of Larval Bloaters (*Coregonus hoyi*) in Southeastern Lake Michigan. *Transactions of the American Fisheries Society*, *95*(4), 388–396. [https://doi.org/10.1577/1548-8659\(1966\)95\[388:saddol\]2.0.co;2](https://doi.org/10.1577/1548-8659(1966)95[388:saddol]2.0.co;2)
- Willis, T. V., & Magnuson, J. J. (2006). Response of fish communities in five north temperate lakes to exotic species and climate. *Limnology and Oceanography*, *51*(6), 2808–2820.
<https://doi.org/10.4319/lo.2006.51.6.2808>
- Withers, J. L., Sesterhenn, T. M., Foley, C. J., Troy, C. D., & Höök, T. O. (2015). Diets and growth potential of early stage larval yellow perch and alewife in a nearshore region of southeastern Lake Michigan. *Journal of Great Lakes Research*, *41*, 197–209.
<https://doi.org/10.1016/j.jglr.2015.08.003>

SUPPLEMENTAL INFORMATION:

Table S1: Number of larval fish collected in Lake Huron in July of 2017 at each transect (Burbot, Rainbow Smelt, coregonine).

	French	Harbor Beach	Maitland	Nottawasaga	Ocqueoc	Parry Sound	Saugeen	Spanish	Thessalon
18 meter surface	(0, 24, 0)	(0, 0, 0)	(0, 5, 3)	(0, 4, 0)	No Tow	(0, 39, 0)	(0, 3, 3)	(0, 28, 0)	(0, 5, 0)
18 meter oblique	(1, 212, 0)	(0, 4, 0)	(0, 14, 2)	(6, 11, 1)	(1, 36, 1)	(0, 148, 0)	(0, 34, 0)	(0, 164, 0)	(0, 1, 0)
46 meter surface	(0, 38, 0)	(2, 0, 0)	(0, 1, 0)	(0, 2, 0)	(1, 2, 0)	(0, 21, 4)	(1, 0, 0)	(0, 32, 0)	(0, 22, 0)
46 meter oblique	(57, 315, 0)	(10, 0, 0)	(10, 12, 1)	(12, 17, 1)	(4, 12, 1)	(6, 54, 2)	(6, 6, 7)	(0, 155, 0)	(0, 272, 0)
68, 73, 82 meter surface	(4, 21, 9)	(2, 1, 1)	(1, 1, 1)	(0, 1, 1)	(2, 5, 8)	(4, 3, 13)	(1, 0, 3)	No Tow	No Tow
68, 73, 82 meter oblique	(100, 91, 7)	(20, 1, 7)	(2, 2, 2)	(26, 10, 2)	(16, 71, 7)	(71, 47, 16)	(17, 2, 5)	No Tow	No Tow
Summary	(162, 701, 16)	(34, 6, 8)	(13, 35, 8)	(44, 45, 5)	(24, 126, 17)	(81, 312, 35)	(25, 45, 18)	(0, 379, 0)	(0, 300, 0)

Table S2: Number of larval fish with stomach contents based on transect (assume a maximum of 30 dissected) (Burbot, Rainbow Smelt, coregonines). All fish were collected from Lake Huron in July of 2017.

	French	Harbor Beach	Maitland	Nottawasaga	Ocqueoc	Parry Sound	Saugeen	Spanish	Thessalon
18 meter surface	(0, 0, 0)	(0, 0, 0)	(0, 0, 0)	(0, 0, 0)	Now Tow	(0, 0, 0)	(0, 0, 0)	(0, 0, 0)	(0, 0, 0)
18 meter oblique	(1, 0, 0)	(0, 3, 0)	(0, 0, 2)	(6, 0, 0)	(1, 2, 0)	(0, 0, 0)	(0, 18, 0)	(0, 0, 0)	(0, 0, 0)
46 meter surface	(0, 2, 0)	(2, 0, 0)	(0, 0, 0)	(0, 0, 0)	(1, 0, 0)	(0, 1, 0)	(1, 0, 0)	(0, 0, 0)	(0, 0, 0)
46 meter oblique	(27, 0, 0)	(9, 0, 0)	(10, 5, 0)	(12, 0, 0)	(4, 5, 0)	(6, 0, 0)	(5, 4, 4)	(0, 1, 0)	(0, 0, 0)
68, 73, 82 meter surface	(3, 0, 9)	(2, 1, 0)	(1, 0, 1)	(0, 0, 1)	(2, 0, 8)	(3, 0, 12)	(0, 0, 0)	No Tow	No Tow
68, 73, 82 meter oblique	(27, 0, 5)	(18, 0, 7)	(2, 1, 2)	(23, 0, 1)	(15, 3, 7)	(29, 0, 13)	(15, 0, 0)	No Tow	No Tow
Summary	(58, 2, 14)	(31, 4, 7)	(13, 6, 5)	(41, 0, 2)	(23, 10, 15)	(38, 1, 25)	(21, 22, 4)	(0, 1, 0)	(0, 0, 0)

Table S3. Results of Welch's T-test comparing the lengths of veligers in fish diets and the environment in North & South Main Basin and Georgian Bay

Basin	Length of veligers in the diets (mm)	Length of veligers in the environment (mm)	Confidence Interval	P-value
North Main Basin	0.1933	0.1428	0.0457 - 0.0553	<0.0001
South Main Basin	0.1949	0.1568	0.0329 - 0.0433	<0.0001
Georgian Bay	0.1672	0.1354	0.0299 - 0.0338	<0.0001

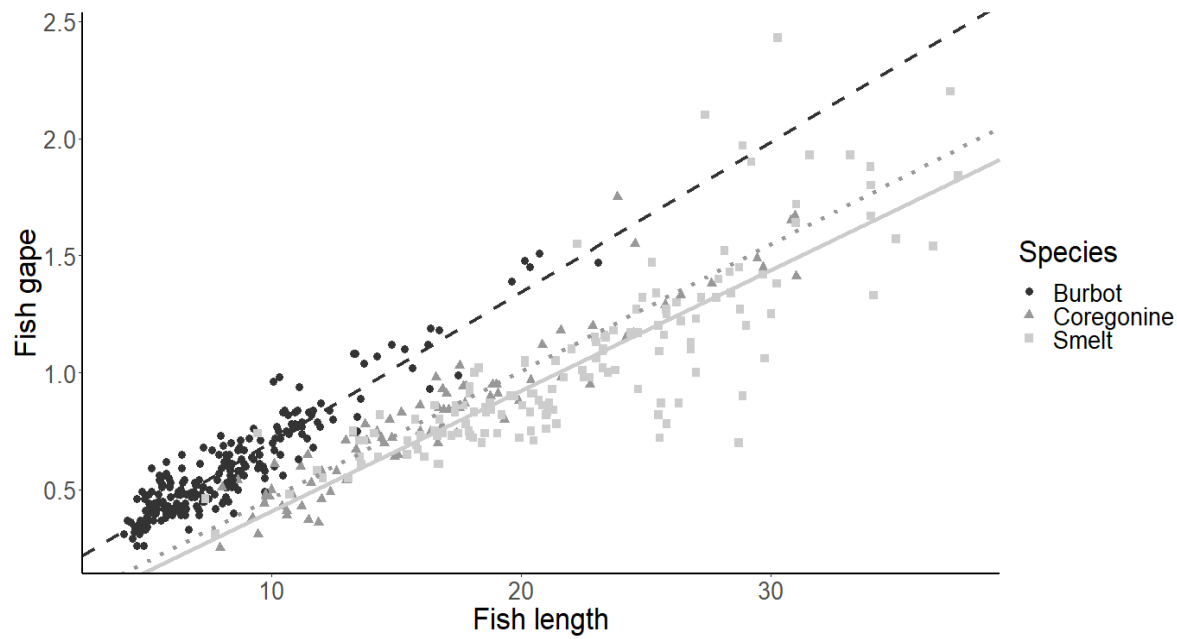


Figure S1: Fish length-gape relationship for dissected larval burbot, smelt, and coregonines sampled in Lake Huron in July of 2017. The dashed line represents this relationship for burbot, the dotted line for coregonines, and the solid line for smelt. The length-gape relationship for each species are as follows: Burbot: $y=0.0643x+0.0611$, Smelt: $y=0.05142x-0.1059$, Bloater: $y=0.0542x-0.0792$.