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Spatiotemporal variability in energetic condition of alewife and round goby in
Lake Michigan

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Abstract

Pelagic-oriented alewife (*Alosa pseudoharengus*) and benthic-oriented round goby (*Neogobius melanostomus*) are two important prey fish in the Laurentian Great Lakes. In 2015, we evaluated their seasonal total energy (TE) across nine Lake Michigan transects. Round goby contained at least 48% more kilojoules of TE than alewife of equal length during spring and summer. TE varied spatially for both species, but only large alewife exhibited a consistent pattern, with higher values along the eastern shoreline. Variation in TE was not explained by site-specific prey densities for either species. Round goby energy density (ED) was higher in Lake Michigan than in central Lake Erie, but comparable to other regions of the Great Lakes. Alewife ED in 2015 was similar to 2002-2004 in Lake Michigan, with the exception of November (small alewife ED was 21% higher) and April (large alewife ED was 30% lower). Despite oligotrophication, our study suggests that starvation of juvenile and adults has not been directly contributing to overall declining prey fish abundance, although future research should evaluate the potential for overwinter starvation.

32 Introduction

33 Multiple ecological drivers can influence population dynamics of fish, including
34 predation, climate, pathogens or disease, and limiting resources. In developed countries,
35 watershed management continues to improve in some regions, causing reductions in nutrient
36 inputs to reservoirs and lakes and even reversing some systems from eutrophication to
37 oligotrophication (Stockner et al. 2000; Anderson et al. 2005) and potentially limiting resources
38 for fishes. Disentangling the effects of limiting resources on a fish population can be difficult
39 among the many other drivers in any given system. Estimating the energetic condition of fishes
40 offers one method to determine the extent to which limiting resources could be influencing
41 individual survival and contribute to population dynamics. This method has been applied to
42 address a diversity of research questions in a broad range of ecosystems, including monitoring
43 the recovery of Atlantic cod populations (Lambert and Dutil 1997), overwinter survival and
44 effects on recruitment (Pangle et al. 2004), and understanding community-level interactions
45 between seabirds and their prey fishes (Wanless et al. 2005).

46 Several Laurentian Great Lakes (e.g., Lake Ontario, Lake Huron, Lake Michigan) have
47 undergone or are undergoing oligotrophication owing to long-term declines in nutrient inputs and
48 changes to internal nutrient recycling associated with the proliferation of dreissenid mussels
49 (Evans et al. 2011)- zebra mussels *Dreissena polymorpha* and then quagga mussels *D. bugensis*.
50 In Lake Michigan, declines in phytoplankton (Fahnenstiel et al. 2010; Pothoven and Fahnenstiel
51 2013) and *Diporeia* spp., a high-energy benthic prey resource (Nalepa et al. 2014), are
52 unambiguous, whereas zooplankton have declined in some regions but not in others (Bunnell et
53 al. 2018). Correlation analyses at the lakewide level reveal declining prey fish biomass to be
54 correlated with declines in nutrients, phytoplankton, zooplankton, and benthic invertebrates, but

more empirical work is required to evaluate whether limiting resources is, in fact, the causal factor (Bunnell et al. 2014). Previous studies have documented declining energy density for different fish species (Hondorp et al. 2005; Madenjian et al. 2006; Rennie et al. 2009; Pothoven et al. 2012; Pothoven and Fahnenstiel 2014), likely resulting from declining *Diporeia* prey resources. Concerned by declines in phosphorus and phytoplankton, Lake Michigan managers are seeking improved knowledge of how changing lower trophic levels could be contributing to the declining abundance of prey fishes (Bunnell et al. 2018) which, in turn, support a recreational fishery targeting Chinook salmon (*Oncorhynchus tshawytscha*), lake trout (*Salvelinus namaycush*), steelhead (*Oncorhynchus mykiss*), Coho salmon (*Oncorhynchus kisutch*), and brown trout (*Salmo trutta*) that invested more than 9 million angler-days of effort in 2015 (U.S. Department of Interior 2016).

In a system as large as Lake Michigan (58,000 km², spanning 4.5 degrees of latitude), spatial heterogeneity in nutrients and prey resources that ultimately support the piscivores is likely. For example, several tributaries in the southeast corner of the lake occur in agricultural watersheds and have been modeled to deliver relatively high loads of total phosphorus inputs (e.g., Saint Joseph, Kalamazoo, Grand) compared to other regions of the lake (Dolan and Chapra 2012; Robertson et al. 2018). Managers have begun to recognize this spatial variability in their decision making. For example, Michigan Department of Natural Resources is implementing a zonal strategy where they will adjust fisheries management to match available habitat within its more than 34,000 km² of water that falls within its state boundary (J. Wesley, Michigan Department of Natural Resources, 621 N. 10th Street, Plainwell, Michigan, USA, personal communication). One possible outcome is to develop zonal stocking strategies that best reflect optimal thermal habitat or prey availability for a given species. In the Great Lakes, previous

studies rarely have analyzed the energetic condition of prey fishes in a spatial context to evaluate whether locally productive areas can translate into higher energy density for a given fish species.

In Lake Michigan, alewife (*Alosa pseudoharengus*) and round goby (*Neogobius melanostomus*) are the two prey fishes that most commonly occur in piscivore diets (see Jacobs et al. 2013; Happel et al. 2018). Both species are nonindigenous, although the alewife proliferated several decades earlier than the round gobies (i.e., 1960s versus 2000s). They differ, however in their habitat use, with alewives being benthopelagic (older alewives spend daytime associated with the bottom and migrate up at nighttime, Janssen and Brandt 1980) and round gobies being benthic. Alewife energy density (ED, typically in kilojoules (kJ)/g wet mass) has been well studied at the lakewide level. Madenjian et al. (2006) reported a 23% decline in ED for large alewife between 1979-1981 and 2002-2004, but no change for small alewife. In a more recent study focused on yearling alewife from a transect in southeastern Lake Michigan, Pothoven and Fahnenstiel (2014) reported lower ED in 2010-2013 than in 1998-1999, as well as steeper declines in first-year overwinter ED in the later years compared to the earlier ones. Both studies attributed the declining ED to declines in *Diporeia* prey, which themselves declined precipitously following the proliferation of dreissenid mussels. Round goby ED, conversely, has not previously been described in Lake Michigan so temporal comparisons are not possible. But we can compare round goby ED in Lake Michigan to other studies in a Lake Michigan watershed (Ruetz et al. 2009), in Lake Huron (Steven A. Pothoven, Great Lakes Environmental Research Laboratory-National Oceanic and Atmospheric Administration, 1431 Beach St, Muskegon, MI, USA, unpublished data), and in central Lake Erie (Johnson et al. 2005).

In this paper, we compare the total energy (TE) content for the two primary prey fishes in Lake Michigan, alewife and round goby. For each species, we will then evaluate the spatial variability in TE across 9 nearshore to offshore transects that putatively differ in their productivity given variable proximity to tributaries with different levels of phosphorus input. We hypothesize that TE values will be positively related to densities of their primary prey (i.e., zooplankton for alewife, quagga mussels for round gobies). Finally, we compare the 2015 ED of alewives and round gobies to previous Lake Michigan studies and studies in other regions, respectively. Given the declining benthic and pelagic resources for alewife (e.g., *Diporeia* and cladoceran zooplankton) in Lake Michigan, we hypothesize that alewife ED will be lower in 2015 than in previous years. For round goby, given that Ruetz et al. (2009) showed higher ED in a Lake Michigan tributary than in central Lake Erie, we hypothesize that the relatively high abundance of quagga mussel prey in Lake Michigan proper will enable the ED of Lake Michigan round gobies to be similar to what Ruetz et al. (2009) reported.

Methods

Alewives and round gobies were collected through bottom and midwater trawling from nine transects around Lake Michigan (Fig. 1), some of which were adjacent to tributaries with historically high phosphorus loading (e.g., St. Joseph, Manitowoc, Kalamazoo; Dolan and Chapra 2012). At each transect, trawling occurred over multiple bottom depths (ranging 9 m to 128 m) and at least three times during 2015, targeting spring (April 16 – May 11), summer (July 18-26), and autumn (October 18-November 3). The standard bottom depths that were sampled during each targeted season and at all sites were 18, 46, and either 91 or 110 m. At some sites, opportunistic fish collections were made at additional depths along the Pere Marquette,

124 Waukegan, Frankfort, and Sturgeon Bay transects during September 13-26, and at the standard
125 depths along the Muskegon transect on May 27, June 30, and August 31. Aboard the research
126 vessel, fishes were sorted by species and processed to obtain a total weight (by species) and up to
127 50 measurements of total length (TL, by species). Alewife and round goby were frozen in water
128 within 30 minutes of capture, and maintained in a -20 °C freezer until processed. These two fish
129 species were not captured in each transect in each season.

130 To estimate % dry weight (%DW), fish were thawed, measured for TL (nearest mm) and
131 intact wet weight (nearest 0.1 g). For alewives, stomachs were excised to prevent biased
132 estimates of %DW or ED, although any fat attached to the stomach was scraped off and kept
133 with the rest of the tissue for drying. For round gobies, we discarded the contents of the
134 digestive tract, but did not remove the stomach tissue. For both species, individual fish were cut
135 into several ~20-mm pieces and placed into a tin that was pre-weighed to the nearest 0.0001 g.
136 The wet weight of the dissected fish was then estimated to the nearest 0.0001 g, and this was the
137 value used to estimate %DW. Individuals were dried in an oven at 65 °C until a constant weight
138 (nearest 0.0001 g) was achieved. Fish were first weighed after 48 hours, and then every 24 hours
139 thereafter. The time to reach a constant weight ranged from 72 to 216 hours. Hence, for each
140 individual fish, %DW equaled (dry weight/dissected wet weight)*100%.

141 A subsample of fish was selected for direct ED estimation, for which %DW is a strong
142 predictor (Hartman and Brandt 1995). The subsampled fish were selected to represent a
143 distribution of fish sizes from each transect and season and were homogenized with either a
144 coffee grinder or mortar and pestle, the latter being used more for smaller amounts of dried
145 tissue. For alewives less than 100 mm, we combined up to 6 fish that were within 10 mm TL of
146 one another to make a composite sample for direct ED estimation. For round gobies, composites

of similar sized fish were made if individual fish were less than 0.2 g dry weight. From either the sample of composited fish or an individually ground fish, up to a 1-g subsample of dried tissue was combusted in a Parr 1261 isoperibol bomb calorimeter that was standardized with benzoic acid. ED was converted to joules per gram of wet weight using the known dry weight : wet weight ratio for that fish. For composite samples, the dry weight : wet weight ratio for a fish equaled the sum of dry weights divided by the sum of the dissected wet weights across the individuals used. Triplicate ED estimates were made for 10 alewife and 10 round goby to estimate within-sample variability. Because the mean coefficient of variation [$100 \times (\text{SD}/\text{mean})$] was less than 1% among replicates, only a single estimate was made for the remainder of the ED determinations.

The relationship between ED (kJ/g wet weight) and %DW was determined for each species, and used to predict ED for individuals where only %DW was known. For alewives, ED vs. %DW was examined separately for small (i.e., ≤ 120 mm TL) and large (i.e., > 120 mm TL) sizes, following the size classes used by Madenjian et al. (2006). For round goby, the best predictive relationship for ED was found when the data were not split into size classes. For the analyses seeking to explain variation in ED, however, we divided the round goby data into two size classes (small = ≤ 70 mm TL and large = > 70 mm TL) because there was such a strong positive relationship between fish size and ED for small round gobies.

Does total energy differ between alewife and round goby?

Total energy (TE, in kJ) for each fish was calculated as the ED (either estimated directly or calculated from %DW) multiplied by the dissected wet weight of the fish. Because energetics of alewives vary seasonally (see Madenjian et al. 2006), we analyzed each season separately for

both species. Because the variance in total energy increased with fish size, we ln-transformed both ED and TL in the model when estimating the relationship with linear regression. The coefficient of determination (R^2) in ln-space revealed the variability in total energy for a given length, in each species and season. We also reported the predicted mean total energy ($\widehat{TE}$) in arithmetic space:

$$\widehat{TE} = e^{(\alpha + \beta \ln(TL) + \frac{MSE}{2})}$$

where α and β equal the intercept and slope of the ln-transformed regression, and MSE equals the mean square error of the regression (Hilborn and Walters 1992). We compared ($\widehat{TE}$) for a “small” (i.e., 100 mm TL) and “large” (i.e., 150 mm TL) fish for each species and season.

Does total energy vary spatially within species?

When summarizing data from a given transect in each season, we required energy estimates from at least five fish for a given size class for spatial analyses. We conducted an Analysis of Variance (ANOVA) to determine whether the residual TE (observed TE – predicted TE) differed across transects. Because the variance in TE increased with fish size, the residuals were calculated in ln-space. Because previous studies have separately analyzed size classes of alewife, and because diets can differ with ontogeny for both alewives and round gobies (e.g., Bunnell et al. 2015), we conducted a separate ANOVA for each species, season, and size class. When TE varied among transects, we conducted Bonferroni t-tests for pairwise comparisons between transects.

For the month with the largest number of transects for a given fish and size class, we used Pearson’s correlation to explore whether the mean residual TE was associated with prey availability: zooplankton biomass for alewife or quagga mussel biomass for round gobies (see

below). This analysis occurred in October for small alewife (N = 6 transects) and small and large round gobies (N = 9 transects). No correlative analysis was possible for large alewife because of limited sample size: the month with the largest number of transects (July) only had an N = 4 because comparable zooplankton data were not available for Muskegon. When prey availability was non-normally distributed, we performed a natural log transformation to improve normality.

To represent alewife prey availability, we averaged both total and “consumed” (taxa = *Epischura lacustris*, *Bythotrephes longimanus*, *Limnocalanus macrurus*, *Bosmina* spp., *Leptodiaptomus sicilis*, *Diacyclops thomasi*) zooplankton across summer and autumn months from the 18 m and 46 m sites, because we assumed that small alewives were not yet born when zooplankton were sampled in the spring and no small alewives were sampled at the 110 m site. For our study, we based “consumed” zooplankton on the zooplankton taxa that occurred in at least 10% of the diet for a give size class in a recent Lake Michigan diet study (Bunnell et al. 2015). During spring, summer and autumn at the 18 m and 46 m sites for each transect, zooplankton were sampled at night with a 153- μ m mesh, 0.5-m diameter, conical net that vertically sampled the water column from 2 m above the bottom to the surface. A flowmeter that was calibrated during each season was mounted within the mouth to estimate total distance sampled such that m³ of water sampled could be estimated. Samples were preserved in 5% buffered formalin after first being narcotized with antacid.

In the laboratory, the entire zooplankton sample was first inspected for aggregations of large predatory cladocerans (i.e., *Bythotrephes*, *Cercopagis*) that could affect subsampling; when aggregations were found, smaller crustacean zooplankton were disentangled and larger predatory cladocerans were removed for subsequent processing. The zooplankton sample was then diluted

with reverse-osmosis water to between 30-750 mL, with the goal of attaining a concentration of 200 zooplankters per mL. After mixing the sample with a glass rod, a 1-mL aliquot was removed with a Hensen-Stempel pipette. All individual crustacean zooplankton from the subsample were identified to the highest taxonomic resolution possible (see below) and counted under a dissecting microscope; copepod nauplii, dreissenid veligers, and rotifers were not enumerated because we believed their densities would be biased too low because of the 153- μ m mesh of the net. All adults were identified to species (except for *Bosmina* spp.) and copepodites (immature copepods) were identified to genus in a few instances (e.g., *Mesocyclops*, *Tropocyclops*, *Limnocalanus*, *Epischura*, *Senecella*) but were otherwise identified as either calanoid or calanoid copepodites. If 200 or more zooplankters were counted in the first aliquot, no additional ones were processed. Otherwise, aliquots were removed in 1-mL increments and processed as described above until at least 200 individuals (total) were counted. The entire sample (including any aggregations that were previously removed) was then processed to enumerate predatory cladocerans, noting the instar for *Bythotrephes* and *Cercopagis*. For all taxa, up to the first 20 individuals encountered were measured using an ocular micrometer, and biomass was estimated using published, taxa-specific length/weight regressions. We calculated the total and preferred crustacean zooplankton biomass for each sampling depth in each season.

To represent round goby prey availability, we used quagga mussel biomass (i.e., no zebra mussels were found in 2015; Karatayev and Burlakova 2017) rather than zooplankton given the predominance of dreissenid mussels in round goby diets (Kornis et al. 2012). Although smaller round gobies (i.e., < 75 mm TL) do not consume as many dreissenid mussels as larger ones, a Lake Michigan diet study in 2010 still reported dreissenids as comprising between 16 and 49% of the diet, depending on the season (Bunnell et al. 2015); other prey that dominated the diets of

small round gobies in at least one season were *Eurycercus lamellatus* and ostracods, but density estimates for those benthic prey were unavailable. Benthic invertebrates were sampled with a ponar grab (sampling area = 0.048 m²) during the summer (only) along each of our transects. At each site, three replicate ponar samples were collected, sieved through a 0.5-mm mesh, and preserved in 10% buffered formalin. In the laboratory, all dreissenid mussels were removed from the sample sediment with the aid of a dissection microscope, identified to species, and then shell length was measured to the nearest 1 mm. The mussels were aggregated within 5-mm size fractions: 0-5 mm, 5-10 mm, up to 35-40 mm. Within each size fraction, the mussels were blotted dry to remove excess moisture, then weighed to the nearest 0.001 g. Thus, biomass is expressed in terms of whole mussel wet weight, which includes soft tissue and shell. We reported biomass of mussels ≤ 15 mm because round gobies are gape limited in the size of mussel they can consume (Djuricich and Janssen 2001). Diet data from a 2010 diet study (Bunnell et al. 2010) revealed that 99.6% of mussels consumed had a shell length of 15 mm or less, which corresponds with other published field studies (Djuricich and Janssen 2001; Andraso et al. 2011). We averaged quagga mussel biomass (g/m²) sampled from sites < 46 m; all small round gobies in autumn were collected at 18 and 46 m depths and although 23% of large round gobies were collected at 110 m we assumed their migration to these deeper waters had occurred very recently (e.g., Walsh et al. 2007) and previously were feeding at shallower depths.

Comparing alewife and round goby energy density to previous studies

Madenjian et al. (2006) estimated the monthly ED from small and large alewives sampled from 8 sites in Lake Michigan in 2002-2004 and compared their ED to those estimated in 1979-1981. For April, May, July, September, and November, we determined whether the 95%

confidence intervals in our mean alewife ED overlapped with the 95% CI reported by Madenjian et al. (2006) for 2002-2004 or with the energy density schedule reported by Madenjian et al. (2006, see Figure 2) from Stewart and Binkowski (1986) and Hewett and Johnson (1992) from 1979-1981.

For round goby, we pooled our data and compared to previous studies that reported an ED versus wet weight relationship. These include round goby from the Muskegon River, Michigan watershed in 2004 (Ruetz et al. 2009), Lake Huron in 2007, and central Lake Erie from 1995-2002 (Johnson et al. 2005).

Results

Percent dry weight was a strong predictor of alewife ED ($r^2 = 0.97$, $P < 0.0001$, Table 1). Alewife ED was directly estimated from 582 individuals or composites, and calculated from %DW for another 524 individual fish. Alewife ED was weakly positively correlated with fish size. For the 286 small alewives (i.e., ≤ 120 mm TL) across all transects and seasons, ED increased with TL, but only 12% of the variation was explained ($F_{1,284} = 40.0$; $P < 0.0001$; $r^2 = 0.12$). For the 820 large alewives, ED was even less related to TL ($F_{1,818} = 63.0$; $P < 0.0001$; $r^2 = 0.07$).

Percent dry weight explained 80% of the variation in round goby ED (Table 1), but the relationship was not as strong as observed for alewife and analyzing the data by size class did not improve the fit. Round goby ED was directly estimated from 585 individuals or composites, and indirectly estimated from another 644 individuals. The relationship between ED and TL differed between size classes (see Fig. 2b). For small round gobies (i.e., ≤ 70 mm TL) ED increased strongly with TL ($F_{1,447} = 161.1$; $P < 0.0001$; $r^2 = 0.26$). For larger round gobies, there was a

statistically significant relationship between ED and fish size ($F_{1,777} = 13.1$; $P = 0.0003$; $r^2 = 0.02$), but probably not ecologically meaningful.

Does total energy differ between alewife and round goby?

Given that TE is the product of WW and ED, we plotted how these two variables were related to fish length for each species. For WW, round gobies always weighed more than alewife at a given TL (Fig. 2a) with the predicted weight for a 100-mm round goby (14.3 g) being 71% greater than for alewife (6.8 g). For a 150-mm fish, round gobies weighed 64% more than alewives (51.9 g. vs 26.8 g). ED of round gobies did not vary markedly by season, and linearly increased from 20 to 80 mm TL, and was relatively constant for larger sizes (Fig. 2b). Alewife ED varied both with season and size (Fig. 2b). For alewives smaller than 100 mm, ED also increased linearly among autumn fish, at a much faster rate than for round gobies, and then largely leveled off at larger sizes. For alewives larger than 100 mm, seasonal effects drove the variability with the highest average ED occurring in autumn (8.1 kJ/g), followed by spring (5.0 kJ/g) and summer (4.0 kJ/g).

During spring, a 100-mm round goby provided about 73% more TE than a 100-mm alewife (64 kJ vs. 30 kJ, Fig. 3a, b), and for a 150-mm fish, round goby provided 81% more TE (273 kJ vs. 116 kJ). Alewives were more variable in TE for a given size ($R^2 = 0.69$) than were round gobies ($R^2 = 0.99$). Post-hoc analysis of covariance of the alewife data indicated no difference in total energy between males and females in spring (size $\times$ sex: $F_{1,133} = 0.67$, $P = 0.41$; sex: $F_{1,133} = 0.69$, $P = 0.41$). Hence variation in alewife ED for a given size was more likely related to spatial differences or to some other factor that caused variation within a site.

During summer, round gobies continued to provide more TE than alewives (Fig. 3c, d). A 100-mm round goby provided 60 kJ, 48% more than a 100-mm alewife (37 kJ). The difference was 90% for 150-mm fishes: 235 kJ vs. 89 kJ for round goby and alewife, respectively, although the round goby estimate was an extrapolation. As found for spring, variability across individual alewife as a function of size ($R^2 = 0.33$) was extremely high compared to round gobies ($R^2 = 0.99$) and differences between sexes did not account for the variability in alewife (size $\times$ sex: $F_{1,133} = 0.81$, $P = 0.37$; sex: $F_{1,133} = 0.79$, $P = 0.38$).

During autumn, differences between round goby and alewife TE were smaller. For 100-mm fish, round gobies provided 66 kJ of TE whereas alewife provided 53 kJ, a 23% difference (Fig. 3e, f). For a 150-mm fish, round gobies provided 279 kJ of TE whereas alewife provided 237 kJ, a 17% difference. Unlike spring and summer, however, total energy as a function of fish size was just as predictable for alewife ($R^2 = 0.98$) as for round gobies ($R^2 = 0.98$). This result suggests that for each species, ED for a similarly sized fish was not very different within and across sampling sites during autumn.

Does total energy vary spatially within species?

For both size classes, mean residuals of alewife TE varied across transects in each season. For small alewife in the spring (likely yearlings), multiple comparisons revealed that residual TE from individuals caught at Frankfort had significantly higher values than those from the Root transect (Fig. 4a), whereas those from Muskegon were not different from the other ones. In autumn, small alewives [likely young-of-year (YOY)] from Waukegan had higher residual TE than those from the Frankfort and Root transects, while those from the other four transects were not different from the other ones (Fig. 4d). For autumn, alewife residual TE was unrelated to

either measure of zooplankton biomass (preferred ZP: $r = -0.77$, $P = 0.07$; total ZP: $r = -0.48$, $P = 0.34$).

For large alewife in the spring, those from Frankfort had significantly higher residual TE than those from the Root and Waukegan transects (Fig. 4b). For summer, none were caught from Frankfort but the highest residual TE was found for alewives in southeast Lake Michigan, St. Joseph and Muskegon, which had higher values than those from Sturgeon Bay, Root, and Waukegan (Fig. 4c). By autumn, large alewives from St. Joseph still had the highest residual TE, along with those from Frankfort and Waukegan (Fig. 4e); those from the Root transect had significantly lower residual TE. For large alewife, the highest mean residual TE was generally along the eastern shoreline transects.

For round gobies, the mean residual TE varied across transects in spring and autumn. For small round gobies in spring (likely yearlings), those from Sturgeon Bay had significantly higher residual TE than those from the Root and Waukegan transects (Fig. 5a). In autumn, small (presumably YOY) round gobies were collected from every transect. Those from the Muskegon transects had higher residual TE than those from the Pere Marquette, Kalamazoo, and St. Joseph transects (Fig. 5d); those from the Root and Manitowoc transects also had higher residual TE than those from the Pere Marquette.

Large round gobies in spring were classified into three groups whose mean residual TE differed from one another (Fig. 5b). Those from Sturgeon Bay had the highest residual TE, followed by those from Manitowoc, Root, Pere Marquette, Waukegan, and Frankfort, and then those from St. Joseph had the lowest residual TE. In summer, large round gobies were only collected from two transects (Waukegan and Muskegon) and their residual TE was not different from one another (Fig. 5c). In autumn, large round gobies from Manitowoc had a higher mean

residual TE than those from Sturgeon Bay, Frankfort, Pere Marquette, Kalamazoo, and St. Joseph transects (Fig. 5e). Curiously, large round gobies from Sturgeon Bay were the highest residual TE in spring but then dropped to among the lowest residual TE in autumn. Round goby residual TE in autumn was not related to quagga mussel biomass for either the small ($r = -0.05$, $P = 0.89$) or large ($r = -0.47$, $P = 0.21$) size classes.

Comparing alewife and round goby energy density to previous studies

Alewife ED differed from previous studies more for small individuals than large ones. For small alewife, ED could only be compared with previous studies for late fall. ED in early November 2015 averaged 6.5 kJ/g wet mass, which was 21% and 23% higher than estimated in 2002-2004 and 1979-1981, respectively (reported by Madenjian et al. 2006). Conversely, large alewife ED has not increased relative to earlier time periods. In fact, the 95% confidence intervals overlapped between 2015 and 2002-2004 for May, July, September, and November (Fig. 6a). In April, the intervals from the two time-periods differed, and large alewife ED was 30% lower in 2015 than in 2002-2004. Averaging the ED of large alewife in 2002-2004 and 2015 and comparing to 1979-1981 reveals the steepest declines occurred in April and May (30-38%) and that ED in autumn (September and November) was only 17% lower in the 2000s than in 1979-1981 (Fig. 6b).

Round goby ED (kJ/g wet mass) in Lake Michigan in 2015 was best described by the equation $3.646 \times W^{0.0736}$, where W equals the wet weight of the fish. Our data overlapped considerably with the best fit ED reported by Ruetz et al. (2009) in the Muskegon River watershed and for Lake Huron (S. A. Pothoven, unpublished data, Fig. 7). For very small round gobies (2 g) the percent difference among these three studies was no more than 4%. For a 15-g

round goby, those from Muskegon River watershed study had 10% greater energy density than our study and those from Lake Huron had 6% greater energy density than our study. We note, however, that the size range and sample size from our study (range = 0.1-83.5 g, mean = 11.6 g, N = 585) was larger than the range from the Muskegon (range = 0.1-16.1 g, mean = 3.3 g, N = 33) and Huron (range 0.7 – 23.8 g, mean = 4.3 g, N = 154) studies. Round goby from central Lake Erie included a relatively broad size range (range = 2.0 – 132.9 g, mean = 31.3 g, N = 46) and were larger, on average, than those from our study. However, 91% of the round goby ED values from 2015 in Lake Michigan were higher than predicted from central Lake Erie. The percent difference between Lake Michigan and central Lake Erie fish declined with size: 60% for 3 g, 17% for 15 g, 4% for 40 g, and no difference by 58 g.

Discussion

Estimating the energetic content of fishes is a helpful tool to evaluate how resources vary across time or space. Our somewhat surprising result was that during spring and summer, a round goby contained at least 48% more kJ of TE for piscivore consumption than an alewife of equal length. By autumn, however, alewife ED had markedly increased and alewife TE was only 17-23% lower than round goby TE of a similar length. This result demonstrates the variability in energetic content between species, and that round goby have the potential to be even more beneficial to piscivores than alewife from an energetics perspective should the availability of these prey species be equal in terms of length distributions. In terms of spatial variability, both species exhibited variability in TE across transects- especially in spring and autumn (summer comparisons were limited by sample size). For large alewives, the only consistent spatial pattern was higher residual TE along the eastern shoreline (i.e., Frankfort, Muskegon, St. Joseph

transects). No spatial pattern was evident for small alewives, and variation in residual TE in the autumn was unexplained by their primary prey: zooplankton biomass. Likewise, no spatial pattern in residual TE was apparent for small or large round gobies, nor was the variation explained by their primary prey: quagga mussel biomass less than 15 mm in length. Pooling round goby ED across our sites in Lake Michigan revealed some spatial variability across the Great Lakes. Round goby ED from central Lake Erie (Johnson et al. 2005) was consistently lower than what we measured in Lake Michigan and Huron or what others have measured in a Lake Michigan tributary (Ruetz et al. 2009). Temporal comparisons of alewife ED in Lake Michigan revealed a 21-23% increase in 2015 for small alewife in November relative to 2002-2004 and 1979-1981, and a 30% decrease in 2015 for large alewife in April relative to 2002-2004; comparisons between 2015 and 2002-2004 for large alewife revealed no differences in the other months.

Across a broad range of aquatic systems, differences in energy density have been noted among key prey fish species (Rand et al. 1994; Lawson et al. 1998; Anthony et al. 2000; Eggleston and Schramm 2002). These differences can sometimes be explained by guilds. For example, in the northern Gulf of Alaska, schooling pelagic species (analogous to alewife) tended to have either very high or low ED, whereas nearshore benthic species (analogous to round goby) had intermediate ED values (Anthony et al. 2000). Since the invasion of round gobies in the Great Lakes basin, studies have compared round goby with other prey fishes and concluded round goby ED is comparatively average (Ruetz et al. 2009) or among the lowest (Forzono et al. 2017). For example, in the Muskegon River watershed that drains into Lake Michigan, round goby ED was intermediate among four native prey fishes (Ruetz et al. 2009). In the upper Niagara River and Buffalo harbor, round goby ranked among the lowest ED among 15 species

and size classes of prey fishes (Forzono et al. 2017). Had we compared only ED between alewife and round goby, we would have concluded that alewife is higher than round goby in all seasons except summer. But because predators consume the entire fish, an equally appropriate comparison is TE, where fish of similar TL are compared given that TL, rather than weight, is the typical dimension considered when analyzing prey size selection by piscivores (see Juanes 1994). Because round goby weighed at least 60% more than an alewife of equal length, the TE of round goby can be more energetically beneficially to piscivores.

Our result that round goby offers more TE than an alewife of equal length has implications for piscivore growth beyond Lake Michigan given that these two species have been important prey species in other systems. From the 1970s through early 2000s, alewives were a key prey fish for Chinook salmon and lake trout in lakes Michigan, Huron, and Ontario (Brandt 1986; Jude et al. 1987; Diana 1990; Madenjian et al. 1998). Alewife densities have undergone some degree of decline in each of these Great Lakes, even to the point of “collapse” in Lake Huron (Riley et al. 2008). Over this time of alewife decline, round gobies invaded and proliferated everywhere but Lake Superior (Kornis et al. 2012) and their prevalence in piscivore diets has increased (Dietrich et al. 2006; Roseman et al. 2014; Happel et al. 2018). Lake trout, for example, appear to have compensated for declining availability of alewife with more frequent consumption of round goby, and scientists have hypothesized how this substitution can benefit thiamine levels in lake trout eggs and improve their reproductive success (Fitzsimons et al. 2009; Happel et al. 2018). To our knowledge, ours is the first study to suggest that substitution of round goby for alewife also can offer an energetic advantage so long as the lengths of alewife and round goby prey are similar. We caution, however, that the assumption of equal length distributions between the species may not be realized. To illustrate, in each season of our 2015

study, the mean size of alewife sampled in our trawls was always larger than the mean size of round goby (spring = 129 vs. 80 mm TL, summer = 147 vs. 88 mm TL, autumn = 98 vs. 74 mm TL). Assuming a piscivore consumed an average-sized fish, an average alewife provided 85%, 74%, and 73% more TE than an average round goby in spring, summer, and autumn of 2015, respectively. This comparison illustrates the importance of length distributions in determining which of these common Great Lakes prey fishes provides a greater energetic benefit to piscivores.

Spatiotemporal variability in TE can indicate differences in quality or quantity of resources available to fish. Alewives were much more variable in TE for a given length in spring and summer than round gobies. One interpretation of this result is that alewives were more resource limited during these seasons than round gobies, perhaps owing to greater spatial variation in the quality or quantity of what is consumed. Perhaps round gobies always have a relatively abundant prey resource, quagga mussels, that contributes to homogenization of TE across the lake for a given length. Conversely, alewife diets may be more diverse, especially when seeking to replace *Diporeia*, a high-lipid prey item that comprised at least 35% of large alewife diets in the spring through the mid-1990s (Rand et al. 1995; Davis et al. 2007; Pothoven and Madenjian 2008). Since the decline of *Diporeia* (Nalepa et al. 2014), alewife spring diets have shifted to include more calanoid copepods and *Mysis diluviana* (Pothoven and Madenjian 2008; Bunnell et al. 2015). We hypothesize that the proportion of mysids in alewife diets could be driving the relatively high variability in TE for a given site, given that mysids are a large and high lipid prey resource. Among the alewife diet studies in Lake Michigan since quagga mussels have become abundant, the percentage of mysids in the diets ranged from 7-51 at different sites and years (Pothoven and Madenjian 2008; Bunnell et al. 2015). Although we did not conduct

diet analyses with the 2015 alewives, we would hypothesize that alewife captured at the Frankfort transect had consumed more mysids during winter into spring, given that alewives from Frankfort had higher than average TE values.

We hypothesized that energetic content of fishes would be reflective of spatial or temporal patterns in prey resources. For plantivorous Pacific herring (*Clupea pallasii*) in Prince William Sound, autumn and winter ED differed among different regions and scientists hypothesized that differences in zooplankton quality and quantity underlie the variation (Paul and Paul 1999; Gorman et al. 2018). Among three southeast Lake Michigan sites in an earlier study, the one with the lowest density of *Diporeia* spp. prey also had the lowest ED for deepwater sculpin and large alewife (Hondorp et al. 2005). Likewise, lipid levels for *Diporeia* spp. were higher in northern Lake Michigan than in southern waters (Nalepa et al. 2001), and the authors posited that greater diatom densities in the north could explain the difference. In our study, the strongest spatial pattern occurred with large alewife, where residual TE was consistently higher on the eastern side of the lake (e.g., Frankfort, Muskegon, St. Joseph transects) in each season. The eastern and western shorelines of the lake are known to differ with respect to upwellings (more frequent on the western shore, Plattner et al. 2006), substrate type (rockier and more complex in the lower western two-thirds of the lake, Janssen et al. 2005), and number of high-phosphorus loading tributaries (more on the eastern shore, Dolan and Chapra 2012). Recent Lake Michigan diet studies for spottail shiner (*Notropis hudsonius*) and yellow perch (*Perca flavescens*) that covered both coastlines indicated more benthic-oriented prey were consumed on the western side and more pelagic-oriented prey were consumed on the eastern side (Happel et al. 2015 a,b). Whether more pelagic prey items enhanced the TE of pelagic-oriented alewife on the eastern side of the lake deserves further research. It is logical that the higher

phosphorus loading along the southeastern coastline (i.e., St. Joseph, Grand, Kalamazoo Rivers) could enhance phytoplankton and even zooplankton productivity. However, we found no relationship between residual TE of small alewife in the autumn and coincident zooplankton biomass from the summer and autumn.

Our comparisons of round goby ED from 2015 to other systems indicated (1) minimal differences with those from the Muskegon Lake watershed (Ruetz et al. 2009) and Lake Huron, and (2) round gobies from central Lake Erie generally have a lower ED. This second result is surprising given that central Lake Erie is more productive, in terms of phosphorus and chlorophyll, than Lakes Michigan and Huron (Bunnell et al. 2014). At the same time, densities of dreissenid mussels at comparable depths were considerably higher in Lake Michigan ($2,053 \pm 697$ per m^2 in the 0 – 30 m depth range in 2015) than in central Lake Erie (608 ± 224 per m^2 basinwide density in 2014; Karatayev and Burlakova 2017). Lower mussel densities in central Lake Erie are likely due to hypoxia that develops at depths greater than 20 m and eliminates dreissenids sensitive to low oxygen (Karatayev et al. 2018). At the same time, surveys in 2014-2015 reported densities for non-dreissenid invertebrates such as chironomids and oligochaetes to be more than twice as high in central Lake Erie (11,357 per m^2) than in Lake Michigan (4,618 per m^2 ; Karatayev and Burlakova 2017), and non-dreissenid invertebrates typically have a higher ED than dreissenid mussels (Johnson et al. 2005). Hence two explanations for lower round goby ED in central Lake Erie are conceivable. First, higher densities of dreissenid mussels in Lakes Michigan may enable round gobies to eat a higher total biomass of prey, which causes more total energy to be consumed. Second, the tolerance of round gobies to hypoxia may low enough that they cannot take advantage of the higher densities of non-dreissenid benthic invertebrate prey that are available during mid-July through mid-

October when hypolimnetic oxygen concentrations in central Lake Erie are diminished (see Arend et al. 2011).

Temporal comparisons of alewife ED in Lake Michigan between 2015 and 2002-2004 indicated differences in only a few comparisons. One likely explanation for the limited decadal differences is that alewife biomass in 2015 was estimated at only 69 kilotonnes, compared to a mean of 255 kilotonnes in 2002-2004 (D.M. Warner, unpublished data), suggesting reduced intraspecific competition prevented alewife ED from eroding despite declines in offshore total zooplankton biomass and no increases in mysids or *Diporeia* spp. (Bunnell et al. 2018). The differences that were documented included small alewife ED in November 2015 being 21% higher than November 2002-2004, and large alewife ED in spring 2015 being 30% lower in 2015 than in spring 2002-2004. The latter difference was consistent with Pothoven and Fahnenstiel (2014) reporting a steeper decline over the first winter of life for yearling alewife in the 2000s than in the 1990s. Given these two studies, we hypothesize that alewives are not able to consume as much energy during winter since 2004 owing to food-web changes. Specifically, during winter and spring when dreissenid mussels can filter more phytoplankton from the water column (Fahnenstiel et al. 2010), this reduction in primary production could reduce the lipids available to overwintering omnivorous copepods that likely sustain alewife as prey overwinter.

Several of the Laurentian Great Lakes are undergoing oligotrophication in the offshore waters. As a result, managers are increasingly asking how reductions in nutrients could influence fish production (Bunnell et al. 2018) and adjusting piscivore stocking rates to more accurately balance predator/prey resources. Although the energetic content of alewife and round goby varied across our nine transects, we were unable to explain this variation with the available estimates of their prey density. Whether this lack of correspondence was due to inaccurate

characterization of the prey density at those sites (i.e., sampling on one date in summer and one date in autumn and comparing to autumn condition) or our inability to measure some other important biological factor (e.g., fish movement in and out of sampling sites) is not clear. We also explored whether density dependence could influence condition but correlations between fish density from each transect and residual TE revealed no pattern for either species. Furthermore, lakewide alewife acoustic densities from August 2015 showed higher mean densities in Michigan waters (i.e., along the eastern coastline) than in Wisconsin and Illinois waters (i.e., along the western coastline) by a factor of 1.7 (D.M. Warner, unpublished data), which is the opposite from what we would have predicted if density dependence regulated TE. Future research should explore the eastern versus western shoreline differences in invertebrate prey resources for pelagic-oriented alewife, given the consistently higher TE we measured for large alewife along the eastern transects. These regional differences in alewife condition support the management of Lake Michigan fisheries at a sub-lake level, as is currently being pursued by Michigan Department of Natural Resources.

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Table 1. Predictive relationship between energy density (ED, kJ/g wet mass) and percent dry weight (%DW) for alewife and round goby collected from Lake Michigan during 2015.

Species	Size Class	Equation	N	Statistics
Alewife	Small (≤ 120 mm, TL)	$ED = -1.931 + 0.331(\%DW)$	220	$F = 6407.7$ $P < 0.0001$ $r^2 = 0.97$
Alewife	Large (> 120 mm, TL)	$ED = -3.143 + 0.370(\%DW)$	362	$F = 13106.2$ $P < 0.0001$ $r^2 = 0.97$
Round goby	n/a	$ED = -0.326 + 0.228 (\%DW)$	585	$F = 2362.0$ $P < 0.0001$ $r^2 = 0.80$

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Figure 1. Location of sampling sites with adjacent tributaries that were sampled in Lake Michigan in 2015. Inset shows where Lake Michigan is located among the Laurentian Great Lakes. Map data: ArcGIS and U.S. Geological Survey.

Figure 2. Comparison of round goby and alewife weight (a) and energy density (b, estimated directly from bomb calorimetry or calculated from % dry weight) as a function of total length based on samples collected from nine transects in Lake Michigan from 2015. Large seasonal differences in alewife energy density were apparent in panel b.

Figure 3. Total energy of alewife (left column) and round goby (right column) as a function of total length. Panels a, b represent fish sampled between April 16 and May 11. Panels c, d represent fish sampled between July 18-26. Panels e, f represent fish sampled between October 18 and November 3. The line represents predicted total energy for a given total length. The coefficient of determination for the relationship and the number of transects from which fish were sampled are shown in each panel.

Figure 4. The mean residual (observed-predicted, in ln-scale) total energy for small (left column, ≤ 120 mm) and large (right column, >120 mm) alewife size classes sampled in eight transects in Lake Michigan in 2015 (noting that alewives were not sampled in all transects in all seasons). Abbreviations for transects [ordered left to right as western shoreline (north to south) and then eastern shoreline (north to south)] are STB (Sturgeon Bay), MNW (Manitowoc), RT (Root), WK (Waukegan), FF (Frankfort), PM (Pere Marquette), MK (Muskegon), and STJ (St. Joseph). Panels a, b represent alewife sampled between April 16 and May 11. Panel c represents alewife

sampled between July 18-26. Panels d, e represent alewife sampled between October 18 and November 3. Small alewives were not collected in summer. Different letters indicate the mean residuals are significantly different from one another.

Figure 5. The mean residual (observed-predicted, in ln-scale) total energy for small (left column, ≤ 70 mm) and large (right column, >70 mm) round goby size classes sampled in nine transects in Lake Michigan in 2015 (noting that round gobies were not sampled in all transects in all seasons). Abbreviations for transects [ordered left to right as western shoreline (north to south) and then eastern shoreline (north to south)] are STB (Sturgeon Bay), MNW (Manitowoc), RT (Root), WK (Waukegan), FF (Frankfort), PM (Pere Marquette), MK (Muskegon), KZ (Kalamazoo), and STJ (St. Joseph). Panels a, b represent round goby sampled between April 16 and May 11. Panel c represents round goby sampled between July 18-26. Panels d, e represent round goby sampled between October 18 and November 3. Small round gobies were not collected in summer. Different letters indicate the mean residuals are significantly different from one another.

Figure 6. Temporal comparisons for large alewife energy density in Lake Michigan. Panel a illustrates the monthly mean energy density ($\pm$ 95% confidence intervals, where available) over three time periods, with 1979-1981 and 2002-2004 values derived from Madenjian et al. (2006). Note that November 2015 represents alewives sampled between 26 October and 3 November. Panel b depicts the percent difference in large alewife energy density between the mean of 2015 and 2002-2004 values and the mean 1979-1981 value.

797 Figure 7. Comparisons between round goby energy density (estimated through bomb
798 calorimetry) as a function of wet weight estimated from nine transects in Lake Michigan in 2015
799 (data are open gray circles; dashed, dark gray line is the best fit curve) to those from Muskegon
800 watershed (dashed line, Ruetz et al. 2009), Lake Huron in 2007 (solid line) and central Lake Erie
801 (dash-dot-dot-dash line, Johnson et al. 2005).
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Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.