

Energy Density of Introduced Round Goby Compared with Four Native Fishes in a Lake Michigan Tributary

CARL R. RUETZ III* AND DANA L. STROUSE¹

Annis Water Resources Institute, Grand Valley State University,
740 West Shoreline Drive, Muskegon, Michigan 49441, USA

STEVEN A. POTHOVEN

National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory,
1431 Beach Street, Muskegon, Michigan 49441, USA

Abstract.—The round goby *Neogobius melanostomus* is an invasive species that has changed Great Lakes food webs and become an important prey for many predators. We tested whether the round goby from a Lake Michigan tributary was energetically equivalent to four native fishes: mottled sculpin *Cottus bairdii*, johnny darter *Etheostoma nigrum*, bluntnose minnow *Pimephales notatus*, and rock bass *Ambloplites rupestris*. We found positive linear relationships between energy density and the percent dry weight of a fish for each species. We also found evidence of temporal and spatial variation in round goby energy density. Energy density was lower in spring and summer than in fall. The spatial variation in energy density may be linked to the inclusion of the low-quality prey, dreissenid mussels, in the diets of larger round goby. For a given size, the johnny darter and bluntnose minnow had the highest energy density while mottled sculpin had the lowest. Our results show that the energy density of the round goby is intermediate to those of the four native fishes, suggesting that the round goby is an energetically average prey in a Lake Michigan tributary.

The round goby *Neogobius melanostomus* is an invasive species in North America and Europe (Corkum et al. 2004). In North America, round gobies are spreading throughout the Great Lakes (Clapp et al. 2001; Schaeffer et al. 2005; Walsh et al. 2007), including connecting lakes and rivers (Phillips et al. 2003; Cooper et al. 2007), and are also invading the Mississippi River basin (Irons et al. 2006). The invasion of round goby into the Great Lakes is altering the food web (Johnson et al. 2005b). For example, round goby can be highly abundant (Lauer et al. 2004; Johnson et al. 2005a; Ruetz et al. 2007), approaching densities greater than 100 individuals/m² (Chotkowski and Marsden 1999; Steinhart et al. 2004a), and may replace native benthic fishes, including mottled scul-

pins *Cottus bairdii* and johnny darters *Etheostoma nigrum* (Janssen and Jude 2001; Lauer et al. 2004). Several piscivores are reported to consume round goby (e.g., Johnson et al. 2005b; Truemper et al. 2006; Hensler et al. 2008), including juvenile smallmouth bass *Micropterus dolomieu* in Lake Erie, which may have led to the latter's increased growth rates and a shift to piscivory at an earlier age (Steinhart et al. 2004b). Thus, invasion of round goby may have both positive (e.g., providing an abundant food resource for piscivores) and negative (e.g., locally extirpating native benthic fishes) effects in the Great Lakes.

Measuring energy density of both predators and prey can be an important tool for quantifying trophic dynamics, assessing effects of ecosystem change on fish production, and evaluating fish health and the flow of energy through the food web (Rand et al. 1994; Shearer 1994; Madenjian et al. 2000; Pothoven et al. 2006). The goal of this study was to determine whether the round goby is energetically equivalent to native fishes as a prey resource. Thus, comparing the energy content of the round goby with other prey fishes will help predict ecological effects of the round goby in areas where they replace native benthic fishes and occur at high densities. Our objectives were to: (1) compare the energy density of the round goby with four native fishes, (2) examine whether energy content of round gobies varied among seasons, and (3) explore whether energy density of round gobies that primarily consume *Dreissena* spp. (i.e., zebra mussels *D. polymorpha* and quagga mussels *D. bugensis*) differs from that of round gobies that do not.

Methods

Sampling.—We collected round gobies and four native fishes in Muskegon Lake and the lower Muskegon River watershed (Muskegon County, Michigan). The round goby was first discovered in Lake Michigan near Muskegon Lake in 1999 (Clapp et al. 2001) and is now abundant in Muskegon Lake (Breen and Ruetz 2006; Ruetz et al. 2007).

* Corresponding author: ruetzc@gvsu.edu

¹ Present address: Michigan Department of Environmental Quality, 350 Ottawa NW, Grand Rapids, Michigan 49503, USA.

TABLE 1.—Sample size (n), fish size, and dates and locations of collections for each species used in calorimetric analysis. Fish were collected during 2004 from Muskegon Lake (ML), the Muskegon River (MR), and Cedar Creek (CC).

Species	n	Total length (cm)		Wet weight (g)		Collection	
		Mean \pm SD	Range	Mean \pm SD	Range	Dates	Locations
Bluntnose minnow	40	5.3 \pm 1.5	2.8–8.0	1.72 \pm 1.48	0.27–5.59	Jul 13–22, Aug 12	ML, MR
Johnny darter	21	3.8 \pm 0.9	2.5–5.3	0.51 \pm 0.36	0.11–1.31	Jul 19–27, Aug 12	MR
Mottled sculpin	19	6.7 \pm 1.9	4.0–10.4	5.16 \pm 4.98	0.70–19.80	Oct 11	CC
Rock bass ^a	32	7.6 \pm 2.1	2.6–12.6	10.29 \pm 7.59	1.77–35.99	Jul 13–22	ML
Round goby	33	5.4 \pm 2.2	2.1–10.1	3.31 \pm 3.80	0.11–16.15	Jul 13–27	ML ^b , MR

^a Includes two fish that were considered outliers when fitting regression models (see Figure 1).

^b Does not include fish collected via angling from the channel connecting Muskegon Lake to Lake Michigan.

We selected native species for energy analysis to represent different habitat uses (benthic versus water-column species) and body morphologies (fusiform versus compressiform, spiny-rayed versus soft-rayed). The johnny darter and mottled sculpin are native benthic species that have been replaced at some locations in Lake Michigan by the round goby (Janssen and Jude 2001; Lauer et al. 2004). The bluntnose minnow *Pimephales notatus* is a common cyprinid in Muskegon Lake (Breen and Ruetz 2006; Ruetz et al. 2007) and is an important prey to many piscivores (Becker 1983). The rock bass *Ambloplites rupestris* has a different morphology than the other prey species selected and is common in Muskegon Lake (Breen and Ruetz 2006; Ruetz et al. 2007). Both the bluntnose minnow and rock bass are water-column species.

In 2004, fishes were collected between July and October primarily with fyke nets (e.g., Breen and Ruetz 2006; Ruetz et al. 2007) in Muskegon Lake (Table 1). To achieve adequate numbers of each species, we supplemented collections of bluntnose minnows by seining both Muskegon Lake and Muskegon River. Additional round gobies and johnny darters were collected by backpack electrofishing in the Muskegon River. Mottled sculpins were captured by backpack electrofishing in Cedar Creek, a tributary of the lower Muskegon River, because none were collected in Muskegon Lake or Muskegon River. In 2005, round gobies were collected by fyke netting in Muskegon Lake during 11–12 May, 20–21 July, and 13–14 September to examine seasonal changes in energy content.

We also collected round gobies by angling at the channel connecting Muskegon Lake to Lake Michigan (hereafter Muskegon Lake channel) on 19 August 2004 ($n = 8$ fish, range = 10.0–14.0 cm total length [TL] and 13.8–40.9 g wet weight) and 22 July 2005 ($n = 10$, range = 9.4–16.0 cm TL and 12.9–49.7 g wet weight) to increase the number of large fish for our analysis because angling is often selective for larger individuals (MacInnis and Corkum 2000; Clapp et al. 2001).

However, these fish were not included in our comparison among species (Table 1) because round gobies collected from Muskegon Lake channel in 2004 had a different relationship between energy density and percent dry weight than did round gobies from Muskegon Lake and Muskegon River (hereafter Muskegon Lake watershed; see Results). Round gobies collected in 2005 at the Muskegon Lake channel were used to test whether the difference we observed in 2004 was related to presence of *Dreissena* in stomachs of round gobies.

Sample processing.—To slow decomposition and reduce water loss, fish were placed in sealable plastic bags with lake water, placed on ice, and transported to the laboratory for storage (Hartman and Brandt 1995). Fish were measured to the nearest 0.01 mm with dial calipers for TL and stored frozen in water individually for calorimetry.

For each species, 21–40 individuals were selected for calorimetric analysis so that size ranges overlapped among species (Table 1). Fish were thawed, patted dry, and weighed to the nearest 0.0001 g. In most cases, rock bass at least 9 cm TL (about 12 g) and round goby at least 10 cm TL (about 13 g) were homogenized with a hand grinder before they were oven dried. Fish were oven dried at approximately 70°C to a constant weight (about 48 h) before measuring dry weight. Dried fish were homogenized with a mortar and pestle. A Parr Model 1261 Isoperibol calorimeter was used to measure energy content. The calorimeter was calibrated using benzoic acid pellets before making energy determinations. Fish larger than 1.25 g dry weight were subsampled to obtain a sample between 1.0 and 1.75 g dry weight. For fish less than 1.25 g dry weight, the entire fish was weighed and combusted to measure energy content. In some cases, an individual fish was too small to be combusted and two to three fish of the same species were combined. We determined which fish needed to be combined by first attempting to combust the smallest individual of each species. If the sample did not combust, then it was combined with the

TABLE 2.—Linear regression models used to explore differences in energy density among the bluntnose minnow (BM), johnny darter (JD), mottled sculpin (MS), rock bass (RB), and round goby (RG) captured during 2004. The number of parameters (K), error sum of squares (SSE), Akaike's information criterion corrected for small-sample bias (AIC_c), AIC difference (Δ_i), and Akaike weights (w_i) are reported for each model. The species models fit unique intercept and slope parameters for each species. For pooled models, a common intercept and slope were fit for the species noted, whereas unique intercept and slope parameters were fit for other species.

Model	K	SSE	AIC_c	Δ_i	w_i
Energy density versus % dry weight					
Species	11	4,390,526	1,501.5	1.8	0.26
JD–MS–RG pooled	7	4,967,769	1,510.0	10.3	<0.01
MS–RG pooled	9	4,899,651	1,512.5	12.9	<0.01
JD–RG pooled	9	4,477,973	1,499.7	0	0.66
MS–JD pooled	9	4,613,761	1,503.9	4.3	0.08
BM–JD–MS–RB pooled	5	16,204,563	1,674.7	175.0	<0.01
BM–JD–MS–RB–RG pooled	3	16,408,041	1,672.2	172.5	<0.01
Log₁₀(energy density) versus log₁₀(wet weight)					
Species	11	0.2547	–881.3	0	>0.99
JD–MS–RG pooled	7	0.3724	–836.1	45.2	<0.01
MS–RG pooled	9	0.3235	–851.7	26.6	<0.01
JD–RG pooled	9	0.2874	–868.6	12.6	<0.01
MS–JD pooled	9	0.3019	–861.6	19.7	<0.01
BM–JD–MS–RB pooled	5	0.4750	–805.7	75.6	<0.01
BM–JD–MS–RB–RG pooled	3	0.5120	–799.2	82.0	<0.01

next smallest fish for combustion. Energy density was reported on a wet-weight basis for each fish (J/g wet weight) along with percent dry weight, which was calculated for each fish (Hartman and Brandt 1995). Estimates of energy density included stomach contents except for round goby collected at the Muskegon Lake channel by angling in 2005. Stomach contents were combusted separately for round goby collected at the Muskegon Lake channel via angling in 2005 to compare energy densities of fish tissues (excluding stomach contents) to stomach contents. Based on 2004 sampling (see Results), we expected that *Dreissena* in stomach contents were lowering estimates of round goby energy density. Round gobies collected by means of fyke netting in 2005 were dried but not combusted because we used percent dry weight as a surrogate for energy density (Hartman and Brandt 1995; this study) to make seasonal comparisons.

Data analysis.—We used the information–theoretic approach (Burnham and Anderson 2002) to evaluate evidence for a set of hierarchical regression models to determine whether energy density differed among fish species (Table 1) or whether energy density of round gobies differed among seasons (collected during 2005 by fyke netting). We used indicator variables to include species or seasons categories in regression models so that both intercept and slope differ for each category in a model (Montgomery and Peck 1992).

We used the procedures outlined by Burnham and Anderson (2002) to compare regression models using the information–theoretic approach. First, we calculated Akaike's information criterion corrected for small-

sample bias (AIC_c) to assess the fit of each candidate model. The best-fitting model had the lowest AIC_c . Next, we calculated the AIC difference (Δ_i), which is AIC_c for candidate model i minus the minimum AIC_c among all candidate models ($i = 1, 2, \dots, n$ for a set of n candidate models) because AIC_c values are only comparable among other AIC_c values in the model set. Models with low Δ_i are most plausible given the data set. Finally, we calculated Akaike weight (w_i), which is the weight of evidence for model i given the data set and the set of candidate models ($0 < w_i < 1$), to select the best-fit model. Models with the highest values of w_i have the greatest support.

To test whether energy content differed among species when controlling for size, we evaluated the evidence for a set of seven competing hypotheses that were expressed as regression models (Table 2). We regressed energy density versus percent dry weight (to account for differences in the water content of a species) and \log_{10} (energy density) versus \log_{10} (wet weight). Two outliers were apparent for rock bass (based on Studentized residuals; Montgomery and Peck 1992), which were excluded from regression models because we suspect they were measurement errors. Our hypotheses on the relationships between energy density and percent dry weight (and between \log_{10} [energy density] and \log_{10} [wet weight]) were that (1) each species differed (species model), (2) native species were similar but differed from the round goby (BM–JD–MS–RB pooled model), and (3) all species were similar (BM–JD–MS–RB–RG pooled model) (abbreviations represent species: BM, bluntnose minnow; JD,

TABLE 3.—Linear regression models used to explore differences in round goby energy density (measured as percent dry weight) among seasons (May, Jul, Sep) during 2005 in Muskegon Lake. Model descriptors are defined in Table 2. The seasonal model fit unique intercept and slope parameters for each season. For pooled models, a common intercept and slope were fit for the months noted, whereas unique intercept and slope parameters were fit for the other months.

Model	K	SSE	AIC_c	Δ_i	w_i
Seasonal	7	252.7	95.4	3.6	0.14
May–Jul pooled	5	254.1	91.8	0	0.86
Jul–Sep pooled	5	327.5	128.5	36.8	<0.01
May–Jul–Sep pooled	3	349.8	133.9	42.1	<0.01

johnny darter; MS, mottled sculpin; RB, rock bass; and RG, round goby). Additionally, we hypothesized that (4) all benthic species were similar, but differed from the other species (JD–MS–RG pooled model), (5) the mottled sculpin and round goby were similar but differed from other species (MS–RG pooled model), (6) the johnny darter and round goby were similar but differed from the other species (JD–RG pooled model), and (7) native benthic species differed from the round goby and the other species (MS–JD pooled model).

To test whether energy content of round gobies differed among seasons when controlling for size, we evaluated the evidence for a set of four competing hypotheses that were expressed as regression models (Table 3). We regressed percent dry weight (i.e., index of energy density) versus TL. One outlier was apparent (based on Studentized residuals), which was excluded from regression models because we suspect it was a measurement error. Our hypotheses on the relationship between percent dry weight and TL were that (1) each season differed (seasonal model), (2) May and July were similar, but differed from September (May–July pooled model), (3) July and September were similar, but differed from May (July–September pooled model), and (4) all seasons were similar (May–July–September pooled model).

We did not use the information–theoretic approach to compare energy density of round gobies collected from the Muskegon Lake watershed in 2004 with round gobies collected from the Muskegon Lake channel in 2004 and 2005 because these comparisons were not planned a priori (see Burnham and Anderson 2002). Therefore, we focus on the relationship and effect size (i.e., difference in energy density between groups) for these comparisons.

Results

We found positive linear relationships between energy density and percent dry weight for all species (Figure 1). Akaike weights indicated that the best-fit

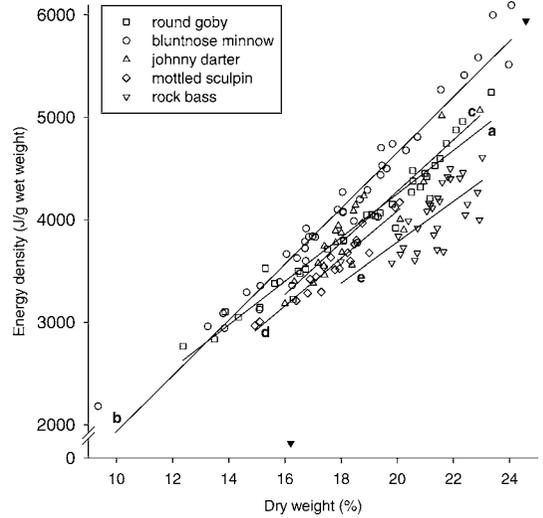


FIGURE 1.—Relationships between energy density (ED) and percent dry weight (DW) for the round goby (a: $ED = 1.77 + 212.55 \cdot DW$; $R^2 = 0.95$), bluntnose minnow (b: $ED = -786.67 + 272.16 \cdot DW$; $R^2 = 0.95$), johnny darter (c: $ED = -743.12 + 251.04 \cdot DW$; $R^2 = 0.82$), mottled sculpin (d: $ED = -530.85 + 230.85 \cdot DW$; $R^2 = 0.92$), and rock bass (e: $ED = -195.97 + 198.84 \cdot DW$; $R^2 = 0.49$). Outliers (shown in black on the graph) were excluded from the regression analysis. The break on the y-axis indicates the omission of values between 500 and 1,925 J/g wet weight. Sample sizes and the sizes of the fish used for analysis are reported in Table 1.

model was JD–RG pooled, although there was also support for the species model (Table 2). The best-fit model indicated that energy density was typically highest for the bluntnose minnow and lowest for rock bass with benthic species intermediate (Figure 1). Energy densities of the johnny darter and round goby were most similar (i.e., can be described by a single regression line; Table 2) and greater than for mottled sculpin (Figure 1).

We found a strong, positive relationship between energy density and wet weight for the round goby, bluntnose minnow, and johnny darter (Figure 2). There was not a clear relationship between energy density and wet weight for the mottled sculpin and rock bass (Figure 2). When we did find a relationship between energy density and wet weight, it was asymptotic rather than the linear relationship between energy density and percent dry weight. Akaike weights indicated that the best-fit model was the species model (Table 2), suggesting that regression lines were different for each species. On average, round goby energy density was intermediate to the other fishes, which is similar to our findings based on the relationship between energy density and percent dry weight (Figure 1), with the

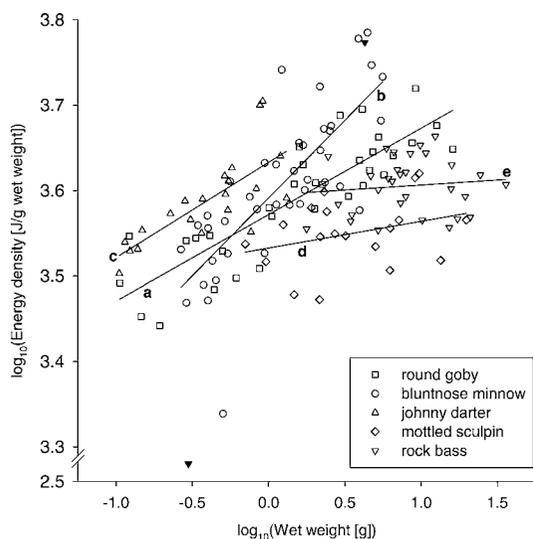


FIGURE 2.—Relationships between energy density (ED) and wet weight (WW) for the round goby (a: $\log_{10}[\text{ED}] = 3.57 + 0.10 \cdot \log_{10}[\text{WW}]$; $R^2 = 0.74$), bluntnose minnow (b: $\log_{10}[\text{ED}] = 3.59 + 0.18 \cdot \log_{10}[\text{WW}]$; $R^2 = 0.60$), johnny darter (c: $\log_{10}[\text{ED}] = 3.63 + 0.11 \cdot \log_{10}[\text{WW}]$; $R^2 = 0.56$), mottled sculpin (d: $\log_{10}[\text{ED}] = 3.53 + 0.03 \cdot \log_{10}[\text{WW}]$; $R^2 = 0.10$), and rock bass (e: $\log_{10}[\text{ED}] = 3.59 + 0.01 \cdot \log_{10}[\text{WW}]$; $R^2 = 0.01$). Outliers (shown in black on the graph) were identified during the first analysis (see Figure 1) and excluded from this regression analysis. The break on the y-axis indicates the omission of values between 2.59 and 3.29 $\log_{10}(\text{J/g wet weight})$. Sample sizes and the wet weights of the fish used for analysis are reported in Table 1.

johnny darter higher and mottled sculpin lower than round goby (Figure 2).

We found that percent dry weight increased linearly with TL of a round goby and this relationship differed among seasons (Figure 3). Akaike weights indicated that the best-fit model was May–July pooled, although there was limited support for the seasonal model (Table 3). The best-fit model indicated that percent dry weight of round gobies during May and July was most similar and less than September (Figure 3). The same general result was obtained when we regressed $\log_{10}(\% \text{ dry weight})$ on $\log_{10}(\text{wet weight})$; therefore, we only reported the relationship between percent dry weight and TL.

Energy density of round gobies collected at Muskegon Lake channel differed from round gobies collected in Muskegon Lake watershed (Figure 4). These relationships were as expected (i.e., positive slopes) when energy density was regressed as a function of percent dry weight (Figure 4A), but were negative with wet weight (Figure 4B). Energy density of round gobies collected from the Muskegon Lake

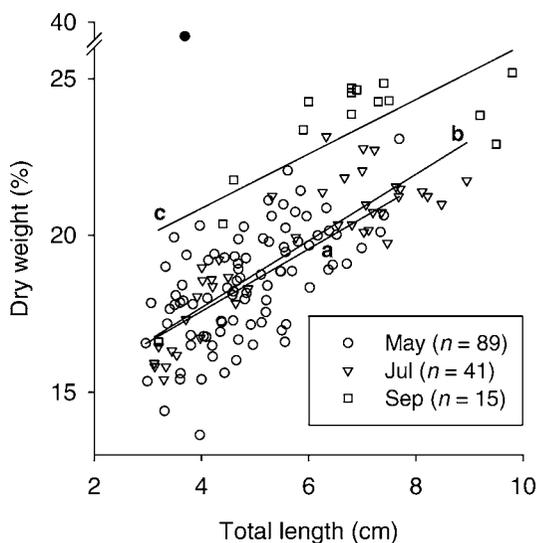


FIGURE 3.—Relationships between percent dry weight (DW) and total length (TL) for round gobies captured during May (a: $\text{DW} = 13.62 + 0.99 \cdot \text{TL}$; $R^2 = 0.37$), July (b: $\text{DW} = 13.45 + 1.06 \cdot \text{TL}$; $R^2 = 0.76$), and September 2005 (c: $\text{DW} = 17.39 + 0.87 \cdot \text{TL}$; $R^2 = 0.51$) in Muskegon Lake. An outlier (shown in black on the graph) was excluded from the regression analysis and not included in sample sizes (n) reported in the legend. The break on the y-axis indicates the omission of values between 26 and 38 percent dry weight.

channel in 2004 averaged 14% lower (between 20 and 23 percent dry weight) than round gobies collected from the Muskegon Lake watershed in 2004 (Figure 4A), which we initially suspected was caused by including stomach contents of larger round gobies containing *Dreissena* in samples used for calorimetry. Excluding stomach contents from round gobies collected from the Muskegon Lake channel in 2005 resulted in an 11% increase in energy density expressed as a function of percent dry weight compared with round gobies collected at the same location in 2004 (Figure 4A), although energy density of the 2005 fish still averaged 4% lower than round goby collected from the Muskegon Lake watershed in 2004 (difference: 10% at 20 percent dry weight and -0.2% at 23 percent dry weight). Similarly, energy density (expressed as a function of wet weight) was greater for round gobies collected from the Muskegon Lake channel in 2005 than for fish collected from the same location in 2004 (Figure 4B). However, energy density of round gobies collected from the Muskegon Lake channel tended to decline with size (Figure 4B) because their water content increased with wet weight (i.e., there was a negative relationship between percent dry weight and wet weight).

Although energy density of *Dreissena* in the

stomach of round gobies was lower than energy density of round goby tissues, the amount of stomach contents did not mainly account for the lower energy density of the round gobies (when controlling for size) collected from the Muskegon Lake channel in 2005 than the round gobies collected in the Muskegon Lake watershed in 2004 (Figure 4). In 2005, the energy density of *Dreissena* in stomach contents of round gobies was 1,730 J/g wet weight (SD = 60, $n = 3$ samples from pooled stomach contents) compared with 4,411 J/g wet weight (SD = 715, $n = 10$ fish) for round gobies with stomach contents excluded. Although stomach contents were almost entirely *Dreissena*, they only accounted for about 3.2% (range = 1.5–5.3%) of the wet weight of a round goby. Thus, adding *Dreissena* in stomach contents to the estimated energy density of round gobies only resulted in a 1.9% decrease in average energy density (fish only: 4,411 J/g wet weight; fish + *Dreissena* in stomach contents: 4,326 J/g wet weight).

Discussion

Round goby energy density was intermediate among the four native fishes we investigated. Unlike the central basin of Lake Erie where the round goby was an energetically inferior prey (Johnson et al. 2005b), the round goby was an energetically average prey in our Lake Michigan tributary. Round goby energy density was more similar to native benthic fishes (especially johnny darter) than either the bluntnose minnow or rock bass when species comparisons were made controlling for water content (Figure 1). When species comparisons were made controlling for size (Figure 2), round goby energy density was typically lower than for the johnny darter and bluntnose minnow and higher than for the rock bass and mottled sculpin.

Although the round goby was an energetically average prey among the fishes we examined, energy density is one of many factors needed to determine the suitability of a prey type in a predator's diet (e.g., Wahl and Stein 1988). Round goby can reach much higher numerical densities than native benthic fishes (Lauer et al. 2004; Steinhart et al. 2004a; Johnson et al. 2005a), which could make them more available to predators (Johnson et al. 2005b). Round gobies were an important component of the diets yellow perch *Perca flavescens* in southern Lake Michigan (Truemper et al. 2006), smallmouth bass (Steinhart et al. 2004b; Johnson et al. 2005b) and northern water snakes *Nerodia sipedon* (King et al. 2006) in Lake Erie, burbot *Lota lota* in Lakes Michigan, Huron, and Erie (Johnson et al. 2005b; Hensler et al. 2008), and double-crested cormorants *Phalacrocorax auritus* (Somers et al. 2003) and lake trout *Salvelinus namaycush* (Dietrich et al. 2006) in Lake Ontario. Nevertheless, consumption of

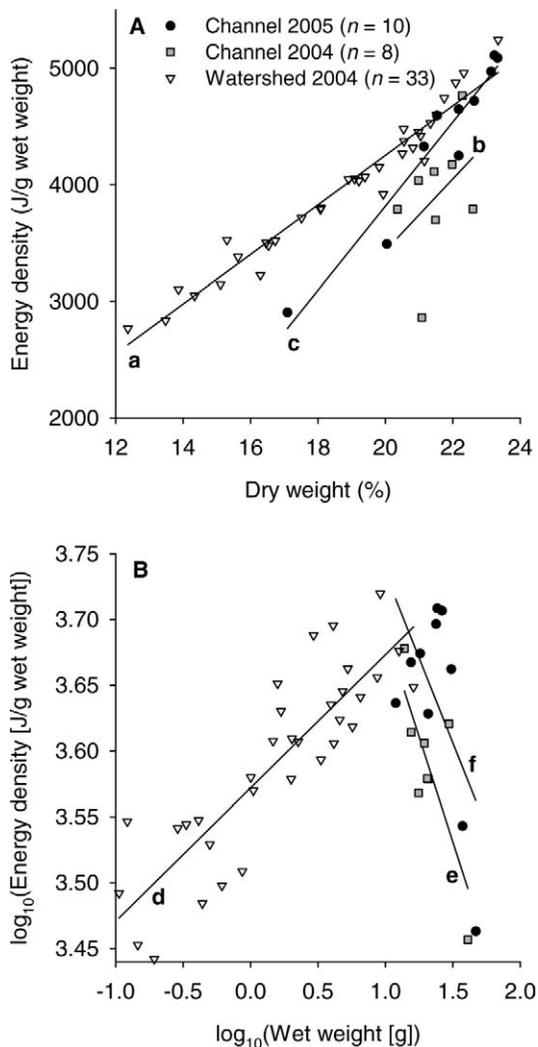


FIGURE 4.—Panel (A) shows the relationships between energy density (ED) and percent dry weight (DW) for round gobies collected from Muskegon Lake watershed in 2004 (a: Figure 1), Muskegon Lake channel in 2004 (b: $ED = -2,715.75 + 307.52 \cdot DW$; $R^2 = 0.18$), and Muskegon Lake channel in 2005 (c: $ED = -3,397.80 + 360.72 \cdot DW$; $R^2 = 0.93$). Panel (B) shows the relationships between ED and wet weight (WW) for round gobies collected from Muskegon Lake watershed in 2004 (d: Figure 2), Muskegon Lake channel in 2004 (e: $\log_{10}[ED] = 4.01 - 0.32 \cdot \log_{10}[WW]$; $R^2 = 0.59$), and Muskegon Lake channel in 2005 (f: $\log_{10}[ED] = 3.99 - 0.26 \cdot \log_{10}[WW]$; $R^2 = 0.34$). Stomach contents were included in estimates of ED in 2004 and excluded in 2005.

the round goby also may have negative effects on predators. The round goby may provide a new pathway for biomagnifications of contaminants in the Great Lakes food web (Hogan et al. 2007; Ng et al. 2008; but see Hensler et al. 2008) and serve as a vector for

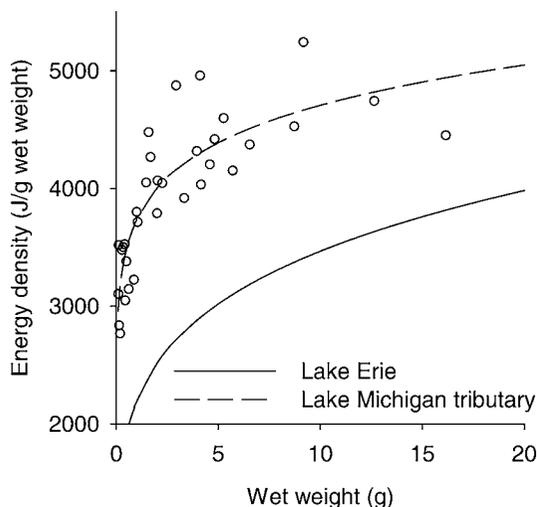


FIGURE 5.—Relationships between energy density (ED) and wet weight (WW) of round goby from the Muskegon Lake watershed, a tributary of Lake Michigan (Table 1; $ED = 3,731.9 \cdot WW^{0.101}$) and the central basin of Lake Erie ($ED = 2,188 \cdot WW^{0.200}$). The relationship for Lake Erie was estimated by Johnson et al. (2005b).

transfer of botulism neurotoxin to fish-eating birds (Yule et al. 2006).

Our results suggest that energy density of round gobies varied among seasons. Energy density was lower in spring and summer than in fall. Energy reserves of many species, including the alewife *Alosa pseudoharengus* (Flath and Diana 1985; Madenjian et al. 2000), Atlantic silverside *Menidia menidia* (Schultz and Conover 1997), and slimy sculpin *C. cognatus* (Madenjian et al. 2000), varied among seasons. Similar to our findings for the round goby, energy density of the rainbow smelt *Osmerus mordax* was shown to increase from summer to fall (Foltz and Norden 1977; Vondracek et al. 1996), although seasonal variation in energy reserves of some species, including lake whitefish *Coregonus clupeaformis* (Pothoven et al. 2006) and bloater *C. hoyi* (Madenjian et al. 2000), can be minimal. We suspect that the observed increase in energy density of round gobies in fall was a result of the fish increasing their reserves for winter and subsequent reproduction in spring and summer. Female round gobies spawn many times over an extended spawning season from spring to midsummer (MacInnis and Corkum 2000), discounting the likelihood that seasonal differences in energy density were primarily due to spawning behavior because the May and July sampling events should have been near the beginning and ending of the spawning season, respectively. Additionally, water temperature, which can affect lipid

storage and metabolic rate (Shearer 1994), was unlikely to cause seasonal differences in round goby energy density because temperatures in Muskegon Lake were lower in spring than in summer (highest) or fall (Ruetz et al. 2007). However, we did not evaluate abundance and nutritional quality of prey consumed by round goby, which could affect seasonal differences in round goby energy density (e.g., Shearer 1994).

In addition to seasonal variation, energy density of round gobies may vary spatially throughout their range. We found that energy density of round gobies from the Muskegon Lake watershed was greater than similarly sized fish from the central basin of Lake Erie (Figure 5). We suspect that the difference in energy density may be due to differences in diet (see later discussion). Energy density of predatory fishes is often a product of prey quality (e.g., Pothoven et al. 2006). Nevertheless, other factors, including round goby density, also could account for the spatial variation in energy density.

The round gobies we collected from Muskegon Lake channel generally had lower energy density than expected based on regression relationships derived from round gobies collected from Muskegon Lake watershed (Figure 4). We found that including stomach contents that had *Dreissena* with whole fish for calorimetric measurement only slightly decreased our estimates of energy density even though energy density of *Dreissena* was 2.5 times less than for fish tissue (i.e., when fish was combusted without stomach contents) because stomach contents comprised a small proportion of the total wet weight of a fish (i.e., fish tissue plus stomach contents). Nevertheless, the cause of the negative relationship between energy density and size for round gobies collected from Muskegon Lake channel (Figure 4B) was unclear—other than water content increased with fish size—but could be related to differences in quality of prey consumed by round gobies (see next paragraph), round goby densities, and depletion of energy reserves from spawning. The ease at which round gobies were captured at Muskegon Lake channel suggests round goby densities were higher than at sites we sampled in Muskegon Lake (Breen and Ruetz 2006; present study). In contrast to our results, the relationship between energy density and wet weight was positive for large (e.g., wet weight, >30 g) round gobies in Lake Erie (Johnson et al. 2005b), although the predicted energy density of a 25.5-g round goby (average size of round gobies collected from Muskegon Lake channel in 2005, Figure 4B) in Lake Erie (4,181 J/g wet weight) was less than what we observed for an average round goby collected in Muskegon Lake channel (2005: 4,326 J/g wet weight).

We hypothesize that consumption of prey with low

energy density (i.e., *Dreissena*) causes larger round gobies to have lower energy density than that in smaller individuals. Small round gobies often consume invertebrates other than mussels, such as cladocerans and dipterans, whereas large round gobies often readily consume *Dreissena* (Jude et al. 1995; Ng et al. 2008). Prey quality often influences the energy density of consumers (e.g., Hondrop et al. 2005). For instance, lake whitefish energy density was suspected to decline, in part, due to including *Dreissena*, which is of low quality, in their diet (Pothoven et al. 2006; Lumb et al. 2007). Round goby preferred amphipods to *Dreissena* in laboratory experiments when encounter rates with the more mobile amphipods were sufficient (Diggins et al. 2002). Difference in energy density between round gobies from a Lake Michigan tributary and Lake Erie (Figure 5) and within a Lake Michigan tributary (Figure 4) could be partially due to different diets. *Dreissena* dominated the diets of round gobies collected in Lake Erie (Bunnell et al. 2005; Johnson et al. 2005b). We suspect this was not true for round gobies used in our main analysis (see Table 1) because few fish were of sufficient size to readily consume *Dreissena* (Jude et al. 1995; Ray and Corkum 1997), which may be typical for Lake Michigan tributaries (Cooper et al. 2007). Only about 3% of round goby diets (based on numbers of prey consumed; $n = 15$ fish, range = 2.6–8.8 cm TL) collected in Muskegon Lake during June 2006 consisted of *Dreissena* (C. R. Ruetz, B. Shafer, D. G. Uzarski, and M. J. Cooper, unpublished data). In contrast, we consistently observed *Dreissena* in the diets of round gobies collected from the Muskegon Lake channel, which is probably due to round goby size and abundant hard substrates in the channel that are colonized by *Dreissena* (Jude and DeBoe 1996).

In conclusion, our results showed that round goby energy density was not markedly different from that of native benthic fishes and can vary both spatially and among seasons. Our regression models of round goby energy density could be used to improve predictions of consumption and growth by round gobies using a recent bioenergetics model, although round goby energy density was not a highly sensitive parameter in the model (Lee and Johnson 2005). As more predators in the Great Lakes basin include the introduced round goby in their diets, understanding spatiotemporal patterns of round goby energy density becomes more important for evaluating predator–prey dynamics.

Acknowledgments

We thank Matt Breen, Melissa Reniski, and Eric Nemeth for assistance with sampling. Much of the fish

sampling was part of the Muskegon Lake Long-Term Monitoring Project, which is supported by the Muskegon Lake Research Endowment Fund managed by the Community Foundation for Muskegon County. Additional support was provided by Sigma Xi Grants-in-Aid of Research program to D.L.S., who was supported by a research assistantship by the Annis Water Resources Institute. This is Great Lakes Environmental Research Laboratory contribution 1510.

References

- Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.
- Breen, M. J., and C. R. Ruetz, III. 2006. Gear bias in fyke netting: evaluating soak time, fish density, and predators. *North American Journal of Fisheries Management* 26:32–41.
- Bunnell, D. B., T. B. Johnson, and C. T. Knight. 2005. The impact of introduced round gobies (*Neogobius melanostomus*) on phosphorus cycling in central Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 62:15–29.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer, New York.
- Chotkowski, M. A., and J. E. Marsden. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. *Journal of Great Lakes Research* 25:26–35.
- Clapp, D. F., P. J. Schneeberger, D. J. Jude, G. Madison, and C. Pistis. 2001. Monitoring round goby (*Neogobius melanostomus*) population expansion in eastern and northern Lake Michigan. *Journal of Great Lakes Research* 27:335–341.
- Cooper, M. J., C. R. Ruetz, III, D. G. Uzarski, and T. M. Burton. 2007. Distribution of round gobies in coastal areas of Lake Michigan: are wetlands resistant to invasion? *Journal of Great Lakes Research* 33:303–313.
- Corkum, L. D., M. R. Sapota, and K. E. Skora. 2004. The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. *Biological Invasions* 6:173–181.
- Dietrich, J. P., B. J. Morrison, and J. A. Hoyle. 2006. Alternative ecological pathways in the eastern Lake Ontario food web: round goby in the diet of lake trout. *Journal of Great Lakes Research* 32:395–400.
- Diggins, T. P., J. Kaur, R. K. Chakraborti, and J. V. DePinto. 2002. Diet choice by the exotic round goby (*Neogobius melanostomus*) as influenced by prey motility and environmental complexity. *Journal of Great Lakes Research* 28:411–420.
- Flath, L. E., and J. S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. *Transactions of the American Fisheries Society* 114:328–337.
- Foltz, J. W., and C. R. Norden. 1977. Seasonal changes in food consumption and energy content of smelt (*Osmerus mordax*) in Lake Michigan. *Transactions of the American Fisheries Society* 106:230–234.
- Hartman, K. J., and S. B. Brandt. 1995. Estimating energy

- density of fish. *Transactions of the American Fisheries Society* 124:347–355.
- Hensler, S. R., D. J. Jude, and J. He. 2008. Burbot growth and diets in Lakes Michigan and Huron: an ongoing shift from native species to round gobies. Pages 91–107 in *Burbot: ecology, management, and culture*. American Fisheries Society, Symposium 59, Bethesda, Maryland.
- Hogan, L. S., E. Marschall, C. Folt, and R. A. Stein. 2007. How nonnative species in Lake Erie influence trophic transfer of mercury and lead to top predators. *Journal of Great Lakes Research* 33:46–61.
- Hondrop, D. W., S. A. Pothoven, and S. B. Brandt. 2005. Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. *Transactions of the American Fisheries Society* 134:588–601.
- Irons, K. S., M. A. McClelland, and M. A. Pegg. 2006. Expansion of round goby in the Illinois Waterway. *American Midland Naturalist* 156:198–200.
- Janssen, J., and D. J. Jude. 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *Journal of Great Lakes Research* 27:319–328.
- Johnson, T. B., M. Allen, L. D. Corkum, and V. A. Lee. 2005a. Comparison of methods needed to estimate population size of round gobies (*Neogobius melanostomus*) in western Lake Erie. *Journal of Great Lakes Research* 31:78–86.
- Johnson, T. B., D. B. Bunnell, and C. T. Knight. 2005b. A potential new energy pathway in central Lake Erie: the round goby connection. *Journal of Great Lakes Research* 31(Supplement 2):238–251.
- Jude, D. J., and S. F. DeBoe. 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):136–141.
- Jude, D. J., J. Janssen, and G. Crawford. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit rivers. Pages 447–460 in M. Munawar, T. Edsall, and J. Leach, editors. *The Lake Huron ecosystem: ecology, fisheries, and management*. SPB Publishing, The Netherlands.
- King, R. B., J. M. Ray, and K. M. Stanford. 2006. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. *Canadian Journal of Zoology* 84:108–115.
- Lauer, T. E., P. J. Allen, and T. S. McComish. 2004. Changes in mottled sculpin and johnny darter trawl catches after the appearance of round gobies in the Indiana waters of Lake Michigan. *Transactions of the American Fisheries Society* 133:185–189.
- Lee, V. A., and T. B. Johnson. 2005. Development of a bioenergetics model for the round goby (*Neogobius melanostomus*). *Journal of Great Lakes Research* 31:125–134.
- Lumb, C. E., T. B. Johnson, H. A. Cook, and J. A. Hoyle. 2007. Comparison of lake whitefish (*Coregonus clupeaformis*) growth, condition, and energy density between Lakes Erie and Ontario. *Journal of Great Lakes Research* 33:314–325.
- MacInnis, A. J., and L. D. Corkum. 2000. Fecundity and reproductive season of the round goby *Neogobius melanostomus* in the upper Detroit River. *Transactions of the American Fisheries Society* 129:136–144.
- Madenjian, C. P., R. F. Elliott, T. J. DeSorcie, R. M. Stedman, D. V. O'Connor, and D. V. Rottiers. 2000. Lipid concentrations in Lake Michigan fishes: seasonal, spatial, ontogenetic, and long-term trends. *Journal of Great Lakes Research* 26:427–444.
- Montgomery, D. C., and E. A. Peck. 1992. *Introduction to linear regression analysis*, 2nd edition. Wiley, New York.
- Ng, C. A., M. B. Berg, D. J. Jude, J. Janssen, P. M. Charlebois, L. A. N. Amaral, and K. A. Gray. 2008. Chemical amplification in an invaded food web: seasonality and ontogeny in a high-biomass, low-diversity ecosystem. *Environmental Toxicology and Chemistry* 27:2186–2195.
- Phillips, E. C., M. E. Washek, A. W. Hertel, and B. M. Niebel. 2003. The round goby (*Neogobius melanostomus*) in Pennsylvania tributary streams of Lake Erie. *Journal of Great Lakes Research* 29:34–40.
- Pothoven, S. A., T. F. Nalepa, C. P. Madenjian, R. R. Rediske, P. J. Schneeberger, and J. X. He. 2006. Energy density of lake whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. *Environmental Biology of Fishes* 76:151–158.
- Rand, P. S., B. F. Lantry, R. O'Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for salmonine energetics. *Transactions of the American Fisheries Society* 123:519–534.
- Ray, W. J., and L. D. Corkum. 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environmental Biology of Fishes* 50:267–273.
- Ruetz, C. R., III, D. G. Uzarski, D. M. Krueger, and E. S. Rutherford. 2007. Sampling a littoral fish assemblage: comparison of small-mesh fyke netting and boat electrofishing. *North American Journal of Fisheries Management* 27:825–831.
- Schaeffer, J. S., A. Bowen, M. Thomas, J. R. P. French, III, and G. L. Curtis. 2005. Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in western Lake Huron, USA. *Journal of Great Lakes Research* 31:414–425.
- Schultz, E. T., and D. O. Conover. 1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). *Oecologia* 109:516–529.
- Shearer, K. D. 1994. Factors affecting the proximate composition of cultured fishes, with emphasis on salmonids. *Aquaculture* 119:63–88.
- Somers, C. M., M. N. Lozer, V. A. Kjos, and J. S. Quinn. 2003. The invasive round goby (*Neogobius melanostomus*) in the diet of nestling double-crested cormorants (*Phalacrocorax auritus*) in Hamilton Harbour, Lake Ontario. *Journal of Great Lakes Research* 29:392–399.
- Steinhart, G. B., E. A. Marschall, and R. A. Stein. 2004a. Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. *Transactions of the American Fisheries Society* 133:121–131.
- Steinhart, G. B., R. A. Stein, and E. A. Marschall. 2004b. High growth rate of young-of-year smallmouth bass in

- Lake Erie: a result of the round goby invasion? *Journal of Great Lakes Research* 30:381–389.
- Truemper, H. A., T. E. Lauer, T. S. McComish, and R. A. Edgell. 2006. Response of yellow perch diet to a changing forage base in southern Lake Michigan. *Journal of Great Lakes Research* 32:806–816.
- Vondracek, B., B. D. Giese, and M. G. Henry. 1996. Energy density of three fishes from Minnesota waters of Lake Superior. *Journal of Great Lakes Research* 22:757–764.
- Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* 117:142–151.
- Walsh, M. G., D. E. Dittman, and R. O’Gorman. 2007. Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. *Journal of Great Lakes Research* 33:83–92.
- Yule, A. M., I. K. Barker, J. W. Austin, and R. D. Moccia. 2006. Toxicity of *Clostridium botulinum* type E neurotoxin to Great Lakes fish: implications for avian botulism. *Journal of Wildlife Diseases* 42:479–493.