Quantifying the predatory effect of round goby on Saginaw Bay dreissenids

Carolyn J. Foley a,b,⁎, Sara R. Andree a,1, Steven A. Pothoven c, Thomas F. Nalepa d,2, Tomas O. Höök a,b

a Purdue University, Department of Forestry and Natural Resources, West Lafayette, IN 47907, United States
b Illinois-Indiana Sea Grant College Program, Purdue University, West Lafayette, IN 47907, United States
c NOAA-GLERL Lake Michigan Field Station, Muskegon, MI 49441, United States
d Water Center, Graham Sustainability Institute, University of Michigan, Ann Arbor, MI 48104, United States

⁎ Corresponding author at: Purdue University, Department of Forestry and Natural Resources, West Lafayette, IN 47907, United States.
E-mail addresses: cfoley@purdue.edu (C.J. Foley), srandree@purdue.edu (S.R. Andree), steve.pothoven@noaa.gov (S.A. Pothoven), nalepa@umich.edu (T.F. Nalepa), thook@purdue.edu (T.O. Höök).
1 Present address: Department of Natural Resources and Environmental Sciences, University of Illinois Urbana-Champaign, 1816 S. Oak St., Champaign IL, 61820, United States.
2 NOAA-GLERL, Ann Arbor, MI 48108, United States.

A B S T R A C T

Invasive dreissenid mussels (D. polymorpha and D. r. bugensis) have fundamentally altered Laurentian Great Lake ecosystems, however in many areas their abundances have declined since the mid-1990s. Another invader, the benthic fish round goby (Neogobius melanostomus), is morphologically adapted to feed on dreissenids and likely affects dreissenid populations; however, the degree of this predatory effect is variable. In 2009 and 2010, we examined round goby abundances, size distributions, diet contents, and diet selectivity in Saginaw Bay, Lake Huron; a shallow bay that has been subjected to numerous anthropogenic stressors. We further used a consumption model to estimate dreissenid consumption by three different size classes of round goby. Round gobies were found throughout the bay and most were smaller than 80 mm total length. Round gobies of all sizes consumed dreissenids (including fish as small as 30 mm total length), though dreissenids were rarely preferred. The relative proportion of dreissenids (by biomass) present in diets of round gobies increased with increasing round goby abundance. We found substrate type, as zebra mussels prefer hard substrates to which they can more firmly attach (Marsden and Lansky, 2000), and are generally less abundant on sand and silt (Wilson et al., 2006). Zebra mussel expansion in North America has often been closely followed by that of the invasive quagga mussel. This congeneric species has not only impacted zebra mussel populations, but also come to dominate benthic communities in many habitats where zebra mussels were rarely found (Nalepa et al., 2010; Benson, 2013). Quagga mussels are able to colonize softer, less structured substrates, and can tolerate and reproduce at lower temperatures (Diggins, 2001; Garton et al., 2013). Lower respiration requirements (Stoeckmann, 2003) and comparatively more efficient filtration capacity at low food densities (Baldwin et al., 2002; Diggins, 2001) and in the presence of predators (Nadda and Rudstam, 2013) have likely also facilitated quagga mussel proliferation throughout the Great Lakes.

Though dreissenids have become dominant members of Great Lakes ecosystems, recent declines in dreissenid density and condition have become apparent in lakes Michigan, Huron, Erie, and Ontario (Glyshew et al., 2015; Karataayev et al., 2014; Nalepa et al., 2010; Pennuto et al., 2012a). Potential explanations for these decreases include that dreissenids have reached carrying capacity and are now food-limited (Bunnell et al., 2013; Hecky et al., 2004; Wilson et al., 2006); have been
negatively influenced by coldwater upwellings in nearshore areas (Wilson et al., 2006) or, especially for quagga mussels, are being preyed upon (Naddaf and Rudstam, 2013; Naddaf and Rudstam, 2014a). Dreissenids serve as prey for a variety of native fish species, including lake whitefish (Coregonus clupeformis) (Madenjian et al., 2010), yellow perch (Perca flavescens) (Morison et al., 1997; Roswell et al., 2013; Withers et al., 2015), freshwater drum (Aplodinotus grunniens) (Morison et al., 1997) and common carp (Cyprinus carpio) (French, 1993), and predation by fishes may be an increasingly important factor influencing dreissenid abundance. Past research in the Great Lakes suggests that round gobies may be particularly effective at culling dreissenid populations (Lederer et al., 2008; Naddaf and Rudstam, 2014b; Wilson et al., 2006). The extent and impact of round goby predation upon dreissenids may vary spatially throughout the Great Lakes Basin (Kipp et al., 2012), and there is an ongoing need to examine the ability of round goby predation to affect dreissenid abundance across a variety of ecosystems (Ruetz et al., 2012).

Round gobies possess a suite of life history traits (e.g., multiple annual reproductive episodes) and behavioral strategies (e.g., nest-guarding and aggression) which allow them to successfully reproduce and thrive in shallow, warmer regions of the Great Lakes (Vanderploeg et al., 2002). Additionally, their preference for hard substrates as feeding and nesting sites (Ray and Corkum, 2001) and the presence of both upper and lower pharyngeal teeth (Ghedotti et al., 1995) likely make them particularly adept at exploiting dreissenids as a food source. Previous studies confirm that dreissenids can comprise a large proportion of round goby diets, especially for larger individuals with fewer morphological limitations (French and Jude, 2001; Lederer et al., 2008; Ray and Corkum, 1997). Some research suggests that round goby predation can drastically reduce dreissenid abundance; in Lake Erie, Barton et al. (2005) observed a 94% reduction of dreissenid density from 2002 to 2004, which coincided with increasing round goby predation upon dreissenids. Conversely, other studies estimate that round goby predation affects only a small proportion of dreissenid populations in Lakes Erie (Bunnell et al., 2005; Johnson et al., 2005b) and Ontario (Pennuto et al., 2012a). Evidence also suggests that smaller round gobies tend to prefer non-dreissenid prey (Barton et al., 2005; Diggins et al., 2002). An ontogenetic diet shift (occurring between 60 and 100 mm total length) from soft-bodied macroinvertebrates to almost exclusively molluscs is typical of round gobies in both their native and invasive ranges (Janssen and Jude, 2001; Jude et al., 1995), and is likely regulated by progressive development of the pharyngeal feeding apparatus (Andrasso et al., 2011a).

Saginaw Bay, a large, shallow embayment of Lake Huron, has undergone many changes due to both anthropogenic activity (Fielder et al., 2000; Johengen et al., 2000), and multiple introductions of nonindigenous species (e.g., Fielder and Thomas, 2000; Ivan et al., 2014). Saginaw Bay remains the largest Area of Concern of the Great Lakes, being persistently impacted by beneficial use impairments including eutrophication, loss of fish and wildlife habitat, and population degradation of fish, wildlife and benthic invertebrates (Selzer et al., 2014). While various remedial activities have begun to ameliorate these conditions, the bay has yet to fully recover and remains an area of unique and ongoing management interest (Selzer et al., 2014). One continued concern is that the bay’s benthic habitat remains largely altered by the presence of dreissenids (Nalepa et al., 2002). Mean density and biomass of dreissenids on hard substrates in Saginaw Bay declined dramatically between the early-to-mid-1990s and 2008–2010. After wide-scale, annual fluctuations in the immediate years after initial establishment, the population stabilized, and in 1993–1996 mean density and shell-free, ash-free dry weight biomass was 4163/m2 (SE = 747/m2) and 7.6 g/m2 (SE = 2.2 g/m2) (Nalepa et al., 2003). However, by 2008–2010 mean density and biomass was only 92/m2 (SE = 444/m2) and 1.6 g/m2 (SE = 0.2 g/m2) (Nalepa et al., in preparation).

As in other systems, the decrease in dreissenid populations over hard substrates in Saginaw Bay was coincident with an increase in round goby size and abundance (Schaefeer et al., 2005). In 2009 and 2010, round gobies were the third most abundant fish caught in annual fall trawling surveys (Fielder and Thomas, 2014). They have become an increasingly important member of the Saginaw Bay fish community, with CPE increasing up to 2-fold between 1997 and 2003 (Fielder and Thomas, 2014; Schaeffer et al., 2005), and continuing to increase since 2005 even as many native prey fish species have declined (Ivan et al., 2014; Fielder and Thomas, 2014). Whether or not round gobies have a major effect on dreissenid populations in Saginaw Bay has been posited (Nalepa et al., 2003), but to date has not been evaluated. The objectives of this study were to infer the predatory effect of round gobies on dreissenid populations in Saginaw Bay by 1) examining round goby feeding patterns in terms of diet composition and prey preference, and 2) estimating round goby consumption of dreissenids and relating this to overall dreissenid population characteristics (e.g., size, abundance, production).

Methods

Field and laboratory methodology

We collected round gobies and potential prey from five sites in Saginaw Bay (Fig. 1), which varied in depth and sediment type (Table 1). We attempted to visit each site once per month, from April through November of 2009 and 2010. We collected fish during the day with a 7.62 m headrope, 4-seam bottom trawl with a 3.175 mm mesh cod liner, performing 3–7 tows per site visit. We measured (to nearest mm) and weighed (to nearest 0.01 g). From each trawl, we randomly selected round gobies for diet analysis (up to 20 round gobies per site per month, spread evenly across trawls collected during a single sampling event). Since round gobies have no distinct stomach, we thawed, measured and weighed each fish, then removed the fish’s entire digestive tract (after Barton et al., 2005; MacInnis and Corkum, 2000). Under a dissecting microscope, we identified (to lowest possible taxonomic level) and counted all diet items with a head or complete shell, and then photographed and measured each item to the nearest 0.1 mm using Image J analysis software (Schneider et al., 2012). We estimated dry weight (DW) of individual diet items using published length-weight relationships or mean dry weight (Roswell, 2011). From these, we calculated the proportion by biomass of dreissenids consumed by individual round gobies.

We processed benthic macroinvertebrate samples in the laboratory within one year of collection. All round gobies were thawed and counted, and up to 30 randomly-selected individual fish per trawl tow were measured (to nearest mm) and weighed (to nearest 0.01 g). From each trawl, we randomly selected round gobies for diet analysis (up to 20 round gobies per site per month, spread evenly across trawls collected during a single sampling event). Since round gobies have no distinct stomach, we thawed, measured and weighed each fish, then removed the fish’s entire digestive tract (after Barton et al., 2005; MacInnis and Corkum, 2000). Under a dissecting microscope, we identified (to lowest possible taxonomic level) and counted all diet items with a head or complete shell, and then photographed and measured each item to the nearest 0.1 mm using Image J analysis software (Schneider et al., 2012). We estimated dry weight (DW) of individual diet items using published length-weight relationships or mean dry weight (Roswell, 2011). From these, we calculated the proportion by biomass of dreissenids consumed by individual round gobies.

We processed benthic macroinvertebrate samples in the laboratory by rinsing with water through a 500 μm mesh sieve and transferring contents to a sorting tray. We examined the tray under a magnifying lamp and removed, identified and counted all whole benthic macroinvertebrates, as well as those with identifiable heads. Animals were then stored in 70% ethanol. We photographed and measured up to 20 randomly selected dreissenids per sample with a dissecting microscope.

We attempted to visit each site once per month, from April through November of 2009 and 2010. We collected these samples to quantify dreissenid abundance and distribution, as well as those with identifi-
camera, and ImageJ analysis software (Schneider et al., 2012). In some samples, we observed very large numbers of 1–3 mm individuals. For these, we photographed and measured 20 of these smaller individuals and up to 20 larger individuals. Dreissenids that were too large to photograph were measured to the nearest mm using a ruler under a dissecting microscope. To estimate biomass, we converted lengths to shell-free dry weights (mg) using published length-weight regressions for quagga ($W = 0.0078L^{2.783}$; Conroy et al., 2005) and zebra ($W = 0.007L^{2.982}$; Mackie, 1991) mussels, determined the mean weight of each taxon, and multiplied the mean weight by the mean density of animals of the taxon in that sample.

**Statistical and selectivity analyses**

To understand potential differences in round goby feeding over the year, we performed an ANCOVA with mean size of dreissenid found in round goby diets as the response variable, month (May, July and September only) as the explanatory variable, and total length of individual fish (mm) as the covariate. We also performed ANOVAs on the mean proportion of dreissenids relative to other items found in round goby diets of three distinct size classes (TL) that correspond roughly to age classes (<70 mm = Age-0, 71–88 mm = Age-1, >88 mm = Age-2 and older; e.g., MacInnis and Corkum, 2000; Taraborelli et al., 2010), with year, month (May, July and September) and size class as between group factors. Proportion data were ln + 0.001 transformed prior to analyses, and all analyses were performed using the ezANOVA package in R (R Core Team, 2013).

To investigate feeding preference, we evaluated selectivity of round gobies for various benthic macroinvertebrate prey by calculating Chesson’s $\alpha$ (Chesson, 1983), as defined by the equation

$$\alpha = \frac{r_i / p_i}{\sum r_i / p_i}$$

where $r_i$ is the proportion (by count) of a prey type found in diets, and $p_i$ is the proportion (by density per m$^2$) found in the environment. Prey availability varied with site and season of sampling (C. Foley, unpublished data), thus values of $\alpha$ were calculated for individual sites each month for which data were available. Neutral selection for each site was determined as one divided by the average of all $\alpha$ values for each site (Chesson, 1983). Prey items were grouped into eight categories which included all macroinvertebrates observed in both diets and the environment. The category “Chironomidae” included both larvae and pupae of this taxon, and the category “Dreissenidae” included both zebra and quagga mussels. The number of fish included in these site-month calculations ranged from 1 to 34.

![Fig. 1. Sites in Saginaw Bay, Lake Huron from which round gobies and benthic macroinvertebrates were collected in 2009 and 2010.](image)

**Table 1** Description of sample sites. Mean depth is calculated over all sampling events. Temperatures are noted as mean (minimum-maximum) experienced over the sampling time frame.

<table>
<thead>
<tr>
<th>Site name</th>
<th>Mean depth (m)</th>
<th>Surface temp. (°C)</th>
<th>Substrate type</th>
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<td>2</td>
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<td>3.6</td>
<td>18.3 (11.7–25.9)</td>
<td>Cobble, gravel, sand</td>
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<td>16.2 (5.6–26.9)</td>
<td>Silt, muck</td>
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<td>3.8</td>
<td>18.9 (12-27.1)</td>
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<td>20</td>
<td>17.7</td>
<td>15.2 (5.6–23.7)</td>
<td>Sandy silt</td>
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Estimates of consumption

Bioenergetics models have often been used to estimate predatory demand on prey taxa (e.g., Johnson et al., 2005b; Stewart and Ibarra, 1991). Lee and Johnson (2005) developed a temperature- and weight-dependent bioenergetics model for round goby in the Great Lakes. We applied this model (using Saginaw Bay-specific data) to estimate round goby consumption under three scenarios (see below). Given that round gobies spawn multiple times per year, it is difficult to follow growth of distinct cohorts and age classes. In addition, in North America, different age classes of round goby often overlap in size (e.g., MacInnis and Corkum, 2000; Taraborelli et al., 2010). In order to assess the potential effect of round goby predation on dreissenid populations, we placed an upper bound on potential round goby consumption by assuming that round gobies were feeding at their maximum daily rate (as estimated by Lee and Johnson, 2005) for a given weight and temperature (after Ryan et al., 2013).

We estimated densities of round gobies per trawl for the three different size classes (previously described) as well as total round goby catch. For trawls in which >30 round gobies were caught (i.e., not all fish were measured), we multiplied total round goby catch by the proportion of fish of a given size class in the subset of fish measured. However, by collecting fish via trawls and sampling some sites dominated by soft substrates, we expect that we underestimated both the true abundances and size distributions of round gobies present in the bay (Steingraeber et al., 1996; Wilson et al., 2005; Young et al., 2010). Round gobies may be able to escape trawls as they move horizontally, or even underneath the trawl. Previous studies have argued that video recordings are the most appropriate way to estimate round goby abundance (Johnson et al., 2005a; Ray and Corkum, 2001), though round goby densities may still be underestimated by up to 60% (Ray and Corkum, 2001). Round gobies have been found in lower densities over sandy substrates (e.g., Johnson et al., 2005a; Penneuto et al., 2012b) and smaller sizes when caught in trawls versus other types of sampling gear (e.g., Clapp et al., 2001; Steingraeber et al., 1996). Given this, our density estimates are likely lower than would be attributed via other methods (i.e., scuba surveys or video recordings over a relatively small area).

We estimated total potential consumption (g) by round gobies of three different size classes (>70 mm, 71–88 mm, and >88 mm) per m² from May 1 through November 1 of 2009 and 2010. To determine daily temperatures for each year, we fit a polynomial equation to observed surface temperature data (Supplementary material). Inner Saginaw Bay is generally well-mixed and not thermally stratified (Nalepa et al., 2003), thus we assume that surface temperatures are roughly the same as those at the bottom, where round gobies typically reside. We then estimated the daily total consumption (g) of a mean-sized individual round goby for each size class for each day (daily mean weight determined by linearly interpolating mean weight between sampling days). This base value we call C_daily. We then modified C_daily for each size class according to the following scenarios:

1. “Observed conditions”: C_daily * observed proportions of dreissenids in diets * observed densities of round gobies
2. “Only dreissenids consumed” (proportions of dreissenids in diets = 1); C_daily * 1 * observed densities of round gobies
3. “Alternate round goby density”: C_daily * observed proportions of dreissenids in diets * 10,000 * observed densities of round gobies

Daily densities of each size class of round goby were determined by linearly interpolating mean density between sampling days for each year. For the “Alternate round goby density” scenario, we sought to modify our round goby density estimates to densities similar to those observed by others in the Laurentian Great Lakes via non-trawl sampling methods (typically swimming over 100–200 m transects; see Table S1 in Supplementary material). The multiplication factor to achieve this was 10,000. For the “observed conditions” and “alternate round goby density” scenarios, we linearly interpolated the mean proportion of dreissenids present in round goby diets of each size class from May through July and July through September (Supplementary material). Given that we did not examine diet contents of round gobies collected in October or November, we assumed that the proportion of dreissenids consumed by an individual in each size class remained constant from September 1 through November 1. We summed the dreissenid consumption estimates (g/m²) for each scenario and size class from May 1 to November 1 of each year, resulting in potential annual consumption estimates for dreissenids in g/m²/year.

We compared the potential annual consumption estimates to estimates of annual dreissenid production in inner Saginaw Bay. Production-to-biomass (P/B) ratios are used to understand how a population

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is replacing itself over time. To estimate mean wet biomass (g/m^2) of dreissenids in Saginaw Bay, we multiplied mean wet weight plus shells of dreissenids by the mean number of dreissenids per m^2 (over all sites and months sampled) for 2009 and 2010. P/B values for dreissenids are scarce in general (Mackie and Schloesser, 1996), but particularly so for populations from the Laurentian Great Lakes. Johannsson et al. (2000) used shell-free wet weight (WW) of dreissenids to calculate a P/B ratio of 5.3 for quagga mussels and 14.2 for zebra mussels (shell length: shell weight ratios taken from site M-25, year 2004, in Nalepa et al., 2010). To make results comparable to round goby consumption estimates, we added shell weight to each dreissenid by multiplying shell length by 8.4 for quagga mussels and 14.2 for zebra mussels, then multiplied by 5.3 (Johannsson et al., 2000) to determine dreissenid production in g/m^2/year.

**Results**

Both round gobies and dreissenids were found ubiquitously throughout the bay during both years (Table 2). Overall round goby densities and catch-per-unit-effort in terms of fish caught per hour trawled varied from month to month and were highest at sites 2, 5 and 14 (i.e., hard-bottomed and/or primarily sandy sites), in June through September (Table 2). The round gobies caught in our trawls were typically smaller than 80 mm (Fig. 2) but ranged from 20 to 135 mm total length. Dreissenid densities were largely stable throughout each year and were also highest at sites 2, 5 and 14 (with one instance of very high densities at site 10 in September; Table 2). The overall makeup of all dreissenids sampled via PONARs was approximately 11% zebra mussel, 89% quagga mussel (by count).

Round goby diet composition varied among months and size classes (Fig. 3). Chironomids accounted for the bulk of diet biomass estimates in most cases, occurring in diets during every season and in each size class. Round gobies usually did not prefer dreissenids over other available prey items (Fig. 4), and only selected for dreissenids in ~15% of all instances analyzed. In 2009, round gobies selected for dreissenids during June (neutral selection = 0.25, α_dreissenid = 0.99) and October (neutral selection = 0.33, α_dreissenid = 0.99), both at site 10. In 2010, round gobies selected dreissenids during May at sites 5 (neutral selection = 0.2, α_dreissenid = 0.83) and 20 (neutral selection = 0.25, α_dreissenid = 0.71), during July at 20 (α_dreissenid = 1), and during September at 2 (neutral selection = 0.33, α_dreissenid = 0.98). Chironomids were the most often preferred prey type, being positively selected ~78% of the time (over all instances analyzed). Other taxa that were preferred include amphipods (~23% of the time), gastropods, sphaeriids, and other, non-chironomid insects (<1% of the time each, Fig. 4).

Though not preferred, dreissenids were consumed by round gobies of all size classes (Fig. 3). Only one zebra mussel was found in all round goby diets examined, thus the vast majority of dreissenids consumed were quagga mussels. The mean number of dreissenids found in an individual round goby diet was 1.6 (SD = 3.7) in 2009, and 2.1 (SD = 5.6) in 2010. We found dreissenids in 39% and 42% of round goby diets from 2009 and 2010, respectively. The mean proportion of dreissenids in diets (by biomass; Table 3) was significantly different.

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**Fig. 2.** Length distributions of round gobies collected from Saginaw Bay, Lake Huron, by month and year. A maximum of 30 fish per trawl were measured (see Methods for details). Weather conditions prevented sampling in April 2009 and October 2010.
by size class ($F_{2, 380} = 14.8, p < 0.001$) but not month ($F_{2, 380} = 1.9, p = 0.15$) or year ($F_{1, 380} = 0.2, p = 0.65$). The largest round gobies had the highest proportion of dreissenids in diets (Fig. 3, Table 3), and, in general, larger round gobies also consumed larger dreissenids (Fig. 5). The overall mean (and range) of dreissenid shell lengths found in round goby diets was 3.4 mm (0.5–14.3 mm). Including total length of round goby as a covariate, there were significant differences in mean size of dreissenid consumed across months ($F_{2, 163} = 3.3, p = 0.04$) but not years ($F_{1, 163} = 0.17, p = 0.68$). In both years, round gobies consumed smaller dreissenids in May than in July or September. There was greater distinction between mean size of dreissenids consumed in July and September in 2009 than in 2010 (Fig. 5). This may be due in part to a large number of very small (i.e., 2–3 mm) dreissenids observed in 2010 samples (C. Foley, unpublished data). Size distributions of dreissenids found in round goby diets closely patterned those available in the environment, up to about 10 mm (Fig. 6).

The mean shell-free wet weight biomass of dreissenids for all sites and months sampled was 210 g/m$^2$ in 2009 and 168 g/m$^2$ in 2010. Adding in shells resulted in a mean biomass of 339 g/m$^2$ in 2009 and 268 g/m$^2$ in 2010. Total annual consumption estimates for individuals from each size class (Table 3) were similar to those calculated by Lee and Johnson (2005) for Lake Erie (17.19 g/m$^2$ for Age-0, 49.34 g/m$^2$ for Age-1, 108.09 g/m$^2$ for Age-2). Model estimates of potential total consumption of dreissenids by round gobies in inner Saginaw Bay under observed conditions were several orders of magnitude lower than the estimates of annual dreissenid production for both years and all size classes (Table 3). Assuming round gobies consumed nothing but dreissenids led to increases in total dreissenid consumption for all

![Fig. 3. Mean proportions by biomass of diet items in three size classes of round gobies collected during May, July, and September of 2009 (left) and 2010 (right) in Saginaw Bay, Lake Huron. Sample sizes noted in top right corner of each plot. Prey categories are the same as those included in selectivity analyses. Dreissenids are highlighted in grey.](image-url)
size classes, but estimates still fell far below production estimates (Table 3). Assuming alternate densities of round gobies resulted in the greatest increase in consumption estimates (Table 3). Under this scenario, estimates of total round goby consumption of dreissenids were 19% of annual dreissenid production in 2009 and 27% of annual dreissenid production in 2010. For all scenarios, consumption of dreissenid biomass by the smallest (and most abundant) size class of round goby was higher than consumption of dreissenid biomass by either of the other two size classes (Table 3).

Discussion

Round gobies and dreissenids overlapped temporally and spatially in Saginaw Bay, suggesting potential for round goby predation on

Table 3

Annual consumption and production estimates for Saginaw Bay, Lake Huron. Consumption estimates assume prey are shelled, wet-weight dreissenids. Production estimates are based on estimates of shelled, wet-weight dreissenid biomass. Densities are based on distance travelled and assume the trawl opened halfway.

<table>
<thead>
<tr>
<th>Year</th>
<th>Size class</th>
<th>Individual estimates</th>
<th>Mean no. of round gobies/m²</th>
<th>Modeled total round goby consumption of dreissenids (g/m²/year)</th>
<th>Dreissenid production (g/m²/year)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean prop. dreissenid in diet by biomass (by count)</td>
<td>Mean total dreissenid consumed (g/year)</td>
<td>Observed conditions</td>
</tr>
<tr>
<td>2009</td>
<td>~70 mm</td>
<td>17.3</td>
<td>0.16 (0.12)</td>
<td>2.8</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>71-88 mm</td>
<td>42.5</td>
<td>0.26 (0.2)</td>
<td>11.1</td>
<td>0.00037</td>
</tr>
<tr>
<td></td>
<td>&gt;88 mm</td>
<td>84.5</td>
<td>0.52 (0.39)</td>
<td>43.9</td>
<td>0.00006</td>
</tr>
<tr>
<td>2010</td>
<td>~70 mm</td>
<td>19.4</td>
<td>0.18 (0.18)</td>
<td>3.5</td>
<td>0.0076</td>
</tr>
<tr>
<td></td>
<td>71-88 mm</td>
<td>42.2</td>
<td>0.24 (0.22)</td>
<td>10.1</td>
<td>0.00043</td>
</tr>
<tr>
<td></td>
<td>&gt;88 mm</td>
<td>76.2</td>
<td>0.55 (0.53)</td>
<td>41.9</td>
<td>0.00011</td>
</tr>
</tbody>
</table>

Fig. 4. Prey selectivity (presented as Chesson’s α) of round gobies at each sampling site and date for which diet information was available. Dashes indicate neutral selectivity for a given prey item. Prey items that were consumed but not adequately sampled in the environment are omitted from this figure, as were prey that were sampled in the environment but not observed in round goby diets.
dreissenid populations. However, low round goby densities at particular locations and certain times of year (presumably due to offshore movement overwinter, e.g., Ray and Corkum, 2001) may lead to decreased predatory effect on dreissenids. Similar to findings from other relatively warm and shallow areas of the Laurentian Great Lakes (e.g., Barton et al., 2005; Lederer et al., 2008), dreissenids were not the primary prey for round gobies collected by our study. We did observe a shift toward greater proportion of dreissenids with increasing round goby total length (as in Janssen and Jude, 2001; Jude et al., 1995), however dreissenids comprised little more than half of total diet contents for even the largest round gobies collected. Chase and Bailey (1999) suggested that quagga mussels would be more vulnerable to predation than zebra mussels, and our results support this. By counting whole dreissenid shells only, we have likely underestimated the total biomass of dreissenids consumed (Hamilton, 1992). However, given that dreissenid shells break down more slowly than other invertebrate prey, it is also possible that we have underestimated the importance of non-dreissenid prey to round goby diets (Brush et al., 2012).

Dreissenids of various sizes were available in the environment, but round gobies seem to focus predation on dreissenids smaller than 10 mm. We also observed no dreissenids larger than 14.3 mm in any round goby diets. Together, these findings complement previous suggestions that predators of dreissenids select individuals from a relatively narrow size range (8–11 mm; e.g. Andraso et al., 2011b; Ray and Corkum, 1997). Naddaf and Rudstam (2014b) found that, while larger round gobies were capable of consuming dreissenids up to 20 mm, they preferred dreissenids between 4 and 8 mm; furthermore, other predators including pumpkinseed sunfish (Lepomis gibbosus) and rusty crayfish (Orconectes rusticus) were only able to consume dreissenids that were smaller than 8 mm. Morrison et al. (1997) observed a similar preference for dreissenids of only 2–6 mm, even by large yellow perch and freshwater drum. In Saginaw Bay, round gobies may be gape-limited predators of dreissenids, given that size distributions of dreissenids up to 10 mm are fairly similar between the environment and those found in round goby diets (i.e., round gobies do not appear to prefer particular sizes, but rather consume what is available). As a result, it seems that many dreissenids in Saginaw Bay have grown to sizes essentially invulnerable to most round goby predation. Given that dreissenids invest similarly in reproduction throughout their adult lifespans (Stoeckmann, 2003) and are considered sexually mature at approximately 8–9 mm in length (Benson et al., 2016), the selective cropping of smaller individuals by round gobies may not have a pronounced impact on overall dreissenid population reproductive ability; especially as thinning of small dreissenids may allow release from density-dependent control and allow for faster growth.

While round gobies often selected for other prey items, they did at times select for dreissenids. These instances did not share common
and prey consumption might in
to that found by others sampling the Great Lakes (e.g., Clapp et al., 2001; Steingraeber et al., 1996), and the relative frequencies of round gobies of particular sizes reflected in our study are comparable to those presented by Schaeffer et al. (2005), Fielder and Thomas (2006), and Cooper et al. (2009) for Saginaw Bay. Schaeffer et al. (2005) and Fielder and Thomas (2006) presented data from the late 1990s to mid-2000s, while Cooper et al. (2009) presented data from 2006. Two of these studies also present trawl data, and thus may have the same biases toward smaller-bodied round gobies as previously noted; however, Cooper et al. (2009) sampled using overnight fyke nets which would presumably be less biased. While multiple studies have described a size structure of round gobies similar to that found in our study, specifically targeting larger round gobies in order to assess both their abundances and dreissenid consumption patterns would be necessary before fully assessing predatory effects of round gobies.

Examining multiple scenarios with bioenergetics modeling allowed us to assess how uncertainty regarding round goby densities and prey consumption might influence their potential predatory impact. In Saginaw Bay, the most sensitive variable by far was round goby density, while uncertainty in consumption rate or diet composition was less influential. The vulnerability (or lack thereof) of round gobies to certain sampling methods makes it difficult for researchers to assess the role of this relatively new invader in Great Lakes food webs. We therefore emphasize the need for improved, less biased collection methods for round gobies. Another source of uncertainty in our study is the P/B ratio of the dreissenid population. The P/B ratio calculated by Johansson et al. (2000) for Western Lake Erie was likely calculated during the exponential growth phase of that dreissenid population. P/B ratios for some zebra mussel populations in Europe are much lower than this (reviewed in Chase and Bailey, 1999; Mackie and Schloesser, 1996). Chase and Bailey (1999) also found variable P/B ratios in Lake Erie, with a mean P/B ratio for Lake Erie of 0.85. If we were to assume a P/B ratio of 1, the dreissenid consumption estimates under the Alternate Round Goby Density scenario in each year would just exceed dreissenid production as estimated over the relatively soft substrates sampled in our study. However, we are likely also underestimating the total biomass of dreissenids present, given that densities over hard substrates are much higher than those observed in our study (Nalepa et al., 2003; Nalepa et al., in preparation).

Given that many of the dreissenids sampled in our study appear to be too large to be preyed upon, it seems unlikely that round goby predation has historically strongly affected dreissenid populations in Saginaw Bay. At the same time, zebra mussels are becoming the dominant dreissenid present in the Great Lakes and are possibly more vulnerable to predation than zebra mussels (e.g., Chase and Bailey, 1999, current study). We demonstrated that all sizes of round goby prey on dreissenids, that round gobies consume smaller dreissenids in early parts of the year (potentially exploiting the first reproductive cohort of a given year), and that round gobies would likely have the greatest impact on dreissenids that are less than one year old (<8–9 mm total length; Benson et al., 2016). As such, we suggest it possible that round gobies will help suppress Saginaw Bay dreissenid populations in years to come. Several other fish species have been known to prey on dreissenids with some regularity (e.g., Madenjian et al., 2010), and yellow perch are a documented predator of dreissenids and dreissenid veligers in Saginaw Bay (Roswell et al., 2013). While not assessed in the current study, it is possible that predation by other fishes could act in concert with predation by round gobies, ultimately contributing to overall decline in dreissenid populations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2016.10.018.

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