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Quantifying the predatory effect of round goby on Saginaw Bay dreissenids

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ABSTRACT

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 fish size, but also throughout the year for all size classes. Despite this, overall consumptive effects of round gobies on dreissenids in Saginaw Bay were low. Many dreissenids present in the bay were larger than those consumed by round gobies. Bioenergetics-based model estimates suggest that the smallest round gobies are responsible for the majority of dreissenid consumption. While our findings are limited to soft substrates and influenced by sampling restrictions, our study design allowed us to put bounds on our estimates based upon these multiple sources of uncertainty.

Introduction

The introduction of zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena r. bugensis*, respectively) throughout the Laurentian Great Lakes has fundamentally altered food webs in many ways, notably by redirecting the flow of nutrients from pelagic to benthic pathways (Hecky et al., 2004; Cha et al., 2011), and altering benthic communities in terms of physical structure and composition (Bially and MacIsaac, 2000; Zhu et al., 2006; Ward and Ricciardi, 2007). After being first reported in Lake St. Clair in 1988 (Hebert et al., 1989), zebra mussels dispersed rapidly among the Great Lakes and throughout the U.S. and Canada (Benson, 2013). However, observed peak densities have varied widely from region to region, spanning several orders of magnitude (Benson, 2013). This variation is likely influenced by 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 (Naddafi 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 (Glyshaw et al., 2015; Karatayev 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

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negatively influenced by coldwater upwellings in nearshore areas (Wilson et al., 2006) or, (especially for quagga mussels), are being preyed upon (Naddafi and Rudstam, 2013; Naddafi 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*) (Morrison et al., 1997; Roswell et al., 2013; Withers et al., 2015), freshwater drum (*Aplodinotus grunniens*) (Morrison 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; Naddafi 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 portion 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 (Andraso 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, 2006; 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., 2003). 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 $4163/\text{m}^2$ ($\text{SE} = 747/\text{m}^2$) and $7.6\ \text{g/m}^2$ ($\text{SE} = 2.2\ \text{g/m}^2$) (Nalepa et al., 2003). However, by 2008–2010 mean density and biomass was only $922/\text{m}^2$ ($\text{SE} = 444\ \text{g/m}^2$) and $1.6\ \text{g/m}^2$ ($\text{SE} = 0.2\ \text{g/m}^2$) (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 (Schaeffer 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 in 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 trawls per site visit. We calculated the area sampled by each trawl by recording start and end coordinates using a GPS unit, then estimating distance travelled using the point distance tool in ArcGIS (ESRI, 2011). Trawl doors do not always fully open, thus we conservatively assumed that the trawl opened halfway during each tow, and multiplied the distance travelled during a trawl by 3.81 m to calculate the area sampled by each trawl (m^2). Immediately after collection, round gobies were separated from all other fish collected, frozen in water and stored at −20 °C until processing. Dreissenids and other benthic macroinvertebrate taxa were collected with duplicate PONAR grabs ($0.052\ \text{m}^2$ opening) either directly before or after trawling. We rinsed PONAR samples through a 500 μm mesh bucket in the field and preserved contents in 10% formalin with rose Bengal stain. Sediment type was determined by examining the contents of the PONAR. We also recorded depth of the site (m), surface temperature (°C) and day of year of sampling (DOY).

Fish and invertebrate samples were processed 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,

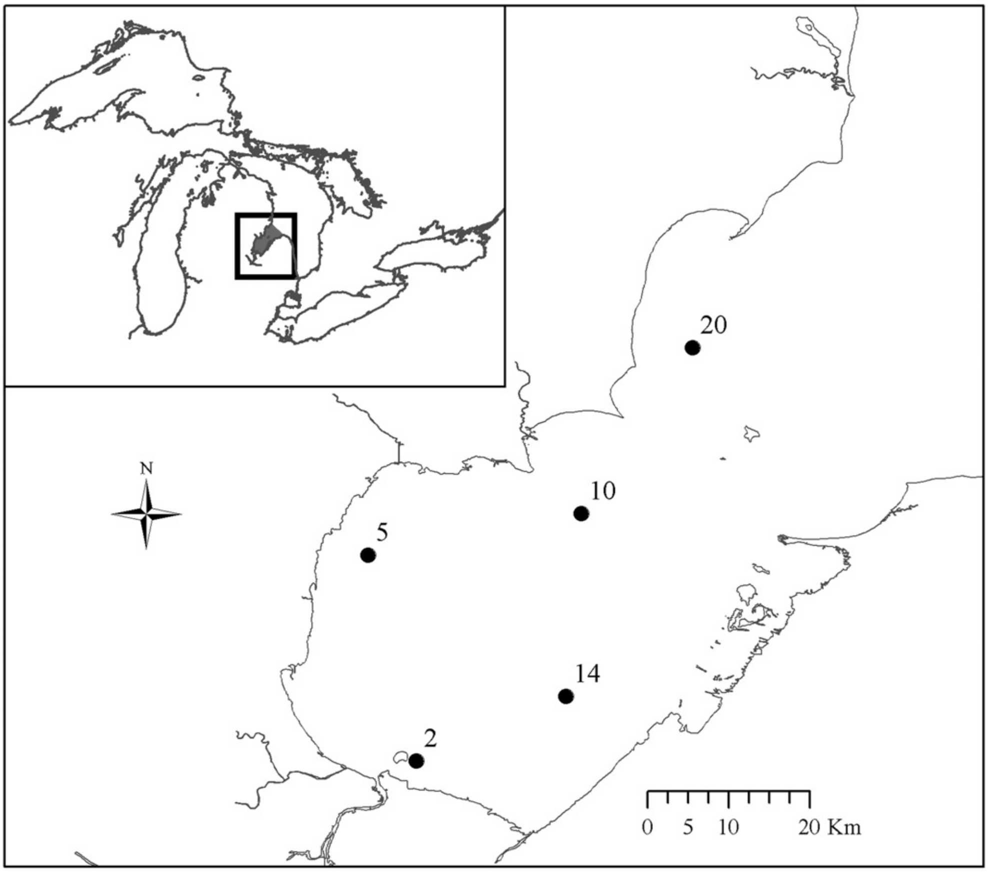

Fig. 1. Sites in Saginaw Bay, Lake Huron from which round gobies and benthic macroinvertebrates were collected in 2009 and 2010.

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 α (Chesson, 1983), as defined by the equation

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

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 α 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 α 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.

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.

Site name	Mean depth (m)	Surface temp. (°C)	Substrate type
2	3.9	17.4 (5.6–26)	Rock, cobble
5	3.6	18.3 (11.7–25.9)	Cobble, gravel, sand
10	12.4	16.2 (5.6–26.9)	Silt, muck
14	3.8	18.9 (12–27.1)	Sand
20	17.7	15.2 (5.6–23.7)	Sandy silt

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., 2006; 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; Pennuto 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 potential total consumption (g) by round gobies of three different size classes (<70 mm, 71–88 mm, and >88 mm) per m^2 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": $C_{Daily} * \text{observed proportions of dreissenids in diets} * \text{observed densities of round gobies}$
2. "Only dreissenids consumed" (proportions of dreissenids in diets = 1): $C_{Daily} * 1 * \text{observed densities of round gobies}$
3. "Alternate round goby density": $C_{Daily} * \text{observed proportions of dreissenids in diets} * 10{,}000 * \text{observed densities of round gobies}$

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/m^2) 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/m^2/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

Table 2
Mean round goby (all size classes combined) and dreissenid abundances for Saginaw Bay at each site and date sampled. "–" indicates that no sampling occurred. Weather conditions completely prevented sampling during April 2009 and October 2010.

Taxon/units	Month	Site 2		Site 5		Site 10		Site 14		Site 20	
		2009	2010	2009	2010	2009	2010	2009	2010	2009	2010
Round goby no./ha	Apr	–	2.1	–	–	–	0	–	–	–	–
	May	19.5	5.7	22.0	2.6	6.3	2.1	8.3	2.2	2.6	2.1
	Jun	93.5	–	31.8	52.6	19.8	0	76.3	–	0	–
	Jul	129	31.8	478	182	16.1	34.6	153	38.8	0	8.4
	Aug	43.2	101	21.7	897	78	58.4	177	58.2	0	99.7
	Sep	76.9	36.1	177	95.3	27.3	253	112	46.1	482	307
	Oct	16.3	–	13.0	–	241	–	70.3	–	–	–
	Nov	–	0	0	0	62.9	6.82	–	–	–	0
Round goby no./trawl h	Apr	–	6	–	–	–	0	–	–	–	–
	May	24	18	51	6	6	6	18	6	6	6
	Jun	162	–	66	126	41	0	147	–	0	–
	Jul	299	93	698	576	32	106	345	123	0	30
	Aug	91	138	45	1857	134	141	384	156	0	290
	Sep	173	81	365	198	63	624	294	105	1008	690
	Oct	33	–	27	–	414	–	156	–	–	–
	Nov	–	0	0	0	108	18	–	–	–	0
Dreissenids no./m^2	Apr	–	1259	–	–	–	9.5	–	–	–	–
	May	1735	1821	3185	1316	296	0	0	114	0	114
	Jun	1297	–	887	1287	9.5	0	3394	–	105	–
	Jul	1726	1001	591	3194	162	0	610	467	181	76
	Aug	2326	3289	1411	1163	0	0	849	1220	172	86
	Sep	2220	267	2145	6503	1850	0	0	601	67	0
	Oct	1535	–	353	–	9.5	–	829	–	–	–
	Nov	–	1545	0	0	0	0	–	–	–	19

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 in Lake Erie. For our production estimate, we adjusted shell-free dry weight dreissenid biomass estimates previously calculated by converting dreissenid dry weight to wet weight (DW = 8.2%WW for quagga mussels, DW = 7.1%WW for zebra mussels; 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 (shell length: shell weight ratios taken from site M-25, year 2004, in Nalepa et al., 2010). After calculating mean wet weights plus shells of dreissenids per m^2 for each year, we 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, $\alpha_{\text{dreissenid}} = 0.99$) and October (neutral selection = 0.33, $\alpha_{\text{dreissenid}} = 0.99$), both at site 10. In 2010, round gobies selected dreissenids during May at sites 5 (neutral selection = 0.2, $\alpha_{\text{dreissenid}} = 0.83$) and 20 (neutral selection = 0.25, $\alpha_{\text{dreissenid}} = 0.71$), during July at 20 ($\alpha_{\text{dreissenid}} = 1$), and during September at 2 (neutral selection = 0.33, $\alpha_{\text{dreissenid}} = 0.98$). 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

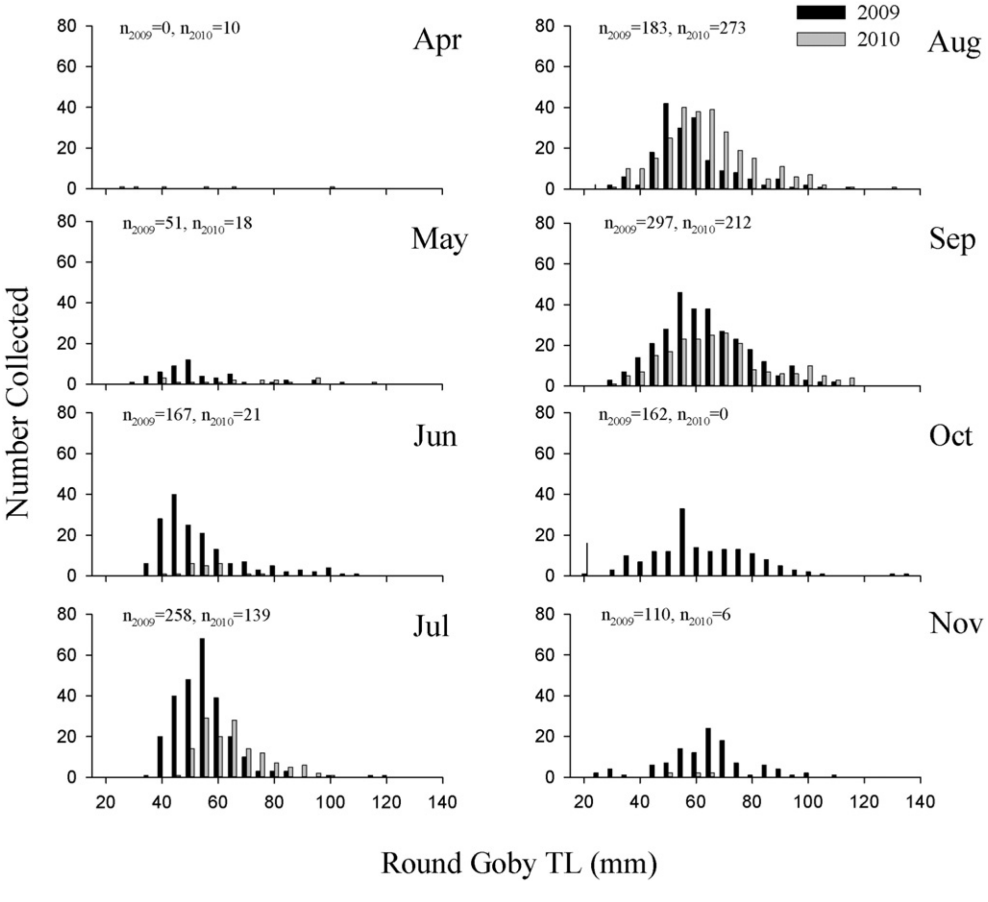

Fig. 2. Length distributions of round gobies collected from Saginaw Bay, Lake Huron, by month and year. A maximum of 30 fish per trawl were measured (see Methods for details). Weather conditions prevented sampling in April 2009 and October 2010.

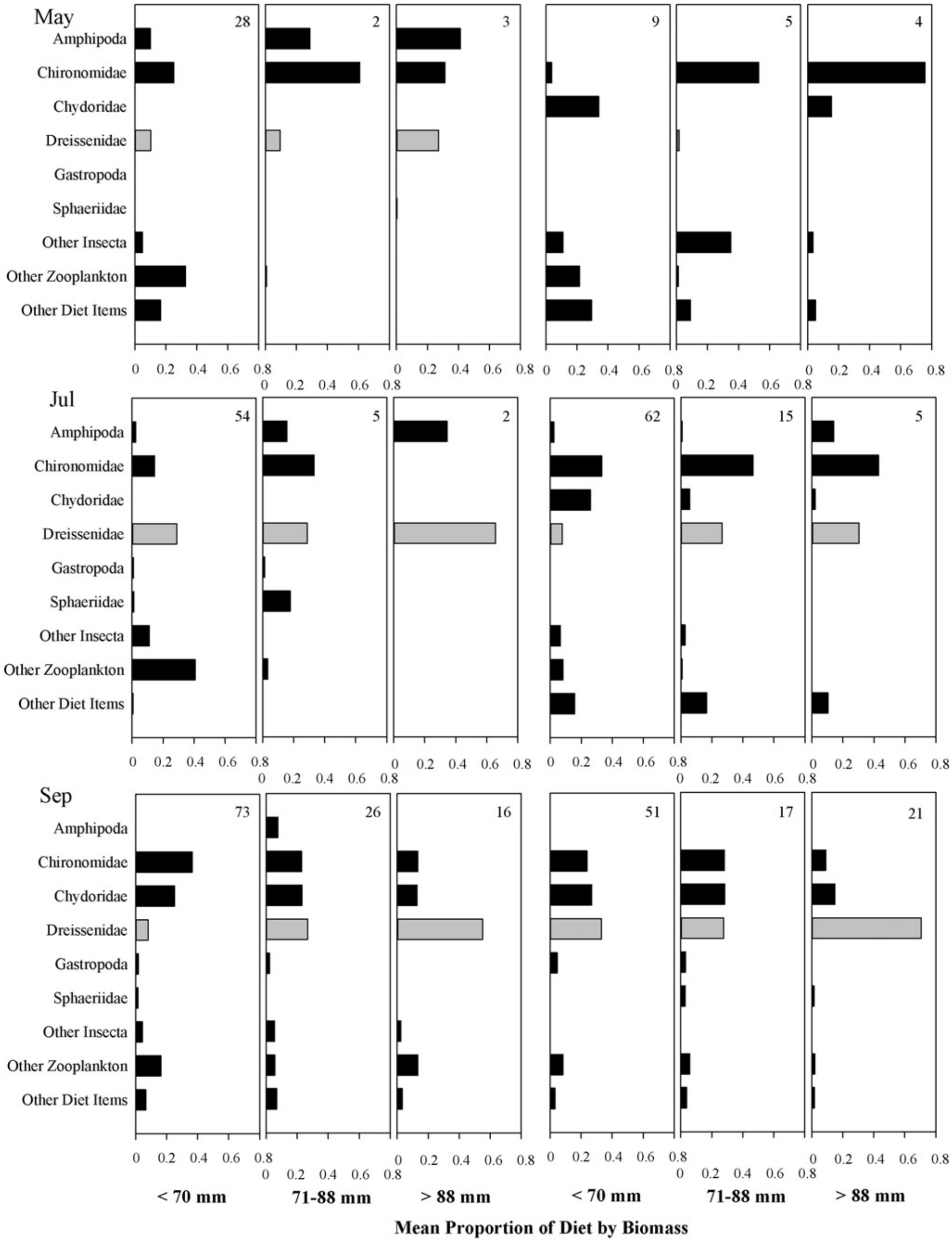

Fig. 3. Mean proportions by biomass of diet items in three size classes of round gobies collected during May, July, and September of 2009 (left) and 2010 (right) in Saginaw Bay, Lake Huron. Sample sizes noted in top right corner of each plot. Prey categories are the same as those included in selectivity analyses. Dreissenids are highlighted in grey.

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

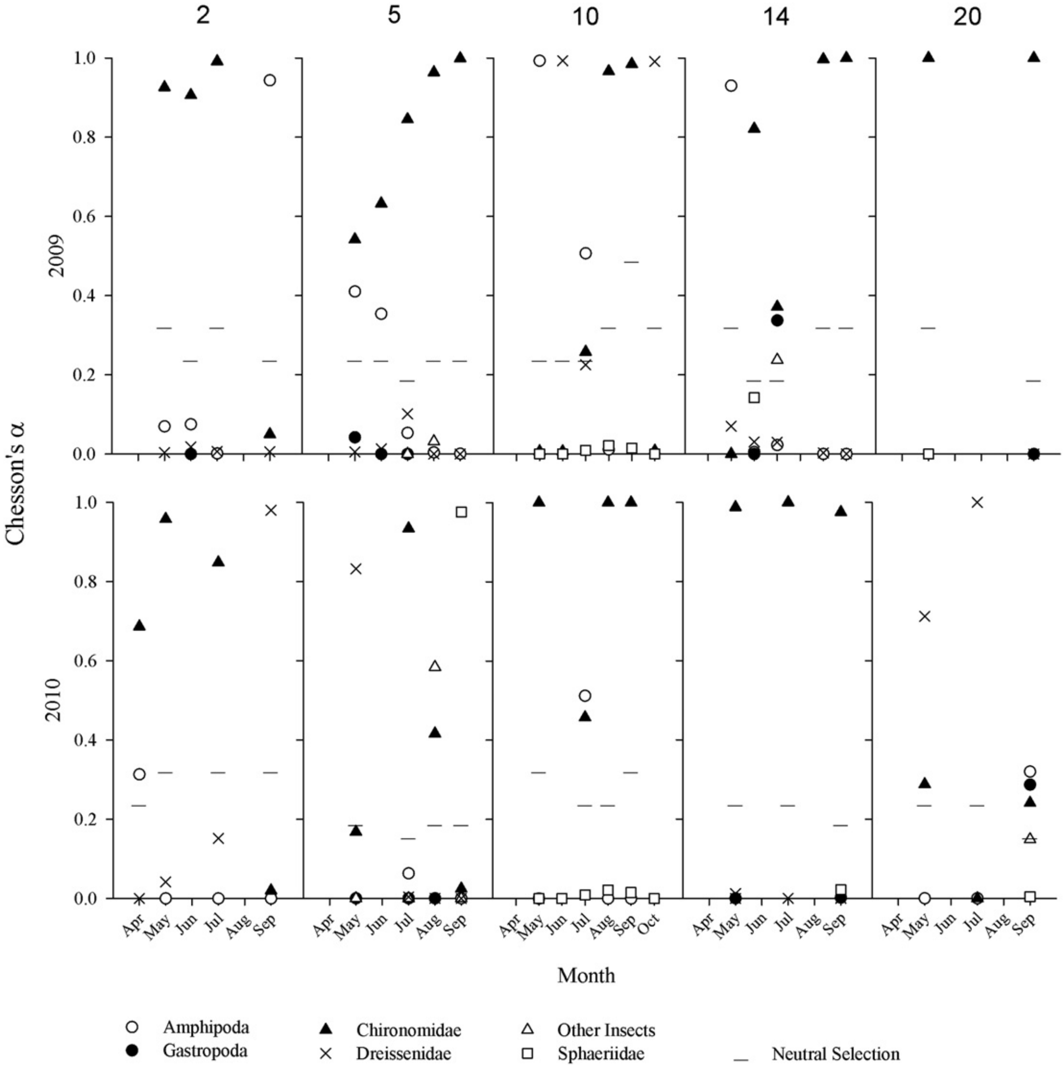

Fig. 4. Prey selectivity (presented as Chesson's α) of round gobies at each sampling site and date for which diet information was available. Dashes indicate neutral selectivity for a given prey item. Prey items that were consumed but not adequately sampled in the environment are omitted from this figure, as were prey that were sampled in the environment but not observed in round goby diets.

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.

Year	Size class	Individual estimates			Mean no. of round gobies/m^2	Modeled total round goby consumption of dreissenids (g/m^2/year)			Dreissenid production (g/m^2/year)
		Total consumption (g/year)	Mean prop. dreissenid in diet by biomass (by count)	Mean total dreissenid consumed (g/year)		Observed conditions	Assume only dreissenids consumed	Assume alt. round goby density	
2009	<70 mm	17.3	0.16 (0.12)	2.8	0.008	0.023	0.16	268	1797
	71–88 mm	42.5	0.26 (0.2)	11.1	0.00037	0.0019	0.018	46.9	
	>88 mm	84.5	0.52 (0.39)	43.9	0.00006	0.0016	0.0049	26.1	
2010	<70 mm	19.4	0.18 (0.18)	3.5	0.0076	0.029	0.13	289	1416
	71–88 mm	42.2	0.24 (0.22)	10.1	0.00043	0.0042	0.016	42.2	
	>88 mm	76.2	0.55 (0.53)	41.9	0.00011	0.0048	0.0079	47.9	

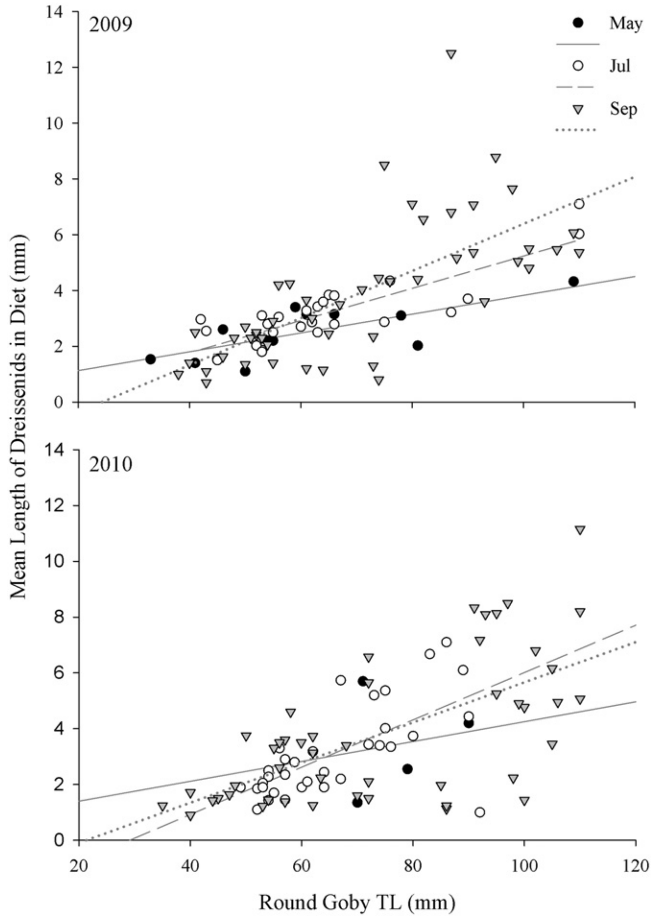

Fig. 5. Individual round goby total length versus mean shell length of dreissenids in diets (for those fish that had dreissenids in diets). Linear regressions are presented for May (solid line, $n_{2009} = 12$, $n_{2010} = 4$), July (dashed line, $n_{2009} = 29$, $n_{2010} = 33$) and September (dotted line, $n_{2009} = 53$, $n_{2010} = 48$).

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). Naddafi 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 (*Oronectes 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

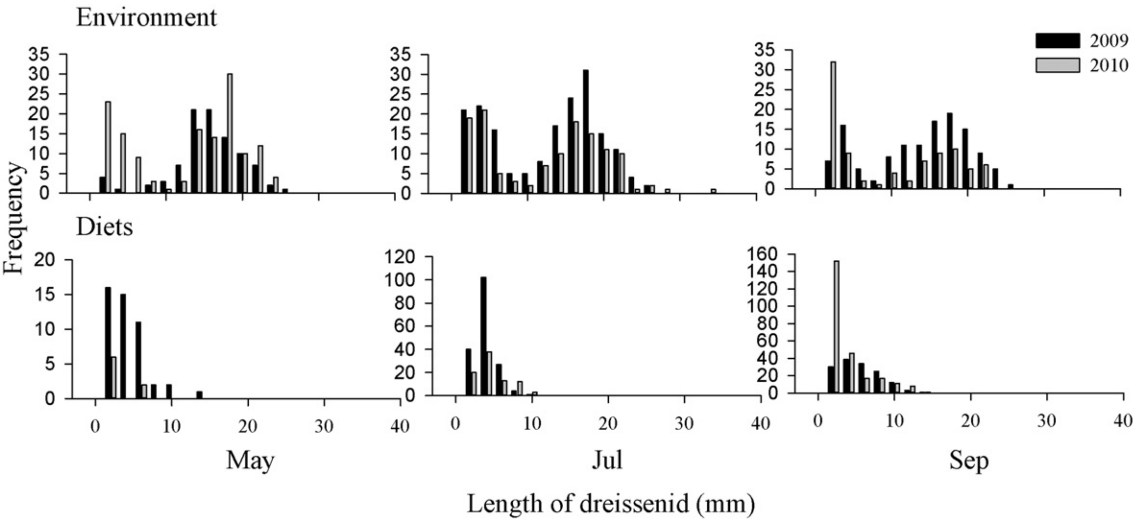

Fig. 6. Length distributions of dreissenids collected from the environment (via PONAR) and observed in round goby diets.

sites or dates, nor did they always coincide with sampling events where we collected greater numbers of large round gobies (which would be expected to prey most heavily on dreissenids). In 2010, round gobies seemed to select more strongly for dreissenids when observed dreissenid abundance was relatively low. It is possible that lower abundances, and thus smaller aggregations, of dreissenids allowed round gobies to more easily harvest individuals that may otherwise have been covered or wedged between larger dreissenids (Andraso et al., 2011b; Ghedotti et al., 1995). However, it also seems plausible that the perceived preference is simply an artifact of the selectivity calculation itself, i.e., similar numbers of dreissenids were consumed by round gobies in these areas as in other areas where the number of available dreissenids was greater.

Even though small round gobies consume fewer dreissenids on an individual basis, our model estimates suggest that their high abundances may ultimately lead to much greater overall consumption of dreissenid biomass than their larger counterparts. One caveat is that our annual consumption estimate excludes the months of November through April. While numbers of round gobies captured did decline during cooler months, presumably due to offshore movement (e.g., Ray and Corkum, 2001), and consumption estimates would likely decrease in cooler temperatures (Lee and Johnson, 2005), individual round gobies may continue to prey on dreissenids during this time period. Another previously mentioned caveat is that we have sampled softer substrates with gear that is not ideal for assessing round goby densities. Our calculations of fishing effort in terms of number of round gobies caught per trawl hour are similar to those 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 Johannsson 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, quagga 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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