Research Article

Feeding ecology of the invasive round goby, *Neogobius melanostomus* (Pallas, 1814), based on laboratory size preference and field diet in different habitats in the western basin of Lake Erie

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Abstract

The round goby, *Neogobius melanostomus*, is an invasive benthic fish species in the Laurentian Great Lakes that is threatening native fish populations through competition, predation, and trophic dynamic change. This study examined the trophic dynamic plasticity of round goby along a depth gradient based on laboratory and field observations to determine prey species consumed and mussel prey size selection. Prey size selection in the laboratory was assessed by presenting individual round goby with quagga mussels (*Dreissena rostriformis bugensis*) of various class sizes (i.e., 6.0–9.9 mm, 10.0–12.9 mm, 13.0–15.9 mm, and 16.0–18.9 mm in length). Round goby exhibited a selection preference for small sized quagga mussels, although in individual trial events, mussels were consumed from all four size classes. Prey species consumed from shallow and deep sites in the western basin of Lake Erie were assessed using individual gut contents to calculate measures of prey importance, diversity, and dominance. Based on the Index of Relative Importance (IRI), Cladocera was found to be the most consumed prey item for both males and females and between study sites. Both sexes consumed a variety of prey items although females exhibited greater prey dominance or reliance on one prey item. Round goby individuals at the shallow, natural shoreline site had the highest trophic diversity, while individuals at the deep site exhibited the highest prey dominance. Diet of round goby in the western basin of Lake Erie are mainly dominated by just a few prey items.

Key words: round goby, feeding ecology, invasive species, Lake Erie

Introduction

Community level trophic dynamics, including feeding ecology, are important in understanding interactions between invasive and native species (Arim et al. 2006; Crowl et al. 2008; France and Duffy 2006; Gido and Brown 1999; Lepak et al. 2006; Parker et al. 1999; Vander Zanden and Olden 2008). Invasive species often have the capacity to process materials differently and consume different prey than native species and subsequently can affect change in how an ecosystem functions (Gonzalez et al. 2008; Taylor et al. 2006; Vitousek 1990). The feeding ecology of an invasive species can influence community interactions including distribution and abundance of a species (Carmen et al. 2006; Shea and Chesson 2002). The limited information available on feeding ecology for most fish species makes it more difficult to accurately assess the stability of fish populations and their vulnerability to changes in prey availability (Charlebois et al. 2001). However, feeding ecology studies can be useful in the management of invasive species by providing key clues on how invasive species can alter system trophic dynamics and can be used to predict interactions especially in sympatric areas with similar habitat and diet preference (Kolar and Lodge 2001; Shea and Chesson 2002; Thompson and Simon 2014). Ecological-envelope model predictions can then be used by ecosystem managers to focus their efforts to mitigate the invasive species' impact.

The round goby, *Neogobius melanostomus* (Pallas, 1814), is one of several species native to the Ponto-Caspian basin that has proven to be a detrimental invasive fish in European and North

American lakes and rivers (Borcherding et al. 2011; Brandner et al. 2013b; Copp et al. 2008; Jude et al. 1992). Research into this species has largely evolved around the significant impacts of goby invasion to the Laurentian Great Lakes and their surrounding tributaries since their first discovery in spring of 1990 and their subsequent spread to all of the Laurentian Great Lakes within the subsequent five years (Corkum et al. 2004; Johnson et al. 2005; Jude et al. 1992; Ricciardi and MacIsaac 2000). Both the round goby (*Neogobius melanostomus)* and the tubenose goby (*Proterorhinus semilunaris*) have established themselves in the region, but the round goby has proven to be more successful and its population levels have increased to the point where they have affected the trophic dynamics of the Laurentian Great Lakes (Charlebois et al. 2001; Janssen and Jude 2001; Kornis et al. 2012). Both the round goby and the tubenose goby directly compete with native benthic fish species for both habitat and prey (Balshine et al. 2005; Bergstrom and Mensinger 2009; Dubs and Corkum 1996; Janssen and Jude 2001).

Round goby is considered to be a threat to several native fish species including mottled sculpin (*Cottus bairdii*) (Janssen and Jude 2001), small-mouth bass (*Micropterus dolomieu*) (Steinhart et al. 2004), and lake trout (*Salvelinus namaycush*) (Chotkowski and Marsden 1999). Management of this invasive species is reliant on understanding the species' life history strategy both in its native habitat and its invasive range (Charlebois et al. 2001; Moran and Simon 2013). Current studies are focusing on the ecology of these invasive fish to assess why invasive species are successful in the Laurentian Great Lakes. A significant focus of these studies is analyzing the relationship between the success of round goby as an invasive species and other invasive species in the Laurentian Great Lakes. The relatively contemporaneous invasion of the Laurentian Great Lakes by dreissenid mussels, including zebra (*Dreissena polymorpha*) and quagga (*Dreissena rotriformis bugensis*) mussels, has been widely credited with sustaining the round goby population in the Laurentian Great Lakes (Ray and Corkum 1997; Wilson et al. 2006).

Many studies of round goby diet in North America have focused on the consumption of bivalves (Janssen and Jude 2001; Naddafi and Rudstam 2014; Ray and Corkum 1997; Ruetz et al. 2012; Walsh et al. 2007; Wilson et al. 2006), while studies of round goby in Europe have focused on amphipod prey (Brandner et al. 2013a). Most North American studies have focused on

the relationships between round goby and invasive *Dreissena*, particularly the zebra and quagga mussels, also natives of the Ponto-Caspian region, which were first found in the United States in the 1980s and are now well established in all of the Laurentian Great Lakes (Bossenbroek et al. 2007; Wilson et al. 2006). Studies of the morphology of the round goby have concluded that the fish are particularly adapted for the consumption of bivalves, leading to conclusions that bivalves, particularly *Dreissena*, are preferred prey (Andraso et al. 2011a; Ghedotti et al. 1995; Simonovic et al. 2001). The relationship between round goby and dreissenid mussels is of particular concern for invasive species management due to projections of the further spread of both species (Bossenbroek et al. 2007; Kornis and Vander Zanden 2010; Kornis et al. 2012). Using the presence of dreissenid mussels to predict the spread of round goby may be an effective strategy, but cannot explain why the species has been found in regions where dreissenid mussels are not present (Carmen et al. 2006). Since round goby can be found in these regions it suggests that their diet can adapt to local prey availability, exhibiting a high plasticity for feeding adaption (Brandner et al. 2013a; Kornis et al. 2012).

This study analyzes the consumption choices of round goby along a depth gradient in the western basin of Lake Erie. Both laboratory and field components were used to evaluate prey selection, prey consumption, and then were used to describe diet based on dominance, frequency, and relative importance of prey items. Our objectives for this study were, 1) to determine the species richness and dominance exhibited in round goby prey in the western basin of Lake Erie and 2) to determine the size selectivity of prey items when goby are presented with varying size classes under laboratory conditions.

Methods and materials

Field study

Field studies of round goby dietary habits were conducted at six sites surrounding the Bass Island archipelago in the western basin of Lake Erie, Ohio, USA. Each site was chosen to represent variation in depth, coastal shoreline structure, and habitat heterogeneity following the pilot study by Thompson and Simon (2014). Prey items consumed by round goby was evaluated to provide an assessment of the prey choices and selected items available for each site based on shallow with

natural substrates (< 2m depth), shallow with anthropogenically-modified substrates (<2 m depth) habitats compared with deep open water natural substrate (>8 m depth) habitats. Three sites (Catawba Island [41.5602 N, -82.8557 W], Green Island [41.629983 N, -82.862817 W], and School-house Bay [41.685633 N, -82.784767 W]) were deep, open water sites (>8m depth), two sites were natural, shallow water with cobble substrates (Alligator Bar, Gibraltar Island [41.65749 N, -82.822291 W] and Dock Beach, Gibraltar Island [41.65775 N, -82.82164 W]), and a single site was an anthropogenically modified, habitat with steel sheet piling and concrete <2 m deep (Oak Point [41.656418 N, -82.824434 W]).

Gear choice is a fundamental concern in designing field experiments in order to reduce size selection bias (Brandner et al. 2013c). Same sized mesh in seines and otter trawls were selected to reduce bias in shallow- and deepwater habitat selection of individuals. Round goby were collected from shallow anthropogenically modified habitats using trotlines and seines. We recognize that sampling using seine show bias in failure to capture large individuals. As a result, trotlines were selected to collect larger individuals from shallow habitats. Three trotlines 10 m in length each with 10 hooks equally spaced 1m apart with #size-6, small shank hooks with a 6.35 mm gape width between the shank and the barb were placed in series parallel to shore (Moran and Simon 2013). Hook size was selected to approximate the size of an age 1 round goby mouth (Ray and Corkum 1997). An approximately 5 mm segment of nightcrawler (*Lumbricus terrestris*) was used as bait for each hook. Lines were checked after 10 minute sets. Common sense minnow seines 4.5 m in length with 3.125 mm mesh were used to collect from shallow habitats by wading to 1.5 m depths parallel to shore and then drawing the seine into the shoreline littoral zone. The combination of trotline and seine provided a sample of all sizes of round goby from shallow habitats, reducing bias related to the use of either single gear-type exclusively (Brandner et al. 2013c). Deepwater habitats were sampled using the Ohio State University Gibraltar III research vessel that towed a 4m otter trawl with 3.125 mm mesh. Timed trawls of 10 minute duration were conducted for distances of 1.6 km. Each individual collected was immediately anesthetized after capture with MS222 and fixed with 10% formaldehyde according to standard procedures (Murphy and Willis 1996).

Specimen Analysis

Individual field-collected fish (n=96) were segregated into two size groups (<65 mm and >65 mm TL) based on hypothesized niche shift size, i.e., pivotal hinge point size, at 65 mm TL (Moran and Simon 2013) and were sexed and measured for total length (TL) to the nearest 0.1 mm using an ocular micrometer outfitted on a Leica Stereozoom 5 dissecting microscope. Fish used in laboratory analysis were soaked in water just prior to being measured then blotted dry to remove excess moisture prior to wet weighing. Somatic weight (µg) and gut weight (µg) was measured using a Sartorius balance with a resolution of 1 µg. Methods for stomach content analysis are based on standard methods (Murphy and Willis 1996). The entire digestive tract was dissected from preserved individuals by making a midventral incision and removing the digestive tract from the esophagus to the anus. Contents were identified and volume and percent frequency of each prey item was calculated (Pinkas et al. 1971). The volume of a prey item was estimated for each fish as a percentage of the gut content. The volume (%) of each prey item for each individual was used to calculate the total volume of that prey item in the sample population. The sample population total was the sum of the volume of that specific prey item divided by the total stomach and intestine volume for all specimens (Pinkas et al. 1971).

Prey consumption and diversity

To analyze diet consumption patterns, individuals from each sample were segregated by sex. Differences in diet were analyzed among the six sites to see if the surrounding environment substantially affected prey consumption. Prey items were grouped by taxonomic order for comparison. Prey items were identified to the lowest taxonomic level, but due to varying states of decomposition due to digestion, organisms were reported at levels to enable consistent reporting. For each prey item, the abundance (percentage of total number of prey items), volumetric importance (percentage of total volume of prey items), and frequency of occurrence (percentage of guts that contained that prey item) were calculated (Armstrong et al. 1996).

The Index of Relative Importance (IRI; Pinkas et al. 1971; Equation 1) was calculated using the prey item abundance, volumetric importance, and frequency of occurrence (Pinkas et al. 1971).

The IRI was calculated as follows,

Equation 1: $IRI = (N + V) F$

where N= abundance, V= volumetric importance, and F= frequency of occurrence. The IRI allowed a comparison of the relative importance of each prey item in the round goby diet.

To analyze round goby trophic diversity the Shannon-Weiner Information Measure (H') was used (Wilson and Bossert 1971; Equation 2. The equation for H' is as follows,

Equation 2: $H' = \Sigma(p_i) \ln(p_i)$

where, the volumetric importance (V) was used for p_i rather than frequency of occurrence or numerical abundance, p_i represents the proportion of the diet for each prey item, and i representing each prey item type.

Prey dominance (d; Wilson and Bossert 1971; Equation 3) was used to assess whether one prey type dominates the diet of the individual. It was calculated using numerical abundance, volumetric importance or frequency of occurrence as follows,

Equation 3: $d = \Sigma(p_i)^2$

where, the volumetric importance (V) was used for p_i, representing the proportion of the diet that each prey item contributes and i represents each prey item type. For the field study, we assessed significant differences between sex and diet characteristics, including: volumetric abundance, numerical abundance, frequency abundance, using a multivariate analysis of variance (MANOVA). To compare sex and our calculated IRI values, we used a multivariate analysis of covariance (MANCOVA). To test for differences in numerical abundances between shallow and deep sites we used a t-test. To test for differences in volumetric and frequency abundances, we used a z-test.

Quagga Mussel Laboratory Size-Selection Experiment

Predation experiments followed the study design of Ray and Corkum (1997) and the field investigation in Andraso et al. (2011b). Our study design is similar but not an exact duplicate of previous studies. For example, we have a longer exposure window for our individuals to consume prey (5 days). We increased the exposure period so that we could determine if goby were selecting specific mussel sizes or if just maximizing the amount of mussels consumed within a limited exposure period. In addition, we did not replace consumed prey since in the ambient environment it is common for select prey items to become rare as resources are depleted. Our study was attempting to represent this observed phenomenon.

Individual round goby were collected from the western basin near Put-in-Bay in June (n=31). Round goby were collected by seining and trotline angling from shallow, natural habitats at Alligator Bar and Dock Beach. Quagga mussels, which are the dominant taxon, were obtained from Gibraltar Island in the western basin by snorkel diving. Rocks were collected with attached mussels and mussels were carefully removed with a scalpel by severing the byssal thread anchor. Quagga mussels were then differentiated from zebra mussels by shell morphology (Domm et al. 1993). Previous studies had used zebra mussels, so quagga mussels were chosen to determine whether findings were comparable between dreissenid species. Quagga mussels were measured and divided into four size classes (6.0–9.9 mm, 10.0–12.9 mm, 13.0–15.9 mm, and 16.0–18.9 mm in horizontal length; Ray and Corkum 1997). For the experimental design, 10 individual mussels for each of the four size classes (n=40 individuals total) were measured and positioned hinge side up in a 28 L aquarium that was covered exteriorly with black, translucent, plastic wrap to prevent proximity interactions between aquaria (Ray and Corkum 1997). Each aquarium was filled with lake water and maintained at ambient temperature (20–22°C). A single round goby was introduced into each aquarium and allowed to feed on mussels without replacement (Ray and Corkum 1997). After 5 days, each round goby was removed from the aquaria, euthanized using MS-222, and measured to the nearest mm total length (TL).

Prey consumption in size-selection experiment

Mussels remaining in the tank were segregated into the assigned size classes and compared to the initial measured mussel shell sizes. A predation index (PI) was calculated for each individual goby.

Equation 4: $PI = \Sigma (C \times N)$

The PI equals the sum of the products of the number of mussels (N) eaten from a specific size class multiplied by the midpoint of that mussel size class (C). For analysis of prey size selected, a Kruskal-Wallis test was used to compare the observed consumption of mussels from each size class. To assess the relationship between prey size preference and the size of the predator, a comparison was made between the PI and TL using a simple linear regression (Zar 2010).

Table 1. Numerical, frequency, and volumetric importance (%), Index of Relative Importance (IRI), and prey dominance (d) based on prey items in the diet of field-collected round goby, *Neogobius melanostomus,* for males, females, and both sexes collected in June of 2011 from the western basin of Lake Erie.

Prey Class	Prey Item	Numerical Importance (%)			Frequency Importance (%)			Volumetric Importance (%)			Index of Relative Importance		
		Males	Females	Both Sexes	Males	Females	Both Sexes	Males	Females	Both Sexes	Males	Females	Both Sexes
Flora	Algae	0.1	0	0	43.5	16.0	36.5	2.7	1.0	2.2	120	16	80
	Plant material	0	0	0	30.4	40.0	21.9	4.9	4.6	5.0	151	184	109
Annelids	Oligochaeta	0.8	0.9	1.0	8.7	4.0	6.3	0.9	0.4	0.7	14	5	11
Crustacea	Amphipoda	0.7	0.4	0.7	26.1	8.0	25.0	5.4	1.9	4.9	160	18	139
	Cladocera	38.2	47.8	41.0	98.6	92.0	47.9	21.8	33.1	24.3	5915	7445	3131
	Copepoda	7.9	6.6	7.4	17.4	8.0	12.5	1.4	1.6	2.4		65	111
	Isopoda	0.6	3.6	1.5	17.4	36.0	12.5	0.2	1.6	0.6	13	188	26
Insecta	Coleoptera	0	0	0	2.9	0	2.1	0.8	0	0.5	2	0	1
	Cotlidae	0	0	0	1.4	0	1.0	1.5	0	1.1		0	1
	Diptera	4.6	1.9	3.9	73.9	8.0	53.1	12.3	.0	12.0	1252	784	844
	Ephemeroptera	0.4	0.6	0.5	17.4	36.0	12.5	2.7	7.4	3.9	53	288	55
	Odonata	0.1	0.1	0.1	4.3	4.0	3.1	0.6	0.8	0.6	3	4	2
	Trichoptera	0.3	0	0.2	5.8	4.0	4.2	2.0	3.6	2.3	13	14	11
Mollusca	Dreissenidae	4.7	4.4	4.6	17.4	28.0	12.5	11.4	15.6	12.2	280	562	211
	Veliger	8.9	2.6	6.9	29.0	24.0	20.8	5.2	3.2	4.6	408	140	240
	Gastropoda	0.7	0.2	0.5	10.1	12.0	7.3	1.4	0.4	1.1	21	7	12
	Helisoma	0.2	0.1	0.2	2.9	4.0	2.1	1.2	0.4	1.0	4	2	2
	Non-dreissenid bivalves	4.7	27.3	29.4	53.6	28.0	38.5	20.1	9.7	17.4	2710	1038	1805
Rotifera	Rotifera	0.4	3.0	1.2	10.1	16.0	7.3	0.2	2.0	0.7	6	79	14
Pisces	Egg bundle	0.5	0.3	0.5	8.7	8.0	6.3	1.2	0.7	1.1	15	8	10
	Osteichthyes	0.4	0.3	0.4	15.9	24.0	11.5	2.2	3.0	2,2	41	79	30
Prey Dominance (d)					1276	1639	1300						

Diet selectivity was assessed using the Strauss Index. The Strauss' Linear Index (L$_i$; Equation 5) is defined simply as:

$$\text{Equation 5: } L_i = r_i - p_i$$

Within the Strauss Index, similar to the Ivlev's index, r$_i$ is the proportion of a particular food item consumed by a predator, and p$_i$ is the proportion of that prey item in the environment. Since mussel shells were sometimes intact and passed through the digestive tract whole and other times were crushed and fragments recovered, we used the pre-experimental trial mussel shell measurements. Our logic was that since only the quagga mussels were introduced into the tank and each individual mussel shell was initially measured and counted that they represented a microcosm comprised of each of the four size classes. This met the criteria for the Strauss Linear Index and represented the information necessary to determine the proportion of each prey size in the environment. Strauss' Linear Index has a possible range of −1 to+1, with negative values indicating avoidance or inaccessibility, a value of zero indicating random

selection, and positive values indicating active selection. Unlike Ivlev's index, extreme values only occur when a prey item is rare but consumed almost exclusively, or when it is very abundant but consumed rarely (Strauss 1979). For the laboratory prey size-selection experiment, a multivariate analysis of covariance (MANCOVA) was performed to determine whether the dreissenid composition of a round goby diet is significantly different based on prey size following similar protocol as Andraso et al. (2011b). Dreissenid shell measurements (average length of whole valves, average length of valves overall, length of the largest whole valve consumed, and length of the smallest valve consumed) were used to calculate the size of mussels consumed by each individual round goby for comparison with the length of the goby (Andraso et al. 2011b). Each parameter of dreissenid size was considered as dependent variables to avoid pseudoreplication (Hurlbert 1984) while round goby length was treated as a covariate. Log transformation of mussel length measurements was used to meet normality assumptions of the MANCOVA test.

Results

Field study

The field study evaluated gut contents of 96 round goby (average TL = 67.7 mm ± 17.3 SD) to determine the types and abundance of prey consumed. Total length ranged from 17 mm to 113 mm, with 44 individuals classified as small (<65 mm) and 52 individuals classified as large (≥65 mm). Males dominated the sex ratio at each location, comprising 71.9% of the overall catch, but this is representative of the sex distribution previously observed in the western basin (Moran and Simon 2013). Of the total round goby individuals (n = 96), 32.3% (n=31) were collected from natural shallow habitats (Alligator Bar: n=3; Dock Beach: n=28 with 26 collected by seine and 2 collected by trotline sampling); 22.9% were collected from shallow, anthropogenically modified habitats (Oak Point: n=22 trotline sampling only); and 40.6% (n=39) were collected by trawling in the open water, deep habitats (Catawba Island: n =22; Green Island: n=7; Schoolhouse Bay: n=10). Male comprised 71.9% (n=69) of individuals (average TL=71.0 mm ± 7.2 SD) and 28.1% (n=27) were female (average TL=61.3 mm ± 14.6 SD).

Prey items included 22 taxa identified during the gut content analysis (Table 1), including invertebrates, such as crustaceans, molluscs, and insects. Multiple prey items were consumed by males, including Cladocera (21.8% by volume) and non-dreissenid bivalves (20.1%; Table 1). Females consumed a variety of prey items, with higher consumption of Cladocera (33.1% by volume) and dreissenids (15.6%; Table 1). Overall, round goby individuals consumed higher volumes of Cladocera (24.3%), non-dreissenid bivalves (17.4%), dreissenids (12.2%), and Diptera (12.0%) than other food sources (Table 1). We did not observe significant differences between sexes for volumetric abundance (MANOVA: F=0.776, p =0.789; skewness =0.129), numerical abundance (MANOVA: F=0.883, p =0.64; skewness =0.378), or frequency abundance (MANOVA: F=0.795, p =0.768; skewness =-0.194).

The volumetric importance of prey varied among the six sites and there were differences in prey consumption between several sites. We did not, however, observe significant differences in volumetric (z =-0.17, p =0.86), numerical (t =-0.26, p = 0.80), or frequency (z =-1.27, p = 0.20) abundances between the shallow and deep sites. At Alligator Bar, Diptera (25.4%) had the greatest
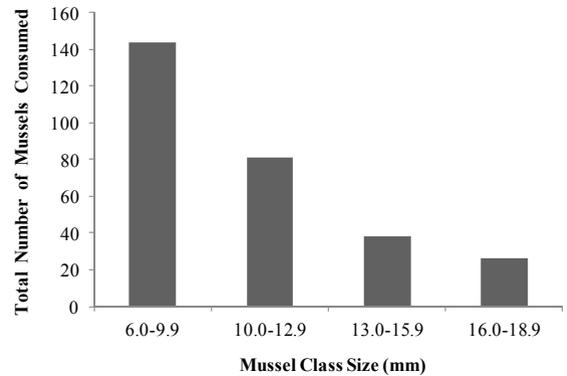

Figure 1. Observed consumption of quagga mussels (*Dreissena rostrifromis bugensis*) (n=289) per size class (mm) by *Neogobius melanostomus* (n=31). Experiments were conducted with individuals collected from Gibraltar Island in the western basin of Lake Erie.
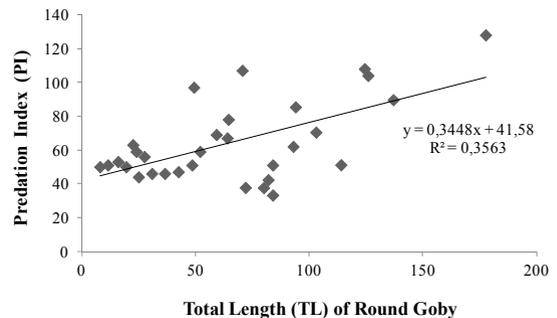

Figure 2. Comparison between the predation index (PI) and total length (TL) for round goby, *Neogobius melanostomus*, (n=31) individual size preference experiments. The predation index was calculated using the number and size class of quagga mussels (*Dreissena rostrifromis bugensis*) consumed by the individuals.

prey volume of shallow-water prey items followed by Ephemeroptera (18.9%) and amphipods (17.8%; Table 2). Cladocera had the greatest prey volume of deepwater prey items at the Catawba Island (45.5%), Green Island (29.1%), and Schoolhouse Bay (52.7%) sites. Non-dreissenid bivalves (39.2%) were the volumetrically most important shallow-water prey item at the anthropogenically-modified Oak Point. At Dock Beach, no prey item comprised more than 12.3% of dietary volume and prey dominance (d) was low there, compared to other sites (Table 2).

Statistically, we did not observe significant differences between round goby sex and IRI values (MANCOVA: F=0.131, p =0.72; skewness =0.318), but we did see some variation in IRI values between sexes. Male individuals consumed Cladocera

Table 2. Volumetric importance (%) for prey items in the diet of field-collected round goby, *Neogobius melanostomus*, for sites in the western basin of Lake Erie in June 2011.

Prey Item	Shallow			Deep		
	Alligator Bar	Dock Beach	Oak Point	Catawba Island	Green Island	Schoolhouse Bay
Flora						
Algae	11.9	5.0	1.2	0	2.5	0
Plant material	1.6	8.3	3.1	4.7	4.9	3.0
Annelids						
Oligochaeta	0	2.4	0.1	0	0	0
Crustacea						
Amphipoda	17.8	10.9	3.7	0.2	1.8	0
Cladocera	5.4	8.8	1.9	45.5	29.1	52.7
Copepoda	0	4.7	0.1	0	0	0
Isopoda	0	0.8	0.2	0.9	0.7	0.1
Insecta						
Coleoptera	0	1.8	0	0	0	0
Cotlidae	0	3.6	0	0	0	0
Diptera	25.4	12.3	13.8	6.8	15.7	22.3
Ephemeroptera	18.9	1.1	0.4	6.8	9.3	0
Odonata	0	0.4	0.7	0.9	0	0
Trichoptera	0	7.0	0.2	0	0	0
Mollusca						
Dreissenidae	10.8	10.1	27.7	11.1	4.4	0
Veliger	0	1.6	0.2	2.9	14.8	13.4
Gastropoda	0	0.2	4.3	0.1	0.7	0
Helisoma	0	3.3	0	0	0	0
Non-dreissenid bivalves	6.5	12.0	39.2	17.2	14.6	0
Rotifera	0	1.6	1.1	0.3	0	0
Pisces						
Egg bundle	0	0.5	1.0	0.2	0	7.2
Osteichthyes	1.6	3.8	1.0	2.2	2.2	1.4
Prey Dominance (d)	1656	813	2544	2624	1666	3515

(IRI=5915), which was the most important prey item followed by non-dreissenid bivalves (IRI=2710) and Diptera (IRI=1252; Table 1). Females exhibited similar dietary preferences for those items, but Cladocera (IRI=7445) comprised greater importance in females than males (Table 1). The IRI score for both sexes showed that Cladocera, Diptera, and non-dreissenid bivalves were the three most important prey items, but with a lesser importance for males than females (Table 1). Among sites, there was variation in the prey item with the greatest IRI value (Table 3). Cladocera was the most important prey item at Dock Beach (IRI=1562), Catawba Island (IRI= 10493), Green Island (IRI=6564), and Schoolhouse Bay (IRI=12985), whereas non-dreissenid bivalves were the most important prey at Alligator Bar (IRI=5016) and Oak Point (IRI=8459; Table 3). For all sites combined, trophic diversity (H') was slightly higher in males (H'=2.40) than in females (H'=2.24) and the combined sexes (H'=2.39; Figure 3). Among the study sites, trophic diversity of diets was highest at the shallow, natural habitat at Dock Beach (H'=2.74) and lowest at the deep, open water at Schoolhouse Bay (H'=1.30; Figure 4). Prey dominance of diets was highest in females (d=1639) with Cladocera being the dominant prey (Table 1). Within sites, prey dominance was highest at Schoolhouse Bay (d=3515) with Cladocera being the dominant prey (Table 2).

Laboratory Size-Selection

Round goby individuals (n=31) consumed quagga mussels from all size classes, but as a nonsignificant statistical trend consumed greater number of mussels from the smallest size class (H=7, d.f.=3, p=0.07; Figure 1). The relationship between TL and the size of mussels consumed was significant (MANCOVA: F=16.79, p <0.01; skewness = 0.770 TL, -0.125 valve length).

Round goby individuals consumed, on average, more quagga mussels from the smallest size class (6.0–9.9 mm: n=144) compared to other size classes (10.0–12.9 mm: n=81, 13.0–15.9 mm: n=38, 16.0–18.9 mm: n=26). Strauss' Linear Index revealed greater selection of mussels from the smaller class sizes (6.0–9.9 mm: L_i=0.215, 10.0–12.9 mm: L_i=0.011) compared to the larger class sizes (13.0–15.9 mm: L_i=-0.127, 16.0–18.9 mm: L_i=-0.166). A positive correlation was observed between the Predation Index (PI) and round goby TL (R^2=0.3563, F=16.049, d.f.=30, p<0.001; Figure 2).
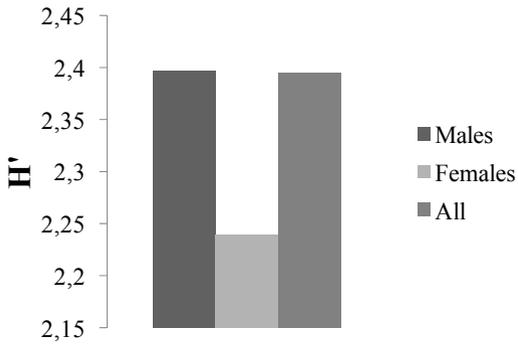
Figure 3. Trophic diversity comparison of Shannon-Weiner Information Index (H') values in the diet of round goby (*Neogobius melanostomus)* between males, females and both sexes combined for fish collected in western basin of Lake Erie, 2011.
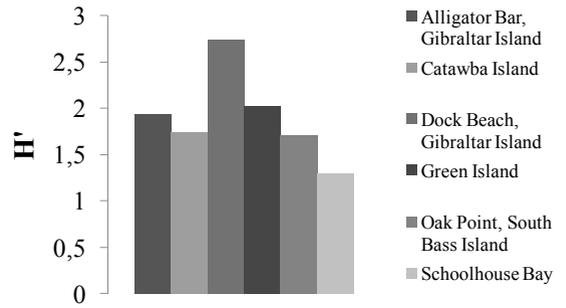

Figure 4. Shannon-Weiner Information Index (H') comparison of trophic diversity in the diet of round goby (*Neogobius melanostomus)* in the western basin of Lake Erie, 2011.

Table 3. Index of Relative Importance (IRI) for prey items in the diet of field-collected round goby, *Neogobius melanostomus*, for sites in the western basin of Lake Erie in June 2011.

Prey Item	Shallow			Deep		
	Alligator Bar	Dock Beach	Oak Point	Catawba Island	Green Island	Schoolhouse Bay
Flora						
Algae	1189	327	50	1	144	0
Plant material	54	149	116	237	114	89
Annelids						
Oligochaeta	0	110	20	0	0	0
Crustacea						
Amphipoda	2933	346	1115	1	78	13
Cladocera	1215	1562	511	10493	6564	12985
Copepoda	0	2035	7	0	0	0
Isopoda	0	65	22	81	67	2
Insecta						
Coleoptera	0	7	0	0	0	0
Cotlidae	0	13	0	0	0	0
Diptera	2230	887	1458	801	1701	2646
Ephemeroptera	1491	5	6	302	606	24
Odonata	0	2	4	4	0	0
Trichoptera	0	82	39	0	0	0
Mollusca						
Dreissenidae	399	120	1363	437	86	0
Veliger	0	55	95	112	2063	2459
Gastropoda	0	6	107	2	15	0
Helisoma	0	43	1	0	0	0
Non-dreissenid bivalves	5016	735	8459	2417	666	0
Rotifera	0	109	0	12	0	0
Pisces						
Egg bundle	0	3	40	4	0	0
Osteichthyes	92	27	24	95	82	15

Table 4. Review of important prey items in the diet of round goby, *Neogobius melanostomus*, in the Great Lakes and major tributary rivers.

Prey Item	Importance	Time of Year	Location	Reference
Zebra mussels	58%	June	Detroit River (MI)	Ray and Corkum 1997
Chironomid larvae	45%	May-August	Flint River (MI)	Carmen et al. 2006
Chironomid larvae	70.6%	August	Mexico Bay, Lake Ontario	Johnson et al. 2008
Daphnia	78%	May	Flint River (MI)	Carmen et al. 2006
Diptera	54%	June	Lake Michigan, Lake Huron	Cooper et al. 2009
Dreissenid mussels	92%	May-October	Lake Erie (Presque Isle, PA)	Andraso et al. 2011

Discussion

Previous studies have focused on consumption of dreissenid mussels by round goby based on sex (Andraso et al. 2011b; Thompson and Simon 2014) but did not find sex to be a significant predictor (Andraso et al. 2011b) or have not evaluated selection of prey organisms compared to relative abundance of organisms in various habitats (Ray and Corkum 1997). Andraso et al. (2011b) assessed dreissenid relative abundance in the environment, but found that non-dreissenid prey comprised a trivial portion of round goby diet. Thompson and Simon's (2014) pilot study did not quantify prey relative abundance availability in the environment, but evaluated general patterns in the western basin of Lake Erie. This study evaluates prey found in the gut of round goby from multiple sites in western Lake Erie based on microhabitat patterns across a variety of sites, but also does not evaluate the prey relative abundance or distribution in the western basin. We found that round goby consume a variety of small prey. Diet analysis of field-collected goby showed that the most consumed prey items were Cladocera, Diptera, and non-dreissenid bivalves. While our collections resulted in more male individuals than females, we believe that our results show general trends of diet consumption in the field.

Previous studies by Andraso et al. (2011b) evaluated patterns based on sex and found that sex did not predict any parameters of dreissenid consumption. Andraso et al. (2011b) found 162 non-dreissenid prey items that comprised 7.7% of the total prey items. In comparison, our study found trophic diversity was highest for the combined sexes, but females had higher prey dominance than males, an indication that females may be more reliant on large volumes of few prey items. Among sites we found that round goby at the Dock Beach site had the highest trophic diversity (H'), while round goby at the Schoolhouse Bay site had the highest prey dominance (Cladocera) with the lowest trophic diversity. These patterns indicate that low trophic diversity (H') in round goby diet is related to high prey dominance.

In the laboratory prey selectivity experiment, an overall preference for smaller quagga mussels was observed, with the highest consumption among the 6.0–9.9 mm quagga mussels. This study also found a positive correlation between the predation index (PI) and the TL of round goby. These results are consistent with other round goby predation

studies (Ray and Corkum 1997; Andraso et al. 2011b). Ghedotti et al. (1995) found that round goby between 60–100 mm would consume zebra mussels up to 7×13 mm, but exhibited preferences for smaller mussels. Ray and Corkum (1997) found an overall preference for smaller zebra mussels (<10 mm) amongst round goby with only the largest fish (85–103 mm SL) consuming mussels from the largest size categories. Andraso et al. (2011b) found preference for smaller dreissenid bivalves occurred in the 8–11 mm class size. Andraso et al. (2011b) also found a relationship between increased round goby length and the consumption of larger bivalves, which indicate that the size of the round goby affected prey size selection. This study showed similar patterns and responded similarly as previous studies based on individuals from riverine (Ray and Corkum 1997) and lake habitats (Andraso et al. 2011b). Based on our results individuals from both riverine and lacustrine habitats respond similarly to size selection of mussels with small round goby individuals feeding exclusively on mussels between 6.0 and 9.9 mm, while large individuals ate mussels between 6.0 and 12.9 mm but selected mussels in the 6.0 to 9.9 mm range.

Previous studies concluded that round goby are feeding specialists, adapted for preying on bivalves (Simonovic et al. 2001). Most studies consider the primary prey of Laurentian Great Lakes round goby as zebra mussels (*Dreissena polymorpha*), another invasive species (Janssen and Jude 2001). The abundance of zebra mussels is correlated with the high relative abundance as one hypothesis for the wide distribution of the round goby (Janssen and Jude 2001). However, other studies have found that round goby will consume other prey items, such as other types of mussels and invertebrates (see summary: Table 4).

There are several examples of studies that have found round goby consuming prey other than *Dreissena*. A study by González and Burkart (2004) showed that aquatic invertebrate populations have been significantly impacted by round goby predation. Brush et al. (2012) found that amphipods, chironomids, and cladocerans were the most important prey items for round goby in Lake Ontario. Comparing results from stomach content and stable isotope analyses of round goby diets, their study suggests that stomach content analyses overestimate the role of dreissenids in round goby diet. Another study by Walsh et al. (2007) found that round goby switch from consumption of *Dreissena* to more profitable prey items in the profundal zone. The variety of dominant prey items

eaten suggests that round goby are adaptable to available prey, a trait enabling survival in waterways lacking zebra or quagga mussels. Round goby are morphologically adapted to prey on bivalves, but consume a wide variety of prey, exhibiting a much more adaptive predation strategy. This behavior may be an example of Liem's Paradox, an adaptive strategy where a specialized species switches to a more generalized role in order to adapt to changing environments (Robinson and Wilson 1998). In this study, dreissenid mussels were not the dominant prey consumed in the goby diet in the western basin of Lake Erie. Instead, the most consumed prey was Cladocera, primarily *Daphnia*, for both sexes and at four out of the six study sites. Many cladocerans are planktonic, suggesting that round goby must be swimming into the water column to consume these invertebrates. These results are consistent with those of Carmen et al. (2006), who conducted a study of round goby feeding behavior in the Flint River, MI. The Flint River does not have zebra mussels and they found that *Daphnia* composed a large proportion (78%) of the diet. Flint River round goby consumed the greatest proportion of *Daphnia* in late spring (May) when *Daphnia* were most abundant in the environment. The food source entered into the river from an upstream reservoir pulse. This seasonal relationship between *Daphnia* abundance and round goby selection may explain why *Daphnia* and other cladocerans were such an important and dominant prey item in this study.

Another plausible explanation for the prey consumed by round goby in the western basin may be the age and size of the individuals. Andraso et al. (2011a) investigated the correlation between pharyngeal morphology and prey items. They found that the pharyngeals of larger goby individuals (>80 mm TL) contained molariform teeth with larger diameters suitable for dreissenid prey consumption. Smaller goby (< 80 mm) had pharyngeal teeth more suited for arthropod prey. In our study, the individuals collected were on average smaller than those in the Andraso et al. (2011b) study. This could indicate that the pharyngeal morphology of our collected gobies made them more suited for consuming smaller crustaceans, such as Cladocera.

Round goby are able to adapt their feeding behavior to available prey based on particle size selection, enabling the consumption of a wide variety of prey item types. The ability to adapt to varying prey is among the strategies that round goby have used to successfully invade the Laurentian Great Lakes. This is a plausible explanation as to why round goby are colonizing waterways that lack zebra mussels. The high consumption of the cladoceran *Daphnia* at several sites demonstrates that a new prey item can be selected when mussels are unavailable, or size may dictate the handling ability of smaller individuals without well developed, molariform pharyngeal teeth. Round goby populations continue to threaten native fish species and invade vulnerable tributary waterways. To prevent their further spread, more studies are needed to assess the habitat and prey tolerances of round goby in tributaries to the Laurentian Great Lakes.

Acknowledgements

References

Andraso GM, Cowles J, Colt R, Patel J, Campbell M (2011a) Ontogenetic changes in pharyngeal morphology correlate with a diet shift from arthropods to dreissenid mussels in round gobies (*Neogobius melanostomus*). *Journal of Great Lakes Research* 37: 738–743, http://dx.doi.org/10.1016/j.jglr.2011.07.011

Andraso GM, Ganger MT, Adamczyk J (2011b) Size-selective predation by round gobies (*Neogobius melanostomus*) on dreissenid mussels in the field. *Journal of Great Lakes Research* 37: 298–304, http://dx.doi.org/10.1016/j.jglr.2011.02.006

Arim M, Abades SR, Neill PE, Lima M, Marquet PA (2006) Spread dynamics of invasive species. *Proceedings of National Acad. of Science* 103: 374–378, http://dx.doi.org/10.1073/pnas.0504272102

Armstrong MP, Musick JA, Colvocoresses JA (1996) Food and ontogenetic shifts in feeding of the goosefish, *Lophius americanus*. *Journal of Northwest Atlantic Fishery Science* 18: 99–103, http://dx.doi.org/10.2960/J.v18.a7

Balshine S, Verma A, Chant V, Theysmeyer T (2005) Competitive interactions between round gobies and logperch. *Journal of Great Lakes Research* 31: 68–77, http://dx.doi.org/10.1016/S0380-1330(05)70238-0

Bergstrom MA, Mensinger AF (2009) Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. *Transactions of American Fisheries Society* 138: 1009–1017, http://dx.doi.org/10.1577/T08-095.1

Borcherding J, Staas S, Krüger S, Ondračková M, Šlapanský L, Jurajda P (2011) Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. *Journal of Applied Ichthyology* 27: 153–155, http://dx.doi.org/10.1111/j.1439-0426.2010.01662.x

Bossenbroek JM, Johnson LE, Peters B, Lodge DM (2007) Forecasting the expansion of zebra mussels in the United States. *Conservation Biology* 21: 800–810, http://dx.doi.org/10.1111/j.1523-1739.2006.00614.x

Brandner J, Auerswald K, Cerwenka AF, Schliewen UK, Geist J (2013a) Comparative feeding ecology of invasive Ponto-Caspian gobies. *Hydrobiologia* 703: 113–131, http://dx.doi.org/10.1007/s10750-012-1349-9

Brandner J, Cerwenka AF, Schliewen UK, Geist J (2013b) Bigger is better: Characteristics of round gobies forming an invasion front in the Danube River. *PLoS ONE* 8: e73036, http://dx.doi.org/10.1371/journal.pone.0073036

Brandner J, Pander J, Mueller M, Cerwenka AF, Geist J (2013c) Effects of sampling techniques on population assessment of invasive round goby *Neogobius melanostomus. Journal of Fish Biology* 82: 2063–2079, http://dx.doi.org/10.1111/jfb.12137

Brush JM, Fisk AT, Hussey NE, Johnson TB (2012) Spatial and seasonal variability in the diet of round goby (*Neogobius melanostomus*): stable isotopes indicate that stomach contents overestimate the importance of dreissenids. *Canadian Journal of Fisheries & Aquatic Sciences* 69: 573–586

Carmen SM, Janssen J, Jude DJ, Berg MB (2006) Diel interactions between prey behaviour and feeding in an invasive fish, the round goby, in a North American river. *Freshwater Biology* 51: 724–755, http://dx.doi.org/10.1111/j.1365-2427.2006.01527.x

Charlebois PM, Corkum LD, Jude DJ, Knight C (2001) The round goby (*Neogobius melanostomus*) invasion: current research and future needs. *Journal of Great Lakes Research* 27: 263–266, http://dx.doi.org/10.1016/S0380-1330(01)70641-7

Chotkowski MA, Marsden JE (1990) Round goby and mottled sculpin predation on trout eggs and fry: field predictions from laboratory experiments. *Journal of Great Lakes Research* 25: 26–35, http://dx.doi.org/10.1016/S0380-1330(99)70714-8

Cooper MJ, Ruetz CR, Uzarski DG, Shafer BM (2009) Habitat use and diet of the round goby (*Neogobius melanostomus*) in coastal areas of Lake Michigan and Lake Huron. *Journal of Freshwater Ecology* 24: 477–488, http://dx.doi.org/10.1080/02705060.2009.9664321

Copp GH, Kovac V, Zweimuller I, Dias A, Nascimento M, Balazova M (2008) Preliminary study of dietary interactions between invading Ponto-Caspian gobies and some native fish species in the River Danube near Bratislava (Slovakia). *Aquatic Invasions* 3: 193–200, http://dx.doi.org/10.3391/ai.2008.3.2.10

Corkum LD, Sapota MR, Skora KE (2004) The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. *Biological Invasions* 6: 173–181, http://dx.doi.org/10.1023/B:BINV.0000022136.43502.db

Crowl TA, Crist TO, Parmenter RR, Belovsky G, Lugo AE (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers of Ecology and Evolution* 6: 238–246, http://dx.doi.org/10.1890/070151

Domm S, McCauley RW, Kott E, Ackerman JD (1993) Physiological and taxonomic separation of two dreissenid mussels in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2294–2297, http://dx.doi.org/10.1139/f93-253

Dubs DOL, Corkum LD (1996) Behavioral interactions between round goby (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). *Journal of Great Lakes Research* 22: 838–844, http://dx.doi.org/10.1016/S0380-1330(96)71005-5

France KE, Duffy JE (2006) Consumer diversity mediates invasion dynamics at multiple trophic levels. *Oikos* 113: 515–519, http://dx.doi.org/10.1111/j.2006.0030-1299.14140.x

Ghedotti MJ, Smihula JC, Smith GR (1995) Zebra mussel predation by round gobies in the laboratory *Journal of Great Lakes Research* 21: 665–669, http://dx.doi.org/10.1016/S0380-1330(95)71076-0

Gido KB, Brown JH (1999) Invasion of North American drainages by alien fish species. *Freshwater Biology* 42: 387–399, http://dx.doi.org/10.1046/j.1365-2427.1999.444490.x

González MJ, Burkart GA (2004) Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species, *Gammarus fasciatus* and *Echinogammarus ischnus. Journal of Great Lakes Research* 30: 100–113, http://dx.doi.org/10.1016/S0380-1330(04)70333-0

Gonzalez A, Lambert A, Ricciardi A (2008) When does ecosystem engineering cause invasion and species replacement? *Oikos* 117: 1247–1257, http://dx.doi.org/10.1111/j.0030-1299.2008.16419.x

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211, http://dx.doi.org/10.2307/1942661

Janssen J, Jude DJ (2001) Recruitment failure of the 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, http://dx.doi.org/10.1016/S0380-1330(01)70647-8

Johnson JH, McKenna JE, Nack CC, Chalupnicki MA (2008) Diel diet composition and feeding activity of round goby in the nearshore region of Lake Ontario. *Journal of Freshwater Ecology* 23:607–612, http://dx.doi.org/10.1080/02705060.2008.9664248

Johnson TB, Allen M, Corkum LD, Lee VA (2005) 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, http://dx.doi.org/10.1016/S0380-1330(05)70239-2

Jude DJ, Reider RH, Smith GR (1992) Establishment of Gobiidae in the Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 416–421, http://dx.doi.org/10.1139/f92-047

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16: 199–204, http://dx.doi.org/10.1016/S0169-5347(01)02101-2

Kornis MS, Vander Zanden MJ (2010) Forecasting the distribution of the invasive round goby (*Neogobius melanostomus*) in Wisconsin tributaries to Lake Michigan. *Canadian Journal of Fisheries & Aquatic Sciences* 67: 553–562, http://dx.doi.org/10.1139/F10-002

Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* 80: 235–285, http://dx.doi.org/10.1111/j.1095-8649.2011.03157.x

Lepak JM, Kraft CE, Weldel BC (2006) Rapid food web recovery in response to removal of an introduced apex predator. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 569–575, http://dx.doi.org/10.1139/f05-248

Moran EA, Simon TP (2013) Size, relative abundance, and catch-per-unit-effort of round goby, *Neogobius melanostomus*, in anthropogenically modified and natural habitats in the western basin of Lake Erie. *Journal of Applied Ichthyology* 29: 1134–1138, http://dx.doi.org/10.1111/jai.12211

Murphy BR, Willis DW (1996) Fisheries techniques, 2nd edition. American Fisheries Society, Bethseda, MD, 732 pp

Naddafi R, Rudstam LG (2014) Predation on invasive zebra mussel, *Dreissena polymorpha*, by pumpkinseed fish, rusty crayfish, and round goby. *Hydrobiologia* 721: 107–115, http://dx.doi.org/10.1007/s10750-013-1653-z

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact toward a framework for understanding the ecological effects of invader. *Biological Invasions* 1: 3–19, http://dx.doi.org/10.1023/A:1010034312781

Pinkas L, Oliphant MS, Irerson ILK (1971) Food habits of albacore, bluefin tuna, and bonita in Californian waters. *Fish Bulletin, California Department of Fish and Game* 152: 105

Ray WJ, Corkum LD (1997) Predation of zebra mussels by round gobies*, Neogobius melanostomus. Environmental Biology of Fishes* 50: 267–273, http://dx.doi.org/10.1023/A:1007379220052

Ricciardi A, MacIsaac HJ (2000) Recent mass invasions of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology & Evolution* 15: 62–65, http://dx.doi.org/10.1016/S0169-5347(99)01745-0

Robinson BW, Wilson DS (1998) Optimal foraging, specialization, and a solution to Liem's paradox. *The American Naturalist* 151: 223–235, http://dx.doi.org/10.1086/286113

Ruetz CR, Reneski MR, Uzarski DG (2012) Round goby predation on *Dreissena* in coastal areas of eastern Lake Michigan. *Journal of Freshwater Ecology* 27: 171–184, http://dx.doi.org/10.1080/02705060.2011.644702

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170–176, http://dx.doi.org/10.1016/S0169-5347(02)02495-3

Simonovic P, Paunovic M, Popovic S (2001) Morphology, feeding, and reproduction of the round goby, *Neogobius melanostomus* (Pallas), in the Danube River basin, Yugoslavia. *Journal of Great Lakes Research* 27: 281–289, http://dx.doi.org/10.1016/S0380-1330(01)70643-0

Strauss RE (1979) Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* 108: 344–352, http://dx.doi.org/10.1577/1548-8659(1979)108<344:REFIEI>2.0.CO;2

Steinhart GB, Marschall EA, Stein RA (2004) Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. *Transactions of American Fisheries Society* 133: 121–131, http://dx.doi.org/10.1577/t03-020

Taylor BW, Flecker AS, Hall RO (2006) Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* 313: 833–836, http://dx.doi.org/10.1126/science.1128223

Thompson HA, Simon TP (2014) Diet shift response in round goby, *Neogobius melanostomus*, based on size, sex, depth, and habitat in the western basin of Lake Erie. *Journal of Applied Ichthyology* 30: 955–961, http://dx.doi.org/10.1111/jai.12441

Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1512–1522, http://dx.doi.org/10.1139/F08-099

Vitousek PM (1990) Biological invasions and ecosystem processes – towards an integration of population biology and ecosystems studies. *Oikos* 57: 7–13, http://dx.doi.org/10.2307/3565731

Walsh MG, Dittman DE, O'Gorman R (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, http://dx.doi.org/10.3394/0380-1330(2007)33[83:OAFHOT]2.0.CO;2

Wilson EO, Bossert WH (1971) A primer on population biology. Harvard University Press, Cambridge, MA, 192 pp

Wilson KA, Howell ET, Jackson DA (2006) Replacement of zebra mussels by quagga mussels in the Canadian nearshore of Lake Ontario: the importance of substrate, round goby abundance, and upwelling frequency. *J. of Great Lakes Research* 32: 11–28, http://dx.doi.org/10.3394/0380-1330(2006)32[11:ROZMBQ]2.0.CO;2

Zar JH (2010) Biostatistical Analysis, 5th edn. Pearson Prentice-Hall, Upper Saddle River, NJ, 960 pp