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Impacts of predation by the Eurasian round goby (*Neogobius melanostomus*) on molluscs in the upper St. Lawrence River

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ABSTRACT

An invasive Eurasian fish, the round goby *Neogobius melanostomus*, has recently spread from the Great Lakes into the St. Lawrence River. We quantified prey preferences of this benthivore and determined whether its predatory impacts on molluscs in the river are similar to those in the Great Lakes. We measured the size structure of gastropods and dreissenid mussels at 13 St. Lawrence River sites where round goby densities ranged from 0 to 6 m^{-2}. For four of these sites, data were available for multiple years before and after invasion. Contrary to studies in the Great Lakes, there were no consistent effects of round goby density on the size structure of dreissenids, although there was an ontogenetic diet shift toward dreissenids. However, the abundance and richness of small gastropods (≤14 mm) was negatively correlated with round goby density across all sites, and declined over time at three of four sites sampled before and after invasion. Median gastropod size also declined across sites with increasing round goby density. Gastropods (as well as chironomid larvae, caddisfly larvae, and ostracods) were consistently among the most preferred prey items consumed by gobies, whereas dreissenids (as well as leeches and freshwater mites) were consistently avoided. These results indicate the major role of the round goby in structuring gastropod populations in the St. Lawrence River, and highlight large-scale spatial variation in its predatory impact on dreissenid populations.

Introduction

The round goby (*Neogobius melanostomus*), a benthivorous fish native to the Black and Caspian Seas region, was discovered in the St. Clair River in 1990 (Jude et al., 1992) and subsequently spread throughout the Great Lakes basin within 5 years (Charlebois et al., 2001). The species was likely introduced in ballast water released by transoceanic vessels (Corkum et al., 2004). Its range extension into the upper St. Lawrence River has occurred slowly, as it was not detected at Cornwall, Ontario until 2004 (Hickey and Fowlie, 2005).

A conspicuous impact of round goby invasion in the Great Lakes has been a negative effect on macroinvertebrate communities (Barton et al., 2005; Ghedotti et al., 1995; Krakowiak and Pennuto, 2008; Kuhns and Berg, 1999; Lederer et al., 2006, 2008). Round gobies consume a broad variety of benthic macroinvertebrates, particularly molluscs, but dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis*) frequently compose the largest proportion of their diet (Barton et al., 2005; Rakauskas et al., 2008; Ray and Corkum, 1997). The relative importance of different prey items varies with round goby size, habitat conditions, season, and time since invasion (French and Jude, 2001; Janssen and Jude, 2001; Jude et al., 1995; Raby et al., 2010). Round goby diet appears to vary across the Great Lakes, reflecting their flexible and opportunistic feeding habits. Indeed, round gobies exploit a wide variety of habitat types within the Great Lakes basin, from stream environments where their diet is composed almost entirely of aquatic insects (Carman et al., 2006; Pennuto et al., 2010; Phillips et al., 2003) to profundal zones of Lakes Ontario and Huron, where they primarily consume molluscs and crustaceans (Schaeffer et al., 2005; Walsh et al., 2007).

Several studies have investigated round goby predation on dreissenids and some have attempted to relate these prey preferences to observed changes in the size structure of dreissenid populations. In the Great Lakes, round gobies generally reach maximum lengths of ~150–180 mm. An ontogenetic shift toward a predominantly dreissenid-based diet occurs at lengths of 60–80 mm (Barton et al., 2005; French and Jude, 2001; Janssen and Jude, 2001; Jude et al., 1995; Ray and Corkum, 1997), although fish as small as 40–50 mm may consume dreissenids (Djuricich and Janssen, 2001; Lederer et al., 2006; Taraborelli and Schaner, 2002). The maximum size of dreissenids consumed is limited by the gape size of the fish and ranges from 10 to 20 mm with a mean of 14 mm across field and

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laboratory studies from the Great Lakes region (Clark, 2007; Djuricich and Janssen, 2001; Ghedotti et al., 1995; Jude et al., 1995; Ray and Corkum, 1997; Taraborelli and Schaner, 2002; Thomas, 1997).

Studies that have examined the impacts of round gobies on dreissenid size distributions generally record larger effects on the smallest mussels. In nearshore eastern Lake Erie, the size distribution of quagga mussels changed through time as round goby density increased from 6 m^{-2} in 2001 to 14 m^{-2} in later years; over this time period, there was a decline in the abundance of mussels of 3–15 mm length (Barton et al., 2005). A subsequent lakewide survey in 2002 found very low abundances of dreissenids in the 3–12 mm range, in combination with an increase in the average size of mature mussels, likely due to round goby predation (Patterson et al., 2005). In nearshore Lake Ontario, Wilson et al. (2006) found that the proportion of young-of-the-year quagga mussels (≤10 mm) was negatively related to round goby abundance. In the Cheboygan River, Michigan, the size distribution of dreissenids peaked at 14–17 mm, while that in round goby GI tracts peaked at 8–11 mm (Clark, 2007). Similarly, in the Bay of Quinte, Lake Ontario, dreissenid size distribution peaked at 12–16 mm, while that in round goby GI tracts peaked at 8–9 mm (Taraborelli and Schaner, 2002). These studies suggest a tendency for gobies to preferentially remove smaller mussels and thus alter mussel size distributions in the field. More recently, Andraso et al. (2011) found that round gobies in Presque Isle Bay, Lake Erie, preferentially selected 8–11 mm dreissenids for consumption.

The work reported here complements a field survey conducted in the upper St. Lawrence River that aimed to investigate impacts of round gobies on the entire macroinvertebrate community (Kipp and Ricciardi, in press). Among other impacts, the field survey found significant negative relationships between the biomass of gastropods and round gobies, and no significant relationships between the biomass of dreissenids and round gobies — which is surprising in view of impacts reported from the Great Lakes. Based on the premise that impacts on dreissenids in the St. Lawrence might be limited to smaller molluscs, we examined differential predation by round gobies on the size distribution of molluscs in the field. Thus, our study linked spatial and temporal patterns of gastropod and dreissenid size structure on cobble substrates to the diets of gobies at multiple sites. We hypothesized that dreissenids and gastropods would rank among the most preferred prey items in round goby diets (i.e. these taxa would comprise a larger proportion of the diet relative to their proportional availability in the field; Ivlev, 1961). We predicted that 1) the size, abundance, and proportion of dreissenids and gastropods consumed by gobies would increase with fish total length; and 2) dreissenid and gastropod consumption would be more prevalent in gobies >70 mm in total length. Moreover, as round goby density increased across sites and over time, 3) the density of small (≤14 mm) dreissenids and gastropods, as well as the taxa richness of small gastropods, would be reduced; 4) gastropod taxa with a maximum size of ≤14 mm would be absent more frequently than larger taxa; and 5) dreissenid and gastropod sizes would increase as smaller molluscs would be disproportionately removed through round goby predation.

Material and methods

Study area

Our study made use of the same sampling techniques and sites as those in a larger field survey that examined impacts of round gobies on the entire macroinvertebrate community in the upper St. Lawrence River (Kipp and Ricciardi, in press). In 2008, we sampled 13 sites across a range of round goby densities in the upper St. Lawrence River between Prescott, Ontario and Montreal, Quebec, in order to determine mollusc size structure (Table 1; Fig. 1). Given that round gobies are frequently associated with rocky substrates (Jude et al., 1992; Ray and Corkum, 2001), and mollusc assemblages on cobble (diameter ~65–260 mm) are diverse in this area (Ricciardi et al., 1997), sites having some cobble were chosen (Table 1). Four of these sites were resampled in 2009 (Table 1). Data from cobble at 3 sites in 2005 (K. Harper and A. Ricciardi, unpublished data) and a blank brick colonization experiment in 2006 (Ward and Ricciardi, 2010) were available for interannual comparisons (Table 1). Calcium ion concentration [Ca^{2+}] was sufficiently high at all sites and in all years (mean 29.6 $mg \cdot L^{-1}$; range 20.6–32.0 $mg \cdot L^{-1}$) such that it was not expected to limit mollusc abundance or diversity (Clarke, 1981; Jones and Ricciardi, 2005; Mellina and Rasmussen, 1994).

Round goby density quantification and diet analysis

Round goby density m^{-2} (Table 1) was quantified visually by a SCUBA diver swimming at a constant depth of 1 m above the substrate along two 30-m transects while holding a 1-m pole at arms' length perpendicular to each transect and parallel to the bottom. All round gobies that passed under the pole were counted (cf. Barton et al., 2005). Round goby counts were always conducted by the same diver at each site on the same day that molluscs were collected, and before molluscs were sampled, in order to avoid disturbing the fish. We recognize that visual estimates of round goby densities using transect counts can be problematic because of the cryptic nature of round gobies (Ray and Corkum, 2001) and their attraction to SCUBA divers (Johnson et al., 2005a). This method was chosen because it is unobtrusive and inexpensive, and allowed density estimates to be compared with each other (although not to those made using other sampling methods in the Great Lakes). Transects were placed in 1–2 m of water parallel to shore, either end-to-end at sites with steep slopes, or at the same points along the shore at sites with gentle slopes. For one analysis, sites were ranked in terms of their degree of invasion. They were classified into two categories based on both round goby density and time since invasion, in which gobies were: (i) present for 0–2 years at densities ≤1.6 m^{-2} at early-invasion sites, or (ii) present for 2 or more years at densities >1.6 m^{-2} at late-invasion sites (Table 1). Time since invasion (Table 1) was estimated using information from Hickey and Fowlie (2005) and Fuller et al. (2010), as well as from personal observations.

In late August 2009, 130 round gobies were sampled for analysis of GI tract contents at four sites in Lac Saint-Louis — a fluvial lake near Montreal. These sites were chosen because they were those for which 2009 macroinvertebrate community and mollusc size structure data were available. Round gobies were captured during the day with unbaited minnow traps or gill nets (length 14.25 m, height 1.80 m, mesh size 5.5 mm) deployed at 1–2 m depth for 1 h (Table 1). We measured the total lengths (to 1 mm) of gobies using a fish ruler and gape height (to 0.1 mm) using digital calipers. Upon dissection in the laboratory, GI tracts were placed in 95% ethanol; within 13 months, their contents were subsequently analyzed under dissecting microscopes (45×). These samples were analyzed randomly so that any potential changes in biomass due to preservation would not exert consistent effects at specific sites. Each prey item was identified to the lowest taxon possible and weighed to the nearest mg (preserved wet weight). The longest axes of all dreissenid mussel fragments and all whole gastropods found in GI tracts were measured to 0.1 mm with digital calipers.

Mollusc collection

Along the transects laid out for round goby density counts, a SCUBA diver haphazardly tossed a 0.25 m^2 quadrat to sample cobbles eight times along one transect and seven times along the other. Only cobbles found entirely inside the quadrat were chosen for sampling and only one cobble per quadrat was retained. Each cobble sample was placed in doubled sealable plastic bags underwater and transported in coolers back to the laboratory. Percent cobble (Table 1)

Table 1
Sampling localities, GPS coordinates[a] and sampling dates (Time)[b], with corresponding site-level data: sample size, *n*; % cobble[c]; round goby density[d]; time since invasion, T.I.[e]; invasion stage, I.S.[f]; sample size for round goby diet analyses, *n* diet; and round goby capture method (C.M.)[g]. Note that no round gobies were observed during sampling at CW and LE in 2008; however, at CW, round gobies were present earlier in the summer and at LE, round goby eggs were found during sampling. In 2008, round gobies were therefore considered present at these two sites.

Site (abbreviation)	GPS coordinates	Time	*n*	% cobble	Round goby density	T.I.	I.S.	*n* diet	C.M.
Sites sampled over time									
Châteauguay E. (CE)	+45°22′31.71″–73°46′34.25″	J 2005	8		0	0	E		
		S 2008	15	50 (25–95)	1.6 (1.3–1.8)	1	E		
		A 2009	15	60 (10–90)	2.4 (2.4–2.5)	2	L	36	g.n.
Les Coteaux (LC)	+45°15′13.89″–74°12′43.67″	J 2005	9		0	0	E		
		A 2008	15	80 (50–90)	1.9 (1.9–1.9)	3	L		
		A 2009	15	60 (40–60)	3.8 (2.9–4.7)	4	L	30	m.t.
Melocheville (ME)	+45°19′9.18″–73°55′39.79″	J 2005	10		0	0	E		
		A 2008	15	100	0.7 (0.6–0.7)	2	E		
		A 2009	15	100 (90–100)	3.3 (2.9–3.7)	3	L	28	g.n.
Pointe-du-Moulin (PD)	+45°21′57.86″–73°51′7.02″	S 2006	10		0	0	E		
		A 2008	15	90 (40–100)	2.6 (1.7–3.5)	2	L		
		A 2009	15	60 (10–100)	2.9 (2.0–3.7)	3	L	36	g.n.
Sites sampled in 2008 only									
Beauharnois (BE)	+45°19′7.06″–73°52′58.64″	A 2008	10	70 (30–95)	4.1 (3.8–4.3)	2	L		
Châteauguay W. (CW)	+45°21′48.30″–73°47′12.78″	A 2008	10	80 (50–100)	0	1	E		
Ile Madore (IM)	+45°23′35.73″–73°53′45.55″	A 2008	10	80 (30–100)	0.1 (0.0–0.1)	1	E		
Léry (LE)	+45°20′7.91″–73°49′6.38″	A 2008	10	50 (30–70)	0	1	E		
Loyalist Park (LP)	+44°52′30.17″–75°13′40.92″	A 2008	10	50 (5–80)	6.0 (3.7–8.3)	6	L		
Moulinette (MO)	+45°1′49.91″–74°51′27.84″	S 2008	10	20 (5–90)	3.0 (2.1–3.8)	5	L		
Prescott (PR)	+44°42′14.68″–75°31′9.58″	A 2008	10	100	2.5 (2.4–2.5)	6	L		
Soulanges Canal (SC)	+45°20′7.53″–73°57′15.62″	A 2008	10	100	0	0	E		
Summerstown (SU)	+45°2′45.72″–74°35′36.58″	S 2008	10	50(5–80)	3.8 (3.4–4.1)	5	L		

[a] In degrees, minutes, and seconds (WGS84 coordinate system; error ~30 m).

[b] Sampling months (J, Jul.; A, Aug.; S, Sep.) and year shown.

[c] Mean percent cobble (range). When no values are shown, this was not estimated by the samplers at that site and time. These data were from other sources: K. Harper and A. Ricciardi (2005, unpublished data): CE 2005, LC 2005, ME 2005; Ward and Ricciardi (2010): PD 2006.

[d] In units m^{-2} (range).

[e] Time since invasion in years, where 1-yr presence indicates arrival of the invasion front in the sampling year.

[f] Invasion stage (E, Early; L, Late).

[g] Capture method (g.n., gill nets; m.t., minnow traps).

was estimated visually inside the 0.25 m^2 quadrat by counting the number of 10 cm × 10 cm squares containing cobble within in a 5 × 5 grid. In 2008 and 2009, sampling was carried out in August and early September. Bricks from the site sampled in 2006 (Pointe-du-Moulin) by Ward and Ricciardi (2010) were returned to the laboratory for analysis in September, after having incubated in shallow water

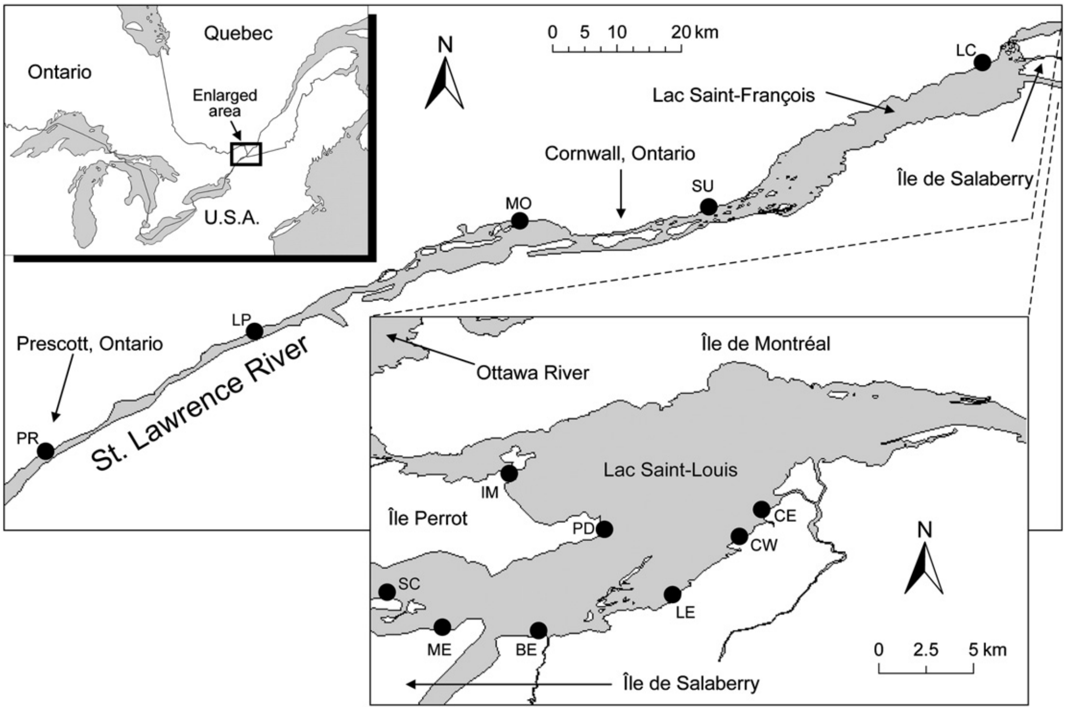

Fig. 1. Map of sites sampled from Prescott, Ontario to Montreal, Quebec in the upper St. Lawrence River. Data are from DMTI Spatial Inc. (2009). Inlaid map modified from Musser (2006). See Table 1 for full site names corresponding to site codes.

in the littoral zone at depths <3 m for 53 days, beginning in July. A SCUBA diver placed these bricks in sealable plastic bags underwater, and they were then transported in a cooler back to the laboratory within 3 h. Cobble samples from the three sites sampled in 2005 (Châteauguay East, Les Coteaux and Melocheville) by K. Harper and A. Ricciardi (unpublished data) were also sampled in the shallow littoral zone <3 m deep. They were sampled from July 10 to July 31 by snorkelers, who placed the cobble in plastic bags underwater for subsequent transport to the laboratory. All samples were thus taken in mid- to late-summer. Differences in timing of sampling between July and September were not important for many gastropods and dreissenids with lifespans greater than 1 year, such as *Elimia* and *Dreissena* (e.g. see Brown and Lydeard, 2010; Clarke, 1981; Cummings and Graf, 2010; Mackie and Schloesser, 1996). For gastropods such as *Amnicola* and *Physella*, which frequently survive for only 1 year, studies indicate that ranges in size distributions are relatively similar in July, August, and September (e.g. see DeWitt, 1955; Pinel-Alloul and Magnin, 1973). Cobble and brick sample sizes varied due to time constraints and the loss of some discarded samples (Table 1). In the laboratory, all molluscs retained by a 500-μm sieve (Nalepa and Robertson, 1981) were removed with forceps from the cobble samples and placed immediately in 95% ethanol. In order to standardize mollusc abundance data for area, cobble surface area was estimated by measuring three orthogonal dimensions of each rock: length, width, and height, in cm (Dall, 1979). Mollusc processing in the laboratory was similar for the 2006 bricks (Ward and Ricciardi, 2010) and the 2005 cobbles (K. Harper and A. Ricciardi, unpublished data). Mollusc taxa were identified to the lowest possible taxon (Clarke, 1981; May and Marsden, 1992), and the shells' longest axes were measured to 0.1 mm with digital calipers.

Statistical analyses

Regression analyses (including multiyear data from the same site) were used to relate dependent variables to round goby density. In order to control pseudoreplication, generalized least squares (GLS) auto-regressive models of order 1 were used to model the temporally correlated error structure at sites that were sampled repeatedly. Likelihood ratio tests were used to ascertain if the temporal correlation in the error structure was statistically significant (Zuur et al., 2009). The false discovery rate (FDR) was calculated for multiple (≥10) tests on the same data, in order to correct the familywise error rate (Benjamini and Hochberg, 1995). Dreissenid data from Pointe-du-Moulin in 2006 were excluded from analyses, owing to the fact that the bricks from the colonization experiment by Ward and Ricciardi (2010) were not deployed in the river long enough for dreissenids to reach similar size and density to those in the surrounding community. Proportional data (e.g. percent gastropod biomass) were transformed as $\sin^{-1}(x^{0.5})$ and absolute abundance and length data were $\log_{10}$-transformed, where appropriate.

Round goby impacts on mollusc size structure and diversity

At four sites, we determined whether the density of small (≤14 mm length) and large (>14 mm) dreissenids and gastropods, and the taxa richness of small and large gastropods, were ranked higher prior to round goby invasion than in post-invasion years. We applied one-tailed, non-parametric Wilcoxon rank sum tests to these data because they comprised a large number of zeros. For all sites and years, ANCOVAs were used to test if site-level mean dreissenid and gastropod density and pooled gastropod taxa richness declined more rapidly in the smaller size class compared to the larger one as round goby density increased. For these analyses, round goby density was the covariate and the single factor tested was size class.

One-factor ANOVAs with Type II sums of squares for unbalanced designs (due to unequal sample sizes; see Table 1) were used to test for variation in rock area among years at each resampled site. The factor tested was therefore 'year'. In the case of a significant result, Tukey's honest significance difference tests were applied to determine between which years rock areas differed at a given site. This analysis was performed to assess if species–(rock) area relationships — rather than changes in round goby density — could explain differences observed in gastropod taxa richness through time, as the latter response variable was not area-corrected. At the site level, we related pooled rock area per site to round goby density using linear regression; thus, we were able to evaluate if the two variables were correlated and hence if pooled species–(rock) area relationships confounded the relationship between round goby density and gastropod taxa richness per site.

Fisher's exact tests were used to determine if there was an association between two invasion stages (early-invasion vs late-invasion) and the number of sites with gastropod families present or absent. Regressions were used to relate mean and median gastropod and dreissenid size for pooled samples to round goby density across sites.

Round goby gape limitation and ontogenetic diet shift

We used simple linear regression to relate the maximum length of the longest dreissenid fragment recovered from each round goby GI tract to round goby gape size. A similar regression on the maximum length of the largest whole gastropod from each GI tract was also performed.

Linear regressions were conducted to relate the biomass, volume, and numerical abundance of both dreissenids and gastropods recovered from GI tracts to round goby total length, using proportions and absolute values. In all cases, we excluded round goby GI tracts that did not contain the mollusc taxon being assessed. Finally, we used Fisher's exact tests to assess whether there was an association between round goby size class (≤70 mm and >70 mm) and the occurrence of dreissenids and gastropods in GI tracts.

Round goby prey preference

Variation in round goby total length among the four sites was tested by using a one-factor ANOVA (with 'site' as the factor) with Tukey's post-hoc comparisons. In order to ascertain whether mollusc taxa were preferred prey items in round goby diets, we calculated prey selectivity using Ivlev's index: $E_{\text{abundance}} = (p_x - r_x)/(p_x + r_x)$, where r_x = percent numerical abundance of a prey category in all GI tracts at a site, and p_x = percent numerical abundance of the resource found at a site (Ivlev, 1961). Positive values of the index indicate prey preference, while negative values indicate avoidance. The index was also calculated for biomass (E_{biomass}) to account for the influence of differential sizes between prey items on prey choice (Ivlev, 1961). Percent contributions of the prey resource were obtained at each of the four sites using mean area-corrected macroinvertebrate density or biomass data from 2009 cobble samples (Kipp and Ricciardi, in press). The four sites used in these analyses were generally dominated by cobble, which comprised 50–100% of the substrate in 2008 and 2009 (Table 1).

We tested whether the rank importance of mollusc prey categories was higher in comparison to categories of other macroinvertebrates available, and were not interested in the absolute values of the prey preference index chosen. Lechowicz (1982) showed that the rank orders, but not the absolute values, of prey categories were similar for various prey preference indices, including Ivlev's E. We emphasize, therefore, that the values of $E_{\text{abundance}}$ and E_{biomass} in our study should be analyzed only in terms of their relative rank. As such, we applied Friedman's non-parametric test (the equivalent of an unreplicated two-way ANOVA) to the selectivity indices to determine if their ranked values varied between prey categories across sites. In this case, the two factors considered were prey category and site. Note that for the Friedman test, using the FDR was not possible due to constraints of the statistics package (R version 2.6.2), and we therefore applied standard Bonferroni correction. Statistical significance at the 0.05 level was also reported, as standard Bonferroni correction is overly conservative (Gotelli and Ellison, 2004; Moran, 2003; Rice, 1989). All statistical analyses were conducted in R version 2.6.2.

Results

Round goby impacts on mollusc size structure and diversity

Genera and families of gastropods recovered across sites and years included: *Ferrissia*, Ancylidae; *Bithynia*, Bithyniidae; *Amnicola* and *Marstonia*, Hydrobiidae; *Stagnicola*, Lymnaeidae; *Physella*, Physidae; *Gyraulus*, *Promenetus*, and *Helisoma*, Planorbidae; *Elimia*, Pleuroceridae; and *Cipangopaludina*, Viviparidae. The latter four genera can attain >14 mm size. However, the only large gastropods recovered from cobble samples across sites were a few individuals of *Elimia* and *Cipangopaludina*. The occurrence of gastropods in all families, except for the two largest (Pleuroceridae and Viviparidae) and the smallest (Hydrobiidae), was correlated with invasion stage (Table 2).

There were no statistically detectable declines observed for either dreissenid size class at Châteauguay East in 2008 or 2009, in comparison to the pre-invasion year (one-tailed Wilcoxon rank sum tests corrected for the FDR on 12 tests; Table 3; Fig. 2a). Statistically detectable declines were more consistent at Les Coteaux (Fig. 2b) and Melocheville (Fig. 2c) for the larger dreissenid size class (Table 3).

In contrast, after round goby invasion, densities (Fig. 2) and taxa richness (Fig. 3) of small gastropods were ranked lower more frequently than densities and taxa richness of large gastropods (one-tailed Wilcoxon rank sum tests corrected for the FDR on 16 tests for each of gastropod density and gastropod taxa richness; Table 3). Châteauguay East was an exception, where no declines in gastropod density or taxa richness were detected (Figs. 2a, 3a).

Likelihood ratio tests indicated that, in general, the temporal correlation in the error structure for ANCOVAs and regressions was not statistically significant, with the exception of two cases: the ANCOVA with dreissenid density as a response variable and regressions between mean and median dreissenid length. Nevertheless, in these cases, GLS tests yielded the same statistical conclusions with regard to accepting or rejecting null hypotheses as linear regressions and ANCOVAs; therefore, for clarity, we present only the results from the latter. GLS outputs are available upon request from the senior author.

For the ANCOVA with dreissenid density as a response variable, the round goby density × mussel size interaction was not significant ($F_{1,36}=0.5$, $n=40$, $p=0.5$; slope $=-0.16$ and -0.07 for large and small dreissenids, respectively; Fig. 4a). Upon removing the interaction term, dreissenid size class was significant ($F_{1,37}=10.4$, $n=40$, $p=0.003$), and round goby density was not significant ($F_{1,37}=3.3$, $n=40$, $p=0.08$).

For the ANCOVA with gastropod density as a response variable, the round goby density × mussel size interaction was significant (slope $=-0.21$ and -0.41 for large and small gastropods, respectively; $F_{1,38}=4.6$, $n=42$, $p=0.04$), but only with the inclusion of the Loyalist Park site (Fig. 4b). When this site was removed, the slopes were statistically indistinguishable across sites ($F_{1,36}=1.9$, $n=40$, $p=0.2$). In the latter case, both gastropod size class

Table 2

Number of sites in two round goby invasion stages for which gastropod families in two size categories were present (P) and absent (A). Those gastropod families in the smaller size category do not exceed 14 mm; gastropod families in the larger size category may exceed 14 mm (Clarke, 1981) and therefore might be able to exploit a size refugium from predation. The *p*-values for Fisher's exact tests on 2×2 contingency tables are shown for each family. Stars indicate significance at the 0.05 level after controlling for the FDR (beginning with 1/10∗(0.05)).

Family	Early-invasion		Late-invasion		p
	P	A	P	A	
a) Smaller gastropod families (maximum lengths ≤14 mm)					
Ancylidae	8	2	3	8	*0.03
Bithyniidae	7	3	0	11	*0.001
Hydrobiidae	10	0	9	2	0.5
Planorbidae	10	0	5	6	*0.01
Valvatidae	9	1	1	10	*0.0003
b) Larger gastropod families (maximum lengths >14 mm)					
Planorbidae	6	4	0	11	*0.004
Lymnaeidae	8	2	2	9	*0.009
Physidae	8	2	2	9	*0.009
Pleuroceridae	9	1	7	4	0.3
Viviparidae	1	9	0	11	0.5

Table 3

Mollusc size and diversity comparisons in two size classes at four sites before and after round goby invasion, using one-tailed Wilcoxon rank sum tests. Stars indicate significant declines in the post-invasion year at the 0.05 level after controlling for the FDR (beginning with 1/12∗(0.05) for dreissenids and 1/16∗(0.05) for each of gastropod density and taxa richness).

Site	Pre-invasion year$_1$	n_1	Post-invasion year$_2$	n_2	W	p
Dreissenid density ≤14 mm						
CE	2005	8	2008	15	40	0.9
CE	2005	8	2009	15	49	0.8
LC	2005	9	2008	15	96.5	0.04
LC	2005	9	2009	15	90	0.09
ME	2005	10	2008	15	107	0.04
ME	2005	10	2009	15	129.5	*0.0008
Dreissenid density >14 mm						
CE	2005	8	2008	15	37	0.9
CE	2005	8	2009	15	56.5	0.6
LC	2005	9	2008	15	103.5	*0.015
LC	2005	9	2009	15	103.5	*0.015
ME	2005	10	2008	15	131	*0.0005
ME	2005	10	2009	15	132.5	*0.0004
Gastropod density ≤14 mm						
CE	2005	8	2008	15	22.5	~1.0
CE	2005	8	2009	15	40	0.9
LC	2005	9	2008	15	135	*<0.0001
LC	2005	9	2009	15	135	*<0.0001
ME	2005	10	2008	15	145	*<0.0001
ME	2005	10	2009	15	150	*<0.0001
PD	2006	10	2008	15	150	*<0.0001
PD	2006	10	2009	15	150	*<0.0001
Gastropod density >14 mm						
CE	2005	8	2008	15	52	~1.0
CE	2005	8	2009	15	44	~1.0
LC	2005	9	2008	15	75.5	0.2
LC	2005	9	2009	15	79	0.1
ME	2005	10	2008	15	73.5	0.5
ME	2005	10	2009	15	110	*0.005
PD	2006	10	2008	15	97.5	0.05
PD	2006	10	2009	15	97.5	0.05
Gastropod taxa richness ≤14 mm						
CE	2005	8	2008	15	19.5	~1.0
CE	2005	8	2009	15	26	~1.0
LC	2005	9	2008	15	133.5	*<0.0001
LC	2005	9	2009	15	135	*<0.0001
ME	2005	10	2008	15	132	*0.0003
ME	2005	10	2009	15	149.5	*<0.0001
PD	2006	10	2008	15	150	*<0.0001
PD	2006	10	2009	15	150	*<0.0001
Gastropod taxa richness >14 mm						
CE	2005	8	2008	15	52	~1.0
CE	2005	8	2009	15	44	~1.0
LC	2005	9	2008	15	73.5	0.5
LC	2005	9	2009	15	78	0.3
ME	2005	10	2008	15	77.5	0.6
ME	2005	10	2009	15	107.5	0.02
PD	2006	10	2008	15	97.5	0.05
PD	2006	10	2009	15	97.5	0.05

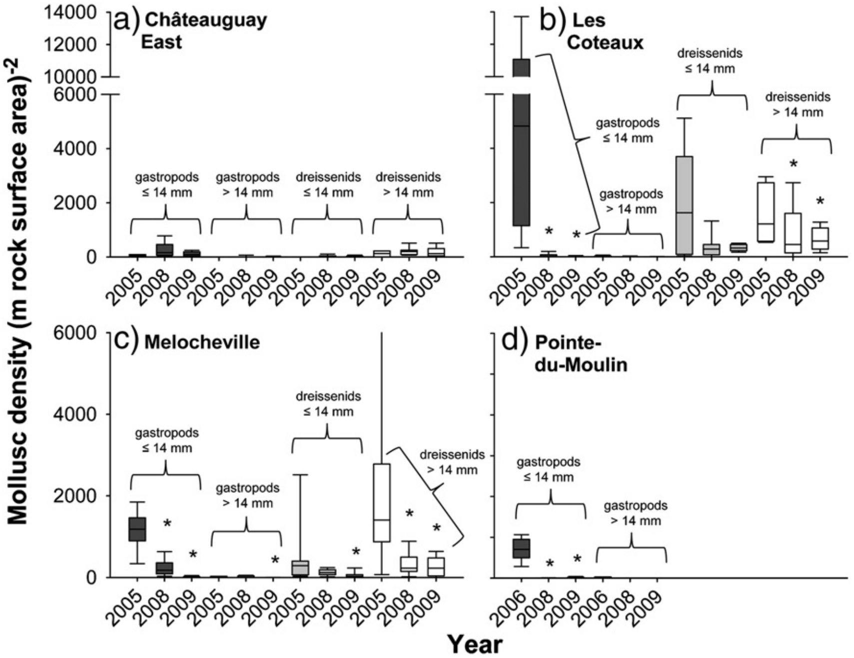

Fig. 2. Density of small and large gastropods and dreissenids before (2005 or 2006) and after (2008 and 2009) round goby invasion, at four sites. Single stars (*) denote densities ranked lower than those in the pre-invasion year according to one-tailed Wilcoxon rank sum tests at the 0.05 level after controlling for the FDR (beginning with 1/16∗(0.05) for gastropods and 1/12∗(0.05) for dreissenids). The boxes show the median, 25th, and 75th percentiles. The whiskers show the 10th and 90th percentiles, excluding outliers. For a) and b), a break is indicated on the y-axis, while for c) and d), no break is shown and the y-axis scale is different. Note that in c), the upper whisker for dreissenids > 14 mm in 2005 lies off the plot, but would end just above 10,000.

($F_{1,37}=64.6$, $n=40$, $p<0.0001$) and the covariate (round goby density: $F_{1,37}=31.3$, $n=40$, $p<0.0001$) were significant.

For the ANCOVA with gastropod taxa richness as a response variable, the round goby density × gastropod size interaction was significant (slope $=-0.18$ and -1.46 for the large and small size classes, respectively; $F_{1,38}=17.7$, $n=42$, $p=0.0002$), and this remained true even when Loyalist Park was excluded ($F_{1,36}=13.5$, $n=40$, $p=0.0008$; Fig. 4c). Therefore, the group effect (gastropod size) was difficult to interpret.

For resampled sites, rock area did not vary across years at Pointe-du-Moulin (mean rock area = 364 cm^2 ± 18 S.E.; ANOVA, $F_{2,37}=1.0$, $p=0.4$); Châteauguay East (mean rock area = 345 cm^2 ± 26 S.E.; ANOVA, $F_{2,35}=1.0$, $p=0.4$); or Melocheville (mean rock area = 330 cm^2 ± 26 S.E.; ANOVA, $F_{2,37}=1.7$, $p=0.2$). For Les Coteaux, there was variation in rock area across years (ANOVA, $F_{2,36}=13.7$, $p<0.0001$); post-hoc comparisons indicated that cobble from 2008 (mean rock area = 215 cm^2 ± 28 S.E., $n=15$) was smaller than that from 2005 (mean rock area = 424 cm^2 ± 52 S.E., $n=9$,

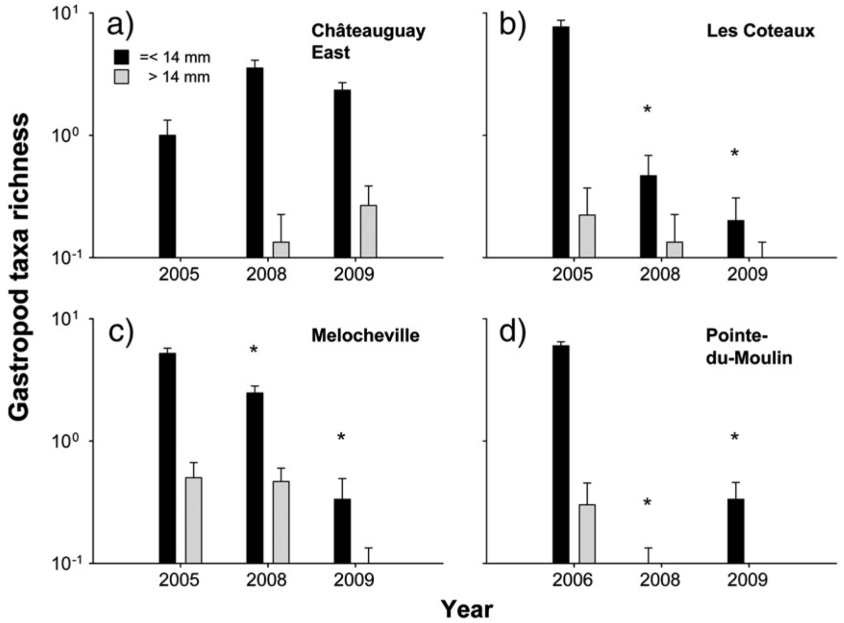

Fig. 3. Taxa richness of small and large gastropods before (2005 or 2006) and after (2008 and 2009) round goby invasion, at four sites. Single stars (*) denote densities ranked lower than those in the pre-invasion year according to one-tailed Wilcoxon rank sum tests at the 0.05 level after controlling for the FDR (beginning with 1/16∗(0.05)). The boxes show the median, 25th and 75th percentiles. The whiskers show the 10th and 90th percentiles, excluding outliers.

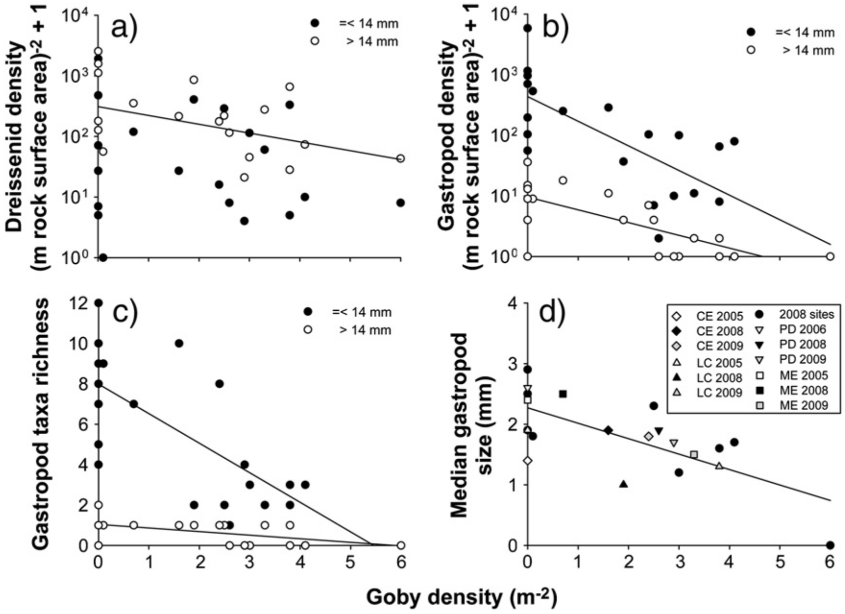

Fig. 4. All lines fitted by least squares regression. a) Density of small and large dreissenids as a function of round goby density. For open circles, log $(y+1)=2.60-0.16\,x$ ($R^2=0.25$, $F_{1,18}=6.1$, $n=20$, $p=0.02$). When the LP 2008 datapoint was excluded, the curve was no longer statistically significant (log $(y+1)=2.60-0.17\,x$, $R^2=0.20$, $F_{1,17}=4.2$, $n=19$, $p=0.06$). For black circles, the relationship was not significant ($F_{1,18}=0.4$, $n=20$, $p=0.5$). b) Density of small and large gastropods as a function of round goby density: for black circles, log $(y+1)=2.64-0.41\,x$ ($R^2=0.58$, $F_{1,19}=26.3$, $n=21$, $p<0.0001$); for open circles, log $(y+1)=0.98-0.21\,x$ ($R^2=0.52$, $F_{1,19}=20.7$, $n=21$, $p=0.0002$). c) Taxa richness for pooled samples of small and large gastropods as a function of round goby density: for black circles, $y=7.98-1.46\,x$ ($R^2=0.56$, $F_{1,19}=23.8$, $n=21$, $p=0.0001$); for open circles, $y=1.04-0.18\,x$ ($R^2=0.32$, $F_{1,19}=8.9$, $n=21$, $p=0.008$). d) Median gastropod size for pooled samples as a function of round goby density: $y=2.27-0.25\,x$ ($R^2=0.50$, $F_{1,19}=19.1$, $n=21$, $p=0.0003$).

$p=0.0005$) and 2009 (mean rock area = 413 cm^2 ± 26 S.E., $n=15$, $p=0.0001$). There was no relationship between round goby density and total pooled rock area at the site level (linear regression, $F_{1,19}=0.9$, $n=21$, $p=0.4$).

There was no relationship between round goby density and dreissenid shell length (linear regressions, mean length vs goby density: $F_{1,18}=0.9$, $n=20$, $p=0.4$; median length vs goby density: $F_{1,18}=0.1$, $n=20$, $p=0.8$). In contrast, median gastropod size declined with increasing round goby density across sites (Fig. 4d). Mean gastropod size also tended to decline with round goby density, but not significantly so ($y=3.73-0.31\,x$, $R^2=0.13$, $F_{1,19}=2.9$, $n=21$, $p=0.1$).

Round goby gape limitation and ontogenetic diet shift

The mean gape height for 130 gobies sampled across the four sites was 7.4 mm (range: 4.5–13.0 mm). A total of 62 individual dreissenids were recovered from the GI tracts. There was a strong positive relationship between round goby gape height and dreissenid fragment size (Fig. 5). Upon examining GI tracts, no whole gastropods >7 mm were found, and gastropod fragments were few and small. There was no relationship between gape height and maximum gastropod size (Fig. 5). A total of 425 recognizable gastropods were recovered from the GI tracts. The most abundant gastropod was the snail *Amnicola*, accounting for 80% of all individuals. The next most abundant was *Gyraulus* (5%), followed by *Physella* (3%) and *Stagnicola* (3%). *Ferrissia* and *Elimia* each accounted for <1% of the total. Unidentified snails accounted for 8% of the total. In no instance did the maximum size of a gastropod found in a GI tract exceed gape height, whereas this occurred in three instances with dreissenid fragments.

There were no significant relationships between round goby total length and log-transformed absolute values of gastropod abundance (linear regression, $F_{1,75}=1.4$, $n=77$, $p=0.2$), biomass ($F_{1,63}=1.4$, $n=65$, $p=0.2$), and volume ($F_{1,48}=0.0$, $n=50$, $p\sim1.0$), or arcsine-transformed proportional values of gastropod abundance ($F_{1,75}=0.0$, $n=77$, $p\sim1.0$) and volume ($F_{1,52}=1.8$, $n=54$, $p=0.2$). There was a tendency for percent gastropod biomass to decline with round goby total length ($\sin^{-1}(y^{0.5})=0.95-0.01\,x$, $R^2=0.06$, $F_{1,63}=4.3$, $n=65$, $p=0.04$), although the relationship was not significant upon FDR correction. In contrast, dreissenid biomass (preserved wet weight) and volume increased with round goby total length, as did percent dreissenid biomass (Fig. 6). The majority of individual fish (46 of 53 in which mussels were present) contained only one mussel, while five fish contained two mussels, and two fish contained three mussels. Given the small range in the number of dreissenids consumed, relationships between round goby total length and the proportional and absolute values of dreissenid abundance in round goby GI tracts were not evaluated.

There were 60 fish ≤70 mm and 17 fish >70 mm that contained no dreissenids, while 20 fish ≤70 mm and 33 fish >70 mm contained dreissenids. There were 37 fish ≤70 mm and 16 fish >70 mm that contained no gastropods, whereas 43 fish ≤70 mm and 34 fish

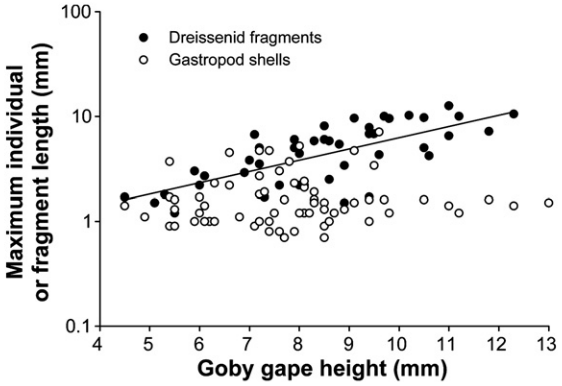

Fig. 5. Dreissenid fragment and gastropod shell lengths for the largest fragment or individual retrieved per fish as a function of round goby gape height. For dreissenids (curve shown), there was a statistically significant relationship between round goby gape height and shell length: log $(y)=-0.28+0.11\,x$ ($R^2=0.47$, $F_{1,44}=39.4$, $n=46$, $p<0.0001$). For gastropods, there was no relationship ($F_{1,65}=0.3$, $n=67$, $p=0.6$).

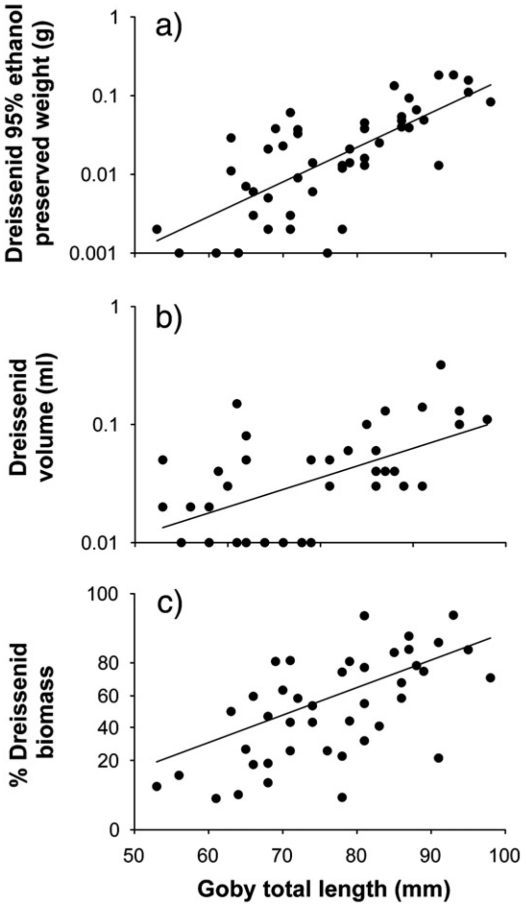

Fig. 6. All lines fitted by least squares regression. a) 95% ethanol wet weight of dreissenids retrieved from round goby GI tracts as a function of round goby total length: $\log(y) = -5.17 + 0.04x$ ($R^2 = 0.54$, $F_{1,45} = 51.9$, $n = 47$, $p < 0.0001$). b) Volume of dreissenids retrieved from round goby GI tracts as a function of round goby total length: $\log(y) = -3.44 + 0.02x$ ($R^2 = 0.32$, $F_{1,37} = 17.8$, $n = 39$, $p = 0.0002$). c) Percent 95% ethanol wet weight of dreissenids retrieved from round goby GI tracts as a function of round goby total length: $\sin^{-1}(y^{0.5}) = -0.52 + 0.02x$ ($R^2 = 0.24$, $F_{1,45} = 14.3$, $n = 47$, $p = 0.0005$).

>70 mm had consumed gastropods. The occurrence of dreissenids in fish stomachs differed with round goby length class (≤70 mm and >70 mm; Fisher's exact test, $p < 0.0001$), but no such difference was observed for gastropods ($p = 0.1$).

Round goby diet and prey preference

Mean total length for the 130 round gobies collected at the four sites sampled in 2009 was 69 mm (range 47–104 mm). At individual sites, mean total lengths were as follows: Châteauguay East, 66 ± 1.54 mm (S.E.), $n = 36$ (range 48–98 mm); Les Coteaux, 77 ± 2.23 mm, $n = 30$ (range 54–104 mm); Melocheville, 73 ± 1.94 mm, $n = 28$ (range 53–95 mm); and Pointe-du-Moulin, 63 ± 1.08 mm, $n = 36$ (range 47–80 mm). There was significant variation among sites (ANOVA, $F_{3,126} = 14.4$, $p < 0.0001$), and Les Coteaux and Melocheville round gobies were larger than those from Châteauguay East (Tukey's post-hoc comparisons, $p < 0.0001$ and $p = 0.03$, respectively) and Pointe-du-Moulin ($p < 0.0001$ and $p = 0.0003$, respectively).

Only two of the 130 round goby GI tracts were empty. Friedman tests indicated that prey categories varied significantly in their rank importance across the four sites, according to Ivlev's prey selectivity index calculated as both $E_{\text{abundance}}$ ($Q_{18} = 4.39$, $n = 19$, $p = 0.0002$) and E_{biomass} ($Q_{11} = 3.15$, $n = 12$, $p = 0.008$) (Table 4). For both indices, there was a tendency for Gastropoda, Chironomidae, Ostracoda, and Trichoptera to rank as the most preferred prey, while Dreissenidae, Hirudinea, and Acari tended to rank as the most avoided prey.

Discussion

Round goby impacts on dreissenid size structure

Surprisingly, there were no consistent trends in dreissenid size structure with increasing round goby density across sites or years. We predicted that declines would be most pronounced for the small size class, as the average maximum size of mussels reported consumed by round gobies in the Great Lakes is 14 mm (Clark, 2007; Djuricich and Janssen, 2001; Ghedotti et al., 1995; Jude et al., 1995; Ray and Corkum, 1997; Taraborelli and Schaner, 2002; Thomas, 1997). Contrary to expectations, significant declines occurred more frequently at Melocheville and at Les Coteaux in 2008 and 2009 for the large dreissenid size class. It is of note that Melocheville and Les Coteaux round gobies were larger than those at the other two sites tested over time. It seems possible that larger round gobies consumed more of the larger mussels, contributing to impacts in the larger size class more frequently. The larger mussel size class also tended to decline across all sites. Our results therefore seemed to suggest only occasional correlation between mussels >14 mm and round goby density.

Some of these results might not have been caused by round goby predation, but rather by other ongoing changes in dreissenid populations in the Great Lakes–St. Lawrence basin. For example, the replacement of *D. polymorpha* by *D. bugensis* in the Great Lakes has occurred in conjunction with general declines in total dreissenid densities in some regions (Haynes et al., 2005). Indeed, evidence suggests that *D. polymorpha* is being replaced gradually by *D. bugensis* across our sites, with increasing round goby density and time since invasion (Kipp and Ricciardi, in press). However, this replacement began years before round gobies became abundant (Ricciardi and Whoriskey, 2004).

The lack of consistent effects of round goby predation on dreissenids could conceivably result from several factors, including: (i) insufficient predation on dreissenids owing to relatively small sizes of fish; (ii) stronger preferences for alternative prey; (iii) insufficient time for impacts to accrue; (iv) relatively low round goby densities; (v) low dreissenid densities in comparison to the Great Lakes, leading to lower encounter rates with optimally sized mussels; and (vi) insufficient statistical power to detect effects. It may have been too early in the invasion for effects to be detected at some sites, as discussed below with respect to gastropods at Châteauguay East. However, round gobies were estimated to have been present at some sites for up to 5 years, which exceeds time frames in studies in which a significant reduction in dreissenids has been attributed to round goby predation (e.g. ~3 years; Lederer et al., 2008). It is possible that round goby densities in the upper St. Lawrence River are still too low to produce strong impacts on dreissenid populations. In two studies where round goby densities were estimated at 14–15 m^{-2}, gobies were the implicated cause of changes in dreissenid densities (Barton et al., 2005; Kuhns and Berg, 1999) and size structure (Barton et al., 2005). In both studies, round goby densities were 2.3–2.5 times higher than that at our highest density site (Loyalist Park). However, we note that because our round goby density estimates were made by visual counts along transects, they were likely imprecise and would need to be verified by other means (e.g. videotaped counts).

Significant impacts might occur only where both dreissenids and round gobies are present at high densities. Dreissenid densities tend to be higher in lentic systems (Mellina and Rasmussen, 1994; Ricciardi et al., 1995), and dreissenid populations in the upper St. Lawrence River might be substantially reduced in density compared to those in the Great Lakes such that round goby predatory impacts in the river are muted by comparison. Prior to round goby invasion

Table 4

Ivlev's E, calculated in two different ways for prey items recovered from round goby GI tracts at four sites (see Table 1 for codes) in 2009. Some prey categories were ranked higher than others for $E_{abundance}$ ($Q = 4.39$, $df = 18$, $n = 19$, $p = 0.0002$) and $E_{biomass}$ ($Q = 3.15$, $df = 11$, $n = 12$, $p = 0.008$) across the four sites. Excluded are all categories not captured in cobble samples, such as Decapoda, Copepoda, Cladocera, inorganic matter and non-invertebrate organic matter. Letters denote prey categories that are not ranked statistically differently (Diffs.) at the 0.05 level after Bonferroni correction (0.05/171 and 0.05/66, for each metric, in order of appearance). Values in bold italics highlight categories that were ranked higher than all other categories before Bonferroni correction.

$E_{abundance}$

Prey	CE	LC	ME	PD	Diffs.
Gastropoda	***0.76***	***0.96***	***0.81***	***0.56***	a
Ostracoda	***0.24***	***0.7***	***0.25***	***0.67***	a,b
Pisidiidae	***1***	***1***	***0***	***0***	a,b
Trichoptera	***−0.11***	***0.09***	***0.64***	***0.18***	a,b,c
Lepidoptera	***1***	***0***	***−1***	***0.5***	a,b,c
Chironomidae	***0.04***	***0.01***	***0.08***	***−0.23***	a,b,c
Nematoda	***0.33***	***0.53***	***−1***	***0***	a,b,c
Odonata	1	0	−1	0	a,b,c
Amphipoda	−0.18	−0.38	−0.51	0.2	a,b,c
Ephemeroptera	0.08	−0.50	−0.29	−0.3	a,b,c
Neuroptera	0	0	−1	0	a,b,c
Coleoptera	−0.87	−1	−0.77	0.64	a,b,c
Nemertea	−1	−1	0	0	a,b,c
Hirudinea	0	−1	0	−1	a,b,c
Acari	−0.68	−0.71	−0.43	−0.75	a,b,c
Dreissenidae	−0.67	−0.82	−0.71	−0.43	a,b,c
Isopoda	−1	−1	−1	0	b,c
Turbellaria	−1	0	−1	−1	b,c
Oligochaeta	−1	−1	−1	−1	c

$E_{biomass}$

Prey	CE	LC	ME	PD	Diffs.
Ephemeroptera	***1***	***1***	***1***	***0.81***	a
Ostracoda	***1***	***1***	***0***	***1***	a
Trichoptera	***0.95***	***1***	***0.96***	***0.78***	a,b
Gastropoda	***0.72***	***0.91***	***0.99***	***1***	a,b
Coleoptera	***0.73***	***0***	***1***	***0.98***	a,b
Amphipoda	***0.91***	***0.94***	***0.94***	***0.93***	a,b
Chironomidae	***0.94***	***0.94***	***0.98***	***0.77***	a,b
Pisidiidae	1	0	0	0	a,b
Lepidoptera	0	0	0	1	a,b
Acari	0	0	1	−1	a,b
Hirudinea	0	0	0	−1	a,b
Dreissenidae	−0.59	−0.13	−0.39	−0.99	b

at the four resampled sites in this study, dreissenid densities in the small size class varied from <10 to 2000 m^{-2} rock surface area, while densities in the large size class varied between ~100 and 2500 m^{-2} rock surface area. These numbers are several times smaller than those in Lake Erie (Barton et al., 2005). In the experiment by Kuhns and Berg (1999), changes in dreissenid density occurred only for tiles colonized by 100,000 individuals m^{-2}, whereas tiles with 10,000 m^{-2} showed no changes in the presence of round gobies. On the other hand, significant impacts were observed in nearshore areas of Green Bay, Lake Michigan where dreissenid densities were ~50–350 m^{-2} immediately prior to round goby invasion (Lederer et al., 2008).

Although it is possible that low statistical power combined with temporal variability in sampling hindered detection of the effects of round goby predation, such factors did not prevent detection of impacts on gastropods. Moreover, bioenergetic models calculate round gobies consume <0.2% of available dreissenid biomass in the Great Lakes (Bunnell et al., 2005; Johnson et al., 2005b). The negative impacts of round gobies on dreissenid densities and size structure might occur only where round goby densities are locally high.

Round goby impacts on gastropod size structure and taxa richness

The data supported our predictions regarding round goby impacts on the structure and diversity of the two gastropod size classes studied in the upper St. Lawrence River. Across sites and time at three of four resampled sites, the small size class generally experienced the strongest declines in density and taxa richness. For tests on taxa richness, because total pooled rock area was not correlated with round goby density, it is unlikely that species–(rock) area relationships could have confounded changes to gastropod taxa richness across sites. Species–area relationships were also unlikely to have affected the results at three of the four resampled sites. Only at Les Coteaux did rock area differ between years; rock area in 2008 was smaller than in 2005 and 2009, which could have biased the observed changes in taxa richness in small gastropods from 2005 to 2008, but does not explain reduced taxa richness in 2009.

One of the resampled sites, Châteauguay East, clearly stood out as an exception to the dominant trends seen for sites sampled before and after round goby invasion. Of the four resampled sites, Châteauguay East exhibited the lowest round goby density and time since invasion in 2009. Thus, round gobies were probably not present at sufficiently high densities long enough to exert strong impacts. Moreover, the pre-invasion samples in 2005 may have been collected too close to the wave swept zone and for this reason comprised an already depauperate macroinvertebrate community (there is no record of the exact depth at which they were taken).

One important environmental factor that potentially affects gastropod distributions is current flow. For example, lymnaeids, planorbids and physids are associated most with low velocity (e.g. Nelson and Lieberman, 2002), while pleurocerids are typically considered more characteristic of lotic habitats (Brown et al., 2008). Nevertheless, gastropods often exhibit great phenotypic plasticity. Pleurocerid snails, for example, can colonize low-flow habitats and sometimes prefer them over high-flow habitats (Brown et al., 2008). We did not measure current velocity at our sites, but observed that it was generally low in mid to late summer. Indeed, all of our sites were situated in littoral zones with some macrophyte cover, often in small embayments or low flow areas. The exception was Pointe-du-Moulin, an exposed site where velocity was relatively high (Ward and Ricciardi, 2010). Nevertheless, prior to round goby invasion, a variety of gastropods — including lymnaeids, physids, and planorbids — were abundant at this site (Ward and Ricciardi, 2010). As at Les Coteaux and Melocheville, two other sites with lower current velocities, smaller gastropods underwent similar changes over time in conjunction with round goby invasion. We recognize that current velocity structures gastropod communities in lotic environments and could have affected relationships between round gobies and gastropods. However, given that gastropod communities across our sites in the upper St. Lawrence River were similarly diverse and abundant prior to round goby invasion (Masson et al., 2009; Pinel-Alloul et al., 1996; Ricciardi et al., 1997; Ward and Ricciardi, 2010), it seems likely that the effects we observed in this study were related primarily to round gobies, rather than current flow.

Overall, the weight of evidence suggests stronger impacts on the small gastropod size class. Indeed, snail families that actually attained a size of >14 mm in the field (Viviparidae and Pleuroceridae) were not correlated with the stages of round goby invasion, while smaller families (with the exception of the Hydrobiidae) did exhibit such a correlation. Surprisingly, the median (but not the mean) size of gastropods was negatively correlated with round goby density across sites, which apparently contradicts the hypothesis that round gobies reduce the abundance of small gastropods. However, the most frequently remaining families at late-invasion sites were large Pleuroceridae and small Hydrobiidae. Despite heavy round goby predation on hydrobiids, this gastropod family remained the most abundant and comprised the smallest individuals. Small individuals may have been relatively difficult for a visual predator to remove from interstitial substrate (cf. Stewart et al., 1999). The median size of the entire gastropod distribution at such sites was thus quite small. For sites in earlier stages of invasion, a larger number of families intermediate in size between hydrobiids and pleurocerids were present (Ancylidae, Bithyniidae, Lymnaeidae, Physidae, and Valvatidae), causing the median to increase.

The most abundant gastropod taxon occurring both at field sites and in round goby GI tracts was the hydrobiid *Amnicola*, which can attain a maximum size of 4.5 mm in the upper St. Lawrence River (Pinel-Alloul and Magnin, 1973; personal observations). Not one of the *Amnicola* collected from round goby GI tracts or cobble samples in 2009 exceeded 3 mm. Given that *Amnicola* occurred at various mid- and late-invasion sites, where it was always considerably smaller than 4.5 mm, it is possible that this species has been able to reproduce successfully at very small sizes. Phenotypic changes have been observed in other gastropods in response to predators. For example, a documented decline in the size of intertidal gastropods has been attributed to predation pressure that made it more advantageous to reproduce at smaller sizes (Rochette et al., 2003). This possible phenotypic change in response to predation highlights the potentially broad range of subtle impacts the round goby could exert in a novel environment.

Although dreissenid mussels themselves can alter the composition and size structure of gastropods (Ricciardi et al., 1997; Ward and Ricciardi, 2007), it is unlikely that changes to the median gastropod size occurred indirectly through declines in dreissenids because there were no major changes to dreissenid density at our sites. Even if larger dreissenids declined with round goby density, we would expect the size of all gastropods to be positively affected, given that large snails tend to be scarce in the presence of high dreissenid densities (Ward and Ricciardi, 2007).

Round goby gape limitation and ontogenetic diet shift

Round goby consumption of dreissenids was gape limited, as suggested by the fact that no whole dreissenids were consumed and that dreissenid fragment size increased with round goby gape size. This result complements a recent study from Presque Isle Bay, Lake Erie, where the size of whole and crushed dreissenids consumed by round gobies increased with the total length of the fish (Andraso et al., 2011). In contrast to dreissenids, the size of consumed gastropods was not related to round goby gape height in our study. Round gobies may prefer gastropods over dreissenids, as suggested by their prey selectivity. An abundance of gastropods that lack the size, crushing resistance, and byssal attachment of dreissenids might be a more energetically profitable prey, particularly for round gobies that are not fully mature. Indeed, other studies have found that various molluscivores prefer smaller snails over larger molluscs including dreissenids, likely because of reduced handling time and shell thickness (Nyström and Pérez, 1998; Stein et al., 1975). In our study, *Physella* and *Ferrissia* are thin-shelled species (Clarke, 1981) that occurred much less frequently at late-invasion sites. Indeed, *Physella* exhibits particularly low crushing resistance with respect to molluscivorous fishes (Huckins, 1997). Although other snails such as *Amnicola* are more compact and may therefore be more resistant to crushing (Huckins, 1997; Lewis and Magnuson, 1999), they lack byssal threads and are considerably smaller than the majority of available dreissenids. Thicker-shelled genera such as *Bithynia*, *Valvata*, *Helisoma* and *Stagnicola* are locally abundant in benthic habitats throughout the St. Lawrence River (Masson et al., 2009; Pinel-Alloul et al., 1996; Ricciardi et al., 1997; Ward and Ricciardi, 2010), but were all reduced in frequency of occurrence at late-invasion sites in our study. These species could have been preferred by round gobies over dreissenids, particularly because of their lack of byssal threads.

The small size of gastropods recovered from GI tracts in this study might simply indicate that larger individuals in the appropriate size range, from ~7–14 mm, were no longer available. In 2009, almost all gastropods available were <5 mm at the four sites sampled, with the exception of the occasional *Elimia* and one *Stagnicola*. Without conducting size-selection experiments, it is not possible to determine whether the observed dietary composition was due to prey preference or prey availability. Only very minimal predation on *Elimia* was observed (one snail <2 mm in length found in a single fish GI tract at each of Châteauguay East and Melocheville), possibly because of their thicker, more compact shells in comparison to other taxa available. Nevertheless, large gastropods — which were almost exclusively *Elimia* — responded negatively to round goby density across sites, suggesting a predation effect.

There was evidence for an ontogenetic diet shift: the biomass proportion of the diet composed of dreissenids increased with round goby length and dreissenid presence in the diet was associated with round goby size class. Round gobies sampled in Lac Saint-Louis were 47–104 mm in total length and showed a substantial shift toward molluscivory at lengths of ~70 mm. The observed ontogenetic diet shift for mid-sized round gobies and the observed range in round goby sizes are comparable to those for populations in the Great Lakes (e.g. French and Jude, 2001; Janssen and Jude, 2001; Jude et al., 1995). This round goby size range is also comparable to those associated with substantial consumption of dreissenids in the laboratory (e.g. 47 mussels day^{-1} per individual round goby; Ghedotti et al., 1995) and significant impacts on dreissenid populations in the field (Lederer et al., 2006, 2008). Altogether, these considerations indicate that the size of round gobies alone probably does not explain the variable effects on dreissenids found in this study, although the combination of relatively small round goby sizes and densities could play a role.

The differences in mean round goby size observed among sites likely resulted from differences in time since invasion rather than gear capture bias. Only minnow traps were used at Les Coteaux to capture round gobies, whereas only gill nets were used at Châteauguay East, Pointe-du-Moulin and Melocheville. Owing to the small mesh size of our gill nets, we employed a modified capture method in which we waited behind the net until a round goby swam into it, and then quickly pulled up the leadline to capture it within the net, before removing it by hand into a bucket. Therefore, the gill nets did not contribute to selective bias in the size of fish captured. Our minnow traps were large enough to capture the largest round gobies present at our sites, but we do recognize that smaller round gobies tend not to enter traps with larger fish (J. Janssen, University of Wisconsin–Milwaukee, 2011, pers. comm.). Nevertheless, times since invasion roughly matched differences in round goby size across sites: Les Coteaux and Melocheville fish were larger than Châteauguay East and Pointe-du-Moulin fish. By 2009, round gobies had been present for 4 years at Les Coteaux, 3 years at Melocheville and Pointe-du-Moulin, and 2 years at Châteauguay East. It seems most likely that differences in round goby size across sites were due more to time since invasion than the size selective bias of the minnow traps at Les Coteaux only.

Round goby diet and prey preference

Gastropods, chironomids, trichopterans and ostracods were the only prey categories consistently ranked the highest prior to Bonferroni correction for all values of Ivlev's E. After Bonferroni correction there were few prey categories ranked significantly differently from one another; in this case, the Bonferroni correction applied to rank tests was so conservative as to obscure differences in prey selection. The ranking of these metrics for gastropods was consistent with our expectations based on studies recording impacts on these taxa in the Great Lakes (e.g. Kipp and Ricciardi, in press; Lederer et al., 2006, 2008), and with our results.

Values of E for dreissenids were negative at all sites. The positive preference for gastropods and chironomids, combined with apparent avoidance of dreissenids, mirrors values of E reported from the Baltic Sea, where round gobies preferred gastropods, chironomids, and annelids, and avoided bivalves and crustaceans (Wandzel, 2003). Similar results were found for a congeneric species, the monkey goby *Neogobius fluviatilis*; in the Vistula River (Poland), where it is introduced, the monkey goby exhibited positive values of E solely for dipteran taxa, even though it is molluscivorous in a number of other habitats (Grabowska et al., 2009). The preference for chironomids was also similar to that recorded for the round goby in a recent study in Great Lakes' tributary streams (Pennuto et al., 2010). However, the lack of preference for dreissenids in our study contradicts laboratory studies that show that round gobies from the Great Lakes prefer dreissenids over native molluscs (Ghedotti et al., 1995). The E_{biomass} values in this study were more consistent with other laboratory experiments in which round gobies preferred amphipods over dreissenids (Diggins et al., 2002; Polačik et al., 2009), although the $E_{\text{abundance}}$ values in this study suggest that round gobies tended to avoid dreissenids and amphipods at most sites. Also contrary to this study, Barton et al. (2005) and Raby et al. (2010) found that round gobies increased the non-dreissenid component of their diet only after mussels became rare, indicating a preference for dreissenids over other macroinvertebrates.

Factors that affect rates at which round gobies encounter prey include: (i) substrate type and visibility (Diggins et al., 2002); (ii) availability of appropriately sized mussels and their occurrence in refugia on the undersides of rocks or in patches (Djuricich and Janssen, 2001); and (iii) the availability of mussel patches or macrophytes as refugia for mobile macroinvertebrates (González and Burkart, 2004; Kestrup and Ricciardi, 2009; Reed et al., 2004). Through their mediation of encounter rates, these factors influence indices that attempt to describe round goby preference or avoidance of prey. As these factors may vary spatially and temporally, round goby prey preferences are highly context dependent.

Implications of the study

Impacts of the round goby on non-dreissenid mollusc taxa have rarely been explored in detail, although Poos et al. (2009) recently reviewed the potential for round gobies to negatively affect freshwater mussels via impacts on their obligate fish hosts in Great Lakes' tributary streams. Research on potential impacts on non-dreissenid molluscs in the St. Lawrence River has also been limited to date. This was the first field study to investigate round goby prey selection in relation to alterations to mollusc size structure in a large river. The consistent effects on smaller gastropods and preference for such prey, combined with the inconsistent effects on dreissenids, demonstrate the heterogeneous impacts of this benthic predator. Our study supports the view that local impacts on dreissenids may occur only where round goby abundances are highly concentrated (Johnson et al., 2005b; Patterson et al., 2005). Furthermore, variation in impacts might be explained by the age structure of local round goby populations. Smaller round gobies likely exert more direct predatory effects on dreissenid-associated macroinvertebrates such as gastropods, whereas larger round gobies consume a greater proportion of dreissenids and exert more indirect effects (Lederer et al., 2006). Therefore, benthic communities in the St. Lawrence River can be expected to undergo further transformations as round goby population structure changes over time.

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