

Impacts of the Eurasian round goby (*Neogobius melanostomus*) on benthic communities in the upper St. Lawrence River

Rebekah Kipp and Anthony Ricciardi

Abstract: An invasive benthivorous fish, the Eurasian round goby (*Neogobius melanostomus*) is abundant throughout the lower Great Lakes – St. Lawrence River system. We examined the round goby's potential to alter benthic communities on cobble substrates in the upper St. Lawrence River. During the summers of 2008 and 2009, macroinvertebrates and benthic algae were sampled across sites with varying goby densities. Archived data from various sites in 2004–2006 (prior to invasion) were available for comparison. Macroinvertebrate community composition varied significantly among samples grouped into categories based on goby density and time since invasion. Macroinvertebrate diversity and dominance by large-bodied taxa declined with increasing goby density. Surprisingly, dreissenid biomass did not vary consistently with goby density, in contrast to studies in the Great Lakes. The biomass of all non-dreissenid taxa was negatively correlated with increasing goby density across sites and over time at three of four sites. Negative effects were most pronounced on the biomass of gastropods. Benthic algal biomass increased with goby density across sites, suggesting a trophic cascade driven by the impacts of gobies on gastropods and other algivores. Our study highlights the potential ecosystem impacts of an expanding goby population in a large river.

Résumé : Le poisson envahissant, consommateur de benthos, le gobie à taches noires d'Eurasie, *Neogobius melanostomus*, est abondant dans l'ensemble du système des Grands Lacs inférieurs et du Saint-Laurent. Nous étudions le potentiel qu'a le gobie à taches noires pour modifier les communautés benthiques sur les substrats pierreux dans la région amont du Saint-Laurent. Durant les étés 2008 et 2009, nous avons échantillonné les macroinvertébrés et les algues benthiques dans un ensemble de sites présentant des densités diverses de gobies. Il existe des données en archives pour plusieurs sites en 2004–2006 (avant l'invasion) pour servir de comparaison. La composition des communautés d'invertébrés varie significativement dans les différents échantillons regroupés en catégories d'après la densité des gobies et le temps depuis l'invasion. La diversité des macroinvertébrés et la dominance des taxons de grande taille diminuent en fonction de l'augmentation de la densité des gobies. De manière inattendue, la biomasse des dreissenidés ne varie pas de manière cohérente en fonction de la densité des gobies, comme elle le fait dans les Grands Lacs selon certaines études. Dans trois de quatre sites, la biomasse de l'ensemble des taxons moins les dreissenidés est en corrélation négative avec l'accroissement des gobies dans les divers sites et les différentes périodes. Les effets négatifs les plus prononcés s'observent sur la biomasse des gastéropodes. La biomasse des algues benthiques augmente en fonction de la densité des gobies dans les différents sites, ce qui laisse croire à une cascade trophique causée par les impacts des gobies sur les gastéropodes et les autres consommateurs d'algues. Notre étude souligne les impacts potentiels sur l'écosystème provoqués par l'expansion d'une population de gobies dans une grande rivière.

[Traduit par la Rédaction]

Introduction

The round goby (*Neogobius melanostomus*) is an invasive benthic fish native to the Black and Caspian seas region. It was discovered in the St. Clair River in 1990 (Jude et al. 1992), presumably after having been introduced in ballast water released from transoceanic ships (Corkum et al. 2004). Populations expanded rapidly throughout the lower Great Lakes (Charlebois et al. 2001) and spread more recently into the upper St. Lawrence River (Hickey and Fowlie 2005). Gobies are generalist predators that consume an increasing pro-

portion of dreissenid mussels (zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*) as they mature (Jude et al. 1995). Despite a preference for smaller mussels (Ghedotti et al. 1995; Ray and Corkum 1997; Djuricich and Janssen 2001), goby foraging can cause local reductions in dreissenid density (Kuhns and Berg 1999; Barton et al. 2005; Lederer et al. 2006). Although negative impacts on other macroinvertebrates have been inferred, the mechanisms involved are often unclear. Macroinvertebrate declines could occur directly via predation or indirectly through the reduction of dreissenid densities, which may re-

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R. Kipp and A. Ricciardi. Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, QC H3A 2K6, Canada.

Corresponding author: Anthony Ricciardi (e-mail: tony.ricciardi@mcgill.ca).

sult in the loss of mussel-generated refugia, habitat, and nutrients to mussel-associated taxa (Kuhns and Berg 1999; Lederer et al. 2006, 2008).

In this study, the first to be conducted in a large river, we examined responses of benthic communities to round goby invasion. Impacts on macroinvertebrate functional feeding groups were analyzed for the first time, allowing us to explore novel indirect mechanisms of goby impacts. Moreover, no studies to date have tested the effects of gobies on the body-size dominance of non-dreissenid macroinvertebrate taxa. By examining this factor, we highlight community-level restructuring similar to that reported for other invasive fishes (Carlisle and Hawkins 1998; Buria et al. 2007). Finally, we examined the potential for community-level changes to produce indirect effects on local primary production, i.e., a trophic cascade. Trophic cascades are instigated by predators through top-down control of herbivores (Shurin et al. 2002) or via negative impacts on the herbivore's foraging behaviour (Schmitz et al. 2004). Aquatic systems are more easily regulated by such top-down control than are terrestrial ones (Strong 1992; Shurin et al. 2006), and trophic cascades are generally stronger when they involve benthic grazers in aquatic environments (Shurin et al. 2002). In Lake Erie, for example, experimental tiles deployed for colonization by macroinvertebrates and exposed to goby predation exhibited significantly lower abundances of algal biomass, which likely explained an observed increase in chlorophyll *a* (a proxy for total algal biomass), compared with the abundances on predator-exclusion tiles (Kuhns and Berg 1999). Conversely, Lederer et al. (2006) found that epilithic dry algal biomass (consisting mostly of the filamentous alga *Cladophora*) was 12-fold lower in the presence of gobies, and Wilson et al. (2006) found a negative relationship between goby abundance and *Cladophora* percent cover. Such negative relationships were likely driven by a reduction in dreissenid-generated nutrients and reduced surface area for *Cladophora* attachment as a result of goby predation on dreissenids. Here, we attempted to clarify these contrasting results by considering direct and indirect trophic interactions in different environmental contexts to explain variation in benthic algal abundance.

Our study examined the effects of increasing round goby densities and time since invasion on local benthic communities on cobble substrates. We predicted that, as these factors increase across sites and over time, (i) macroinvertebrate biomass and diversity decline; (ii) non-dreissenid macroinvertebrate communities become increasingly dominated by smaller-bodied taxa; and (iii) benthic algae increase in biomass.

Materials and methods

Study area and data sets used

Data used in this study were obtained from archived studies (2004–2006) and sampling conducted in 2008 and 2009 at sites with cobble substrates and varying goby densities in the upper St. Lawrence River between Prescott, Ontario, and Montreal, Quebec (Fig. 1). Sites having cobble (diameter 65–260 mm) covering at least 10% of the substrate were chosen because gobies are frequently associated with cobble (Jude et al. 1992; Jude and DeBoe 1996; Ray and Corkum 2001).

Epilithic macroinvertebrate communities exploiting dreissenid beds are also diverse in this region on such substrates (Ricciardi et al. 1997), and sites with cobble substrates are common in the St. Lawrence River (Mellina and Rasmussen 1994; Jones and Ricciardi 2005). For all data employed in this study, dreissenid beds were neither deliberately sampled nor avoided; however, dreissenids were present at all sites sampled and ranged in density from 10^1 to 10^3 individuals·(m² cobble surface area)⁻¹ in 2008 and 2009. Finally, at all sites sampled for benthic macroinvertebrates, calcium concentration ([Ca²⁺]) was >20 mg·L⁻¹, which is not limiting to the freshwater species in the river (Clarke 1981; Mellina and Rasmussen 1994; Jones and Ricciardi 2005).

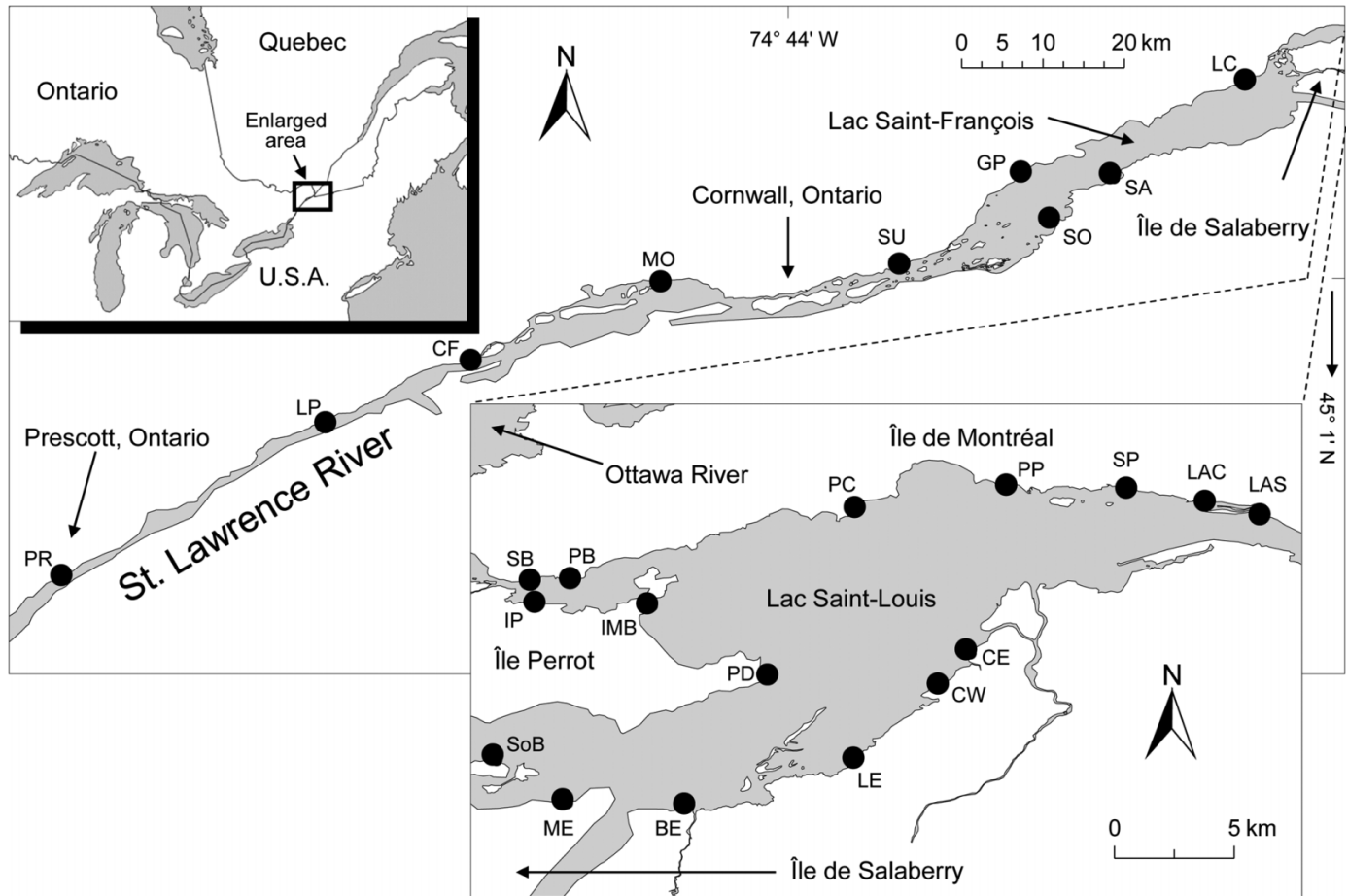
Macroinvertebrate data from the nearshore zones of sites sampled prior to goby invasion were assembled from archived studies using sampling techniques that were similar to those employed in the sampling protocol of this study. These baseline data were essential, as only one site we sampled had no gobies present in 2008, and none did in 2009. Macroinvertebrate data from cobble at three sites in 2005 were used (K. Harper and A. Ricciardi, unpublished data). Cobbles were sampled by snorkelers, who exercised caution to avoid losing actively mobile macroinvertebrates when they placed them into sealable plastic bags underwater. Macroinvertebrate data from artificial substrates (blank cement bricks) from colonization experiments at one site in 2004 and 2006 were also available for quantification of pre-goby invasion benthic communities (Ward and Ricciardi 2010). The bricks' dimensions (19.0 cm × 9.0 cm × 5.7 cm) were comparable to that of cobble in this study. They were deployed in the St. Lawrence River for macroinvertebrate colonization after significant dreissenid settlement had occurred, for purposes related to that study's experimental design; the bricks remained in the water for a duration sufficient for colonization of all other macroinvertebrates (i.e., 53–70 days, from July to September). Therefore, data from this experiment excluded dreissenids. A SCUBA diver retrieved these bricks, placing them underwater into sealable plastic bags. Finally, our sampling of macroinvertebrate communities on cobbles took place in 2008 at 13 St. Lawrence River sites. In 2009, we returned to the four sites for which preinvasion data from 2004, 2005, or 2006 were available, to quantify whether effects measured in 2008 remained similar in 2009.

Benthic algae were collected at 21 sites in 2008 and 17 in 2009, 13 of which were resampled from one year to the next. The 13 resampled sites were also those sampled for macroinvertebrates in 2008. A larger number of sites were sampled for benthic algae than for macroinvertebrates because sample processing was more rapid for the former. Eight sites were not resampled in 2009 for benthic algae because we realized that these sites were highly turbid and could have affected the results, as we note later. Instead, we included four new sites in 2009 that were not turbid and where gobies were present. Benthic algal biomass data were also available from the colonization experiments at one site in 2004 and 2006 (Ward and Ricciardi 2010) (Table 1).

Round goby quantification

To estimate local goby density (m⁻²), a SCUBA diver

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



swam along two 30 m transects while holding a 1 m pole perpendicular to each transect and counted all gobies that passed under the pole. Transect counts are commonly used to quantify goby densities (Barton et al. 2005; Lederer et al. 2006; Kestrup and Ricciardi 2009). Ray and Corkum (2001) suggest that they likely underestimate abundances because of the cryptic behaviour of gobies, whereas Johnson et al. (2005) note that they may overestimate abundances if divers stir up sediments, owing to the curiosity of the fish. For this reason, counts were conducted before macroinvertebrate sampling, on the same day as cobbles were taken, and the SCUBA method on each transect involved a single pass only. Counts were thus undertaken once in the sampling year. Nevertheless, we carried out presampling visits to all our sites and observed that goby densities were similar throughout the sampling season. Our transects were placed in 1–2 m of water; they were placed end-to-end and parallel to the shore at sites with steep slopes, and stacked parallel to each other and along the shore at sites with gentle slopes.

Time since invasion at each site was estimated using either published data (Fuller et al. 2010; Hickey and Fowle 2005) or personal observations based on site visits from earlier in 2008 and 2009, as well as visits in previous years. When 1-year presence is indicated, the invasion front arrived in the year of sampling, no matter the month of arrival. When 2-year presence is indicated, the invasion front arrived in the year prior to sampling, and so on. If gobies were detected at

a site in one month and not detected at a subsequent sampling date, they were still considered present, as the population could have exerted some impact earlier in the year. Furthermore, if we found no gobies at a site but noted the presence of egg masses, we considered the population to be present (Table 1). Gobies arrived at different sites at various times. Consequently, we decided for some analyses to classify sites into categories, using a combined approach to incorporate abundance and time since invasion. The latter is typically ignored in impact studies but is essential for explaining variation in impact (Strayer et al. 2006). We decided on four a priori categories. The first would evidently comprise sites with no round gobies present, as control (preinvasion) sites. “Late-invasion” sites were defined based on the time gobies had been present in the upper St. Lawrence River in Ontario (i.e., 4 years or more), where we expected chronic impacts (sensu Strayer et al. 2006) to have accrued and to be most similar to those recorded in the Great Lakes. The remaining downstream sites sampled in 2008, where gobies were known to have been present for only 1–3 years, were divided into two further categories, “early invasion” and “mid-invasion”, to discern whether density could exert an important effect in the earlier years of invasion. Therefore, these sites were assigned a priori as those having lower goby densities (early invasion) and those having higher goby densities (mid-invasion). Based on these criteria, early-invasion sites all had gobies present for 1–2 years at densities ≤ 1.6 fish·m⁻²,

Table 1. Sampling localities, with corresponding site-level data and characteristics.

| Site (abbreviation) | GPS coordinates ^a | Time ^b | <i>n</i> | [Ca ²⁺] (mg·L ⁻¹) ^c | % cobble ^d | Goby density ^e (m ⁻²) | TI (years) ^f | IS ^g | D ^h | Algal biomass ⁱ |
|------------------------------------|--------------------------------|-------------------|--------------------|--|-----------------------|--|-------------------------|-----------------|----------------|----------------------------|
| Beauharnois (BE08) | 45°19'7.06", -73°52'58.64" | A 2008 | 15 ^k | 30.2(1.7) | 70(10) | 4.1(0.3) | 2 | M | D, B | 50.41(7.53) |
| Beauharnois (BE09) | 45°19'7.06", -73°52'58.64" | A 2009 | 15 | 31.0 | 80(<10) | 2.3(0.4) | 3 | M | | 66.55(7.69) |
| Châteauguay E. (CE05) ^j | 45°22'31.71", -73°46'34.25" | J 2005 | 8 | 30.4 | | 0 | 0 | P | D, B | |
| Châteauguay E. (CE08) | 45°22'31.71", -73°46'34.25" | S 2008 | 15 | 30.2(1.9) | 50(10) | 1.6(0.3) | 1 | E | D, B | 30.17(7.01) |
| Châteauguay E. (CE09) | 45°22'31.71", -73°46'34.25" | A 2009 | 15 | 30.9(0.4) | 60(10) | 2.4(<0.1) | 2 | M | D, B | 46.26(5.76) |
| Châteauguay W. (CW08) | 45°21'48.30", -73°47'12.78" | A 2008 | 15 ^k | 29.9(0.9) | 80(<10) | 0 ⁿ | 1 ⁿ | E ⁿ | D, B | 43.05(7.10) |
| Châteauguay W. (CW09) | 45°21'48.30", -73°47'12.78" | A 2009 | 15 | 32.2 | 50(10) | 1.6(<0.1) | 2 | E | | 24.01(5.41) |
| Crysler Farm (CF09) | 44°56'33.49", -75°4'4.68" | A 2009 | 15 | 29.8 | 50(10) | 2.0(0.5) | 7 | L | | 10.45(1.80) |
| Glengarry Pk (GP09) | 45°9'5.63", -74°27'33.20" | A 2009 | 15 | 35.6 | 70(10) | 2.7(0.5) | 5 | L | | 46.97(6.87) |
| Île Madore B (IMB08) | 45°23'35.73", -73°53'45.55" | A 2008 | 15 ^k | 20.6(3.6) | 80(10) | 0.1(<0.1) | 1 | E | D, B | 5.88(1.32) |
| Île Madore B (IMB09) | 45°23'35.73", -73°53'45.55" | A 2009 | 15 | 23.3(5.1) | 80(<10) | 0.4(<0.1) | 2 | E | | 27.51(3.84) |
| Île Perrot (IP08) | 45°23'37.22", -73°56'18.80" | A 2008 | 15 | 11.2(1.4) | 100(0) | 0 | 0 | P | | 11.19(1.94) |
| Lachine (LAC08) | 45°26'0.49", -73°41'11.19" | A 2008 | 15 | 15.4(2.5) | 60(10) | 0 | 0 | P | | 18.47(3.69) |
| Lasalle (LAS08) | 45°25'41.80", -73°39'57.68" | A 2008 | 15 ^l | 14.3(1.9) | 60(<10) | 0 | 0 | P | | 0.15(0.06) |
| Léry (LE08) | 45°20'7.91", -73°49'6.38" | A 2008 | 15 ^k | 31.9(2.5) | 50(<10) | 0 ⁿ | 1 ⁿ | E ⁿ | D, B | 10.64(4.70) |
| Léry (LE09) | 45°20'7.91", -73°49'6.38" | A 2009 | 15 | 30.8 | 50(<10) | 0.5(<0.1) | 2 | E | | 31.74(6.81) |
| Les Coteaux (LC05) ^j | 45°15'13.89", -74°12'43.67" | J 2005 | 12 ^m | 28.8(1.6) | | 0 | 0 | P | D, B | |
| Les Coteaux (LC08) | 45°15'13.89", -74°12'43.67" | A 2008 | 15 | 28.6(1.4) | 80(<10) | 1.9(<0.1) | 3 | M | D, B | 93.99(9.80) |
| Les Coteaux (LC09) | 45°15'13.89", -74°12'43.67" | A 2009 | 15 | 32.0(2.1) | 60(10) | 3.8(0.9) | 4 | L | D, B | 29.02(3.59) |
| Loyalist Park (LP08) | 44°52'30.17", -75°13'40.92" | A 2008 | 15 ^{k, l} | 29.4(1.3) | 50(10) | 6.0(2.3) | 6 | L | D, B | 52.92(9.52) |
| Loyalist Park (LP09) | 44°52'30.17", -75°13'40.92" | A 2009 | 15 | 32.3 | 40(10) | 7.0(0.8) | 7 | L | | 38.57(4.93) |
| Melocheville (ME05) ^j | 45°19'9.18", -73°55'39.79" | J 2005 | 10 | 29.6(1.9) | | 0 | 0 | P | D, B | |
| Melocheville (ME08) | 45°19'9.18", -73°55'39.79" | A 2008 | 15 | 30.7(1.6) | 100(0) | 0.7(0.1) | 2 | E | D, B | 27.50(4.39) |
| Melocheville (ME09) | 45°19'9.18", -73°55'39.79" | A 2009 | 15 | 29.6(0.7) | 100(<10) | 3.3(0.4) | 3 | M | D, B | 18.39(2.19) |
| Moulinette (MO08) | 45°1'49.91", -74°51'27.84" | S 2008 | 15 ^k | 30.3(2.8) | 20(10) | 3.0(0.9) | 5 | L | D, B | 7.95(3.87) |
| Moulinette (MO09) | 45°1'49.91", -74°51'27.84" | A 2009 | 15 | 36.0 | 10(<10) | 1.4(0.1) | 6 | L | | 7.06(0.90) |
| Parc Bertold (PB08) | 45°24'12.34", -73°55'30.10" | A 2008 | 15 | 12.0(1.6) | 70(10) | 0 | 0 | P | | 2.92(1.37) |
| Pine Park (PP08) | 45°26'21.73", -73°45'39.66" | A 2008 | 15 ^l | 13.9(2.0) | 100(<10) | 0 | 0 | P | | 1.28(0.79) |
| Pointe Claire (PC08) | 45°25'49.29", -73°49'5.12" | A 2008 | 15 | 13.3(0.4) | 60(<10) | 0 | 0 | P | | 5.51(1.97) |

Table 1 (concluded).

| Site (abbreviation) | GPS coordinates ^a | Time ^b | <i>n</i> | [Ca ²⁺] (mg·L ⁻¹) ^c | % cobble ^d | Goby density ^e (m ⁻²) | TI (years) ^f | IS ^g | D ^h | Algal biomass ⁱ |
|--------------------------------------|--------------------------------|-------------------|-----------------|--|-----------------------|--|-------------------------|-----------------|----------------|----------------------------|
| Pointe-du-Moulin (PD04) ^j | 45°21'57.86", -73°51'7.02" | S 2004 | 19 ^l | | | 0 | 0 | P | D | 27.20(3.82) |
| Pointe-du-Moulin (PD06) ^j | 45°21'57.86", -73°51'7.02" | S 2006 | 10 | | | 0 | 0 | P | D, B | 9.13(3.43) |
| Pointe-du-Moulin (PD08) | 45°21'57.86", -73°51'7.02" | A 2008 | 15 | 27.9(0.2) | 90(10) | 2.6(0.9) | 2 | M | D, B | 12.33(4.05) |
| Pointe-du-Moulin (PD09) | 45°21'57.86", -73°51'7.02" | A 2009 | 15 | 31.1(0.9) | 60(10) | 2.9(0.8) | 3 | M | D, B | 19.08(4.05) |
| Prescott (PR08) | 44°42'14.68", -75°31'9.58" | A 2008 | 15 ^k | 28.9(2.4) | 100(0) | 2.5(<0.1) | 6 | L | D, B | 41.38(7.34) |
| Prescott (PR09) | 44°42'14.68", -75°31'9.58" | A 2009 | 15 | 30.4 | 90(<10) | 3.6(0.9) | 7 | L | | 30.37(3.51) |
| Saint-Anicet (SA09) | 45°8'29.43", -74°21'38.61" | A 2009 | 15 | 26.4 | 70(10) | 2.8(0.7) | 4 | L | | 8.75(1.16) |
| Ste-Ann-de-Bellevue (SB08) | 45°24'10.02", -73°56'25.78" | A 2008 | 15 ^l | 12.1(0.9) | 70(10) | 0 | 0 | P | | 2.33(0.71) |
| Somerville (SO09) | 45°5'34.49", -74°25'42.17" | A 2009 | 15 | 27.2 | 100(<10) | 6.4(0.6) | 4 | L | | 26.53(4.06) |
| Soulanges B (SoB08) | 45°20'7.53", -73°57'15.62" | A 2008 | 15 ^k | 30.5(1.9) | 100(0) | 0 | 0 | P | D, B | 10.28(3.07) |
| Soulanges B (SoB09) | 45°20'7.53", -73°57'15.62" | A 2009 | 15 | 35.0 | 100(<10) | 0.1(0.1) | 1 | E | | 7.35(1.18) |
| Summerlea Pk (SP08) | 45°26'15.09", -73°42'57.11" | A 2008 | 15 | 17.3(4.7) | 60(10) | 0 | 0 | P | | 19.07(8.70) |
| Summerstown (SU08) | 45°2'45.72", -74°35'36.58" | S 2008 | 15 ^k | 30.7(1.7) | 50(10) | 3.8(0.4) | 5 | L | D, B | 73.07(12.15) |
| Summerstown (SU09) | 45°2'45.72", -74°35'36.58" | A 2009 | 15 | 27.6 | 50(10) | 4.1(1.9) | 6 | L | | 79.92(11.69) |

^aIn degrees, minutes, and seconds (WGS84 coordinate system; error ~30 m).

^bSampling month (J, July; A, August; S, September) and year shown.

^cConcentration for water samples taken at the site (standard error (SE) provided when two or three values from separate months were available).

^dMean percent cobble (SE).

^eFish density (m⁻²) values are means (SE).

^fTime since invasion, where 1-year presence indicates arrival of the invasion front in the sampling year.

^gInvasion stage (P, pre; E, early; M, mid; L, late).

^hData available (D, macroinvertebrate density; B, macroinvertebrate biomass).

ⁱMean benthic algal dry biomass (g·(m² rock surface area)⁻¹) (SE).

^jData from other sources. K. Harper and A. Ricciardi (unpublished data): CE05, LC05, ME05; Ward and Ricciardi (2010): PD04, PD06.

^kTen samples only analyzed for macroinvertebrate communities.

^lNumber of samples available for algal biomass: 14 at LAS08, LP08, PP08, and SB08; 9 at PD04.

^mNine samples available for macroinvertebrate biomass.

ⁿNo gobies observed during sampling; however, at CW08, gobies were present earlier in the summer and at LE08, goby eggs were found during sampling.

and mid-invasion sites all had gobies present for 2–3 years at densities >1.6 fish·m⁻² (Table 1).

Collection and analysis of benthic macroinvertebrates and algae

We conducted macroinvertebrate sampling in August and early September 2008 and 2009. Data from Ward and Ricciardi (2010) were collected in September, while unpublished data from K. Harper and A. Ricciardi were taken after 10 July. All samples were therefore collected in mid- to late summer, when macroinvertebrate communities typically develop high abundance and diversity in the upper St. Law-

rence River (Ricciardi et al. 1997; A. Ricciardi, unpublished data). A SCUBA diver haphazardly tossed a 0.25 m² quadrat to sample cobble 8 times along the first transect and 7 times along the second transect, yielding 15 cobble samples per site. Each cobble sample was carefully lifted from the substrate after placing doubled, sealable plastic bags around it (stones embedded in sediment were not sampled), and the bags were sealed quickly before being lifted from the bottom to prevent escape of swimming macroinvertebrates. Cobble samples were then transported in coolers back to the laboratory. Percent cobble was estimated visually per quadrat by counting the number of squares (each 10 cm × 10 cm) within

a 5 × 5 grid that contained cobble. Most sites had low current velocity such that a SCUBA diver would not have to swim continuously to remain stationary.

For each of the four sites resampled in 2009, macroinvertebrate analyses were performed on all 15 cobbles per site for both years. However, owing to time constraints, only 10 of the 15 cobbles were fully processed at the remaining 9 sites sampled exclusively in 2008. Sample sizes varied from 8 to 19 for 2004, 2005, and 2006 data (Table 1). The length, width, and height (in cm) of each rock were measured so that total surface area could be estimated (Dall 1979), to adjust numerical abundance and biomass data for area. Because we sampled only cobbles that were not embedded in finer substrate, the entire rock surface area (including the bottom surface) was available for colonization. In the laboratory, macroinvertebrates retained by a 500 µm sieve (Nalepa and Robertson 1981) were removed with forceps and placed immediately in 95% ethanol (no water from the sample was added). Each macroinvertebrate was identified to the lowest possible taxon with dichotomous keys under a dissecting microscope (50×) and assigned to the primary functional feeding group to which it belonged (Clarke 1981; Merritt and Cummins 1984; Pennak 1989). The functional feeding groups were classified as follows: insect algivores, gastropod scrapers, dreissenid filter-feeders, non-dreissenid filter-feeders, omnivores, predators, and deposit-feeders.

The 70% (2005 and 2006 data) or 95% ethanol wet mass (2008 and 2009 data) of each taxon was recorded per rock using an electronic balance (0.001 g). Samples from 2005 and 2006 remained in 70% ethanol for 3–4 years, while samples from 2008 and 2009 remained in 95% ethanol for 1–9 months before weighing. Ethanol preservation can affect macroinvertebrate biomass, but changes occur relatively quickly, and after 2–4 weeks in 70% ethanol further change is minimal (Howmillier 1972; Stanford 1973; Wetzel et al. 2005). We assessed the potential effects of storage in ethanol on relationships between biomass and goby density. For samples from 2008 and 2009 only, there was no correlation between goby density and \log_{10} -transformed mean number of months in ethanol ($p = 0.6$, $n = 17$). When the preinvasion samples from 2005 and 2006 were included, there was a significant negative relationship: $\log_{10} y = 1.11 - 0.13x$ ($R_{\text{adj}}^2 = 0.24$, $p = 0.01$, $n = 21$); in this case, the potential biomass change in ethanol occurred in the direction opposite to the expected effect of goby density. For all molluscs, wet masses included shells, following Jones and Ricciardi (2005) and Wilson and Ricciardi (2009). Recognizing that biomass loss of shelled invertebrates in ethanol would be proportionally smaller than biomass loss of taxa lacking shells, we analyzed shelled invertebrates in separate functional feeding groups (dreissenid filter-feeders and gastropod scrapers) from soft-bodied taxa (insect algivores and non-dreissenid filter-feeders).

Benthic algae were scraped from cobble surfaces using forceps and bristle brushes (Dudley et al. 1986), placed in individual plastic bags, and stored in a freezer at -20 °C. Upon thawing, algae samples were dried at 70 °C for 24 h, and the biomass was recorded (to 0.001 g). Dry biomass was adjusted for cobble area. We measured dry biomass (rather than ash-free dry mass) to be consistent with Ward and Ric-

ciardi (2010), whose data were used for comparison and were collected in a similar manner to the technique we employed.

Statistical analyses

All analyses were performed in R version 2.6.2, unless otherwise stated (The R Project for Statistical Computing, <http://www.r-project.org/>). We tested the effects of goby density on benthic community variables, including macroinvertebrate body size dominance, biomass, and diversity, as well as algal biomass, using regression analyses and including data collected over different years at the same site. To control pseudoreplication, generalized least squares (GLS) autoregressive models of order 1 were used for modeling temporally correlated error structures at sites that were sampled repeatedly over time (Zuur et al. 2009). GLS models were evaluated using log-likelihood ratio tests to ascertain whether they were a better fit to the data than simple linear regression models. We estimated the false discovery rate (FDR; Benjamini and Hochberg 1995) when multiple (≥ 10) tests were conducted on the same data.

Round goby impacts on community diversity, composition, and body size dominance

Changes to taxa richness and Shannon diversity across sites were determined by comparing rarefaction curves with 95% confidence intervals computed in EstimateS version 8.2.0 (Colwell 2006). When final error bars did not overlap, rarefaction curves were considered significantly different (cf. Wilson and Ricciardi 2009). Taxa richness and Shannon diversity were calculated for each level of sample pooling (one cobble sample), adding samples at random without replacement over 50 runs to calculate the mean and standard deviation. The effect of goby density on maximum taxa richness and maximum Shannon diversity was tested by regression analysis. Maximum taxa richness was extrapolated from curves fitted in EstimateS using a Michaelis–Menten type equation and employing maximum likelihood methods (Raaijmakers 1987; Colwell and Coddington 1994). Using this method, the estimate for the final sample pooling level was calculated analytically one time only. Final Shannon diversity was obtained from rarefaction curves that had reached apparent asymptotes (Colwell 2006).

To determine whether variation in substrate size (rock area) between years explained the observed differences in macroinvertebrate diversity, we used linear regression to test whether mean rock area across sites was confounded with goby density. One-factor analyses of variance (ANOVA) with type II sums of squares for unbalanced designs were used to test for variation in rock area amongst years at each resampled site. In the case of a significant result, Tukey's honestly significance difference tests were applied to determine between which years rock areas differed at a given site.

We conducted a constrained discriminant canonical analysis of principal coordinates (CAP) in PERMANOVA+ version 1.0.1 (Anderson et al. 2008) to test whether benthic macroinvertebrate community composition varied according to the four invasion stages. Rare taxa (defined as those present in fewer than three samples) were excluded. Bray–Curtis similarity values were calculated on square-root transformed density data (Clarke and Warwick 2001). In total, 999 iterations with cross-validation of each sample were per-

formed to calculate the misclassification error rate of the model. Taxa (Pearson correlation >0.2) were plotted on the first two CAP axes to visualize their associations with samples across invasion stages.

Abundance–biomass comparison (ABC) curves (Warwick 1986) were constructed in PRIMER 6 version 6.1.11 (Clarke and Gorley 2006) to determine whether non-dreissenid macroinvertebrate communities became increasingly dominated by relatively smaller-bodied organisms as goby density increased across sites in space and time. Species ranks on a \log_{10} -scale were placed on the x -axis, and percent cumulative abundance and biomass were placed on the y -axis for each site. The W statistic (Clarke 1990), or the scaled and summed difference between the two curves, was calculated in PRIMER. W takes into account the biomass dominance of a community relative to its dominance in terms of abundance and reveals the position of the community along a response continuum to a stressor without having to make a comparison to a reference condition (Warwick 1986; Yeman et al. 2005). W is positive when communities are dominated by larger-bodied taxa (i.e., cumulative biomass lies above cumulative abundance), which often occurs when such communities are free from negative stressors or disturbances. W becomes negative as communities are dominated by smaller-bodied taxa (i.e., cumulative abundance lies above cumulative biomass), which signifies the effect of negative stressors on larger-bodied, slower-growing organisms in the community. We excluded dreissenids from this particular analysis, because dreissenid biomass can be an order of magnitude greater than that of all non-dreissenid macroinvertebrates (e.g., Nalepa et al. 2003) and ABC curves may be sensitive to the dominance of a small minority of large taxa (Clarke 1990). In addition, we preferred to focus on changes in body size dominance in mobile macroinvertebrates living amongst dreissenid beds, given that mobile large-bodied macroinvertebrates are often those targeted by visual predators (Meissner and Muotka 2006; Herbst et al. 2009). W was calculated using means per site for all taxa, after adjusting for rock area. Effects of goby density on W were tested using regression. Major changes in the most dominant taxa by biomass and density across invasion stages were ascertained using G tests with Williams' correction for small sample sizes.

Round goby impacts on macroinvertebrate biomass

Using regressions with FDR correction, we determined whether goby density explained variation in the mean site-level biomass of macroinvertebrate functional feeding groups, as well as the mean site-level biomass of all non-dreissenid taxa. Taxa that were positively associated with the late-invasion stage in the CAP were excluded from the functional feeding group analyses to see whether the remaining taxa, as a group, responded negatively to gobies. We also tested for rank declines in the same measures of macroinvertebrate biomass from preinvasion (2004, 2005 and (or) 2006) to post-invasion years (2008 and 2009) in association with increasing goby density over time at four sites. One-tailed nonparametric Mann–Whitney tests with FDR correction were performed. Nonparametric tests were chosen because of the large number of zeros in the data set.

Indirect effects of round gobies on benthic algae

The association between goby density and site-level \log_{10} -transformed mean benthic algal biomass was tested using regression analysis of data from 2008 and 2009, respectively. Sites with $[\text{Ca}^{2+}] < 25 \text{ mg}\cdot\text{L}^{-1}$ were influenced by humic water from the Ottawa River (Fig. 1; see also Jones and Ricciardi 2005) and were relatively more turbid. Since water clarity could affect algal biomass and no turbidity measurements were available, $[\text{Ca}^{2+}]$ was used as a proxy variable for turbidity and was included with goby density in a multiple regression model for all sites and years. The inclusion of algal biomass data from the same site sampled in different years is justified because of strong temporal within-site variation: benthic algae exhibit seasonal die-offs, interannual variability in response to small fluctuations in nutrients, and seasonal variability in response to temperature (Hecky et al. 2004; Higgins et al. 2006). For Pointe-du-Moulin in 2004 and 2006, $[\text{Ca}^{2+}]$ was unavailable and was estimated from a mean value from previous years (2003 (Jones and Ricciardi 2005), 2008, and 2009), because this site receives only St. Lawrence River water that has consistently high $[\text{Ca}^{2+}]$ (Table 1). Changes to site-level \log_{10} -transformed mean algal biomass in relation to similarly transformed dreissenid, insect algivore, and gastropod scraper density were tested using multiple regression analysis.

Results

For all regression analyses, statistics for simple linear regression and GLS models are described in the supplemental materials (Supplemental Table S1¹). Hereafter, for clarity, GLS model results are mentioned only when they were a better fit than the simple linear regression model.

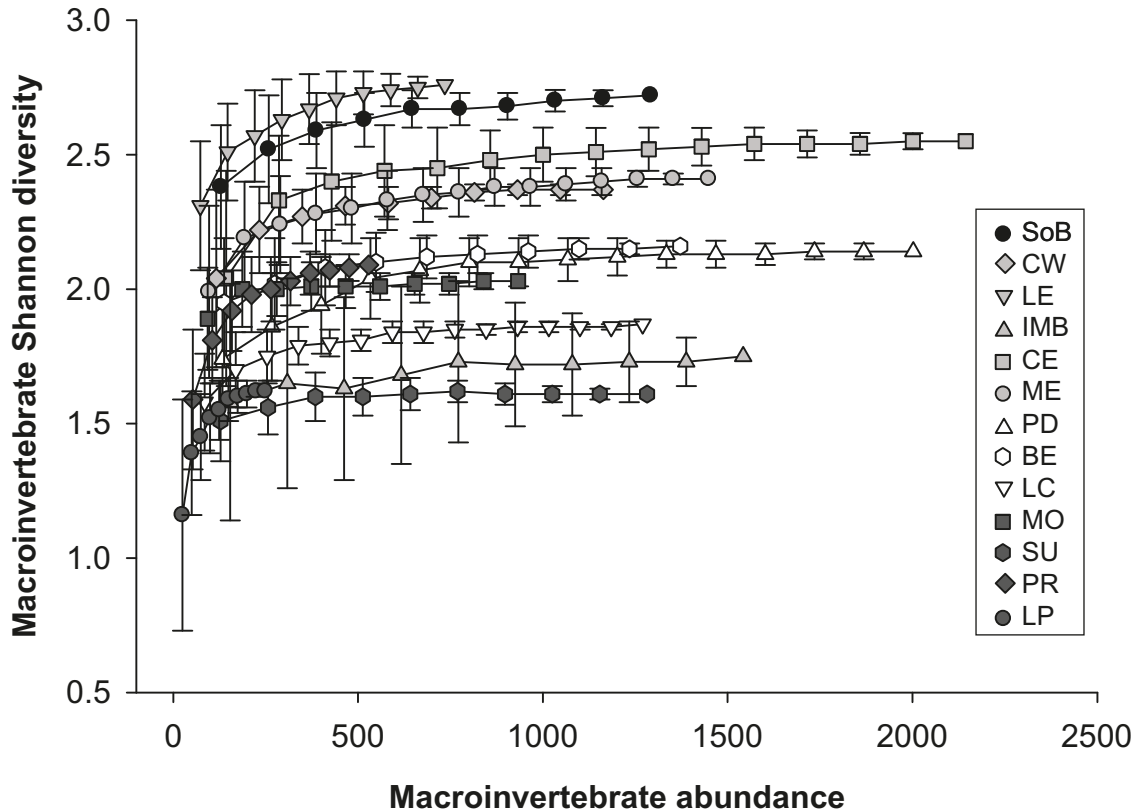
Round goby impacts on community diversity, composition, and body size dominance

Rarefied Shannon diversity varied across sites sampled in 2008 such that diversity measures were frequently lower for sites that were in later stages of invasion (Fig. 2). Rarefied taxa richness showed a similar trend. For three of four sites sampled over time (Châteauguay East, Les Coteaux, and Melocheville), rarefied taxa richness in 2009 was lower than in the preinvasion year. At Pointe-du-Moulin, rarefied taxa richness in 2009 was not different from either of the two preinvasion years (2004 and 2006) for which data were available. For all sites sampled over time, rarefied Shannon diversity in 2009 was lower than in preinvasion years. Maximum estimated taxa richness ($y = 43.31 - 3.26x$; $R_{\text{adj}}^2 = 0.28$, $p = 0.007$, $n = 22$) and final Shannon diversity (Fig. 3a: $R_{\text{adj}}^2 = 0.35$, $p = 0.002$, $n = 22$) were negatively correlated with goby density.

There was no relationship between goby density and mean rock area ($p > 0.9$, $n = 22$). Rock area did not vary across years at Pointe-du-Moulin (mean rock area \pm SE = $364 \pm 18 \text{ cm}^2$, $F = 1.01$, $p = 0.4$), Châteauguay East (mean rock area \pm SE = $345 \pm 26 \text{ cm}^2$, $F = 0.99$, $p = 0.4$), or Melocheville (mean rock area \pm SE = $330 \pm 26 \text{ cm}^2$, $F = 1.73$, $p = 0.2$). However, rock area differed amongst years at Les Coteaux ($F = 13.65$, $p < 0.0001$); cobble from 2008 (mean

¹Supplementary data are available with the article through the journal Web site (<http://nrcresearchpress.com/doi/suppl/10.1139/f2011-139>).

Fig. 2. Rarefied Shannon diversity curves for macroinvertebrate communities on cobble at 13 sites in 2008. Error bars indicate 95% confidence intervals. Invasion stages are represented as follows: preinvasion, black shapes; early invasion, light grey shapes; mid-invasion, white shapes; late invasion, dark grey shapes.



rock area \pm SE = 215 ± 28 cm²) was smaller than that from 2005 (mean rock area \pm SE = 424 ± 52 cm², $p = 0.0005$) and 2009 (mean rock area \pm SE = 413 ± 26 cm², $p = 0.0001$).

As predicted, W was generally negative at sites in mid- and late-invasion stages (where goby densities were >2.5 fish·m⁻²). W was lower in 2009 in comparison to that in the preinvasion year at the four sites sampled over time, excluding Les Coteaux. Comparisons between preinvasion conditions and 2008 varied more (see Supplemental Fig. S1¹ for details). In spite of this variability, W decreased as a function of goby density (Fig. 3b: $R_{adj}^2 = 0.21$, $p = 0.02$, $n = 21$). There was no evidence that the taxa dominating macroinvertebrate density were associated with invasion stage ($G = 9.61$, $p = 0.1$, $n = 21$), although sites in the late-invasion stage were the only ones where freshwater mites (Acari) were most frequently dominant. Other dominant taxa in different invasion stages included crustaceans and insects. In contrast, the taxa that dominated macroinvertebrate biomass varied with invasion stage (Fig. 4: $G = 14.25$, $p = 0.03$, $n = 21$). Gastropods dominated biomass at sites in the pre-invasion and early-invasion stages, whereas insects most frequently dominated biomass at sites in the mid- and late-invasion stages.

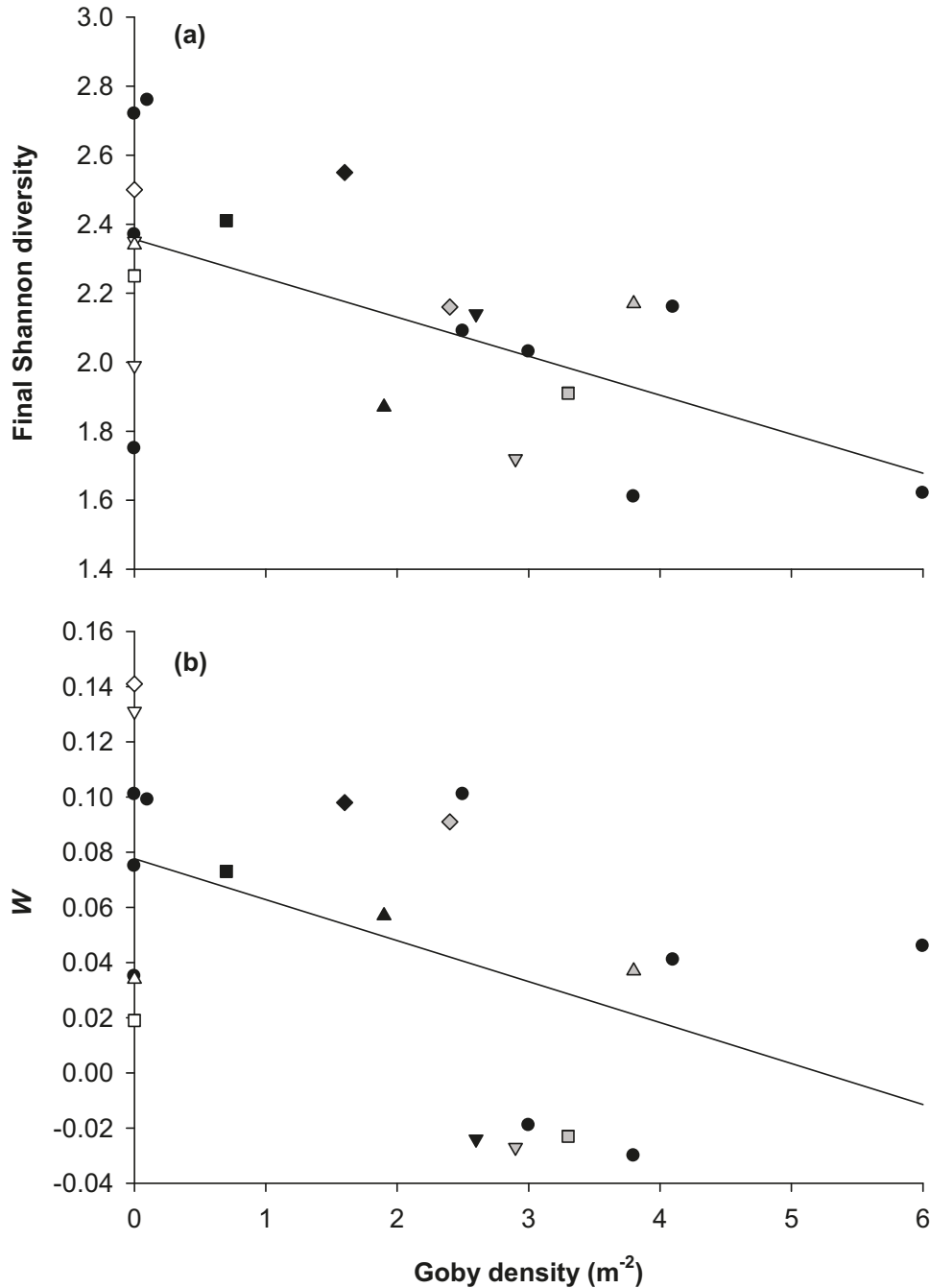
The four invasion stages described macroinvertebrate community composition well (Fig. 5a: trace statistic = 1.73, $\delta_1^2 = 0.81$, $p = 0.001$, n permutations = 999, n samples = 269, misclassification error rate = 17.1%). Furthermore, of the 46 (of 269) misclassified samples, only 6 were incorrect by two

or more invasion stages. The first axis ($\delta_1 = 0.90$) discriminated best between preinvasion and mid- to late-invasion samples, while the second ($\delta_2 = 0.76$) discriminated best between early-invasion samples and those in other invasion stages. Eight gastropod taxa were associated most with preinvasion samples, while the pleurocerid snail *Elimia livescens* was associated most with early-invasion samples (Fig. 5b). Only two taxa, the mayfly (*Caenis*) and mites, were associated most with late-invasion samples.

Round goby impacts on macroinvertebrate biomass

In order not to obscure hypothesized negative relationships of most taxa with gobies, *Caenis* and Acari were excluded from the deposit-feeder and predator functional feeding groups, respectively, because the CAP (Fig. 5b) indicated that these two groups were positively associated with the late-invasion stage. Filter-feeders other than dreissenids occurred at such low abundances that they were not analyzed. Macroinvertebrate predator biomass (Fig. 6a: $R_{adj}^2 = 0.57$, $p < 0.0001$, $n = 21$) decreased with goby density. For gastropod biomass, the GLS model was a better fit to the data ($p = 0.04$) and showed that gastropod biomass decreased significantly with goby density (Fig. 6b: $t = -6.51$, $p < 0.0001$, $n = 21$). The biomass of total non-dreissenid macroinvertebrates also exhibited a strong negative relationship with goby density (Fig. 6c: $R_{adj}^2 = 0.59$, $p < 0.0001$, $n = 21$). Even when the site with highest goby density, Loyalist Park, was excluded from any of these tests, the regressions remained significant. Omnivore and dreissenid biomass also

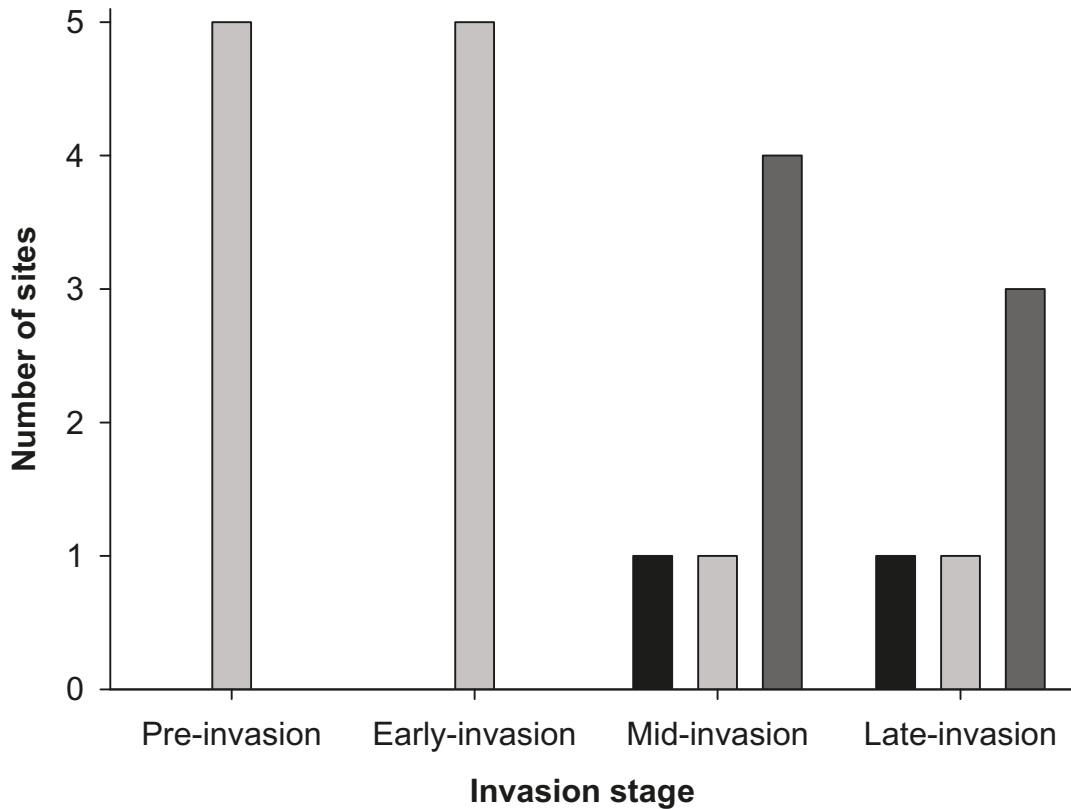
Fig. 3. (a) Final Shannon diversity as a function of goby density. Line fit by least-squares regression: $y = 2.36 - 0.11x$ ($R_{\text{adj}}^2 = 0.35$, $p = 0.002$, $n = 22$). If LP08, the site with highest goby density, is excluded, the result remains significant ($R_{\text{adj}}^2 = 0.25$, $p = 0.01$, $n = 21$). (b) The W statistic, or the scaled and summed difference between cumulative abundance and biomass curves, as a function of goby density. W is positive when the biomass curve lies above the abundance curve and negative when the opposite is true, indicating dominance by larger-bodied organisms in the former case and by smaller-bodied organisms in the latter. Line fit by least-squares regression: $y = 0.08 - 0.01x$ ($R_{\text{adj}}^2 = 0.21$, $p = 0.02$, $n = 21$). If LP08 is excluded, the regression remains significant ($R_{\text{adj}}^2 = 0.29$, $p = 0.008$, $n = 20$). Open shapes are sites sampled prior to invasion, black shapes are 2008 sites, and grey shapes are 2009 sites. Circles are different 2008 sites, diamonds are CE, triangles facing up are LC, squares are ME, and triangles facing down are PD.



tended to decline with goby density. However, these relationships were not significant either upon exclusion of Loyalist Park or with FDR correction (see Supplemental Table S1 for details¹). No correlations were found between goby density and biomass of either algivorous insects or deposit-feeders ($p > 0.1$ in both cases).

Gastropod biomass showed rank declines in 2008 and 2009 in comparison to preinvasion years at three of four sites sampled over time, while declines for biomass of dreissenids, predators, and omnivores were less consistent overall (Fig. 7). Total biomass decreased in rank in 2008 and 2009 at Melocheville, Les Coteaux, and Pointe-du-Moulin relative

Fig. 4. Number of sites for which the most dominant taxon by biomass belonged to different taxa, organized by invasion stage. The association between invasion stage and dominant taxon type is significant ($G = 14.25$, $p = 0.03$). Taxa are represented as follows: black, Crustacea; light grey, Gastropoda; dark grey, Insecta.



to preinvasion years for which data were available, while it did not at Châteauguay East.

Indirect effects of round gobies on algae

Algal biomass was related to goby density across sites in 2008 (Fig. 6d; $R_{adj}^2 = 0.25$, $p = 0.01$, $n = 21$) but not in 2009 ($p = 0.2$, $n = 17$). In a linear multiple regression model, both $[Ca^{2+}]$ ($p = 0.002$) and goby density ($p < 0.05$) explained variation in algal biomass ($R_{adj}^2 = 0.39$, $p < 0.0001$, $n = 40$). Significant variation was not explained by the inclusion of densities of dreissenids ($p = 0.6$), insect algivores ($p = 0.5$), or gastropod scrapers ($p = 0.6$) in a multiple regression model.

Discussion

Round goby impacts on the macroinvertebrate community as a whole

Our analyses revealed major alterations to the composition, diversity, and biomass of macroinvertebrate communities following round goby invasion. The CAP had an allocation success rate of 82.9%, which is substantially higher than the rate expected by chance (25%) for a model with four discriminant categories (Anderson et al. 2008). Preinvasion and early-invasion samples were clearly different in species composition from mid- and late-invasion samples, especially in terms of gastropod taxa.

Moreover, community diversity indices changed substantially with goby invasion. The effect of goby density on

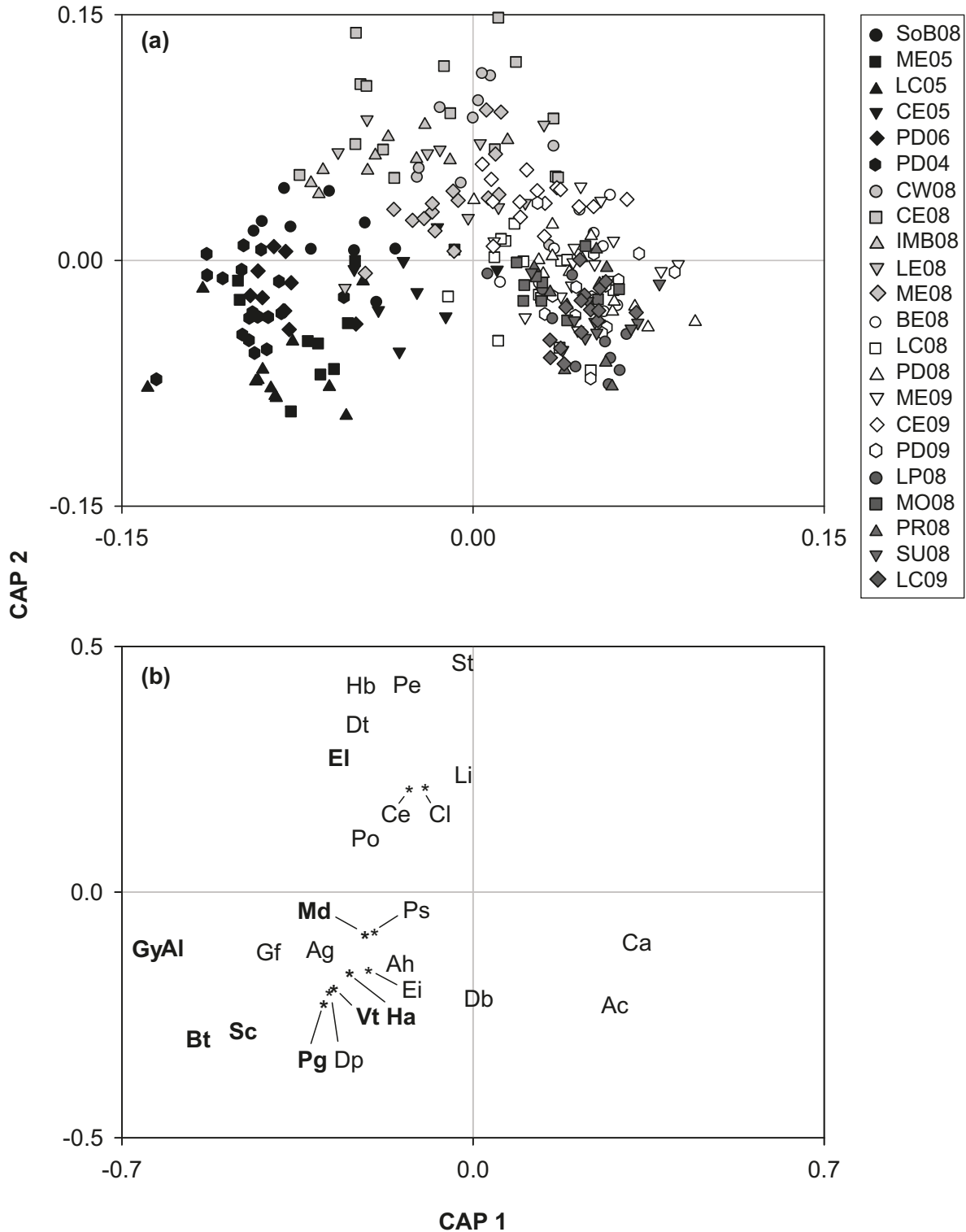
diversity was unlikely to be confounded by species-(rock) area effects, given that there was no relationship between goby density and mean rock area per site. Overall, these results agree with a study on streams in the Lake Erie watershed where Shannon diversity was reduced in the presence of round gobies (Krakowiak and Pennuto 2008).

We observed consistent declines in total non-dreissenid biomass across sites as well as at three of four sites sampled before and after invasion. The anomalous site in this analysis, Châteauguay East, was where gobies were present for the shortest length of time and at the lowest density of the four resampled sites. In addition, samples from this site in 2005 (K. Harper and A. Ricciardi, unpublished data) might have been taken too close to the wave-swept zone, where communities are relatively depauperate. Indeed, this site contributed the most samples misclassified by two or more invasion stages in the CAP. It is striking that consistent patterns in total non-dreissenid biomass occurred across sites despite the inclusion of Châteauguay East. Only one other study has measured changes to total non-dreissenid biomass following round goby invasion, and it also recorded a decline (Kuhns and Berg 1999).

Round goby impacts on body size dominance

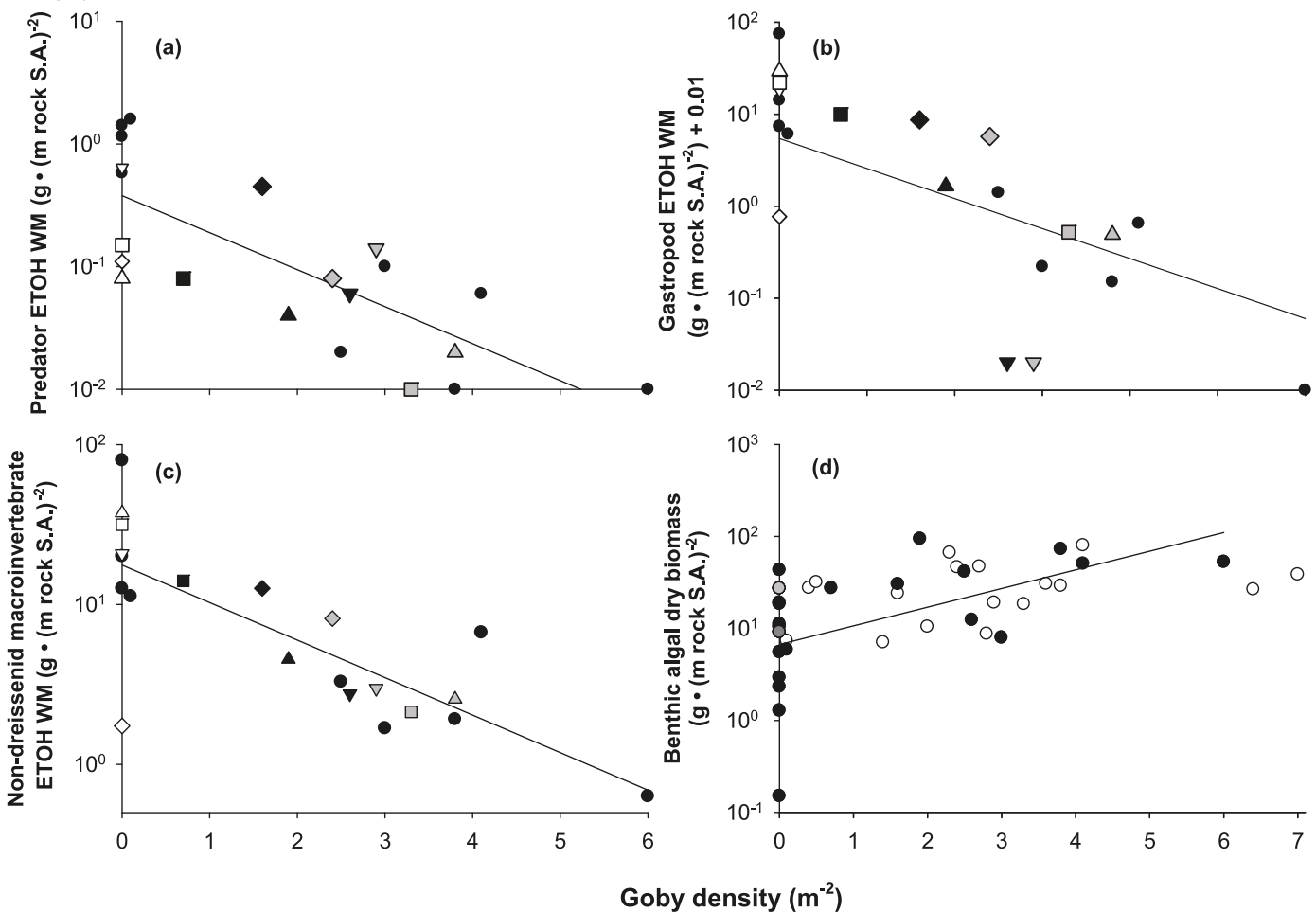
Body size dominance, represented by the W statistic, declined across sites with increasing goby density, and by 2009 it was reduced in comparison to preinvasion conditions at three of four sites sampled over time. We note that at the sites and times for which W was negative, goby densities

Fig. 5. (a) Cobble samples in x - y space after a discriminant canonical analysis of principal coordinates. Samples organized as follows: black shapes, preinvasion stage; light grey shapes, early-invasion stage; white shapes, mid-invasion stage; dark grey shapes, late-invasion stage (trace statistic = 1.73, $\delta_1^2 = 0.81$, $p = 0.001$, n permutations = 999, $n = 269$, misclassification error rate = 17.1%). (b) Loading values for taxa with Pearson correlation >0.2 ($n = 26$ out of 73). Taxa are represented as follows: Ac, Acari; Ag, *Agraylea*; Ah, *Alboglossiphonia heteroclita*; Al, *Ammicola limosa*; Bt, *Bithynia tentaculata*; Ca, *Caenis*; Ce, non-sponge-feeding *Ceraclea* spp.; Cl, *Cloeon*; Db, *Dreissena bugensis*; Dp, *Dreissena polymorpha*; Dt, *Dugesia tigrina*; Ei, *Echinogammarus ischnus*; El, *Elimia livescens*; Gf, *Gammarus fasciatus*; Gy, *Gyraulus* spp.; Ha, *Helisoma anceps*; Hb, *Helicopsyche borealis*; Li, *Lirceus*; Md, *Marstonia decepta*; Pe, *Petrophila*; Pg, *Physella gyrina*; Po, *Polycentropus*; Ps, *Psychomyia*; Sc, *Stagnicola catascopium*; St, *Stenelmis*; and Vt, *Valvata tricarinata*. Bold characters emphasize gastropods.



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Fig. 6. (a) Macroinvertebrate predator (excluding Acari) preserved wet mass (WM); (b) gastropod preserved WM; (c) total non-dreissenid preserved WM; and (d) benthic algal dry biomass in response to goby density. In (a) to (c), preserved wet masses are in ethanol (ETOH). In all cases, biomass is corrected per square metre of rock surface area (S.A.). For (a), (c), and (d), lines were fit by least-squares regression: (a) $\log_{10} y = -0.42 - 0.30x$ ($R^2_{\text{adj}} = 0.57$, $p < 0.0001$, $n = 21$); excluding LP08: $R^2_{\text{adj}} = 0.52$ ($p = 0.0002$, $n = 20$); (c) $\log_{10} y = 1.25 - 0.23x$ ($R^2_{\text{adj}} = 0.59$, $p < 0.0001$, $n = 21$); excluding LP08: $R^2_{\text{adj}} = 0.49$ ($p = 0.0004$, $n = 20$); (d) $\log_{10} y = 0.83 + 0.20x$ ($R^2_{\text{adj}} = 0.25$, $p = 0.01$, $n = 21$; 2008 data only). For (b), the line was fit by generalized least-squares regression: $\log_{10}(y + 0.01) = 1.12 - 0.49x$ ($t = -6.51$, $p < 0.0001$, $n = 21$); excluding LP08: $t = -5.29$ ($p < 0.0001$, $n = 20$). Regressions on macroinvertebrate biomass remained significant upon FDR correction, beginning with $1/24 \times 0.05$. For (a), (b), and (c), open shapes are preinvasion sites, black shapes are 2008 sites, and grey shapes are 2009 sites. Circles are different sites sampled in 2008, diamonds are CE, triangles facing up are LC, squares are ME, and triangles facing down are PD. For (d), data from 2008 are represented as black circles; from 2009 as white circles; from 2004 as light grey circles; and from 2006 as dark grey circles.



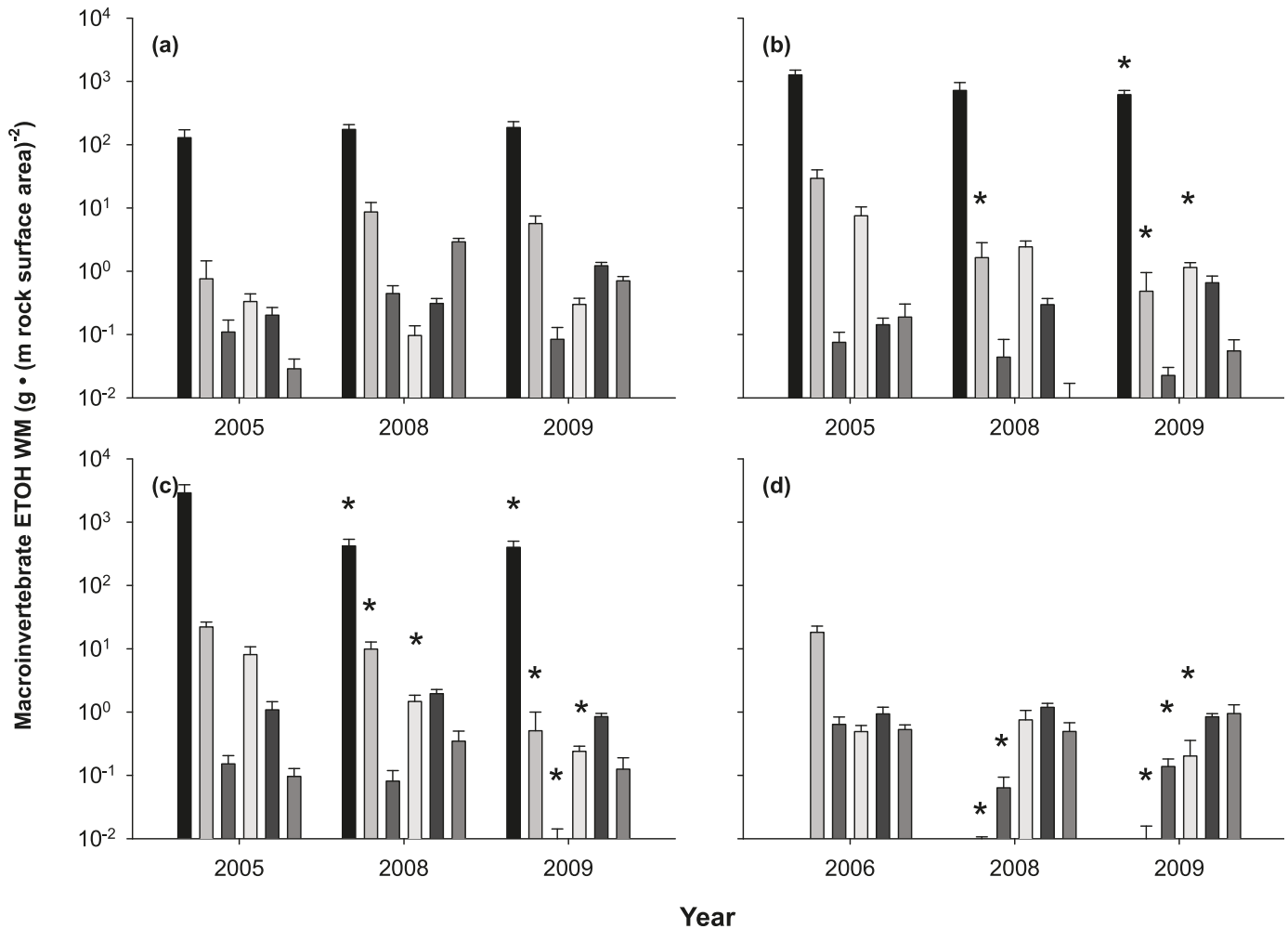
ranged from 2.6 to 4.0 fish·m⁻², while three sites with goby densities of 3.8–6.0 fish·m⁻² unexpectedly had positive values of W . In four out of five instances where W was negative, the most dominant taxon in terms of biomass was chironomids, while the caddisfly *Nectopsyche* dominated in the fifth instance. When goby density was high and W was positive, chironomids dominated biomass in only one case. In the remaining cases, the amphipod *Gammarus fasciatus* and the caddisfly *Nectopsyche* dominated biomass. Therefore, in most cases at goby densities >2.5 fish·m⁻², chironomids become the most dominant taxon by biomass, and W is typically negative. When biomass dominance is replaced by a taxon other than chironomids, the response of W is sometimes positive, perhaps because these other taxa are larger than chironomids in body size. Indeed, changes to W often occur because of shifts in community dominance of one

taxon in relation to others (Warwick and Clarke 1994). As there was a clear decline in biomass dominance of gastropod taxa from preinvasion and early-invasion stages to mid- and late-invasion stages, it seems most likely that declines in W in this study reflect a shift in dominance from large-bodied gastropods to smaller-bodied taxa, particularly chironomids, as a result of selective goby predation. This conclusion is supported by another study that measured a decline in the median size of gastropods with increasing goby density across the same St. Lawrence River sites; this size shift was linked to selective predation by gobies (suggested by diet analysis; Kipp et al. 2011).

Round goby impacts on different functional feeding groups

Our study showed generally consistent effects of gobies on

Fig. 7. Preserved ethanol (ETOH) wet mass (WM) per square metre of rock surface area of functional feeding groups prior to invasion (2005 and 2006) and after invasion (2008 and 2009), for (a) CE, (b) LC, (c) ME, and (d) PD. Asterisks indicate significant declines from the pre-invasion conditions based on one-tailed Mann–Whitney tests at the $\alpha = 0.05$ level upon FDR correction (starting with $1/54 \times 0.05$). Functional feeding groups are represented, in order, as follows: black, filter-feeding dreissenids; second lightest grey, gastropod scrapers; second darkest grey, predators; lightest grey, omnivores; darkest grey, deposit-feeders; medium grey, algivorous insects. Error bars indicate standard error.



gastropods through time and space. Eight gastropod species were associated with samples in the preinvasion category in the CAP, while a ninth, *E. livescens*, is a relatively large and thick-shelled species that was rarely consumed by gobies in Lac Saint-Louis in 2009 (Kipp et al. 2011). This snail was associated with early-invasion samples, apparently experiencing negative impacts of gobies later into the invasion than the other gastropod taxa. Negative effects of gobies on gastropod density have been observed in the Great Lakes, either owing to direct consumption or indirect negative effects through goby destruction of dreissenid beds (Lederer et al. 2006, 2008). In our study, changes to dreissenids were less consistent than changes to gastropods, so it is likely that the latter resulted from selective goby predation (Kipp et al. 2011).

Impacts on predators, excluding freshwater mites, were substantial across sites and became evident at some sites over time. Freshwater mites, in contrast, were associated most with late-invasion samples. These taxa feed predominantly on larval Diptera (Pennak 1989; Di Sabatino et al. 2000). Chironomids, the majority of dipterans available, were apparently unaffected by gobies, and there was no neg-

ative impact on deposit-feeders as a functional feeding group (comprising 83% chironomids by biomass). Freshwater mites were therefore probably not subjected to a loss in their principal prey. No study in the Great Lakes has examined the effects of gobies on the macroinvertebrate predator functional feeding group as a whole, although the only significant taxon-level effect in the experiments by Kuhns and Berg (1999) was on the predatory caddisfly *Oecetis*. In Lac Saint-Louis in 2009, gobies were not found to consume any predatory macroinvertebrates except certain caddisflies (Kipp et al. 2011). Impacts on macroinvertebrate predators other than caddisflies were therefore likely driven by declining prey availability. For example, the leech *Alboglossiphonia heteroclita* was correlated with samples from preinvasion sites in the CAP; this predator feeds predominantly on gastropods, isopods, and oligochaetes (Wrona and Calow 1988), and gastropods in particular were negatively associated with gobies. The decline in macroinvertebrate predators across sites, and at some sites over time, suggests that gobies can truncate benthic food webs through competition with macroinvertebrate predators for prey.

It was surprising to find inconsistent effects of gobies on the density and biomass of omnivores, insect algivores, and dreissenids, as most taxa in these groups have undergone substantial impacts in the Great Lakes attributable to goby predation (Kuhns and Berg 1999; Barton et al. 2005; Lederer et al. 2006). A goby's ability to capture prey such as amphipods (which constitute 99.9% of omnivores, by density, in this study) is affected largely by refugia, water clarity, and habitat complexity (Diggins et al. 2002; González and Burkart 2004; Kestrup and Ricciardi 2009). Variation in these factors across the Great Lakes – St. Lawrence system should thus generate variable impacts. Low goby densities of 0–6 fish·m⁻² at our sites (compared with densities as high as 14–15 fish·m⁻² in the Great Lakes; Kuhns and Berg 1999; Barton et al. 2005) may also explain the lack of detectable impacts on certain taxa. Dreissenids may also have escaped substantial predation because of goby preference for other prey, combined with smaller fish size (and therefore limited gape size) in this study in comparison to that observed in the Great Lakes. Total lengths of gobies at sites in Lac Saint-Louis in 2009 ranged up to 104 mm (Kipp et al. 2011), while gobies in the Great Lakes frequently grow to ~180 mm in length (Barton et al. 2005).

Evidence of a trophic cascade?

A trophic cascade occurs when predation limits herbivory and herbivory limits primary producers such that primary producers increase in the presence of predators (Flecker and Townsend 1994; Townsend 1996). In this study, gobies apparently reduced gastropods, although there was no detectable effect on insect algivores. Omnivorous crustaceans such as amphipods (Summers et al. 1997) and crayfish (Creed 1994) may also consume benthic algae and thus might contribute to a trophic cascade. In this study, amphipods did not decline significantly as goby density increased, although amphipod species were associated most with rocks sampled at preinvasion sites. We observed the presence of crayfish across St. Lawrence River sites but did not quantify their abundances. Although there were no strong relationships between algivores and benthic algae, there was a positive correlation between goby density and benthic algae across all sites even after accounting for changes in water clarity. If the largest change in algal biomass occurs from preinvasion to postinvasion conditions, the lack of preinvasion sites in 2009 could explain why the goby–algae correlation observed for 2008 data was not significant for 2009.

Trophic cascades may result from the inhibition of foraging behaviour of dominant algivores by the presence of an introduced predator (McIntosh and Townsend 1996; Diehl et al. 2000; Nyström et al. 2003). Such an indirect trait-mediated interaction (Schmitz et al. 2004) would not require a link between algivore abundance and algal biomass, nor even one between predator and algivore abundance — although in our study there was evidence for this relationship between gobies and gastropods. If refugia are available, algivorous invertebrates may spend less time on substrates exposed to fish (Stewart et al. 1999; Turner et al. 1999) and thus less time foraging, particularly when predators are at high densities (Richardson and Brown 1992). Thus, gobies may have affected algivorous insects' foraging behaviour without changing their abundance.

In spite of some small-scale negative effects of dreissenids on benthic algae (Ward and Ricciardi 2010), positive effects are generally considered most common (Hecky et al. 2004; Wilson et al. 2006; Higgins et al. 2008). In this study, there was no relationship between dreissenids and benthic algae, and there were no consistent relationships between gobies and dreissenids. In the two studies that detected negative goby–algae relationships (Lederer et al. 2006; Wilson et al. 2006), gobies apparently reduced either the density or the size structure of dreissenids. For example, Lederer et al. (2006) found consistent impacts of gobies both on dreissenids and most non-dreissenid macroinvertebrates; their study indicated that a positive association between dreissenids and benthic algae was larger than any negative correlation between algivores (snails) and algae. In the only experimental study in which a trophic cascade has been detected (Kuhns and Berg 1999), gobies exerted negative impacts on dreissenids occurring on high-density tiles (10⁵ m⁻²) and not on low-density tiles (10⁴ m⁻²). The authors did not report whether the relative magnitude of the effect of gobies was larger on dreissenids or on algivores. In our study, the negative impact of gobies on algivorous gastropods, in particular, was consistently larger than that on dreissenids.

The palatability of benthic algae might account for differential effects of algivores at different locations. Wilson et al. (2006) measured percent cover of *Cladophora* and Lederer et al. (2006) measured total algal biomass, comprising mainly *Cladophora*. In our study, all benthic algae were collected, and although some sites were dominated by *Cladophora* (Pointe-du-Moulin in 2004 and 2006; Ward and Ricciardi 2010), algal species composition varied greatly across sites. We did not attempt to identify individual taxa, but detected at least four distinct morphotypes during sample collection. Scraping rock surfaces of all algae likely captured the large majority of benthic macroalgae and microalgae (the latter of which frequently grow epiphytically on the former; Dodds 1991; Marks and Power 2001), including those that are more palatable to algivorous macroinvertebrates. Kuhns and Berg (1999) measured algal abundance as chlorophyll *a* concentration, by removing algae from 25% of their experimental tiles without discriminating between macroalgae and microalgae or different species. Thus it is possible that trophic cascades reflect the ability of algivores to control benthic algae that are more palatable than *Cladophora*, which is avoided by most algivores once it is mature (Dodds 1991; Feminella and Resh 1991; Haynes et al. 1999).

Limitations of the study

An obvious limitation is the heterogeneity in data sets employed to test our hypotheses in this study. Sampling techniques and seasons for macroinvertebrate collections at preinvasion sites in 2004, 2005, and 2006 varied in comparison to those used in 2008 and 2009, possibly affecting some results. Nevertheless, we believe that in all cases where our results might have been influenced by this heterogeneity, the expected trends were potentially reduced in magnitude and never exaggerated. For example, at Pointe-du-Moulin, taxa richness did not differ in 2009 compared to preinvasion conditions; this might be because the preinvasion experimental substrates (bricks) were all of equivalent size, shape, and surface roughness and lacked sufficient microhabitat heterogene-

ity to support an assemblage as diverse as would occur on natural rock substrates (Douglas and Lake 1994). Furthermore, we used online software (<http://www.degree-days.net>, which uses temperature data from <http://www.wunderground.com>) to calculate the number of cooling degree-days for a base temperature of 0.0 °C at Montreal airport in different years for which data existed. For 2004, 2006, 2008, and 2009, the number of degree-days at which sampling took place was very close in time, ranging from around 2600 to 2800. For 2005, the number of degree-days at which sampling took place was approximately 1800. Therefore, 2005 macroinvertebrate assemblages could have been smaller or less diverse than later in the summer, when maximal biomass and diversity are typically achieved. However, because all 2005 data served as preinvasion data, if sampling had taken place later in the season, the apparent impact on biomass and diversity would likely have been magnified.

Given the correlative nature of this study, in no instance is any observed relationship between goby density (or time since invasion) and a community metric necessarily causal. Our study did not quantitatively address other environmental factors (such as food availability, habitat variables, and current velocity) that could influence macroinvertebrates, gobies, and algae. We attempted to limit the heterogeneity of such variables by focusing sampling at sites with similar flow velocities and substrates (presence of cobble habitats conducive to abundant macroinvertebrate and goby communities); nevertheless, owing to difficulties associated with site access, we were not always capable of sampling sites with these same attributes. All sites sampled had little to no exposure to current, except Pointe-du-Moulin, Lasalle, and Saint-Ann-de-Bellevue, where current speeds were appreciable. Lasalle and Saint-Ann-de-Bellevue served as sites where only macroalgal biomass was sampled, while Pointe-du-Moulin served as a site at which both macroalgae and macroinvertebrates were sampled. However, we believe that current speed would not have confounded relationships of macroinvertebrates with goby density or time since invasion, because gobies appear to either be little affected by flow rates or prefer low-flow habitats (Marsden et al. 1996; Tierney et al. 2011), and gastropods, which were most negatively affected by gobies, also generally prefer low-flow habitats (Clarke 1981). Furthermore, changes over time in the benthic community at Pointe-du-Moulin were still comparable to those at low-flow sites such as Melocheville and Les Coteaux.

The proportion and surface roughness (interstitial habitat) of cobble varied across sites. These substrate characteristics could have exerted an effect on both gobies and macroinvertebrates and conceivably could have affected our estimation of algal biomass. However, it is unlikely that they confounded or biased our results, because it is expected that they similarly influenced gobies (Ray and Corkum 2001) and macroinvertebrates (Ricciardi et al. 1997; Ward and Ricciardi 2010).

Finally, rock area between years at resampled sites did not vary except at Les Coteaux, where rocks collected in 2008 were smaller than those collected in 2005 and 2009. This difference could have contributed to observed changes in macroinvertebrate metrics between 2005 and 2008, but not between 2005 and 2009. The difference in rock area between years suggests that this site's substrate was highly heterogenous.

The Les Coteaux site was unusual because its shallow near-shore zone was much larger in area, and thus possessed a greater range of substrate size, than any other site we sampled.

Implications of the study

Our study revealed substantial changes to benthic community composition, biomass, and diversity in the upper St. Lawrence River correlated with the recent round goby invasion. These changes include severe declines in the biomass of gastropods (likely via direct predation) and most predatory macroinvertebrates (potentially via indirect effects of declining prey availability). Overall, size structure of macroinvertebrate communities was significantly altered in later stages of goby invasion, such that there was a depletion of larger-bodied macroinvertebrates, particularly gastropods. Negative impacts of gobies on algivorous macroinvertebrates may have triggered an increase in benthic algal biomass across sites. This evidence points to an ongoing transformation of benthic communities and trophic interactions in the river. Given that benthic macroinvertebrates are essential to the diets of a large number of fishes in this region (Latour et al. 1980; Boisclair and Leggett 1989; Boisclair and Rasmussen 1996), strong local reductions in benthic macroinvertebrate communities by an expanding round goby population could exert negative effects on other fishes, including some threatened molluscivores (e.g., see COSEWIC 2004, 2006).

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