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Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour

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ABSTRACT

The invasive round goby, *Neogobius melanostomus*, consumes eggs and fry of other fishes, competes for resources with native fish species, and hence poses a threat to Great Lakes aquatic communities. We provide the first description of round goby demographic patterns in Hamilton Harbour, in the western tip of Lake Ontario, and the connected Cootes Paradise Marsh, a recently restored wetland. By monitoring round goby populations on a variety of distinct habitats for 7 years (2002–2008), we found that populations have declined at all sample locations and that average fish body size also has decreased. We also related abundance, body size, and reproductive patterns to seasonality, to substrate types (mud, sand, cobble and boulder) and to water quality in all locations. Round gobies were found on all substrates sampled including mud, although they were less abundant on mud than on other substrates, and to date have not extensively colonized Cootes Paradise Marsh. Our work confirms previous studies, which have suggested that habitats lacking hard structures will have fewer round gobies because they lack substrates on which round gobies can breed. However, our results also indicate that muddy and sandy substrates are not resistant to round goby invasion and will not prevent round goby colonization, a potential concern for Cootes Paradise Marsh an important spawning, nursery, and refuge habitat for warmwater native fishes and for other similar wetlands.

Introduction

Round gobies are native to the Black and Caspian Seas (Berg, 1949) and were accidentally introduced to North America via ballast water in the early 1990s (Jude et al., 1992). They have subsequently spread to all five of the Great Lakes faster than any previously introduced fish species (Charlebois et al., 2001; Dillon and Stepien, 2001). Round gobies were first detected in Lake Ontario in 1998 (Mills et al., 2003) and by June 2002 they were one of the most frequently caught species in the littoral zone in Hamilton Harbour (Balshine et al., 2005).

The abundance of round gobies in Hamilton Harbour is of particular concern because the harbour is attached by a narrow man-made channel, Desjardins Canal, to Cootes Paradise Marsh, a large wetland and important breeding ground for native fishes in Lake Ontario (Fig. 1; Holmes, 1988; Lougheed et al., 2004). Cootes Paradise was previously one of the most degraded areas in the Great Lakes (Holmes, 1988), but ongoing restoration (such as extensive planting of native species, and the construction of a fishway/barrier to exclude common carp *Cyprinus carpio*) has improved the physical habitat and stemmed the decline of native species such as yellow perch, *Perca flavescens* (Brousseau and Randall, 2008; Holmes, 1988). Previous research has shown that round gobies can negatively impact other species of fish in part by eating their eggs and young (Chotkowski and Marsden, 1999; French and Jude, 2001; Steinhart et al., 2004a). As well, several studies have shown that, as round gobies have increased in density, other species such as mottled sculpin, *Cottus bairdii* (Janssen and Jude, 2001) and caddisfly, *Oecetis* spp. (Trichoptera; Kuhns and Berg, 1999) have declined. In recent years, in an effort to improve conditions so that Hamilton Harbour might be delisted as an Area of Concern by 2015 (International Joint Commission, 1999), a fisheries management plan (Bowlby et al., 2009) has been created to help support a sustainable and productive fish community. Large round goby populations in Hamilton Harbour and Cootes Paradise Marsh could compromise native fish breeding success as well as the goals of the Hamilton Harbour Remedial Action Plan (RAP; Hall et al., 2006) and other restoration efforts.

In both their native and introduced habitats, round gobies have been found on many different substrate types including rock, coarse gravel, sand, on shell beds, and among macrophytes (Clapp et al., 2001; Jude and DeBoe, 1996; Miller, 1986). A number of studies suggest that round gobies prefer structurally complex, hard, rocky habitats, with ample shelter for breeding (Miller, 1986; Vanderploeg

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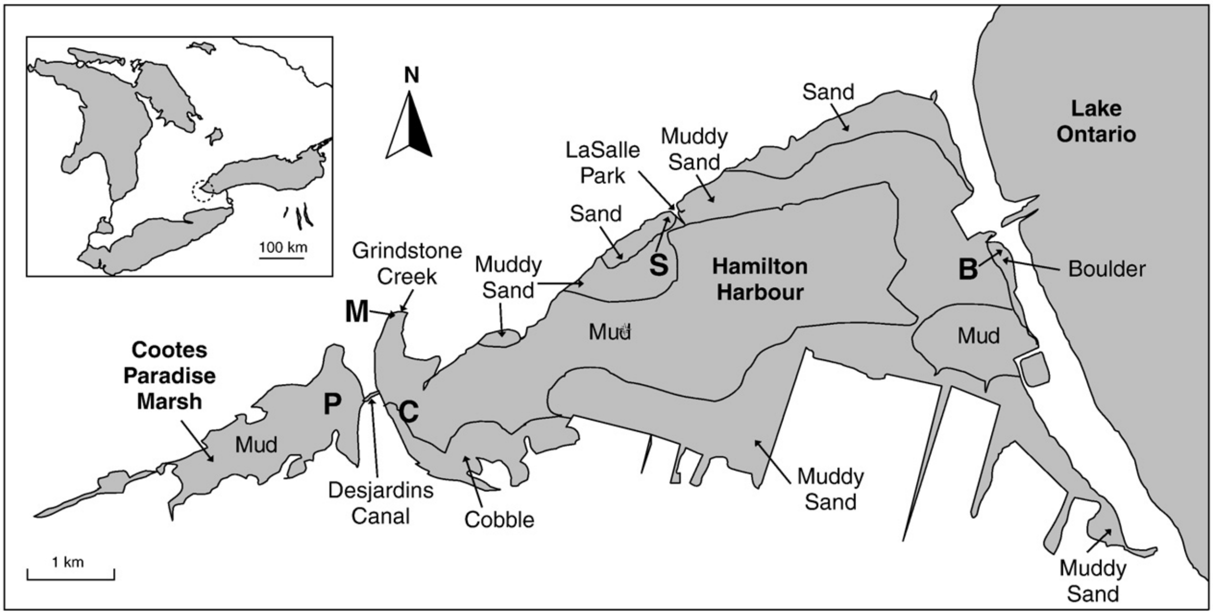

Fig. 1. A map of Hamilton Harbour (43°N, 79°W) with the sampling locations and substrate types indicated. M refers to sites sampled with mud substrate, S refers to sites sampled with sand substrates, C refers to sites that were sampled with cobble substrates, B to sites with boulder substrates, and P refers to sampling sites in Cootes Paradise Marsh.

et al., 2002). In lakes Michigan and Erie, adult round gobies were most abundant on rock while juvenile round gobies were found to be more abundant on sandy substrates, and it has been argued that adult round gobies will displace juveniles from favored, structurally complex habitats onto open, sandy substrates (Charlebois et al., 1997; Ray and Corkum, 2001). However, a recent study, near Pelee Island, Lake Erie, found round gobies to be as abundant on mud as on rock (Johnson et al., 2005). To date, explicit laboratory tests for substrate preference have not been conducted, but such preferences, or lack thereof, could influence the speed and success of the round goby range expansion.

The aims of this study were threefold. 1) To track changes in the abundance of the round goby in Hamilton Harbour over the course of its Lake Ontario invasion (2002–2008). 2) To compare abundance across four different substrate types: mud, sand, cobble, and boulder. 3) To examine how the body size of round gobies varied over time and season, and across the various substrate types. As our study began not long after the round goby was first detected in Hamilton Harbour (in 1999, OMNR, 2000), we hypothesized that round goby populations would initially increase and then eventually stabilize as they reached saturation (Begon et al., 1996). We also considered the possibility that populations might even decline as predators adapted to the presence of a new food source (Jaksic, 1998; Reusch, 1998). We also hypothesized that round gobies would prefer, and be most common on, hard, complex substrates on which they could deposit and guard eggs (e.g., boulder and cobble) and where they could best hide from predators. Finally, we hypothesized that these hard substrate habitats would harbour the largest round gobies, as these individuals could exclude smaller round gobies from preferred sites (Ray and Corkum, 2001).

Methods

Demography and habitat affinity

Round gobies in Hamilton Harbour were sampled from 2002 to 2008 and collected at least twice each month from May to October, with the exception of 2003 when sampling occurred only once each month. In all seven years we used baited minnow traps set out at four sites around Hamilton Harbour. Each site represented a different substrate type: mud, sand, cobble, and boulder (Fig. 1), defined by particle size following the substrate scale proposed by Krumbein and Sloss (1951). Substrate was measured using either a measuring tape (cobble, boulder), or a stage micrometer on a dissecting microscope (mud, sand). Boulders ($N=10$) were on average 137 cm long, 127 cm wide and 48 cm high. The average size of the cobble ($N=10$) was 19.6 cm (length) × 14.2 cm (width) × 10.1 cm (height). Sand grains ($N=20$) were on average 733 µm in diameter, and mud particles ($N=8$) measured on average 29 µm in diameter. The sampling sites used were identical from year to year. At each site, two (2002–2004) or four (2005–2008) minnow traps, baited with approximately 25 g of frozen corn, were placed on the benthos 8–9 m from the shore, in water 60- to 100-cm deep. Although some mark recapture studies have reported capturing gobies up to 67 m from the initial point of tagging (Wolfe and Marsden, 1998), one study that specifically addressed high site fidelity in round gobies reported a minimum home range of approximately 5 m^2 (Ray and Corkum, 2001). Based on the information from this latter study, traps were placed at least 10-m apart. All fish captured in each trap were collected 24-hr later. Additionally, traps (two in 2003–2004 and eight in 2005–2007) were placed in Cootes Paradise Marsh (at the eastern end of the marsh closest to the mouth of the Desjardins Canal; see Fig. 1). Water quality was assessed at each site and on each sampling occasion (2004–2008) by monitoring water temperature, dissolved oxygen, pH (with a YSI 550A field meter), and water clarity (using a Secchi disk).

All round gobies caught were counted, sexed, and measured. The sex of each fish was determined by visually examining the urogenital papilla between the anus and the base of the anal fin (Miller, 1984). Fish that could not be sexed were recorded as juveniles. The standard lengths of the fish were measured to the nearest mm. Body mass was measured by drying the fish with a towel and placing it on a portable digital balance, accurate to 0.1 g. Body condition was determined using Fulton's body condition index ($10^5 \times$[body mass (g) / standard length (mm)^3]; Ricker, 1975). Gonad mass was measured from 2004 to 2008, and the gonadosomatic index (GSI) was calculated ($100 \times$[gonad mass (g)] / [body mass (g) − gonad mass (g)]; Schreck and Moyle, 1990). Fish were considered to be in reproductive condition if their GSI exceeded 8% (for females) or 1% (for males), as these represent minimum GSI values found for reproductive round gobies in other studies (Gammon et al., 2005; MacInnis, 1997; Marentette and Corkum, 2008).

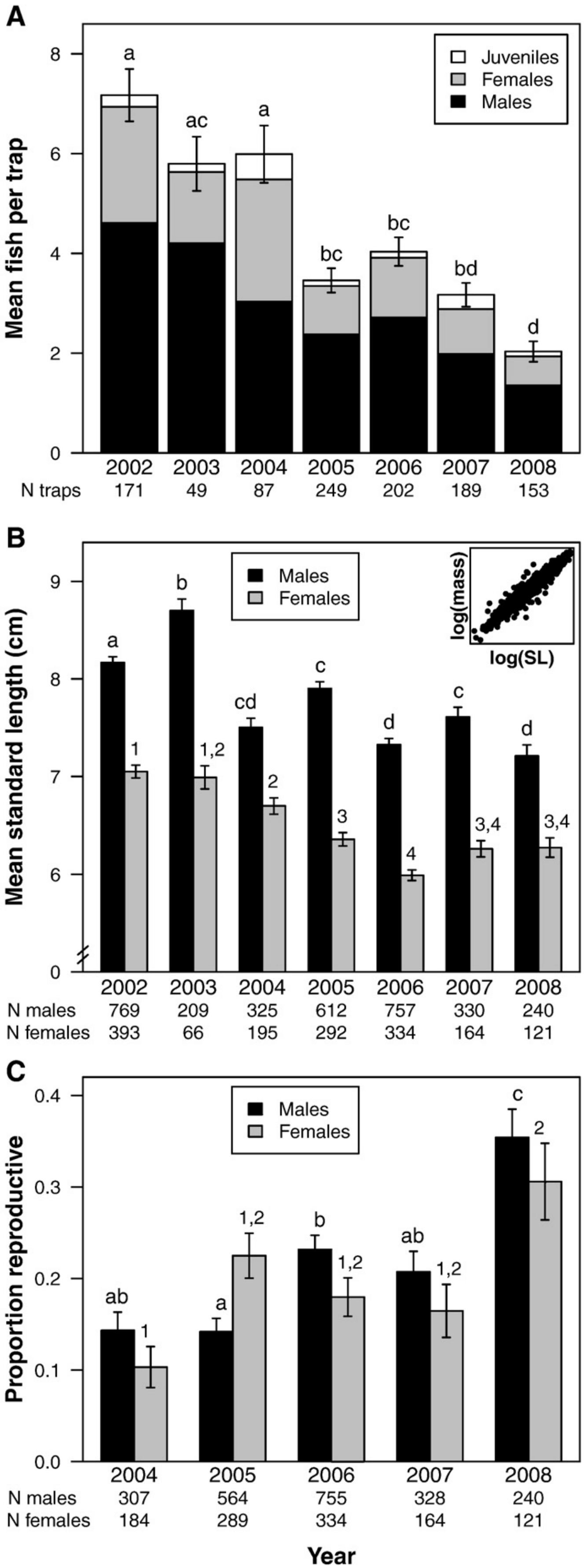

Fig. 2. (A) Mean number (±SE) of round gobies/trap by year of collection, all four substrates combined. Juveniles could not be sexed, and so are included in abundance figures only. Letters the bars show statistical significance; bars that do not have a letter in common differ significantly at $p<0.05$ (based on multiple all-pair *post hoc* comparisons with Bonferroni corrections). (B) Mean (±SE) standard length in cm of both males and females by year of collection, with all four substrates combined. Means shown have been reverse-transformed to show original body lengths. Bars that do not have a letter (for males) or number (for females) in common differ significantly at $p<0.05$ (based on multiple all-pair *post hoc* comparisons with Bonferroni corrections). Inset: The relationship between fish standard body length and body mass (log-transformed). (C) The proportion of fish (±SE) that were reproductive in each year of collection. Fish were considered reproductive if their GSI exceeded 1% (males) or 8% (females). Statistical significance is denoted as in panel b.

Table 1
Mean fish caught per trap by year and substrate type.

Substrate	2002	2003	2004	2005	2006	2007	2008
Mud	4.2	3.3	5.8	1.5	1.7	0.9	0.5
Sand	6.3	6.3	3.9	4.8	5.8	3.9	2.8
Cobble	8.2	4.9	6.8	4.1	4.9	4.1	3.1
Boulder	9.7	7.7	7.5	3.9	3.8	3.6	1.8

Statistical analyses

Statistical tests were performed using the statistical programming language R, version 2.7.1. Data were checked for normality, transformed whenever necessary and parametric statistics were used whenever possible, i.e., where assumptions for parametric tests (normality and sample homoscedasticity) were met. Standard length data was log-transformed and body mass was transformed with log (mass + 1). Males and females were compared using χ^2 tests for abundance statistics, *t*-tests for standard length and body mass, and Mann–Whitney *U* tests for body condition. Abundance (count) data were fit to a quasi-Poisson general linear model (GLM), and percent data to a binomial GLM (logistic regression; Fox, 2002, pp. 155–190; Agresti, 2002). Type II, 3-factor ANOVAs were performed on all parametric statistics using the R-package "car" (Fox, 2008) with year, site, and month as factors. Type II ANOVAs are preferable to use when there is an unbalanced design. They test the significance of each term in the model after all others, except for the term's "higher-order relatives" (i.e., they follow the principle of marginality; Fox, 2008). Multiple all-pair *post hoc* comparisons were performed using the R-package "multcomp" (Hothorn et al., 2008) with Bonferroni corrections for simultaneous inference. Kruskal–Wallis tests were used for body condition, GSI, water temperature, and clarity data (as these could not be normalized), and these tests were followed by multiple comparison between treatments (Siegel and Castellan, 1988, p. 213). All tests were two-sided, and were considered significant at *p* values less than or equal to 0.05.

To account for sampling irregularities such as trap theft, drift, or breakage, fish per trap was used as the measurement of abundance. The traps were placed in identical locations each week and each year for the abundance study. Occasionally, extra traps were set at the four sites (away from the abundance study traps) to collect fish for experiments. These fish were excluded from the abundance counts but were measured and included in analysis of morphological data. Hence, the sample sizes for body characteristics and abundance were not identical.

Results

Patterns across years

During the 7 years of study, a total of 4617 round gobies were caught in Hamilton Harbour. There was a 72% decline in mean fish per trap between 2002 and 2008, and this decline was linear (Fig. 2A, Table 1; 3-factor ANOVA, overall model: $F_{77,\ 1022}=7.0$, $p<0.0001$; effect of year: $F_{6,\ 1022}=30.2$, $p<0.0001$; linear trend analysis on year:

Table 2
Mean body measurements by year and by gender.

Body measurement		2002	2003	2004	2005	2006	2007	2008
Standard length (cm)	Males	8.2	8.7	7.5	7.9	7.3	7.6	7.2
	Females	7.1	7.0	6.7	6.4	6.0	6.3	6.3
Body mass (g)	Males	12.6	16.1	11.3	12.7	10.5	10.9	10.1
	Females	7.9	8.6	7.9	6.3	5.6	6.0	6.4

$F_{1,\ 1093} = 135.5$, $p < 0.0001$; see Maxwell and Delaney, 2004, pp. 243-274 for further statistical details on linear trend analyses).

Of the fish caught, 4403 could be sexed. The remaining 214 fish were sexually immature and recorded as juveniles. More males ($n_{\text{males}} = 2979$) were caught than females (Fig. 2A; $n_{\text{females}} = 1424$, chi-square test: $\chi^2 = 549.2$, $df = 1$, $p < 0.0001$), giving an overall sex ratio of approximately two males for every female. Indeed 71% of the catches were male-biased (of a possible 396 sampling occasions, 280 resulted in a male-biased catch, where an 'occasion' includes all fish caught at one site on a given day, $\chi^2 = 67.9$, $df = 1$, $p < 0.001$). Despite the overall decline in fish numbers, the sex ratio (number of male fish/female fish) remained strongly male-biased and relatively constant over time apart from one year (2004) when the male bias was less extreme (Fig. 2A; test for constant proportion across years: $\chi^2_{2004} = 5.5$, $df = 1$, $p = 0.02$; χ^2 for all other years > 47.0, $p < 0.0001$).

Round gobies caught in Hamilton Harbour averaged 74.4 ± 0.2 mm [mean ± SE] in standard length (range 31–132 mm) and 12.0 ± 0.1 g in body mass (range 0.6–64.8 g). Overall, males were longer, heavier, and in better condition than females (Table 2; two-sample *t*-tests, $n_{\text{males}} = 3241$, $n_{\text{females}} = 1564$: standard length, $t = 28.9$, $p < 0.0001$; body mass, $t = 30.1$, $p < 0.0001$; body condition, $t = 5.2$, $p < 0.0001$). Body mass and length were highly correlated (Fig. 2B, inset; linear regression: $R^2 = 0.96$, $p < 0.0001$). The decline in overall round goby abundance was mirrored by a decline in body size; there was a 10% decrease in standard length and a 16% reduction in body mass between 2002 and 2008 (Table 2, Fig. 2B, standard length shown; effect of year, male standard length: $F_{6,\ 3164} = 36.2$, $p < 0.0001$; female standard length: $F_{6,\ 1487} = 37.9$, $p < 0.0001$). The downward trend in body size was confirmed in both males and females by a linear regression (standard length and body mass versus year of capture, $p < 0.001$ for males and females). While body size and abundance of round gobies decreased over time, the proportion of reproductive fish was higher in 2008 than in 2004 (Fig. 2C; 3-factor ANOVA with data fit to a binomial GLM, testing for constant reproductive proportions across years, for males: $n = 2195$: $\chi^2 = 31.8$, $df = 4$, $p < 0.0001$; for females: $n = 1094$: $\chi^2 = 12.8$, $df = 4$, $p = 0.01$).

Patterns across the breeding season

Round goby abundance did not differ across the months that were sampled (Fig. 3A inset; effect of month: $F_{5,\ 1022} = 1.1$, $p = 0.38$).

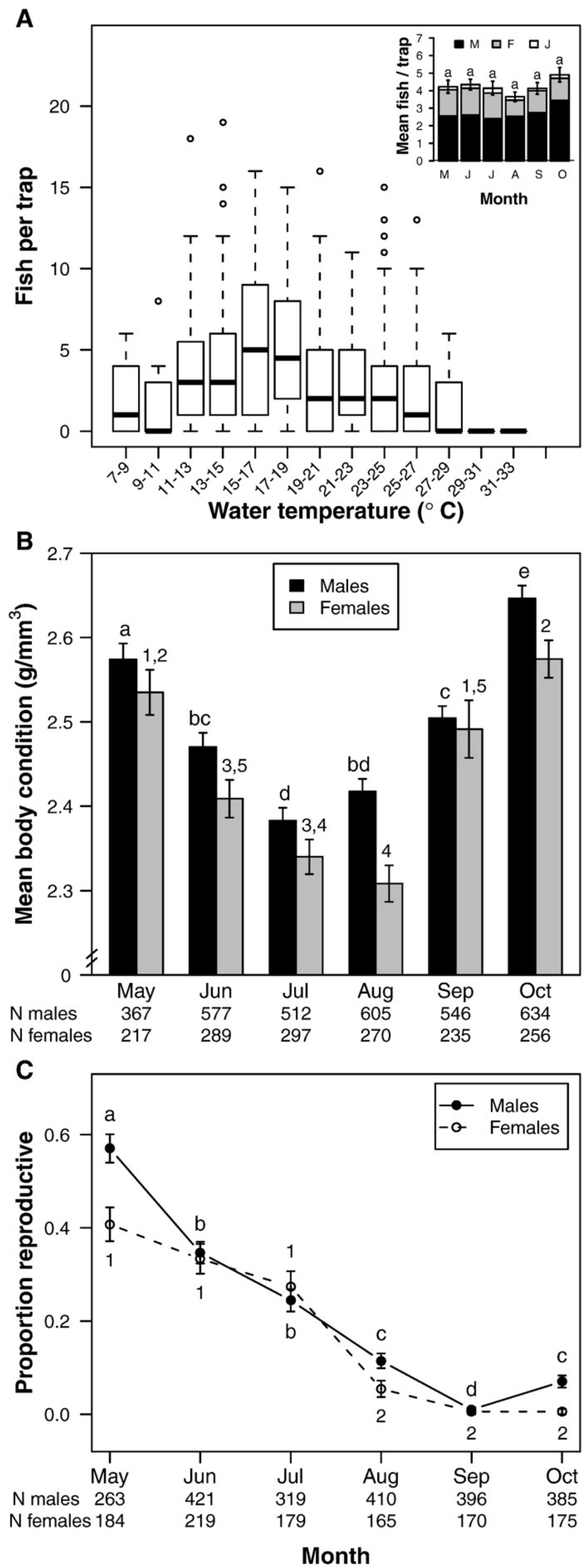

Fig. 3. (A) Boxplots of number of round gobies caught in each trap by water temperature at time of collection. Boxes show medians and 25th/75th percentile. Dashed lines extend to the most extreme data point which falls within 1.5 times the interquartile range. Outliers (values beyond this range) are shown with open circles. Temperatures are binned into 2-degree intervals (ex. (7–9), (9–11), etc.). Temperature was related to abundance ($R^2 = 0.026$, $F_{1,\ 841} = 22.14$, $p < 0.0001$), and including the term (temperature)^2 significantly improved the fit ($R^2 = 0.055$; comparison of models: $F_{1,\ 841} = 25.9$, $p < 0.0001$), suggesting a quadratic (parabolic) function relates temperature to catch rate. Inset: mean number (±SE) of round gobies/trap by month of collection, years, and substrates combined. Statistical significance is denoted as in Fig. 2A. (B) Mean (±SE) fish body condition (Fulton's index: $10^5 \times [\text{g/mm}^3]$) by month of collection. Means shown have been reverse-transformed to show values in the original scale. Males differed from females in condition in June ($p = 0.03$), August ($p < 0.0001$), and October ($p = 0.007$). Bars that do not have a letter (for males) or a number (for females) in common differ significantly at $p < 0.05$ (based on Kruskal-Wallis *post hoc* comparisons). (C) Proportion of all fish that were reproductive (when GSI exceeded 1% for males or 8% for females) in each month of collection. Statistical significance is denoted as in panel B.

Temperature, however, was significantly related to fish abundance (Fig. 3A; effect of temperature, controlled for year, site, month: $F_{1, 829}=4.2$, $p=0.04$), with the highest catch rates in waters between 15 and 17 °C. A strong seasonal pattern was observed in body condition; fish of both sexes tended to be lightest and in poorest condition just after the peak of the breeding season (June–August) and were heaviest and in the best condition early in the season (May) as well as late in the season in September/October (Fig. 3B; male body condition: Kruskal–Wallis test, $H=239.0$, $n=3241$, $p<0.0001$; female body condition: $H=130.7$, $n=1564$, $p<0.0001$). There were also seasonal changes in reproductive patterns; the proportion of reproductive fish (males and females) decreased steadily from May to September, increasing again slightly in October in males (Fig. 3C; testing for constant reproductive proportions across month, data fit to a binomial GLM, for males: $\chi^2=426.3$, $df=5$, $p<0.0001$; for females: $\chi^2=218.3$, $df=5$, $p<0.0001$).

Patterns across substrate types

Fewer round gobies were captured on mud than on boulder, cobble, or sand (Fig. 4A; effect of substrate: $F_{3, 1022}=41.8$, $p<0.0001$). The observed decline in round goby abundance occurred on all substrates in Hamilton Harbour with the smallest decline on sand, and the largest decline on boulder (Table 1). In total, 199 round gobies were caught in Cootes Paradise Marsh, and the average number of fish/trap (0.8 ± 0.1, mean ± SE) was significantly lower than the average number of fish/trap (2.0 ± 0.2, mean ± SE) caught on mud habitats within Hamilton Harbour (Fig. 4A; Mann–Whitney *U* test: $W=42650$, $p<0.0001$). Furthermore, most fish caught in the marsh were found in traps near the mouth of the canal leading to the harbour.

The overall population male sex bias was apparent on sand, cobble and boulder habitats. On these substrates, at least two males were caught for every one female (Fig. 4A; $df=1$, all χ^2 values > 159.6, and all p values < 0.0001). More males than females were also caught on mud, but the bias was less extreme (1.5 males to every female caught: $\chi^2=22.4$, $df=1$, $p<0.0001$). In Cootes Paradise Marsh, for every female caught, there were 1.9 males caught ($\chi^2=18.6$, $df=1$, $p<0.0001$).

Fish captured on mud and boulders in Hamilton Harbour were smaller, lighter, and in worse body condition compared to fish from sand and cobble (Fig. 4B, standard length shown; effect of substrate: male standard length $F_{3, 3164}=16.5$, $p<0.0001$; male body mass $F_{3, 3166}=18.5$, $p<0.0001$; male body condition, Kruskal–Wallis test: $H=73.6$, $n=3241$, $p<0.0001$; female standard length: $F_{3, 1487}=19.5$, $p<0.0001$; female body mass: $F_{3, 1488}=20.2$, $p<0.0001$; female body condition: $H=24.0$, $n=1563$, $p<0.0001$). Interestingly, female round gobies caught in Cootes Paradise Marsh were some of the largest and heaviest females caught (Fig. 4). Conversely, male round gobies caught from Cootes Paradise Marsh were among the smallest and lightest males caught. The proportion of females that were reproductive did not vary across substrates (Fig. 4; testing for constant reproductive proportion across substrate, binomial GLM: $\chi^2=6.56$, $df=4$, $p=0.16$), but a higher proportion of males found to be

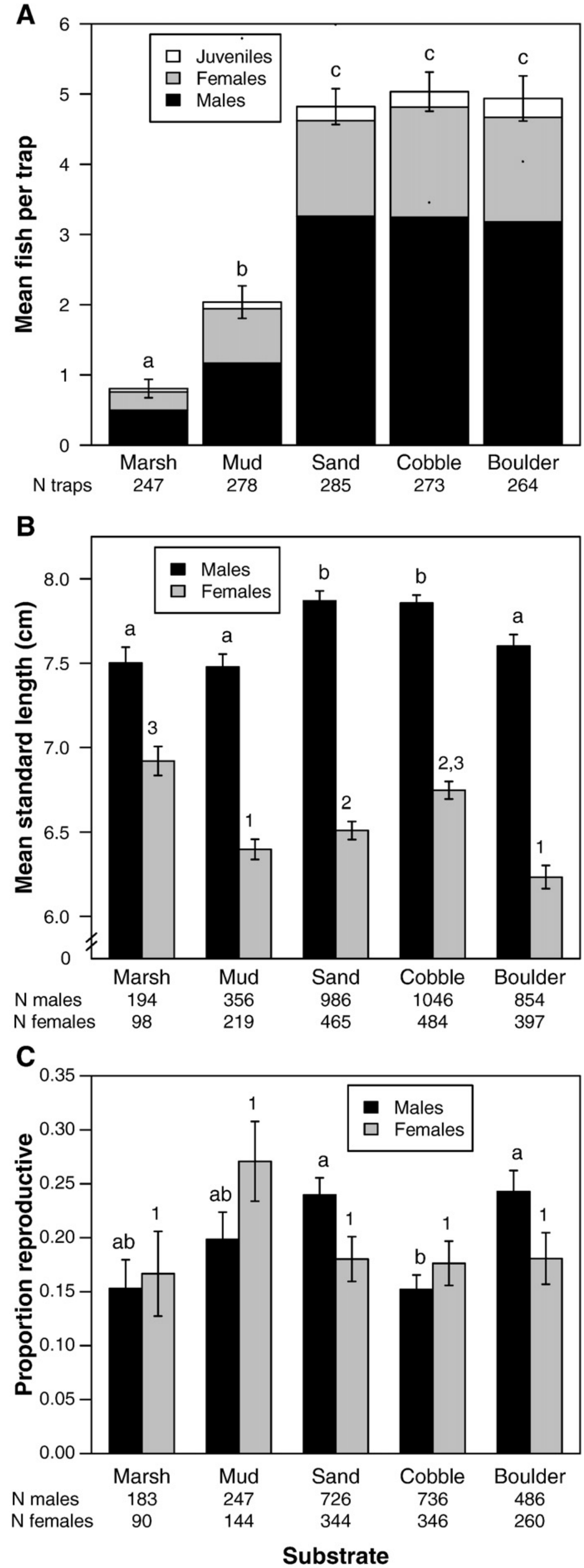

Fig. 4. (A) Mean (± SE) number of round gobies per trap caught on various substrates in Hamilton Harbour and Cootes Paradise Marsh. Bars that do not have a letter in common differ significantly at $p<0.05$ (based on multiple all-pair *post hoc* comparisons with Bonferroni corrections). (B) Mean (± SE) standard length in cm of males and female round gobies across substrate types. Bars that do not have a letter (for males) or a number (for females) in common differ significantly at $p<0.05$ (based on multiple all-pair *post hoc* comparisons with Bonferroni corrections). The picture is similar for both mass and body condition. (C) Proportion of fish that were reproductive (when GSI exceeded 1% for males or 8% for females) by substrate type. Bars that do not have a letter in common differ significantly at $p<0.05$ (based on multiple all-pair *post hoc* comparisons with Bonferroni corrections).

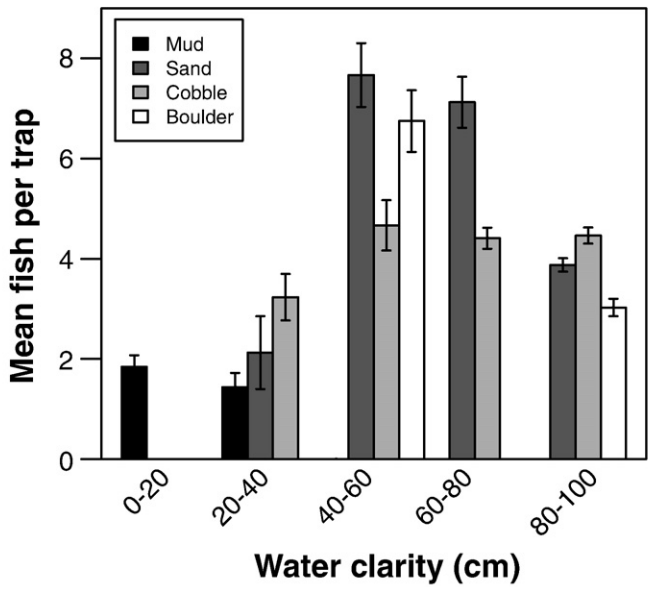

Fig. 5. Mean number (±SE) of round gobies per trap by substrate and clarity of water (in cm) at time of collection, as measured using a Secchi disk.

reproductive on boulder and sand compared with cobble ($\chi^2=20.4$, $df=4$, $p<0.001$).

Water temperature, pH, and dissolved oxygen levels did not differ between substrates/locations (data pooled across years; temperature: Kruskal–Wallis test, $H=7.3$, $df=3$, $n=320$, $p=0.06$; dissolved oxygen: $F_{3,166}=0.89$, $p=0.45$; pH: $F_{3,94}=1.1$, $p=0.36$). Water clarity, however, did vary across sites (Fig. 5; Kruskal–Wallis test, $H=185.6$, $n=310$, $p<0.0001$); it was least clear on mud and clearest on sand and boulder. Temperature correlated with fish abundance (Fig. 3A), but neither pH nor dissolved oxygen explained the variance in fish abundance (pH: $R^2<0.0001$, $F_{1,\ 308}=0.01$, $p=0.91$; dissolved oxygen: $R^2=0.006$, $F_{1,\ 564}=3.3$, $p=0.07$). Substrate type and water clarity both related to abundance (in a collinear manner), but the effect of substrate was much stronger (Fig. 5; effect of clarity alone: $R^2=0.086$, $F_{1,\ 718}=67.2$, $p<0.0001$; effect of clarity after controlling for other factors: $F_{1,\ 692}=1.6$, $p=0.21$; effect of substrate after controlling for other factors: $F_{3,\ 715}=16.3$, $p<0.0001$).

Discussion

Between 2002 and 2008, round gobies in Hamilton Harbour decreased in terms of their abundance and body size. The significant decline in abundance occurred on all substrates. Conversely, investment in reproduction has increased over time. Round goby abundance in the near shore was related to temperature with the highest catch rate observed at water temperatures between 15 and 17 °C. In Hamilton Harbour, round gobies were least abundant on mud, and even fewer were caught in Cootes Paradise Marsh.

Population decline

Our initial hypothesis of a population increase followed by a period of stabilization was not met. The tandem declines in abundance and body size suggest that the round goby population in Hamilton Harbour may have reached, or even exceeded, its maximum carrying capacity before 2005. Our observations of decline may also represent an overshoot of carrying capacity, which may eventually settle to a stable level in coming years. Other fish species have recently increased in Hamilton Harbour (Brousseau and Randall, 2008), suggesting that the observed decline in round goby numbers is not merely a reflection of region-wide declines in fish abundance.

Factors such as predation or food supply may have influenced the abundance trends across years, and it is possible that these factors might even select for earlier maturation or reduced growth. Aging studies are currently underway to test this suggestion. Studies have shown that predators such as smallmouth bass (*Micropterus dolomieu*), double-crested cormorants (*Phalacrocorax auritus*), and water snakes (*Nerodia sipedon insularum*) have begun to consume round gobies (King et al., 2006; Somers et al., 2003; Steinhart et al., 2004b). The strongest declines in round goby abundance were observed on boulders near a large colony of water birds (e.g., double-crested cormorants, Caspian terns, *Hydroprogne caspia*, ring-billed gulls, *Larus delawarensis*, and herring gulls, *Larus argentatus*). It is possible that, before 2005, round gobies were more successful at escaping predation, but that in recent years, potential predators have learned to recognize them as a new available diet item. Alternatively, the round goby decline may have more to do with the recent decline of zebra muscles (*Dreissena polymorpha*, a major diet item for round gobies) in Hamilton Harbour and in other areas of the Great Lakes (Charlebois et al., 1997; Petri and Knapton, 1999). To determine whether predation and food availability are contributing to the decline of round gobies and to explore any compensatory responses in growth, fecundity, and timing of sexual maturity, additional experimental studies (manipulating the presence of predators and diet restrictions) are now needed. It should also be noted that our own harvest of 4617 round gobies may have in part contributed to the observed decline of round gobies in our study sites. However, we suspect that our removal of round gobies was not solely responsible for the observed decline. First, we sampled only a small fraction of the entire study area. Second, the prolific reproductive capacity of round gobies (they spawn multiple broods per year) as well as their relatively high clutch survival rates (as a result of paternal care; Charlebois et al., 1997) argues against the idea of our removals having a massive affect on this rapidly reproducing species.

We used minnow traps for this study, which may have led to some sampling bias. Capture in a minnow trap requires that fish actively explore the trap to be caught. Previous studies have suggested that minnow traps have a low catch rate compared to other sampling methods (Johnson et al., 2005). As a result, while our study can be used as a comparison of relative abundance across years and substrates, our catch rate is likely an underestimate of the true density of round gobies in Hamilton Harbour and Cootes Paradise Marsh. Only one sampling method was used in this study; however, pilot work has shown that sampling with minnow traps yields similar numbers to electrofishing and higher numbers than seining. Also, these other sampling methods were not equally successful on all substrates (electrofishing had poor yields on mud, and seining is not possible on boulder or cobble). Finally, temperature was more strongly related to abundance than was month of year and may influence round goby catchability. Round gobies may reduce general activity in very warm or very cold waters, making them less likely to explore, forage, and swim into a trap. Alternatively, our results could reflect a true preference for intermediate temperatures, with round gobies frequenting waters deeper than our traps (>1 m) when temperatures are more extreme.

Male bias

The strong male bias observed in this study and reported by Corkum et al. (2004) may be related to male round goby territoriality and paternal care. Like other goby species, only males defend a territory and care for eggs by fanning and defending the eggs (Corkum et al., 1998; Kangas and Lindström, 2001; Kvarnemo and Forsgren, 2000; Marentette et al., 2009; Miller, 1984). Males, therefore, will occupy the nesting areas in the shallow littoral zone for much longer (days and weeks rather than hours) than visiting females. Females may enter the shallow breeding sites only briefly to deposit eggs, remaining mainly in deeper water to avoid predation (Kovtun, 1979). Indeed, the male bias was less extreme during the peak of the breeding season, suggesting females migrate to deeper waters earlier than males (Fig. 3A, inset). Although a territorial guarding male may have somewhat restricted movement compared to a non-reproductive male or a female, such males are more likely to interact with the trap near their nests as they are in these areas for longer periods.

Another explanation for the male bias may be because male round gobies are generally more active and explorative in the laboratory than are females (JR Marentette, unpublished data). Interestingly, pilot work using different fish sampling techniques (see Balshine et al., 2005) revealed a similar male-biased catch of round gobies. Male territoriality, exploration and paternal behaviours all may work together to make males more likely to enter minnow traps compared to females (see Balshine-Earn, 1996, for similar results for African cichlids).

Implications for Cootes Paradise Marsh and other wetlands

Our study suggests that mud alone will not exclude round gobies from wetlands/marshes like Cootes Paradise. Hamilton Harbour has been extensively colonized by round gobies (Balshine et al., 2005), including areas with muddy substrates previously thought to be devoid of round gobies. Although previous studies found that round gobies prefer structurally complex environments with many refuges and nesting sites (Cooper et al., 2007; Miller, 1986; Ray and Corkum, 2001; Wickett and Corkum, 1998), we found that round gobies had successfully colonized muddy substrates. In western Lake Erie, Johnson et al. (2005) found round gobies on mud near Pelee Island, and they were even more abundant on mud than on sand. Soft substrates may actually provide effective hiding places from predators as round gobies can bury themselves (Jude et al., 1992). Furthermore, any lack of shelter on muddy substrates may be partially compensated for by more turbid waters reducing the effectiveness of predators that rely on visual or auditory detection (Jude and Pappas, 1992).

In our study, fewer round gobies were found on mud and fewer still were found in nearby Cootes Paradise Marsh. One possible explanation for the much lower numbers in the marsh is that round gobies may have to migrate to seek refuge in tributaries or back into the Harbour when much of the shallow water column in the marsh freezes each winter (Bowen and Theysmeyer, 1998). The average depth in the Cootes Paradise Marsh is only 0.7 m and the maximum depth is 2 m (Chow-Fraser, 1999; Holmes, 1988). When the water levels in the marsh drop during the winter months, the majority of the fish communities are forced to migrate to deeper and warmer areas of Hamilton Harbour (Chow-Fraser, 1999). This need to repeatedly re-invade the marsh each year may have prevented the same scale of establishment as in the Harbour. In Lake Michigan, Cooper et al. (2007) found fewer round gobies in wetlands than in adjacent lake habitats and hypothesized that a lack of hard substrates in the wetlands may be responsible for these results. They argued that wetlands may act as barriers to invasion. Two other studies have suggested that wetlands might be barriers to round gobies as a result of their rich species diversity (Carman et al., 2006; Jude et al., 2006). The numbers of round gobies found on muddy habitats in Hamilton Harbour suggest that the muddy substrates of wetlands such as Cootes Paradise will not provide a barrier to invasion, but may slow down the rate of colonization and establishment.

Cootes Paradise is the largest and most important warm water native fish breeding ground in western Lake Ontario (Holmes, 1988). If round gobies establish in larger numbers in Cootes Paradise Marsh, this could impact current restoration efforts. The round goby's generalized invertebrate feeding niche means that major impacts on the basal food web structure would be unavoidable. In some areas, native fish species have indeed declined where round gobies have become abundant (Crossman et al., 1992; Janssen and Jude, 2001). If round gobies invade the marsh in large numbers, native fish species will have to compete with round gobies for food (French and Jude, 2001), shelter, and breeding habitat (Balshine et al., 2005). In addition, round gobies have been known to disrupt spawning and decrease reproductive success of native species by eating their young (Steinhart et al., 2004a). Species particularly at risk include sticklebacks (Gasterosteidae), darters (*Etheostoma* spp., *Ammocrypta* spp.), and logperch (*Percina caprodes*) (Balshine et al., 2005; Chotkowski and Marsden, 1999; Janssen and Jude, 2001).

This longitudinal study traced population dynamics of an invasive fish species, the round goby, in Hamilton Harbour and began at a presumed early time point in the round goby invasion of Lake Ontario. We have shown that the population appears to be declining in Hamilton Harbour. Nevertheless, the high densities of round gobies, their prolific reproduction and tolerance to a wide range of ecological conditions suggest that they are likely to persist. Given the round goby's potential for negative impacts on ecosystem function (as a result of competition with and predation on native species) as well as possible positive impacts on native fish and bird populations (as a result of the availability of a new plentiful food source), it is imperative that efforts to monitor round goby population dynamics, and the factors influencing these dynamics, are maintained. Such efforts will lead to a better understanding of the underlying causes of the trends described here and will shed light on how to control the spread of this invasive species in other water bodies.

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