

# Invasion success and impact of an invasive fish, round goby, in Great Lakes tributaries

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## ABSTRACT

**Aim** Environmental and biological characteristics interact in complex ways to determine ecosystem susceptibility to invasive species, and a greater understanding of their relative roles in invader spread and impact is needed. We evaluated relationships between environmental characteristics, biodiversity of indigenous species, and the abundance and ecological impact of an invasive fish, round goby (*Neogobius melanostomus*).

**Location** Tributaries to Lake Michigan, WI, USA.

**Methods** We assessed the distribution and abundance of round gobies and native fishes in tributaries via electrofishing. We compared fish community composition and diversity in streams with ( $n = 30$ ) and without ( $n = 52$ ) round gobies and examined how trends in round goby abundance from 2007 to 2010 correlated with changes in abundance of five native benthic fishes. We used redundancy analysis to determine how indigenous stream communities related to environmental characteristics and round goby abundance.

**Results** Round goby abundance was best explained by environmental characteristics, with watershed area and temperature explaining 22.4% of the variation. Species richness and Shannon diversity only explained 6.9% of the variation in round goby abundance and only an additional 2.3% after considering environmental characteristics. Round goby abundance was not a significant predictor of fish community composition, which was best explained by seven environmental variables (30.3% of the variation). Invaded communities had significantly higher indigenous species richness than uninvaded communities (8.38 vs. 6.54). Round goby abundance was low compared with estimates from other studies, but showed an increasing trend in many tributaries (average 10.8-fold increase from 2007 to 2010). Surprisingly, there were no temporal trends in native benthic fish abundance despite increases in round goby abundance.

**Main conclusions** Environmental characteristics favouring high fish diversity (e.g. resource availability and warm water temperature) were positively associated with round goby abundance. However, round goby density and impact are relatively low in most tributaries at present, emphasizing the importance of considering heterogeneity in an invader's abundance when assessing invasion success.

## Keywords

Biodiversity, biological invasions, community composition, environmental characteristics, Great Lakes, *Neogobius melanostomus*, round goby.

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## INTRODUCTION

Invasive species inflict huge economic and ecological costs world-wide (Vitousek *et al.*, 1996; Pimentel *et al.*, 2005; Lodge *et al.*, 2006) in part by altering the composition of communities and reducing ecosystem services (Chapin *et al.*, 2000). Understanding factors related to invader abundance and impact remains an important goal in ecology (Parker *et al.*, 1999; Byers *et al.*, 2002; Kulhanek *et al.*, 2011). Ecological niche models are often employed to assess ecosystem susceptibility to invasion based on environmental conditions (Peterson, 2003; Mercado-Silva *et al.*, 2006; Kornis & Vander Zanden, 2010). However, biotic factors such as community composition and diversity can also play a role in susceptibility to invasion. Theory predicts diverse and intact assemblages of native species should be resistant to species invasions at local scales (Elton, 1958); this is supported by models (Case, 1990) and experimental studies (Tilman, 1997; Stachowicz *et al.*, 1999; Kennedy *et al.*, 2002). At larger scales, however, environmental factors related to high native species diversity may facilitate species invasions (Levine, 2000; Hooper *et al.*, 2005). Thus, invasion success, in terms of invader establishment, spread and abundance, is likely determined by a combination of environmental conditions, resource availability and biotic community composition at multiple spatial scales (Shea & Chesson, 2002).

Although invasive species commonly invade ecosystems similar to their native habitat, species may act unpredictably outside of their native range (Mooney & Cleland, 2001; Peterson & Vieglais, 2001). Invasion of habitats dissimilar from a species' native range is not uncommon, complicating our ability to predict ecosystem susceptibility (Urban *et al.*, 2007; Loo *et al.*, 2007; Kornis & Vander Zanden, 2010). Invasive species are often characterized by genetic plasticity, allowing rapid adaptation to novel environments (Lee *et al.*, 2003; Lavergne & Molofsky, 2007; Prentis *et al.*, 2008; Facon *et al.*, 2008). Broad physiological tolerance (Reid & Orlova, 2002) and release from predators, competitors or parasites (Keane & Crawley, 2002; Blumenthal, 2006) can also lead to invasion of unexpected habitats. Ecological niche theory suggests that species are not equally suited to multiple habitats; for invasive species, lower density and impact would be expected in suboptimal habitats (Yokomizo *et al.*, 2009). Comparing a single species' invasion in multiple habitats could provide valuable insight into the heterogeneity of invasion effects.

Round goby (*Neogobius melanostomus*) invasion of the Laurentian Great Lakes provides a unique opportunity to compare invasion of multiple ecosystem types. Native to the Black and Caspian Seas, round gobies are associated with numerous negative effects in the Laurentian Great Lakes (Kornis *et al.*, 2012), including local extirpations of native fishes (Janssen & Jude, 2001; Lauer *et al.*, 2004) and declines in fish and invertebrate abundance (Balshine *et al.*, 2005; Lederer *et al.*, 2008). Round gobies are becoming increasingly common in Laurentian Great Lake tributaries (Kornis & Vander Zanden, 2010; Poos *et al.*, 2010) an unexpected

secondary invasion considering round gobies are largely a lentic species (Charlebois *et al.*, 1997; Harka & Biró, 2007). Few studies have examined round goby invasion success in tributaries. Kornis & Vander Zanden (2010) found watershed area and stream gradient to be the strongest predictors of round goby presence/absence, Krakowiak & Pennuto (2008) concluded stream size was a good predictor of presence, and Baldwin *et al.* (2012) added that streams with low concentrations of dissolved ions such as calcium resist invasion. Conflicting evidence exists with regard to biotic factors: several studies have suggested that round gobies tend to invade low diversity streams (Carman *et al.*, 2006; Krakowiak & Pennuto, 2008), but Poos *et al.* (2010) documented an invasion of species diversity hot spots in Ontario tributaries. Thus, the respective roles of abiotic and biotic factors in round goby invasion success remain undetermined.

The ecological impacts of round gobies in Laurentian Great Lake tributaries are also unclear. Potential impact on tributary communities is large (Poos *et al.*, 2010) but may not translate into realized impact. Krakowiak & Pennuto (2008) found significantly reduced invertebrate diversity in four goby-invaded tributaries of Lake Erie compared with four non-invaded streams. This study also suggested decreased fish diversity in invaded systems, but this trend proved statistically insignificant. Further comparison of biological communities in streams invaded and not invaded by round gobies is warranted because Krakowiak & Pennuto (2008) only studied sites within 2–3 km of Lake Erie. Round gobies have invaded farther upstream (> 10 km) in many tributaries (Kornis & Vander Zanden, 2010), and upstream sites often differ from downstream sites in terms of environmental factors, habitat complexity and biological community structure (Harrel *et al.*, 1967; Gorman & Karr, 1978; Vannote *et al.*, 1980).

We pose two overarching questions in this study: (1) do biological characteristics such as community diversity and abundance affect round goby invasion success? and (2) are invaded communities in turn affected by round goby invasion? These intertwining issues are common in invasion biology, as native communities can both affect and be affected by an invader, and both issues can be addressed by viewing the same data from different perspectives. We address question one by describing the amount of variation in round goby density explained by biotic and abiotic factors. Question two is addressed by describing the composition of stream fish communities in terms of their relationship with round goby density and environmental conditions, by comparing indigenous fish species densities in invaded and uninvaded systems, and by evaluating changes in the density of five indigenous benthic fishes at invaded sites over time. We also compare fish community diversity in streams with and without round gobies, with implications for both questions. In this study, 'non-native species' refers to species outside of their native range, while 'invasive species' refers to non-native species with documented negative ecological effects. 'Establishment' will be used to describe a

species' presence/absence, 'spread' a species' range and 'abundance' a species' density. 'Invasion success' encompasses high degrees of establishment, spread and abundance.

## METHODS

### Site selection and fish collection

Sites used in this study (Fig. 1) represent a subset of sites from a 2007 census of all Wisconsin tributaries of Lake Michigan, with sampling designed to ascertain the distribution of round gobies in these streams (Kornis & Vander Zanden, 2010). In the current study, we only evaluated wadeable sites (< 1 m maximum depth) where the stream bottom was visible (82 sites from 58 distinct streams). Sites were sampled using a battery-powered backpack electrofishing unit with pulsed DC current, the most widely used method in studies of riverine fish communities (Zalewski, 1983). Sites from Kornis & Vander Zanden (2010) that were too deep or turbid to sample via electrofishing were excluded because they were sampled using minnow traps, a sampling method with considerable bias towards small benthic fishes and thus not suitable for studies of fish communities. As physical barriers such as dams impede the spread of round gobies, only sites downstream of such barriers were considered in our analysis such that all sites were connected to Lake Michigan without interruption. Each site was electrofished for 20 min, working upstream and sampling from bank to bank so as to cover all microhabitats (mean area sampled was  $268 \text{ m}^2 \pm 28 \text{ SE}$ ). All fish captured were identified, measured, enumerated and released at the site of capture except for round gobies, which were euthanized with tricaine methanesulfonate (MS-222) and retained. Catch per unit effort (CPUE, measured in individuals captured per minute of electrofishing) was used as a proxy for species density throughout.

Round goby absence at some sites may have been due to lack of colonization time or failure to detect round goby presence. We estimated a 75% probability of detection when round gobies were rare, based on twelve 20-min electrofishing samples at sites with the minimum CPUE ( $0.05 \text{ fish min}^{-1}$ ) detected by our method (Kornis & Vander Zanden, 2010). We found round gobies at  $0.05 \text{ CPUE}$  at 8 of 30 goby-present sites; if our 75% detection probability for such sites is accurate, we would anticipate only a handful of absences (two to three sites) owing to detection failure. Regarding colonization time, sampling conducted in 2008 detected round goby presence at five of our 2007 absence sites, and these sites were considered 'invaded' in this study. Most absence sites (44/52) occurred in streams where round gobies were not observed, however, and the eight absence sites that occurred upstream of a presence site typically had suboptimal goby habitat (high stream gradient, sandy/silty substrate). Although we cannot rule out lack of colonization time or inability to detect presence as sources of goby absences, unfavourable environmental conditions likely played a much larger role.

A total of 23 sites were selected for the multi-year monitoring portion of this study. At these sites, round gobies co-occurred with at least one of five indigenous benthic stream fishes during summer 2007: Johnny darter (*Etheostoma nigrum*), mottled sculpin (*Cottus bairdii*), logperch (*Percina caprodes*), blackside darter (*Percina maculata*) and fantail darter (*Etheostoma flabellare*). These five indigenous species were selected because of previous studies from the Great Lakes indicating negative effects of round gobies (Janssen & Jude, 2001; Lauer *et al.*, 2004; Balshine *et al.*, 2005) or because of suspected diet and habitat overlap (Poos *et al.*, 2010). Each of these 23 sites was sampled again in 2010 using identical electrofishing methods, allowing for comparison of round goby and native species CPUE between years. We examined the change in round goby and native fish CPUE from 2007 to 2010, expressed as a ratio, such that positive values indicate an increase and negative values indicate a decrease in CPUE. Ratios were calculated by

$$+ \frac{2010 \text{ CPUE}}{2007 \text{ CPUE}}$$

when CPUE increased from 2007 to 2010 and calculated by

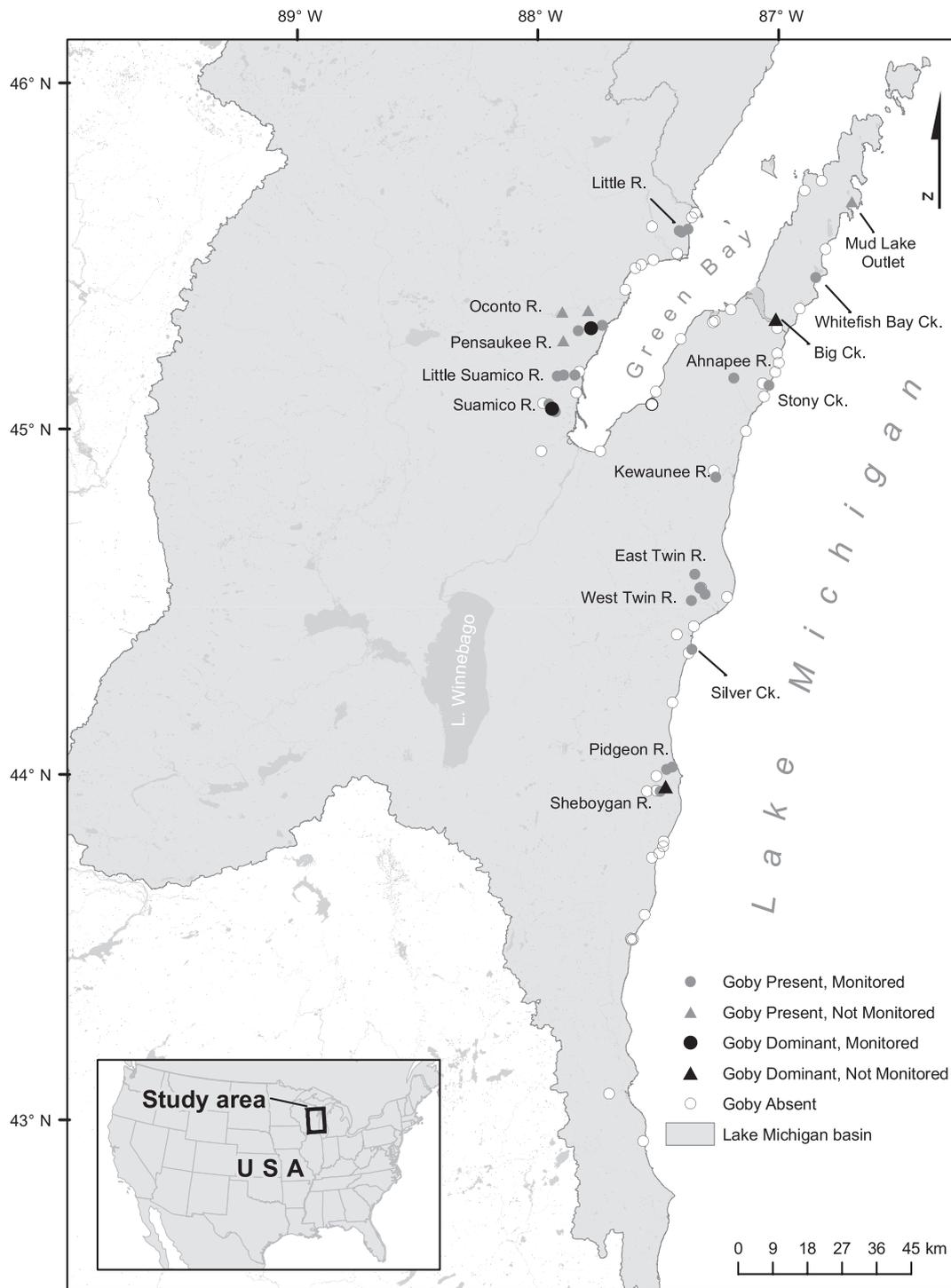
$$- \frac{2007 \text{ CPUE}}{2010 \text{ CPUE}}$$

when CPUE decreased from 2007 to 2010. To allow a ratio calculation when native species absence resulted in a 0 denominator, absences were assigned a CPUE value of  $0.05 \text{ fish min}^{-1}$ , equivalent to the minimum possible capture (one fish) in a standard 20-min electrofishing survey.

Round goby density was estimated in four rivers (three sites in each river) through depletion electrofishing methods following Bohlin *et al.* (1989). At each of these 12 sites, a reach was cordoned off with two block nets and sampled in three consecutive electrofishing passes. A tow boat electrofishing unit with gas-generated pulsed DC current was used instead of the battery-powered backpack unit to provide a larger electrical field, resulting in greater capture efficiency and reducing the number of passes needed to observe clean depletion curves. These sites had predominantly run geomorphology, were comparable in terms of environmental characteristics and represented sites with above-average round goby CPUE. Average area sampled was  $202 \pm 60 \text{ (SD) m}^2$ , mean substrate size was  $123 \pm 43 \text{ mm}$ , water temperature  $19.4 \pm 3.5 \text{ }^\circ\text{C}$ , stream width  $10.5 \pm 2.1 \text{ m}$  and mean depth  $0.38 \pm 0.11 \text{ m}$ .

### Environmental variables

Several landscape-scale variables [watershed area, watershed slope, watershed soil permeability, mean July air temperature (a correlate of water temperature), baseflow index (90% exceedance flow/watershed area), stream gradient and watershed land use (categorized as per cent urban, agricultural, wetland and



**Figure 1** Round goby (*Neogobius melanostomus*) presence (grey and black symbols) and absence (white circles) in Wisconsin tributaries of Lake Michigan. Site locations represent the 82 electrofished sites used in our analysis. Circles represent the 23 sites monitored for the comparison of indigenous fish catch per unit effort (CPUE) from 2007 to 2010, while triangles are goby-presence sites used strictly for the comparison of community diversity. Black circles/triangles are the four sites at which round gobies were the numerically dominant community member. Only streams with goby presence are named. Sampling occurred from June to August 2007, and watersheds were sampled at discrete sites upstream from the coast until absence was detected. Figure adapted from Kornis & Vander Zanden (2010).

forested land)] were considered in our multivariate analysis of fish community composition. These data were obtained from a geographical information system (GIS) database (US

Geological Survey, Great Lakes Aquatic GAP Analysis Project) and were calculated on the scale of confluence-bound stream segments, with each segment between the confluence of two

streams considered as one unit. Conductivity, water temperature and per cent substrate composition, assessed at each site, were also considered potential predictors of fish community structure. Per cent substrate composition was visually assessed into the following categories: silt, sand, gravel, rock (cobble and boulder) or bedrock. Conductivity and water temperature were measured using a YSI 85 metre (YSI Inc., Yellow Springs, OH, USA). Watershed area values were log-transformed to produce a non-skewed distribution, and each environmental variable was z-standardized to convert all environmental data to the same unitless scale.

### Statistical methods

Stream fish communities were related to environmental conditions and round goby CPUE using a redundancy analysis (RDA; Van den Wollenberg, 1977). RDA is a direct gradient analysis technique that partitions variation in community composition into components associated with multiple predictor variables. The response variables in a RDA can be expressed as a linear combination of the predictor variables, and the approach handles species abundance data, sample sites and environmental data simultaneously (Borcard *et al.*, 1992). It is especially useful in understanding patterns of community composition and has been applied to fish communities in several contexts (Angermeier & Winston, 1999; Sharma *et al.*, 2011). Rare species (species occurring in < 5% of sites) were removed from the analysis, as they can have a disproportionate effect on ordinations (Jackson & Harvey, 1989). Tubenose gobies (*Proterorhinus semilunaris*), a Great Lakes invader in the same family as round goby (Gobiidae), were not captured at any of our sites. Species CPUE data were transformed using Hellinger distance, which decreases the importance of the most abundant species, as recommended by Legendre & Gallagher (2001). The subset of seven

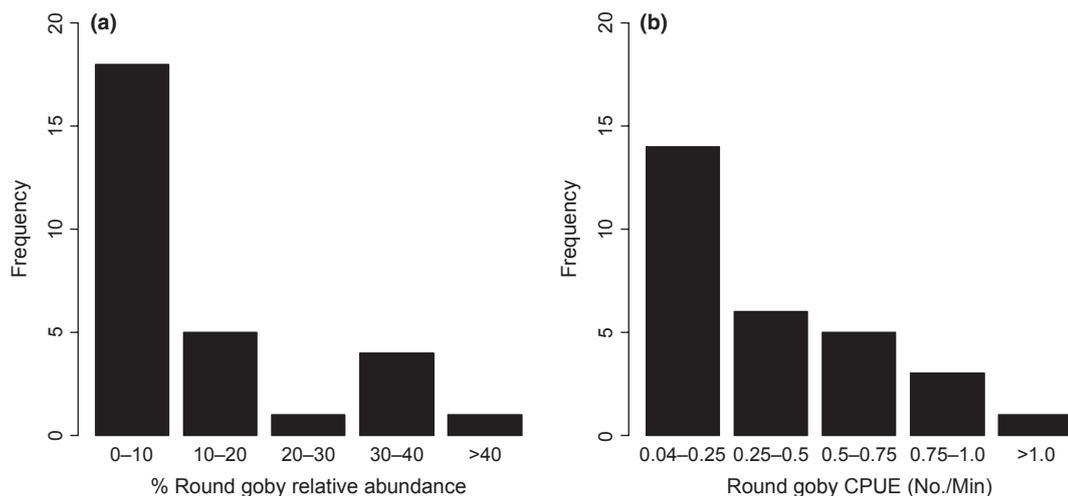
environmental predictors used for this analysis were selected because they explained a significant amount of variation in the community data ( $P < 0.05$ ) and were minimally correlated (Pearson correlation coefficient, all  $r^2 < 0.35$ ). The 'packfor' R package (creators: Stéphane Dray, Pierre Legendre and Guillaume Blanchet) was used for the RDA analysis and included a forward selection procedure (env.sel) from which our subset of environmental variables was chosen. The package is available at <http://www.bio.umontreal.ca/legendre/indexEn.html>.

Redundancy analysis, correlation analysis and linear regressions were performed using the R statistical package (version 2.13.2; [www.r-project.org/](http://www.r-project.org/)). The map depicting round goby presence/absence and sample sites was constructed using ARC-GIS software (ESRI, Redlands, CA, USA).

## RESULTS

### Patterns of round goby abundance

Round goby CPUE (number of fish captured per minute of electrofishing) and % relative abundance (% of total numerical catch) had strongly right-skewed distributions, with low CPUE and % relative abundance values at most invaded sites (Fig. 2). Round gobies were the numerically dominant species at four of the 30 invaded sites (sites in Big Creek, Pensaukee R., Sheboygan R. and Suamico R.). At these four sites (Fig. 1), round goby relative abundance ranged from 31.5 to 83.3% of all individuals captured, and CPUE was significantly greater at these sites (mean of 0.83 fish  $\text{min}^{-1}$ ) than at sites where gobies were not dominant (mean of 0.31 fish  $\text{min}^{-1}$ ) ( $P = 0.02$ ,  $t = 2.56$ , d.f. = 27, two-tailed Student's  $t$ -test assuming equal variance). Round goby relative abundance was 15.3% of all individuals captured on average, but this value drops to 8.8% excluding the four sites



**Figure 2** Frequency distribution of round goby (*Neogobius melanostomus*) relative abundance (a) and catch per unit effort (CPUE) (b) at invaded sites. Round gobies were absent from 52 of the 82 sites sampled, but these absence sites were excluded from these figures to illustrate the frequency distribution of round goby relative abundance and CPUE at sites where they are present ( $n = 30$ ).

where they are numerically dominant. See Table S1 for stream names, global positioning system (GPS) coordinates and round goby CPUE of all sites.

Round goby density was estimated through 3× depletions at a subset of sites ( $n = 12$  sites in 4 streams) to provide a value comparable with other studies and ranged from 0.07 to 0.36 fish  $m^{-2}$ . These sites represent areas with comparatively high round goby CPUE (mean of 0.53 in subset vs. 0.27 at goby-present sites not in subset).

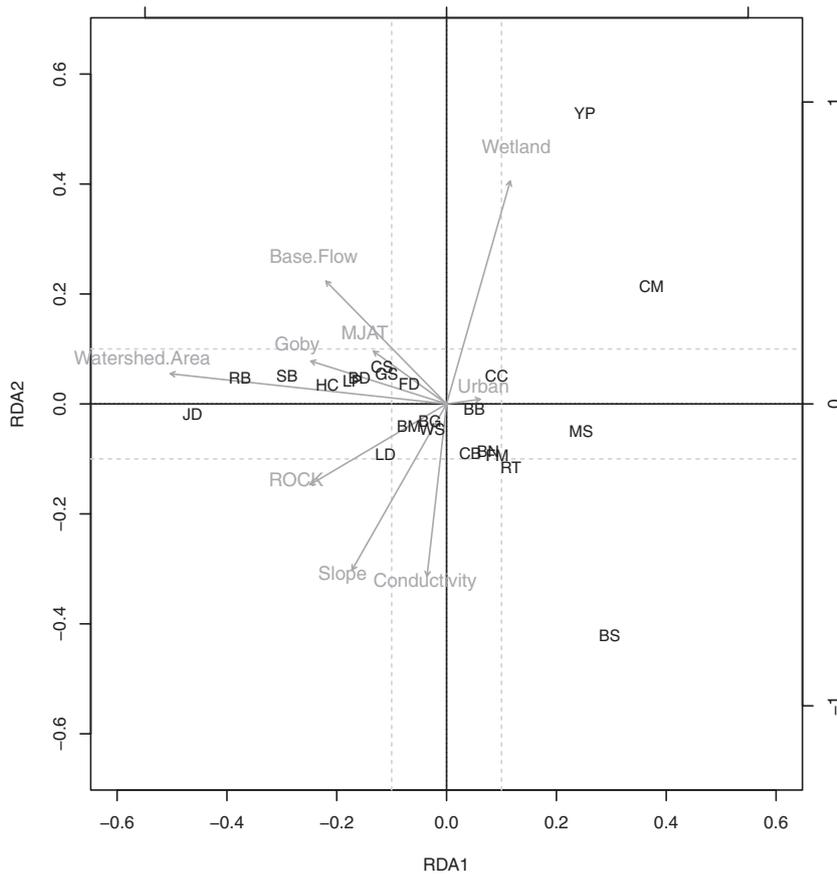
### Predictors of round goby CPUE

A RDA found only two environmental characteristics, watershed area and water temperature, to be significant predictors of round goby CPUE. These two predictors explained

22.4% of the variation in round goby CPUE. Two biological predictors, species richness and Shannon diversity (Shannon & Weaver, 1949), only explained an additional 2.3% of the variation in round goby CPUE when added to the analysis. A RDA using only the two biological predictors explained 6.9% of the variation in round goby CPUE, and neither biological characteristic was a significant predictor.

### Patterns in native fish communities

Three community metrics, Shannon diversity, fish species richness and total fish CPUE, were compared for invaded and non-invaded sites (Table 2). Round goby sites had significantly greater Shannon diversity (1.56 vs. 1.23) and species richness (9.38 vs. 6.54) compared with non-invaded sites



**Figure 3** Redundancy analysis (RDA) axes one and two showing the association of fish catch per unit effort (CPUE) with both environmental data and round goby (*Neogobius melanostomus*) CPUE. Black letters represent non-goby species found in at least 5% of streams sampled (minimum of five sites); see Table 1 for abbreviations. Species located close together on the RDA axes are associated with each other, whereas species found at opposite ends of the RDA axes are very unlikely to be found together. Grey letters correspond with arrows and represent the environmental variables that were significant predictors of fish CPUE at  $\alpha = 0.05$ . Length of each arrow indicates the strength of a given environmental variable; the direction of the arrow indicates how well species correlate with environmental conditions. Species that fell within 0.1 RDA units of the origin (denoted by light dashed grey lines) were considered generalists relative to the predictor variables included in the RDA. Overlapping species codes at  $(-0.15, 0.05)$  are LP and BD. Overlapping species codes near  $(0.1, -0.1)$  are BN and FM. Predictor abbreviations: Wetland = % watershed covered by wetlands, MJAT = mean July air temperature, Goby = round goby CPUE, ROCK = % of substrate that is cobble or boulder, Urban = % of watershed covered by urban land, Slope = watershed slope. RDA explained 31.2% of the variation in species CPUE. The first two axes (displayed in this figure) explained 15.3% of the variation.

**Table 1** Species-specific differences in per cent occurrence and catch per unit effort (CPUE) between sites invaded and not invaded by round gobies (*Neogobius melanostomus*).

Taxa	Abrv.	No. of sites	% of goby-present sites with taxa	% of goby-absent sites with taxa	Mean CPUE at goby-present sites (SE)	Mean CPUE at goby-absent sites (SE)	P-value for CPUE data (d.f.)
Catostomidae							
White Sucker	WS	32	36.0	39.0	0.49 (0.28)	0.35 (0.09)	0.55 (30)
<i>Catostomus commersonii</i>							
Centrarchidae							
Bluegill	BG	16	12.0	22.0	0.77 (0.49)	0.53 (0.17)	0.59 (14)
<i>Lepomis macrochirus</i>							
Green Sunfish	GS	23	36.0	23.7	0.20 (0.08)	0.47 (0.18)	0.27 (21)
<i>Lepomis cyanellus</i> <sup>†</sup>							
Rock Bass	RB	26	56	20.3	0.47 (0.13)	0.26 (0.04)	0.17 (24)
<i>Ambloplites rupestris</i> <sup>†</sup>							
Smallmouth Bass	SB	32	15.3	35.6	0.26 (0.05)	0.69 (0.24)	0.12 (30)
<i>Micropterus dolomieu</i> <sup>†</sup>							
Cottidae							
Mottled Sculpin	MS	18	16.0	23.7	1.28 (0.96)	1.28 (0.29)	0.99 (16)
<i>Cottus bairdii</i> <sup>‡</sup>							
Cyprinidae							
Western Blacknose Dace	BN	8	0.0	13.6	0	0.85 (0.32)	n/a
<i>Rhinichthys obtusus</i>							
Bluntnose Minnow	BM	20	36.0	18.6	1.90 (1.03)	0.70 (0.17)	0.22 (18)
<i>Pimephales notatus</i> <sup>*</sup>							
Common Carp	CC	10	4.0	15.3	0.2 (n/a)	0.42 (0.14)	0.64 (8)
<i>Cyprinus carpio</i>							
Common Shiner	CS	15	28.0	13.6	0.68 (0.31)	0.37 (0.12)	0.35 (13)
<i>Luxilus cornutus</i> <sup>†</sup>							
Creek Chub	CB	22	16.0	30.5	0.10 (0.04)	1.10 (0.54)	0.41 (20)
<i>Semotilus atromaculatus</i> <sup>*</sup>							
Fathead Minnow	FM	13	12.0	16.9	0.38 (0.09)	1.20 (0.34)	0.22 (11)
<i>Pimephales promelas</i>							
Hornyhead Chub	HC	18	36.0	15.3	0.86 (0.37)	0.45 (0.21)	0.35 (16)
<i>Nocomis biguttatus</i> <sup>†</sup>							
Longnose Dace	LD	22	32.0	23.7	0.17 (0.06)	0.55 (0.19)	0.16 (20)
<i>Rhinichthys cataractae</i>							
Gasterosteidae							
Brook Stickleback	BS	25	16.0	35.6	0.12 (0.06)	3.29 (1.13)	0.24 (23)
<i>Culaea inconstans</i> <sup>*‡</sup>							
Ictaluridae							
Black Bullhead	BB	11	16.0	11.9	0.25 (0.09)	0.36 (0.11)	0.50 (9)
<i>Ameiurus melas</i>							
Percidae							
Blackside Darter	BD	16	32.0	13.6	0.40 (0.12)	0.51 (0.11)	0.56 (14)
<i>Percina maculata</i> <sup>†</sup>							
Fantail Darter	FD	6	16.0	3.4	0.21 (0.10)	0.54 (0.09)	0.13 (4)
<i>Etheostoma flabellare</i>							
Johnny Darter	JD	41	60.0	44.0	1.75 (0.63)	1.64 (0.44)	0.88 (39)
<i>Etheostoma nigrum</i> <sup>†</sup>							
Logperch	LP	12	28.0	8.5	0.25 (0.06)	0.27 (0.14)	0.90 (10)
<i>Percina caprodes</i> <sup>†</sup>							
Yellow Perch	YP	21	36.0	20.3	0.22 (0.09)	1.27 (0.36)	0.02 (19)
<i>Perca flavescens</i> <sup>*‡</sup>							
Salmonidae							
Rainbow Trout	RT	13	12.0	16.9	0.73 (0.53)	0.75 (0.34)	0.98 (11)
<i>Oncorhynchus mykiss</i> <sup>‡</sup>							

Table 1 Continued.

Taxa	Abrv.	No. of sites	% of goby-present sites with taxa	% of goby-absent sites with taxa	Mean CPUE at goby-present sites (SE)	Mean CPUE at goby-absent sites (SE)	P-value for CPUE data (d.f.)
Umbridae							
Central Mudminnow <i>Umbra limi</i> <sup>‡</sup>	CM	40	32.0	54.2	0.43 (0.17)	1.13 (0.33)	0.30 (38)

Abbreviations correspond to those used in the redundancy analysis (RDA) (Fig. 3). Taxa denoted with a '†' were positively associated with round goby CPUE in the RDA, those denoted with a '‡' were negatively associated, and those without denotation were generalists with respect to the RDA. CPUE data are mean values from sites where the listed species was present; absences were removed because they likely derived from over-arching environmental variables and not goby presence/absence. *P*-values are from two-tailed Student's *t*-tests, assuming equal variance, comparing CPUE of listed taxa in goby-present and goby-absent sites; significance is determined at  $\alpha = 0.002$  (Bonferroni correction). In many cases, sample size differed drastically between round goby-present and -absent sites, and any taxa with a mean difference in CPUE of at least 1.0 fish  $\text{min}^{-1}$  between goby-present and goby-absent sites are denoted with an \* to highlight trends that may be biologically relevant despite statistical insignificance.

( $P = 0.003$  and  $< 0.001$ , respectively). Excluding gobies from diversity and richness calculations produced similar though less significant results (species richness, 8.38 vs. 6.54,  $P = 0.02$ ; Shannon diversity, 1.44 vs. 1.23,  $P = 0.07$ ). Neither total CPUE nor non-goby CPUE differed significantly between invaded and non-invaded sites.

A RDA examining how the CPUE of 23 fish species related to seven environmental variables and round goby CPUE explained 31.2% of the variation in species-specific CPUE (Fig. 3). 15.3% of the variation was explained in the first two axes. Round goby CPUE was not a significant predictor of stream fish community composition ( $P = 0.28$ ) but was included in the RDA because of biological relevance. Round goby CPUE was most strongly related to watershed area and mean July air temperature, although rocky substrate and baseflow index were also positively associated. Species that fell within 0.1 RDA units of the origin were considered generalists relative to the predictor variables included in the RDA. As the round goby CPUE aligns primarily with the *x*-axis of the RDA plot, species with RDA1 values of less than  $-0.1$  were considered positively associated with round gobies while species with RDA1 values of greater than 0.1 were considered negatively associated with round goby. In total, eight taxa were positively associated with round goby CPUE, including three members of Percidae (Johnny darter, logperch and blackside darter), two members of Cyprinidae (hornyhead chub and common shiner) and three members of Centrarchidae (green sunfish, rock bass and smallmouth bass). Five species were negatively associated with round goby CPUE, including yellow perch, one species tolerant of low oxygen conditions (central mudminnow) and three taxa that are associated with cooler water temperature and higher gradient systems (rainbow trout, mottled sculpin and brook stickleback). Four species had differences in CPUE of at least 1.0 fish  $\text{min}^{-1}$  between goby-present and goby-absent sites: yellow perch, bluntnose minnow, brook stickleback and creek chub, although no statistically significant differences were found (Bonferroni-corrected  $\alpha$  of 0.002). Sites where native species were absent were not included in these comparisons

because our RDA indicated that such absences are far more likely to be due to environmental characteristics than round goby presence/absence.

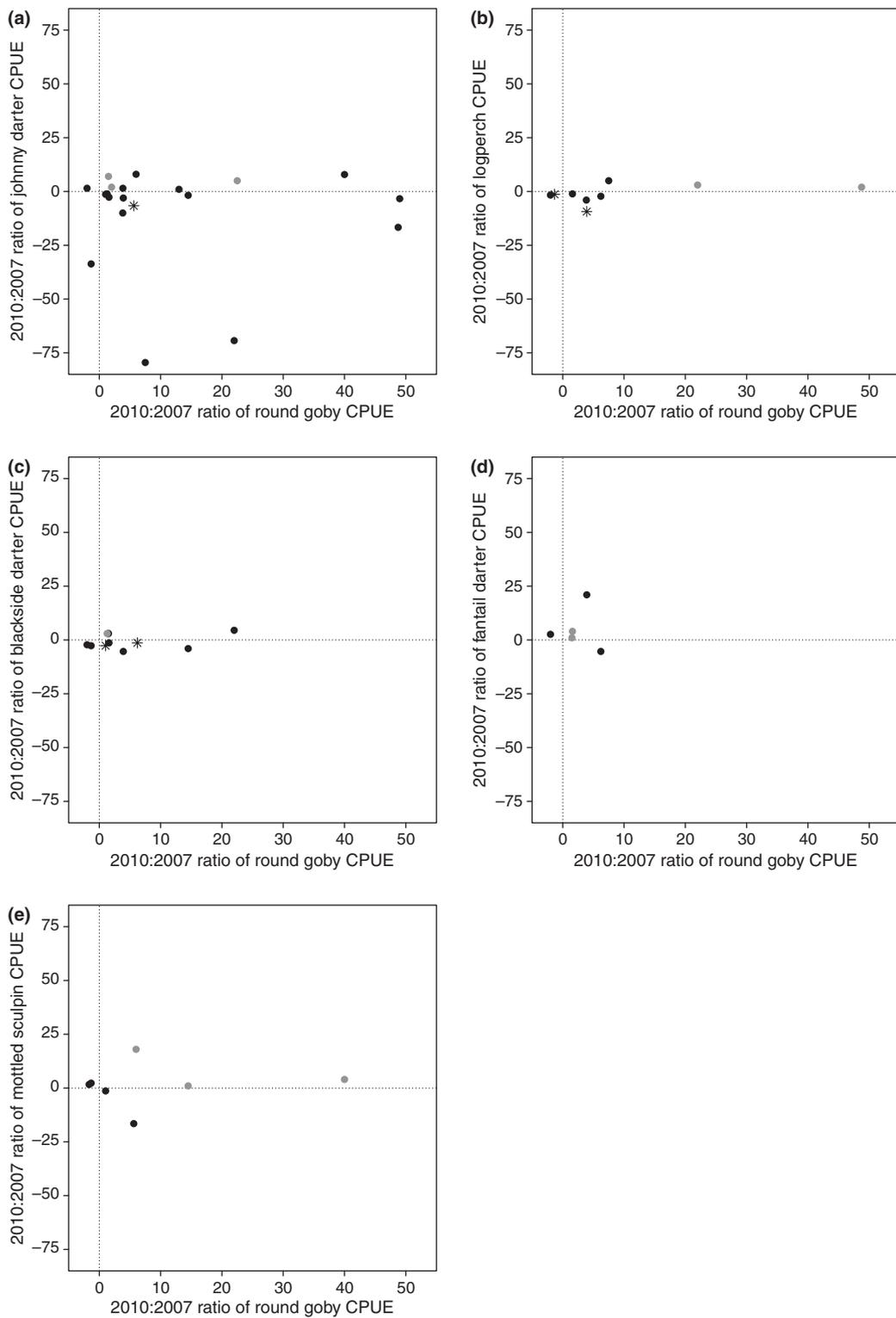
### Impact of round gobies on native benthic fishes

We compared the change in CPUE from 2007 to 2010 for round gobies to that of five indigenous species: Johnny darter, mottled sculpin, logperch, fantail darter and blackside darter (Fig. 4). Between 2007 and 2010, round goby abundance increased at 19 of 23 sites, with at least a doubling of round goby CPUE at 65% of sites (15 of 23). On average, round goby CPUE was 10.8 times higher in 2010 than in 2007; at five sites, CPUE had increased more than 20-fold from 2007 to 2010. Despite increases in round gobies CPUE, native species CPUE showed no major trends. The change in CPUE of Johnny darter ( $P = 0.87$ ), mottled sculpin ( $P = 0.81$ ), logperch ( $P = 0.24$ ), blackside darter ( $P = 0.40$ ) and fantail darter ( $P = 0.99$ ) did not significantly correlate with the change in round goby CPUE.

We also compared species richness at three of the four round goby-dominated sites (Fig. 1) to other sites located within the same river ( $n = 4$  sites per river). Sites where round gobies were numerically dominant had 2.9 fewer native species on average when compared to other sites in the same rivers ( $P = 0.08$ , d.f. = 2, two-tailed paired *t*-test). This difference was at least partially explained by the absence of darter species (one or two of Johnny darter, fantail darter, blackside darter or logperch, depending on the stream) at the goby-dominated site compared with other sites in the river (average of 1.11 fewer darter species at the goby-dominated site).

### DISCUSSION

We found round gobies were associated with high diversity streams, and we attribute this result not to high species diversity per se, but rather to round gobies inhabiting streams with an environmental profile that facilitates high



**Figure 4** Trends in round goby (*Neogobius melanosotmus*) and (a) Johnny darter (*Etheostoma nigrum*), (b) logperch (*Percina caprodes*), (c) blackside darter (*Percina maculata*), (d) fantail darter (*Etheostoma flabellare*) and (e) mottled sculpin (*Cottus bairdii*) catch per unit effort (CPUE) from 2007 to 2010. Each site was sampled once during summer 2007 and once during summer 2010 with 20 min of backpack electrofishing. Data presented represent the ratio of CPUE between years, with positive ratio values indicating an increase in CPUE from 2007 to 2010 and negative values indicating a decrease. Grey points represent cases where the native species was not present in 2007, while asterisks indicate the native species was not present in 2010. To avoid dividing by zero in the ratio calculation, these absences were assigned a CPUE value of 0.05 fish min<sup>-1</sup>, equivalent to the minimum possible capture (one fish) in a standard 20-min electrofishing survey.  $n = 20, 7, 9, 10$  and  $5$  for Johnny darter, mottled sculpin, logperch, blackside darter and fantail darter, respectively.

species richness. Although the potential for diverse species assemblages to resist species invasions is well documented (Tilman *et al.*, 1996; Hooper & Vitousek, 1998; Knops *et al.*, 1999; Kennedy *et al.*, 2002), environmental characteristics are often a greater structuring force than biodiversity (Moyle & Light, 1996; Holway *et al.*, 2002), and abiotic factors favouring diversity can favour invasion success (Levine & D'Antonio, 1999; Foster *et al.*, 2002; Marchetti *et al.*, 2004). Our results corroborate this: a RDA of round goby abundance based on environmental characteristics explained three times as much variation as a RDA based on biological descriptors. Additionally, we observed greater native species richness (number of taxa) in streams invaded by round gobies ( $P = 0.02$ , Table 2). This may be related to a positive association between round goby abundance and watershed area and a negative association with environmental variables (i.e. high slope, cool temperature) typical of lower order streams (Fig. 3). Fish diversity, resource availability and habitat complexity tend to increase with watershed area (Gorman & Karr, 1978; Schlosser, 1982; Fauch *et al.*, 1984; Lamberti & Steinman, 1997), though specific sites may be exceptions (Bott *et al.*, 1985). Round gobies also have an energetic optimum temperature of about 26 °C (Lee & Johnson, 2005) and appear to avoid colder streams (Kornis & Vander Zanden, 2010), which tend to support fewer species (Magnuson *et al.*, 1979). Our findings therefore support recent evaluations of the diversity/resistance hypothesis suggesting abiotic factors positively correlated with species diversity improve invasion success, and often override the resistance effects of species richness (Stohlgren *et al.*, 1999; Levine & D'Antonio, 1999; Hooper *et al.*, 2005).

We report a positive relationship between round goby presence and native species diversity, contrasting the finding that invasive species often contribute to biodiversity loss (Ricciardi & Rasmussen, 1998; Clavero & García-Berthou, 2005; Dextrase & Mandrake, 2006). Round gobies have been implicated in localized species extirpations and abundance declines in the Laurentian Great Lakes by several studies (Janssen & Jude, 2001; Lauer *et al.*, 2004; Balshine *et al.*, 2005). In contrast, we found stream fish community composition was strongly associated with environmental variables and not goby abundance. RDA only explained 30.3% of the varia-

tion in species-specific abundance, likely because the sampling strategy did not account for variables such as the chance distribution and establishment of individuals, animal activity, local disturbances or fine-scale environmental heterogeneity (Gauch, 1982).

Although round goby abundance was not a significant factor in shaping stream communities, our analysis highlights several associations between round gobies and native species. Species positively associated with round goby abundance likely to be found in systems susceptible to invasion and may be vulnerable to negative effects. Amongst these species are three small, benthic Percid species – Johnny darter, logperch and blackside darter – that are particularly at risk because of dietary and habitat overlap with round goby (French & Jude, 2001; Poos *et al.*, 2010). However, our study found no changes in the abundance of these species despite increases in round goby abundance from 2007 to 2010. Species negatively associated with round gobies are unlikely to co-occur because of preference for habitat characteristics suboptimal for round goby, including tolerance of low oxygen conditions (central mudminnow), watersheds with higher slope and faster flow (rainbow trout, brook stickleback) and cooler temperature (mottled sculpin). We also observed a negative association between yellow perch and round gobies, a finding opposite to that of one Great Lakes study (Dopazo *et al.* 2008). Similarly, limited co-occurrence of mottled sculpin and round goby in streams is particularly interesting as mottled sculpin declines in Lake Michigan were associated with round goby invasion (Janssen & Jude, 2001). This suggests round gobies, mottled sculpin and yellow perch share habitat preferences in the Great Lakes but not in tributaries.

Impact assessments are emerging as an important component of understanding and managing invasive species, but impacts are often heterogeneous across an invaded range. Parker *et al.* (1999) define an invader's impact by its range, abundance and per-capita effect. High abundance is often considered a defining quality for invasive species (Kolar & Lodge, 2001; Valéry *et al.*, 2008), but recent evidence (G.J.A. Hansen, M.J. Vander Zanden, M.J. Blum, M.K. Clayton, E.F. Hain, J. Hauxwell, M. Izzo, M.S. Kornis, P.B. McIntyre, A. Mikulyuk, E. Nilsson, J.D. Olden, M. Papes, and S. Sharma,

**Table 2** Shannon diversity, species richness and overall catch per unit effort (CPUE) for fish species in goby-present ( $n = 30$ ) and goby-absent ( $n = 52$ ) streams.

Index	Mean (goby-present) $\pm$ 1 SD	Mean (goby-absent) $\pm$ 1 SD	<i>P</i> -value
Shannon diversity	1.56 $\pm$ 0.45	1.23 $\pm$ 0.50	0.003
Number of taxa	9.38 $\pm$ 3.60	6.54 $\pm$ 2.80	< 0.001
CPUE (no per min)	5.28 $\pm$ 4.38	5.50 $\pm$ 4.96	0.83
Shannon diversity	1.44 $\pm$ 0.48	1.23 $\pm$ 0.50	0.07
No. of taxa	8.38 $\pm$ 3.60	6.54 $\pm$ 2.80	0.02
CPUE (no per min)	4.9 $\pm$ 4.36	5.50 $\pm$ 4.96	0.57

Data above the dashed line include round gobies in the computation of each index, while data below the dashed line do not include round gobies in index computation. *P*-values are from two-tailed Student's *t*-tests, assuming equal variance, comparing goby-present and goby-absent sites.

in review) suggests aquatic invasive species across a wide range of taxa (plants, molluscs, crustaceans and fishes) tend to have high abundance at few locations and low abundance at most locations throughout their range. This follows the same general trend observed for most native species (Brown *et al.*, 1995, 1996). Our results suggest differences between round goby abundance and impact between the Laurentian Great Lakes and some of their tributaries. Round gobies are rapidly increasing in abundance in Lake Michigan tributaries, but current densities (0.07–0.36 fish  $m^{-2}$  at sites with above-average round goby CPUE) are low when compared to estimates from the Laurentian Great Lakes. Johnson *et al.* (2005) reported round goby densities ranging from 0.62 fish  $m^{-2}$  in sandy habitat to 6.94 fish  $m^{-2}$  in rocky habitat in western Lake Erie, while Taraborelli *et al.* (2009) reported densities from 0.63 to 3.88 fish  $m^{-2}$  across depth and substrate gradients in the Bay of Quinte, Lake Ontario. This comparison is limited by different density estimation methods (video transects vs. depletion electrofishing) and by a low number of studies reporting density (most report relative abundance). Relative abundance and CPUE data from our study can be compared with values reported from the downstream sections of Lake Erie tributaries owing to similar sampling methods. Round goby relative abundance is greater in these tributaries, with a mean of 33.5% vs. 15.3% reported from our study (Lake Erie mean combined from Phillips *et al.*, 2003 and Krakowiak & Pennuto, 2008). CPUE is also greater, with abundance increasing from spring to autumn and peaking at 7.2 and 12.6 fish  $min^{-1}$  in October. At 96% of our invaded sites, round goby CPUE was  $< 1$  fish  $min^{-1}$ , with 1.8 fish  $min^{-1}$  the maximum observed value. This demonstrates heterogeneity in round goby abundance amongst tributaries, which may be due to differences in habitat suitability or population residence time.

Our ability to compare impact between Great Lake and tributary habitats is limited to comparing short-term effects on native benthic fishes; nevertheless, trends were notably different in these two habitat types. Johnny darter and mottled sculpin populations precipitously declined within 1–2 years following the discovery of round gobies in southern Lake Michigan (Janssen & Jude, 2001; Lauer *et al.*, 2004). Round gobies have also been associated with declines in logperch abundance (Balshine *et al.*, 2005) and were predicted to negatively impact blackside and fantail darter abundance (Poos *et al.*, 2010). Conversely, we observed no significant change in the abundance of five indigenous benthic fishes from 2007 to 2010 despite dramatic increases in round goby abundance. Although our comparisons are limited in scope, the density and impact discrepancies between ecosystems described here highlight the importance of considering an invader's density when managing for their impacts.

Although we report limited round goby abundance and impact on fishes in Lake Michigan tributaries thus far, this could potentially be due to sites only recently becoming invaded (e.g. short residency time). The observed increase in round goby abundance from 2007 to 2010 raises concerns

that more prominent impacts will develop over time. There is often a time lag between invader establishment and growth in abundance (Crooks & Soulé, 2001), and other studies have reported high round goby abundance in tributaries with longer resident populations (Phillips *et al.*, 2003; Carman *et al.*, 2006; Pennuto *et al.*, 2010). Although major goby-related changes to fish communities have been reported over short time periods in areas of the Great Lakes (Janssen & Jude, 2001; Lauer *et al.*, 2004), similar changes may take longer to develop in stream ecosystems. Our comparison of invaded and uninvaded communities/habitats is also limited by the short residency time of round gobies in tributaries. As of 2007, round gobies only occupied about 20% of their forecasted range in habitats downstream of impassable barriers (Kornis & Vander Zanden, 2010). Although many uninvaded sites examined by our study fit an environmental profile unfavourable to round gobies (e.g. cooler water temperature, high stream gradient), several of these sites may become invaded as the range expands in the region. This is especially likely for the 11 of our 52 absence sites that were predicted to be invaded by the range forecast model presented by Kornis & Vander Zanden (2010). Assessments of early-stage invasions tend to underpredict potential range and impact compared with those conducted at later stages (Václavík & Meentemeyer, 2012). However, early-stage characterization of an invader's impact and preferred habitat provides a greater opportunity to use gained information for preventative management, a distinct advantage over late-stage studies. We recommend further investigation into the effects of invader residency time on the accuracy of invasion assessments, with a focus on identifying stages of invasion that maximize the trade-off between accuracy and utility.

This study highlights several challenges in studying and managing species invasions. An invader's abundance and impact will likely vary at multiple spatial scales, and assessments of this variability could better inform decision makers. In the case of round gobies, we highlighted different short-term impacts on native benthic fishes between lake and stream ecosystems, provided evidence that abundance could differ between these systems and described variability in abundance among stream sites. Management decisions often take place at local scales, and evaluation of invader impact at this scale may be essential to this process. In addition, greater clarity is needed when referring to invasion success, which can be defined by either presence or abundance. This and other studies (Moyle & Light, 1996; Foster *et al.*, 2002; Hooper *et al.*, 2005) point to environmental characteristics as the predominant factor in the establishment of invasive species, a relationship that can produce positive associations between invader presence and indigenous species diversity. What promotes invader presence will not necessarily promote abundance, however, as competitor density and diversity may limit invader abundance by reducing niche opportunity. The relative importance of environmental and biological factors will differ on a species-by-species basis. Incorporating both environmental and biological factors in

understanding the spread, abundance and impact of invasive species will lead to improved ability to assess, predict and effectively manage for their effects.

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## BIOSKETCHES

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Author contributions: M.S.K. and J.V.Z. conceived the ideas, M.S.K. led the field collection team, S.S. and M.S.K. performed the multivariate analysis, M.S.K. performed other analyses, M.S.K. wrote the first draft of the paper, and all authors contributed substantially to subsequent revisions.

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