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PRIMARY RESEARCH PAPER

Occupation, body size and sex ratio of round goby (*Neogobius melanostomus*) in established and newly invaded areas of an Ontario river

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Abstract Invasive species represent a challenge because the particular characteristics of a species' invasion are often unknown before the invasion. To provide some clarity as to how invasive species demographic structure might change as a population advances its range, we compared the proportion of occupied sites, size structure and sex ratio of round gobies in the area where they first invaded with more recently invaded areas at the extent of their range in a river in south-eastern Ontario. We used a standardized angling technique to sample gobies larger than 45-mm total length in the summer and early autumn of 2007. Round goby at the upstream and downstream extent of their range occupied a lower proportion of randomly selected sites, and contained a wider distribution of sizes as well as significantly larger individuals. Sex ratios in all areas were male-biased and the male-to-female ratio was significantly higher in the upstream segment of the river (2.2:1) compared to the area of first introduction (1.4:1). The difference between the newly invaded and the established sites suggests that round goby population structure may be affected by density. The results of this study help us further describe the demographic characteristics of biological invasions whilst examples of population structure and behaviour in gobies and other species provide a basis for generating hypotheses for range expansion.

Keywords Dispersal · Gobiidae · Invasive · Non-indigenous · Range expansion

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Introduction

Hundreds of aquatic species have established populations outside of their native range, many of which are prolific because they possess key attributes including the ability to rapidly expand their population's range (Kolar & Lodge, 2002). The study of invasive species range expansion has recently gained momentum in the aquatic sciences with literature topics ranging from descriptions of a population's spread (Correa & Gross, 2008; Franch et al., 2008) to the investigation of traits associated with range expansion (Kolar & Lodge, 2002) and examinations of population demography at different stages of an invasion (e.g. Bøhn et al., 2004; Bergstrom et al., 2008). Theoretical research also offers a powerful tool for modelling range expansion (Hastings et al., 2005; Phillips et al., 2010); however, many new invasions are investigated empirically to provide the basis for developing management programmes that are appropriate to the invasion (Shea et al., 2010).

The round goby (*Neogobius melanostomus*) is native to the Ponto-Caspian sea region and was likely introduced to North America through the ballast of transoceanic ships (Charlebois et al., 1997; Hensler & Jude, 2007). Although known to exhibit high site fidelity (Wolfe & Marsden, 1998; Ray & Corkum, 2001), the round goby has spread rapidly since its discovery in 1990 in the St. Clair River, Michigan (Jude et al., 1992). By 1996, this small benthic fish was found throughout the Laurentian Great Lakes (Charlebois et al., 1997) and today its range expansion continues into tributaries (Phillips et al., 2003; Carmen et al., 2006; Krakowiak & Pennuto, 2008; Poos et al., 2009). European populations have also managed to expand their range, making the round goby an invasive species on two continents (Corkum et al., 2004; L'avrinčíková & Kováč, 2006).

Many traits contribute to the tremendous success of the round goby, including a life history that favours high rates of reproduction during an invasion (MacInnis & Corkum, 2000a, b; L'avrinčíková & Kováč, 2006), the ability to produce eggs multiple times during a reproductive season (Kovtun, 1977; Miller, 1986), aggressive nest-guarding behaviour and an acute sensory system that allows for nocturnal activity (Charlebois et al., 1997). Range expansion has also been fuelled by human-assisted transport (e.g. bait–bucket transfer), natural spread, and the now common invasive zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*), which are prey for adult round goby (Charlebois et al., 1997). Whilst the economic impact of this species is yet to be determined, its impacts on invaded ecosystems have been identified to include egg and larval consumption (Chotkowski & Marsden, 1999; Steinhart et al., 2004), the ability to outcompete native fishes (Janssen & Jude, 2001; Balshine et al., 2005; Karlson et al., 2007; Bergstrom & Mesinger, 2009), and the alteration of benthic invertebrate communities (Krakowiak & Pennuto, 2008; Lederer et al., 2008).

During the process of an aquatic species' range expansion, one would expect to see dynamic shifts in demographic traits in response to changes in population size and food availability as the species becomes locally abundant (Bøhn et al., 2004), but there are few studies available to assess such shifts in invasive fish populations. Whilst such comparisons along an invasion pathway do not exist for the round goby, studies of body size differences between early- and late-invaded sites for the Wels catfish (*Silurus glanis*) and the vendace (*Coregonus albula*) have demonstrated larger asymptotic length (Bøhn et al., 2004) and faster growing, larger-bodied individuals (Carol et al., 2009) in the more recently invaded sites. In the case of the round goby, a recent 7-year study of population and demographic changes in an area invaded by the species showed a decline over time in the mean body length of individuals (Young et al., 2010), but the study did not monitor such traits in the outward expanding areas newly occupied by the population.

One of the inland waterways that the round goby has invaded is the Trent River in southeastern Ontario. Rather than the population of gobies reaching the upper portion of the river by natural movement from Lake Ontario, this aggregation is believed to have originated from a bait–bucket introduction (F. MacDonald, Ontario Federation of Anglers and Hunters (OFAH), personal communication). Range expansion of this population has been rapid and in the 4 years it had been monitored, round gobies were found many kilometres from the area of first introduction in both an upstream and a downstream direction (Raby et al., 2010). Thus, the population presented the opportunity to examine a biological invasion and assess changes in occupation patterns and demographic parameters at different locations along a dynamic invasion pathway.

In this study, we compare frequency of occurrence, size and size–class distribution, and sex ratio in the portion of the river where the round goby was first introduced with that of upstream and downstream segments of the population range. We predicted that the area of original introduction would contain a significantly higher proportion of occupied sites than the more recently occupied upstream and downstream areas. We also compared body size and sex ratio of round gobies between the originally introduced and the newly occupied areas to characterize the demographic structure of the population.

Methods

Study area

The Trent River is approximately 90 km in length and connects Rice Lake to the Bay of Quinte, Lake Ontario (Fig. 1). The river has a drainage area of 12,550 km^2 and is the principal source of inflow to the Bay of Quinte (Minns et al., 2004). The Trent River is also the largest river in the Trent–Severn waterway, which is a historic commercial and recreational boating route that spans 386 km from Lake Ontario to Georgian Bay, Lake Huron. The river itself contains 18 Locks, five of which are found within the current extent of the Trent River round goby range. Shoreline development along the study area is limited to houses, cottages and farmland. The Trent River contains areas of both relatively fast (e.g. near Hastings) and slow flow (e.g. Lake Seymore) depending on river bed morphology and river width (Fig. 1). The average depth of the Trent River navigational channel is 4.1 m (map data, Canadian Hydrographic Service), and the mean monthly flow of the river varies but is normally the highest (167 m^3 s^{-1}) in April and the lowest (32 m^3 s^{-1}) in August (Parks Canada, unpublished data). The river would be considered mesotrophic, based on a mean annual total phosphorus concentration of 21 μg l^{-1} (Ontario Ministry of Environment, unpublished 2001–2006 data).

The Trent River contains a warm water fish community that includes walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), muskellunge (*Esox masquinongy*), longnose gar (*Lepisosteus osseus*), redhorse (*Moxostoma carinatum*), brown bullhead (*Ameiurus nebulosus*), channel catfish (*Ictalurus punctatus*), lake sturgeon (*Acipenser fulvescens*), black crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), northern logperch (*Percina caprodes*) and a variety of cyprinid species (Ontario Ministry of Natural Resources (OMNR) 2009). The bed of the Trent River contains a mix of hard and soft substrate, many species of native aquatic macrophytes, periphyton [e.g. macroalgae (*Chara* spp.)] and invasive zebra and quagga mussels.

Round gobies were first discovered downstream of Lock 18 (44°18′38″N, 77°57′10″W) in the town of Hastings in 2003, and the introduction is believed to be the result of anglers who used bait buckets to transport gobies from infested waters in Lake Ontario to the Trent River (F. MacDonald, OFAH, personal communication). Following the discovery, round goby sightings indicated both upstream and downstream range expansion from the original area of introduction.

To compare the demographic characteristics of the round goby population in the originally established and the newly occupied sites, we selected three areas for population sampling: the area of first introduction (hereafter known as the CORE area) and the most recently identified upstream and downstream extents of the species' river range. The investigations began with a collection of sighting records from the Ontario Federation of Anglers and were supplemented by seine net and extensive angling surveys that were conducted in 2008. Whilst one cannot rule out the possibility that outward range expansion was aided by additional bait–bucket transfers, the pattern of the new goby observations was progressive in an outward direction and with the exception of a few individuals too small to be bait–bucket transfers, there was no indication of new sightings that were part of a distinct group disconnected from the main body of the population and spreading backwards in the direction of the CORE area (Raby et al., 2010).

The area of first introduction was defined as a 4-km length of river that encompasses the area occupied by gobies within 2 years of the first sighting in the river (Fig. 1). The lengths of the upstream and downstream segments were defined by the distance between round goby sightings, which had been documented by OFAH and by the seine net and angling surveys in 2007. This originally resulted in 10-km segment lengths that were compared against the CORE area. However, the stretch of river considered to be the downstream segment had to be modified later, when subsequent information from the OMNR revealed that round gobies had occupied an area as far downstream as the Hamlet of Trent River and part of Lake Seymore since at least 2005. This meant that gobies in this part of the downstream sampling area were known to have several years of establishment time ahead of those in the upstream sampling area. All of the samples from the upstream

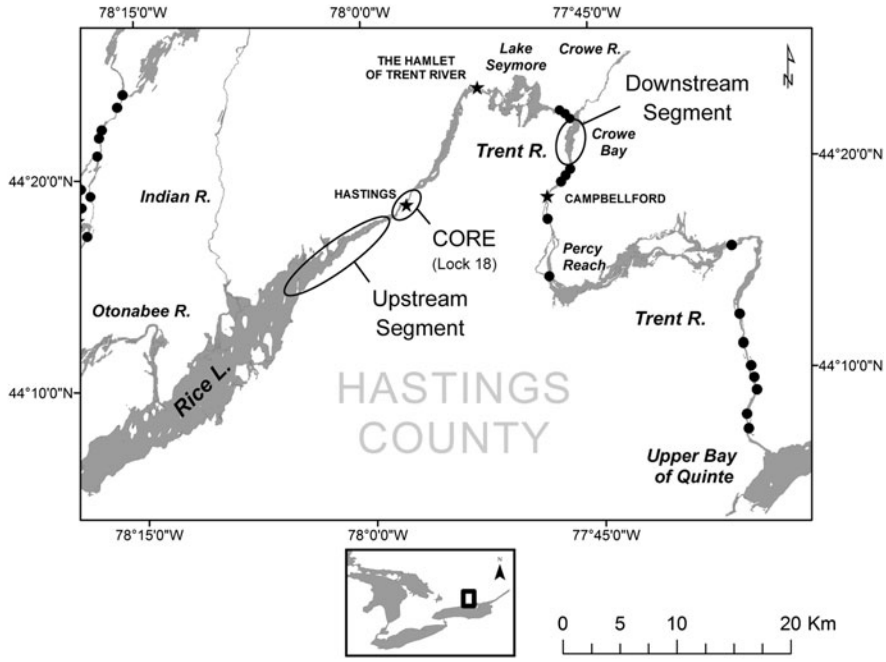

Fig. 1 Round goby study areas in Trent River. The area of first introduction (CORE) and the upstream and downstream extent of the round goby range as of 2007 are delineated by *ellipses*. The approximate location of Trent–Severn waterway Locks is identified by *black circles*. Specific locks within the study area include Lock 18 (located beneath the star that denotes Hastings); Locks 17, 16 and 15 (located at the northeast portion of the river entering Crowe Bay); and Lock 14 (located at the bottom of the ellipse that delineates the downstream segment)

segment and the area of first introduction were retained for analysis; however, only samples taken downstream of the Hamlet of Trent River and Lake Seymore were analysed for comparability between the two reaches and to maintain consistency with the study design (Fig. 1).

The habitat available to gobies is similar amongst sampling areas, and mainly consists of small and large rocks usually colonized by zebra mussels. River morphometry and shoreline development varies amongst areas. The upstream segment widens and becomes less developed near Rice Lake and the CORE area is narrower and most of the shoreline is developed with houses, resorts, and cottages. The downstream segment is a wide pool with some deep pockets ($\approx$15 m), scattered housing along the shoreline, and a campground at the north end near Lock 15. The Crowe River enters the downstream segment at the north end of Crowe Bay (Fig. 1).

Site selection and sampling method

The study was conducted from June to October 2008. Sampling sites were selected within the three study areas with a random point-generator program. Randomly generated sites containing dense macrophyte cover were not used, as our sampling method would not work under such conditions. The number of sites originally sampled in each area was 33, but owing to the aforementioned adjustment of the downstream area boundary, only 20 samples from that area could be taken for this study.

Sampling was conducted by angling from a bow and stern-anchored 16′ Jon boat with a fixed 1.5 m^2 floating quadrat that was used to delineate the sampling area. Following a 5-min settling period, two anglers fished simultaneously with lightweight rods, a small weight attached to the line and a size-20 hook baited with a small scented plastic maggot. This apparatus was found to effectively capture age 1 and older round gobies; i.e. those $\geq$45 mm total length (TL) during the study period.

Angling was conducted for a 20 min period in each site because it was found in a pre-test to be a sufficient period to capture all gobies present in most test sites in the river. Sampled sites were checked with an Aquaview S-series colour underwater video camera (Nature Vision Inc., Brainerd, MN) to search for gobies that remained following the 20 min period. The camera was also used to assess the dominant substrate type, e.g. rock, gravel, sand or macrophytes.

Upon capture, total length (nearest mm) and sex [by examination of the urogenital papilla (Charlebois et al., 1997)] of each goby was recorded. Round gobies captured during a given sampling period were retained in a pail of water, and angling was resumed for the full 20-min sampling period. Although in Ontario it is illegal to possess round gobies and they should be dispatched upon capture, angled gobies in this study were released (in accordance with our permit) at the end of the sampling period so that ongoing population studies were not biased by removing large numbers of gobies from localized areas.

Data analysis

Round goby occupancy was defined by presence/absence at a given sample site. The proportion of occupied sites in the CORE area was compared with that of the upstream and downstream segments using Fisher's exact tests. Size-class distributions (10-mm size classes) amongst locations were compared qualitatively using histograms with males and females pooled from sites within a given area. To test for differences in the mean length of gobies, captured gobies were separated by time of season (June–July and August–October) and compared with Kruskal–Wallis non-parametric tests, followed by a post-hoc comparison of mean ranks (Siegel & Castellan, 1988). Low sample sizes in downstream segment restricted this examination to the upstream segment and the CORE area. For sex ratio analysis, differences were examined with chi-square tests. The level of significance for all statistical tests was set at $P < 0.05$.

Results

Site occupancy

Eighty-six samples were compared with a combined catch of 607 round gobies. The proportion of sample sites containing gobies was the highest in rock and gravel sites, and these were the predominant substrates in all three areas sampled (Table 1). Round gobies were present in 97% of sampled sites in the CORE area; this occupancy rate was almost 50% greater than that found in the upstream segment and more than twice that of the downstream segment. These differences between the CORE area and upstream and downstream segments were significant (Fisher's Exact Test, $P = 0.001$ and $P < 0.001$, respectively), whereas there was no significant difference between upstream and downstream segments in the proportion of sites that contained round goby ($P = 0.10$).

Body size and sex ratio

Total body lengths of captured gobies varied from 51 to 160 mm in males, and from 48 to 115 mm in females. Size distribution was normally distributed in females (Lilliefors, $P > 0.05$) but not in males (Lilliefors, $P < 0.05$), in the CORE area. With the exception of females from the downstream area, all groups from the newly invaded areas were normally distributed (Lilliefors, $P > 0.05$) and males and females in the newly invaded areas were more evenly distributed across size-classes than those in the CORE area (Fig. 2). The largest individuals of each sex were captured in the upstream segment, followed by the downstream segment, and not in the CORE area as might be expected from the larger sample size of gobies captured there (Table 2).

Mean body length of males was greater than that of females in all the three sample sites (Table 2; Fig. 2). The mean length of gobies sampled from the CORE area was approximately 8% smaller than those

Table 1 The number of sites in which round gobies were present/absent in each area of river sampled and dominant habitat type

Habitat	Area sampled					
	Upstream segment		CORE		Downstream segment	
	Present	Absent	Present	Absent	Present	Absent
Sand	0	2	–	–	0	1
Gravel	1	2	3	1	4	1
Rock	19	4	28	0	5	5
Macrophytes	2	3	1	0	0	4
Total	22	11	32	1	9	11

Cells denoted with dashes (–) were not sampled

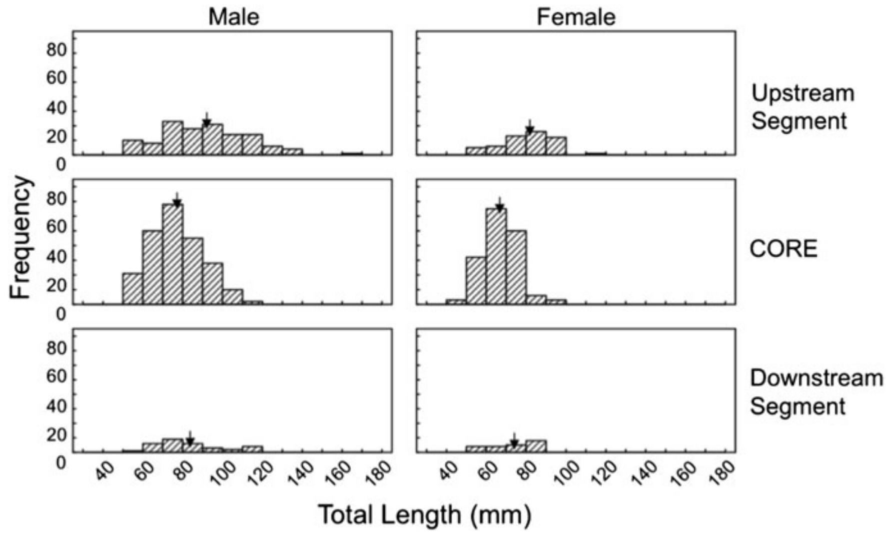

Fig. 2 Round goby frequency in total length (mm) size classes for each study location. Means of each sex are indicated by an *arrow*

Table 2 Descriptive statistics of the mean total length (mm) ± 1 SE by sex for round gobies ($n = 607$) angled from the Trent River in 2008

Location	♂ TL ± 1 SE	♀ TL ± 1 SE
Upstream segment	91.8 ± 2.0 (119)	81.1 ± 1.7 (53)
CORE	77.6 ± 0.91 (224)	68.1 ± 0.69 (159)
Downstream segment	84.0 ± 3.0 (31)	74.5 ± 2.4 (21)

Total number of gobies is indicated in parentheses

sampled from the downstream segment and 16% smaller than those collected in the upstream segment (Table 2). Mean body length did not differ significantly amongst areas during the summer period (Kruskal–Wallis $H = 5.79$, $P = 0.055$, $n = 165$) but was significantly different in the fall (Kruskal–Wallis $H = 80.5$, $P < 0.001$, $n = 440$). Fall sampled gobies in the upstream segment were significantly larger than those in the CORE area (multiple comparison of mean ranks, $Z = 8.96$, $P < 0.001$) and downstream segment (multiple comparison of mean ranks, $Z = 2.62$, $P = 0.03$). A qualitative examination of total length over the sampling periods showed that males and females exhibited a similar pattern of change in size, which differed between CORE and upstream sample areas (Fig. 3).

Sex ratios were male-biased in all the three areas and were 1.4:1 in the CORE, 1.5:1 in the downstream segment, and 2.2:1 in the upstream segment. The ratio of males to females in the upstream segment was significantly higher than the CORE area (χ^2, $P = 0.02$), but there was no significant difference between the CORE area and the downstream segment (χ^2, $P = 0.87$), or between the upstream and downstream segments (χ^2, $P = 0.19$).

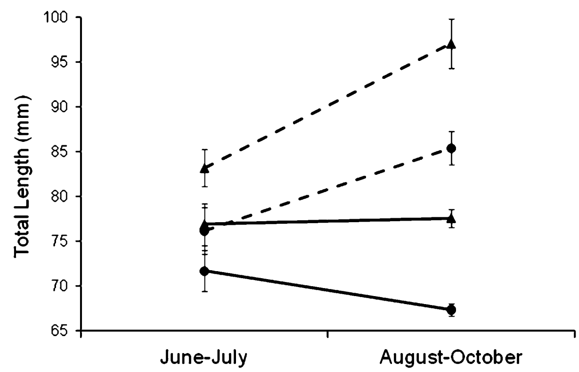

Fig. 3 Round goby mean total length (mm) ± 1 SE by location and sampling period. The locations are represented by a *solid line* (CORE area) or *dashed line* (upstream extent) and the sexes are further represented as ♂ (*filled triangle*), ♀ (*filled circle*)

Discussion

The greatest proportion of samples containing at least one round goby was found in the area of first introduction (Table 1), which corresponded to the relatively high adult abundance found when angling in the CORE area (12.0 gobies/20 min ± 1.4 SE) compared to the other two locations (upstream segment: 7.8 gobies/20 min ± 1.1 SE; downstream segment: 5.1 gobies/20 min ± 1.2 SE; Gutowsky et al., 2011). Colonization is followed by population growth and eventual saturation (Shigesada & Kawasaki, 1997), and it would appear that the area of first introduction has nearly reached saturation with over 97% of sampling sites occupied by round goby. As expected, sites containing no gobies were common at the invasion front, especially in the downstream segment. According to our results, rather than only increasing in numbers in small localized aggregations, round gobies may also continue to seek new territory during population range expansion. Short-distance migration from high-density areas into lower-density marginal habitat, followed then by further range expansion from the marginal habitat has been suggested in at least two other studies (Ray & Corkum, 2001; Bergstrom et al., 2008), and may also occur from areas of low density present at the edges of the range. Invasive species can exhibit complex range expansion processes which in some cases have been studied in depth; for example, the flat bottom sea star (*Asterias amurensis*; Dunstan & Bax, 2007), cane toad (Phillips et al., 2008; Llewelyn et al., 2010), and marine macrophytes (Mineur et al., 2010); however, the particular mechanisms of round goby range expansion are still largely unknown. In our study, the downstream segment is disconnected from the CORE area whereas the upstream segment is almost immediately adjacent (Fig. 1). Although we chose to sample in this way to isolate the farthest known upstream and downstream extent of the round goby's range, the scarcity of gobies in the smaller downstream segment suggests that this area is more representative of the 'edge' of the range whilst the upstream segment, although never identified as hosting round goby before 2007, represented more of a continuum. This is also explained by low abundance and occupancy at the outermost sampling sites of the upstream segment (data not shown).

In this study, we simultaneously considered spatial and temporal variation during an invasion, and we found intrapopulation variation with respect to body size (Fig. 3). Similar to round goby in the Trent River, intrapopulation differences in body size were identified between established and establishing populations of invasive European catfish (*Silurus glanis*), where newly invaded water bodies contained significantly larger individuals than long established ones. It is thought that food resource depletion by the catfish leads to slower growth in well established populations (Carol et al., 2009). Resource depletion does occur in terrestrial nonindigenous species as well, e.g. reindeer (*Rangifer tarandus*; Klein, 1968) and Argentinean ants (*Linepithema humile*; Tillberg et al. 2007). For the round goby, studies have shown that invasive populations can deplete local resources and alter their forage base (Kuhns & Berg, 1999; Djuricich & Janssen, 2001; Gonzalez & Burkart, 2004; Krakowiak & Pennuto, 2008; Lederer et al., 2008). Furthermore, gut fullness of round goby in the area of first introduction in the Trent River was shown to be significantly lower than the upstream area of range expansion and the density of dreissends, a favoured prey item of the round goby, was an order of magnitude lower in the CORE area than in the areas of upstream and downstream range expansion (Raby et al., 2010). The results of these studies provide good evidence that the pressure this species places on its environment could lead to intrapopulation demographic variability during the invasion and that an altered forage base could be a factor in further facilitate range expansion (Dwyer & Morris, 2006).

Whilst the differences in mean goby length between the CORE and range expansion areas can be potentially explained by differences in population density (Gutowsky et al., 2011) and stomach fullness (Raby et al., 2010), these factors cannot fully explain why the largest-bodied individuals were found in the upstream, but not the downstream range expansion area. One possibility is that the individuals most physiologically or morphologically capable of dispersal (Llewelyn et al., 2010) are disposed to travel in an upstream direction. A second possibility is that abiotic factors are influencing round goby growth, as the upstream and downstream areas of range expansion differ in shape, riverbed morphometry, water velocity, and perhaps productivity. For instance, food availability may be highest for gobies in the upstream segment near Rice Lake, whilst inflow from the Crowe River at the downstream segment may contain fewer nutrients and thus, reduced productivity. Two alternative explanations are that the larger individuals present in the downstream area were not represented in the relatively small number of individuals captured (see Fig. 2), or that goby growth was inhibited in the downstream area by the high abundance of northern logperch (*Percina caprodes semifasciata*) in that section. The northern logperch is a native species that competes with the round goby for benthic prey resources (Bergstrom & Mesinger, 2009).

All locations in the Trent River were male dominated, which has similarly been observed in several other systems invaded by the round goby. Corkum et al. (2004) reported male dominated sex ratios of 3:1 in the invaded Gulf of Gdansk in the Baltic Sea and 6:1 in the Western Basin of Lake Erie and the Detroit River. Young et al. (2010) also reported a 2:1 male to female ratio in Hamilton Harbor, Ontario. A study in the Duluth-Superior Harbor area of Lake Superior reported the round goby population to be strongly female-biased (Bergstrom et al., 2008); however the authors attribute at least part of this trend to trawl sampling, which did not permit the sampling of rocky habitats where guarding males are typically located. Gear bias inherently exists with all sampling systems; in fact there is a bias towards females using the technique described in the current study (Gutowsky et al., 2011). Beam trawl collections in the round goby's native range have shown the male to female ratio was closer to 1:1 (Kovtun, 1979), demonstrating that established and establishing populations may indeed differ in adult sex ratio. Given that the area of first introduction remains male biased after 6 years of occupation, it may be that compared to its native range conspecifics, the Trent River round goby population continues to maintain a male bias as a whole. This is also seen in most North American goby populations and in other invasive species [e.g. the Cuban tree frog (*Osteopilus septentrionalis*); Salinas, 2006].

Given the behavioural characteristics of round goby (e.g. aggression and paternal brood care), the significantly male biased upstream extent may result from density-dependant intraspecific competition amongst competitive males (see Stammler & Corkum, 2005) and/or a propensity for some individuals to seek new territory (e.g. 'movers' versus 'stayers' or boldness, Wilson et al., 1994; Fraser et al., 2001). Boldness has been suggested as a mechanism for dispersal in an invasive crayfish (*Pacifastacus leniusculus*; Pintor et al., 2009) and invasive *Gambusia* spp. (Schöpf Rehage & Sih, 2004). Boldness has yet to be examined in round goby, however long distance movement by a tagged individual in Lake Michigan may provide anecdotal evidence of this behaviour during an invasion (Wolfe & Marsden, 1998). Although our explanations suggest that the downstream reach in the Trent River should have the most male-biased sex ratio, the relatively low ratio may be a result of small sample sizes in this location.

Density-dependent competition and boldness provide two testable hypotheses to explain the relatively high male to female ratio and size differences seen at the low density 'edge' of the population range. However, strong inferences about behaviour, gender, and the patterns of range expansion cannot be drawn without also examining the influence of microhabitat selection by individuals, alternative reproductive strategies, the effect of predation [e.g. smallmouth bass (Steinhart et al., 2004) and cormorants (*Phalacrocorax auritus*; Somers et al., 2003)], propagule pressure during an invasion, the magnitude of environmental disturbance (MacDougall & Turkington, 2005), and abiotic factors (Moyle & Light, 1996) that can aid or restrict population spread (e.g. Argentinean ants, Holway, 1998).

The lowest frequency and minimum catchable size-class was 40–50 mm, meaning that angling was unable to effectively sample small round gobies. The underwater video camera used in the current study is adequate for detecting medium to large-bodied gobies, but is deficient at detecting individuals smaller than 50-mm TL (Schaner et al., 2009). To sample a greater array of size-classes, we recommend that another method be deployed (e.g. minnow traps; Dianna et al., 2006) to see whether the body size differences between the area of first introduction and areas of recent range expansion detected in our study still apply when juveniles are also considered.

The spatial and temporal heterogeneity of rivers can pose logistical constraints to studies on fish and their assemblages. By using angling, we were able to effectively sample an expanding population of large riverine round goby in all habitat types where they were found. We found that round goby are similar to other invasive species in that the largest individuals occupy the outermost reaches of the population's range and that males dominate the population. The patchy occurrence of round gobies in the newly invaded areas suggests that range expansion may result from a combination of small scale movement to marginal habitat (Ray & Corkum, 2001), larger scale range expansion, and by resource depletion, which are characteristic of range expansion in a variety of other invasive species (Dwyer & Morris, 2006). The mechanisms of such movements are hypothesized to result from intraspecific competition and behavioural differences amongst individuals (e.g. boldness and reproductive strategy). Furthermore, based on the distance from the area of first introduction, round gobies appear to disperse further downstream than upstream in a given period of time. Larval drift has been proposed as a means of range expansion (Bergstrom et al., 2008; Hayden & Miner, 2009), and our capture of only two very small ($\approx$30 mm TL) round gobies approximately 13 km downstream of any previous sighting in 2008 suggests that this may yet be another mechanism of dispersal for round goby. Based on the observations in this study, round gobies appear to successfully expand their range through mechanisms that parallel those used by other invasive populations, which makes the round goby a good candidate to test both empirical and theoretical hypotheses about species' invasions.

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References

Balshine, S. A., V. Verma, V. Chant & T. Theysmeyer, 2005. Competitive interactions between round gobies and logperch. Journal Great Lakes Research 31: 68–77.

Bergstrom, M. A. & A. F. Mesinger, 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. Transactions of the American Fisheries Society 138: 1009–1017.

Bergstrom, M. A., L. M. Evrard & A. F. Mensinger, 2008. Distribution, abundance, range of the round goby, *Apollonia melanostoma*, in the Duluth-Superior Harbor, St. Louis River Estuary, 1998–2004. Journal Great Lakes Research 34: 535–536.

Bøhn, T., O. T. Sandlund, P. Amundsen & R. Primicerio, 2004. Rapidly changing life history during invasion. Oikos 106: 138–150.

Carmen, S. M., J. Janssen, D. J. Jude & M. B. Berg, 2006. Diel interactions between prey behaviour and feeding in an invasive fish, the round goby, in a North American river. Freshwater Biology 51: 742–745.

Carol, J., L. Benejam, J. Benito & E. Garcia-Berthou, 2009. Growth and diet of European catfish (*Silurus glanis*) in early and late invasion stages. Archiv fur Hydrobiologie 174: 317–328.

Charlebois, P. M., J. E. Marsden, R. G. Geottel, R. K. Wolfe, D. J. Jude & S. Rudnicka, 1997. The round goby, *Neogobius melanostomus* (Pallas), a review of European and North American literature. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey. INHS Special Publication No. 20.

Chotkowski, M. A. & J. E. Marsden, 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. Journal of Great Lakes Research 25: 26–35.

Corkum, L. D., M. R. Sapota & K. E. Skora, 2004. The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. Biological Invasions 6: 173–181.

Correa, C. & M. R. Gross, 2008. Chinook salmon invade southern South America. Biological Invasions 10: 615–639.

Dianna, C. M., J. L. Jonas, R. M. Claramunt, J. D. Fitzsimons & J. E. Marsden, 2006. A comparison of methods for sampling round goby in rocky littoral areas. North American Journal of Fisheries Management 26: 514–522.

Djuricich, P. & J. Janssen, 2001. Impact of round goby predation on zebra mussel size distribution at Calumet Harbor, Lake Michigan. Journal Great Lakes Research 27: 312–318.

Dunstan, P. K. & N. J. Bax, 2007. How far can marine species go? Influence of population biology and larval movement on future range limits. Marine Ecology Progress Series 344: 15–28.

Dwyer, G. & W. F. Morris, 2006. Resource-dependant dispersal and the speed of biological invasions. The American Naturalist 167: 165–176.

Franch, N., M. Clavero, M. Garrido, N. Gaya, V. López, Q. Pou-Rovira & J. M. Queral, 2008. On the establishment and range expansion of oriental weatherfish (*Misgurnus anguillicaudatus*) in NE Iberian Peninsula. Biological Invasions 10: 1327–1331.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le & G. T. Skalski, 2001. Leptokurtic Movement Distributions: Intrapopulation Variation in Boldness and Exploration. The American Naturalist 158: 124–135.

Gonzalez, M. J. & G. A. Burkart, 2004. Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species, *Gammarus fasciatus* and *Echinogammarus ischnus*. Journal Great Lakes Research 30: 100–113.

Gutowsky, L. F. G., J. W. Brownscombe & M. G. Fox, 2011. Angling to estimate the density of round goby (*Neogobius melanostomus*). Fisheries Research 108: 228–231.

Hastings, A., K. Cuddington, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. Freestone, S. Harrison, M. Holland, J. Lambrinos, U. Malvadkar, B. A. Melbourne, K. Moore, C. Taylor & D. Thomson, 2005. The spatial spread of invasions: new developments in theory and evidence. Ecology Letters 8: 91–101.

Hayden, T. A. & J. G. Miner, 2009. Rapid dispersal and establishment of a benthic Ponto-Caspian goby in Lake Erie: diel vertical migration of early juvenile round goby. Biological Invasions 11: 1767–1776.

Hensler, S. R. & D. J. Jude, 2007. Diel vertical migration of round goby larvae in the great lakes. Journal Great Lakes Research 33: 295–302.

Holway, D. A., 1998. Factors governing rate of invasion: a natural experiment using Argentine ants. Oceologia 115: 206–212.

Janssen, J. & J. D. Jude, 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. Journal of Great Lakes Research 27: 319–328.

Jude, D. J., R. H. Reider & G. R. Smith, 1992. Establishment of Gobiidae in the Great Lakes Basin. Canadian Journal of Fisheries and Aquatic Science 49: 416–421.

Karlson, A. M. L., G. Almqvist, K. E. Skora & M. Appelberg, 2007. Indication of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES Journal of Marine Science 64: 479–486.

Klein, D. R., 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management 32: 350–367.

Kolar, C. S. & D. M. Lodge, 2002. Predictions and risk assessment for alien fishes in North America. Science 298: 1233–1236.

Kovtun, I. F., 1977. On the fecundity of the round goby, *Gobius* ([*sic*] *Neogobius*) *melanostomus* (Pallas), from the Sea of Azov. Journal of Ichthyology 17: 566–573.

Kovtun, I. F., 1979. Significance of the sex ratio in the spawning population of the round goby in relation to year-class strength in the Sea of Azov. Journal of Ichthyology 19: 161–163.

Krakowiak, P. J. & C. M. Pennuto, 2008. Fish and macroinvertebrate communities in tributary streams of eastern Lake Erie with and without round gobies (*Neogobius melanostomus*, Pallas 1814). Journal of Great Lakes Research 34: 675–689.

Kuhns, L. A. & M. B. Berg, 1999. Benthic invertebrate community response to round goby (*Neogobius melanostomus*) and zebra mussel (*Dreissena polymorpha*) invasion in southern Lake Michigan. Journal of Great Lakes Research 25: 910–917.

L'avrinčíková, M. & V. Kováč, 2006. Invasive round goby *Neogobius melanostomus* from the Danube mature at small size. Journal of Applied Ichthyology 23: 276–278.

Lederer, A. M., J. Janssen, T. Reed & A. Wolf, 2008. Impacts of the introduced round goby (*Apollonia melanostoma*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and on macroinvertebrate community between 2003 and 2006 in the littoral zone of Green Bay, Lake Michigan. Journal of Great Lakes Research 34: 690–697.

Llewelyn, J., B. L. Phillips, R. A. Alford, L. Schwarzkopf & R. Shine, 2010. Locomotor performance in an invasive species: cane toads from the invasion front have greater endurance, but not speed, compared to conspecifics from a long-colonised area. Oecologia 162: 343–348.

MacDougall, S. & R. Turkington, 2005. Are invasive species drivers or passengers of change in degraded ecosystems? Ecology 86: 42–55.

MacInnis, A. J. & L. D. Corkum, 2000a. Fecundity and reproductive season of the round goby *Neogobius melanostomus* in the Upper Detroit River. Transactions of the American Fisheries Society 129: 136–144.

MacInnis, A. J. & L. D. Corkum, 2000b. Age and growth of round goby (*Neogobius melanostomus*) in the Upper Detroit River. Transactions of the American Fisheries Society 129: 852–858.

Miller, P. J., 1986. Gobiidae. In Whitehead, P. J. P., M. L. Bauchot, J. C. Hureau, J. Nielson & E. Tortonese (eds), Fishes of the Northeastern Atlantic and the Mediterranean. UNESCO, Paris: 1019–1085.

Mineur, F., A. J. Davies, C. A. Maggs, M. Verlaque & M. P. Johnson, 2010. Fronts, jumps and secondary introductions suggested as different invasion patterns in marine species, with an increase in spread rates over time. Proceedings of the Royal Society B-Biological Sciences 277: 2693–2701.

Minns, C. K., J. E. Moore & K. E. Seifried, 2004. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1972-2001. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2694. Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, Burlington, ON

Moyle, P. B. & T. Light, 1996. Fish invasions in California: do abiotic factors determine success? Ecology 77: 1666–1670.

OMNR, 2009. Fisheries management plan for fisheries management zone 17: 2010-2020: 7.0 other fish species management strategy. Peterborough, Aurora and Bancroft Districts, ON, CA.

Phillips, E. C., M. E. Washek, A. W. Hertel & B. M. Niebel, 2003. The round goby (*Neogobius melanostomus*) in Pennsylvania tributary streams of Lake Erie. Journal of Great Lakes Research 29: 34–40.

Phillips, B. L., G. P. Brown, J. M. J. Travis & R. Shine, 2008. Reid's paradox revisited: the evolution of dispersal kernels during range expansion. American Naturalist 172: S34–S48.

Phillips, B. L., G. P. Brown & R. Shine, 2010. Life-history evolution in range-shifting populations. Ecology 91: 1617–1627.

Pintor, L. M., A. Sih & J. L. Kerby, 2009. Behavioral correlations provide a mechanism for explaining high invader densities and increased impacts on native prey. Ecology 90: 581–587.

Poos, M., A. J. Dextrase, A. N. Schwalb & J. D. Ackerman, 2009. Secondary invasion of the round goby into high diversity Great Lakes tributaries and species at risk hotspots: potential new concerns for endangered freshwater species. Biological Invasions 12: 1269–1284.

Raby, G. D., L. F. G. Gutowsky & M. G. Fox, 2010. Diet composition and consumption rate in round goby (*Neogobius melanostomus*) in its expansion phase in the Trent River, Ontario. Environmental Biology of Fishes 89: 143–150.

Ray, W. J. & L. D. Corkum, 2001. Habitat and site affinity of the round goby. Journal of Great Lakes Research 27: 329–334.

Salinas, F. V., 2006. Breeding behaviour and colonization success of the Cuban treefrog (*Osteopilus* septentrionalis). Herpetologica 62: 398–408.

Schaner, T., M. G. Fox & A. C. Taraborelli, 2009. An inexpensive system for underwater video surveys of demersal fishes. Journal of Great Lakes Research 35: 317–319.

Schöpf Rehage, J. & A. Sih, 2004. Dispersal behaviour, boldness, and the link to invasiveness: a comparison of four *Gambusia* species. Biological Invasions 6: 379–391.

Shea, K., E. Jongejans, O. Skarpaas, D. Kelly & A. W. Sheppard, 2010. Optimal management strategies to control local population growth or population spread may not be the same. Ecological Applications 20: 1148–1161.

Shigesada, N. & K. Kawasaki, 1997. Biological Invasions: Theory and Practice. Oxford University Press, Oxford: 205.

Siegel, S. & N. J. Castellan, 1988. Nonparametric Statistics for the Behavioral Sciences, 2nd ed. McGraw-Hill, NY.

Somers, C. M., M. N. Lozer, V. A. Kjoss & J. S. Quinn, 2003. The invasive round goby (*Neogobius melanostomus*) in the diet of nestling double-crested cormorants (*Phalacrocorax auritus*). Journal of Great Lakes Research 29: 392–399.

Stammler, K. L. & L. D. Corkum, 2005. Assessment of fish size on shelter choice and intraspecific interactions by round gobies *Neogobius melanostomus*. Environmental Biology of Fishes 73: 117–123.

Steinhart, G. B., E. A. Marschall & R. A. Stein, 2004. Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. Transactions of the American Fisheries Society 133: 121–131.

Tillberg, C. V., D. A. Holway, E. G. LeBrun & A. V. Suarez, 2007. Trophic ecology of invasive Argentine ants in their native and introduced ranges. Proceedings of the National Academy of Sciences of the United States of America 104: 20856–20861.

Wilson, D. S., A. B. Clark, A. Coleman & T. Dearstyne, 1994. Shyness and boldness in humans and other animals. Trends in Ecology & Evolution 9: 442–446.

Wolfe, R. K. & J. E. Marsden, 1998. Tagging methods for the round goby (*Neogobius melanostomus*). Journal of Great Lakes Research 24: 731–735.

Young, J. A. M., J. R. Marentette, C. Gross, J. I. McDonald, A. Verma, S. E. Marsh-Rollo, P. D. M. Macdonald, D. J. D. Earn & S. Balshine, 2010. Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. Journal of Great Lakes Research 36: 115–122.