Intra-population variability of life-history traits and growth during range expansion of the invasive round goby, *Neogobius melanostomus*

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Abstract Fish can undergo changes in their life-history traits that correspond with local demographic conditions. Under range expansion, a population of non-native fish might then be expected to exhibit a suite of life-history traits that differ between the edge and the centre of the population's geographic range. To test this hypothesis, life-history traits of an expanding population of round goby, *Neogobius melanostomus* (Pallas), in early and newly established sites in the Trent River (Ontario, Canada) were compared in 2007 and 2008. Round goby in the area of first introduction exhibited a significant decrease in age at maturity, increased length at age 1 and they increased in GSI from 2007 to 2008. While individuals at the edges of the range exhibited traits that promote population growth under low intraspecific density, yearly variability in life-history traits suggests that additional processes such as declining density and fluctuating food availability are influencing the reproductive strategy and growth of round goby during an invasion.

KEYWORDS: aquatic invasion, Gobiidae, life-history trade-off, non-native species, phenotypic plasticity, river.

Introduction

Many invasive species of fish have common characteristics that allow for successful colonisation of novel ecosystems (Sakai *et al.* 2001; Kolar & Lodge 2002; Olden *et al.* 2006). Some of these characteristics include a broad diet and aggressive behaviour (Beamish *et al.* 2005; Leunda *et al.* 2008) or phenotypic changes in life-history traits; for example, the mosquitofish, *Gambusia affinis* (Baird & Girard), stone loach, *Barbatula barbatula* (L.), and vendace, *Coregonus albula* L., exhibit changes to life-history traits in response to freshwater niche, salinity, seasonal temperature, intraspecific density and food availability or anthropogenic changes in lacustrine and fluvial habitats (Mills & Eloranta 1985; Haynes & Cashner 1995; Bøhn *et al.* 2004; Alcaraz & García-Berthou 2007).

Life-history theory can be used to predict an invasive species' phenotypic response (e.g. changes in age at maturity, reproductive allocation, growth) to the demographic and environmental conditions present following an invasion event (see Bøhn *et al.* 2004 and Fox *et al.* 2007). Life-history traits in fishes can vary in response to different environments and demographic conditions, as evidenced by differences in life-history traits between native and non-native populations of the same species (MacInnis & Corkum 2000a,b; Fox *et al.* 2007) and within a single population through time or in different habitats (Bøhn *et al.* 2004; Becker *et al.* 2008; Johnston & Post 2009). These observations suggest that fishes in the process of invasion might also be expected to experience predictable alterations to life-history traits.

The round goby, *Neogobius melanostomus* (Pallas), is a small benthic fish native to the Ponto-Caspian region of Eastern Europe (Charlebois *et al.* 1997). This fish was first observed in Lake St. Clair, Michigan, USA in 1990 and quickly spread throughout the

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Laurentian Great Lakes and many tributaries. Consequences of the invasion include altered benthic communities (Kuhns & Berg 1999; Djuricich & Janssen 2001; Gonzalez & Burkart 2004; Krakowiak & Pennuto 2008; Lederer *et al*. 2008) and uptake and transfer of toxins through the food web (Kwon *et al*. 2006). The round goby exhibits complex reproductive behaviour (e.g. paternal nest guarding) and a short generation time in invasive populations (MacInnis & Corkum 2000b). Its more precocial life-history traits have been suggested to give this species a short-term advantage over another invasive goby, *Neogobius kessleri* (Günther) (Kováč *et al*. 2009). Invasive round goby can also exhibit a suite of life-history traits that are different from native populations [e.g. earlier maturity at a smaller size (MacInnis & Corkum 2000a,b; L'avrinčíková & Kováč 2007)] and may shift from a highly precocial (i.e. well-developed fry) to less precocial life history (Kováč *et al*. 2009).

In this study, intra-population variations in growth and life-history traits were examined during a 2-year period in a river where the population was actively expanding its range. In the Trent River, round goby in the area of first introduction existed at densities that were 1.7–2.5 times those at the edges of the expanding population (Gutowsky *et al*. 2011). Given that demographic parameters, such as population density, can influence life-history traits (Charlesworth 1994; Rose & Cowan 2000; Abdoli *et al*. 2005) and that demographic parameters, somatic growth rates and life-history traits can change over the course of an invasion (Bøhn *et al*. 2004), it was hypothesised that life-history traits and growth rates would differ between established and less established segments of the population. Specifically, it was predicted that round goby occupying the pioneering edges of an expanding population would possess life-history traits that promote population growth (i.e. early maturity and high reproductive effort) and show higher somatic growth rates relative to individuals occupying the earliest established portion of their range. It was also predicted that, as the expansion front moves outward, round goby from the former edge of the range would show life-history traits similar to those occupying the earlier-established portion of their range.

Methods

Study location

The Trent River is part of a 12 550 km² watershed in southeastern Ontario, Canada (Minns *et al*. 2004). The main navigation channel is approximately 90 km in length from the eastern end of Rice Lake to the outlet in the Bay of Quinte, Lake Ontario (Fig. 1). The river also contains a number of dams and locks that are part of the Trent–Severn waterway. The diverse fish community includes pumpkinseed, *Lepomis gibbosus* L., bluegill, *Lepomis macrochirus* (Rafinesque), yellow perch, *Perca flavescens* (Mitchill), black crappie, *Pomoxis nigromaculatus* (Lesueur), rock bass, *Ambloplites rupestris* (Rafinesque), river redhorse, *Moxostoma carinatum* (Cope), brown bullhead, *Ameiurus nebulosus* (Lesueur), channel catfish, *Ictalurus punctatus* (Rafinesque), lake sturgeon, *Acipenser fulvescens* (Rafinesque), American eel, *Anguilla rostrata* (Lesueur), the introduced common carp, *Cyprinus carpio* L., and a variety of other cyprinids. Recreational game fishes include largemouth bass, *Micropterus salmoides* (Lacepède), smallmouth bass, *Micropterus dolomieu* (Lacepède), muskellunge, *Esox masquinongy* (Mitchill), northern pike, *Esox lucius* L., longnose gar, *Lepisosteus osseus* L., and walleye, *Sander vitreus* (Mitchill) (OMNR 2009).

The substrate in the river is generally composed of small and large rocks that are often colonised by quagga mussel, *Dreissena bugensis* (Andrusov), and zebra mussel, *Dreissena polymorpha* (Pallas). Common aquatic vegetation in the littoral zone includes watermilfoil, *Myriophyllum* spp., water plantain, *Heteranthera dubia* (Jacq.) MacMillan, water lily, *Nymphaea* spp., pondweed, *Potamogeton* spp., pickerelweed, *Pontederia cordata* L., and coontail, *Ceratophyllum demersum* L. Between Rice Lake (44°15′53″ N, 78°2′25″ W) and Crowe Bay (44°21′46″ N, 77°45′56″ W), the Trent River has a maximum depth of approximately 16 m and an average channel depth of 4.4 m (calculated from contour maps prepared by the Canadian Hydrographic Service, http://www.charts.gc.ca/). The mean monthly flow of the river is highly variable, but it is usually highest in April (167 m³ s⁻¹) and lowest in August (32 m³ s⁻¹; unpublished 1994 to 2004 data, D. Ness, Trent-Severn Waterway, Parks Canada). Sampling in 2007 and 2008 showed water temperature in the Trent River was similar throughout the system, with June and July temperatures averaging 24 °C.

Round goby were first reported in the river in 2003 at a location just downstream of Lock 18 in the town of Hastings (Fig. 1; Ontario Federation of Anglers & Hunters, unpublished data). It is believed that the initial introduction was the result of one or more bait bucket releases by anglers that brought round goby from the infested waters of Lake Ontario (F. MacDonald, Ontario Federation of Anglers & Hunters, personal communication). Since their discovery, round goby has undergone range expansion both upstream

Figure 1. The Trent River between Rice Lake and the Bay of Quinte, Lake Ontario, Ontario, Canada. Sampling locations with sampling year(s) are indicated by arrows and dashed ellipses. Samples were collected from the area of first introduction (CORE), the upstream edge (USE), and the downstream edge (DSE). The downstream edge in 2005 is also indicated. The general location of round goby isolated from the main population body are denoted by $\oplus$ for those identified in 2007 and by $\otimes$ for those identified in 2008. Stars represent a human settlement, diamonds represent the approximate location of locks (except Lock 18 which is located in Hastings), and the inset map shows the location of the study area relative to the Laurentian Great Lakes.

and downstream of the area where it was originally introduced (Gutowsky & Fox 2011). Potential obstacles to range expansion include Healey Falls and Locks 14–18.

Site selection

Extensive surveys to identify the distribution of round goby in the Trent River began in May 2006 using angling and beach seining at random locations, starting as far downstream as Lock 13 (Campbellford, Fig. 1) and working upstream towards the area of first introduction (Gan 2006). In 2006, round goby were found consistently up to 6 km downstream from the area of first introduction (herein referred to as the centre of range expansion, or CORE area). No surveys were completed upstream of Lock 18 (Hastings) in 2006. In 2007, surveys were conducted by seine netting, snorkelling and angling with small hooks (Gutowsky *et al.* 2011), beginning from the CORE area and working upstream and downstream of Lock 18. Seining took place in nearshore locations that comprised mainly small rocks, gravel and sand habitat, while snorkelling was used to survey nearshore sites where seining was impractical, e.g. water >2 m deep. Angling surveys targeted the central portion of the river and were

conducted in randomly selected locations from a 14.3-m boat. Surveys were conducted weekly in May and June 2006–2008 and also in August 2008.

Range edges in the Trent River were defined from the spring surveys as the furthest upstream or downstream areas in a given year where round goby could no longer be located up to 1 km beyond the main body of the population. Although small aggregations or individual goby were known to exist beyond the edges defined each year (Fig. 1), range expansion of the main body of the population was evident each subsequent year. Prior to 2007, round goby was not known to occur upstream of Lock 18, but by May of 2007, round goby could be consistently found approximately 2.4 km upstream of the original site of introduction. Surveys conducted downstream of the CORE area in 2006 showed that round goby could be found approximately 8 km from the CORE area. In 2007, the species was found 4 km further downstream, and by 2008, it was found downstream as far as the southern end of Crowe Bay.

Sampling

In 2007, round goby were collected from the CORE area and the upstream edge. In 2008, they were

collected from the former upstream edge established in the spring of 2007 (a strategy to examine whether life-history traits would remain consistent or change between years) and from the new downstream edge at the southern end of Crowe Bay.

Sampling occurred from 1 June to 8 August to correspond with the spawning period determined in a previous survey of the Trent River in 2006 (Gan 2006). Collections were made with a 15 m × 2 m, 6.4-mm^2 mesh bag seine. The actual sampling sites within the CORE, upstream edge and downstream edge areas were selected for accessibility from land, accessibility to spawning fish (depths < 1.5 m; Charlebois *et al.* 1997) and the absence of large obstructions. Although this technique does not capture round goby taking refuge under or beside rocks (e.g. some nest-guarding males), it was believed to be the most effective for sampling goby in the littoral zone. Sites were also standardised by habitat to minimise differences among the portions of the range sampled; all sampled sites contained a mix of sand, gravel and a minimum of rocks, with sparse aquatic macrophyte cover (mainly pondweed, coontail and watermilfoil). The slope of the littoral zone restricted most seining to within 5 m of shore.

Round goby was sampled at 10–14-day intervals during their reproductive period to account for this species' protracted spawning season (Charlebois *et al.* 1997). To ensure that localised removal did not have an effect on growth and life-history traits of the fish, multiple sites were seined within a location on a given date, and none were sampled more than twice per year.

Collection and processing

In the field, 15–30 fish were randomly selected from the seine net, euthanised using MS222 and transported on ice to Trent University where they were subsequently frozen. In the laboratory, a random selection of 10-20 frozen females were thawed and measured for TL (mm) and wet mass (0.01 g). Females were used to assess reproductive allocation, age at maturity, length at maturity, length at age and annual growth increment between age 1 and age 2. Females were the focus of this study, because the majority of their seasonal reproductive energy is allocated to egg production. Unlike females, males allocate their energy to sperm production, brood care (see Bertschy & Fox 1999) or the sneaker-male strategy where some males do not guard a brood but possess larger testis with more sperm (Marentette *et al.* 2009). However, males were also used to allow comparison of length at ages 1 and 2 and seasonal growth increment (age 1) between CORE

and edge areas. Annual growth increment could not be estimated for males because of small sample sizes of age-2 individuals.

Reproductive allocation was assessed using mature females and compared among locations using the gonadosomatic index (GSI; Fox & Crivelli 1998). GSI was calculated as 100 times the gonad mass divided by the body mass minus gonad mass (Snyder 1983). Maturity was assessed during ovary extraction. Females were considered mature if the ovaries contained yolked eggs and distinguishable red blood vessels, or if they were flaccid, indicating a past spawning event.

Scales were used to determine the age of sampled round goby, as well as to estimate length at age and growth increment. To estimate mean age at maturity, all of the females captured during the spawning season in a given location were pooled after first determining that there was no significant relationship between elapsed date and percent maturity. Mean age at maturity (α) was calculated from the percentage of mature fish of each age class using the formula from DeMaster (1978):

$$\alpha = \sum_{x=0}^{w} (x)[f(x) - f(x - 1)],$$

where x is the age in years, $f(x)$ is the proportion of sexually mature animals at age x and w is the maximum age of the sample. Length at maturity was also calculated with the DeMaster (1978) formula by using the percentage of mature females in 10 mm TL size classes in place of age (Trippel & Harvey 1987).

Mean length at age was estimated using the Fraser–Lee method of back calculation. The intercepts were calculated by regressing total length against scale length for all goby in a given year. In 2007 and 2008, the intercepts were 6.47 and 14.5, respectively. Lengths at ages 1 and 2 were estimable for males and females. Mean annual growth increment was calculated separately for CORE and edge areas for age-1 individuals (the age when most goby first matured) during their second year of life by estimating the change in back-calculated lengths between first and second annulus formation in age-2 individuals. A second growth indicator, seasonal growth increment (SGI), was calculated as per Fox and Crivelli (2001):

$$SGI = \frac{\sum_{i=1}^{N} [TL_{1i} - LBK_{1i}]}{N},$$

where TL_{1i} is the total length of the ith age-1 goby, LBK_{1i} is the Fraser–Lee back-calculated length at age

1 (Bagenal & Tesch 1978) of the ith age-1 goby and N is the total number of age-1 goby in the sample. Large samples of age-1 males allowed for the calculation of seasonal growth increment in 2008, but the small number of age-2 males restricted the estimation of annual growth increment to only females.

Data analysis

To test for differences in reproductive allocation among study areas, a mixed-model analysis of covariance was used with ovary mass as the dependent variable, somatic mass as the covariate, location as an independent variable, the location–somatic mass interaction term to test for parallelism and the date–location interaction as the error term. The analysis included dates from June to the end of July, as gonad mass was almost nil in August. To satisfy the assumption of linearity, somatic weight and ovary weight data were $\log_e$ transformed prior to analysis. As the downstream edge of expansion was not sampled in 2007, reproductive allocation was compared between the CORE area and the upstream edge of expansion in that year. A Tukey post hoc test was used to check for significant effects in the ANCOVA used to analyse reproductive allocation in 2008. The level of statistical significance for all tests was set at $P < 0.05$. The programme Statistica 8.0 (StatSoft, Tulsa, OK, USA) was used to conduct all statistical analyses.

Differences in age and length at maturity between females captured in the CORE and edge areas were assessed with the G-test (log-likelihood ratio). Maturity comparisons were based on the number of mature and immature females in a 'pivotal' age and size class, where pivotal represents the earliest class that achieved 50% maturity in a given year (Fox & Keast 1991). A significantly higher proportion of mature individuals in the pivotal age or size class in a given area was interpreted as earlier maturity or maturity at a smaller size, respectively, in that area.

Length at age between the CORE area and the upstream edge in each year was compared for age-1 and age-2 goby using fully factorial ANOVAs with year and location as the independent variables and length at age as the dependant variable. Because there were no available data for the downstream edge in 2007, comparisons for length at age between the CORE area and downstream edge were made for 2008 using independent t-tests for age-1 and age-2 females. No statistical analysis was carried out on age-3 individuals because of the small sample size.

Location and year (2007 and 2008) effects were tested on female annual growth increment using a two-way ANOVA. Because of a non-normal distribution at the downstream edge, a Mann–Whitney U test was used to compare annual growth increment between the downstream edge and the CORE area in 2008. Seasonal growth increments were compared between the CORE and edge areas (each sex, 2008 only) using independent t-tests.
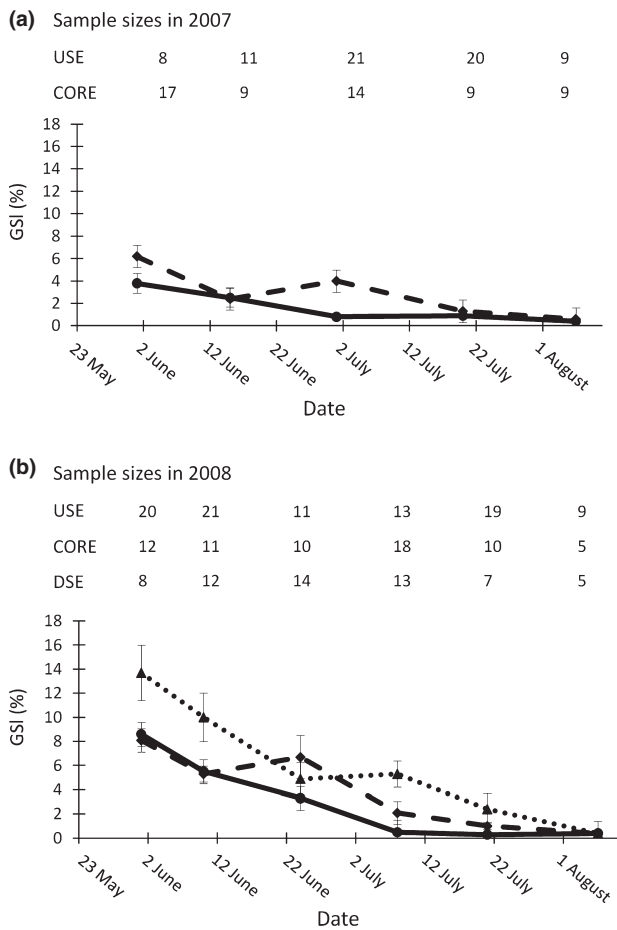
Results

Comparison of life-history traits

In 2007, female round goby that occupied the upstream edge matured earlier ($G = 2.91$, $P = 0.027$) and at a smaller size ($G = 6.22$, $P = 0.013$) than those in the CORE area (Table 1). The GSI of females declined in the CORE area throughout the month of June and was almost nil in July, whereas females from the upstream edge of their distribution exhibited GSI peaks at the beginning of June and again in the beginning of July (Fig. 2a). GSI in the upstream edge was higher than in the CORE area on every assessment date, and the seasonal mean GSI was about 29% higher at the upstream edge (2.80% $\pm$ 0.35 SE) than at the CORE (1.99% $\pm$ 0.35 SE). Analysis of covariance showed no violation of the assumption of homogeneity of slopes and no significant date effect, but there was a significant difference between the upstream edge and CORE area females in soma-adjusted ovary mass ($F_{1,3} = 8.55$, $P = 0.031$).

Unlike female goby sampled from the CORE and upstream edge in 2007, there was no significant difference between these locations in either age ($G = 0.547$, $P = 0.46$) or length at maturity ($G = 0.013$, $P = 0.91$) in 2008. Females from the downstream edge also exhibited no significant difference in age ($G = 0.047$, $P = 0.83$) or length at

Table 1. Mean age and total length at maturity for female round goby collected from the area of first introduction (CORE) and expanding upstream (USE) and downstream (DSE) edges of the population range in the Trent River in 2007 and 2008

	2007		2008	
	Age at maturity (year)	Length at maturity (mm)	Age at maturity (year)	Length at maturity (mm)
Location				
USE	1.2 (80)	63 (80)	1.3 (129)	62 (129)
CORE	2.0 (154)	83 (154)	1.5 (106)	68 (106)
DSE			1.2 (83)	63 (83)

Values in brackets are sample size.

(a) Sample sizes in 2007

USE	8	11	21	20	9
CORE	17	9	14	9	9

(b) Sample sizes in 2008

USE	20	21	11	13	19	9
CORE	12	11	10	18	10	5
DSE	8	12	14	13	7	5

Figure 2. Mean gonadosomatic index (GSI) $\pm$ 1 SE of female round goby collected from the area of first introduction [CORE, (—●—)], and the expanding upstream (·-◆-·) and downstream edges (····▲····) of the population in the Trent River in 2007 and 2008.

maturity ($G = 0.585$, $P = 0.44$) from those in the CORE area. In addition, a significantly lower proportion of females from the CORE area in 2007 were mature at age 1 (the pivotal age class) than in 2008 ($G = 28.6$, $P < 0.001$), whereas a significantly higher proportion of females (96%) were mature at age 1 at the upstream edge in 2007 than in the following year (72%; $G = 28.6$, $P < 0.001$). A greater proportion of females from the CORE area reached maturity at larger size (61–70-mm TL size class) in 2007 than in 2008 ($G = 5.49$, $P = 0.019$), whereas the number of goby that reached maturity in this size class did not differ at the upstream edge in 2007 compared with 2008 ($G = 2.30$, $P = 0.13$) (Table 1).

As was the case in 2007, GSI for females during the 2008 breeding season from the CORE area was highest at the beginning of the breeding season and showed no other peaks, whereas females from the upstream and downstream edges showed modest secondary peaks in reproductive allocation in the middle of the season (Fig. 2b). Once again, analysis of covariance showed no violation of homogeneity of slopes, but a significant difference among locations in soma-adjusted ovary mass ($F_{2,8} = 4.43$, $P = 0.025$), as well as a significant date effect ($F_{4,8} = 19.3$, $P = 0.004$). In 2008, female goby from the former upstream edge and the CORE area exhibited no significant difference in adjusted ovary mass (Tukey test, $P > 0.05$). However, even though GSI was almost equal on the first two sampling dates and the mean difference between these areas was lower in 2008 (approximately 22%) than in 2007, the shift was more a result of increasing GSI at the CORE area rather than decreasing GSI at the upstream edge. Mean GSI in females from the new downstream edge was greater than that of females from the CORE area on every date. The mean difference in GSI was also greatest between these two locations. The mean GSI in females increased from 2007 to 2008 in the CORE area (2007: 1.99% $\pm$ 0.35 SE; 2008: 3.44% $\pm$ 0.54 SE) and upstream edge (2007: 2.80% $\pm$ 0.35 SE; 2008: 4.39% $\pm$ 0.47 SE), and the mean GSI of females from the downstream edge was the highest of any location in both years (2008: 6.33% $\pm$ 0.79 SE; Fig. 2b).

Comparison of length at age and growth increment

Comparing length at age 1 of female goby between the CORE area and upstream edge showed a significant year–location interaction ($F_{1,342} = 4.98$, $P = 0.026$). Females at age 1 were almost 20% larger at the upstream edge than at the CORE area in 2007 (Tukey test, $P = 0.002$), whereas no difference existed in 2008 (Table 2). In addition, length at age 1 for females from the upstream edge did not differ between 2007 and 2008, whereas length at age 1 in the CORE area increased from 2007 to 2008 in the CORE area.

The length attained by age-2 females from the CORE area and upstream edge decreased from 2007 to 2008 ($F_{1,117} = 17.1$, $P < 0.001$), and there was no significant year–location interaction ($F_{1,117} = 0.702$, $P = 0.41$). Age-2 females from the upstream edge were significantly larger than those in the CORE area in 2007 and 2008 ($F_{1,117} = 24.6$, $P < 0.001$). Females at the downstream edge in 2008 were not significantly different in length at age 1 ($t_{144} = 1.16$, $P = 0.247$), but were significantly larger at age 2 than those at the CORE ($t_{48} = 3.32$, $P = 0.002$).

There was no location–year interaction for annual growth increment in females from age 1 to age 2 ($F_{1,124} = 0.40$, $P = 0.52$). In 2007, mean annual growth increment of females from the upstream edge

Table 2 Mean total length (mm) at age for female and male round goby collected from the area of first introduction (CORE) and expanding upstream (USE) and downstream (DSE) edges of the population in the Trent River in 2007 and 2008

		2007		2008	
	Location	Age 1	Age 2	Age 1	Age 2
♀	USE	47.4 (1.62, 57)[a,x]	84.4 (2.96, 20)[a,x]	48.2 (0.92, 109)[a,x]	78.1 (1.86, 27)[a,y]
	CORE	40.0 (1.60, 105)[b,x]	76.6 (1.61, 43)[b,x]	47.0 (1.2, 76)[a,y]	67.2 (1.13, 31)[b,y]
	DSE			49.0 (1.18, 70)[c]	72.8 (1.12, 19)[d]
♂	USE			49.2 (1.26, 57)[a]	74.3 (4.06, 2)
	CORE			48.1 (1.08, 55)[a]	64.9 (8.21, 4)
	DSE			53.7 (1.56, 55)[b]	79.9 (2.86, 3)

Values in brackets are SE, n.

[a,b]Means with different letters for fish of the same age and within the same year are significantly different ($P < 0.05$) between locations.

[x,y]Means with different letters for fish of the same age and within the same areas significantly different ($P < 0.05$) between years.

[c]Mean total length not significantly different from CORE area, t-test, $P > 0.05$.

[d]Mean total length significantly different from CORE area, t-test, $P < 0.05$.

was 42.6 mm ± 2.73 SE, whereas females from the CORE area had a mean annual growth increment of 35.0 mm ± 1.74 SE. Mean annual growth increment then decreased in both locations, as females from the upstream edge had a mean annual growth increment of 36.4 mm ± 1.39 SE and those from the CORE area had a mean annual growth increment of 31.1 mm ± 0.69 SE (Table 3). Overall, the mean annual growth increment of females in their second year of life was significantly higher in the upstream edge (39.3 mm ± 1.53 SE) than in the CORE area (33.4 mm ± 1.09 SE; $F_{1,124} = 12.7$, $P < 0.001$). The significant year effect resulted from faster growth in 2007 than in 2008 at both locations ($F_{1,124} = 8.00$, $P = 0.005$). Age-2 females from the downstream edge also had a significantly greater annual growth increment (37.0 mm, range 30–51 mm) than those in the CORE area (31.0 mm, range 22-38; Mann–Whitney $U = 4.22$, $n = 50$, $P < 0.001$).

Table 3 Mean annual growth increment in the second year of life determined from age-2 female round goby collected from the area of first introduction (CORE) and upstream edge (USE) of the population in the Trent River in 2007 and 2008

Location	2006–2007	2007–2008
CORE	35.0 (1.74, 46)[ax]	31.1 (0.69, 31)[ay]
USE	42.6 (2.73, 24)[bx]	36.4 (1.39, 27)[by]

Values in brackets are SE, n.

[a,b]Means with different letters for fish of the same age and within the same year are significantly different ($P < 0.05$) between locations.

[x,y]Means with different letters for fish of the same age and within the same areas significantly different ($P < 0.05$) between years.

Similar to the patterns seen with females, the length at age and seasonal growth increment of males indicated that those occupying edge locations experienced faster growth than those occupying the CORE area (Table 2; Fig. 3). Analysis of the final sampling dates in 2008 showed that the seasonal growth increment of age-1 males from the upstream edge (28.9 mm ± 1.7 SE) was significantly greater than those occupying the CORE area (22.1 mm ± 0.69 SE, $t_{26} = 3.5$, $P < 0.01$). Although the mean seasonal growth increment of males from the downstream edge was higher throughout the season, there was no
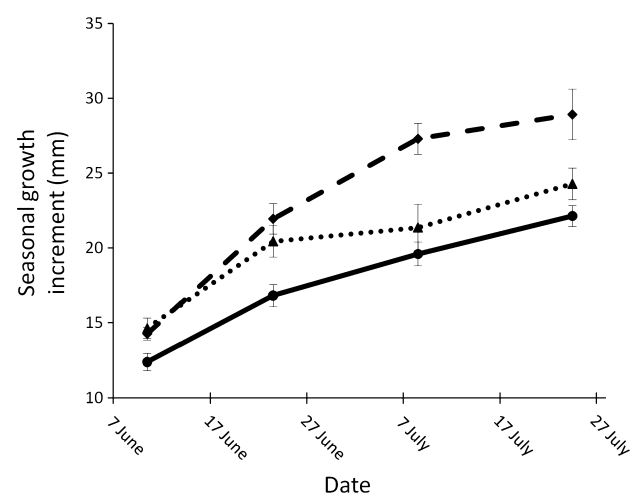
Figure 3. Seasonal growth increment ± 1 SE of age 1 male round goby collected from the area of first introduction (━●━), and expanding upstream (-◆-) and downstream (-▲-) edges of the population in the Trent River, 2008.

significant difference in growth increment between the downstream edge and CORE area males on the final sampling date ($P > 0.05$). In the case of females, individuals from the CORE area (25.8 mm ± 3.0 SE) showed no significant difference in seasonal growth increment on their final sampling date in 2008 compared with females from the upstream edge (26.2 mm ± 1.8 SE, $P > 0.05$), whereas females from the downstream edge (16.1 mm ± 1.6 SE) differed from those in the CORE ($t_{21} = 2.9$, $P < 0.05$).

Discussion

The round goby population in the Trent River exhibited significant differences in life-history traits and somatic growth between the area where it was first introduced and the edges of its expanding range. Population density at the periphery of an expanding invasive population should be lower than the area of first introduction (see Shigesada & Kawasaki 1997); and estimates generated by a stationary angling technique that depletes the local aggregation of large (> 45 mm TL) goby demonstrated this difference, with the highest densities in the CORE area (10 m^{-2}) and lower densities at the edges (upstream: 6 m^{-2}; downstream: 4 m^{-2}; data from 2008; Gutowsky et al. 2011). The interpretation is that the differences in life-history traits are partly functions of density and the intensity of intra-specific competition for resources. For instance, Raby et al. (2010) found that Trent River goby at the edges of the population's range had significantly fuller stomachs than goby in the CORE, which is compatible with the greater growth and higher GSI at the edge locations. In the current study, the edges of the round goby range generally showed the predicted trends in life-history traits. In 2007, the CORE area and upstream edge of the species' range exhibited the predicted differences in each of the investigated life-history traits, including smaller size at maturity, earlier maturity and significantly higher GSI at the upstream edge. A year later, the differences between these areas in the same life-history traits had shrunk. Concurrently, females from the downstream edge of the species' range exhibited the lowest density (4 m^{-2}), the earliest maturity and the highest annual GSI of the three study areas (Fig. 2). Early maturity, high reproductive investment and fast growth have been associated with low-density conditions in other fishes (see Weeks 1993; Museth et al. 2002), and increasing densities have been shown to lead to later age at maturity and even increased frequency of skipped spawning events (Johnston & Post 2009). Given the results of the current study, the life-history traits of round goby appear to be at least partially affected by intraspecific density during the invasion.

Although the life-history traits of round goby occupying the upstream edge of its river range became similar over time to those occupying the CORE area, this occurred because females in the CORE area shifted to become similar to those of the upstream edge while, at the same time, mean GSI increased in females caught from both areas from 2007 to 2008. Females at the upstream edge also showed delayed maturity but higher GSI in 2008 compared with 2007 (Fig. 2). One might expect little yearly variation in life-history traits in round goby at the CORE area, but goby here matured earlier and had a higher GSI in 2008 (3.44% ± 0.54 SE) than in 2007 (1.99% ± 0.35 SE). Density in an introduced species might be predicted to increase at the edges and remain relatively constant in the area where it was first introduced, but decreases in density are also known to occur years after establishment (Cox 2004; Simberloff & Gibbons 2004). For example, Johnson et al. (2005) demonstrated that round goby in central Lake Erie reached a relatively steady population size that was far lower than the peak observed in 1999. A similar but less extreme decline was observed in the round goby population occupying Hamilton Harbour (Lake Ontario, ON, Canada) over a 7-year monitoring period (Young et al. 2010). Round goby in the area of first introduction in the Trent River could have experienced an initial boom in population during the early years of colonisation (circa 2003), which was likely characterised by the same reproductive strategies seen in the current edge locations. Indeed, round goby could experience a variety of stressors during the establishment and expansion phases of an invasion, which would subsequently influence reproductive tactics. For instance, decreased reproductive effort accompanied by emigration from the high density CORE area in 2007 could have resulted in a shift back to life-history traits that promote population growth. Alternatively, an increase in benthic prey could have resulted in a trade-off between significantly lower growth and higher GSI in both the upstream edge and CORE area in 2008 compared with 2007. Other factors such as habitat or density-related differences in predation risk (Reznick & Endler 1982; Reznick et al. 1990; Brownscombe 2011) and environmental variability independent of invasion stage need also be considered as potential explanations for the observed changes in round goby life-history traits during this invasion.

Compared with the CORE area, round goby occupying both population edges showed relatively high

growth rates. Similar to the round goby in the Trent River (Gutowsky & Fox 2011) invasive wels catfish, *Silurus glanis* L., in Spain (Carol *et al.* 2009) and vendace in northern Scandinavia (Bøhn *et al.* 2004) have been found to attain larger maximum size in newly invaded areas. These authors hypothesised that greater sizes were attainable through increased food availability or lower population density in newly invaded sites. In the current study, the decline in growth increment from 2007 to 2008 in both CORE and upstream edge areas may reflect a trade-off between high GSI and post-maturational growth or a reduction in resource availability, as goby continue to exploit food resources (see Krakowiak & Pennuto 2008; Lederer *et al.* 2008). In addition to showing that Trent River round goby contained fuller stomachs and a greater number of high-quality food items (e.g. benthic invertebrates) at the edge of the range than in the area of first introduction, Raby *et al.* (2010) conducted an assessment of dreissenid mussels in the spring of 2008 and found that their density in the CORE area was about 10% of that in the upstream and downstream edges. Male seasonal growth increment seems to also indirectly reflect how round goby at the edges of its range are benefiting from greater food availability or higher quality food (Raby *et al.* 2010). Initially abundant, high-energy food resources, such as benthic invertebrates, may have declined with the expansion of the round goby population, which seems to result in decreased growth potential for round goby (see Ylikarjula *et al.* 1999). Further investigations into the changing round goby population and the benthic community along an invasion pathway would provide valuable insight into the impacts of round goby on native species.

The observed spatial and temporal life-history changes in the Trent River round goby population provide an example of how an invasive fish can exhibit life-history variation related to the stage of invasion. It is likely that density-dependent processes, biotic factors (e.g. changes in predation risk and food availability) and seasonal variability in abiotic factors [e.g. temperature (Angilletta *et al.* 2004) and flow velocity (Jonsson *et al.* 2001)] interact to influence the life-history traits observed at different stages of the invasion. Future research could examine life-history traits in response to diet (Raby *et al.* 2010), specific changes in density (Johnson *et al.* 2005), survivorship of adults relative to juveniles [e.g. brook trout, *Salvelinus fontinalis* (Mitchill) (Hutchings 1993) and pumpkinseed (Bertschy & Fox 1999)], the onset of disease such as viral haemorrhagic septicaemia (OMNR 2008) or the transitioning of predators to include the round goby as a major food source (King *et al.* 2006; Truemper *et al.* 2006; Taraborelli *et al.* 2010). Currently there are numerous round goby populations moving along multiple invasion pathways. It is recommended that these populations be the subject of research to bolster or contend theories in invasion biology and identify how population dynamics could be used to predict community-level reactions to an advancing invasion front.

Acknowledgments

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