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Consistent life history shifts along invasion routes? An examination of round goby populations invading on two continents

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Abstract

Aim: Many invasive populations exhibit dynamic life history shifts along their invasion route. We investigated whether these shifts represent consistent biological responses of a given species to range expansion, even in systems located in different geographic regions.

Location: North-eastern France, Central Ontario (Canada).

Method: We investigated population density, life history traits and age-specific reproductive investment in expanding populations of round goby at three invasion stages (expansion front, area colonized one year earlier and area colonized for ~five years) along the invasive routes in two river systems differing in climate and system productivity. Interindividual variability, shown to affect range expansion rates, was also investigated along the invasion routes. The study was based on female round gobies collected in three locations within each invasion stage twice monthly throughout the reproductive season (March/May to July).

Results: In both systems, reproductive investment was highest in the newly colonized area and decreased with time since colonization. A faster decrease in reproductive investment was found in the warmer, more productive system behind the invasion front, potentially associated with faster population growth and increased intraspecific competition. In both systems, individual variability in growth and reproductive traits increased from the newly colonized area to the areas of earlier colonization.

Main conclusions: The patterns observed in the two systems suggest a common invasion strategy independent of environmental conditions and highlight the dynamic nature of invasive populations' life history behind the invasion front. Common energetic allocation strategies can be expected at the invasion front. Range expansion may be associated with population growth induced by rapid acclimation to biotic conditions associated with range shift.

KEYWORDS

age-specific reproductive investment, biological invasion, interindividual variability, range expansion, range margin, round goby

1 | INTRODUCTION

Mechanisms that drive the expansion of invasive populations are a focus of research in reaction to the consequences of biological invasions. These mechanisms also attract scientific interest because of the implications of range expansion in other ecological phenomena such as climate change and the recolonization of locally extinct populations. An important but poorly understood element of the invasion process is its spatio-temporal context, which integrates the interaction of ecological processes occurring at various spatio-temporal scales (Levin, 1992; Pauchard & Shea, 2006). Once established, invasive species expand their range and are exposed to landscape heterogeneity in climate, resources, habitat types, connectivity and species interactions (Grosholz, 1996; Smith, Lucey, Waller, Childs, & Real, 2002). Changes in selection pressure are also induced by increases in population density following arrival (Bøhn, Sandlund, Amundsen, & Primicerio, 2004). Invasion dynamics (i.e., range expansion and population dynamics in newly colonized areas defining the expansion rate, and the lag time to further colonization and carrying capacity) are likely affected by the biotic and abiotic conditions encountered and the rate of population growth and depend on how individuals respond to selection pressure (Dwyer & Morris, 2006).

Phenotypic plasticity is important for enabling organisms to maintain fitness when confronted with environmental conditions differing from the species' native range, as well as conditions that change spatially and across invasion phases (Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006; Sakai et al., 2001). Shifts in life history traits along invasion routes are often facilitated by phenotypic plasticity (e.g., Bøhn et al., 2004), with shifts from an opportunistic strategy (*sensu* Winemiller & Rose, 1992) in a newly colonized area to an equilibrium strategy in areas where the species has been established for several years. At the invasion front, a population at low density experiences lower energetic costs related to reduced intraspecific competition and other factors (e.g., defence against pathogens), inducing changes in energy allocation to increase fitness (Llewellyn, Thompson, Brown, Phillips, & Shine, 2012). Offspring from consecutive generations develop under different biotic conditions due to the rapid population growth after arrival, likely inducing variation in the expression of life history traits.

Range expansion has been increasingly associated with the concept of population heterogeneity in movement, most notably the separation of stationary and mobile components (Rodriguez, 2002; Skalski & Gilliam, 2000). Spatial sorting theory predicts that organisms at the expansion front are selected for their ability to disperse, assembling individuals with traits directly related to range expansion such as speed, endurance and directional movement (Brown, Phillips, & Shine, 2014; Phillips, Brown, Webb, & Shine, 2006), but not necessarily those conferring benefit in reproduction (Shine, Brown, & Phillips, 2011). However, some theoretical studies suggest that selection operates on life history strategies at the invasion front and that the reproductive rate influences the rate of spread (Clark, Lewis, & Horvath, 2001; Dytham, Travis, Mustin, & Benton, 2014).

Population demography, dispersal rate and other biotic and abiotic conditions can influence invasion dynamics (Hastings et al., 2005; With, 2002). For example, Urban, Phillips, Skelly, and Shine (2008) demonstrated that the rate of range expansion by the cane toad (*Rhinella marina*) in Australia accelerated in regions with high temperatures, heterogeneous topography (including suitable water bodies for breeding), low elevation, high road density and high patch connectivity. Invasion dynamics can also be affected by the interindividual variability in the invasive population, induced by genetic divergence or phenotypic plasticity (Clark et al., 2001; Dytham et al., 2014).

In this study, we explore the phenomenon of range expansion of an invasive species by characterizing demography and life history shifts exhibited in two river systems, one in North America and the other in Europe. The round goby (*Neogobius melanostomus*), which is known to undergo rapid population growth and range expansion, was used as a model species. As a successful invader on both sides of the Atlantic Ocean (Corkum, Sapota, & Skora, 2004), the round goby has become a management priority because of the threat it represents to aquatic ecosystems (Kornis, Mercado-Silva, & Vander Zanden, 2012). We hypothesized that population density along both invasive routes would be affected by the time since colonization and that the pattern of shifts in life history traits along the two invasion routes would be similar, despite the differences in biotic and abiotic conditions between the two systems. Based on previous studies on range expansion of invasive species (Bøhn et al., 2004; Brownscombe & Fox, 2012), we predicted that (1) round goby density would be low, when an area is initially colonized, and then increase over time in both systems. We also predicted that (2) life history shifts along the invasion routes of the two systems would follow a common pattern, with individuals exhibiting a more opportunistic life history strategy (earlier maturation, smaller size at maturation, greater batch fecundity, lower investment in each oocyte and greater energetic reproductive investment relative to somatic growth) at the invasion front and shifting towards an equilibrium strategy with time since colonization (Burton, Phillips, & Travis, 2010; Phillips, Brown, & Shine, 2010). Finally, we predicted that (3) interindividual variability would be lowest at the invasion front and increase with time since colonization in the two systems.

2 | METHODS

2.1 | Study systems

The North American system used in this study is the Trent–Severn Waterway, a series of connected lakes, rivers and canals in a 12,550 km² watershed in south-eastern Ontario, Canada (Minns, Moore, Seifried, & Road, 2004). The round goby was first recorded in the Trent–Severn Waterway in 2003 near Hastings (Figure 1a). Brownscombe, Masson, Beresford, and Fox (2012) and previous annual surveys since 2005 localized the expansion front of the population of round goby each year until 2011. The expansion front was located on the upper part of the system in the Otonabee River.

The European system used in the study is the Moselle River. The Moselle originates at Bussang in the Vosges Mountains in France and

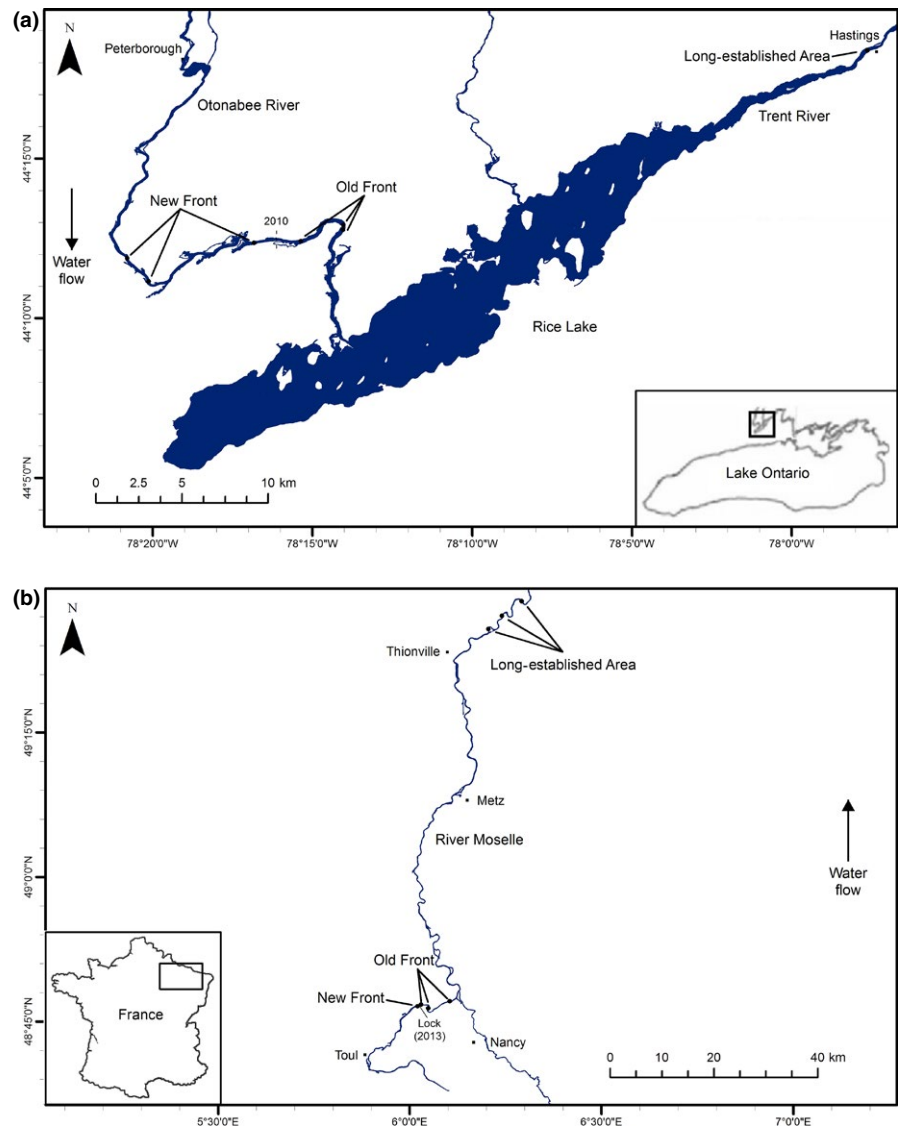


FIGURE 1 Location of the sampling sites in the new and old invasion fronts and the long-established area of the populations of round goby (*Neogobius melanostomus*) in expansion (a) in the Trent–Severn Waterway (Central Ontario, Canada) and (b) in the Moselle River (France) [Colour figure can be viewed at wileyonlinelibrary.com]

flows north for 560 km into Luxembourg and Germany to its mouth in the Rhine River, covering a 28,286 km² watershed (Uehlinger, Wantzen, Leuven, & Arndt, 2008). The Moselle has a warmer thermal regime (water temperature: Moselle, 6 months > 9°C; Otonabee, 5 months > 9°C, 9° being the temperature threshold for round goby to be active and reproduce [Charlebois et al., 1997]) and higher system productivity than the Trent–Severn, as indicated by the assessed average total phosphorus concentration in the sampling sites (Moselle: 0.10 mg/L (range: 0.08–0.12); Otonabee 0.02 mg/L (range: 0.005–0.032) and total nitrate concentration (Moselle: 4.31 mg/L (range: 2.50–6.30); Otonabee 0.02 mg/L (range: 0.01–0.38); see Appendix S1).

Study sites were located in the French section of the Moselle River (Figure 1b). The round goby was first recorded in the Koenigsmacker Reach of the river in 2011 (Manné, Poulet, & Dembski, 2013). Prior to initiating the study, we assessed the invasion history of round goby in the Moselle River and located its expansion front in 2014 using information from anglers (questionnaire and interviews) and field sampling (angling, seining and electrofishing).

2.2 | Fish collection

In the Trent–Severn Waterway, data on female gobies collected during the Gutowsky and Fox (2012) study from the area of first introduction (2003) from May to July in 2008 (Otonabee long-established area, LEA) and data on female gobies collected from May to July in 2011 during the Masson, Brownscombe, and Fox (2016) study from the two fronts were used in this study (Figure 1a). These gobies were sampled from the area that constituted the limit of range expansion detected in the autumn of 2010 (Otonabee old front, OF) and from the area constituting the limit of expansion detected in spring 2011 (Otonabee new front, NF), in the year sampling was conducted. In the spring of 2011, the round goby had moved 7.6 km upstream from the previous year's front.

Sampling in the Moselle River was conducted in 2014 for this study, using the same basic design as that of the aforementioned studies in the Trent–Severn. Female round goby were sampled from a long-established area (LEA) where it was first detected in 2011 in the Moselle River near the Luxembourg border. We believe that round

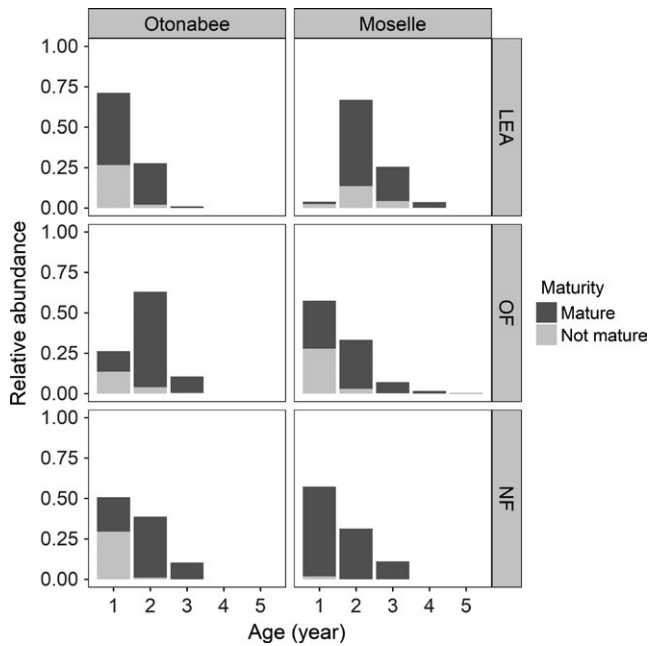


FIGURE 2 Distribution of age classes in female round gobies (*Neogobius melanostomus*) sampled from the long-established area (LEA), old front (OF) and new front (NF) in the Moselle and Otonabee rivers pooled over the reproductive season with proportion of mature female

goby had been present at that location since 2010, based on observations by local anglers. Females were also sampled from the upstream expansion front detected in autumn 2013 (Moselle old front, OF) and from the new expansion front detected in spring 2014 (Moselle new front, NF; Figure 1b). In the spring of 2014, the round goby had moved 4.5 km upstream the previous year's front.

Three sites were selected within each invasion stage area (i.e., LEA, OF and NF) with the following exceptions. Only one site had been sampled in the Otonabee LEA in the study of Gutowsky and Fox (2012), and only one site could be sampled in the Moselle NF due to limited expansion of the round goby from the OF. Sampling sites were standardized by habitat; all contained a mix of sand, gravel and rocky substrates (see Appendix S2). Substrate composition was determined by visual assessment from the river bank when fish were collected in shallow water or using an Aquaview S-series colour underwater camera (Nature Vision Inc., Brainerd, MN) when fish were collected in deeper water.

Round goby collection in the Moselle River followed the sampling protocol used in the Otonabee River in Gutowsky and Fox (2012) and Masson et al. (2016). Assessment of the maturity status of females began when the water temperature approached 9°C, and regular sampling commenced once females were found with maturing ovaries. Round gobies were sampled by angling twice monthly from March to July 2014 in the LEA and OF sites to account for their protracted spawning season. Collection of round gobies in the NF started in May when the population passed the limit of the previous year's front and lasted till July. Collections ceased when no female was found to contain maturing ovaries. Sex was determined by examination of

the urogenital papilla (Charlebois et al., 1997). A sample size of 20 females per site per collection date was targeted, with a minimum of 10 females in low-density areas. Round goby density was estimated at the end of May at each site using the stationary angling method described in Gutowsky, Brownscombe, and Fox (2011), consistent with the Masson et al. (2016) study. As only one site was sampled in the NF of the Moselle, two more density assessments were made for this site between the end of May and the beginning of June. No density data were available in the LEA of the Otonabee when it was sampled by Gutowsky and Fox (2012). Fish were euthanized using MS222 and were frozen for later analysis.

2.3 | Fish processing

In the laboratory, gobies were thawed, measured (total length, nearest mm) and weighed (nearest 0.01 g), and scales were collected from both sides of the fish in the anterior area between the lateral line and the dorsal fin. Females were considered mature if the ovaries contained yolked oocytes and distinguishable red blood vessels, or if ovaries were flaccid, indicating a past spawning event (Crivelli & Mestre, 1988). Mature females with flaccid ovaries and no maturing oocytes were removed from the analysis of reproductive allocation, reproductive effort and batch fecundity. Ovaries were preserved in modified Gilson's fluid (Macinnis & Corkum, 2000) to allow oocyte count and measurement. The maturation state of females from the studies of Gutowsky and Fox (2012) and Masson et al. (2016) was reassessed to standardize the maturity state among all sampling areas based on re-examination of the descriptive notes and photographs of the ovaries.

Scale annuli were used to determine the age of each female and to estimate the mean length-at-age and the growth increment (length increase after formation of the most recent annulus; Taraborelli, Fox, Johnson, & Schaner, 2010). Mean length-at-age was assessed using the Fraser-Lee back-calculation method (Bagenal & Tesgh, 1978). Mean seasonal growth increment was calculated separately for all invasion stages in the two systems for the fish collected in June and July.

Mean age-at-maturity (α) in each site and sampling area was estimated using all females captured during the breeding season using the formula of 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 mature females at age x , and w is the maximum age in the sample. The DeMaster formula was also used to calculate mean length-at-maturity from the percentage of mature females in 10-mm TL size classes (Trippel & Harvey, 1987).

Reproductive allocation was assessed in mature females only, using soma-adjusted ovary mass (ovary mass relative to a body mass covariate) and gonadosomatic index (GSI; Fox & Crivelli, 1998), calculated as the gonad mass divided by the body mass minus gonad

mass. The development stage of the oocytes was assessed based on the classification from Tomczak and Sapota (2006). Fecundity was assessed as soma-adjusted batch fecundity (batch fecundity relative to a body mass covariate) and weight-specific batch fecundity, calculated as the batch fecundity divided by the body mass minus gonad mass. Batch fecundity was assessed by counting the number of stage-3 and stage-4 oocytes (Masson et al., 2016). The largest diameter of 15 stage-3 and stage-4 oocytes per ovary was measured in both ovaries using Motic Images Advanced 3.2 from images captured via Moticam 480 camera.

Reproductive effort (RE) can be defined as the fraction of the total energy flux allocated to reproduction (Clarke, 1987), which is different from the reproductive allocation metric that is based on gonad and body mass. Reproductive effort was calculated as per Masson et al. (2014) and Masson et al. (2016):

$$RE = \frac{\Delta w_o}{\Delta w_o + \Delta w_s}$$

where RE is the reproductive effort over a given period, Δw_o is the change in ovary mass between the time of annulus formation and the time of sampling, and Δw_s is the change in somatic mass (eviscerated mass minus gonad mass) between the time of annulus formation and the time of sampling. A best-fit relationship between ln-transformed TL and ovary mass of immature individuals of a given population was generated to estimate the ovary mass of immature females at the time of annulus formation; Δw_o was calculated by subtracting the estimated immature ovary mass at TL of annulus formation from the ovary mass of mature females at the time of sampling. A best-fit relationship between ln-transformed TL and ln-transformed somatic mass of mature females of a given population and age was generated to estimate the soma mass at the back-calculated TL at the time of annulus formation.

Only the reproductive effort (RE) of females maturing for the first time in the season could be used for these energy estimates. RE was estimated on the month marking the start of the reproductive season (first month with at least five mature females). RE was estimated on the same month for all females of the same age (consistent among invasion stages and between systems). As delayed seasonal maturation is characteristic of small-bodied individuals of other species occupying warm water systems in the north temperate zone (Danylchuk & Fox, 1994; Ridgway, Shuter, & Post, 1991), we used an earlier sampling period to assess reproductive effort for age-2 and age-3 females than for age-1 females.

To investigate individual variability along the invasion routes, a coefficient of variation was calculated for each trait, invasion stage, sampling month and age. A coefficient of variation was calculated for reproductive (GSI, RE and weight-specific batch fecundity) and somatic growth parameters (seasonal growth increment and length-at-ages 1 and 2).

2.4 | Statistical analysis

To test the prediction that there is an increase in round goby density from NF to OF, differences in population density between invasion

stages and systems were tested with a two-way analysis of variance. To test our hypothesis that female round goby life history characteristics differ across the invasion route, we used a series of generalized linear mixed effect (GLMM) and linear mixed effect (LMM) models (see Appendix S3). Ovary mass relative to a body mass covariate and batch fecundity relative to a body mass covariate were used to analyse reproductive allocation and batch fecundity, respectively. For all these models, we first used AICc to establish the optimal structure of the random component with restricted maximum likelihood estimation (REML), including site, sampling month and/or individual fish as random effect (intercept) when supported ($\Delta AICc < 2$, Akaike, 1974; Burnham & Anderson, 2004). A random intercept was assumed to be normally distributed with a mean of zero and variance σ^2 . The optimal structure of the fixed components with maximum likelihood estimation (ML) was then established using stepwise backwards model selection (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We began with the full models (containing all terms) and conducted single-term deletions based on the importance of the terms as determined by their likelihood ratio (L-ratio). This procedure isolates only significant terms. Models were then validated by plotting residuals against fitted values and all independent variables (Zuur et al., 2009).

We used a three-way ANOVA to test whether the coefficient of variation of life history traits in female round goby differs along the invasion route. In the model, system, invasion stage, nature of the traits (reproductive traits or somatic growth traits) and the interaction terms were included as fixed effects.

Ovary mass, oocyte count and back-calculated length-at-age were ln-transformed to meet model assumptions. To carry out all statistical analyses on sufficient sample sizes, consecutive sampling dates were paired within each month. Due to small sample sizes, age-3 and older females were excluded from age-specific statistical analyses. All analyses were conducted using R3.1.1 (R CORE Development Team 2016), and significance was set at $p < .05$. GLMM and LMM were run using the "lme4" and "nlme" R packages, respectively; and all graphs were drawn with "ggplot2" package in R.

3 | RESULTS

3.1 | Timing of reproduction, range expansion and demographics

In the Moselle River, round gobies started to reproduce in March, but individuals were not detected above the previous years' expansion front until May. In the Otonabee River, round gobies did not start to reproduce until May, by which time individuals had already dispersed to the new front. The age structure of the two populations was similar in the NF, but differed by month (not shown in Figure 2) and in the OF and LEA (Figure 2).

Round goby density did not differ significantly between systems ($F_{1,8} = 2.5$, $p = .20$) and showed the same pattern of lower density at the NF and higher density at the OF in the Moselle (OF: 9.8 per $m^2 \pm 1.45$ SE; NF: 2.7 per $m^2 \pm 0.73$ SE) and Otonabee rivers (OF: 6.3 per $m^2 \pm 1.76$ SE; NF: 2.7 per $m^2 \pm 1.76$ SE; invasion stage: $F_{1,8} = 25.6$,

TABLE 1 Mean age and length-at-maturity, weight-specific batch fecundity, back-calculated length-at-age 1 and 2 and seasonal growth increment of females from the long-established area (LEA), old front (OF) and new front (NF) of the Moselle and Otonabee rivers. SE, number of sites and number of females are given in brackets for age and length-at-maturity. SE and number of females given for other parameters

System	Invasion stage	Age-at-maturity (year)	Length-at-maturity (mm)	Weight-specific batch fecundity (oocytes/g)		Oocyte diameter (mm)	Length-at-age (mm)			Seasonal growth (mm)		
				Age-1	Age-2		Age-1	Age-2	Age-3	Age-1	Age-2	
Moselle River	LEA	2.13 (0.12, 3.439)	83.40 (3.39, 3.447)	-	-	-	33.6 (3.4, 6)	77.5 (0.6, 294)	94.8 (0.9, 128)	38.5 (3.6, 13)	10.4 (0.7, 69)	
	OF	1.59 (0.10, 3.294)	70.27 (1.56, 3.334)	28.5 (2.6, 16)	27.2 (1.7, 35)	2.03 (0.01, 33)	44.2 (1.0, 87)	75.6 (1.0, 98)	111.9 (2.3, 27)	34.9 (1.9, 74)	6.5 (0.5, 54)	
	NF	1.04 (NA, 1, 54)	68.30 (NA, 1, 69)	32.1 (2.1, 19)	35.6 (2.1, 13)	2.00 (0.01, 29)	40.0 (1.5, 30)	83.1 (0.9, 17)	97.2 (4.2, 6)	40.1 (1.8, 26)	6.7 (0.9, 15)	
Otonabee River	LEA	1.47 (NA, 1, 94)	58.40 (NA, 1, 94)	-	-	-	47.4 (1.9, 42)	65.0 (1.1, 26)	85.4 (NA, 1)	25.1 (2.7, 43)	10.5 (1.2, 17)	
	OF	1.58 (0.13, 3.198)	65.83 (1.88, 3.257)	42.6 (3.2, 10)	28.1 (1.2, 52)	1.62 (0.01, 56)	42.0 (2.5, 25)	74.1 (0.9, 125)	84.9 (1.6, 21)	23.1 (2.6, 47)	8.1 (0.2, 91)	
	NF	1.63 (0.05, 3.268)	70.17 (2.07, 3.325)	43.1 (3.4, 29)	29.6 (1.5, 30)	1.65 (0.01, 40)	47.1 (1.4, 57)	78.8 (0.9, 104)	92.3 (1.4, 28)	20.0 (1.1, 126)	9.3 (0.4, 55)	

$p < .001$; system*invasion stage: $F_{1,8} = 3.0$, $p = .10$). Mean population density was also much higher in the LEA than in other invasion stages in the Moselle (29.8 per $m^2 \pm 7.6$ SE). No density data were available for the Otonabee LEA.

3.2 | Life history traits

In the analysis of age-at-maturity, the optimum model for maturity state included age (L -ratio = 242.1, $df = 4$, $p < .0001$), system (L -ratio = 27.7, $df = 4$, $p < .0001$), invasion stage (L -ratio = 42.5, $df = 6$, $p < .0001$) and the interactions between system and invasion stage (L -ratio = 25.8, $df = 3$, $p < .0001$) and between age and invasion stage (L -ratio = 37.7, $df = 3$, $p < .0001$). In the analysis of length-at-maturity, the optimum model for maturity state included length (L -ratio = 300.0, $df = 2$, $p < .0001$), system (L -ratio = 22.6, $df = 2$, $p < .0001$), invasion stage (L -ratio = 22.5, $df = 4$, $p < .001$) and the interactions between system and invasion stage (L -ratio = 21.9, $df = 2$, $p < .0001$) and between length and system (L -ratio = 48.7, $df = 1$, $p < .0001$; see Appendix S4). In the Moselle River, females in the NF were maturing at a younger age than those in the OF, which in turn were maturing younger than in the LEA (Table 1). Females in the Otonabee did not show the same pattern in that mean age-at-maturity was similar among invasion stages. In the Moselle River, females in the NF and OF were maturing at a smaller size than in the LEA, and in the Otonabee River, females in the NF and OF were maturing at a larger size than in the LEA.

Site was maintained as random effect ($AIC_{c,full\ model} = 1015.1$; $AIC_{c,full\ model+random\ effect} = 1015.2$). Ovary mass increased with soma mass (LMM, $F_{1,583} = 647.2$, $p < .0001$). There was a significant difference among invasion stages in ovary mass (soma-adjusted) of all mature females pooled (LMM, $F_{2,8} = 10.96$, $p = .005$) with no significant difference between systems (LMM, $F_{1,8} = 0.13$, $p = .73$), nor interaction between invasion stage and system (LMM, $F_{2,8} = 0.91$, $p = .44$). Soma-adjusted ovary mass increased from the LEA to the OF and from the OF to the NF in both systems, although the latter was not always the case in GSI plots of Moselle River gobies (Figure 3). Soma-adjusted ovary mass also decreased over the breeding season (LMM, $F_{4,583} = 13.19$, $p < .0001$), with a significant interaction between body mass and sampling month (LMM, $F_{4,583} = 2.98$, $p = .02$). In the Moselle River, soma-adjusted ovary mass was higher in the NF than in the OF in age-1 females, but no significant difference was found in the Otonabee River (Table 2; Figure 3). In the Moselle and Otonabee rivers, age-2 females in the NF had a higher soma-adjusted ovary mass than in the OF and LEA (Table 2; Figure 3). In the Moselle and Otonabee rivers, age-1 and age-2 females in the NF exhibited greater reproductive effort than those in the OF (Table 2, Figure 4). The later results highlight that, from the end of winter until spawning, a period of geographic separation between individuals in the NF and OF and likely a period of dispersion for individuals arriving in the NF, females from the NF allocated more energy into their reproduction relative to their growth than in the OF.

In the Moselle, age-1 and age-2 females from the NF exhibited a greater batch fecundity (soma-adjusted) than in the OF, but the

difference was not found in the Otonabee (Tables 1 and 2). The optimal model for oocyte diameter included individual fish as random effect ($AIC_{c_{FM}} = -22005.0$, $AIC_{c_{FM} + EF} = -28,111.0$) and system (L -ratio = 35.3, $df = 4$, $p < .0001$) and sampling month (L -ratio = 27.6, $df = 4$, $p < .0001$) as fixed effects. Oocytes in Moselle River females were larger in diameter than those of Otonabee River females (ANOVA, $F_{1,152} = 97.0$, $p < .0001$; Table 1).

3.3 | Length-at-age and seasonal growth

In the Moselle River, mature age-1 and age-3 females in the NF were smaller at annulus formation than in the OF, and in the Otonabee River, mature age-1 and age-3 females in the NF were larger than in the OF (Tables 1 and 3). No significant difference in back-calculated length-at-age 2 was found among invasion stages in either system. No significant difference in seasonal growth increment of mature age-1 or age-2 females was found among invasion stages in either system (Tables 1 and 3). Age-1 females grew more in their first year in the Moselle than in the Otonabee.

3.4 | Interindividual variability

Individual variability in both systems (as indicated by coefficient of variation) was found to be lower in the NF than in the LEA when considering reproductive traits and the traits associated with somatic growth (ANOVA, $F_{2,143} = 3.32$, $p = .033$; Figure 5). OF was intermediate (or equal for reproduction in Otonabee River) between the LEA and the NF. No difference in individual variability was found between the two systems (ANOVA, $F_{1,143} = 0.001$, $p = .97$). Overall, individual variability in reproductive traits was greater than that of traits associated with somatic growth (ANOVA, $F_{1,143} = 30.90$, $p < .0001$).

4 | DISCUSSION

The mechanisms driving range expansion and establishment of invasive species remain unclear, in part because of the differences in source populations and in biotic and abiotic conditions encountered in different systems (Monzón-Argüello et al., 2015; Stepien, Brown, Neilson, & Tumeo, 2005; With, 2002). In our study, the results demonstrate that life history shifts along the invasion routes of round goby on two different continents follow a similar pattern, with a more equilibrium life history strategy in the longer-established area to a more opportunistic life history strategy at the expansion front. Moreover, the results support our prediction that interindividual variability in growth and reproductive traits would be lower at the invasion front and increase with time since colonization in the two systems.

In both systems, shifts in life history traits from the longer-established area to the newly colonized area were mainly demonstrated by an increase in reproductive investment (reproductive allocation, reproductive effort and batch fecundity). Females in the NF exhibited greater reproductive allocation than in the OF, which in turn was greater than in the LEA. Females in the NF also exhibited higher batch fecundity than in the OF in the two systems, with no difference in oocyte diameter. Although no significant difference in the soma-adjusted batch fecundity of age-1 and age-2 females was found between the OF and the NF in the Otonabee, batch fecundity increased from the OF to the NF when analysing all female ages pooled (see Masson et al., 2016). Mean seasonal growth increment was found to decrease from the LEA to the invasion fronts and not to differ significantly between the NF and OF in both systems. These data indicate that reproduction was prioritized over somatic growth at the front. It is likely that resource availability was reduced with the rapid increase in population density in the OF, inducing a shift towards a more equilibrium strategy (Winemiller & Rose, 1992). The higher reproductive

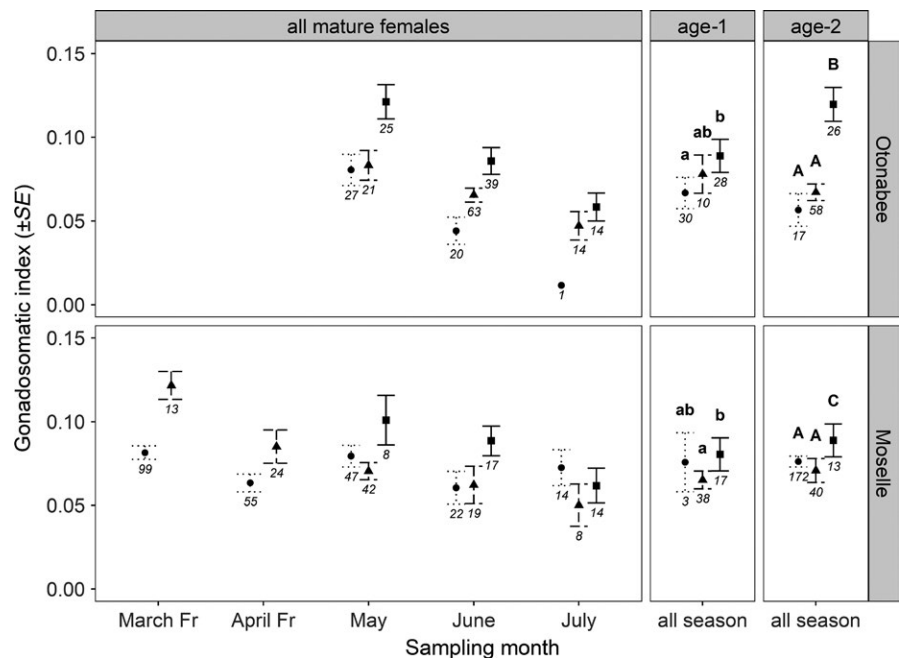


FIGURE 3 Mean gonadosomatic index of mature female round gobies (*Neogobius melanostomus*) sampled from the long-established area (LEA: circle, dotted line), old front (OF: triangle, dashed line) and new front (NF: square, solid line) in the Moselle and Otonabee rivers during the reproductive season. Panels from left to right show all mature females pooled by sampling month; age-1 females pooled over the sampling period; and age-2 females pooled over the sampling period. Error bars are SE. Sample size is indicated below each data point

TABLE 2 Linear mixed effect models of the effects of body mass (M), invasion stage (I) and system (Sy) on reproductive allocation (RA, estimated as gonad mass) and batch fecundity (estimated as the number of stage-3 and stage-4 oocytes) and of invasion stage (I) and system (Sy) on reproductive effort (RE) of age-1 and age-2 mature female round goby. The random effect(s) used in each model was indicated with the AICc of the full model with ($AICc_{FM+random\ effect}$) and without ($AICc_{FM}$) random effect(s). Significant model terms are shown in boldface

Trait	Random effect		Model term	df	F	p
RA	None ($AICc_{FM} = 244.7$; $AICc_{FM+REff(site)} = 247.3$)	Age-1	Body mass	1,115	120.78	<.0001
			Invasion stage	2,115	2.85	.028
			System	1,115	2.04	.16
			Sampling month	3,115	2.11	.10
			M × Sy	1,115	3.47	.07
			I × Sy	2,115	3.22	.044
	Site ($AICc_{FM} = -41.3$; $AICc_{FM+REff(site)} = -39.3$)	Age-2	Body Mass	1,306	2000.38	<.0001
			Invasion stage	2,8	10.36	.006
			System	1,8	0.15	.71
			Sampling month	4,306	8.32	<.0001
			M × Sy	1,306	1.05	.31
			I × Sy	2,8	2.35	.16
RE	None ($AICc_{FM} = -81.5$; $AICc_{FM+REff(site)} = -79.3$)	Age-1	Invasion stage	1,47	18.76	<.0001
			System	1,47	11.09	.0017
			I × Sy	1,47	0.49	.5
	None ($AICc_{FM} = -31.0$; $AICc_{FM+REff(site)} = -28.6$)	Age-2	Invasion stage	2,88	3.70	.03
			System	1,88	0.65	.42
			I × Sy	2,88	2.06	.13
Batch fecundity	None ($AICc_{FM} = 291.2$; $AICc_{FM+REff(site)} = 293.8$)	Age-1	Body Mass	1,63	114.16	<.0001
			Invasion stage	1,63	4.94	.03
			System	1,63	0.65	.42
			Sampling month	2,63	4.50	.01
			I × Sy	1,66	1.19	.28
			Site ($AICc_{FM} = 77.1$; $AICc_{FM+REff(site)} = 78.6$)	Age-2	Body Mass	1,101
	Invasion stage	1,6			7.45	.034
	System	1,6			3.15	.13
	Sampling month	2,101			5.12	.008
	I × Sy	1,6			9.97	.02

investment in the NF in both the Otonabee and Moselle populations indicates that life history traits are dynamic at the invasion front and that the gradient from opportunistic to equilibrium life history traits along invasion routes is not unique to a particular system. Given their geographic separation, the two populations may have originated from different sources and may therefore have had pronounced genetic differences (Snyder & Stepien, 2017). The same patterns found in the two systems suggest a similar biological response to range shift despite the difference in environmental conditions and likely genetic differences. The mechanism inducing the similar pattern in life history shifts was either phenotypic plasticity (Bøhn et al., 2004; Cotto, Kubisch, & Ronce, 2014), spatial sorting (Shine et al., 2011) or the two acting in tandem as enhanced spatial selection (Perkins, Phillips, Baskett, & Hastings, 2013; Quinn, Kinnison, & Unwin, 2001).

An increase in interindividual variability in life history traits from the invasion front to the longer-established area was exhibited by

both expanding populations. This finding suggests that specific traits, such as high reproductive investment, are assembled at the expansion edge, independent of the biotic and abiotic conditions encountered. Spatial sorting predicts that individuals exhibiting dispersal-enhancing traits accumulate at the expansion edge (Shine et al., 2011). Spatial sorting may also assemble individuals at the expansion front that are able to exhibit high reproductive investment despite the energetic cost of dispersal (Clark et al., 2001; Phillips et al., 2010). Alternatively, the greater degree of life history variation in the longer-established area may have been induced by density-dependent resource limitation; as under density-dependent conditions, the variation in size structure, growth rate, ovary size and egg number can increase due to unequal consumption of resources among individuals (Keeley, 2001; Rubenstein, 1981). Dytham et al. (2014) used an individual-based model to investigate the spatial dynamics of species' range shift to demonstrate that range expansion

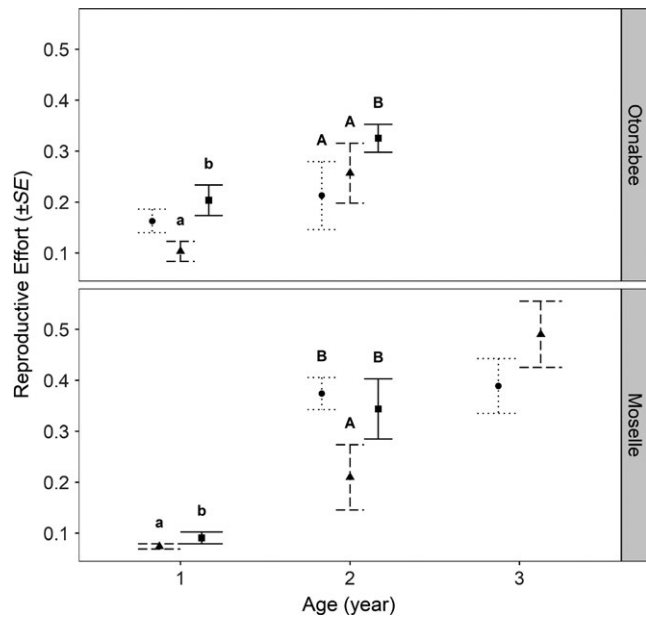


FIGURE 4 Mean reproductive effort \pm SE of age-1, age-2 and age-3 mature female round gobies (*Neogobius melanostomus*) sampled from the long-established area (LEA: circle, dotted line), old front (OF: triangle, dashed line) and new front (NF: square, solid line) in the Moselle and Otonabee rivers. Error bars are SE

would slow when interindividual variability is removed. Whether driven by genetic variation or resource limitation, variation in the expression of life history traits may influence invasion dynamics (Dytham et al., 2014).

Warmer temperatures in the Moselle River undoubtedly extended the duration of the round goby reproductive season relative to the

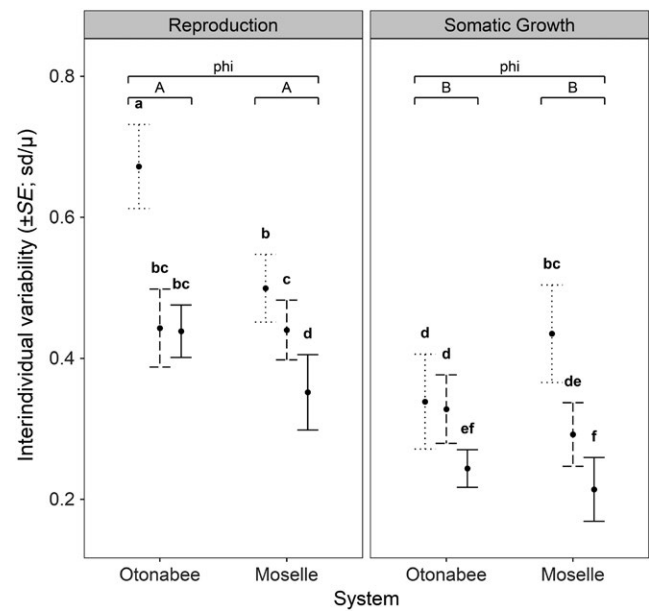


FIGURE 5 Variation in the expression of life history traits of female round goby (*Neogobius melanostomus*) sampled from the long-established area (LEA: circle dotted line), old front (OF: triangle, dashed line) and new front (NF: square, solid line) in the Moselle and Otonabee rivers. Traits were grouped into reproductive investment and somatic growth categories. (See text for details.) Error bars are SE. Capital letters indicate statistical significance between systems and Greek letters between reproductive and somatic growth traits

Otonabee River, due to an earlier occurrence of the 9°C threshold for round goby to be active and reproduce (Charlebois et al., 1997). The longer reproductive season in the Moselle would likely induce

TABLE 3 Linear mixed effect models of the effects of invasion stage (I) and system (Sy) on length-at-age 1 and seasonal growth of age-1 mature females, length-at-age 2 and seasonal growth of age-2 females and length-at-age 3 of age-3 female round gobies. The random effect(s) used in each model was indicated with the AICc of the full model with ($AICc_{FM+REF}$) and without ($AICc_{FM}$) random effect(s). Statistically significant model terms are highlighted in boldface

Trait	Random effect	Model term	df	F	p	
Length-at-age	Sampling month ($AICc_{FM} = 1,877.3$; $AICc_{FM+REF(sampling\ month)} = 1846.9$; $AICc_{FM+REF(site)} = 1,849.0$; $AICc_{FM+REF(sampling\ month + site)} = 1,877.3$)	Age-1	Invasion stage	2,242	0.44	.64
		mature	System	1,242	5.58	.019
			I × Sy	2,242	6.20	.002
	Site + Sampling month ($AICc_{FM} = 4,938.8$; $AICc_{FM+REF(sampling\ month)} = 4,917.0$; $AICc_{FM+REF(site)} = 4,896.5$; $AICc_{FM+REF(sampling\ month + site)} = 4,848.4$)	Age-2	Invasion stage	2,4	1.10	.41
			System	1,5	11.00	.02
			I × Sy	2,4	0.89	.48
	Site ($AICc_{FM} = 589.9$; $AICc_{FM+REF(sampling\ month)} = 592.2$; $AICc_{FM+REF(site)} = 590.8$; $AICc_{FM+REF(sampling\ month + site)} = 597.7$)	Age-3	Invasion stage	1,6	0.09	.27
			System	1,6	34.53	.001
			I × Sy	1,6	10.26	.02
Seasonal growth increment	Sampling month ($AICc_{FM} = 180.3$; $AICc_{FM+REF(sampling\ month)} = 151.9$; $AICc_{FM+REF(site)} = 164.0$; $AICc_{FM+REF(sampling\ month + site)} = 154.1$)	Age-1	Invasion stage	2,147	0.64	.53
		mature	System	1,147	101.32	<.0001
			I × Sy	2,147	1.80	.17
	Site + Sampling month ($AICc_{FM} = 383.9$; $AICc_{FM+REF(sampling\ month)} = 362.8$; $AICc_{FM+REF(site)} = 364.8$; $AICc_{FM+REF(sampling\ month + site)} = 364.9$)	Age-2	Invasion stage	2,9	0.45	.65
			System	1,9	0.51	.49
			I × Sy	2,9	2.17	.17

greater fecundity over the season. Furthermore, individuals hatching earlier in the season have a greater chance to survive the winter, especially if the overwinter period is shorter as it is in the Moselle, allowing more energy to be accumulated during a longer growing season (Post & Evans, 1989; Shuter, Maclean, Fry, & Regier, 1980). Round goby recruitment in the Moselle may therefore be greater than in the Otonabee, which would explain the tendency for faster population growth in the Moselle after first arrival (from NF to OF). Population growth in the Moselle River should be facilitated by high ecosystem productivity, which likely induces greater resource availability than in the Otonabee (see Appendix S1).

Age-specific energetic allocation along the invasive routes revealed a delayed ecological adjustment behind the invasion front in the Otonabee relative to the Moselle. Our results suggest a faster increase in energetic investment into somatic growth relative to reproduction after first colonization and a tendency for greater shifts in age and length-at-maturity in the Moselle than in the Otonabee River. Bøhn et al. (2004) also identified a delay in life history shifts associated with slower population growth of vendace (*Coregonus albula*) in the system with lower resource availability. The warm thermal regime and high system productivity in the Moselle may allow faster population growth, inducing the population to more rapidly reach conditions where resource availability is largely density-dependent.

In summary, the pattern of decrease in reproductive investment from the newly colonized to the longer colonized area at both fine and coarse scales suggests a common response to similar changes in biotic and abiotic conditions due to range expansion, characterized by a shift from density-independent to density-dependent conditions. The more rapid shifts in life history traits and increased life history variation observed in the Moselle relative to the Otonabee River highlight the dynamic nature of life history traits behind the invasion front. Previous studies suggested that the difference in invasion dynamics may be associated with differences in selection pressure along invasion routes and in the traits favoured at the expansion front (Urban et al., 2008). In our study, in two expanding populations of round goby, the same life history traits aggregate at the expansion front but do not dissipate at the same rate. The pattern of shifts in life history traits and the progression of interindividual variability characterized along the invasive routes provide valuable knowledge about the characteristics of invading species populations. Further research is needed to determine whether the type of differences observed between the two systems is driven by differences in temperature, system productivity, differences in gene pools or other factors.

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BIOSKETCH

The coauthors of this study share research interest in understanding invasion dynamics in aquatic systems. We investigate the invasion dynamics (range expansion and population dynamics) and impacts of aquatic invasive species on native communities in various environments and systems. Our research aims to improve understanding of the role of micro-evolutionary processes in the range expansion of invasive populations into novel environments. We also aim to investigate how aquatic system management may favour dispersion of invasive species through habitat destruction, canalization, ship transportation and diverse hydraulic structures. We use novel survey tools (environmental DNA) and data analysis (occupancy models) to investigate the detection potential at an early invasion stage in diverse environments, which can serve to develop survey protocols.

Author contribution: LM, GM, JNB and MGF conceived the ideas. LM and GM collected the data. LFGG provided data for one site. LM performed the analysis with advice provided by LFGG. LM led the writing with contribution from all authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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