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ORIGINAL PAPER

Testing a personality-dispersal hypothesis: behavioural comparisons along a round goby invasion gradient

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Abstract Behaviour is thought to drive dispersal of invasive species and populations, with bold, exploratory and active individuals pushing expansion range. We tested this hypothesis in the round goby (*Neogobius melanostomus*) along an invasion gradient in Ontario, Canada. We collected fish from a core population established two decades ago, and from an edge population representing a six-month-old invasion front, and we compared the personality traits of a subset of size-matched males from these core and edge populations. Four behaviours assessed showed significant repeatability (after a one-week interval) and they were correlated together in a behavioural syndrome. Based on these correlated traits, we calculated a proactivity score (*based on* boldness and activity) for each fish. In contrast to expectations, the core and edge fish did not differ in their proactivity levels. We did uncover a strong correlation between body size and behaviour, in which the smallest fish were the most proactive. Our results show that after controlling for sex and size there was no clear influence of personality facilitating dispersal along the investigated round goby invasion gradient. Our results challenge the idea that personality always drives range expansion, warranting further exploration into the strength of this association.

Keywords Biological invasion · Invasive fish species · Proactivity · Dispersal syndrome · Body size · Trent-Severn Waterway

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Introduction

Biological invasions occur when a species is intentionally or accidentally introduced outside of its native range, manages to establish and spread within this new environment, and begins to cause harm to the recipient ecosystem, to the economy or to human health (Blackburn et al. 2011; Pyšek et al. 2020, Convention on Biological Diversity 2008). Invasions have profound ecological impacts, by influencing factors such as local species richness and food webs structure (Bellard et al. 2016; Crystal and Lockwood 2020; Wainright et al. 2021), and can cause a massive economic burden (Diagne et al. 2021; Bodey et al. 2025). The pervasiveness of biological invasions is now recognized as a leading cause of biodiversity erosion (Jaureguiberry et al. 2022), and the number of invasions per year has been increasing with no clear signs of deceleration (Seebens et al. 2017, 2021). Hence, understanding the mechanisms underlying range expansion is an essential step that will help select and streamline cost-effective mitigation strategies (Cuthbert et al. 2022; Garcia-Lozano et al. 2025).

Over thirty different hypotheses have been proposed to explain what drives the successful establishment and spread of non-native species (Enders et al. 2018). One notable theme across these hypotheses is the idea that animal personality influences the invasion process (Holway and Suarez 1999; Chapple et al. 2012; Sih et al. 2012; Wong and Candolin 2015; Weis and Sol 2016; Ruland and Jeschke 2020). Animal personality is defined as showing consistent behavioural tendencies over time and across contexts (Carere and Maestripieri 2013). There is accumulating evidence suggesting that proactive behavioural tendencies (*e.g.* being bold, active, exploratory, asocial and aggressive towards intra and interspecific individuals) are associated with invasive populations (Duckworth and Badyaev 2007; Juette et al. 2014; Michelangeli et al. 2017; Damas-Moreira et al. 2019; Grabowska et al. 2019; Bensky and Bell 2022; Dickey et al. 2025). Dispersal has also been linked to sociality in some contexts with asocial individuals dispersing further than more social individuals (Cote and Clobert 2006; Cote et al. 2010). This idea that it is active, aggressive, antisocial and bold individuals who are moving the invasion front forward, highlights the role of invasion as a selective filter of behavioural traits (Chapple et al. 2022). Indeed, animals possessing a risk-taking personality are more likely to disperse through different abiotic and biotic conditions even if these conditions are markedly different from their native ecological settings (Juette et al. 2014). However it remains possible that the opposite occurs during range expansion and shy or non-aggressive individuals are instead the individuals that move the invasion front (hereafter, "edge") forwards as they are excluded from established (hereafter, "core") and possibly optimal habitats by more aggressive conspecifics (Cote et al. 2010; Hudina et al. 2015). A number of studies have reported more proactive personalities among the dispersing individuals at the edge of the range expansion, and these results align with unifying theories, such as the pace-of-life syndrome, which relate behavioural traits to physiological and life history traits in animals (Biro and Stamps 2008; Réale et al. 2010). For example, the high foraging rates commonly reported in invasive populations are likely associated with energy-demanding physiological traits and/or with personalities that facilitate resource acquisition (Careau et al. 2008; Careau and Garland 2012; Myles-Gonzalez et al. 2015; Taylor and Dunn 2018; Behrens et al. 2020; Moran and Behrens 2024; Dickey et al. 2025). Particular trait associations in invasive populations support the existence of a dispersal syndrome (Ronce and Clobert 2012; Stevens et al. 2014). However, it is worth mentioning that strong dispersal abilities likely come with trade-offs, including a higher exposure to predation and parasites in certain contexts, greater energy requirements, and increased oxidative stress (Réale et al. 2010; Brandner et al. 2013; Lagos et al. 2017; Błońska et al. 2024).

Invasion gradients provide an ideal opportunity to investigate whether personality or behavioural syndromes as claimed are truly associated to the invasion success. Along an invasion gradient, one can study how traits differ using an intra-specific approach, which will reduce potential confounding factors related to phylogenetic divergences that can arise when comparing distinct non-native and native species. Moreover, the best dispersers are expected to overrepresented at the edge (Shine et al. 2011) resulting in a pattern of assortative mating caused by spatial sorting, also known as the "Olympic village effect" (Phillips et al. 2008). This Olympic village idea would result in genetic structure along the invasion gradient with individuals sorting according to their ability to disperse. The process will further

favour the persistence of dispersal-enhancing traits, such as boldness and aggression, across generations at the invasion edge (Berthouly-Salazar et al. 2012; Courant et al. 2019).

In this study we examined behavioural syndromes in the round goby (*Neogobius melanostomus*) along an invasion gradient in Canada. The round goby is a fish species native to the Ponto-Caspian region, and is invasive in large parts of the European continent, including the Baltic Sea and rivers in central Europe (Sapota and Skóra 2005; Borcherding et al. 2011). Round goby have been intensively studied in both Europe and North America where it is suspected to have arrived in the ballast water of commercial ships (Jude et al. 1992; Kornis et al. 2012). Ecological concerns surrounding the round goby stem from its rapid rate of expansion (Kornis et al. 2013), significant predation pressure affecting native species (Chotkowski and Ellen Marsden 1999; Balshine et al. 2005), its capacity to act as a vector for diseases (Poste and Ozersky 2013; Hebert et al. 2014), and its contribution to bioaccumulation of environmental contaminants via food web dynamics (Kwon et al. 2006; McLean et al. 2025). Thus, understanding how behavioural variation impacts the spread of the round goby and which types of individuals form the invasion edge could be a pivotal step to mitigate habitat damage and anticipate future economic impacts from this species (Cuthbert et al. 2025).

Previous research has identified personality biases in round goby populations, with one study finding individuals with proactive traits at the edge of invasion pathway (Myles-Gonzalez et al. 2015). However, subsequent studies revealed conflicting results, showing that edge populations do not consistently exhibit these proactive individuals (Groen et al. 2012; Thorlacius et al. 2015; Galli et al. 2023). For instance, Galli and colleagues found that individuals from the core population were in fact bolder than those from the invasion edge. In contrast, Groen et al. (2012) found similar levels of boldness and activity between core and edge populations. Thorlacius et al. (2015) found personality traits to be correlated with dispersal in a four-year-old population, but this relationship was absent in an older population established over twenty years ago. These contrasting results may stem from various methodological differences and temporal factors that have not been consistently addressed in previous studies. The temporal dimension highlighted by Thorlacius et al. (2015) suggests that the relationship between personality traits and invasion dynamics may vary with population establishment time. Their findings indicate that behavioural traits associated with dispersal may weaken or disappear as populations mature and environmental pressures shift. Behavioural tendencies will change from initial colonization to long-term establishment, possibly as a result of genetic homogenization over time (Björklund and Almqvist 2010). This temporal effect on behaviour implies that studies examining populations at different invasion stages may yield fundamentally different conclusions about personality-invasion relationships, potentially explaining the contradictory findings across the literature. Furthermore, methodological inconsistencies across studies could also generate conflicting results. Notably, Myles-Gonzales et al. (2015) and Groen et al. (2012) did not assess the repeatability of their behavioural measurements, a critical requirement for establishing true personality traits (Dingemanse and Wright 2020). Without demonstrating temporal consistency in an individual's behavioural responses, conclusions about personality-driven invasion patterns remain tentative. Additionally, Galli et al. (2023) focused solely on comparisons between different edge populations rather than contrasting edge populations with well-established core populations, limiting the ability to detect invasion-stage specific behavioural differences. These methodological gaps underscore the importance of conducting comprehensive studies that compare recent edge invasive populations with long-established core populations using repeatable behavioural assays. Such comparative approaches, incorporating multiple behavioural tests with demonstrated repeatability across temporally distinct invasion stages, are essential to clarify whether consistent personality-invasion relationships exist and how they may change throughout the invasion process.

Here, we investigated the behavioural phenotypes of two connected populations of round goby collected along an invasion pathway in the Trent-Severn Waterway in Ontario, Canada. The core population we studied has been established at this site for over twenty years, whereas the edge population was first reported much more recently (less than one year prior to sampling). Although other invasion core and edge populations have been compared before, to our knowledge our edge population represents one of the most recent fronts to have been examined in a round goby behavioural study (Myles-Gonzalez et al. 2015). Based on

the arguments presented above, we predicted that individuals from the edge site, would exhibit more proactive and asocial personality traits compared to those from the core site, thus facilitating range expansion for these dispersing individuals.

Material and methods

Fish collection and housing

Round goby were collected between the 21st to 24th of May, 2024 at two field sites along the Trent-Severn Waterway, Peterborough County, Canada (Fig. 1). One field site sampled was at an invasion front ("edge") at Young's Point, downstream from Lock 27 (44°29′17.5"N 78°13′58.1"W) while the second site sampled was an established ("core") population at Hastings Village Marina upstream of Lock 18 (44°18′32.0"N 77°57′21.1"W). Round goby were first reported at the Hastings core site in 2003 (Raby et al. 2010; Gutowsky and Fox 2011) while this species was not observed at Young's Point until November 2023, six months prior to our study (Jacob Bowman, personal communication, 2024). To our knowledge this study represents one of the most recently

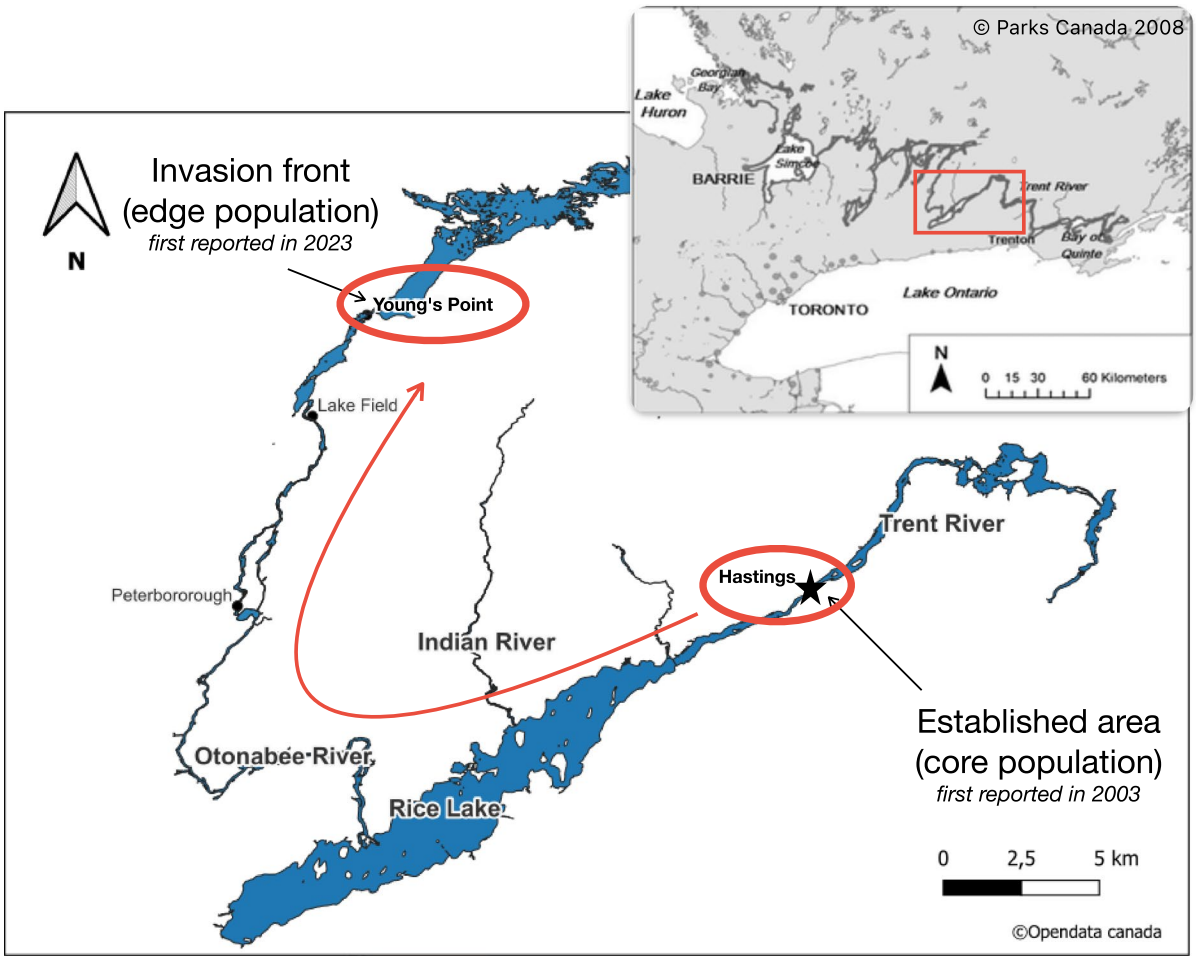

Fig. 1 Map of the two sites used to sample round goby from edge and core populations. The initial introduction site into the Trent-Severn Waterway in 2003 is indicated by a black star. From Hastings, round goby dispersed upstream through Rice Lake, then Peterborough and they were first reported in Young's Point in 2023 (following a trajectory represented by the red arrow). The inset area provides an overview of the Trent-Severn Waterway, with the studied section of the river system found within the red ellipse

invaded front ever examined in a round goby behavioural study (along with Myles-Gonzalez et al. 2015). Round goby were introduced into the Trent-Severn Waterway at Hastings (our core site) as the result of a bait-bucket transfer by anglers, and not a natural dispersal from Lake Ontario (Gutowsky and Fox 2011). In contrast, the fish at Young's Point (our edge site) represent secondary range expansion, thought to be a result of active dispersal by round goby from the core site (Gutowsky and Fox 2011). At the time of sampling, Young's Point represented the upstream limit of the round goby's range in the Trent Severn Waterway, with no round goby found above the lock.

Fish were captured using black and silver minnow traps baited with frozen corn and small pieces of chicken liver. Traps were tied by rope to structures such as trees on the shore and thrown offshore to depths of 1–2 m. Traps were placed approximately 3–10 m apart and left for 2 to 12 h before collection. All captured round goby were sexed based on the shape of their urogenital papilla (Miller 1984). We selected 40 size matched males from each population for this experiment, from the fish collected. All remaining fish were used in another study, see Appendix 1 Table S1 for further information. In this study to avoid any potential confounding influences of sex when exploring behavioural differences related to dispersal, we chose to focus on males. Males were selected because they were overall easier to catch, and are more commonly captured in traps than females (Corkum et al. 2004; Gutowsky and Fox 2011; Azour et al. 2015), probably because males are more active than females (Marentette et al. 2011). We also selected to tightly size match the fish from the two populations because of the strong morphometric differences observed between edge and core populations (see Table 1 and Appendix S1). Body size is known to influence behaviour and physiology in fishes and other vertebrates (Brown and Braithwaite 2004; Uiterwaal et al. 2017; Meuthen et al. 2019; Darby and McGhee 2019; Synyshyn et al. 2021; Galli et al. 2023; Navarro et al. 2025) and we wanted to avoid body size driven behavioural differences between the core and edge fish. Morphological information about the size matched males used in this study is provided in Table 1. Population level morphometric measures of the fish captured in the field (*i.e.* populations) for core and edge can be found in Appendix 1, Table S1. The 80 size matched male fish for the experiment were then transported to McMaster University (Hamilton, Canada) in large, aerated coolers.

Upon arrival at McMaster University, the fish were placed in 84.2 L holding tanks (61 × 46 × 30 cm) that were equipped with an air supply, a thermometer, an external Aqua Clear filter, gravel substrate, and shelters made of 5–10 cm diameter PVC tubes. Fish were held at densities of 7–9 fish per tank with fish separated by collection site. Fish were housed in dechlorinated municipal tap water maintained at room temperature of 19.4 ± 0.2 °C (mean ± SD) and a 16 h:8 h light:dark cycle with 30 min progressive dawn and dusk periods (Marentette et al. 2011). Fish were inspected several times a day and fed *ad libitum* with commercial pellets (Corey Optimum, Corey Nutrition Company, Fredericton, Canada) six days a week but were fasted for 14–23 h prior to the start of the behavioural trials. The length of the fast time depended on when the fish were tested the next day.

After a 4–7 day acclimation period at McMaster University, fish were weighed (to the nearest 0.01 g), measured (to the nearest 0.01 cm) and tagged with subdermal injection of Visible Implant Elastomers (VIE, Northwest Marine Technology Inc., Anacortes, USA) or non-toxic acrylic paint. This unique identifier facilitated individual fish recognition and allowed for repeated behavioural testing. Fish were given 4–20 days to recover following this handling before being used in the experiment. The time given to recover did not impact fish behaviour (see Results).

We ran 68 fish in total out of the 80 that were originally transferred to the lab (with the remaining 12 fish used as conspecifics in the sociability assay, see sections below). One fish turned out to be a female, so we excluded it from the study so in the end we analysed the data from 67 fish. Despite our best attempts to size match the fish brought back to the lab, edge fish were still marginally longer than core fish, but they had similar body mass and body condition (Table 1).

Behavioural tanks

The fish were individually run through a series of four behavioural assays (see description below), which collectively we refer to as a trial. The trials were conducted in four identical 150 L experimental tanks (92 × 45 × 38 cm, Fig. 2a) so replicate trials on four fish were run simultaneously. The four fish

Table 1 Morphometric measures of the subset of core and edge fish used in this study (*i.e.* experimental groups). Body condition is calculated using Fulton's condition index, a standard metric in fish biology based on the relationship between the mass and the length of the fish (Rizzo and Bazzoli 2020). The mean ± standard deviation is presented as well as the range of the measures in square brackets. Comparisons between core and edge fish include Cohen's d and associated 95% confidence interval for effect size, and results of linear models

	Body mass (g)	Total body length (cm)	Fulton body condition ($g.cm^{-3}$)
Core (n = 34)	5.81 ± 2.50, [2.30; 11.88]	8.16 ± 1.17, [6.20; 11.90]	1.01 ± 0.13, [0.71; 1.43]
Edge (n = 33)	6.96 ± 2.72, [2.17; 12.40]	8.73 ± 1.10, [6.90; 10.70]	0.99 ± 0.13, [0.63; 1.42]
Core *vs.* edge	d = -0.42, 95%CI = [-0.92; 0.07], $F_{1,65}$ = 3.28, p = 0.075	d = -0.52, 95%CI = [-1.02; -0.03], $F_{1,65}$ = 4.25, p = 0.04	d = 0.15, 95%CI = [-0.34; 0.64], $F_{1,65}$ = 0.38, p = 0.54

could not see each other during the trials because the tanks were covered on the back and sides with an adhesive opaque plastic material, which also reduced glare and improved contrast in the video recordings (see below). The four experimental tanks were maintained at the same temperature as the housing tanks (19.1 ± 0.4 °C) and the water was aerated by a bubbler in each tank. Clear acrylic fixed partitions and second removable black opaque partitions subdivided each behavioural tank into three compartments (a left side, a central and a right side compartment, Fig. 2a). Focal fish were introduced into the central compartment (42 × 42 × 38 cm). In each side compartment we placed a 20 L tank (40 × 20 × 25 cm) filled with oxygenated water. Both tanks were hidden by the black partitions. One non-focal social stimulus fish was placed in one of these side tanks, while the other tank remained empty. The side containing the stimulus fish was randomly selected by coin toss. The interior glass tanks ensured that no chemical cues could be transferred between compartments.

All the trials were recorded using eight Canon digital camera (VIXIA HF R800, Canon Inc., Tokyo, Japan) in high-definition mode, with one camera being placed 50 cm above the tank and another being placed 1 m from the front of the tank. Experimenters

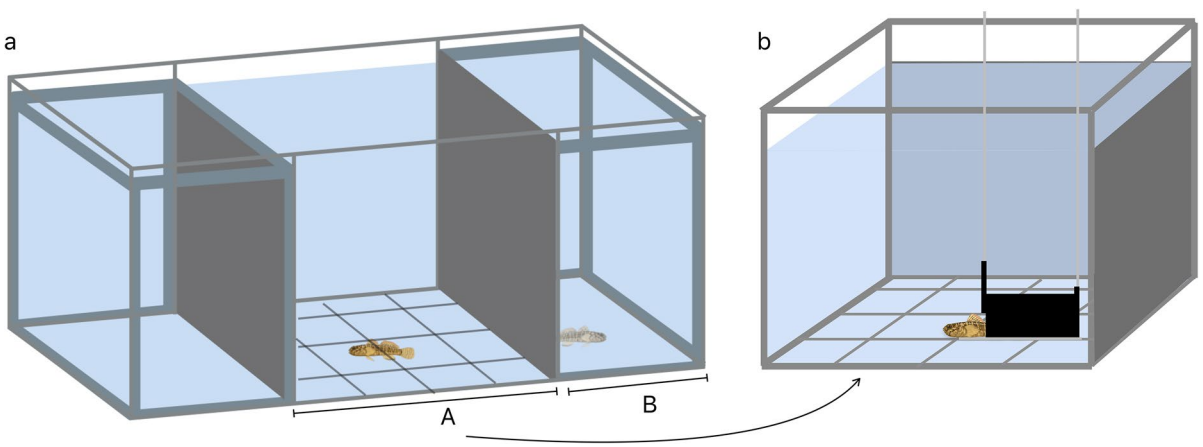

Fig. 2 **a—** Experimental tank setup used for behavioural trials. The focal fish was kept in the central compartment (A) while the conspecific used in the sociability assay was housed in a randomly chosen side tank (B) with the clear partition covered with another opaque partition. Opaque partitions obstructed the view of the focal fish to the adjacent sections. The black grid on the bottom of the tank allowed quantification of horizontal movement (locomotor activity and exploration) in the open field assay. **b—**View of the experimental set-up used for the shelter assay

remained outside of the room or behind an opaque blind during the trials.

Behaviour trials

Each trial consisted in four consecutive behavioural assays followed in the same order: a shelter assay, an open field assay, a startle response assay, and a sociability assay. These assays are described in detail below and were adapted from Synyshyn et al. (2021). We tested eight to twelve fish per day, with half of the fish from the core and the other half from the edge experimental group.

Shelter Assay. At the beginning of each trial, the focal fish was captured from its holding tank and gently guided into a PVC black tube shelter (15 cm long, 5 cm diameter) with one end closed off. Once the fish were inside the tube, we closed off the open end with a removable barrier, and then a focal fish inside its tube shelter was placed in the center of the middle compartment of each experimental tank for a one-hour acclimation period. After this one hour, the removable barrier was lifted remotely, allowing the fish to emerge from the shelter (Fig. 2b). Following Moran and Behrens (2024), the latency to emerge from the shelter was recorded. We considered the fish to have emerged when at least ¾ of its body had left its shelter. If the fish had not emerged within the 25-min allotted trial period, we remotely lifted the entire shelter from the back and forced the focal fish to swim out and leave the shelter.

Open Field Assay. After 25 min, the shelter was removed. Each focal fish was then given an additional 30 min in the empty open compartment. We recorded the fish's movement from above during these 30 min to evaluate its locomotor activity and space use. Each tank was positioned over a grid made of 16 squares with 10.5 cm sides, which was visible on the top mounted video camera recordings. We used the number of grids squares the fish entered during the first, middle, and final five minutes of this 30-min trial as an estimate of each fish's activity. A fish was considered to have entered a grid square when its pectoral fins had moved beyond the grid line. To quantify exploratory behaviour, we followed measures developed in other studies (Beukeboom and Benhaïm 2024; Jones and Godin 2010) and scored the latency until half of the unique squares (*i.e.* eight out of sixteen) had been entered by the focal fish. We used the amount of time taken to visit half of the squares, not the time taken to visit *all* the squares, because the first measure showed a much greater degree of interindividual variability.

Startle Response Assay. Following the open field assay, we rolled a coloured glass marble (1.5 cm diameter) down a plastic pipe which was placed perpendicularly to the side wall of the tank (Schweitzer et al. 2015). The tube was placed above the water (resting on the top edges of the tank walls) and was used only to ensure that the marble would drop in the center of the tank and would drop at the same speed across trials. Once the marble was dropped the tube was removed. We chose to drop the marble at the center of the tank regardless of where the fish was in relation to the tank center, for consistency across trials and repetitions. We recorded each fish's startle response to the marble drop by quantifying the total time fish spent frozen in place after the drop (*i.e.* before the fish initiated its first movement following freezing (Thorlacius et al. 2015; Galli et al. 2023)). Note that 22% of the fish assayed (15 out of 67) immediately darted away from the marble after it was dropped, making a fast and spontaneous movement forward before freezing. For all the fish that darted first, we recorded the duration of this secondary freezing. This assay lasted for 15 min and all the fish started to move well before the end of this period.

Sociability Assay. Finally, we ran a 20-min sociability assay by removing the two black opaque partitions at the same time, which allowed the focal fish see into the right and left compartments. One compartment always held a conspecific that was size matched to the focal fish while the other compartment remained empty (following procedures used in Thorlacius et al. 2015). The conspecific used as a social stimulus was placed in the side tank before any of the assays in the trial began, and this fish came from a separate and dedicated holding tank. The clear partitions remained in place throughout this assay to prevent the focal fish from becoming trapped between the glass walls of the side tanks and the larger experimental tank. We scored the amount of time the focal fish spent in the social zone, defined as the four grid squares nearest to the conspecific compartment, as well as the number of visits to the social zone, the latency to enter the social zone, and the latency to cross a square within the social zone (as a way to capture if fish already in the social zone were moving).

We scored the first ten minutes of the sociality assay, and started immediately after the opaque partitions removal because we wanted to capture the focal's first visual contact with the conspecific as this was a key aspect of our sociality assay, often resulting in movement towards the conspecific. As in the open field assay, a fish was considered to have entered a square when its pectoral fins had moved beyond the grid line.

Between trials, the water in each experimental tank was thoroughly mixed, and the shelters and marbles were rinsed and cleaned. At the end of each day, half the tank water was exchanged with fresh dechlorinated water, and an external filter (Aqua Clear 50) was placed on the tank until the next morning.

To assess the degree of repeatability in individual behavioural responses, the four behavioural assays were re-run with the same focal fish for a second time one week later. Fish were always tested in a different tank in their second test but with the same assay order. In total, we conducted 134 trials between June 3rd and June 24th, 2024. In the startle response assay, most fish initially avoided the marble, but eventually some would investigate it. To maximize neophobia in this assay, each fish was first tested with one marble colour (blue or green) and then on the second repeated measure of this assay each fish was tested with the opposite marble colour. For the sociability assay, we ensured the focal fish was exposed to a different size-matched conspecific across the two trials. When not being tested fish remained in the same holding tank with the same group of fish across the entire duration of the study.

All procedures used were approved by the McMaster Animal Research Ethic Board and followed the Canadian Council of Animal Care guidelines (AUP 22–04-11). Fish behavioural observations from the videos were manually scored using BORIS software (Friard and Gamba 2016) in a randomized order. To minimize experimenter bias, all videos were scored by one observer (CS) who remained blind during video scoring to the order (first or second trial) and the experimental group origin. Due to various video and apparatus technical issues during the trials, data from eight videos had to be excluded from the analyses: two videos had to be completely excluded (*i.e.* 1.5% of the trials) and six videos had time chunks that had to be excluded (*i.e.* 4.5% of the trials). See Appendix 2 for additional details about exclusion criteria.

Statistical analysis

All statistical analysis were conducted in R v.4.5.1 (R Core Team, 2025). Normality and heteroscedasticity assumptions were checked for each model residuals with the "qqplot()" and "qqnorm()" functions, and transformations (*e.g.* logarithmic, square root) were applied when needed to meet normality assumptions. Total body length was used as an explanatory covariate in all our statistical models due to the edge experimental group being significantly longer, despite our attempts to size match fish between populations (see Table 1).

For each behaviour metric measured in the trials, we assessed the repeatability (*i.e.* the consistency of individual responses over time, Bell et al. 2009; Dingemanse and Wright 2020) after a one-week interval. We used the rptRGaussian() function from the "rptR" package (Stoffel et al. 2017), based on mixed effect models with 500 bootstraps which included total body length as a fixed factor, and the fish's identity as random variable. As mentioned above, the data were normalized when needed using the appropriate transformation (*e.g.* logarithmic, square root, Table 2). Repeatability results for each behaviour metric are reported as the repeatability score R and the associated bootstrapped 95% confidence intervals. We calculated p-values for the repeatability scores R, using likelihood ratio tests ($p < 0.05$ indicating significant results).

For each of the repeatable behaviour metrics used, we calculated a mean score for each fish across the two trials that were conducted at a one-week interval, and we based all subsequent analyses on these mean scores (Laubu et al. 2016, 2017). These mean behavioural scores, representing the average responses to the two behavioural trials, are presented in Fig. 3. We verified that the repeatable behaviours were correlated in a syndrome by making pairwise correlations, assessing the strength relations using Pearson correlation coefficients, for all fish, and when considering each experimental group separately. Given that the risk of type I error (false positive) is greatly increased by multiple comparisons arising from systematically testing the difference between fish groups for each behavioural measure, we reduced the dimensionality of the dataset by calculating a composite behavioural score. To do so, we performed a principal component analysis (PCA) on our behavioural data. We used the

"ade4" package (Dray and Dufour 2007), taking into account all repeatable and correlated behaviours and we used the reciprocal of PC1 scores as a measure of proactivity scores along the proactive–reactive *continuum* (Schweitzer et al. 2015; Laubu et al. 2016; Monceau et al. 2017).

We compared the edge and core groups based on the proactivity scores using linear models' analyses. We incorporated the experimental group and total body length in the models and tested the effect of each variable by removing sequentially it from the model (*i.e.* stepwise backward model selection) and assessing its significance with likelihood ratio tests. We computed Cohen's d as an effect size index to compare between experimental groups (Nakagawa and Cuthill 2007) using the "effsize" package (Torchiano 2020). Results are reported as a Cohen's d effect size with confidence interval, an F-value statistic, degrees of freedom, and a p-value.

To assess if the fish from the core and edge groups differed in their behavioural plasticity over the one week held in laboratory conditions between the first and second trial, we compared their reaction norms over time across experimental groups for each of the repeatable behaviour metrics. The "glmmTMB()" function from the "glmmTMB" package (McGillycuddy et al. 2025) was employed to fit linear mixed models. For each of the behaviours tested, the fixed effects included the experimental group, the trial of testing (one or two), as well as their interaction. The model included a random slope (Schielzeth and Forstmeier 2009) for trial of testing by individual fish to account for variation in behavioural change over time. Since our primary interest lies in quantifying the plasticity estimated from the slope of the reaction norm, we did not include a random intercept. We computed the interaction contrasts using "emmeans" package (Lenth 2025). Since we wanted to assess the plasticity over time, we did not perform these analyses on the mean behavioural scores between the first and second trials, but we included all the behavioural measures obtained in both trials. We performed these analyses on each of the behaviour metrics because the PCA was conducted using the mean behavioural scores across the first and second trials, and it made more sense to link each response within its trial. Note that out of 134 trials, data was not used for seven shelter assays and for three open-field and startle response assays, due to a small number technical and fish behaviour exclusions outlined in the Appendix 2.

Results

Repeatability of behavioural measures

The latency to completely emerge from the shelter (a measure taken during the shelter assay), the total number of squares entered, the latency to visit half of the central compartment surface (both measures taken in the open field assay), and the duration of freezing (from the startle response assay), all exhibited significant repeatability scores ranging from 0.29 to 0.47 (Table 2). For each of these behaviours, by comparing overlapping confidence intervals we also verified that the repeatability scores obtained for edge and core fish separately were close to the values obtained when all the fish were analysed together (Appendix 3, Table S2).

In contrast, behaviours scored from the sociability assay exhibited very low and non-significant repeatability values (from 0.08 to 0.21, see Appendix 3 Table S3) and we therefore we excluded these altogether from the subsequent analyses.

We calculated the mean across the first and second trials for the four different repeatable behavioural

Table 2 Transformations used on the data and the overall repeatability score of the four behaviours included in our comparative analyses. Repeatability scores R are given with their bootstrapped 95% confidence interval in square brackets.

Assay	Behaviour	Transformation	Repeatability score	p-value
Shelter	Emergence latency	Log(Y + 1)	$R = 0.47$; [0.26, 0.65]	$p = 4.2e\text{-}05$
Open field	Number of squares crossed	$\sqrt{Y}$	$R = 0.31$; [0.07, 0.51]	$p = 0.007$
	Latency to explore half of the surface	Log(Y)	$R = 0.29$; [0.03, 0.51]	$p = 0.018$
Startle response	Freezing duration	Log(Y)	$R = 0.31$; [0.09, 0.50]	$p = 0.010$

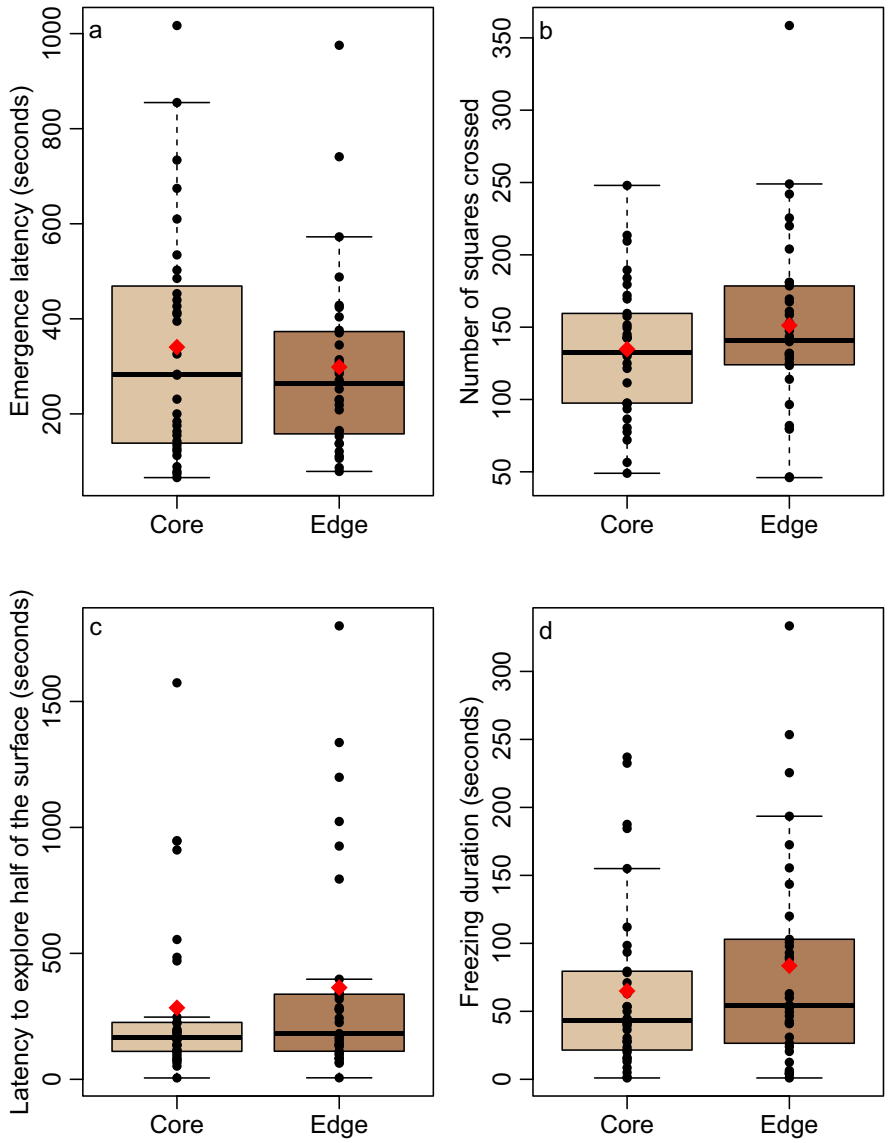

Fig. 3 Mean behavioural scores across the first and second trial for each group for the **a** emergence latency in the shelter assay, **b** number of squares crossed in the open field assay, **c** latency to explore half of the surface in the open field assay, **d** freezing duration in the startle response assay. In the boxplots, boxes represent the range between the upper and the lower quartiles. The median is indicated by the thick middle lines and the mean by the red diamonds

metrics and we based the subsequent analyses on these mean behavioural scores (Fig. 3).

Correlations between behaviours in a syndrome

When we examined all the fish assayed, we found correlations between the different repeatable traits strongly suggesting there is a behavioural syndrome for round goby, and consistently with previous findings (Synyshyn et al. 2021; Galli et al. 2023). For instance, the longer a fish would freeze after the marble dropped (startle response assay), the less exploratory this fish would be (Pearson correlation coefficient: $r = 0.51$, 95%CI = [0.31; 0.67], $p < 0.001$, Fig. 4a). As well, the fish with the longest freezing durations in the startle response assay were also the least active in the open field assay (*i.e.* had the lowest number of squares entered or gridlines crossed, $r = -0.26$, 95%CI = [−0.47; -0.02], p = 0.03). Additionally, the more active a fish was, the earlier it would emerge from the shelter ($r = -0.34$; 95%CI = [−0.53; -0.11], $p = 0.005$). However, when examining the edge and core experimental groups separately, we found that behaviours tended to be

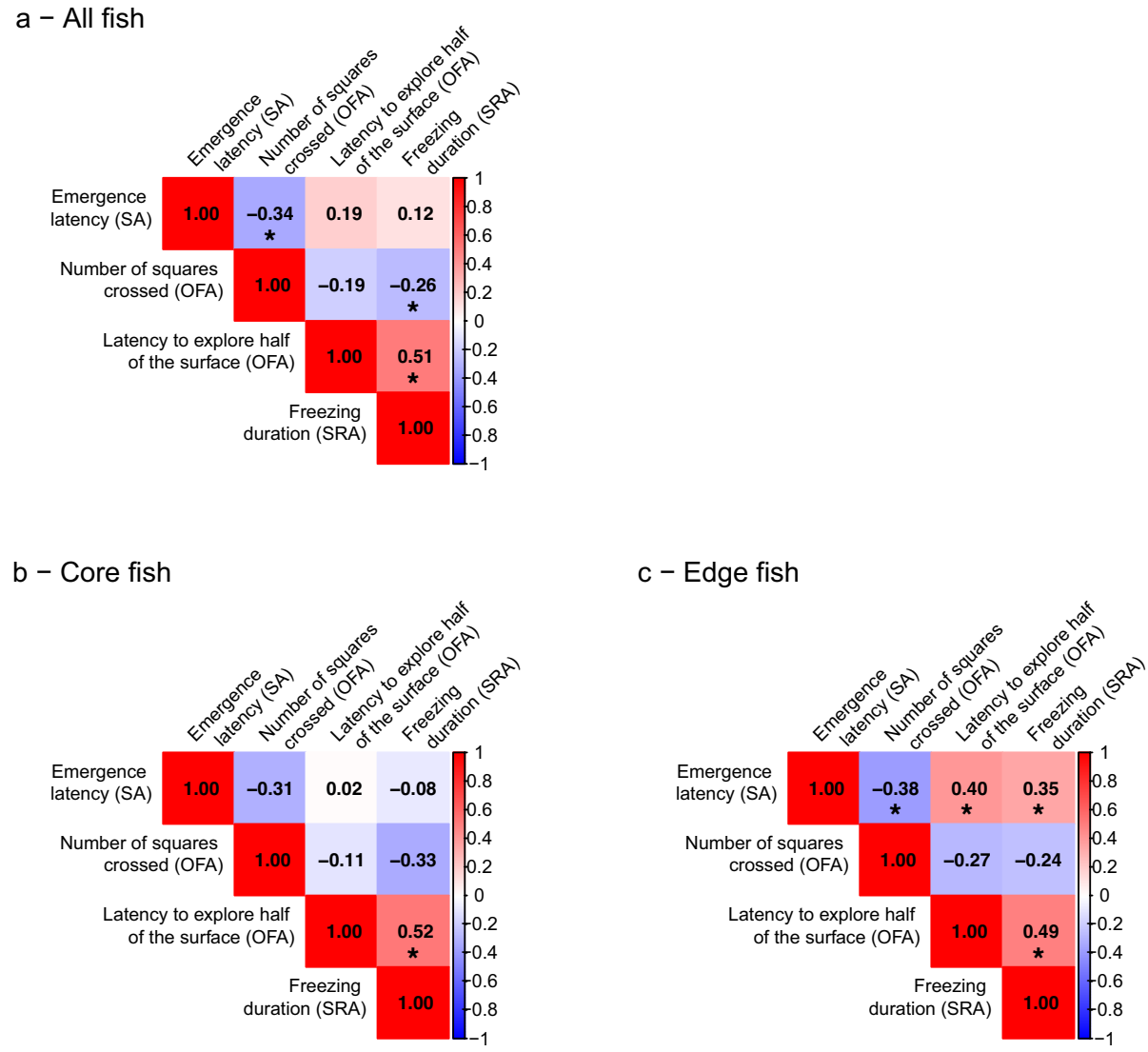

Fig. 4 Correlation matrices of the behaviours included in the comparative analysis for **a** all fish, **b** just core fish (n = 34) or **c** just edge fish (n = 33). The acronyms SA, OFA and SRA stand for shelter assay, open field assay and startle response assay, respectively. The numbers inside the coloured boxes of the heat map refer to the Pearson correlation coefficients calculated on the mean behaviour scores between the first and second trials of testing. A positive correlation between two behaviours is indicated by a positive number and a box in a shade of red while a negative correlation between two behaviours is indicated by a negative number and a blue shaded box. Non-significant correlation between two behaviours is indicated by a white box. Stars indicate p-values < 0.05. Associated 95% confidence intervals and statistics are reported in Appendix 4, Table S4.

more strongly correlated in edge fish (see Fig. 3bc), indicating a more pronounced behavioural syndrome as compared to the core group of the invasion gradient. For instance, there was a strong correlation between emergence latency and exploration in edge fish ($r = 0.40$, 95%CI = [0.07; 0.66], $p = 0.002$) but not in fish from the core ($r = 0.02$; 95%CI = [−0.32; 0.35], $p = 0.93$). The correlation between latency to emerge and freezing duration also tended to be higher in edge fish ($r = 0.35$, 95%CI = [0.01; 0.62], $p = 0.046$) than in core fish ($r = -0.08$; 95%CI = [−0.41; 0.26], $p = 0.64$).

Proactivity scores at the edge *versus* the core

To reduce the number of analyses needed we performed a PCA on the mean behavioural scores presented in Fig. 3. The first two principal components (PC1 and PC2) of the PCA represented 42.8% and 26.7% of the variance, respectively (Fig. 5). For all subsequent comparative analyses, the reciprocal of PC1 (factor loadings for emergence latency: 0.42; squares crossed: -0.43; exploration latency: 0.57; freezing time: 0.56, Fig. 5a) was used as a proactivity score. This followed methods established by Schweitzer et al. 2015, Laubu et al. 2016 and Monceau et al. 2017, with highly positive values indicating proactive individuals that were the most active, exploratory and bold as reflected by a rapid emergence from the shelter, with a propensity to move a lot and rapidly explore the middle compartment in the open field assay, and short freezing times following the marble drop (Fig. 5a). On the other hand, highly negative value corresponded to reactive individuals on the proactive–reactive *continuum*.

When the mean scores of the four behaviours were analysed using a PCA, we found that proactivity scores (*i.e.* the reciprocal of PC1) were strongly predicted by fish size (scaled estimate $\beta = -0.46$, 95%CI = [−0.68; -0.23], $F_{1,\ 65} = 17.00$, $p = 0.0001$), with the longest fish exhibiting the least proactive behaviours (Fig. 6a). However, we found that the edge and core fish did not differ in a clear way in their proactivity scores (Cohen's d = −0.05, 95%CI = [−0.54; 0.44], $F_{1,64} = 0.68$, $p = 0.41$, Fig. 5b and 6b). This can be visualized by projecting individual scores on the principal component plane (Fig. 5b). The effect of fish body length on behavioural scores was the same between the edge and core groups (*i.e.* there was no significant interaction, $F_{1,\ 63} = 0.094$, $p = 0.76$). The order in which the trial was conducted during the day had no effect on proactivity scores ($F_{2,64} = 0.74$, $p = 0.48$) and were consistent across both edge and core fish ($F_{2,61} = 0.30$, $p = 0.75$). The recovery time (between tagging and the first behavioural trial) also had no effect on proactivity scores ($F_{1,65} = 2.73$, $p = 0.10$) and was similar in edge and core fish ($F_{1,63} = 0.30$, $p = 0.94$). Results related to PC2 scores were similar to the proactivity scores (the reciprocal of PC1, Appendix 5, Fig. S1).

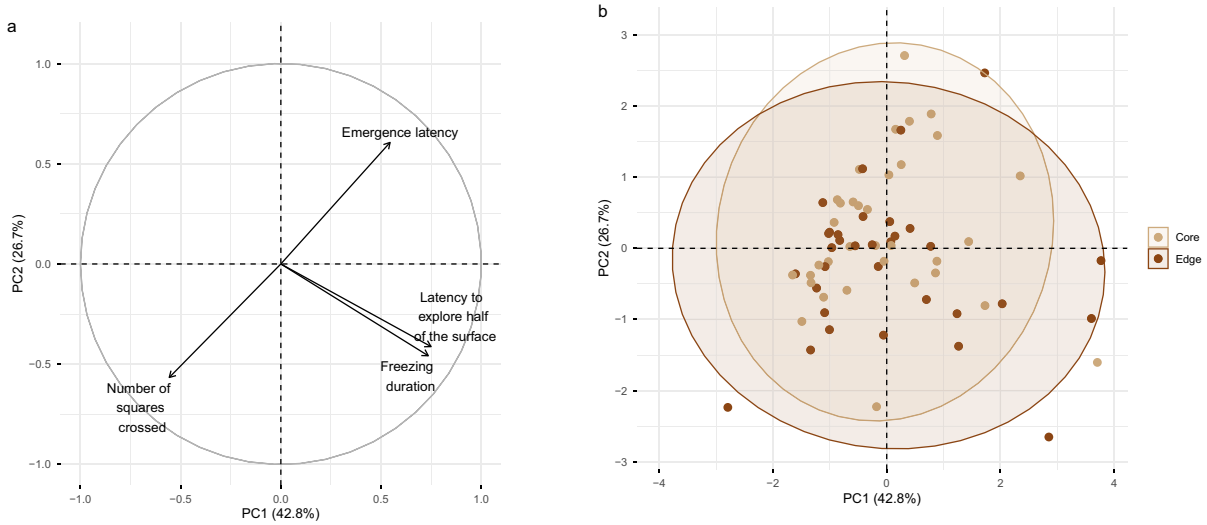

Fig. 5 **a** Correlation circle associated to the four behaviour metrics selected to perform the PCA. PC1 corresponds to the reciprocal of the proactivity score (*i.e.* highly negative values indicating proactive individuals). **b** Projection of individuals on the principal component plan (PC1;PC2), specifying the experimental groups. Core fish are indicated in light beige dots and edge fish in brown dots.

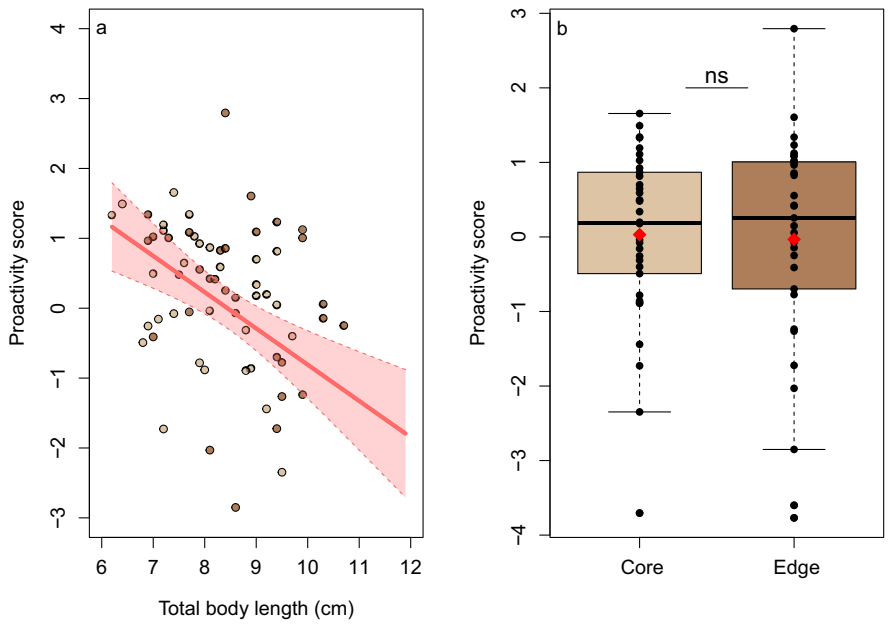

Fig. 6 **a** A linear regression showing the negative correlation between proactivity scores (reciprocal of PC1) and fish total body length (cm). The longest fish were the least proactive. Core fish are indicated in light beige dots and edge fish are represented by brown dots. **b** Proactivity scores (reciprocal of PC1) of fish from the core (n = 34) and edge (n = 33) groups. This graphical representation does not account for total body length of the fish, but the "non-significant" statistical label refers to the results of the best model, which accounts for total length. In the boxplots, boxes represent the range between the upper and the lower quartiles. The median value is indicated by the thick middle lines of the boxplots and the mean by the red diamonds.

Plasticity and Reaction norms of edge vs core fish

Edge and core fish also did not differ in their behavioural plasticity (*i.e.* the slopes) between the first and second trials (Appendix 6, Fig. S2). There was no significant difference in plasticity among groups, over the week that the fish were kept in the laboratory between the two trials, including the latency to emerge from a shelter (change in behaviour relative to the edge group, model estimate: 0.19, 95%CI = [−0.16; 0.54], $t_{119} = 1.10$, $p = 0.27$), the number of squares crossed (0.05, 95%CI = [−1.67; 1.77], $t_{123} = 0.058$, $p = 0.95$), the latency to explore half of the surface (-0.38, 95%CI = [−1.03; 0.27], $t_{123} = -1.16$, $p = 0.25$), and the freezing duration after the marble drop (0.37, 95%CI = [−0.42; 1.16], $t_{123} = 0.93$, $p = 0.36$).

Discussion

In this study we assessed whether individuals at the edge of a biological invasion exhibit distinct personality traits compared to individuals from the core where the expansion first began. We sampled round goby specimens along a Canadian invasion gradient comparing the behaviour of fish from a long-established core population (where fish had been for over two decades) to fish at an edge population, a recently formed invasion front (where fish had been less than one year). We measured repeatable and consistently correlated behavioural traits supporting the notion of a behavioural syndrome (Sih et al. 2004; Bell et al. 2009; Dingemanse and Wright 2020), which was more pronounced (but not statistically so) in edge fish. Contrary to the prevailing theoretical framework and an extensive empirical literature linking invasive individuals with proactive behavioural traits (Cote et al. 2010; Chapple et al. 2012; Damas-Moreira et al. 2019), we did not observe any clear behavioural differences between individuals from the edge *versus* those from a core site. In addition, despite the fish having repeatable (*i.e.* consistent over time) responses, core and edge fish had similar level of behavioural plasticity in terms of how their

responses changed across one week between the two trials.

Although we carefully controlled for body size differences across experimental groups, we still found a significant effect of body size on behaviour, with the largest individuals demonstrating the least proactive tendencies along the proactive–reactive behavioural spectrum. This result aligns with previous findings on other species (Brown et al. 2005; Meuthen et al. 2019), and two previous studies on the round goby (Synyshyn et al. 2021; Galli et al. 2023).

Our findings differ from past empirical evidence showing that proactive traits are associated with invasion success across multiple taxa, including reptiles (Michelangeli et al. 2017; Damas-Moreira et al. 2019), birds (Duckworth and Badyaev 2007; Burstal et al. 2020) and also fishes (Rehage and Sih 2004; Bensky and Bell 2022; Sales et al. 2023). However, other rare contradictory results, including our own, suggest this relationship may not be as straightforward. For instance, similar to our findings, Lopez et al. found no boldness differences between edge and core populations across an invasion gradient, in an African jewelfish (2012). In another invasion gradient, crayfish from the core behaved more aggressively than front populations (Hudina et al. 2015). In round goby, a previous study from the same river system, found that fish from the edge were more aggressive than those from core populations (Groen et al. 2012) but like our current findings these fish showed similar levels of boldness and activity as fish from the core. Note, we did not assess aggressivity in our groups and Groen et al. (2012) did not consider repeatability of the behaviour over time. Similar to our results, Galli et al. (2023) reported equivalent activity levels between edge individuals and fish from a core population in the Baltic Sea, but these researchers also found the edge fish to be the shyest. In contrast, a third study, also focused on round goby from the Trent River system, showed that fish from the expanding edge were bolder (emerged from a shelter sooner), and were more active (moved farther and faster in the flume), compared to individuals from core areas (Myles-Gonzalez et al. 2015).

So why did our study not show these classically reported differences in activity and boldness? It is possible that our edge population, albeit young, had already entered its boom phase (Strayer et al. 2017) and we were not sampling the first individuals to arrive. As time elapses following the initial invasion, potential behavioural differences might become increasingly obscured due to population turnover and demographic growth resulting from the arrival of individuals following the real first "pioneers" to the edge. Round goby had first been detected at our edge site in very low numbers in November 2023, six months prior to our May 2024 sampling (Jacob Bowman, personal communication, November 2024). To our knowledge, our study reports on one of the most recent edge populations in the round goby. Previous studies examining behavioural differences examined edge populations that ranged in age from one-year (Myles Gonzalez et al. 2015) to five years after first colonization (Galli et al. 2023). Therefore, we think it is unlikely that time elapsing since the invasion impacted our ability to detect behavioural differences.

One plausible explanation for the lack of differences may be that by size- and sex-matching the fish we may have eliminated all behavioural differences between populations. We found that the smallest individuals in both of our groups were the most proactive (*i.e.* active and bold), a result consistent with other studies in other fish species (Brown et al. 2005; Meuthen et al. 2019). Galli et al. (2023) too found round goby activity and freezing time to decrease with body size, and that the more active and bold core fish were smaller. In addition, Marentette et al. (2012) and Synyshyn et al. (2021) also reported that smaller round goby were more active, more exploratory, and bolder – although in the second case this may be due to the smaller fish having a different reproductive strategy (*i.e.* they were sneaker males) rather than body size alone. The observation of smaller, more active, and bold fish is often attributed to a negative allometric scaling between body mass and metabolic rate, where smaller individuals have higher metabolic rates per unit of body mass. These smaller fish might exhibit greater boldness to their meet increased energetic demands (Brown and Braithwaite 2004; Réale et al. 2010). However, in the field, we noted that the edge population in fact contained significantly larger fish and was also heavily male-biased compared to the core population (Farley et al., *In prep*), a pattern which has also been documented in other round goby invasion gradients (Brandner et al. 2013; Azour et al. 2015) and also in a study on the same Trent Severn River system used in our study (Gutowsky and Fox 2011). Consequently, the negative correlation we

found between body size and proactivity suggests that the edge population, which is mainly dominated by larger fish, might be populated with more reactive (*i.e.* shy, weakly active) fish when taken as a whole. Note that whether these fish are large because they are reactive, or become more reactive as they grow, remains unknown, and deserves future study. By sub-sampling only the smaller fish from the edge to closely match the fish sizes found in the core areas, we may have introduced a behavioural bias, as we may have selected only the most proactive individuals, who are potentially less representative of the more common behavioural phenotypes present at the edge. However, by matching fish sizes we were able to control for these sources of variation in behaviour, which we believe is crucial to disentangle the contribution of behaviour in shaping the invasion process. Our study suggests that behaviour alone does not always appear to drive the invasion process. To untangle the influences of sex and size on potential behavioural differences that are likely to be subtle, large demographic sampling would be necessary. These results invite us to reevaluate the often-cited link between personality and invasion potential (Holway and Suarez 1999; Chapple et al. 2012). Therefore, there is a crucial need to conduct more comparative behavioural studies along invasion gradients, and perhaps a cross species meta-analysis to clarify the ubiquity of this pattern which is nowadays accepted in the invasion ecology conceptual framework. In addition, even though we found most of our behaviours assessed repeatable, it is worth remembering that the degree repeatability decreases with time (Bell et al. 2009). Thus, it would be valuable if future studies could assess repeatability over longer time intervals, as this would increase the robustness of our conclusions about the implications of personality in invasion contexts.

Finally, it is possible that behavioural differences between populations arise because of density-dependent effects. Our edge fish were captured more rapidly than core fish (0.5 versus 1.5 days), suggesting there were higher densities at the invasion front consistent with the boom or growth phase of the invasion (Strayer et al. 2017). Such density variations could drive divergent personality phenotypes through differential intraspecific competition, as demonstrated in round goby, where high-density sites exhibited greater voracity (Paton et al. 2019), in another goby species where competition promoted subordinate dispersal (Grabowska et al. 2019), and in an invasive crayfish where local population density was shown to positively affect dispersal (Galib et al. 2022). Such a density-related bias could have led us to overestimate proactivity in the edge population. Although quantifying density impacts was beyond the scope of this study, the potential demographic disparities between core and edge populations underscore the need for future research examining the complex interplay among density, sex, and behaviour in invasion dynamics.

In conclusion, we did not detect any differences in personality between core and edge groups of the invasive round goby. Both populations exhibited highly heterogeneous morphological and demographic characteristics, suggesting that these traits influence individual personality. As a result, the average phenotype (behavioural and otherwise) between the two populations could still differ when considered at the population level. However, after removing the impact of size and sex, personality did not explain dispersal tendencies. Importantly, this finding calls into question the common assumption that dispersing individuals predominantly exhibit proactive traits. Before concluding that behaviour has a role as a ubiquitous driver of invasion, if specific behavioural traits are preferentially found at the boundary of the expansion range, future research should also investigate the contribution of individual life history traits (*e.g.* body size, sex, age, physiological traits), or local social conditions (*e.g.* sex ratios, density, degree of competition) in shaping these behavioural phenotypes along invasion gradients.

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Authors contribution All authors contributed to the study conception and design. CS and JD ran the experiments. CS scored the behavioural data. CS, SB and F-X DM analysed the data. The first draft of the manuscript was written by CS and all authors edited the manuscript and gave their approval for submission.

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Data availability The datasets and R script for the analysis are available on Zenodo: https://doi.org/10.5281/zenodo.14806 24

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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