Is there a role for aggression in round goby invasion fronts?

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Abstract

The role of aggression as a factor promoting invasiveness remains hotly debated. Increased aggression or a lack of tolerance for conspecifics may promote population spread. Some previous research suggests that more aggressive or bold individuals are increasingly likely to disperse and as such these individuals may be overrepresented at the invasion front. In contrast, it has also been argued that individuals at the invasion front represent the least aggressive or least competitive individuals in the population, as these animals are excluded from established areas. Accordingly, the invasion front should be made up of shy, submissive individuals that exhibit reduced aggression. In this study we explore these alternative predictions by quantifying the levels of intra-specific aggression in the round goby (*Neogobius melanostomus*), an invasive fish that continues to spread rapidly through the Laurentian Great Lakes region in North America. We collected size matched male round goby from an invasion front as well as from an area with an established population, and we staged resource contests between them. Invasion front fish won 65% of the contests and tended to perform more aggressive acts overall. Invasion front fish were not more active or bold prior to the contest, and used the same types of aggressive displays as fish from established areas. Our results also showed that body size asymmetry was an overriding determinant of competitive outcomes, and that body size rather than individual variation in aggressiveness might be the most important contributing factor determining the composition of round goby invasion fronts throughout the Laurentian Great Lakes and its tributaries.

1. Introduction

Species that are successfully introduced into an environment beyond their native range and become so abundant that they become a disturbance, are classified as invasive (Davis & Thomson, 2000; Mack et al., 2000). Characteristics that make species more likely to be successful invaders include a wide environmental tolerance, a generalist diet, and a short generation time (Kolar & Lodge, 2001). Species-typical behaviours such as dispersal tendencies, aggression and conspecific tolerance have also been put forth as traits that promote the success of invasive species (Holway & Suarez, 1999; Rehage & Sih, 2004; Pintor et al., 2009). More recently, the theory of behavioural syndromes (also known as animal personalities or temperaments) has been applied to understand the process of invasion itself (Pintor et al., 2009; Cote et al., 2010a,b). A behavioural syndrome is a collection of correlated traits that can be observed or predicted to occur in a consistent manner in individuals tested across different situations or contexts, even when those behaviours may not be optimal (Sih et al., 2004a,b, 2010; Réale et al., 2007; Dingemanse & Wolf, 2009; Wolf et al., 2012). Within an invasive species range, individuals with particular behavioural syndromes may be more likely to make up the population right at the invasion front and consequently mediate the colonization of new habitat (Rehage & Sih, 2004).

Aggressiveness, boldness and dispersal tendency are often positively correlated and comprise a behavioural syndrome (Sih et al., 2004a,b), but the role of this syndrome in the expansion of invasion fronts is not yet clear. Some studies have suggested that individuals on the invasion front are more aggressive than their counterparts inhabiting established areas. For example, western bluebirds (*Sialia mexicana*) were more aggressive and displaced than their less aggressive sister species, mountain bluebirds (*Sialia curcoides*), and the males in new populations were more aggressive than males in older, established populations (Duckworth & Badyaev, 2007). Hence in bluebirds, aggressive individuals were driving the range expansion (Duckworth & Badyaev, 2007). Other studies suggest quite the opposite, showing that invasive populations may be populated by less aggressive individuals

(Suarez et al., 1999; Cote et al., 2010b). Less competitive, or less aggressive individuals may in fact drive the range expansion simply by being displaced or competitively excluded from established optimal habitats (Holecamp & Smale, 1998; Schradin & Lamprecht, 2002; Guerra & Pollack, 2010; reviewed in Cote et al., 2010a), and being forced to settle in potentially less ideal habitats at the edges of a species' range.

It has been argued that the general tendency for a species to have low aggression towards conspecifics may in fact help foster high densities, and help invasive species simply numerically outcompete less dense populations of native species. Invasive populations of the Argentine ant (*Liniepithema humile*) in southern California are such an example where the invasive species exhibits reduced intraspecific aggression, relative to native populations of *L. humile* in South America (Suarez et al., 1999), and this reduced intraspecific aggression may facilitate growth of the invasive population (Holway et al., 1998). However, in these instances, aggressivity is considered as a species- or population-wide trait, not as a trait that varies among individuals. When individual differences have been examined, asocial tendencies rather than tolerance or gregariousness appear to drive dispersal and promote invasion into new habitats. For example, in mosquitofish populations, *Gambusia affinis*, the least social individuals disperse (Cote et al., 2010b).

The aim of our study was to determine whether there were differences in aggressive tendencies and competitive abilities between individuals from an invasion front and those from a more established area. We used the round goby (*Neogobius melanostomus*), an invasive fish in the Laurentian Great Lakes. Round goby are native to the Ponto-Caspian region of Europe (Jude et al., 1992) and have rapidly invaded North America and Western Europe. Their invasion has been mediated through unintentional human transfers in the ballast water of shipping vessels (Corkum et al., 2004). Although the saltatory appearances of the round goby through the Great Lakes over a five year period was probably aided by human-assisted dispersal (Hensler & Jude, 2007; Hayden & Miner, 2009), round goby also undergo natural range expansions in invaded habitats through unassisted dispersal (Bronnenhuber et al., 2011; Gutowsky et al., 2011; LaRue et al., 2011). Individual variation in aggressiveness and dispersal tendencies may mediate this expansion.

We compared aggressiveness and competitive ability in the round goby by means of a resource contest over access to shelter. Male round goby that are reproductively active will guard a territory that contains a nest/shelter

(Wickett & Corkum, 1998; MacInnis & Corkum, 2000). Round goby are strongly motivated to compete for and actively defend these shelters from heterospecifics (Dubs & Corkum, 1996; Balshine et al., 2005; Savino et al., 2007) and conspecifics (Stammler & Corkum, 2005; Sopinka et al., 2010). We predicted that if aggression is important in mediating round goby range expansions, then round goby from an invasion front would (1) be bolder than, (2) be more aggressive than and (3) outcompete round goby from established areas. However, given that round goby are highly aggressive and territorial, less competitive individuals could be forced out of prime habitat and, thus, contribute to range expansion (Ray & Corkum, 2001; Johnson et al., 2005; Brownscombe & Fox, 2012). If invasion front round goby are indeed the displaced, less competitive fish, then alternatively we predicted they would be (1) less bold, (2) less aggressive and (3) lose contests more often compared to fish from established populations.

2. Methods

2.1. Animal collection and housing

Round goby (*N. melanostomus*) were collected on June 9 and June 29, 2010 from two areas in the Trent-Severn waterway (Ontario, Canada; Figure 1). Fish from an established and reliably sampled round goby population (since 2003) were caught in three locations in the Trent River centered around Hastings (44°17′54″N, 077°58′02″E; 44°17′43″N, 077°58′29″E; 44°18′30″N, 077°57′28″E; Figure 1 Established Area Inset, Raby et al., 2010). Fish from the invasion front were caught at four locations in the Otonabee River (44°11′49″N, 078°14′22″E; 44°12′22″N, 078°14′22″E; 44°12′36″N, 078°14′11″E; 44°12′46″N, 078°14′01″E; Figure 1 Invasion Front Inset). Round goby were first detected in the Otonabee River only in the spring of 2010 despite this site being previously surveyed for round goby in 2009 and earlier (Brownscombe, 2011). The Trent River population has been there for at least seven years and is thought to have been initially established by a bait bucket transfer from one of the Great Lakes. Round goby from the Otonabee River invasion front site have spread down from the original introduction site in the Trent River near Hastings. The movement of this invasion front has tracked since 2003 (Raby et al., 2010; Brownscombe, 2011; Gutowsky & Fox, 2011). Although more established round goby populations exist in North America (for example, Lake Erie was colonized by round goby in
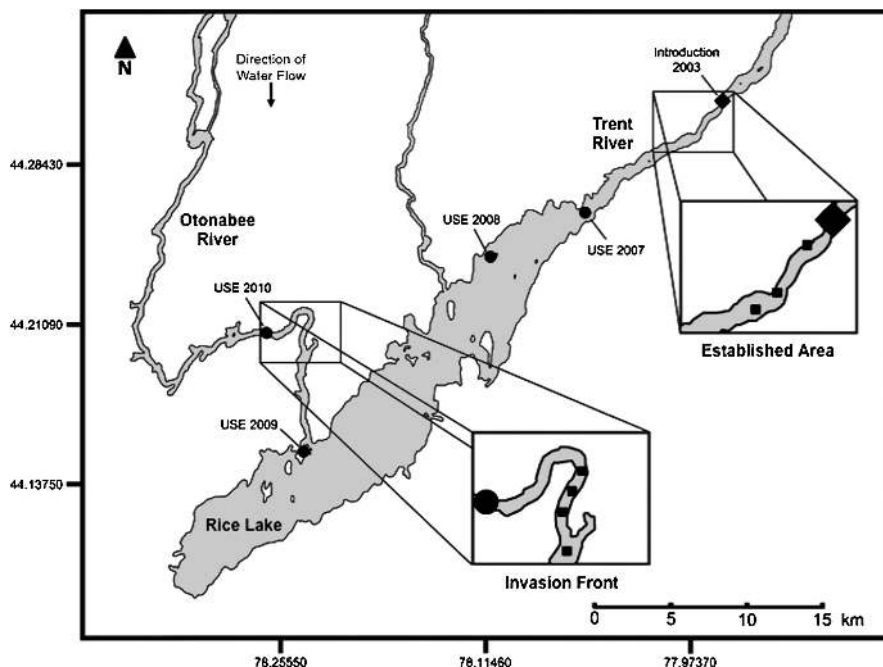
Figure 1. A map of the round goby collection sites used in this study. Inset areas are a magnified view of the invasion front and established area collection sites. The initial introduction of round goby into the Trent River in 2003 is denoted with a diamond (♦). The upstream edges (USE) of the round goby population (the invasion front) between 2007 and 2010 are indicated by circles (●) labelled with the year the population reached the edge location. Insets: Squares (■) represent individual sampling locations within each collection site. Invasion front round goby were sampled from 4 separate areas along the Otonabee River and round goby from the established area were collected from 3 separate areas within the Trent River.

1993; Corkum et al., 1994), we chose to examine fish from these two nearby areas to control for environmentally induced differences in behaviour (Alvarez & Bell, 2007). The two chosen areas are within the same drainage system, and have similar habitat characteristics.

Round goby were caught using angling and baited minnow traps and were then sorted by sex and reproductive status. Males and females were distinguished based on urogenital papilla shape (pointed in males, square in females; Miller, 1984) and the reproductive status of males was assessed using papilla length, head width and body colouration (Marentette & Corkum, 2008; Marentette et al., 2009). Males were transported to McMaster University (Hamilton, Ontario) and held in 66 l aquaria in groups of four to six

fish from the same collection site. Aquaria contained gravel to a depth of 1 cm, 15-cm sections of PVC piping as shelter, an AquaClear 50 external box filter, and a thermometer (water temperature maintained between 22 and 24°C). Round goby were fed flake food (Nutrafin) ad libitum once daily and were allowed at least 72 h to acclimate in the lab prior to behavioural testing.

2.2. Behavioural trials

In total, 36 resource competition trials were conducted. Fish were placed in size-matched pairs with one competitor from the invasion front population and its opponent from the established area. We size-matched fish using body mass (to the nearest 0.01 g) because body size differences of as little as 3% have been shown to influence the outcomes of competitive interactions in this species (Stammler & Corkum, 2005). Size differences between competitors ranged from 0.01 to 2.0 g in body mass (mean difference 0.57 ± 0.49 g, paired t-test; $t = 0.14$, $N = 36$, $p = 0.89$). In order to further account for the effect of size differences on contest outcomes, we selected contestants such that the marginally larger individual of the pair was from the invasion front in half the trials and from the established area in the other half of the trials. To facilitate identification during the contests, each individual was marked subcutaneously with either green or yellow non-toxic acrylic paint just below the dorsal fin spines (see Wolfe & Marsden, 1998). The colour of paint used for each fish and the placement of the fish into the left versus the right end chamber of the aquarium (see below) were randomized.

Twenty-four hours prior to the start of a behavioural trial, size-matched marked opponents were placed into one of two end chambers in a 66-l experimental aquarium divided into thirds by removable, black opaque barriers. Each chamber contained a black opaque shelter box (5 cm long, 15 cm wide, 5 cm high) with a small opening that was oriented to face the front of the aquarium (Figure 2A). The next morning an observer, blind to the origin of the fish, recorded all the behavioural data while seated 1 m away from the aquarium (following protocols used in Sopinka et al., 2010). Data were recorded in person and trials were also videotaped for further analyses on Mini DV cassettes using a Sony Digital Camcorder (model DVR-VX2000NTSC).

Behavioural trials always began between 9:00 and 10:00 h. Each trial started when the shelters were removed from the end chambers (Figure 2B). We observed each focal fish for a 5-min post shelter removal period and
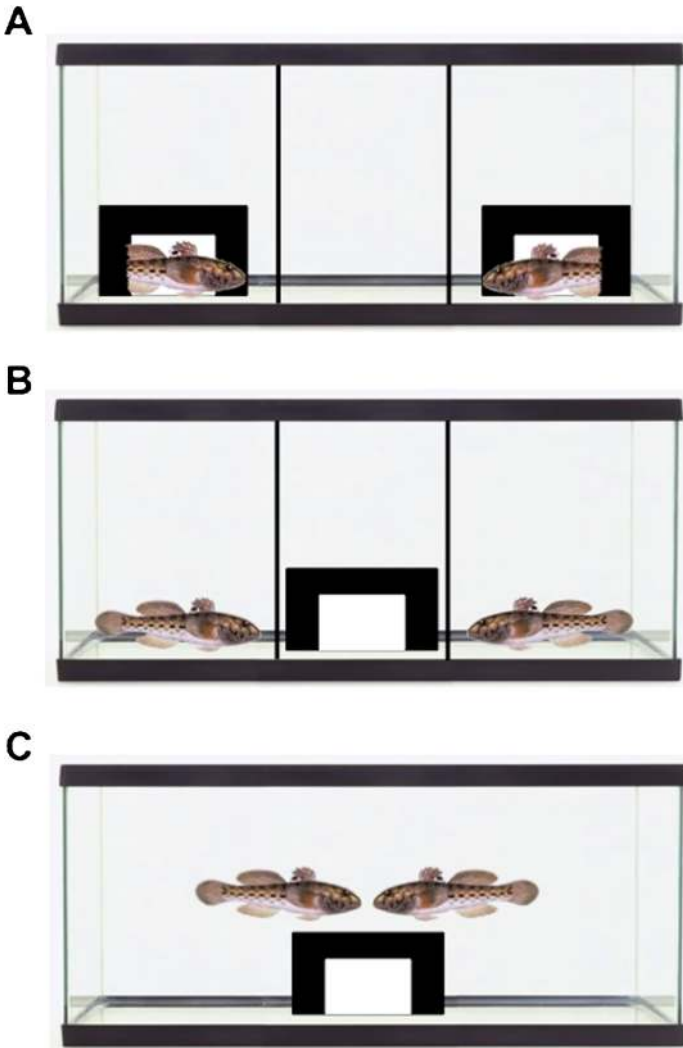
Figure 2. Experimental set-up. (A) Competitors were placed in the outer compartments of the contest tank to acclimatize overnight. (B) Shelters were removed from the compartments and the time to recover activity as well as activity levels were recorded as a measure of boldness. (C) The two barriers were then removed so fish could engage, interact and compete over the shelter. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1568539x/149/7.

recorded the time taken to initiate movement following removal of the shelter as well as all behaviours exhibited (see below). Following the 5-min boldness

evaluation, we removed the two opaque barriers allowing both fish access to the central chamber and shelter and to see and interact with one another (Figure 2C). Each fish was observed for 10 min in a pre-determined, randomized order (20 min total). The identity of the fish that crossed over to the opposite side of the tank first was noted, along with which fish initiated the first aggressive act, the latency to the first aggressive act (in s), and the total duration of the first aggressive interaction that occurred (in s). All aggressive, submissive, and locomotor behaviours were recorded (see Sopinka et al., 2010 for an ethogram of the behavioural repertoire of this species). The time spent in the shelter was noted (in s) for each fish throughout the 20-min trial as well as the total number of shelter entries completed by each fish. At 1.5 and 3 h following the start of the trial each fish was observed for an additional 2 min to determine the rate of aggressive behaviours and note which fish was occupying the shelter. This also allowed us to determine the stability of the dominant-subordinate relationship between the two competitors. After 3 h the trial was terminated, the fish were killed in benzocaine (Sigma Aldrich Canada, Oakville, ON, Canada), and total body mass (to the nearest 0.01 g) was reassessed and sex was confirmed. Between behavioural trials, all barriers and shelters were rinsed thoroughly and one-third of the aquarium water was changed.

2.3. Behavioural assessment

We used activity following a disturbance (i.e., the removal of the shelters from the end chambers prior to each resource contest and removal of the opaque barriers) to quantify boldness, under the assumption that bolder fish would recover from disturbance faster than would shy animals. Boldness was evaluated in three ways: (1) following removal of the shelters from the end chambers, time to resume movement, if any, during the 5-min evaluation period, (2) the level of activity following this disturbance and (3) which fish first crossed into the middle chamber following the removal of the opaque barriers. We disturbed the fish by removing their shelter. Shelter is a critical resource for round goby and is used by the fish for both breeding and avoiding predators (Corkum et al., 2004). Hence, we propose that the tendency to move across an open tank in the absence of shelter is an appropriate measure of individual boldness in this species. At the end of each resource contest the winner was determined based on the following criteria: (1) the fish performing the most aggression during the first 20-min observation period and (2) the fish that monopolized the shelter 3 h following the start of

the trial. Both contact aggression and non-contact displays (see Sopinka et al., 2010) were tallied to determine total aggression. Contact aggression included mouth-fighting, biting and chasing behaviours. Non-contact display aggression included displacements (where the focal fish's movement caused its opponent to retreat/move away), mouth gapes, also known as opercular flares or frontal displays (where the focal fish spread out its operculum and lower jaw while orienting toward its opponent), and parallel displays (when the focal fish arch the front of their body upwards and maximally extends their first dorsal fin within 10 cm of their opponent). Duration of an aggressive interaction (s) was defined as the time from which the first aggressive act (either contact or non-contact) was performed to the time when fish ceased interacting with one another. Following Fuxjager et al. (2010), an 'aggression intensity index' was determined for each contestant during the first 20-min observation period using the formula: total aggressive behaviours performed minus total submissive behaviours performed divided by the sum of all submissive and aggressive behaviours performed.

2.4. Statistical analysis

Statistical analyses were performed using JMP (Version 5.0.1, 2001; SAS Institute, Cary, NC, USA) and R 2.12.2 (R Development Core Team, 2011). Data were checked for normality and transformed when necessary. When data could not be transformed to meet parametric assumptions, non-parametric tests were used. Means and standard errors are reported for all data. Fulton's body condition (K) was calculated for each fish using the formula $K = ((\text{body mass (g)})/(\text{total length (mm)}^3)) \times 10^6$ (Neff & Cargnelli, 2004). Wilcoxon signed ranks tests, chi-squared tests and t-tests were used to assess differences in boldness, aggression and contest wins between invasion front and established area fish. Spearman rho correlations were used to examine relationships between boldness and aggression, and between body mass and duration of aggression interactions, aggression rates and aggression intensity. To explore the effects of collection site and body size on the probability of winning, we calculated a logistic regression of the probability of the individual from the invading population winning the contest, with size difference as the continuous predictor variable. Note that the sample sizes varied across analyses. In three trials, the pairs of fish did not engage aggressively within the 20-min observation period and, therefore, behavioural data could not be recorded for those pairs. However, a winner could be determined on the basis of shelter monopolization for all trials by the end of

the 3-h trial period. In five trials it was unclear which fish first crossed into the opposing half of the chamber as both fish seemed to do so at once, and similarly in eight trials it was not possible to determine which fish initiated aggression.

3. Results

3.1. Boldness, aggression and contest wins

After the disturbance (removal of shelters) round goby from both the invasion front and the established area resumed activity at a similar rate ($z = -0.36$, $N = 36$, $p = 0.72$, Figure 3A). Also, the frequency of activity ($z = -1.28$, $N = 36$, $p = 0.20$) and the number of fish that first crossed into the middle chamber were similar between sites ($\chi^2 = 1.06$, $N_{Inv} = 20$, $N_{Est} = 14$, $p = 0.30$).

Round goby from the invasion front tended to perform more aggressive behaviours ($z = -1.533$, $N = 36$, $p = 0.07$, Figure 3B) but they did not have a higher aggression intensity index than size-matched individuals from the established population ($z = 0.16$, $N = 33$, $p = 0.87$). Round goby from the invasion front did not initiate the contests more frequently ($\chi^2 = 0.57$, $N_{Inv} = 12$, $N_{Est} = 16$, $p = 0.58$) nor did they initiate aggression earlier ($t = 0$, $N_{Inv} = 12$, $N_{Est} = 16$, $p = 1.00$). No significant correlation was observed between aggression rates during the contest and any of the three measures of boldness exhibited in the 5 min prior to the trial (time to resume activity: $r_s = -0.05$, $N = 58$, $p = 0.70$; overall activity performed: $r_s = -0.06$, $N = 58$, $p = 0.68$; crossing over the line: $t = 0.26$, $N = 34$, $p = 0.80$). Also, individuals that initiated the contests were not more aggressive than those that did not initiate the contests ($t = 0.117$, $N = 52$, $p = 0.91$). Invasion front fish won a similar number of contests as the established area fish regardless of whether winning was based on aggression in the first 20 min or shelter monopolization after 3 h (aggression in first 20 min: $z = -1.533$, $N = 36$, $p = 0.07$; shelter monopolization: $\chi^2 = 1.88$, $N_{Inv} = 21$, $N_{Est} = 13$, $p = 0.17$, Figure 3C).

3.2. The influence of competitor asymmetry

Body mass was not significantly correlated with aggression performed ($r_s = -0.11$, $N = 36$, $p = 0.34$) or with aggression intensity ($r_s = 0.16$, $N = 36$, $p = 0.19$). Although differences in body mass had a significant effect on
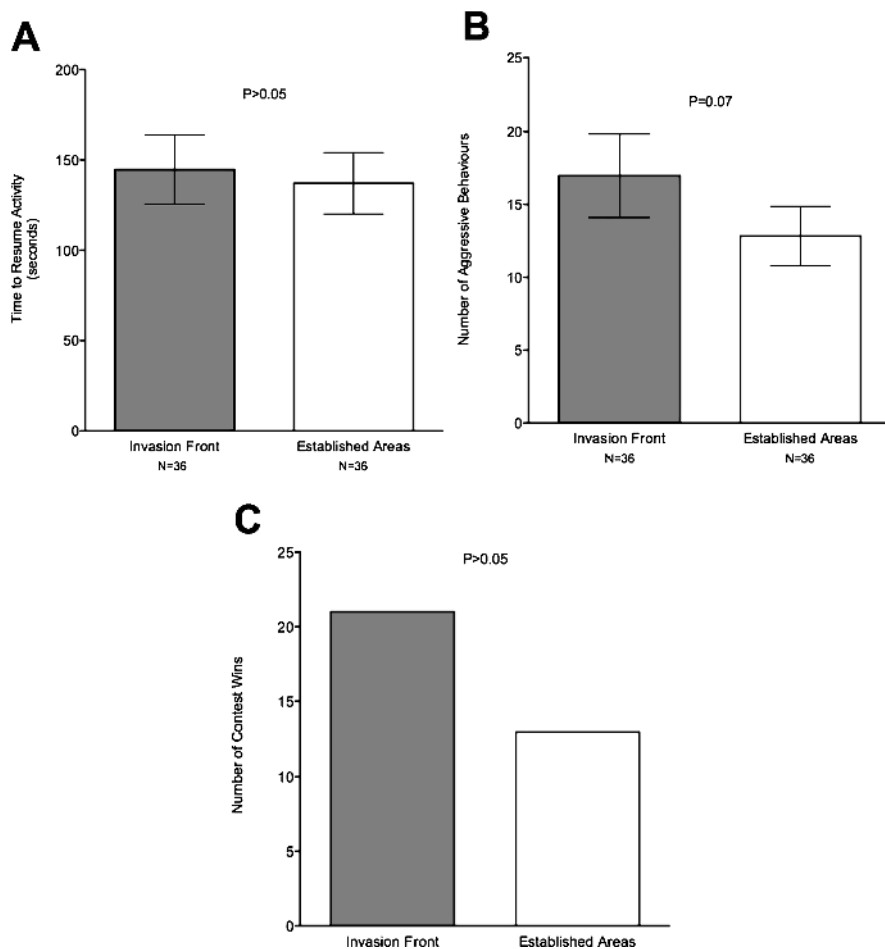
Figure 3. (A) Time (s) for established and invasion front fish to resume activity (a measure of boldness) following removal of the shelter (Figure 2B). (B) Number of aggressive acts displayed by established and invasion front fish during the first 20-min observation period. (C) Number of contests won (based on shelter monopolization after 3 h by established ($N = 13$) and invasion front ($N = 21$) fish.

winning probability (logistic regression of the invasion fish winning with size differences as a continuous predictor variable, $z = 2.21$, $N = 36$, $p = 0.027$), the site the round goby came from only had a marginal and non-significant effect on winning probability ($z = 0.72$, $N = 36$, $p = 0.07$, Figure 4).

The duration of aggressive interactions decreased with an increase in the size discrepancy between competitors ($r_s = -0.49$, $N = 36$, $p = 0.002$).
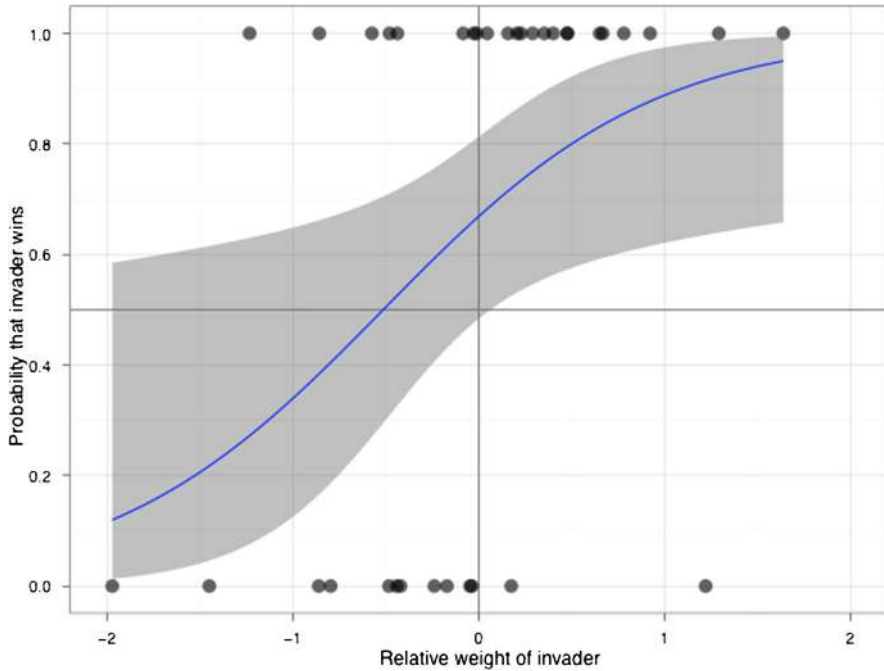
Figure 4. Logistic regression model of the probability of invasion front fish winning a contest with body mass differences as a continuous predictor. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1568539x/149/7.

However, there was no significant correlation between the total aggressive acts performed and competitor size asymmetry ($r_s = -0.18$, $N = 36$, $p = 0.29$). Also, there was no relationship between the degree of competitor asymmetry (by body mass) and either total contact aggression ($r_s = 0.02$, $N = 36$, $p = 0.91$) or total non-contact display aggression ($r_s = -0.20$, $N = 36$, $p = 0.24$) observed in a trial. Interestingly, when considered separately, the aggression frequency in the contest was not significantly correlated with body mass of either the winner ($r_s = -0.25$, $N = 36$, $p = 0.14$) or the loser ($r_s = -0.25$, $N = 36$, $p = 0.13$). Similarly, body condition, which did not differ significantly between individuals from the two collection sites (invasion front versus established area, $x_{inv} = 22.2 + 0.5$ vs. $x_{est} + SE = 23.1 + 0.5$; $z = -1.90$, $N = 36$, $p = 0.06$), did not relate to aggression levels observed in winners ($r_s = -0.27$, $N = 36$, $p = 0.11$) or losers ($r_s = 0.09$, $N = 36$, $p = 0.59$).

4. Discussion

In competition for shelter, round goby from an invasion front tended to perform more aggression, but were otherwise competitively similar to round goby from a more established population. There were also no boldness measure differences between fish from the different sites, suggesting that boldness may not play an important role in the spread of round goby into new habitats. However, it is worth noting that our measures of boldness before the resource contests did not correlate with aggressive behaviour exhibited during the contests, despite the large body of literature that implies that these behavioural traits are often related (Huntingford, 1976; Wilson et al., 1994; Wilson, 1998; Sih et al., 2004a,b; Wolf et al., 2007, 2012; but see Bell & Sih, 2007). The lack of a correlation between aggression and boldness could mean that there is no behavioural syndrome in round goby or that these two traits as quantified in this study did not capture the existing syndrome found at invasion fronts. Further tests of fish personality from more invasion front and established areas are definitely warranted. In addition, it would be valuable to compare round goby populations in North America with ancestral populations from Eastern Europe to see how these would differ.

Body size was an extremely important determinant of contest outcome. As the body size asymmetry between competitors increased, contest duration decreased. Our study shows that even small differences in resource holding power (i.e., body size asymmetries of 3% or smaller) frequently dictate contest outcomes in this species (Stammler & Corkum, 2005). This finding provides ethological support for a proposed invasion mechanism whereby younger, smaller round goby are forced to disperse after losing territorial battles with older, larger fish (Ray & Corkum, 2001; Johnson et al., 2005; Brownscombe & Fox, 2012). The tendency for round goby to not interact aggressively for extended durations but to move on to another area, even when an opponent is only slightly larger, could help explain this species successful colonization capacity.

Given that body size is a good predictor of contest outcome, examination of the size distribution in established versus invasion front areas could provide a test of the ontogenetic theory of range expansion. If it is the less competitive and smaller individuals that expand the range when they are pushed out of established areas, then invasion fronts would be populated by younger, smaller individuals. The results are currently mixed. A few studies have observed younger and smaller round goby at invasion fronts or in newly

invaded areas compared to the fish found in the more established areas (Ray & Corkum, 2001; Bergstrom et al., 2008; Brownscombe & Fox, 2012). However, larger than average round goby have been detected in expansion areas where the species has been present for a year or more (Gutowsky & Fox, 2011). It is possible that fish at invasion fronts might be smaller only on a short time scale, as they probably enjoy rapid growth rates (and high survival rates) as a consequence of lowered conspecific density, reduced conspecific competition for food and shelter, and presumably naïve predators, at the invasion front.

Interestingly, the round goby populations at invasion fronts studied to date appear to be female-biased (Brownscombe & Fox, 2012). In contrast, established round goby populations are typically male-biased (Corkum et al., 2004; Young et al., 2010) and males move more than females (Marentette et al., 2011). It is possible that differences in the degree of competition for mates between invasion fronts and established areas may also shape selection for male aggressivity. Future studies should aim to quantify aggression between invasion front and established site fish across a wider range of body sizes, operational sex ratios and under several ecological contexts (aggression over mates, space and food).

A critical assumption of this study is that each round goby located at the invasion front had dispersed from a region with a more established round goby population (around Hastings). Our study, thus, indirectly assessed the relationship of (current) aggression and (inferred past) movement distance in this fish. As round goby may move larger distances as juveniles than adults (Ray & Corkum, 2001; Hensler & Jude, 2007), there could be a relationship between aggression and dispersal distance as a juvenile that is simply no longer apparent in adult round goby. It would be useful to uncover whether fish that behave more boldly or aggressively in the laboratory, then disperse more readily or move further distances in the field. Establishing this behavioural link is crucial, because other factors such as human-mediated transfers in bait buckets may play a major role in initial round goby invasion fronts. As human-mediated transfers often move fish large distances regardless of their behavioural traits, such human-moved fish could impair our ability to detect the natural dispersers and the influence of behavioural syndromes on the phenotypic structure of invasion fronts. It is also possible that the apparent lack of a behavioural syndrome resulted from a genetic bottleneck of the small founding population.

The ability to rapidly disperse is one of the attributes of successful invasive species (Kolar & Lodge, 2001). This study aimed to further understand the factors influencing the dispersal of round goby, one of the Laurentian Great Lakes' most abundant invaders. Our study did not support the idea that individual variation in aggressiveness or boldness influences the composition of the invasion front. Instead, our data suggest that invasion front fish are comprised of all behavioural types which may have a considerable influence on the social dynamics of expanding invaders, and in turn have consequences for the progression and outcome of biological invasions (Rehage & Sih, 2004; Marentette et al., 2011). Finally, other abiotic and biotic factors that affect dispersal need to be considered. For example, reproductive status and sex (controlled for in our study) are known to influence contest behaviour (Figler et al., 2005) and will impact dispersal and range expansion. Habitat variables (temperature, rugosity, predation risk, prey density) may also influence dispersal and could drive or hinder range expansion. Understanding the contribution of these factors as well as the behavioural and personality differences among individuals inhabiting established and expanding regions may lead to better predictions about where invasions are likely to be most successful and insights on the general population dynamics of invasive species.

Acknowledgements

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