BRILL
Behaviour 152 (2015) 127–146
Behaviour
brill.com/beh

Aggression and sociality: conflicting or complementary traits of a successful invader?

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Accepted 24 July 2014; published online 9 October 2014

Abstract
Invasion biology research has identified two juxtaposing behavioural traits, aggressiveness and sociality, that may both increase the success of species invasions. Highly aggressive invaders can out-compete native species for resources, while social gregarious invaders can tolerate high conspecific density. In order to tease apart the effects of aggressive versus social tendencies on the success of invasive species, we studied round goby (*Neogobius melanostomus*), a highly successful invasive fish species now common in the Laurentian Great Lakes. While round goby are well known for being aggressive, much less is known about their tendency to affiliate with conspecifics, in spite of the fact that they thrive in extremely high densities in many of their invaded habitats. We collected round goby from Hamilton Harbour, ON, Canada and conducted three separate experiments to explore group-forming behaviour by measuring preference for conspecifics. We found that round goby have a strong preference to associate with a single conspecific, and that both males and females showed this preference. No overall preference was detected for large versus small groups of conspecifics. Females chose the safety of a shelter over associating with a conspecific but males were equally attracted to conspecifics as shelter. Our results provide new insight into how interactions between aggressive and social behaviours play a role in the rapid spread of invasive round goby.

Keywords
invasive species, social preference, grouping, sex differences, round goby, Gobiidae, Lake Ontario.

1. Introduction

Behaviour has been identified as an important factor for understanding invasion processes (Holway & Suarez, 1999; Chapple et al., 2012). Studying how behaviours influence invasion dynamics can further our understanding

DOI 10.1163/1568539X-00003235

of why particular species succeed to establish (Sol et al., 2008), but detailed information about an invasive species' behavioural repertoire is often missing. Sociality, or the tendency to live in groups, has been proposed as one behavioural attribute facilitating the colonization and establishment of an invasive species (Holway & Suarez, 1999; Chapple et al., 2012). Social species that are highly gregarious are thought to rapidly colonize and build up in population density, competitively displacing other species due to their numerical advantage (Holway & Suarez, 1999; Tsutsui et al., 2000). However, this idea has rarely been assessed empirically. Much more research has focused on aggressiveness, another classic behavioural characteristic of invasive species, with a number of studies showing that high interspecific aggression allows invasive species to out-compete and displace native species (Capelli & Munjal, 1982; Dick et al., 1995; Usio et al., 2001; Gherardi & Daniels, 2004; Duckworth & Badyaev, 2007; Weis, 2010). Both sociality and aggressiveness are proposed to propel invasion success (Chapple et al., 2012), yet these traits seem to stand in contrast. Successful invaders displaying high aggression to heterospecifics should also show high aggression towards conspecifics (Pintor et al., 2009), limiting the ability of a species to reach high densities. Exploring social and aggressive behaviours will help elucidate the mechanism of how successful invaders rapidly colonize new areas.

Most often, aggression is assessed in a given invasive species, rather than sociality. For example, among ants (Rowles et al., 2007; Carpintero & Reyes-Lopez, 2008), crustaceans (Capelli & Munjal, 1982; Dick et al., 1995; Usio et al., 2001; Gherardi & Daniels, 2004; reviewed in Weis, 2010) and birds (Duckworth & Badyaev, 2007; Duckworth, 2009), invasive species are known to dominate in aggressive contests with native species. In invasive western bluebirds (*Sialia mexicana*), biased dispersal of aggressive individuals at the invasion front led to the displacement of less aggressive native species, but levels of aggression decreased in the established invasive population in subsequent generations (Duckworth & Badyaev, 2007). The few existing studies linking sociality and invasion success have focused on the influence of sociality across different stages of invasion. For example, asocial invasive mosquitofish (*Gambusia affinis*) were found to disperse further than social individuals, showing that the successful spread of an invader is associated with individuals who are not social (Cote et al., 2010, 2011). Successful establishment has been associated with high sociality and low intraspecific aggression in social insect species (Holway et al., 1998, 2002; Perdereau et al., 2011). Invasive Argentine ant (*Linepithema humile*) populations experienced a genetic bottleneck that facilitated the formation of large and dense colonies lacking intraspecific aggression while still displaying high levels of interspecific aggression, allowing them to out-compete native populations (Tsutsui et al., 2000). Taken together, the above work demonstrates the potential for sociality to facilitate invasion and establishment alongside aggression and underscores the need to empirically evaluate the importance of both aggression and social tendencies as traits in successful invasive species.

To this end, we examined social preferences in round goby (*Neogobius melanostomus*), an invasive fish species to the Laurentian Great Lakes that is well known to be highly aggressive (Charlebois et al., 1997; Corkum et al., 1998, 2004; Kornis et al., 2012). Round goby are native to the Black and Caspian Seas of Europe and were accidentally introduced into the St. Clair River via ballast ship water in 1990 (Jude et al., 1992) and rapidly spread to all five Laurentian Great Lakes (Corkum et al., 2004). Round goby are thought to be responsible for the decline of several native fish species that rely on similar resources (French & Jude, 2001; Janssen & Jude, 2001). The ability of round goby to out-compete native species has been attributed in part to their highly aggressive nature during interactions with native fish species (Dubs & Corkum, 1996; Janssen & Jude, 2001; Balshine et al., 2005; Bergstrom & Mensinger, 2009). To date, behavioural research on this species has focussed mainly on interspecific competition between round gobies and native fish species, while far less research has explored round goby intraspecific interactions. Since round goby are a benthic, nest-guarding fish that are not thought to form tight social aggregations (Charlebois et al., 1997), it is surprising that they have been observed living at high densities in the Great Lakes Basin. They have been reported at densities of 0.80 to 7.76 fish/m^2 in western Lake Erie (Johnson et al., 2005), at densities of 3.88 to 9.64 fish/m^2 in the Bay of Quinte (Schaner et al., 2009; Taraborelli et al., 2009), and the highest densities have been reported in the Trent River at 9.6 and 17.0 fish/m^2 (Gutowsky et al., 2011; Brownscombe & Fox, 2012). Males have been reported sometimes nesting within centimetres of each other (Wickett & Corkum, 1998), indicating that round goby males in the Great Lakes may be highly tolerant of conspecifics even during the breeding season. In laboratory contests, round goby are able to perceive even very small (3%) size differences between themselves and a conspecific opponent, eliminating the need for prolonged or overt aggression (Stammler & Corkum, 2005; Groen et al., 2012). If round goby do indeed have a high tolerance of conspecifics, this may be another factor contributing to their rapid establishment and proliferation (Marentette & Corkum, 2008). However, a recent study examining the effects of density on competition found that at higher densities, round goby showed decreased growth and emptier digestive tracks (Kornis et al., 2014), suggesting that there is a cost to grouping and living at high density. This finding highlights the importance of studying intra-, as well as interspecific interactions to determine whether round goby simply tolerate conspecifics, or whether they have a natural tendency to move towards and affiliate with conspecifics because of possible benefits from grouping.

Using an established population of round goby, we sought to assess social aggregation decisions in this species and to provide an initial quantification of their potential for sociality. The specific aims of this study were to address three questions about grouping decisions in round goby: (1) Do round goby prefer to affiliate with a single conspecific or remain solitary? (2) Do round goby prefer to affiliate with small or large groups of conspecifics? (3) Do round goby prefer to affiliate with a conspecific more than inhabiting a shelter? We tested grouping preferences in three separate laboratory experiments using a well-established social preference assay (Svensson et al., 2000; Buckingham et al., 2007; Gomez-Laplaza & Gerlai, 2011; Reddon et al., 2011). Given the high density of round goby in the wild (Johnson et al., 2005), their apparent tolerance of conspecifics (Stammler & Corkum, 2005; Marentette & Corkum, 2008), and theoretical anti-predatory benefits from grouping (Hamilton, 1971; Foster & Treherne, 1981; Morgan & Godin, 1985), we predicted that round goby (of both sexes) would prefer to affiliate with a conspecific over remaining alone. Because large groups often provide better protection against predators compared to small groups (Foster & Treherne, 1981; Magurran & Pitcher, 1987), we also predicted that round goby would prefer a larger group of conspecifics compared to a smaller group. Although round goby may receive anti-predation benefits from grouping, they typically avoid predators by sheltering under rocks (Charlebois et al., 1997) and have a strong preference for rocky substrate and will use and defend rock shelters year round (Ray & Corkum, 2001; Young et al., 2010, *personal observations*). Therefore, we predicted that round goby would prefer to spend time in a shelter versus affiliating with a conspecific. However, we anticipated a sex difference in the degree of shelter preference because although both males and females use shelters to hide from predators, males actively protect eggs in these shelters during the breeding season (Charlebois et al., 1997).

2. Methods

2.1. Fish collection and housing

We collected round goby from LaSalle Park Marina, in Hamilton Harbour, Ontario, Canada (43°18′1″N, 79°50′47″W). Round goby have been sampled at this site for over a decade (Young et al., 2010; McCallum et al., 2014) and it has a mixture of rocky cobble and sandy substrate. Round goby were collected between 15 May and 20 August 2013 using minnow traps baited with frozen corn kernels (see Young et al., 2010; McCallum et al., 2014 for additional details of the collection protocol). We transported the fish in lake water to the laboratory at McMaster University and housed them in 75-l tanks (61 × 46 × 30 cm) with dechlorinated tap water containing a static renewal filter (Aquaclear), a layer of natural gravel substrate (approx. 1 cm deep), and polyvinylchloride (PVC) tubes as shelters. Water temperature was maintained at 20–22°C. All fish were fed Nutrafin basix Staple Food once per day and were maintained on a 14:10 h light-dark schedule. Focal fish were housed in same-sex groups of three and were always housed separately from stimulus fish. After 24 h of acclimation to laboratory conditions, focal fish were individually marked with an injection of non-toxic acrylic paint (Wolfe & Marsden, 1998). Morphological measurements (total length, standard length and body mass) were taken at this time using callipers accurate to the nearest 0.01 cm and a digital scale accurate to the nearest 0.01 g (Scout Pro SP202).

2.2. Testing apparatus

To explore social preferences, round goby were tested in a 150-l tank (90 × 44 × 38 cm; Figure 1A and 1B) in experiments 1 and 2, and in a 75-l tank (61 × 46 × 30 cm; Figure 1C) in experiment 3. Testing tanks contained a layer of gravel substrate (approx. 1 cm deep) and a static renewal filter that was turned off before the start of each trial. Each trial was recorded with a video camera (Canon HD Vixia HFS100 8.0 Megapixel) concealed behind a blind with a hole for the camera that limited disturbance from the experimenter and the video camera. Video recordings were used later for behavioural scoring and analysis.

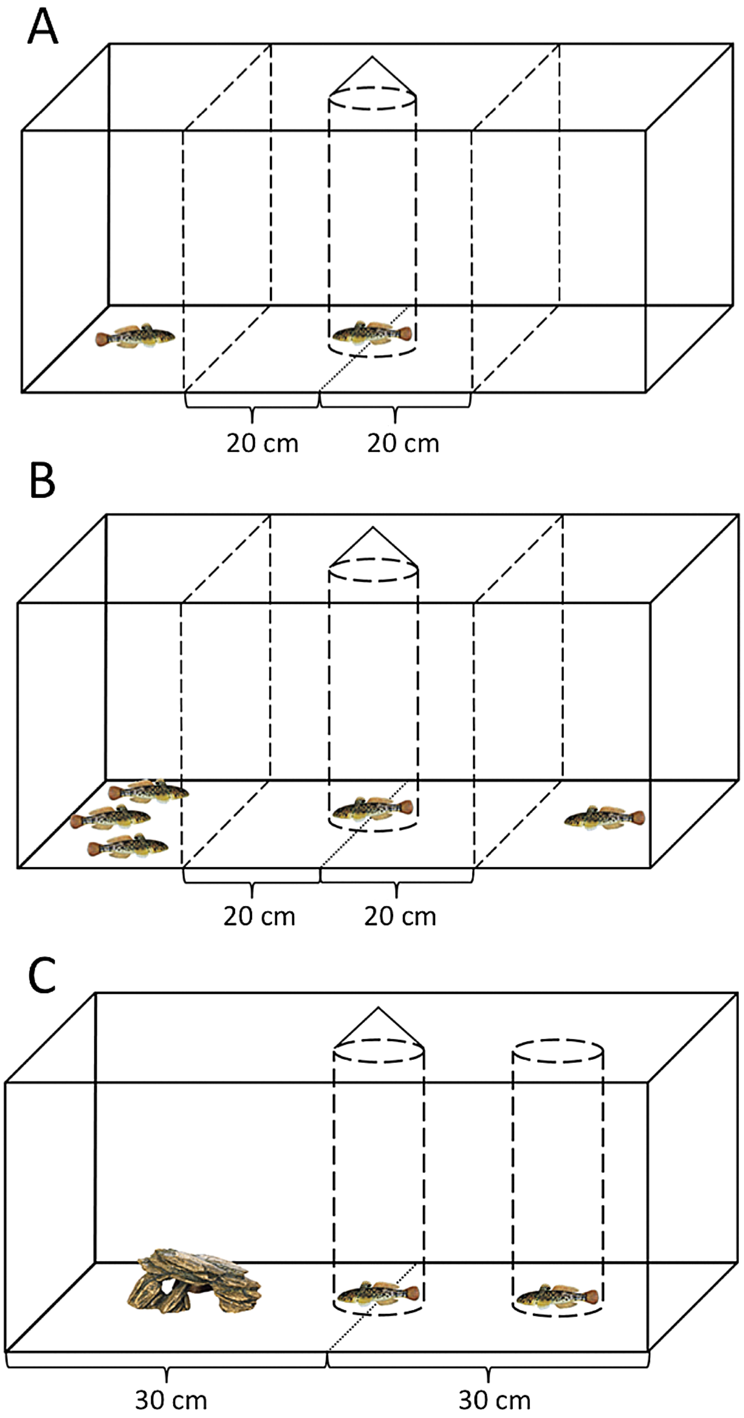

Figure 1. Experimental tank set-up for (A) one fish vs. empty chamber experiment; (B) three fish vs. one fish experiment; and (C) shelter vs. one fish experiment. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

2.3. Testing procedure

2.3.1. General protocol

All fish were housed in the laboratory for a minimum of 48 h before testing. We chose unfamiliar, size-matched, same-sex fish as stimulus fish to ensure that social preference reflected social partner choice and not mate choice (Reddon et al., 2011). Each stimulus fish was used for only three trials, ensuring that overall focal fish were exposed to many different stimulus fish. The side chosen to contain a particular stimulus was randomly assigned by a coin toss. Each focal fish was placed in a perforated cylindrical tube (13 cm diameter, 20 cm height) in the center of the testing tank and left to habituate for 15 min. During this habituation period the fish could see the rest of the tank and the stimuli on both sides of the tank. The central tube was then lifted remotely using a pulley from behind the blind, and the focal fish was free to navigate the exploration area for a 15-min period. Time spent in each half of the exploration area was recorded and used as a measure or index of preference for each stimulus. We also scored focal and stimulus fish movements as well as any behavioural acts performed across the barrier (Table 1).

2.3.2. Experiment 1: one fish versus an empty chamber

A total of 60 focal fish (30 males: mean ± SD total length = 6.3 ± 3.3 cm; 30 females: mean ± SD total length = 6.9 ± 2.9 cm) were used in this experiment. Two transparent perforated plastic barriers divided the testing tank into three compartments (two end compartments that were each 25 cm wide and a central exploration compartment that was 40 cm wide). The perforations allowed for the transfer of visual, olfactory, and limited tactile cues. One stimulus fish was added to one of the testing tank's end compartments, while the other end compartment remained empty. To track each focal fish's preference and number of switches during the trial, a grid was drawn along the central exploration compartment dividing it into two equal zones measuring 20 cm each. In addition, to track focal fish fine scale movement and activity rates, the central compartment was further divided into five equal grid zones measuring 8 cm each (average round goby length). The focal fish was considered to have changed zones when at least 50% of its body — including its head — crossed a grid line and entered a new one on the grid. After testing, focal fish were euthanized using an overdose of benzocaine (0.025% in solution; Sigma Aldrich), and dissected to confirm reproductive status. Gonad weight was taken to the nearest 0.001 g (Acculab Vicon Digital

Table 1.
Ethogram used to score focal fish and stimulus fish behaviours during sociality assays.

	Behaviour	Description
Locomotor and maintenance	Hop (H)	Smooth locomotion on substrate driven by pectoral fins. Forward or sideways movement of distance less than one body length.
	Swim (Sw)	Sustained locomotion in the water column using all fins. Forward or sideways movement of distance greater than one body length.
	Dart (D)	A spontaneous, rapid swim along the substrate not directed at anything.
	Scrape (Sc)	Focal fish very quickly scrapes its side or underside against a surface.
	Glass Swim (GS)	Focal fish orients towards the side of the tank and repeatedly moves vertically, nose to the glass. Episode stops when fish comes to rest on bottom.
	Bury (Bu)	Focal fish vigorously wiggles its body into the substrate, partially or completely hiding its body.
	Dig (Dg)	Focal fish picks up object from the substrate, or pieces of substrate, in mouth and spits it out or moves it to a different location.
Aggressive	Ram (R)	Focal fish orients towards stimulus fish at transparent barrier and very quickly and forcefully rams nose at barrier. Ram is usually accompanied by a bite motion with puffing of the cheeks.
	Glass ram (GR)	Ram is accompanied by an aggressive vertical glass swim with nose to the barrier.
	Parallel display (PD)	Focal fish aligns itself parallel to barrier (usually during interaction with stimulus fish) and flaps tail against barrier using an S-curve body motion.

Scale), and used to calculate gonadosomatic index (GSI: (gonad mass/body mass) − gonad mass). Males were considered to be reproductive if their GSI was greater than 1%, and greater than 8% for females (MacInnis, 1997; Marentette & Corkum, 2008).

2.3.3. Experiment 2: large (3) fish versus small (1) fish groups

A total of 42 focal fish (18 males: mean ± SD total length = 7.4 ± 2.9 cm; 24 females: mean ± SD total length = 7.5 ± 3.9 cm) were used in this experiment. Testing tank set up was identical to experiment 1, except that a group of three stimulus fish were added to one end compartment, and one stimulus fish was added to the other end compartment. As in experiment 1, we scored focal and stimulus fish movement and activity as well as behavioural acts between the focal fish and stimulus fish. After testing, all fish were returned to their housing tanks for future experiments.

2.3.4. Experiment 3: one fish versus shelter

A total of 24 focal fish (12 males: mean ± SD total length = 6.0 ± 2.4 cm; 12 females: mean ± SD total length = 6.4 ± 3.6 cm) were used in this experiment. This tank was not divided into three compartments. A cylindrical, perforated tube (13 cm diameter, 20 cm height) containing one stimulus fish was placed on one side of the tank, while a plastic shelter (20 × 10 × 8 cm, see Figure 1) was located on the opposite side of the tank. During the 15-min trial, each focal fish could interact with the stimulus fish across the perforated barrier of the tube as well as enter and explore the shelter. To track stimulus preference, lines were drawn along the front wall of the entire tank to divide the tank into two equal zones measuring 30 cm. We also tracked focal fish movement and activity by dividing the tank into six equal zones measuring 10 cm each. We scored focal fish and stimulus fish movements, behavioural acts between the focal fish and stimulus fish, time the focal fish spent in the shelter, and number of shelter visits. After testing, all fish were returned to their housing tanks for use in future experiments.

2.4. Statistical analyses

We assigned each focal fish a categorical stimulus preference on the basis of where they spent the majority of time and compared these patterns using a chi-square goodness of fit test. The magnitudes of the preferences were investigated by converting the raw time spent near each stimulus to a preference index value. In experiment 1, the preference index was calculated as the time spent near the stimulus fish side/(time spent near the stimulus fish side + time spent near the empty side), and a preference index value of greater than 0.5 indicates that the focal fish preferred to affiliate with the conspecific. In experiment 2, the preference index was calculated as the time spent near the three fish side/(time spent near the three fish side + time spent near the one fish side), and a preference index value of greater than 0.5 indicates that the focal fish preferred to affiliate with the larger group. In experiment 3, the preference index was calculated as the time spent near the stimulus fish side/(time spent near the stimulus fish side + time spent near the shelter side), and a preference index value of greater than 0.5 indicates that the focal fish preferred to affiliate with the stimulus fish. Focal fish that never moved during the 15 min trial were excluded from analyses, resulting in a final sample size of 55 for experiment 1 (27 males, 28 females), 35 for experiment 2 (17 males, 18 females), and, 20 for experiment 3 (9 males, 11 females). All statistical analyses were conducted using R version 3.0.2 (R Core Development team, 2013). Quantile–quantile and residuals-versus-fitted diagnostic plots were used to visually inspect preference index values for normality and homogeneity of variance. Preference index values from experiment 1 and experiment 3 were logit transformed (Warton & Hui, 2011) to meet normality criteria. Preference index values were split by sex for each experiment and tested against the null hypothesis of no preference (0.5) using a two-tailed one-sample t-test. Average number of tank half switches, grid line crossings (activity), and aggressive acts by the focal fish were compared between sexes and across experiments using a negative binomial logistic regression.

3. Results

3.1. Experiment 1: one fish vs. an empty chamber

Forty-seven fish preferred to affiliate with the conspecific while eight fish preferred the empty chamber (chi square test: $\chi_1^2 = 27.65$, $p < 0.001$). Both males and females spent more time in close proximity to the conspecific (one-sample t-test: $t_{\text{males}(26)} = 4.54$, $p < 0.001$; $t_{\text{females}(27)} = 4.14$, $p < 0.001$; Figure 2). Stimulus fish did not affect preference results, as when preference scores from focal fish experiencing the same stimulus fish were averaged and tested against the null hypothesis of no preference, we still found a preference for associating with a conspecific (one-sample t-test: $t_9 = 2.78$, $p = 0.021$).

Fish were active in this experiment, crossing an average of 35 grid squares, and switching between sides of the exploration compartment an average of 7 times per trial. There were no sex differences in activity level (negative binomial logistic regression: $Z_{53} = 1.5$, $p = 0.13$; Table 2) or the number of side switches (negative binomial logistic regression: $Z_{53} = 1.3$, $p = 0.19$; Table 2). Of the focal fish tested, 60% (33 out of 55 fish, 16 males and 17 females) displayed aggressive behaviours towards the stimulus fish. Males

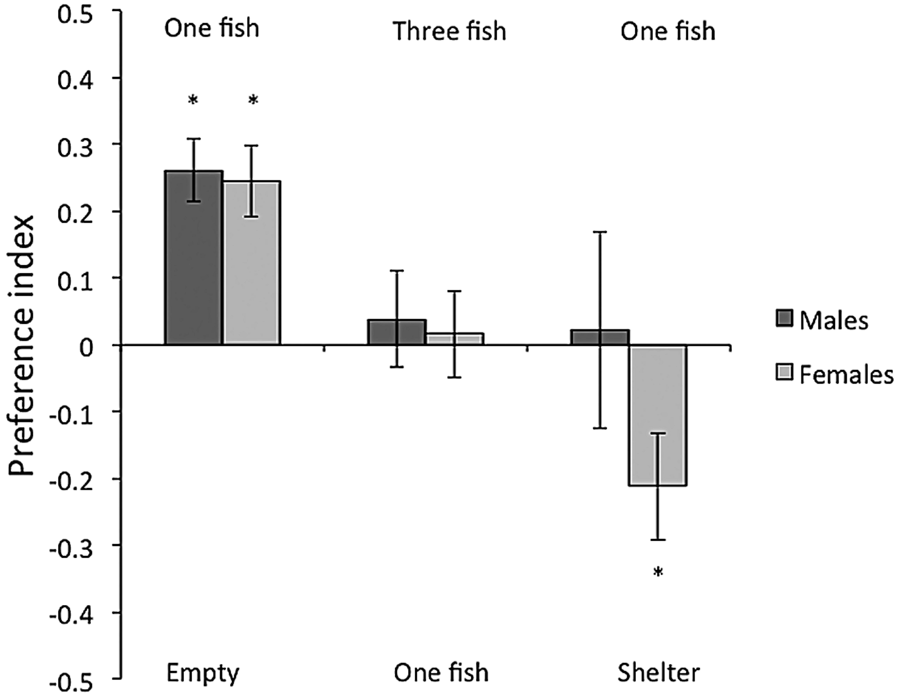

Figure 2. Average (± 1 SE) proportion of time focal fish spent near the stimulus fish compared to the empty chamber in experiment 1, three fish compared to one fish in experiment 2, and the stimulus fish compared to a shelter in experiment 3. For ease of interpretation, preference index values were scaled by 0.5 to produce absolute values where zero indicates no preference. Values above zero indicate a stronger preference for the stimulus fish in experiment 1, large group of three stimulus fish in experiment 2, and the stimulus fish in experiment 3. Significant differences from null hypothesis of no preference (zero) are indicated by asterisks.

Table 2.
Average ± 1 SE and *p*-values from negative binomial regression analyses for focal fish aggressive behaviours towards stimulus fish, tank half switches, and activity observed during each sociality assay.

♀		Aggressive displays		Tank half switches		Total activity	
One vs.	♂	10.48 ± 3.36	$p = 0.54$	8.93 ± 1.79	$p = 0.19$	42.00 ± 7.91	$p = 0.13$
empty	♀	14.57 ± 3.96		5.82 ± 1.24		28.25 ± 5.21	
Three vs.	♂	8.35 ± 3.42	$p = 0.035$	15.47 ± 3.47	$p = 0.38$	53.41 ± 8.99	$p = 0.46$
one	♀	24.50 ± 6.88		11.61 ± 2.29		44.06 ± 7.36	
Shelter vs.	♂	15.89 ± 8.03	$p = 0.76$	1.78 ± 0.72	$p = 0.005$	17.22 ± 4.37	$p = 0.017$
one	♀	12.36 ± 4.36		6.45 ± 1.60		34.55 ± 6.53	

performed an average of 10 aggressive acts while females performed an average of 15 aggressive acts during the 15-min trial, and there was no overall sex difference in aggression (negative binomial logistic regression: $Z_{53} = -0.6$, $p = 0.54$; Table 2).

Dissections confirmed that focal fish were mainly non-reproductive. Males had an average GSI of 0.45%, with 4 out of 27 males reaching the reproductive threshold of a GSI greater than 1%, while females had an average GSI of 3.86%, with 5 out of 28 females reaching the female reproductive threshold of a GSI of 8% or greater.

3.2. *Experiment 2: three fish vs. one fish*

Round goby did not show preference for larger groups. Twenty fish preferred to affiliate with the large group of conspecifics while fifteen fish preferred to affiliate with the small group (chi square test: $\chi^2_1 = 0.71$, $p = 0.40$). Neither males or females showed a preference for the large group or the small group, spending approximately equal time in proximity to large and small groups (one-sample t-test: $t_{\text{males}(16)} = 0.54$, $p = 0.60$; $t_{\text{females}(17)} = 0.26$, $p = 0.80$; Figure 2).

Focal fish were highly active in this experiment, crossing an average of 49 grid squares, and switched between sides of the exploration compartment an average of 14 times. Males and females showed similar activity levels (negative binomial logistic regression: $Z_{33} = 0.73$, $p = 0.46$; Table 2) and similar number of side switches (negative binomial logistic regression: $Z_{33} = 0.88$, $p = 0.38$; Table 2). Of the 35 focal fish, 27 or 77% (12 males, 15 females) behaved aggressively towards either the single or group of stimulus fish, and females performed more aggressive acts on average than males (negative binomial logistic regression: $Z_{33} = -2.10$, $p = 0.035$; Table 2).

3.3. *Experiment 3: shelter vs. one fish*

Twelve fish preferred to seek safety in the shelter while eight fish preferred to affiliate with the conspecific (chi square: $\chi^2_1 = 0.80$, $p = 0.37$). Females preferred to spend time in close proximity to the shelter over the conspecific (one sample t-test: $t_{10} = -2.68$, $p = 0.02$; Figure 2), while males showed no such preference and spent equal time near the shelter and conspecific (one sample t-test: $t_8 = 0.47$, $p = 0.65$; Figure 2). Females made an average of three visits to the shelter while males made an average of only one visit to the shelter during the trial period (Table 3).

Table 3.
Sex differences observed during experiment 3 in average (± 1 SE) number of visits to shelter, time spent inside shelter, and time spent interacting with conspecific across barrier.

	No. of shelter visits	Time in shelter (s)	Time with conspecific (s)
♂	1.11 ± 0.56	60.44 ± 33.25	69.00 ± 39.26
♀	3.36 ± 0.65	105.91 ± 24.81	34.82 ± 12.15

Focal fish crossed an average of 27 grid squares and switched between tank halves an average of 4 times. In general, females were more active than males (negative binomial logistic regression: $Z_{18} = -2.39$, $p = 0.017$; Table 2) and made more switches between stimuli (negative binomial logistic regression: $Z_{18} = -2.83$, $p = 0.005$; Table 2). Out of the, 20 fish, 13 or 65% interacted aggressively with the conspecific (6 males, 7 females) and males and females displayed a similar number of aggressive acts (negative binomial logistic regression: $Z_{18} = 0.30$, $p = 0.76$; Table 2).

4. Discussion

Using three sociality assays, we demonstrate that round goby do exhibit social preferences for conspecifics. As predicted, in our first experiment, we show that both male and female round goby have a strong preference for affiliating with a conspecific as opposed to remaining solitary. In our second experiment, we surprisingly found that round goby showed no preference for a larger group of conspecifics over a smaller group of conspecifics. Finally, in our third experiment we probed the value of conspecific affiliation against the value of protection in a shelter resource, and discovered that females preferred the shelter while males showed no such preference for the shelter over a conspecific.

In the laboratory, many fish species prefer to associate with conspecifics (Griffiths & Ward, 2011). Additionally, when given the choice, fish often prefer to affiliate with the larger of two groups (Hager & Helfman, 1991; Krause et al., 1998; Svensson et al., 2000; Agrillo et al., 2007; Buckingham et al., 2007; Reddon et al., 2011). Starting as low as 2:1, fish are capable of using the ratio of group size to make affiliation and group-joining decisions (Buckingham et al., 2007; Gomez-Laplaza & Gerlai, 2011). While we found that round goby affiliated with a conspecific instead of remaining solitary, they had no preference for group size at a 3:1 ratio of conspecifics. Since round goby avoid predation mainly by using rocks as shelter or burying into the substrate (Charlebois et al., 1997), it is likely that benthic round goby rely less on grouping to minimize predation risk compared to most pelagic shoaling fish species. Supporting this notion, Magoulick et al. (2004) found that many benthic fish species were less susceptible to predation than pelagic fish species due to their benthic habit and cryptic colouration. Therefore, round goby may not need to discriminate between groups of different sizes or join a large group of conspecifics to gain protection from predators. Though round goby did not make grouping decisions based on group size in our experiment, they may still discriminate between groups based on other criteria such as conspecific body size or under specific situational circumstances like predation risk (Pitcher & Paris, 1986; Lima & Dill, 1990; Krause & Godin, 1994; Hoare et al., 2000; Ward & Krause, 2001; Reddon et al., 2011).

We had expected that round goby — especially males — would prefer affiliating with a shelter over a conspecific. However, contrary to our prediction, female round goby preferred to be near the shelter, while males showed no such preference for the shelter. Sex differences in reproductive and predator avoidance behaviours are common in fish (Hanson et al., 2008). In teleost species with paternal care, such as rock bass (*Ambloplites rupestris*, Noltie & Keenleyside, 1987), three-spined stickleback (*Gasterosteus aculeatus*, Pressley, 1981), and sand goby (*Pomatoschistus minutus*, Lindström & Hellström, 1993), reproductive males spend more time in and around their nest preparing or caring for offspring (Blumer, 1979). Our shelter trials were conducted in August, which is at the end of the breeding season for round goby in the Laurentian Great Lakes (MacInnis & Corkum, 2000; Young et al., 2010). It is possible that the reproductive condition of the fish may be why males did not show a strong preference shelter. Only fish from experiment 1 were dissected, and most often males were non-reproductive. Although fish were not dissected in experiment 2 or 3, given the time in the season, their mottled body colour, small size and flaccid shape of their genitalia (Marentette et al., 2011), it is likely that most fish in both experiment 2 and 3 were also not in reproductive condition. Consequently, non-reproductive males may have been less motivated to spend time near or inside a shelter. Alternatively, we had also predicted that round goby would seek shelter as that is a typical behaviour when seeking refuge from predation. Though we collected our round goby from a site with known fish and avian predators (Somers et al., 2003; Brousseau & Randall, 2008), the absence of predation pressure in the lab may have led some fish in our sample to explore the entire tank and not take-up shelter during our trials.

In all three experiments, 60% or more of the interactions between focal and stimulus fish across the barrier were aggressive in nature, and most focal fish showed some level of aggression towards a lone conspecific or the group of conspecifics. Surprisingly, females showed similar levels of aggression as males, and even performed more aggressive acts than males on average in one of the experiments, revealing the importance of including females in future work on aggression. The high levels of aggression combined with the fact that round goby showed no preference for larger group sizes may indicate that although round goby tend to aggregate, high intraspecific competition will occur with increased densities due to round goby's aggressive nature (Fitzsimons et al., 2006; Kornis et al., 2014). In this case, both social attraction and aggression towards conspecifics may combine to facilitate invasive behaviour. It is possible that round goby may aggregate until they reach a certain density threshold where high intraspecific aggression leads to the dispersal of asocial individuals, further facilitating the colonization of new populations (Cote et al., 2010; Fogarty et al., 2011).

We have assessed grouping preferences in invasive round goby, a fish known to be highly aggressive but also to thrive in high densities in the Great Lakes. Our work has shown that although round goby are a benthic, non-shoaling species, they have a tendency to affiliate with conspecifics but show no preference for large groups and following the initial approach may be aggressive to nearby conspecifics. Our results have important implications for understanding round goby behaviour, especially in terms of characteristics contributing to their invasion success. We demonstrate that round goby aggregate and this may account for their ability to thrive in high densities, and have played a role in their establishment and spread in the Great Lakes. It is likely that an interaction between high interspecific aggression and tolerance of conspecifics allowed round goby to competitively displace native species and spread rapidly. Future work will focus on cues that drive and motivate round goby intraspecific interactions, such as predator cues and reproductive status, in order to further understand the circumstances in which aggressive and social behaviours could lead to population growth and spread in this invasive species. We will continue to probe how round goby make group joining decisions by further manipulating stimulus group size and joining size-rank in the group, as both of these factors may contribute to social aggregation (Pitcher & Parish, 1993; Hoare et al., 2000; Griffiths & Ward, 2011). Our work has provided an initial assessment of the social tendencies of round goby in the Great Lakes, but it would be beneficial to explore whether these social behaviours vary across different stages of their invasion (or in fish from established areas versus the invasion front) and how they compare to fish from the native range. In sum, we have demonstrated that characterising behaviours, like sociality, in invasive species can allow us to better understand the potential factors contributing to invasive species establishment and success.

Acknowledgements

The first two authors contributed equally to this manuscript. The authors would like to thank R. Caldwell and O. Petric for field assistance, S. Gulas and R. Marchant for help with video scoring, and S. Marsh-Rollo and M. Ciko for lab assistance and logistics. E.M. was supported by an Ontario Graduate Scholarship. P.C. was supported by the McMaster Work study program and a Natural Sciences and Engineering Research Council of Canada Discovery Grant awarded to S.B. S.B. is further supported by the Canada Research Chair Program.

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