Assessment of fish size on shelter choice and intraspecific interactions by round gobies *Neogobius melanostomus*

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Synopsis

We examined shelter occupancy and behavioural interactions in non-reproductive male round gobies, *Neogobius melanostomus*, an invasive fish, to determine if gobies can assess one another's prowess effectively. Results of laboratory experiments revealed a significant, positive relationship between body size (total mass) and time for individual fish to occupy shelters. Shelter size selection did not vary with body size, but males that abandoned shelters were smaller than those that remained. Overall, the number of interactions between residents and intruders were low with most interactions occurring between large residents and large intruders. A size differential between residents and intruders of 3% was sufficient to predict the proportion of victories in conflicts between round gobies. This ability of the round goby to perceive size differences between themselves and potential opponents reduces the number of interactions and may account for the occurrence of high densities of round gobies observed in the field.

Introduction

Advantages in enhanced survivorship and fitness of animals have been attributed to territories and an individual not holding a territory should be motivated to fight for one (Johnson & Forser 2002). Animals that engage in interactions make assessments about contested territories (or resources) and the fighting ability of the owner relative to the intruder (Parker 1974, Barlow 1983). Winners in territorial disputes are determined by the effect of prior residence (Braddock 1949, Figler & Einhorn 1983), body size (Parker 1974, Faria et al. 1998), previous experience (Beacham 1988, Beaugrand & Goulet 2000) or combinations of factors (Takahashi et al. 2001).

Game theory models predict that animals assess relative resource holding power during fights through informative displays and trials of strength (Parker 1974, Barlow et al. 1986, Sigmund 1993). This information is used to determine fight length and intensity by allowing competitors to assess their relative ability to inflict costs on their rival and to incur fewer costs on themselves, thereby increasing their individual fitness. Thus, weaker or smaller individuals should give up a resource to avoid the costs of fighting and fights should be longer when individuals are closer in size (Neat et al. 1998).

The round goby, *Neogobius melanostomus* (Pallas), is a benthic fish that is presumed to have arrived in the Laurentian Great Lakes in ballast water from the Black and Caspian seas (Jude et al. 1992). The species, first reported from the St. Clair River in 1990, has spread to all five Great Lakes and is invading the Mississippi basin (Charlebois et al. 2001). Reasons for the proliferation of the round goby include its broad diet and availability of molluscan prey (adults eat mainly dreissenids), aggressiveness, high fecundity, multiple spawning habits (up to six times per year), and male parental care (Corkum et al. 2004).

Because round gobies are abundant (up to 90 fish m⁻²) in rocky habitats (Ray & Corkum 2001, Johnson et al. 2005) and both juvenile and adult gobies feed on eggs of lake trout, *Salvelinus namaycush* (Chotkowski & Marsden 1999), lake sturgeon, *Acipenser fulvescens* (Nichols et al. 2003), and smallmouth bass, *Micropterus dolomieu* (Steinhart et al. 2004), round gobies may reduce the recruitment of native fishes (Vanderploeg et al. 2002). Round gobies also may alter ecological function by transferring energy and contaminants from the benthos to higher trophic levels and so represent a health concern (Morrison et al. 2000).

SCUBA observations reveal that round gobies of different sizes co-occur and that the species exhibits high site fidelity (Wolfe & Marsden 1998, Ray & Corkum 2001). Round gobies breed throughout the spring and summer months and males maintain and guard shelters for extended periods (MacInnis & Corkum 2000). Because breeding males aggressively occupy natural and artificial shelters positioned on a variety of substrate types (bare, sand, mud, till or rock) (MacInnis & Corkum 2000, Johnson et al. 2005), shelters may be a limited resource for non-reproductive round gobies.

Round gobies display aggressive behaviour when they co-occur with other fishes (Janssen & Jude 2001). For example, non-reproductive round gobies can displace similarly sized native mottled sculpins, *Cottus bairdi*, from shelters (Dubs & Corkum 1996). Preliminary evidence suggests that large round gobies induce smaller conspecifics to leave preferred rocky habitat and move to less optimal sand habitat (Ray & Corkum 2001). However, conspecific interactions between nonreproductive round gobies have not yet been evaluated.

Although invertebrate benthic taxa are known to select different sizes of shelters (Nakata & Goshima 2003), it is rare to investigate shelter occupancy among non-reproductive fishes. Certainly, shelter size in gobies and in other species is important for parental males because lager males are able to defend larger nests. For species such as round gobies that deposit eggs in a single layer, these large nests can contain more fertilized eggs and result in higher reproductive success (cf. Hamilton 1998). Given that shelters may be limiting in the field, we conducted a laboratory experiment to determine whether or not nonreproductive round goby males would select shelters of different sizes and if time to enter a shelter was a function of body size. In another laboratory experiment, we determined if behavioural interactions were a function of body size or shelter residency. If aggressive interactions are not exhibited by non-breeding male round gobies, it would help to explain the colonial habits of this fish.

Materials and methods

We collected round gobies from May to September, 2000 and 2001, by angling at several shoreline sites along the Detroit River in Windsor, Ontario. Several authors have shown that angling for round gobies is the most effective and efficient method to catch round gobies compared with other types of gear (Clapp et al. 2001, Johnson et al. 2005). Fish were sexed by the shape of the urogenital papilla, which is pointed in males and broad in females (Miller 1984). We restricted our investigation to non-reproductive males and confirmed their status by the lack of secondary sexual traits and low gonadosomatic (GSI) index (determined after experiments). Mean $(\pm SE)$ GSI value of male round gobies used in our experiments was 0.17 (± 0.02) compared with the GSI of reproductive males (2.29 ± 0.59) (W. Arbuckle, University of Windsor, unpublished data). In the laboratory, we sorted males into two arbitrary size classes (small: 8-10 cm, 5-12 g; large: 10.5-14.5 cm, 15-38 g)and maintained them separately.

We held the fish in dechlorinated flow through tanks (210 cm \times 20 cm \times 60 cm) lined with gravel. We provided PVC tubing for shelter and fed fish Tetramin[®] once a day. We selected a 16 h L: 8 h D light regime and at 18 °C to match field conditions.

Shelter choice

We hypothesized that there was no relationship between fish size and shelter size occupied. We placed artificial shelters made of tiled sides and clear Plexiglas[®] tops in one of four wading pools (area: 0.55 m²) containing aerated dechlorinated



Figure 1. The arrangement of shelters (each with an entrance size of $5 \text{ cm} \times 5 \text{ cm}$) in a pool. The shelters (S, small (10 cm × 15 cm: 150 cm²), M, medium (15 cm × 20 cm: 300 cm²), ML, medium-large (20 cm × 22.5 cm: 450 cm²), and L, large (25 cm × 24 cm: 600 cm²) were grouped together in the centre of the pool. We positioned the S, M, and ML shelters within a large sized shelter and covered all four shelters with tiles so that a fish could not distinguish among shelters unless the interior was explored.

water. In each pool, we placed four different sized shelters (each with an entrance size of $5 \text{ cm} \times 5 \text{ cm}$: small (10 cm \times 15 cm: 150 cm²), medium (15 cm \times 20 cm: 300 cm²), medium-large $(20 \text{ cm} \times 22.5 \text{ cm}: 450 \text{ cm}^2)$, and large (25 cm) \times 24 cm: 600 cm²). We grouped shelters together in the centre of a pool with the entrance to each shelter facing a different direction (Figure 1). We chose the position of the shelters randomly and changed it for each replicate. We positioned each small, medium, and medium-large shelter within a large-sized shelter and covered each shelter with a ceramic tile so that fish could not distinguish among shelter sizes unless the interior was explored. We placed 2-ply window screen over the pool to better mimic light conditions in the field. For each replicate, we added one male round goby, chosen at random, to the centre of a pool, recorded the time taken to enter a shelter, and recorded which shelter was occupied every 30 min for 6 h. To reduce the handling of fish, we measured fish size after each trial; each fish was used only once (n = 26 fish).

We analyzed the data using linear regression (after testing for equal variances) to determine the relationship, if any, between fish size and time to enter a shelter when no other fish was present. A *t*-test was used to determine if fish size differed between those that remained in shelters and those that abandoned shelters. An analysis of variance (ANOVA) test, with a 0.05 type I error rate, was used to determine if there were differences in mean fish size among the shelter sizes occupied.

Behavioural interactions

In a second laboratory experiment, we compared behavioural interactions between different fish sizes (large and small) and residency status (resident and intruder) of non-reproductive round gobies in shelters in the day and night. We hypothesized that there would be no differences in time spent in a shelter between fish of different residency status or size and no differences in the frequency of behavioural types (approach, chase, bite) between resident and intruder. The four treatments were Large Resident-Large Intruder (LR-LI, n = 27 replicates: 15 day, 12 night), LargeResident–Small Intruder (LR–SI, n = 27: 15 day, 12 night), Small Resident-Large Intruder (SR-LI, n = 26: 14 day, 12 night), and Small Resident-Small Intruder (SR–SI, n = 27: 15 day, 12 night). Whether or not interactions occurred, a winner was designated by the fish in possession of the shelter at the end of the observation period. Each day, coin tosses were used to determine which of the 4 treatments would be examined. Nighttime observations were made using a 25-W red bulb. We retrieved the fish at random from the holding tanks using a dip net. We marked the fish with an acrylic paint (Wolfe & Marsden 1998) to facilitate identification. Each marked fish was kept in a separate tank for 12 h before experiments began.

We conducted the experiment in two 150-1 tanks (40 cm \times 38 cm \times 90 cm) containing aerated, dechlorinated water, no substrate and one shelter. There was one observer for each tank and assignment of replicates among treatments was randomized. We covered the tanks (but left a narrow opening for observation) with an opaque plastic sheet to avoid outside stimuli. Because round goby males did not show a preference for shelter size (shelter choice experiment), we arbitrarily selected the medium-sized shelter (300 cm²) to be used in all replicate trials, recognizing that shelter size may have an effect on territorial disputes. We placed the shelter in the middle of the tank with the rear of the shelter against the back of the tank; the entrance faced the front of the tank.

A fish, predetermined as the resident, was added to the experimental tank and allowed to acclimate for 1 h. Another fish, predetermined as the intruder, was added at the end of the acclimation period. Round gobies, like other gobiids (Amundsen & Forsgren 2001), quickly acclimate to aquaria. For example, in the shelter choice experiment, 50% of round gobies entered a shelter within 2.5 min and 90% entered a shelter within 15 min. In an earlier laboratory study, we showed that activity patterns of the round goby were consistent from 1 to 72 h (Krause & Corkum, University of Windsor, unpublished data).

After the acclimation period, interactions between individuals were recorded for 1 h by scoring the number of approaches (slow movement or advance of one fish toward the other), chases (quick movement or dart of one fish toward the other), and bites (when a fish with an open mouth closed its mouth on another fish) (Dubs & Corkum 1996).

We used a two-way ANOVA test (type III sum of squares for unbalanced designs, Shaw & Mitchell-Olds 1993) to examine the effect of fish size (large, small) and status (resident, intruder) on the mean time (min) a fish spent in a shelter. Next, we used a G-statistic to determine if the frequency of the three behavioural types (approaches, chases, bites) was independent of residency status ($R \times C$ test of independence, Sokal & Rohlf 1969) for each of the four treatments. We assumed that the behavioural types were independent events. Lastly, we examined the proportion of victories (wins) by the size differential (*d*) between contestants for all four treatments combined using logistic regression analysis (Beacham 1988):

[(the size of the resident – the size of the intruder) /(size of the intruder) \times 100].

Results

Shelter choice

There was a significant, positive relationship between the size (mass) of males and time to enter



Figure 2. Relationship between total mass of round goby males and the time to enter a shelter (n = 26). Y = 0.27 X - 0.33. Closed circles represent fish that remained in shelters; open circles represent fish that abandoned shelters.

the first shelter (p = 0.003; $r^2 = 0.31$) (Figure 2). Males that abandoned shelters were smaller (14.4 \pm 3.13 g) than those that remained (23.4 \pm 2.44 g) (Mann Whitney *U*-test = 29.50, p = 0.03). Results of the one-way ANOVA (variances did not differ significantly, Barlett's test = 2.754, p = 0.431) test showed that there was no significant difference in mean body size among round gobies that occupied the four different shelter sizes ($F_{3,26} = 0.674$, p = 0.576).

Behavioural interactions

Because there were no significant differences in behavioural interactions for experiments conducted in the day or night, data were pooled. Results of the two-way ANOVA test revealed that fish size ($F_{1,210} = 5.89$, p = 0.016) and residency status ($F_{1,210} = 338.28$, p < 0.0001) significantly affected the mean time that a fish spent in a shelter. Overall, residents spent significantly more time in a shelter than intruders for each treatment and large fish spent more time in a shelter than small fish (Figure 3).

Large intruders were successful in usurping smaller residents (11 out of 11 cases), and small intruders were unsuccessful in usurping large residents (0 out of 11 cases). Intruding fish were successful in only a small percentage of attempts when intruders and residents were close in size. For example, small intruders were successful in entering the shelter occupied by a small resident in



Figure 3. Mean (+SE) time (min) spent in a shelter for large and small non-reproductive round gobies. Black bars represent residents; open bars represent intruders. Results of the two-way ANOVA test showed that fish size (p = 0.016) and residency status (p < 0.0001) significantly influenced the time spent by a fish in a shelter.



Figure 4. Mean number of interactions (approaches, chases, or bites) for large residents and large intruders (LR/LI). The frequency of the behavioural classes differed significantly between the resident and intruder in the LR/LI treatment (G = 13.816, p < 0.005). The solid horizontal bar indicates that there were no significant differences in approaches between residents and intruders.

3 of 14 attempts and large intruders were successful in entering the shelter occupied by a large resident in 3 of 13 attempts.

There were no significant differences between the frequency of behavioural classes (approach, chase, bite) and residency status for three (LR–SI, SR–LI, SR–SI) of the four treatments. However, the frequency of the behavioural classes differed significantly between resident and intruder in the LR–LI treatment (G = 13.816, p < 0.005) and so the null hypothesis that behaviour is independent



Figure 5. Logistic function $Y = \exp(2.079 + (0.0342) * X/(1 + \exp(2.079 + (0.0342) * X))$. Points represent the proportion of conflicts won for the % size difference between residents and intruders.

of residency status was rejected for this case. The largest number of interactions occurred in the LR/LI treatment, where numbers of interactions were <3 per hour and large residents were more aggressive (i.e., they scored more chases and bites, but not approaches) than large intruders (Figure 4).

Results of the logistic regression showed that the proportion of victories can be predicted using the size differential (*d*) between residents and intruders ($X^2 = 23.33$, p < 0.001). Whenever *d* is greater than 3% the logistic equation predicts victory, however for values of d < 3%, the outcome is uncertain (Figure 5).

Discussion

Animals often enter shelters to reduce the risk of predation (Godin 1997). However, shelters also reduce interactions between conspecifics (Corkum & Cronin 2004). Although the shelters used in the laboratory experiment were artificial, our earlier studies (MacInnis & Corkum 2000) showed that these shelters are readily occupied by round gobies in the field. We were unable to detect any preference for shelter size by non-reproductive round gobies; however, it is likely that competition for shelters may exist among reproductive males if nest sites are limiting (Janssen & Jude 2001). Time to enter a shelter was a function of body size with small fish entering shelters more quickly than large fish. Small fish tended to abandon shelters when they were alone. However, when small resident fish and an intruder of the same size occupied the tank, small gobies stayed in the shelter as long as larger fish. Thus, the tendency for small gobies to occupy shelters changes when conspecifics are present.

Both fish size and residency status significantly influenced the time spent in a shelter. As expected, residents and large fish spent the most time in shelters. Overall, behavioural interactions between residents and intruders were low. The largest number of interactions (albeit low) was observed between large residents and large intruders where the number of chases and bites by the resident were significantly greater than those exhibited by the intruder. Beaugrand & Goulet (2000) suggested that winning or losing against a well-matched opponent provides more 'experience' than winning to a weak opponent or losing to a strong one. There were no significant differences between the frequency of behavioural interactions and residency status in the other three treatments (LR/ SI, SR/LI, SR/SI). In contrast to the low number of interactions between conspecifics in our study, Dubs & Corkum (1996) showed that non-reproductive round goby residents and intruders were significantly more aggressive (i.e. larger numbers of approaches, chases and bites) with similarly sized mottled sculpin, Cottus bairdi.

The outcome of interactions between residents and intruders is a function of several factors including developmental stage, breeding status, sex, species, time in isolation and physiological state of the animal (Gómez-Laplaza & Morgan 2000). Although parental round gobies are territorial, territoriality among non-reproductive individuals in the field was unknown (Wickett & Corkum 1998). In our laboratory study, we showed that a size differential between residents and intruders of 3% was sufficient to predict the proportions of victories between non-reproductive round gobies. Thus, the round goby resident always wins if it is at least 3% larger than a conspecific intruder. In other fishes, residents can be about 10% smaller than intruders and still defend their shelter (Barlow 2000).

The round goby is distinctive among Great Lakes fishes in the types of neuromasts distributed throughout its body and head. Neuromasts in the head are enclosed within a canal system, while the superficial neuromasts in the body are open (Charlebois et al. 1997). The expectation is that round gobies will be more sensitive to movement than other fishes (cf. Jannsen 1990, Jude et al. 1995). Thus, the ability of round gobies to both detect and assess the presence of organisms moving in the water in day or night may explain the reduction of fights among conspecifics.

In the field, round gobies occur at high densities in rocky habitats (with many sheltered areas) where site fidelity is high (Ray & Corkum 2001). When individuals remain in a group, a stable hierarchy forms as each member is able to discriminate among its neighbours, yet reinforcing displays may be initially frequent (Beaugrand & Goulet 2000). The ability of the round goby to perceive small differences in size between potential opponents may reduce the number of interactions among conspecifics and might account for the colonial habits of the species.

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