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Laboratory and field evidence of sex-biased movement in the invasive round goby

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Abstract Activity levels are modulated by trade-offs between reducing predation risk and the need to move in order to find food or mates. Because these trade-offs affect males and females differently, many species show sex-specific movement, dispersal patterns, and spatial navigation capacities, with the sex that gains the most from territory ownership often dispersing less. Unlike mammals and birds, sex differences in movement among fishes remain poorly studied, and the connections between tests of movement propensity in the laboratory and in the field are rarely made. Here, we examine the differences in movement between male and female round goby (*Neogobius melanostomus*) in both laboratory and field settings. This fish species is invasive in North America and currently undergoing further range expansions. In the laboratory, round goby males were more active and explored a novel environment more readily than did females. A large-scale mark–recapture study in Lake Ontario over two years revealed that males moved more than females between years, but there were no within-year sex differences. Thus, round goby display male-biased movement patterns, providing a comparison point to dispersal patterns in other taxa. Understanding sex-specific

movement of round goby in the field will also help predict dispersal and population dynamics, both in areas where round goby have already become established and where they are continuing to invade.

Introduction

Greater levels of activity, exploration, and dispersal can increase foraging or mating opportunities, but may also increase predation (Werner and Anholt 1993; Smith and Blumstein 2008). The influence of this trade-off on reproductive success differs for males versus females, and as a result, sexes frequently differ in movement patterns and spatial abilities (Jones et al. 2003). Natal and breeding dispersal, two major types of movement, are typically greater for the sex that has more to gain in terms of increasing mate encounter rates or reducing inbreeding and kin competition. The benefits of philopatry also influence dispersal patterns, with the more philopatric sex often having more to gain from a well-known territory or home range with access to familiar shelter and food (Greenwood 1980; Clobert et al. 2001; Dingle and Holyoak 2001; Bowler and Benton 2005). Sex differences in movement are not limited to large-scale dispersal events. Home range or territory size, general activity levels, and spatial navigation capacity are often greater in one sex, usually the dispersing sex (Gaulin 1992; Jones et al. 2003).

Sex-specific movement patterns are frequently generalized by taxon and mating system. Male-biased dispersal predominates in polygynous mammals, while dispersal is often

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female-biased in socially monogamous birds (Greenwood 1980). Sex-specific movement patterns among fish taxa, however, are much less frequently studied. In a wide variety of polygamous species where males do not care for young, males appear to disperse, or range, further (African lions, *Panthera leo*, Pusey and Packer 1987; brook trout, *Salvelinus fontinalis*, Hutchings and Gerber 2002; túngara frogs, *Physalaemus pustulosus*, Lampert et al. 2003; mosquitofish, *Gambusia affinis*, Cote et al. 2010b). In monogamous species or those with sex role reversal (male parental care and a female-biased operational sex ratio), the opposite pattern is found, with greater movement by females (Florida scrub-jays, *Aphelocoma coeruslescens*, Woolfenden and Fitzpatrick 1984; red-necked phalaropes, *Phalaropus lobatus*, Reynolds and Cooke 1988; cardinalfish, *Apogon niger*, Okuda 1999). Fishes provide an opportunity to decouple parental care from mating behavior, as many species exhibit both male-only parental care and typical sex roles (with male-biased operational sex ratios, where males are the more competitive sex). In such systems, males may still range over greater areas than females, particularly outside of the breeding season, and simply reduce their movements and territory range during breeding (fluvial sculpins, *Cottus pollux*, Natsumeda 2001 and Natsumeda 2007; gobiid fish, *Rhinogobius* spp., Osugi et al. 1998), when female movements may exceed males (blenniid fish, *Blennius sanguinolentus*, Santos and Almanda 1988; smallmouth bass, *Micropterus dolomieu*, Savitz et al. 1993).

Measurements of sex-specific or individual spatial ability or activity in the laboratory can be used as a tool for understanding and predicting movements in the field (Jones et al. 2003; Cote et al. 2010a, b). To date, however, only a few studies have done this (Cote et al. 2010a, b). Time to navigate a maze (meadow voles, *Microtus pennsylvanicus*, Gaulin and Fitzgerald 1986), laboratory dispersal (mosquitofish, *Gambusia* spp., Rehage and Sih 2004), exploration (female great tits, *Parus major*, Dingemanse et al. 2003; bullhead fish, *Cottus perifretum*, Kobler et al. 2009), asociality (common lizard, *Lacerta vivipara*, Cote and Clobert 2007), and boldness (killifish, *Rivulus hartii*, Fraser et al. 2001) have all been linked to greater home ranges and/or dispersal for individuals, sexes, or species in the field.

The aims of our study were twofold. (1) To explore sex differences in movement in an understudied group of vertebrates, the fishes—and thus build a picture of how fishes fit in the theoretical framework for dispersal. (2) To link behavior in the laboratory with those observed in the field. We also wished to consider how sex differences in movement may impact patterns of invasion. We used the round goby (Gobiidae: *Neogobius melanostomus*) to address all three issues. The round goby is a benthic, euryhaline fish found in Ponto-Caspian Europe and invaded

regions of both Western Europe and the North American Great Lakes basin (Jude et al. 1992; Corkum et al. 2004). Males exhibit alternative reproductive tactics (Marentette et al. 2009), which may affect movement. Nest-guarding males are dark in color and exhibit both territoriality and parental care (hereafter, guarding males), and a light female-like morph that may parasitize, or sneak, spawnings and exploit the paternal efforts of guarding males (hereafter, sneaker males; Marentette et al. 2009). Competition for nest sites and females is believed to favor larger guarding males (Charlebois et al. 1997; Corkum et al. 1998). Round goby undergo seasonal migrations from deeper water to shallow nearshore rocky areas to spawn during the spring and summer (Pinchuk et al. 2003). During the breeding season, the site fidelity of adults is thought to be high (e.g., Ray and Corkum 2001) though long-distance movement (>1 km) of adults has also been observed (Wolfe and Marsden 1998; Balshine et al., unpublished data). Round goby continue to invade new habitats (Poos et al. 2009), and if sex differences in exploration, ranging, and dispersal exist in the round goby, then differences in sex composition may distinguish an invasion front from more established populations.

In this study, we explored activity differences between male and female round goby in a small-scale laboratory context and a large-scale field context, where natural movements were evaluated through a two-year mark–recapture study. In the two-year period of the field study, we evaluated movement within and outside the breeding season, as well as across years. We had three major predictions. First, we predicted that males would move more than females in most circumstances: over the long term and outside of the breeding season. This prediction was based on the fact that round goby are polygamous and sexually dimorphic, with males growing larger (Young et al. 2010) and faster (MacInnis and Corkum 2000) than females. Larger, faster-growing individuals may move more than smaller ones because they have greater metabolic needs (McNab 1963; Gittleman and Harvey 1982). Moving over a greater home range may mean greater access to food and faster growth, which may be particularly important for males because females prefer large males (Corkum et al. 1998) and larger males fare better in competition for resources such as nest sites (Gaulin 1992; Bowler and Benton 2005; Clobert et al. 2009). Larger individuals are also better able to escape predation by gape-limited predators (Persson et al. 1996), reducing the costs of movement. Second, we predicted that during the breeding season only, guarding males would move less than females as they would be limited by the need to defend small territories and nests (Natsumeda 2001; Sunobe and Nakazono 1999; Taru and Sunobe 2002). Females, on the other hand, continue to forage through the breeding season and are likely to visit multiple nests over a large area to spawn up to six times over

the breeding season (Charlebois et al. 1997; Natsumeda 2001). Third, we predicted that, among males, sneakers might move more than guarding males during the breeding season, as sneakers need not be constrained to a single nest territory and may access and parasitize the spawning efforts of more than one guarding male. Outside of the breeding season, however, larger guarding males were predicted to move more than the smaller sneaker males.

Materials and methods

Collection of fish

Round goby were collected from three locations in Hamilton Harbour, Lake Ontario, Canada (43°17′ N, 79°50′ W; Fig. 1), where they have been present since the mid-1990s (Vélez-Espino et al. 2010), and breed from May to early August (Young et al. 2010). The nearshore littoral population of round goby is male-biased (Young et al. 2010). Collection locations were approximately 4 km apart, had mixed sand, cobble, and boulder substrates, and were similar in water parameters such as turbidity, oxygen concentration, and temperature (Marentette et al. 2010). Fish were collected in commercial minnow traps baited with 30 g frozen corn, set at a depth of 1 m or less, for 24 h. Round goby were transported back to the laboratory and maintained in groups of three to six fish separated by sex. Fish were housed in 60 L aquaria equipped with AquaClear 50 external box filters and two airstones at $21 \pm 1°C$, with a gravel substrate and several 15-cm long, 5-cm diameter PVC tubes for shelter. Male and female round goby are readily distinguished by an examination of the external urogenital papilla, which is pointed in males and blunt in females. Males were assigned one of three reproductive states based on external characteristics: guarding male (erect urogenital papilla, black nuptial coloration, and swollen cheeks), sneaker male (erect urogenital papilla but no secondary sex characteristics), and nonreproducing male (a small, flat papilla; Marentette et al. 2009; Young et al. 2010). Male reproductive status was further confirmed after experiments based on dissection and the presence or absence of well-developed testes and accessory glands during the breeding season (a gonadosomatic index or GSI, gonad (testes) weight (in grams)/somatic weight (in grams)×100, of >1%=reproducing males; Young et al. 2010). Female reproductive status was assigned as gravid or nongravid after dissection based on a GSI of >8% for gravid females (Young et al. 2010). Fish were allowed to acclimate to the laboratory for at least 2 days and no more than 7 days prior to testing and were fed once daily ad libitum with Nutrafin Basix fish flakes, except on the day of testing.

Movement in the laboratory

This experiment was conducted between 16 May and 25 July 2008. Round goby ($N=198$) were maintained under a reversed 16L:8D light schedule to facilitate behavioral observations under nocturnal breeding conditions. This species is more active at night (Dubs and Corkum 1996; Diana et al. 2006). Fish were tested in a five-chambered arena under red light (total dimensions, 2.5 m long, 75 cm wide, 15 cm deep; each segment, 50 cm long and 75 cm wide; Fig. 2a). The arena had sand substrate up to 1 cm depth. Each chamber was equipped with one AquaClear Mini filter and three clear half-tube acrylic shelters. Chambers were separated by transparent dividers; each with a 25×15-cm central gap in the center as an entrance to the next chamber. The water within the arena was changed

Fig. 1 A map of round goby collection sites in Hamilton Harbour, Ontario, Canada, including the three locations where round goby for laboratory experiments were obtained and the mark–recapture study was run (*white circles*). *Inset* the lower Laurentian Great Lakes: from the *left*, Huron, Erie, and Ontario, with the location of Hamilton Harbour *circled*. The scale in kilometers is indicated
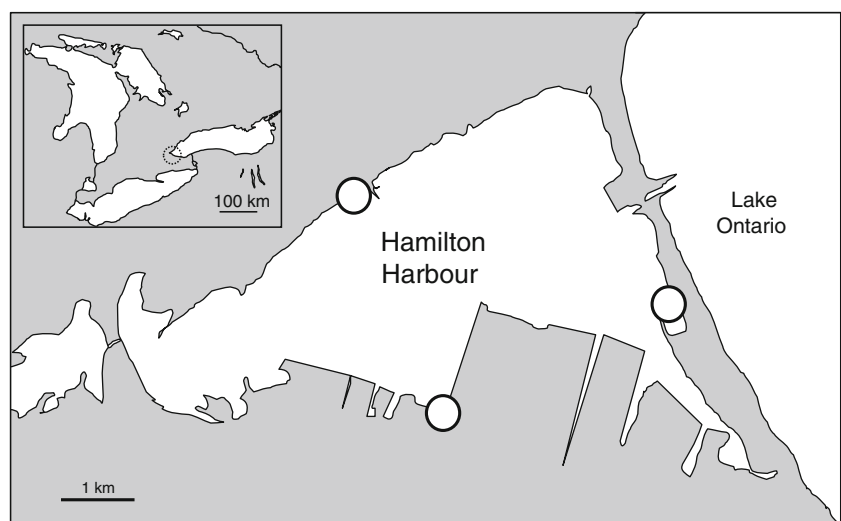
Fig. 2 a Schematic representation of the 2.5-m long testing arena with five chambers of length 0.5 m each. Fish were placed in sex-matched triads in one chamber (*1*) and were able to enter other chambers (*2–5*) after acclimation. Fish in image are not to scale. b Differences in mean±SE exploratory swims per minute for males and females. c The number of male (*N*=99) and female (*N*=99) round goby to move from one to five chambers during the experimental test period of 30 min, representing distances of 0.5 to 2.5 m. An *asterisk* indicates significant differences between the sexes. Males *gray bars*, females *white bars*
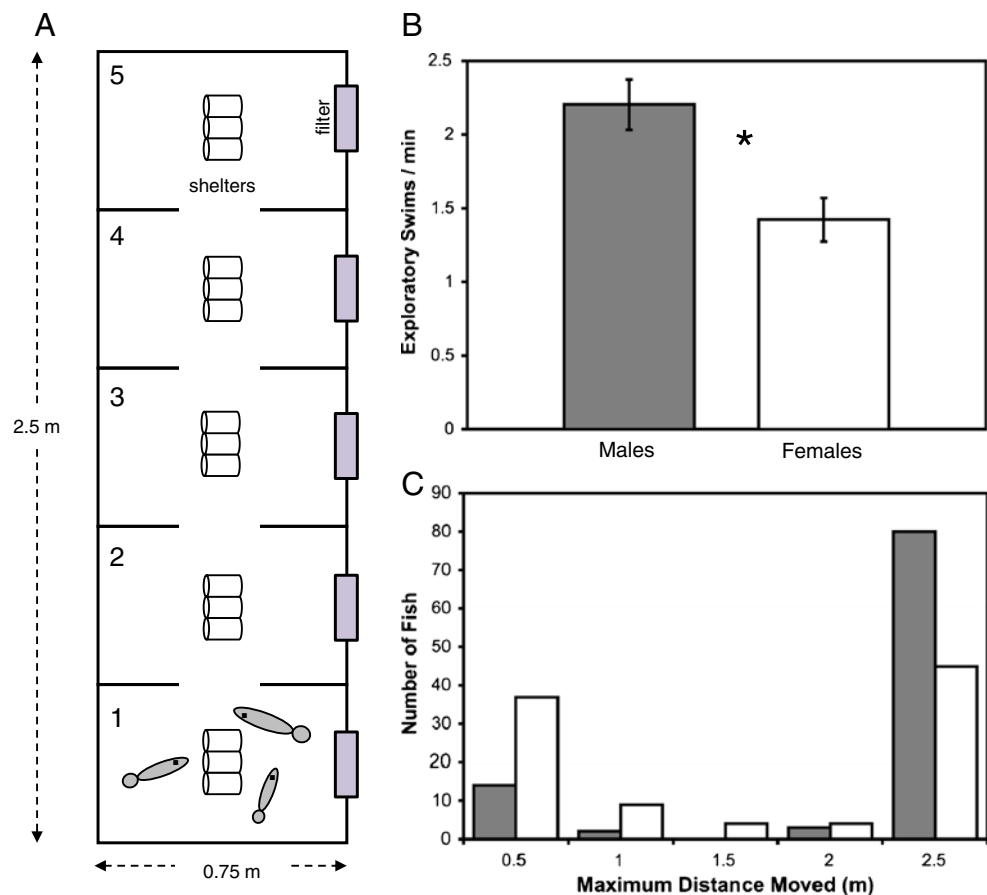
once daily to reduce the influence of fish odors between trials and fish were started from alternating ends of the arena in subsequent tests.

In each trial, a group of three sex-matched fish were tested together. Groups rather than single fish were used because round goby naturally exist in high densities (Chotkowski and Marsden 1999) and pilot studies indicated that fish in triads were more active than when observed individually (a mean increase of 2.0±0.6 movements/min, *N*=81, 95% confidence interval of 0.8–3.1 movements/min). The three individuals in each group were not matched in size, to facilitate individual identification. The observer was blind to the sex of the fish during testing.

Each group of three was placed in one of the end chambers, with access to the rest of the arena temporarily blocked by barriers, to acclimate for 30 min. During the last 15 min of the acclimation, each individual was observed (in randomized order) for 5 min and all behaviors exhibited were recorded. Behavior (obtained for *N*=180 fish) was classed as social interactions, horizontal locomotion, exploration, and sheltering (for details, see Table 1). In a pilot study of 20 individual fish, each introduced to a 90-L testing aquarium and observed for 1-min periods at 15-min intervals over a 1-h trial, exploration occurred at high rates after entry into a novel environment and then declined over the hour (repeated-

measures analysis of variance, $F_{4,76}$=6.7, $P<0.0001$), but horizontal locomotion did not ($F_{4,76}$=0.4, $P=0.80$).

At the end of the acclimation period, the temporary barrier blocking the opening to the second chamber was removed, allowing all three fish to freely disperse within the arena for 30 min. The experimenter noted the time at which each fish first left the starting chamber (time to begin dispersal, in seconds), the furthest chamber each fish reached in the test period (maximum dispersal), and the total number of chamber switches made. At the end of each trial, the fish were removed, euthanized, and dissected to confirm both sex and reproductive status.

Movement in the field

Between May 5 to November 6, 2009 and May 5 to November 3, 2010, we conducted a large-scale mark–recapture study of round goby in Hamilton Harbour. We selected a mark–recapture technique to study round goby movement in the field because this methodology has been used by many other studies and offered many logistic advantages (Hutchings and Gerber 2002; Croft et al. 2003; see below). Traps were set at each of three sites along a 30-m stretch of shoreline (six traps, each 6 m apart) and all fish caught were tagged as above with a unique identifying

Table 1 Behavioral categories for round goby experiments

Category	Behavior	Description
Horizontal locomotion	Hop	Fish movement of ≤1 body length
	Swim	Sustained horizontal movements in water column of >1 body length
	Dart	Rapid swim of >1 body length
Exploration	Swim	Sustained, repeated, frequently vertical movements in water column with mouth oriented at perimeter of aquarium
Sheltering	Dig	Fish inserts snout into substrate, takes mouthful of substrate, and ejects it
	Self-burial	Fish rapidly shimmies to bury body in substrate
Social interactions	Bite	Following a rapid approach, one individual opens and closes its mouth on another; the bitten fish darts away
	Chase	One individual rapidly approaches another without contact; the approached fish darts away

visible implant elastomer (VIE; Northwest Marine Technologies, Inc.) four-mark tag in 4 of 12 possible locations on the body. Fish were tagged in five cohorts between May 5 and August 21, 2009; recaptures continued to be monitored weekly (2009) or twice monthly (2010) until the end of the study. In total, 881 fish were tagged (N=539 males, 328 females, 14 juveniles). Each fish was sexed and its total mass, total length, and reproductive condition (based solely on the external appearance of the urogenital papilla and secondary sexual characteristics; Marentette et al. 2009) were noted. Recaptured individuals were identified, reweighed and measured, their recapture location recorded, and then they were released at that same recapture location. Traps for other round goby studies were also occasionally set in the same general area. Any tagged round goby opportunistically collected in these traps that were not part of the mark–recapture study were reweighed and measured as usual, and the distance along the shore to the nearest mark–recapture trap was calculated in determining the total distance moved by the fish. All recaptured fish were assigned a maximum distance traveled across all capture events (in meters), a maximum number of elapsed days between first and last captures as measures of residence time and site fidelity, and a traveling rate (maximum distance traveled (in meters) per week, with weekly units defined as maximum days elapsed per 7 days).

For the first year of the study, recaptured fish could be assigned to one of three mutually exclusive seasonal categories based on the dates at which they were first and last seen. These categories were (1) breeding season residents, (2) post-breeding season residents, or (3) year-long residents for fish that were first observed during the breeding season and last seen after the breeding season. A fourth category encompassed all fish seen in the second year of the study, (4) returning residents. Previous research has indicated that the number of gravid females in the study area declines dramatically by August (Young et al. 2010), and male sperm is reduced in number and speed in this

month (Marentette, personal observation; Sopinka 2010). Based on these findings, August 15 was selected to demarcate the end of the breeding season.

Two additional supporting studies were also conducted. To evaluate whether tags influenced mortality or would be lost over time, a group of 10 VIE-tagged fish were maintained and monitored in the laboratory from June 2009 to April 2010 when the last round goby in the laboratory died. No tag losses were observed in this period, and no mortalities occurred in the first 2 months of the study. To examine potential sex differences in trap response, a laboratory study was run between July 10 and August 27, 2010. Groups of four fish (two males, two females) were given two 16-h overnight trials spaced 2 days apart. In a trial, each group of four was placed in a 90-L aquarium equipped with an AquaClear 50 filter and a sand substrate to a depth of 2 cm. Groups were placed either inside or outside a minnow trap baited with 30 g frozen corn. Both entrances to the minnow trap were open, and the order of trial presentation (inside or outside the trap) was randomized. After 16 h, the fish that successfully entered or escaped the trap were identified. Of 52 fish, 38% of females (N=10) and 58% males (N=15) entered the trap, but only one individual (a male) was observed to escape the trap. There were no sex differences in rates of laboratory trap entry (χ^2=1.9, P=0.17) or escape (χ^2=1.0, P=0.31).

Statistical analyses

All data analysis was performed using the program JMP 5.0.1a for MacIntosh (SAS Institute, Inc., 2002). Behavioral data (rates per minute) and morphological data (e.g., fish total length) from the laboratory experiment were log or arcsine square root transformed to normalize where possible. As individual fish were observed as part of a group of three, behavioral data were examined with linear mixed models (residual maximum likelihood method) incorporating sex and collection site as fixed main effects and group ID as a random

effect, nested within sex to account for the fact that all members within a group were of the same sex. Differences in laboratory behavior between fish of different reproductive states were examined in linear mixed models separately within each sex, using status as fixed main effect and group ID as a random effect. Fish were given a binary score for some measurements, such as reaching the furthest point of the laboratory apparatus (i.e., "yes" or "no") and these data were analyzed with a logistic regression model followed by post hoc Wald chi-square tests to determine the effect of sex. Male round goby are larger than females (Charlebois et al. 1997; Young et al. 2010) and so a covariate of log total length was used in models, but removed where it was not significant. The number of days spent in the laboratory, which varied between two and seven, was never a significant covariate in models of fish behavior and was, therefore, removed. Nonsignificant interaction terms were also removed from models. Post hoc differences between sexes or reproductive states were identified, where necessary, using Tukey HSD tests or a nonparametric equivalent (Zar 1999). Where data could not be normalized through transformation, and in the case of field movement data, nonparametric statistics, such as the Kruskal–Wallis test, normal approximation to the Wilcoxon rank-sum test, or Spearman rho correlations, were used. Comparisons of numbers recaptured (male versus female) were achieved using chi-square tests.

Ethical note

Animal handling protocols for these studies were approved by the McMaster University Animal Research Board (AUP # 06-10-61) in accordance with the Canadian Council for Animal Care guidelines.

Results

Movement in the laboratory

Male fish explored more than females in the acclimation phase ($F_{\text{sex } 1,56}=6.7$, $P=0.01$; Fig. 2b), although the sexes did not differ in horizontal locomotion ($F_{\text{sex } 1,56}=1.3$, $P=0.27$) or in sheltering behavior ($F_{\text{sex } 1,56}=1.3$, $P=0.12$). Males showed greater dispersal through the arena than females in the test phase: they made chamber switches ($F_{\text{sex } 1,62}=16.3$, $P=0.0001$) and those that dispersed began dispersal sooner than females ($F_{\text{sex } 1,57}=8.0$, $P=0.007$). More males than females reached the fifth and furthest chamber of the testing arena (logistic regression, Wald $\chi_{\text{sex}}^2=25.2$, $P<0.0001$; Fig. 2c).

Reproductive status had little impact on round goby behavior in this experiment. Gravid and nongravid females did not differ from each other on any measure, nor did female

GSI correlate with any behavioral data (analysis of covariances, effect of status P's>0.10; Spearman rho, P's>0.30). Sneaker males showed the most horizontal locomotion among males in the acclimation phase ($F_{\text{status } 2,58}=7.1$, $P=0.002$), but did not disperse differently from other males in the test phase. Guarding males made more chamber switches than nonreproductive males ($F_{\text{status } 2,63}=4.5$, $P=0.02$). Male GSI also did not correlate with any behavioral data (Spearman rho, P's>0.10).

Behavior during the acclimation phase and the testing phase was correlated. Fish that exhibited more exploration in the acclimation phase began dispersal sooner ($r_s=-0.22$, $N=132$, $P=0.01$), dispersed farther ($r_s=0.51$, $N=180$, $P<0.0001$), and made a greater number of chamber switches ($r_s=0.45$, $N=180$, $P<0.0001$) in the test phase.

Body size did not correlate with round goby movement. Fish total length did not relate to exploration behavior, the time to begin dispersal, the distance dispersed, or the number of chamber switches (Spearman rho, all P's>0.10). Aggression was size-based and generally directed by larger individuals toward smaller individuals, with the smallest of three fish receiving the most aggressive acts in a group ($r_s=0.40$, $P<0.0001$). However, the amount of aggression received did not affect how soon fish dispersed, how far they dispersed, or the number of chamber switches made (Spearman rho, all P's>0.10).

Movement in the field

Of the 881 fish tagged, 19.0% ($N=167$) were recaptured the same year (2009). About one third ($N=54$) were recaptured more than once, with three individuals being caught six times after tagging (two females, one male). Male ($N=106$, 19.7%) and female ($N=61$, 18.6%) return rates were similar ($\chi^2=0.2$, $P=0.70$). Among the reproductive males, more guarding males ($N=34$, 23%) than sneaker males ($N=20$, 11.6%) were ultimately recaptured ($\chi^2=7.2$, $P=0.007$). No juveniles were recovered.

In 2010, the second year of the study, 1.5% ($N=13$, 9 males and 4 females) of the original 881 fish were recaptured. All fish possessed a complete set of four VIE tags. Seven fish had not previously been recaptured, increasing the total recapture rate for the study to 20.0% ($N=176$). Of the four fish that had been recaptured in 2009 as well as 2010, three had been year-long residents and one was a post-breeding season resident.

Across the study, known residence times varied from 1 to 168 days in 2009 and up to 386 days in 2010, and absolute distances moved ranged from 0 to 18 m (Table 2). To control for the amount of time elapsed between sightings, we used traveling rate in meters per week to compare movement distances between sexes or among male reproductive tactics in round goby residents.

Table 2 Median (and range) values for the absolute distances moved, in meters, and the number of days elapsed between first and last captures, categorized by round goby sex, reproductive tactic, and whether the fish was a resident (1) during the breeding season, (2) after the breeding season, (3) year-long in 2009, or (4) a returning resident in 2010

Time of residence	Measure	All males	All females	Guarding males	Sneaker males	Nonreproductive males
Breeding season	Distance (m)	0 (0–18)	0 (0–18)	0 (0–9)	0 (0–18)	0 (0–12)
	Days	17 (1–71)	20 (1–85)	14 (1–58)	19.5 (1–71)	29.5 (7–70)
	N	29	21	9	10	10
Post-breeding season	Distance (m)	0 (0–12)	0 (0–6)	0 (0–12)	0 (0–3)	0 (0–12)
	Days	22.5 (1–64)	14 (1–64)	36.5 (1–63)	13 (3–50)	20 (1–64)
	N	58	21	20	6	32
Year-long	Distance (m)	0 (0–9)	3 (0–15)	6 (3–9)	0 (0)	0 (0–3)
	Days	57 (25–134)	79 (28–168)	89 (57–134)	59 (25–93)	47.5 (27–91)
	N	19	19	5	4	10
Returning	Distance (m)	6 (0–12)	1.5 (0–6)	12 (6–12)	n/a	6 (0–12)
	Days	290 (233–386)	322 (282–386)	282 (233–386)	n/a	321 (271–386)
	N	9	4	5	0	4

Days elapsed between captures for returning residents were calculated as the difference between the last capture in 2009 and the first capture in 2010

1. Breeding season residents

    Males and females did not differ in their rate of travel ($Z=0.06$, $P=0.95$). The traveling rate of guarding, sneaker, and nonreproductive males were similar ($H_3=0.24$, $P=0.89$), and guarding males and females moved at similar rates ($Z=10.45$, $P=0.66$; Fig. 3a).

2. Post-breeding season residents

    Males traveled faster than females, but not significantly so ($Z=1.69$, $P=0.09$), after the breeding season ended. Among male tactics, there were no differences in rates of travel ($H_3=2.37$, $P=0.31$). Post-breeding season guarding males traveled faster than did females ($Z=2.16$, $P=0.03$; Fig. 3b).

3. Year-long residents

    In fish present over the entire 2009 sampling period, males and females moved at similar rates ($Z=1.02$, $P=0.31$). Guarding males moved faster than either sneaker males or nonreproductive males ($H_3=10.43$, $P=0.005$). Guarding males, however, did not move differently than females ($Z=2.03$, $P=0.15$; Fig. 3c). In no measure did year-long residents differ from fish found only in either the breeding or post-breeding season. Year-long residents were similar in total length to other residents, controlling for sex ($F_{2,163\ resident}=1.87$, $P=0.16$), nor did they differ from breeding or post-breeding season fish in the rate of travel per week, within each sex or reproductive status (Kruskal–Wallis tests, P's>0.10).

4. Returning residents

   Males moved farther and faster than females ($Z=2.25$, $P=0.024$; Fig. 3d). Larger fish in general traveled faster, but not significantly so (Spearman rho, $r_s=0.48$, $N=13$, $P=0.09$). Three of the males were identified as guarding males in both years, four as nonreproducing in both years, and two males were identified as nonreproducing in 2009 and as guarding males in 2010. Males that presented as nonreproducing in both years grew more than males that presented as guarding males by the second year (measured as a percent change in total length; $Z=2.3$, $P=0.02$). The sex difference in movement between years was driven by guarding males, which moved more than females, and not by nonreproductive males ($H_3=7.0$, $P=0.03$; Fig. 3d).

Discussion

In the laboratory, round goby males exhibited more exploratory behavior, dispersed farther, and dispersed sooner in a novel laboratory environment than did females. In the field, males also moved greater distances than females. Guarding males did not move more than sneaker males in the laboratory, but did so over a year in the field. Although larger round goby are thought to aggressively displace smaller round goby to suboptimal habitat in the field (Ray and Corkum 2001), neither body size nor the amount of aggression received appeared to modulate round goby movements in our laboratory studies.

In the laboratory, where males were not given the opportunity to reproduce or guard territories, our predictions were supported—males moved more than females. In the field, our predictions of greater male movement were supported for post-breeding season movements and movement between years. Our predictions of greater female movement during the breeding season were not supported. Why did we not see less movement in guarding males relative to females? First, there may be no difference in
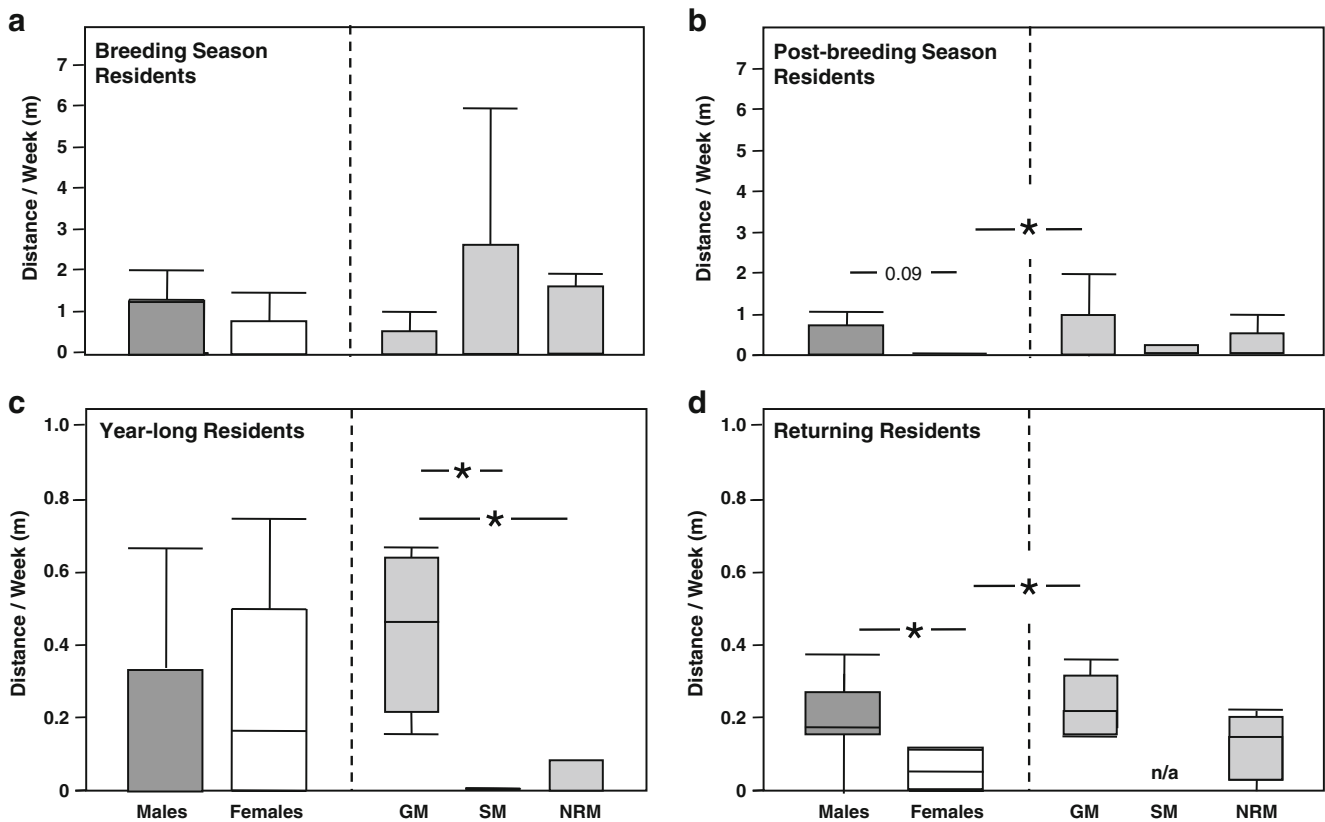
Fig. 3 Median, quartile, and 95% percentile box plot distributions of rate of travel (in meters per week) across sexes (*left*; males *dark gray*, females *white*) and male reproductive states (*right*; light gray) in **a** the breeding season (May–August), **b** the post-breeding season (August–November), **c** year-long residents who spanned the breeding and post-breeding seasons, and **d** returning residents recaptured in the second year of the study. *GM* guarding males, *SM* sneaker males, *NRM* nonreproductive males. *Lines between pairs with an asterisk* indicate significant differences (*P*<0.05) between pairs (based on Wilcoxon rank-sum tests), and one nonsignificant result is indicated as *P*=0.09

home ranges or territorial behavior between guarding males and females. This may be particularly true for guarding males that at the time of capture did not currently have egg clutches in their nest due to clutch loss, not having yet spawned, or having reared a previous clutch to the juvenile stage. Males with eggs are believed to reduce feeding (Charlebois et al. 1997; Corkum et al. 1998) and we felt these were unlikely to be trapped. A reduction in movement around a territory may only be apparent for that window of time when guarding males are actively parenting.

The differences in movement rates or space use between males adopting alternative reproductive tactics have rarely been examined or quantified (see Gladstone 1987; Petersen 1987; Mboko and Kohda 1999; Sunobe and Nakazono 1999; Manabe et al. 2009). In our study, guarding and sneaker male round goby were equally explorative in the laboratory. In the field, guarding males moved more than sneaker males, as predicted, but the pattern was only obvious over the course of an entire year. It may be the case that sneaker males associate closely with one or a few nests only, thus also showing relatively restricted home ranges (as has been observed with ruff, *Philomachus pugnax*, Van

Rhijn 1973; blennies, *B. sanguinolentus*, Santos and Almada 1988; and cichlids, *Telmatochromis vitattus*, Ota and Kohda 2006).

Mark–recapture was preferred as a low-impact methodology for our study. Surgical introduction of ultrasonic or passive integrated transponder (PIT) tags is more invasive than VIE tag injection and thus can affect fish health and ability to move. Accurate individual fish identification based on in-person watches have been used successfully with cottid fish in shallow rivers (e.g., Natsumeda 2001) but would be difficult to achieve in deeper lakes for this rock-dwelling, cryptic, and primarily nocturnal fish species. The distances between traps (6 m) used in our study were smaller than the reported mean 48-h distance moved by round goby in a seminatural enclosure (7.3 m; Cookingham and Ruetz 2008). However, a finer-scale assessment of movement may have been necessary to detect subtle but real differences in movements between sexes or across male tactics within a single year or season. Although the close physical monitoring required for in-person PIT tag detection is known to disturb round goby and could disrupt the maintenance of normal behavior like ranging (e.g., Cookingham and Ruetz 2008), the use of

stationary arrays to detect PIT tags could be useful in this species.

We recaptured 20% of tagged round goby. Tag loss or handling-related mortality seems unlikely to have significantly influenced our recapture rate estimates, as control fish tagged and maintained in the laboratory showed no tag loss even after several months. Also, all fish recaptured in the second year of this study had a complete set of tags. The 80% of fish not recaptured may have remained in the area, but simply avoided or escaped traps. Our laboratory control studies indicated that trap escape is a possibility but may happen only at low rates (<2%) and also that not all fish enter a baited trap even when it is within close quarters. Some other fish probably dispersed out of the mark–recapture study area. In a 2003 mark–recapture study in the same study location of Hamilton Harbour (Balshine et al., unpublished data), three long-distance dispersers were opportunistically captured (one female traveling 50 m, and two males, 4 and 8 km) from a population of 231 tagged fish. Long-distance dispersers may mediate round goby invasion fronts, estimated to move at a rate of 1.0 km/year (Bergstrom et al. 2008).

How do sex differences in movement in this species compare with other taxa? Greater male movement in round goby exhibited in the laboratory and in the field matches up with predictions based on the round goby's polygamous mating system. Like most other polygamous species (mammals, fishes) where males compete more vigorously for access to mates (Greenwood 1980; Dobson 1982), male goby move more than females, both in a short-term spatial task and over the long term (across years) in a natural environment. Sex biases in movement may represent dispersal away from kin toward new mating opportunities or an attempt to access better resources. Passive dispersal of round goby larvae over many kilometers is considered to be a major contributor to genetic exchange among populations (Hensler and Jude 2007; Hayden and Miner 2009), when not driven by human transport (LaRue et al. 2011), so adult movement away from kin may be unnecessary and unlikely for round goby. The effects of 6–12 m movement differences on reproductive success of males versus reproductive success of females are not known. Movement between years may represent the establishment of newer, higher-quality home ranges and nesting territories in rocky nearshore regions where our study was conducted. It is worth noting that the 0–18 m linear nearshore movements revealed in this study are within the same spatial scale as home ranges identified for other benthic fish species of similar body sizes, such as slimy sculpins (*Cottus cognatus*, Cunjak et al. 2005), fluvial sculpin (*C. pollux*, Natsumeda 2001, 2007), and other gobiids (Osugi et al. 1998; Sunobe and Nakazono 1999).

To our knowledge, this study represents the largest-scale and longest-lasting study of adult round goby movement in

the field, where much is not yet known, and the only to take into account fish sex and reproductive tactic. A mark–recapture study of round goby in Lake Michigan yielded only 6.2% recaptures (Wolfe and Marsden 1998); one individual was recovered 2 km away after 213 days. Cookingham and Ruetz (2008) observed that 85% of stocked round goby dispersed out of a 20×20-m area in Muskegon Lake after 2 weeks. A third study recovered 58% of fish in the Detroit River over a 5-week period and calculated the mean diurnal home range of these fish to be 5 m^2 over 1 h (Ray and Corkum 2001). Round goby may move more widely at night, however (Natsumeda 1998). Our study indicated moderate site fidelity on the basis of recapture rates, home ranges with a linear axis of 6 m or less, and very high site fidelity in terms of actual distances moved within and between years. Assuming a winter migration to deeper waters, our study suggests that the round goby has strong annual homing abilities or may simply be undergoing far shorter winter migrations in North America than in its native range (Pinchuk et al. 2003).

Movement at all life stages is key to understanding the dynamics of established as well as invading populations of many species. Upriver invasion fronts of round goby (e.g., Poos et al. 2009) may be mediated primarily through natural dispersal of adults or older juveniles (range expansion) as well as human-assisted transfers because these occur in areas where passive dispersal of larvae cannot occur. The sex of the first round goby to be recorded in newly invaded areas is not often reported; however, Ojaveer (2006) described the first three fish collected from the northeast Baltic Sea to be male. Our experimental behavioral data and field records of long-distance dispersers both suggest that movement of males may precede that of females at the invasion front, like that of male coho salmon (*Oncorhynchus kisutch*, Anderson and Quinn 2007) or male western bluebirds (*Sialia mexicana*, Duckworth and Badyaev 2007), both species undergoing range expansions into non-native habitats. This predicted greater male bias has been found in round goby invasion fronts (Gutowsky and Fox 2011). It is possible that other factors independent of sex, such as asociality (Cote et al. 2010b) or increased aggression (Duckworth and Badyaev 2007), play important roles in determining which round goby first enter new habitats. Invasion fronts thus offer a novel context in which to examine whether field predictions of sex- or individual-specific differences in movement are borne out.

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