

Does the reproductive status of male round gobies (*Neogobius melanostomus*) influence their response to conspecific odours?

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Abstract While pheromone communication has been well documented in the female round goby, male responses have not been examined. We determined if male round gobies responded to odours of their conspecifics, and whether that response varied with their reproductive status (reproductive and non-reproductive). No significant differences were observed for any treatment (dechlorinated water, or water conditioned by reproductive males (RM) and non-reproductive males (NRM) and females), although RM spent more time inside shelter than NRM ($p < 0.05$). Morphologically, length and weight did not vary, but gonadosomatic index, seminal vesicle somatic index and relative head width did differ between the two male groups ($p = 0.000$). Round goby males guard nests in cavities, and so a preference for shelter with increasing reproductive status is expected. Also, a lack of male responses to conspecific odours may be adaptive in this species, since males nest together in high densities, where increased aggression might prove detrimental for nesting males.

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Introduction

A change in reproductive status in teleost fishes is often accompanied by dramatic changes in physical and behavioural characteristics, particularly in males (Liley and Stacey 1983). Reproductive maturity may be accompanied by differences in colour, territoriality or aggression to other conspecifics, fin length and other body proportions in comparison to immature or non-reproductive males (NRM) (Constantz 1975; Liley and Stacey 1983). Similarly, mature males representing different reproductive strategies will also exhibit differences in form and behaviour (Neat et al. 2003).

Status-based physical and behavioural differences are most relevant for intraspecific interactions such as male–male aggression, and attraction of females (Liley and Stacey 1983; Neat et al. 2003). Although information can be passed between individuals in many ways, the release and detection of pheromones are a major means of intraspecific communication in teleosts (Sorensen and Stacey 1999). These chemical signals may be particularly important in eliciting reproductive behaviours (Liley and Stacey 1983). Numerous studies have examined the effect of

pheromones, and substances containing them, on males and females of various species. Male channel catfish, *Ictalurus punctatus*, will concentrate their movements around the introduction point of gravid female washings (Timms and Kleerekoper 1972). Female sea lampreys *Petromyzon marinus*, react with searching behaviour to a sex attractant produced by males (Li et al. 2002).

Members of the teleost family Gobiidae provide some striking examples of male responses. Reproductive male frillfin gobies, *Bathygobius soporator*, were found to respond to odours of gravid females with a courtship display (Tavolga 1956). Work by Locatello et al. (2002) on the black goby, *Gobius niger*, indicated that parental males of this species responded to the pheromone-containing ejaculate of other parental males with an aggressive display of tail-beating and biting. However, they did not find that parental males responded to the ejaculate of sneaker males, so the response was not simply male to male, but depended on their reproductive state.

The round goby, *Neogobius melanostomus* (Pallas) invaded North America from the Ponto-Caspian region of Eurasia by at least 1990 (Jude et al. 1992). This bottom-dwelling fish lives in an environment with little light, and so pheromone-mediated responses are expected to be a major, if not dominant, form of communication in this species. Early work by Kulikova (1985) hinted at a possible link between pheromones and the reproductive state of the round goby, when it was found that males were stimulated to become reproductive merely by the presence of females made gravid through hormone injections. It was not known, though, what combination of physical and chemical cues induced this change. Male round gobies were also found to increase gill ventilation rates when exposed to either gonadal extracts of gravid females (Belanger et al. 2006), or the pheromones E1, E2-3g, and ETIO (Murphy et al. 2001), which may indicate that males are able to detect gender and/or reproductive status of conspecifics (particularly gravid females) at a distance. However, the only behavioural studies to date of the round goby in response to pheromones have concentrated on

the female. Recent work has shown that gravid females respond to reproductive male odour, and non-reproductive females (NRF) to gravid female odour, by increasing swimming velocity and concentrating movement near the odour source (Gammon et al. 2005). This demonstrates that both genders are capable of releasing pheromones detected by conspecifics, but thus far only in a reproductive state.

We determined if male round gobies responded to odours of their conspecifics, and whether that response varied with their reproductive status. It was hypothesized that, like some other gobiids (Tavolga 1956; Locatello et al. 2002), reproductive male round gobies would swim more actively, orient towards the odour source, and spend more time near the introduction point of conditioned water, when that water contained the odours of reproductive males (RM) or reproductive females (RF), but not for water conditioned by NRM and NRF. NRM were hypothesized not to respond by changes in swimming speed, orientation or location to any odour.

Materials and methods

Collection of animals and odour source

Round gobies were collected by angling between May and July 2005 from Lake Erie (Leamington, Ontario) and the Detroit River (Windsor, Ontario). The period of collection coincides with the peak reproductive season of round goby (MacInnis and Corkum 2000). Animal care was in accord with guidelines from the University of Windsor Animal Care Committee. Once in the laboratory, round gobies were sorted by sex and presumed reproductive status into four separately housed categories: RM, NRM, RF and NRF. Gender was determined by means of the urogenital papilla (pointed in males, blunt in females), while reproductive status was inferred from other traits: RM are dark to black in colouration with swollen cheeks, while RF have swollen abdomens (Miller 1984; Gammon et al. 2005). Reproductive status was confirmed by dissection and the calculation of the gonadosomatic index (GSI) [gonad mass (testes + seminal vesicles):total body

mass \times 100%), which measures relative gonad investment (Miller 1984). The GSI of a fish is easily obtained, although it cannot account for allometry within a species (Stoltz et al. 2005) and can only be determined post mortem. In this study, GSI was used as a post hoc measure to validate the reproductive state of male and female round gobies as inferred from external traits. In addition, the seminal vesicle somatic index (SVSI) (seminal vesicle mass:total body mass \times 100%) was calculated for males. The SVSI has been used in other gobiids to distinguish between mature males of different mating tactics (Mazzoldi and Rasotto 2002). All fish were maintained at temperatures of $19 \pm 2^\circ\text{C}$ with a photoperiod of 16 L:8 D, and fed ad libitum on alternate days with Nutrafin[®] flakes.

Conditioned water was obtained from 24 randomly selected individuals of each sex and reproductive status in a manner similar to that of Belanger et al. (2004). Each fish was kept in 1 L of aerated, dechlorinated tap water for 4 h. The water was filtered using Whatman paper (Whatman Inc., Ann Arbor, MI, USA) to remove debris, then frozen at -20°C in 1 L Nalgene containers (Nalge Nunc International, Rochester, NY, USA) for storage until needed. Frozen water was used within 2 weeks of collection, and thawed to ambient temperature before use. Odour donors were used only once ($n = 96$ fish).

Behavioural trials

Each male was placed in a plastic shelter (16 cm long \times 11 cm wide \times 5 cm high, opaque black sides, transparent roof) at one end of a flume (90 cm long \times 29 cm wide \times 30 cm high) with 15 L of dechlorinated aerated tap water. Stimulus water (1 L of conditioned or control water) was introduced from tubes connected to an elevated carbuoy at the opposite end of the flume from the shelter. An airstone was placed in the flume by the odour source to aid dispersal. The entrance of the plastic shelter faced the odour source, while the rear wall of the shelter had small holes allowing passage of water through the shelter. Inflow of stimulus water was controlled by a Gilmont[®] 6.5 mm Industrial flow meter (Gilmont Instruments, Racine, WI, USA); mean flow varied

but ranged from 30 to 35 mL min⁻¹. Valves at the shelter end of the flume were kept open to remove water at a rate equal to the addition of stimulus water. Dye tests showed that at this flow rate, introduced water would be distributed throughout the tank in 8 min.

Trials consisted of three sequential periods of 20 min each (following the protocol of Gammon et al. 2005): an acclimation period with no water added, a control period with dechlorinated tap water added and a stimulus period where either conditioned water or dechlorinated tap water was added. The control period was used to acclimate the tested males to the addition of water alone. Each male was used only once. Reproductive status of the tested males was determined within 24 h after the trial; males were euthanized in MS-222, and the GSI was determined after dissection. Twelve replicates were obtained for both RM ($n = 60$) and NRM ($n = 60$) fish for each of five treatments (control; and conditioned water from RM, RF, NRM and NRF round gobies; $n = 120$ trials). However, males displayed a wide range of values for GSI and it was not immediately obvious what limits defined a RM or NRM by GSI alone. To eliminate males of questionable or intermediate reproductive state, all males within each treatment ($n = 24$) were ranked by GSI, and only the trials of the highest eight (RM) and lowest eight (NRM) tested males by GSI were considered in those status categories (eight replicates; $n = 80$ trials). By removal of the middle third ($n = 8$) fish from each treatment, the bimodal GSI frequency distribution was more clearly separated into high (RM) and low (NRM) regions (Fig. 1).

Morphometric analyses

The following measurements were collected from male round gobies: GSI, total length to the nearest 0.1 cm, weight to the nearest 0.01 g ($n = 168$), SVSI ($n = 56$ RM, 59 NRM) and a head width index (breadth of the head as taken behind the eyes:total length \times 100%; $n = 36$ RM, 33 NRM). Fulton's condition factor, $K = 100 \times \text{mass (g):total length (cm)}^3$ (Danylchuk and Fox 1996), was calculated for males to test the assertion that RM become more emaci-

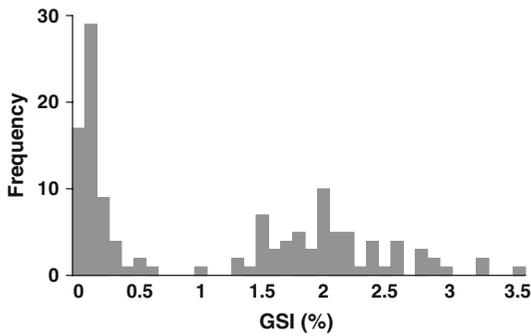


Fig. 1 Frequency histogram for the gonadosomatic index (GSI) of tested and donor reproductive males (RM; GSI $\geq 1\%$, $n = 64$) and non-reproductive males (NRM; GSI $< 1\%$, $n = 64$), after removal of the eight intermediate male GSI from each treatment

ated than NRM during the reproductive season (Miller 1984; Charlebois et al. 1997), while head measurements were taken to examine how strongly the degree of head swelling correlated to reproductive status.

Females with a GSI of 8% or above were considered RF (MacInnis 1997); below this value, NRF. Males which appeared to be reproductive but had small gonads (GSI $\ll 1\%$) were considered as NRM; males which appeared to be reproductive and had large, well developed gonads (GSI $> 1\%$) were considered RM. Those NRM with gonad or seminal vesicle weights of < 0.01 g were given a GSI or SVSI of 0%. Seven males were found in the course of the study which appeared to be NRM, but had large gonads (GSI range 1.36–5.69%)—these males are considered anomalous (AM) and only their morphological measurements (GSI, total length and weight) are contrasted with the other males.

Trial and data analyses

Trials were videotaped for computer analysis. The first minute of the stimulus period was ignored to permit the experimenter to adjust trial equipment, and thereafter the next 15 min were analysed. The stimulus period was examined for three variables: preference for different areas of the flume (measured as number of seconds spent in each specified region, the far half of the tank and the shelter), activity level (or the proportion

of seconds the fish spent swimming) and fish head orientation relative to the odour source (Fig. 2). Location preference data were obtained for the last 8 min (480 s) of the 15 min examined, corresponding to the time when conditioned water would have reached all areas of the experimental flume. Activity level and orientation were scored per second for 1-min periods in minutes 3, 6, 9, 12 and 15. Time spent in different areas and activity level data were obtained using the program FishTracker 2.0 (Shen 2005), with activity level defined as the proportion of seconds where velocity exceeded 1.05 cm s^{-1} (thus allowing for errors in determining fish movement when fish were stationary). Fish orientation was scored by hand in 45° intervals. Data for activity level and orientation were grouped into the categories ‘before odour dispersal’ (minutes 3 and 6), and ‘after odour dispersal’ (minutes 9, 12 and 15).

Location preference data were $\log(X + 1.1)$ transformed before analysis to account for 0 values, while activity level data were arcsine transformed according to Freeman and Tukey’s

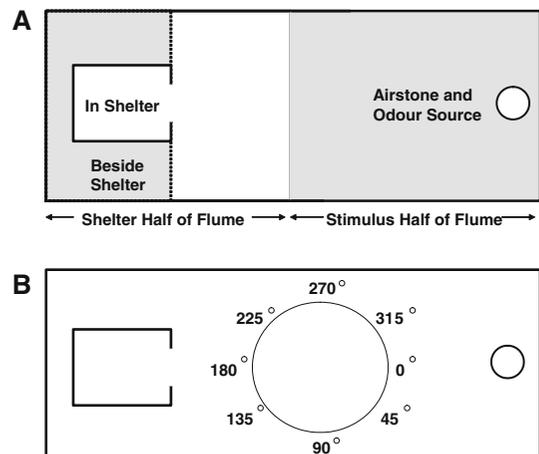


Fig. 2 The experimental apparatus used for behavioural trials. **(A)** Defined regions of the flume used to establish location preference among tested males (in shelter, beside shelter and the shelter or stimulus halves of the flume). **(B)** The circle within the flume indicates the angles used to establish preferred head orientation of the tested males (0° indicating the fish faced the odour source, 180° indicating the fish faced away from the source, etc.). Orientation scores per second were given according to one of these eight angles

(1950) equation $p' = \frac{1}{2}[\arcsin\sqrt{(X/n + 1)} + \arcsin\sqrt{(X + 1/n + 1)}]$ to account for 0.0 and 1.0 values (Zar 1999). Both location preference and activity level were analysed by two-factor (treatment and reproductive status) ANOVA using the computer program Statistica (Statsoft 1998). Where results were significant, Student–Newman–Keuls (S–N–K) post hoc tests were used to identify differences among groups. Mean orientation scores were examined for directionality using tests for second order circular data, and also for differences in angular distance to the odour source, after odour dispersal, for each treatment contrasted against the control. To test for angular distance from the odour source, data on a 0–360° scale were reduced to a 0–180° scale, with values of 180–360° converted to their mirror image angle, after Di Maio and Corkum (1997).

Results

Morphological variation with reproductive status

The two groups of males (RM and NRM) were contrasted morphometrically (Table 1). There were significant differences between the mean GSI ($t_{126} = 29.469, p = 0.000$) for RM and NRM. RM had the highest mean (\pm SE) GSI of $2.094 \pm 0.063\%$, while NRM had the lowest with $0.133 \pm 0.020\%$. After $\log(x + 1)$ transformation to account for right skew, 95% of the GSI measurements fell between the mean ± 1.96 (SD) of 1.239–3.169% for RM, and 0–0.429% for NRM. A one-factor ANOVA contrasting GSI among RM, NRM and AM ($F_{2,132} = 265.148,$

$p = 0.000$) showed that AM, with a mean (\pm SE) GSI of $2.190 \pm 0.591\%$, had significantly greater GSI than NRM (S–N–K test, $p = 0.000$) but were not significantly different from RM (S–N–K test, $p > 0.50$). Values for SVSI also differed between the groups of RM and NRM ($t_{105} = 15.885, p = 0.000$), as did the head index indicating relative head width ($t_{68} = 10.287, p = 0.000$). The GSI was positively correlated with the head index among all males ($y = 0.396x - 6.442, R^2 = 0.619, F_{1,89} = 144.7, p < 0.001$). RM had larger SVSI ($0.711 \pm 0.041\%$) and wider heads ($20.481 \pm 0.186\%$), while NRM had smaller SVSI ($0.010 \pm 0.009\%$) and narrower heads ($17.280 \pm 0.169\%$).

Although gonad measurements and head widths varied between male groups, total length, weight and Fulton’s condition factor K did not vary between RM and NRM (Student’s t tests, $p > 0.5$). One-factor ANOVAs revealed that AM were shorter than all other fish with a mean length of 11.86 ± 0.60 cm (S–N–K tests, $p < 0.05$) but did not differ in weight or Fulton’s condition factor K from RM and NRM ($p > 0.10$).

Preference for different locations within the flume

Tested males were scored for the number of seconds spent in both the stimulus half and the shelter half of the flume, as well as the number of seconds spent within or beside the shelter, after odour dispersal was complete, for a maximum 480 s. Two-factor ANOVA tests were performed using reproductive status (two categories) and treatment (five categories) as factors. Many tested males never left the shelter; 29 RM and 20 NRM

Table 1 Comparison of mean (SE) male round goby body measurements between different reproductive states

	GSI (%)	SVSI (%)	Head index (%)	Length (cm)	Weight (g)	K (g cm ⁻³)
RM	2.094 (0.063) ^a	0.711 (0.041) ^a <i>n</i> = 56	20.481 (0.186) ^a <i>n</i> = 36	13.60 (0.26) ^a	36.137 (2.237) ^a	1.338 (0.017) ^a
NRM	0.133 (0.020) ^b	0.010 (0.009) ^b <i>n</i> = 59	17.280 (0.169) ^b <i>n</i> = 33	13.37 (0.23) ^a	34.626 (1.100) ^a	1.345 (0.017) ^a

RM, $n = 64$; NRM, $n = 64$. Exceptions to group sizes are indicated where applicable. Superscript letters in common indicate no difference among groups according to Student’s t tests; different letters indicate significant differences at $p < 0.001$ (GSI, SVSI and head index)

(of 40 fish) were in the shelter for the entire 8 min of the stimulus period examined. Neither treatment ($F_{4,70} = 0.706$, $p = 0.590$), reproductive status ($F_{1,70} = 0.022$, $p = 0.883$) nor the interaction factor ($F_{4,70} = 2.230$, $p = 0.074$) affected time spent near (in or beside) shelter in RM or NRM. However, NRM spent more time than RM ($F_{1,70} = 6.504$, $p = 0.013$) beside shelter irrespective of treatment ($F_{4,70} = 1.095$, $p = 0.366$) or the interaction factor ($F_{4,70} = 0.278$, $p = 0.891$), and RM spent more time (mean \pm SE time 373.3 ± 30.8 s) than NRM (240.6 ± 38.3 s) inside shelter ($F_{1,70} = 7.849$, $p = 0.007$) irrespective of treatment ($F_{4,70} = 1.437$, $p = 0.231$) or the interaction factor ($F_{4,70} = 0.873$, $p = 0.485$) (Fig. 3).

The amount of time spent in the stimulus half of the flume, nearest the odour source, was influenced by the interaction factor between reproductive status and treatment ($F_{4,70} = 3.057$, $p = 0.022$), but neither status ($F_{1,70} = 2.857$, $p = 0.095$) or treatment ($F_{4,70} = 0.957$, $p = 0.437$) alone (Fig. 4). Tested males did not spend much time in the stimulus half of the flume (mean \pm SE time for RM 17.2 ± 12.4 s, NRM 46.6 ± 19.2 s). Time spent by RM near the stimulus did not vary with treatment (S-N-K tests, $p > 0.05$). NRM given RM odour spent significantly less time near the stimulus than NRM given NRM or RF odour

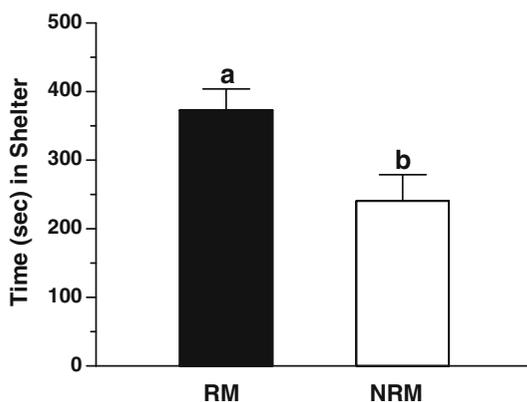


Fig. 3 Differences in mean (+SE) time spent inside the shelter during the stimulus period after odour dispersal, over all five treatments, between reproductive males (RM) and non-reproductive males (NRM), of a maximum 480 s. RM spent significantly more time in the shelter than NRM ($F_{1,70} = 7.849$, $p = 0.007$)

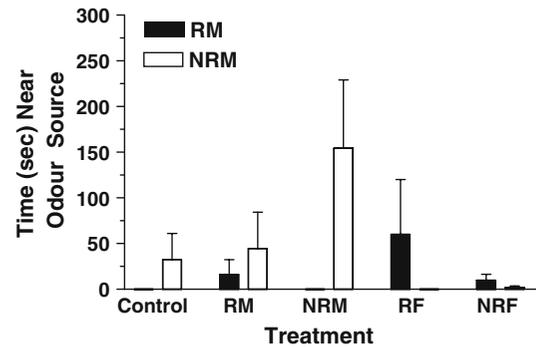


Fig. 4 Differences in mean time (+SE) spent near the odour source after stimulus odour dispersal between reproductive males (RM) and non-reproductive males (NRM) of different treatments, of a maximum 480 s. Time spent by RM near the stimulus did not vary with treatment (S-N-K post hoc tests, $p > 0.05$), but NRM given RM or reproductive female (RF) odour spent significantly less time near the stimulus than NRM given NRM odour (S-N-K tests, $p < 0.05$). Bars are absent where all eight tested males in a given group did not approach the odour source

(S-N-K test, $p < 0.05$), but no group differed from NRM given control water (S-N-K test, $p > 0.05$).

Activity level

Tested round goby males regardless of reproductive status spent much of their time (>90%) immobile, resting on the flume bottom. A two-factor ANOVA on activity levels before and after odour dispersal showed no difference between male groups due to reproductive status ($F_{1,70} = 0.1247$, $p = 0.268$ before; $F_{1,70} = 3.101$, $p = 0.083$ after), treatment type ($F_{4,70} = 0.271$, $p = 0.896$ before; $F_{4,70} = 0.341$, $p = 0.849$ after) or the interaction factor ($F_{4,70} = 1.829$, $p = 0.133$ before; $F_{4,70} = 1.933$, $p = 0.114$ after).

Orientation to odour source

Mean fish orientation scores were tested for randomness with Moore's modification of the Rayleigh test, a non-parametric test suitable for second order data (Zar 1999). After odour dispersal within the flume, only two of ten groups (two male categories \times five treatments) exhibited significant directionality: RM given RF odour ($R' = 1.11$, $p < 0.05$) and NRM given NRM odour ($R' = 1.10$, $p < 0.05$). After conversion of fish

orientation scores to their angular distance from the odour source (i.e. all degrees 0–180°), each treatment group (RM, NRM, RF and NRF stimulus odours) within a reproductive status category was compared with the respective control ($n = 4$ comparisons) using a two-sample Watson's U^2 test adjusted for second order data with ties (Zar 1999). Allowing for Bonferroni adjustment of the significance level ($\alpha = 0.05/4 = 0.0125$), there were no significant differences for RM or NRM after odour dispersal between the control and any treatment group ($U^2 < 0.18$ and $p > 0.05$ in all cases).

Discussion

Mature reproductive status in the male round goby is commonly characterized by black nuptial colouration and a swollen head (Miller 1984). The degree of head swelling as quantified in this study did increase with increasing reproductive status, as expected—although a swollen head was not a guarantee of a high GSI value in any one fish. Dark colouration was not always a useful distinguishing trait, since many freshly caught fish appeared dark regardless of reproductive status. Body size in the round goby had no correlation to male reproductive maturity. In particular, a lack of difference in body weight among males of different reproductive states was unexpected. Although others have reported that nesting (reproductive) round goby males do not feed during episodes of reproduction, resulting in body emaciation (Miller 1984; Charlebois et al. 1997), there was no difference in body weight or Fulton's condition factor between RM and NRM.

An alternative reproductive tactic involving sneaking has been observed in the round goby (C. Murphy, personal communication in MacInnis 1997), but is not well documented. In this study, seven apparent NRM (with mottled colouration and narrow heads) were discovered upon dissection to have well developed gonads comparable to RM, qualities similar to males reported in the gobiid *Pomatoschistus* as evidence of such a sneaker strategy (Miller 1984). Owing to the small sample size, these AM males could not be contrasted behaviourally with the three groups of

males in this study, but their occurrence is reported as further evidence of a sneaker tactic in this species.

Behaviour of round goby males did vary with reproductive status; RM round gobies preferred to stay inside shelter compared to NRM. This finding is not unexpected—in round goby, reproductive or parental males are territorial and establish nests in shelters, from where they will court females and tend eggs (Charlebois et al. 1997). What is surprising is the complete lack of a vigorous response on the part of RM round gobies to odours of other RM and RF. This is in contrast to what has been found in some other gobiids (Tavolga 1956; Locatello et al. 2002). All results of the present study indicate that males simply do not respond to conspecific odours, by increasing their activity levels, by changing their orientation or by choosing different locations in a flume.

If pheromones are not producing changes in behaviour (releaser effects), they might still be influencing physiological processes (primer effects; Liley and Stacey 1983). The lack of an active response does not mean that information is not being passed on, especially since it has been established through gill ventilation studies that round goby males can detect conspecific odours (Murphy et al. 2001; Belanger et al. 2006). Adding support to the possibility of primer effects is a study which reported that male round gobies were induced to become reproductive simply by exposure to RF, which may have been a pheromone-mediated change (Kulikova 1985). Similarly, in the black goby, the presence of parental males has been shown to inhibit the change of reproductive tactics in sneakers, a physiological effect which again may be mediated through chemical signals (Immler et al. 2004).

The absence of potent behavioural responses to conspecific odours is also consistent with what is known of round goby behaviour in the wild and in the laboratory, where it might serve an adaptive purpose in this species. Round gobies are known to nest in high densities (Johnson et al. 2005). A study on round goby spawning on shipwrecks revealed that nests can be so close together they are contiguous—and the respective nest-holding RM did not aggressively interact

until the nest cover was removed (Wickett and Corkum 1998). Nesting densities in other gobiids have not been well reported. Stammer and Corkum (2005) showed that round gobies simply do not interact aggressively as often as they do with fish of other species, such as sculpins (Dubs and Corkum 1996) or logperch (Balshine et al. 2005). By avoiding interactions with male neighbours, nest-guarding males reduce the vulnerability of nest eggs to predators. Nesting males distracted by intruders lost more eggs to predation than at other times (Wickett and Corkum 1998). Moreover, nesting aggregations may also prove beneficial for round goby males, as a concentrated RM odour plume might attract more RF than would be found in regions with more dispersed nests (Gammon et al. 2005). Given such a situation, it makes sense that RF would be attracted to RM odour (Gammon et al. 2005), but not the reverse; parental males would not exit their territories to seek out mates (leaving nests vulnerable) but instead let gravid females approach them, circumstances which may also occur in the black goby (Colombo et al. 1980). Parental males would be expected to aggressively interact with intruders such as sneaker males (Scaggiante et al. 2005), but this would not be an odour-based reaction since sneakers are probably chemically silent (Locatello et al. 2002).

Signals other than odour, or in combination with odour, may be important for conspecific interactions in the round goby. For example, male freshwater gobies, *Padogobius martensii*, responded to both visual and chemical stimuli from females when given playback of male courtship vocalizations (Lugli et al. 2004). Frillfin goby males responded with a courtship display not only to female odours but also to female visual stimuli, while female frillfin gobies increased their activity levels in response to playbacks of male calls (Tavolga 1956).

The development of reliable indicators of male reproductive status, to which the current study contributes, will help to clarify our understanding of pheromone production in round goby males. Pheromone communication in this nuisance species continues to be an important focus of research, not only in the interest of understanding

how round goby reproductive behaviour and intraspecific interactions contributes to its spread into North America's inland waters, to the detriment of native species (Charlebois et al. 2001), but also, from the conservation aspect, as a potential means of chemical control (Corkum 2004). The lack of male behavioural responses to pheromones demonstrated in this study provides evidence that this otherwise aggressive gobiid may be quite tolerant of high conspecific densities, potentially facilitating the burgeoning population of the round goby in the Great Lakes and elsewhere.

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