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ORIGINAL ARTICLE

The role of fanning behavior in water exchange by a nest-guarding benthic fish before spawning

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Abstract

Displacement fanning (fanning during courtship before eggs are deposited) by fish may be an indicator of parental ability. Fanning may be used for ventilation or for the dispersal of chemical messages. We used particle image velocimetry to visualize and characterize flow fields generated by courting male Neogobius melanostomus. *Once flow fields were characterized, we conducted a laboratory experiment to determine if caudal and pectoral fanning behavior was modulated by the presence of a female near the nest. There were significant differences between caudal and pectoral fanning ($F_{1,11} = 54.696$, $p < 0.001$) as was the interaction term, fanning type x distance ($F_{2,\ 22} = 9.870$, $p < 0.001$), on water entering and leaving the nest. The presence of a single female near the nest entrance had no effect on fanning rates. The velocity of water exiting the nest induced by caudal fanning (with the tail at the nest entrance) was 6.0 ± 0.96 (mean ± SD), 5.6 ± 1.18, and 3.1 ± 1.05 mm s^{-1} at 5, 10, and 15 cm away from the nest opening, respectively. In contrast, the mean velocity of water entering the nest via pectoral fanning (with the head at the nest entrance) was –3.9 ± 0.69, –0.2 ± 0.45 and –0.1 ± 0.28 mm s^{-1} at the respective distances. Caudal fanning pushes water out of the nest and pectoral fanning pulls water into the nest. We speculate that these are specializations of locomotive structures that lead to water stirring (pectoral fins) and pumping (caudal fin) to disperse odors.*

Keywords: fanning current, flow visualization, particle image velocimetry, Round Goby

Introduction

[1] Chemical communication has been linked to various behavioral and physiological functions in both invertebrates and vertebrates, for example, courtship behavior (Stadler 1999), mate recognition and attraction (Haberli and Aeschlimann 2004), social interactions (Breithaupt and Thiel 2011), and spawning (Carolsfeld et al. 1997), enabling organisms to track odors over great distances even in dark or turbid environments (Wyatt 2003; Johnson and Li 2010). In particular, odor tracking behaviors in which individuals use odor plumes to locate food, mates, or predators are well developed in fish and crustaceans (Weissburg 2000; Zimmer and Butman 2000; Johnson and Li 2010). Odors may carry qualitative information about a signaler (i.e., reproductive status), but may differ in the directional guidance provided for a receiver. Odors can be actively expelled as pulses or jets (Moore and Atema 1991; Weissburg and Zimmer-Faust 1994) or passively released in a

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leaky manner (Atema 1986). The active or passive release of odors results in different distributions of olfactory compounds within the dispersion plume, requiring different tracking strategies by the receiver to locate its source (Finelli et al. 1999; Johnson and Li 2010). Recent studies have used tracking apparatus to examine how animals process chemical information and track the source of an odor in turbulent environments (Breithaupt and Thiel 2011; Webster et al. 2012).

[2] Fanning behaviors in animals are used for ventilation and to disperse chemical messages that are important in aggression, courtship, foraging, mate choice, and parental care (Wyatt 2003). For example, information may be conveyed by currents using fan organs such as the exopodites of mouthparts in crayfish (Breithaupt and Eger 2002), wings in insects (Tallamy and Denno 1982), or fins in fish (Wantola et al. 2013). Many animal species ventilate enclosures, whether individuals are feeding, courting, or providing parental care. Alldredge (1977) described both house morphology and feeding in tunicates, whereby water is pumped into the house by the "sinusoidal beating of the animal's tail," allowing water to enter through the feeding filter and exit via the pharynx through spiracles and gill slits. In fish, ventilation often occurs by movement of pectoral fins (i.e., Wootton 1976; Karino and Arai 2006). For example, the male Round Goby (*Neogobius melanostomus*, Gobiidae) is known to exhibit fanning behavior (Meunier et al. 2009; Wantola et al. 2013). The challenge for the goby is to push out stagnant water and to pull in fresh water without generating thrust (cf. Videler et al. 1999).

[3] *Neogobius melanostomus* is a small benthic fish with parental care that occupies and defends a nest – an enclosed cavity with a single opening – to which females are attracted to spawn (Miller 1984; MacInnis and Corkum 2000; Charlebois et al. 2001). Because Round Goby spawn in turbid waters, and males are concealed in a nesting cavity, finding a mate is a challenge for conspecific females. Field observations showed that up to 15 different females enter a nest to spawn with a parental male (MacInnis and Corkum 2000). To lure multiple gravid females to a nest, even in low-visibility conditions, spermiating Round Goby males produce sex pheromones (Arbuckle et al. 2005; Gammon et al. 2005). Males release pheromones via urine, gills, and mucus secretions into the environment without the animal leaving the breeding nest or cavity (Gammon et al. 2005; Meunier et al. 2009; Katare et al. 2011). However, the mechanism by which males disperse sex pheromones into surrounding waters to reach potential receivers is unknown.

[4] One mechanism through which odor dispersal can be achieved is the ventilation of the nesting cavity. Meunier et al. (2009) observed that reproductive male gobies exhibit intense fanning behavior by using both pectoral and caudal fins in the hours and days preceding spawning. In nesting fish, fanning typically consists of an individual beating its fins to oxygenate the egg mass and to remove waste from the nest cavity (i.e., urine, feces, and sediments) (Gibson 1993). Fanning behavior is rarely observed prior to egg deposition (Blumer 1979), but has been reported in male Florida Flagfish, *Jordanella floridae* (St. Mary et al. 2001) and Threespine Stickleback, *Gasterosteus aculeatus* (Sevenster 1961). In both studies, prespawning fanning during courtship was positively correlated with male mating success, but it was not known if reproductive success was related to pheromone dispersal or superior egg fanning ability by the male. Displacement fanning (i.e., fanning by males before eggs are deposited in the nest) is thought to be an honest indicator of male parental abilities (Sevenster 1961; Bakker and Mundwiler 1999). Thus, males send honest signals to females about their energy reserves (quality) through courtship intensity (Sargent 1997).

[5] In the present study, we hypothesized that the function of fanning pectoral and caudal fins by nest-holding, prespawning Round Goby males differs, enabling males to both draw in and push out water from the nest. We used particle image velocimetry (PIV) to investigate how water and presumably waterborne olfactory signals are dispersed by mature males. We also examined whether fanning behavior was modulated by the presence of a female.

Methods

[6] We used a PIV technique adapted from Breithaupt and Ayers (1996) to visualize and characterize flow fields generated by the fanning male Round Goby. Detailed analysis of flow velocity, direction, and vorticity

(the tendency for fluid elements to spin) by one mature male Round Goby allowed us to establish whether currents generated by fanning behavior were consistent with the proposed function of pheromone dispersal. Subsequently, we determined if flow patterns resulting from caudal and pectoral fanning were similar among males ($n = 8$) and if flow patterns were influenced by the presence of a female.

[7] Fish were collected by angling along the Detroit River (42°18′ N, 83°04′ W) and Lake Erie (42°15′ N, 81°54′ W). Artificial nests also were deployed and retrieved at Erieau, Ontario, Canada (north shore of Lake Erie) in June and July to capture nest-guarding males (cf. Yavno and Corkum 2011). Fish were transported in coolers (2 h), containing aerated lake water and PVC shelters (4.5 cm × 10 cm) to the Animal Care Facility at the University of Windsor.

[8] Because displacement fanning exhibited during the courtship phase of development was to be characterized, only mature males (retrieved from the artificial nests in which eggs were absent) were used in experiments. The selected males exhibited secondary sexual traits (black coloration and well-developed genital papilla). The reproductive status of males was determined after fanning trials by calculating the gonadosomatic index (GSI) on dissected fish. We considered males with GSI $> -1.0\%$ to be reproductive (Marentette and Corkum 2008). The GSI value of the males used was 1.51 ± 0.25 (mean ± standard error).

PIV Analysis

[9] A 35-L glass tank (51 cm long × 25.4 cm wide × 30 cm high) was filled (28 cm) with dechlorinated tap water at 20 ± 1 °C and lined with black aquarium gravel to provide spawning substrate and to ensure good contrast for the white polyamide particles used in the PIV analysis (Fig. 1). Water was continuously aerated, ensuring a dissolved oxygen level of 75% saturation or more. A black PVC (polyvinyl chloride) rectangular shelter (21 cm × 11.5 cm × 4.5 cm) was placed at one end of the tank to serve as a nest for the male. The nest opening was rectangular and measured 5 cm × 4.5 cm.

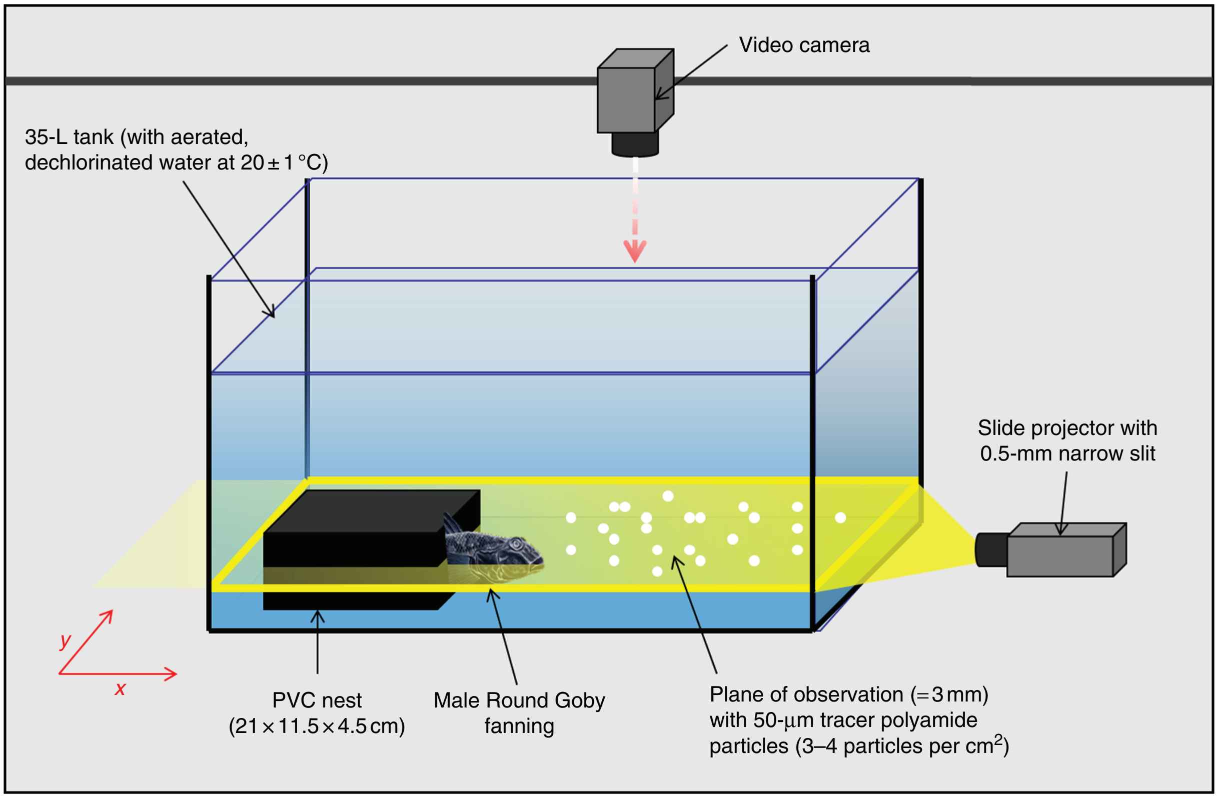

Fig 1. Experimental setup for particle image velocimetry.

[10] A reproductive male Round Goby was placed in the tank with 4 gravid females (characterized by a swollen belly and orange urogenital papilla) to induce male reproductive behaviors, which were monitored using remote video equipment. After 4–5 d of cohabitation, the male started displaying typical reproductive behaviors, including nest guarding, mound building at the nest entrance, vocalizations, and fanning (Meunier et al. 2009). Once fanning behaviors were well established (∼50 fanning bouts per hour), females were removed so that the currents observed in the tank were only those generated by the fanning male.

[11] A sheet of light was created using the light from a 500-W slide projector (Kodak Carousel 800) shining through a thin horizontal layer of water (∼3 mm thick) created by mounting 2 razor blades in parallel on a photographic slide mount. White tracer polyamide particles with a density of 1.03 g cm^{-3} and a diameter of 50 μm (Dantec Dynamics, Denmark) were used to track the direction and speed of fanning currents in the plane of observation. The characteristics of the particles provided near-neutral buoyancy, negligible drag, and a clear contrast between the particles and the black gravel at the bottom of the tank. The particles were added and thoroughly mixed with the water until a seeding density of 3–4 particles cm^{-2} was achieved in the plane of observation. The seeding density was verified by taking images of the plane of observation and counting the number of visible particles on the images. The slide projector was adjusted so that the plane of observation was at the same elevation as the fish's lateral line when the male rested at the bottom of the tank.

[12] Image Video Machine (DanDans Digital Media, USA) was used to capture images at a frequency of 25 frames s^{-1} on the camera, which also represented the maximum rate images could be extracted for the PIV analysis. The PIV analysis was conducted between 0 and 250 mm from the nest opening. Within this area, fanning currents did not appear to be affected by the increase of hydraulic pressure caused by the damming effect at the end of the experimental tank. We used JPIV (Java particle image velocimetry) software (Vennemann et al. 2006, 2007; http://www.jpiv.vennemann-online.de) to batch process the series of images resulting from each PIV trial. We performed PIV analyses of the fanning currents for randomly selected fanning bouts of various durations. Of the 32 caudal fanning bouts and 18 pectoral fanning bouts from one male, 6 bouts of each were randomly selected. For each fanning bout, results of the PIV analysis were time-averaged over the entire duration of the bout.

The Effect of the Presence of a Female on Fanning Behavior of Males

[13] A repeated-measures (distances) fixed model (Model 1) analysis of variance was used to examine the effects of females (presence and absent), fanning type (caudal and pectoral), and their interactions on the flows entering or leaving the nests at different distances from the nest opening by using Statistica version 7 (StatSoft, USA). Flow patterns were measured at three distances (5, 10, and 15 cm) from the nest entrance. The maximum distance represented the total length of a large goby. Eight males were tested, including 4 males in the "female present" treatment and 4 males in the "female absent" treatment.

[14] We used a nonreproductive female Round Goby in trials because reproductive females are difficult to obtain from the field; the operational sex ratio is male biased (Corkum et al. 2004). However, we added conditioned water (CW) from reproductive females to the female present trials. The CW was obtained from 3 reproductive females that were each placed in 1 L of dechlorinated, aerated tap water for 4 h. After filtering the CW to remove debris, samples were pooled and frozen at −20 °C, following the procedure of Gammon et al. (2005). We confined a female in a 12-cm-long PVC tube (3 cm in diameter) with nylon mesh at each end of the tube to prevent escape and added 125 mL of reproductive CW at the front of the tube by using a 60-mL syringe attached to the inflow tubing.

[15] For both with and without female treatments, a reproductive male was placed into the aerated tank with black aquarium gravel, and flow patterns were monitored using PIV. The male was allowed to acclimatize overnight (16 h). The female and CW were added to the tank 1 h before the PIV recordings began. The tube with female was placed near the entrance to the male goby nest at a 45° angle so that the female could be seen, but potential interference with outflow from the male

nest would be minimized. The plane of the light coming from the projector was aligned with the midpoint to the entrance of the goby nest.

Results

Caudal Fanning

[16] The flow visualization technique revealed that vigorous tail strokes by the fish produced a strong current directed outward from the nest (shown in red in Fig. 2). The time-averaged flow fields calculated for each fanning bout (orange shapes in Fig. 2) were characterized by a bell-shaped velocity distribution with lateral spread downstream of the nest, and an area of flow interaction at the boundary with the stagnant ambient water. These characteristics are consistent with those of a jet flow discharging in a stagnant environment with the nest entrance acting as a rectangular nozzle (e.g., Antoine et al. 2001).

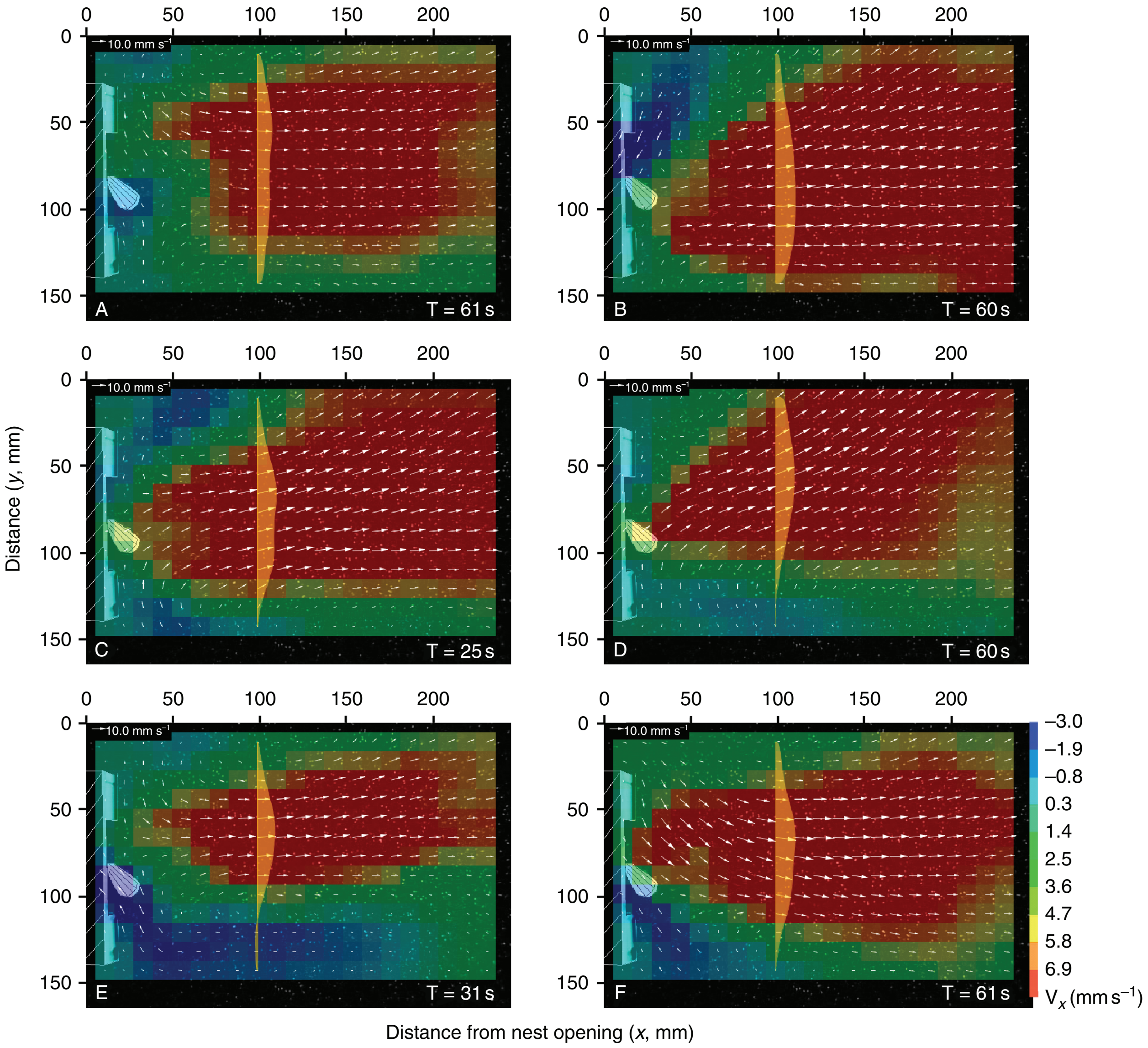

Fig. 2. Horizontal flow visualization. Time-averaged velocity fields for six different caudal fanning bouts (A–F). The nest opening and caudal fin are on the left side of each diagram. The scale of the coordinate system is 1 pixel per 0.343 mm (top and left axis). The color code represents the velocity of the particles in the *x*-direction. The temporal resolution of data acquisition is 0.04 s (25 frames per s). T is the duration of each fanning bout in seconds. The orange shape is the velocity distribution at 100 mm from the nest entrance. The surface area of the velocity distribution is proportional to the in-plane flow per unit length in the *z*-direction.

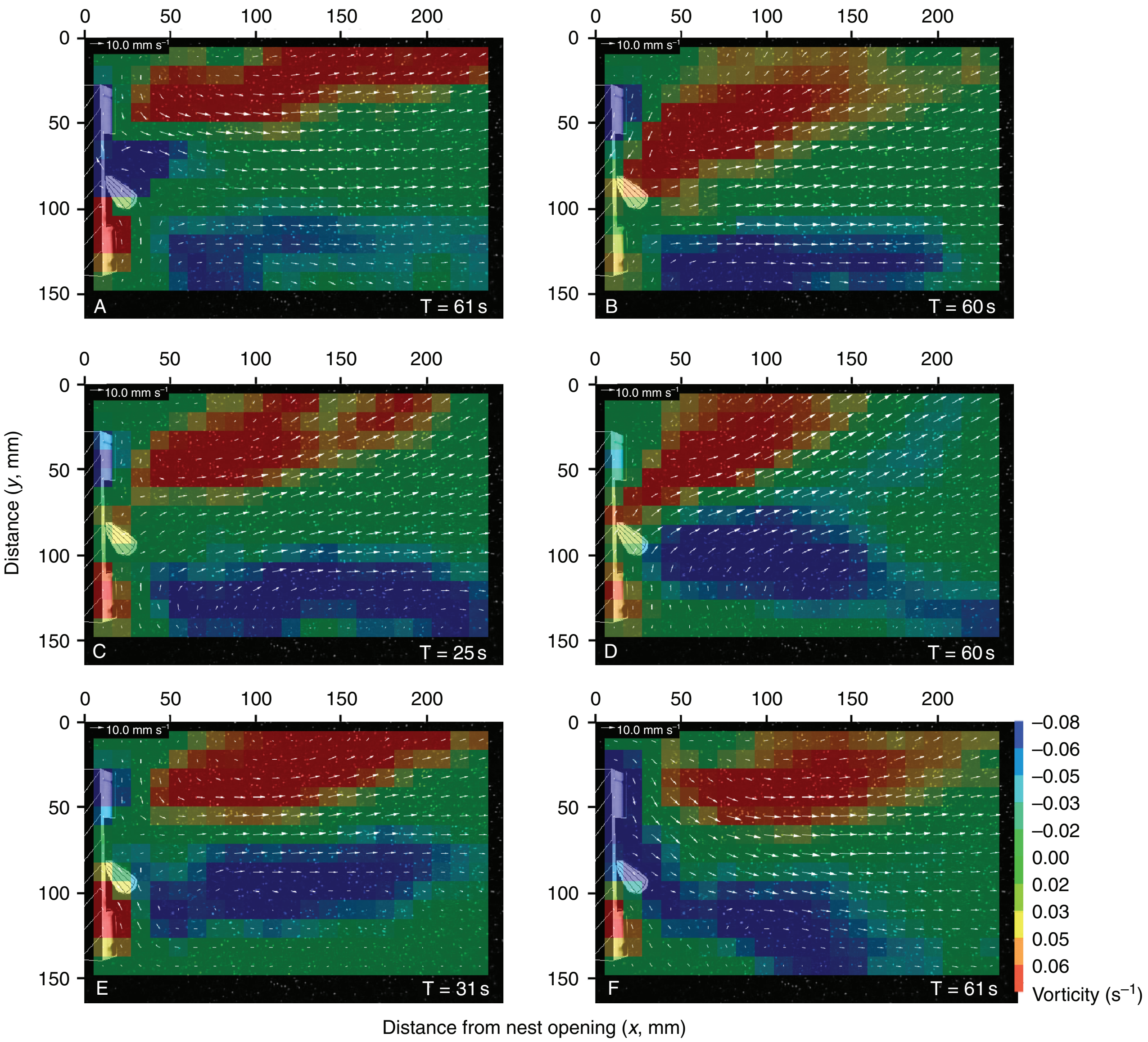

Fig. 3. Horizontal flow visualization. Time-averaged vorticity fields for six different caudal fanning bouts (A–F). The nest entry and caudal fin are on the left side of each diagram. The scale of the coordinate system is 1 pixel per 0.343 mm (top and left axis). The temporal resolution is 0.04 s (25 frames per s). T (29–61) is the duration of the fanning bout in seconds. The color code represents the orthogonal vorticity of the flow.

[17] PIV analysis in the vertical plane ($n = 2$) revealed that the flow field in the vicinity of the nest had a limited spread along the vertical axis (data not shown). Most of the flow occurred in a 50-mm water layer at the bottom of the experimental tank. These observations are consistent with the hydrodynamic characteristics of a jet discharged tangentially over a rough surface (e.g., Launder and Rodi 1983).

[18] The average velocity measured at 100 mm from the nest entrance was 7.7 ± 0.66 mm s^{-1} (mean ± SD, $n = 6$). Assuming that the average velocity remained constant along the vertical axis of the nest entrance, we estimated that the average discharge produced by caudal fanning was 36.7 ± 3.2 cm^3 s^{-1} ($n = 6$). The assumption of constant average velocity along the vertical axis of the nest entrance was supported by PIV

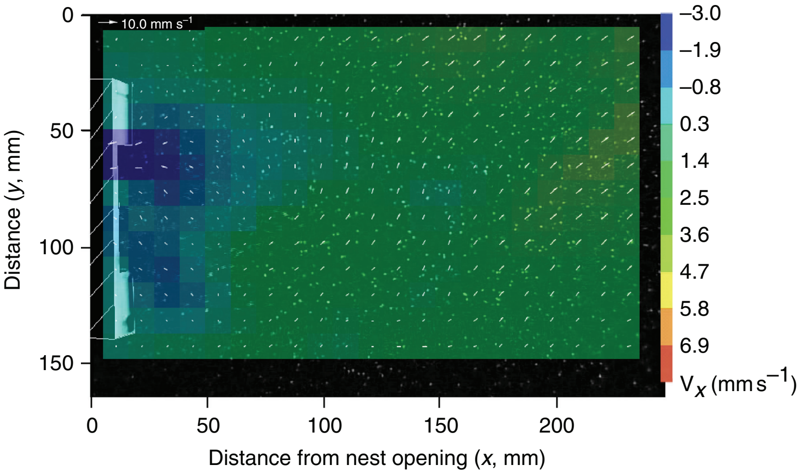

Fig. 4. Horizontal flow visualization. Time-averaged velocity fields for a pectoral fanning bout. The nest entry is on the left side of the diagram. The scale of the coordinate system is 1 pixel per 0.343 mm (top and left axis). The temporal resolution is 0.04 s (25 frames per s). The color code represents the velocity of the particles in the *x*-direction. T is the duration of the fanning bout.

observations in the vertical plane. The time-averaged maximal velocity measured in the central portion of the jet was 13.8 ± 1.9 mm s^{-1} ($n = 6$). The lateral spread of the flow field downstream of the nest was relatively constant across fanning bouts with an average horizontal propagation angle of 57.6 ± 1.8° ($n = 6$).

[19] The difference of velocity between the current and the stagnant environment created a shear layer, resulting in zones of high vorticity at the edges of the flow field (Fig. 3). This flow interaction was quantified by measuring the average vorticity (amount of rotation) across each flow field. At the right and left edges of the two-dimensional flow field, the average vorticity was –0.06 ± 0.002 s^{-1} ($n = 6$; clockwise) and 0.07 ± 0.002 s^{-1} ($n = 6$; anticlockwise), respectively. The average vorticity at the center of the outflow current was zero. This pattern was consistent among fanning bouts.

[20] Velocity measured at incremental distances from the nest revealed that a maximum velocity along the *x*-axis was reached at 150 mm from the nest. The velocity started to decrease beyond 150 mm. This pattern was consistent among fanning bouts. A polynomial regression was used to estimate the velocity decay in the flow field along the *x*-axis. Velocity decreases were described as: $V = -2.5 \times 10^{-4} L^2 + 7.84 \times 10^{-2} L + 2.33$ where V is the velocity and L is the distance from the nest. The regression accounted for 18.8% of the variance of velocity between fanning bouts and the coefficient of determination, R^2, was 0.99. Based on this regression equation, we estimated that outbound currents generated by the caudal fanning propagated at least 344 mm from the nest entrance.

[21] Weaker inbound currents were also observed on both sides of the nest entrance during caudal fanning bouts (blue in Fig. 2). These currents indicated an inflow of ambient water into the nesting cavity during caudal fanning. The velocity of inbound currents varied among fanning bouts with an average maximal velocity of 5.4 ± 1.9 mm s^{-1} ($n = 6$).

Pectoral Fanning

[22] In contrast to caudal fanning bouts, horizontal PIV analysis of the currents generated by pectoral fanning behavior bouts revealed no flow exiting the nest cavity (Fig. 4). Pectoral fin strokes did not create well-defined water circulation as seen with caudal fanning. Instead, we observed a weak stream of water entering the nest with a maximum velocity of 4.1 mm s^{-1}.

The Effect of the Presence of a Female on Fanning Behavior of Males

[23] Results of the repeated-measures analysis of variance revealed significant differences in caudal compared with pectoral fanning type ($p < 0.001$) and in an interaction term (fanning type × distance, $p = 0.001$) on water flow in and out of the nest (Table 1). The presence of a female with reproductive female CW had no effect on flow (Table 1). Caudal fanning, in which a nest-holding male oriented his body facing into the nest with the tail at the nest opening, resulted in water being pushed out of the nest. During caudal fanning, males held the fused pelvic fin against the smooth surface of the tank (the floor of the nest) and continued to fan with pectoral fins. When males faced outward with the head and snout at the nest opening, males engaged

Table 1 Summary of the repeated-measures (distance), Model I, analysis of variance test to examine the effect of female (absent and present), and fanning type (pectoral and caudal) on flow generated by males at three distances out from the opening of the nest (5, 10, and 15 cm).

Effect	Sum of squares	Degrees of freedom	Mean squares	*F*	*P*
Female	4.95	1	4.95	0.489	0.499
Fanning type	554.31	1	554.31	54.696	<0.001
Female × fanning type	0.25	1	0.25	0.025	0.877
Error	111.48	11	10.13		
Distance	6.18	2	3.09	0.858	0.438
Distance × female	21.72	2	10.86	3.017	0.070
Distance × fanning type	71.08	2	35.54	9.870	<0.001
Distance × female × fanning type	3.66	2	1.83	0.508	0.609
Total	79.22	22	3.60		

only in pectoral fanning. Here, we observed male ventilation. As water entered the mouth of the fish, the gill flaps flared so that water was exchanged.

[24] Water that enters and exits the nest is a function of the type of fanning. The mean velocity of water exiting the nest as a result of caudal fanning was 6.0 ± 1.0, 5.6 ± 1.2, and 3.1 ± 1.0 mm s^{-1} at 5, 10, and 15 cm away from the nest opening, respectively. In contrast, mean velocity of water entering the nest via pectoral fanning was –3.9 ± 0.7, –1.9 ± 0.4, and –0.9 ± 0.3 mm s^{-1} at increasing distances away from the nest. Mean outflow was faster than mean inflow. Caudal fanning resulted in water pushed out of the nest, whereas pectoral fanning resulted in water pulled into the nest (Fig. 5). The interaction term (fanning type × distance) revealed that mean current velocity pushed out of the nest declined with increasing distance from the nest, and mean water velocity was in the opposite direction at the nest entrance (Fig. 5).

Discussion

[25] This study supported the hypothesis that the function of caudal and pectoral fanning differs with caudal fanning pushing water out of the nest and pectoral fanning pulling water into the nest. Our study demonstrated that males exhibit consistent fanning patterns during courtship behavior (before eggs are deposited) despite the presence of a nonreproductive female with reproductive female CW near the nest. Specifically, the presence or odor of a female does not modulate fanning behavior by a mature male. Earlier, Marentette and Corkum (2008) showed that in contrast to similarly sized nonreproductive males, mature nest-holding males did not increase their activity levels or orientation in a laboratory flow chamber in response to conspecific odors (males or females), regardless of reproductive status. Because reproductive males become territorial and occupy nests at maturity, it is expected that males would remain within nests during courtship and spawning (MacInnis and Corkum 2000; Meunier et al. 2009). Despite the lack of movement (Marentette and Corkum 2008) and unaltered fanning response (this study) by mature male gobies to the presence of conspecific

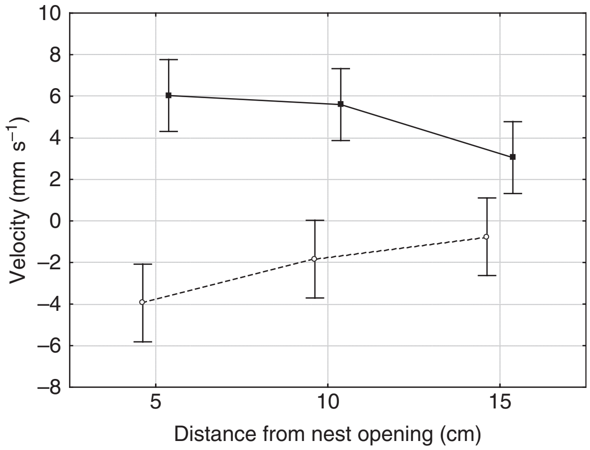

Fig. 5. The relationship between water velocity and increasing distance away from the opening of the nest. Caudal fanning is depicted with solid squares and straight line; pectoral fanning is depicted with open circles and dashed line. Fanning for 8 males was analyzed (4 males used for cases with and without the female treatment). Seven of the 8 fish exhibited both pectoral and caudal fanning. In the female treatment absent case, 1 of 4 males exhibited only caudal fanning; 3 of 4 exhibited both fanning types. Points indicate mean and vertical bars are standard deviation.

females or odors, female signals are likely perceived by males through gill ventilation (Murphy et al. 2001; Belanger et al. 2006).

[26] Murphy et al. (2001) suggested that gill ventilation in the Round Goby may be analogous to "sniffing" behavior to facilitate odor detection as proposed for some species of flounders (Nevitt 1991). During gill ventilation, the mouth of the male opens and closes continuously with gill openings beating in concert. Aleyev (1977) showed that injected dye entered into the oral cavity of fish and escaped through the gill slits with expired water. The inflow of water observed during pectoral fanning may help enhance the detection of female signals by increasing the amount of water entering the fish's mouth during gill ventilation. Belanger et al. (2006) showed that extracts of gonadal tissue from female Round Goby elicited a noticeable increase in gill ventilation in reproductive males; however, male ventilation declined significantly after nasal occlusion (i.e., when males were unable to smell).

[27] Recently, Wantola et al. (2013) demonstrated that reproductive and nonreproductive Round Goby males can be distinguished by the proportionately larger surface areas of pelvic and caudal fins in mature fish. Thus, elaborate fins may be an honest indicator of male parental care quality (Turner 1993; Bakker and Mundwiler 1999). We suggest that the relatively larger pelvic and caudal fins of reproductive males function in the dispersal of wastes and odors into the surrounding environment to lure potential mates.

[28] The fused pelvic fin, a distinguishing trait in the family Gobiidae, is important for attachment to vertical surfaces (Gee and Gee 1995) and facilitates ascent on vertical waterfalls (Blob et al. 2007). The fused fin also aids in the deposition of egg and milt in a single layer when male and females spawn on the ceiling and sides of enclosed cavities (Meunier et al. 2009). In this study, the function of the fused pelvic fin appears to function in stabilizing the fish during caudal fanning. The combined effect of pectoral fanning and the suction of the fused pelvic fin stabilize and anchor the fish so that caudal fanning may pump water while avoiding thrust. Based on our observations, the slow and steady fanning by the pectoral fins appears to fulfill a stirring function within the nest cavity, whereas the short and vigorous fanning by the caudal fin creates strong water circulation outside the nest. This denotes a strong specialization of these locomotive structures as water stirring and pumping appendages.

[29] In order for the pelvic fin to anchor the fish during bouts of caudal fanning, the suction disk of the fin must be against a smooth surface. Interestingly, Round Goby males (and other gobiids; Svensson and Kvarnemo 2007) remove gravel from the bottom of a nest by spitting individual stones just outside the nest entrance (Meunier et al. 2009). This activity, which creates a mound of gravel at the nest entrance, reduces the size of the nest opening. Jones and Reynolds (1999) argued that large openings into cavities aid in ventilation, yet the reduced nest opening is thought to deter intruders (including sneaker males) and to conceal the nest (Svensson and Kvarnemo 2007). An additional benefit of gravel removal from the bottom of the nest is to ensure a smooth surface on which the fused pelvic fin can more easily be anchored. A smooth surface on the floor of the nest provides additional space for egg deposition. MacInnis and Corkum (2000) showed that fertilized Round Goby eggs are deposited on ceiling, walls, and floor of nests.

Significance to Aquatic Environments

[30] Fanning currents generated by male Round Goby were consistent with the proposed function of pheromone dispersal. We observed that vigorous caudal fanning strokes generate strong circulatory currents exiting the nest. These currents were propagated at a relatively high velocity, at a wide angle (in the horizontal plan) and over a distance of at least 34 cm from the nest ($R^2 = 0.99$). This distance corresponds to 2–3 times the typical body length of a mature Round Goby. Under such flow conditions, any waterborne chemical released inside the nesting cavity would be quickly expelled from the nest and dispersed in the surrounding water. Turbulent stirring processes such as the one observed here play an important role in the distribution of olfactory compounds in odorant plumes and their interpretation by organisms (Webster and Weissburg 2009). For species living close to the substrate like the Round Goby, a pulse initiated by the pumping of the tail, which is an active release superior to ambient flow, results in a more

homogenous odor plume (Webster and Weissburg 2001) and may facilitate the detection of olfactory signals by receivers. A sharp flavored current is known to provide a more effective signal to receivers than loose patches of odors passively drifting in the ambient flow (Atema 1996).

[31] Our results also revealed that currents generated by male Round Goby are analogous to water jets characterized by a strong shear flow in the center of the flow field and areas of flow interaction at the boundaries with the surrounding water. Such flow carries intrinsic spatiotemporal information that also could be exploited by female Round Goby to orientate toward males. Tracking organisms dwelling in turbulent environments often exploit a combination of flow direction and chemical stimulation to infer a direction of travel, a behavior referred as odor-gated rheotaxis (Webster and Weissburg 2009). The Round Goby is particularly well suited for the detection of such stimuli, thanks to a high density of superficial neuromasts throughout their body (Charlebois et al. 1997). The modalities of female Round Goby tracking response to chemical and physical stimuli from nesting males remain to be determined.

[32] In addition to providing tracking cues to gravid females, male fanning currents could also play a role in mate selection. The association of fanning behavior and sexual selection has been documented in other fish species including Sand Goby *Pomatoschistus minutus* (Pampoulie et al. 2004), Threespine Stickleback *Gasterosteus aculeatus* (Sevenster 1961) and Florida Flagfish *Jordanella floridae* (St. Mary et al. 2001). The intensity of fanning behavior is directly correlated with male reproductive success in each of these species. In the case of Round Goby, we speculate that the intensity of male fanning currents is likely dependent on health, size and maturity of the male so that females may assess male reproductive fitness and that stronger currents may reach a larger number of females.

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