The role of mounds in promoting water-exchange in the egg-tending burrows of monogamous goby, *Valenciennea longipinnis* (Lay et Bennett)

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Abstract

*Valenciennea longipinnis* spawns monogamously in a burrow. After spawning, the paired female constructs a conspicuous mound on the burrow by carrying and piling up substratum-derived materials while the male tends eggs in the burrow until hatching occurs. In this study, the mounds of *V. longipinnis* were tested in the field to confirm their function of promoting water-exchange in the burrow, and their ecological role was examined in relation to egg care by the male. The mound of *V. longipinnis* promoted water-exchange in the burrow, contributing to the provision of external oxygenated sea water into the burrow. Therefore, dissolved oxygen (DO) concentrations in the burrow with a mound were significantly higher than those without a mound. Although male egg-tending behavior (e.g., fanning) may also promote water-exchange in the burrow, the water-exchange appeared to depend mainly on the hydrodynamic effect. Removals of the mound and paired female on the day of spawning led to high rates of egg-desertion by males. Since the frequency and time of fanning increase with a decrease of DO concentration in the burrow, the egg-desertion may result from an increased parental cost to males due to the decrease of water-exchange without a mound. This was supported by the fact that the DO concentrations on the day after mound removal were significantly lower in the egg-deserted burrows (measured before desertions) than in burrows not deserted by the male. Moreover, removals of paired females only also led to higher desertion rates. After removal of the female, the mound gradually collapsed by wave action and other factors, and the surface of the mound was covered with planktonic materials. Such a mound of poor quality may provide little water-exchange, which may lead to the egg-desertion by males. These results indicated that mound maintenance by females during the egg-tending period has an important role in the success of parental care by males. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

For burrowing animals, water-exchange or ventilation within the burrow is one of major problems. So far, a variety of ways to cope with the problem have been reported. For example, some thalassinidean shrimp species promote water-exchange in the burrow by their own pumping behavior in response to hypoxic conditions (Koike and Mukai, 1983; Forster and Graf, 1995; Astall et al., 1997). The mudskipper fish *Periophthalmus schlosseri* transports air by mouth into their mudflat burrows to maintain DO levels in the burrow (Ishimatsu et al., 1998). On the other hand, some animals harness hydrodynamic and aerodynamic forces to promote the exchange of water or air through their burrows. The black-tailed prairie dog (*Cynomys ludovicianus*, Vogel et al., 1973) and thalassinidean shrimps (*Upogebia africana*, Allanson et al., 1992; *Callianassa truncata*, Ziebis et al., 1996a) pile up sand or mud around one of the burrow openings. These mounds have a function of promoting the ventilation or water-exchange within their burrows through an external stream of fluid. At least two physical mechanisms may induce this function (Vogel and Bretz, 1972; Vogel et al., 1973; Vogel, 1978, 1994). First, a mound piled up around one burrow opening induces asymmetry of external flow velocity between openings, and then, by Bernoulli’s principle, develops a pressure gradient. This gradient produces unidirectional flow in the burrow. Second, the fluid in the burrow will be pulled out of the burrow opening by viscous entrainment, which depends on the viscosity of the fluid.

*Valenciennea longipinnis* is a goby that lives in the near-shore moat on coral reefs. The species is distributed in the west Pacific Ocean, including the Ryukyu Islands (Yoshino, 1984), being found in pairs in shallow sandy areas (Hoese and Larson, 1994; Takegaki and Nakazono, 1999a). Takegaki and Nakazono (1999a) have reported the reproductive ecology of *V. longipinnis* in detail. A paired male (112–184 mm SL) and female (93–170 mm SL) excavate several burrows under coral pavement and rubble within their home range. Each burrow has several openings; however, the pair covers all but entrance with substratum-derived materials: dead-coral fragments, pebbles, shells, sand and algae. The pair spawns monogamously in one of the burrows. The male shows parental care, such as fanning, for the eggs on the ceiling of the burrow continuously until hatching (3–5 days). During the male’s care, the female closes the entrance and constructs a conspicuous mound (60–130 mm high) by carrying and piling up the substratum-derived materials onto one of the other burrow openings, away from the main entrance (Figs. 1 and 2). The remaining openings are thinly covered with the same materials. Although, before spawning, the mound is constructed mainly by the male, only the female continues in its construction following spawning until hatching. Takegaki et al. (1999), using flume experiments, showed that a model mound made of the same substrate-derived materials promotes water-exchange in the burrow, as reported in some mound building animals (Vogel et al., 1973; Allanson et al., 1992; Ziebis et al.,
Fig. 1. (a) Mound construction by female *Valenciennea longipinnis*. (b) The mound on the day before hatching.

1996a). Similar mound construction has been reported in other *Valenciennea* species (Tanaka et al., 1982; Shiobara and Tanaka, 1995; Reavis, 1997; Clark et al., 2000), but the functions of the mound have not been discussed.

We hypothesized that the water-exchange function of *V. longipinnis* mound may contribute to male egg-tending behavior from the following two points: (1) the mound is constructed only on the spawning burrow from just before spawning until hatching occurs (i.e., mainly egg-tending period; see Section 3); (2) egg-tending males adjust
their fanning frequency and duration in response to DO concentrations in the burrow (Takegaki and Nakazono, 1999c). Because the DO concentrations in the egg-tending burrow are lower than those out of the burrow (Takegaki and Nakazono, 1999c), the supply of external oxygenated sea water into the burrow should reduce the parental burden of males.

In this study, we first tried to confirm the water-exchange function of the *V. longipinnis* mound in the field, and its effect on DO concentration in the burrow. Second, to examine the ecological roles of the mound, mound and/or female removal experiments were conducted.

2. Materials and methods

2.1. Study sites

Field studies were carried out on the coral reefs at Kunri Beach, Sesoko Island (26°39′N, 127°52′E) in 1994 and 1995, and at Nagahama Beach (26°42′N, 127°57′E), northern coast of Motobu Peninsula, Okinawa, Japan in 1996 and 1997. At both study sites, *V. longipinnis* were distributed in the near-shore moat at depths of 1–3 m; the substratum consisted mainly of sand and dead-coral fragments, with scattered coral colonies and rocks.
2.2. Ink-injecting experiment

To confirm the effect of the mound on water-exchange in the field, ink was injected into burrows at Nagahama Beach in 1996. Before spawning, a tube (Teflon pipe: about 30–40 cm long, 3.0 mm in outside diameter, 2.0 mm in inside diameter) was inserted into the potential spawning burrows through one of the several openings of each burrow. Blue-black ink (5 ml; mean density± S.D. = 1.02574±0.00404 g/mm³, n=10) was injected using a syringe through the tube between 2 h before and after high tide (flow velocity is about 10–15 cm/s). The site from which ink subsequently appeared was recorded. To exclude and examine the influence of male fanning activity on water-exchange (see Section 3), the experiments were performed both on vacant burrows (1 day after egg care; n=25) and egg-tending burrows (n=19). Eight of 25 trials on the vacant burrows were conducted after removal of the mound to clarify the effect of the mound on the water-exchange. The mound materials were carefully removed by hand so as not to reveal the burrow opening.

2.3. Measurements of DO in the burrow

To investigate the effect of water-exchange function of the mound on DO in the burrow, we compared DO concentration in a burrow before and after removal of the mound. The burrow used in these experiments was situated about 50 m from shore and in water 2.5 m deep at Nagahama Beach. We conducted two experiments here: (1) just after egg-hatch (vacant burrow) and (2) during the egg-tending period with a male and eggs inside to examine the effect of male fanning behavior on water-exchange in the burrow.

2.3.1. Experiment 1: vacant burrow

A pair (male, 157 mm in SL; female, 152 mm) spawned on 31 April, 1996 and the male finished egg-care on 3 May. The pair was removed on 3 May so they could not affect the burrow and mound. We measured DO 12 times at 37–54-min intervals on 4 May (09:15–17:32 h) with a mound (37 cm in major axis, 35 cm in minor axis, 13 cm high) and 10 times at 35–57-min intervals on 7 May (09:43–17:06 h) without the mound. The mound was removed by hand on 6 May without any of materials falling into the burrow. We also measured DO out of the burrow and flow velocity on the sea floor to control for these factors. DO in the burrow was measured by sampling sea water (about 110 ml) in the burrow with a syringe through the same Teflon tube used for ink injection (above). Before sampling the water, we exhausted the bubble from the syringe completely, and then withdrew about 5 ml water from the burrow to flush out the syringe. The sampling tube allowed the water to be sampled from the burrow without further disturbance. In preliminary experiments, more than 3000 ml of polyester resin were used to make casts of four spawning burrows; therefore, removal of 110 ml during sampling approximately once per hour should have little influence on the DO in the burrow. In an aquarium experiment, DO in the water sampled by syringe was not different from that sampled by siphon (the differences were less than 3.7%, Wilcoxon signed ranks test, P=0.39, n=11). Sea water outside the burrow was collected on the
sea floor adjacent to the burrow by syringe. We fixed samples chemically on each sampling occasion, and analyzed the DO by the Winkler method in the laboratory. Flow velocity was calculated from the distance ink flowed per unit time on the sea floor. This velocity was measured 3–5 times for every measurement of DO.

2.3.2. Experiment 2: egg-tending burrow

The same pair spawned on 21 May in the same burrow. Measurements of DO were taken 11 times at 42–55-min intervals on 22 May (09:40–17:40 h) on a burrow with a mound (29×25×9 cm) and 11 times at 40–53-min intervals on 23 May (10:24–18:14 h) on a burrow without a mound. We removed the paired female on 21 May to prevent her from reconstructing the mound, and removed the mound on 22 May. DO in and out of the burrow and the flow velocity on the sea floor were measured as in Experiment 1.

2.4. Female mound maintenance behavior after spawning

To estimate the costs of female mound construction and maintenance, we compared the rates of feeding and burrow mending behavior (primary mound construction and maintenance behavior; see Takegaki and Nakazono, 1999b) during the egg-tending periods with other periods for the same female. Underwater observations were carried out by snorkeling at Kunri Beach during 25 May–25 August, 1994, and 6 June–4 July, 1995. The study area (300×100 m) was situated in the near-shore moat at depths of 1.0–2.5 m. We captured seven paired females (mean SL±S.D. = 143.0±14.6 mm, range = 130–161 mm, n = 7) with a barrier net and hand net, measured their body size (standard length, SL mm) and determined sexes by the shape of the genital papillae (see Takegaki and Nakazono, 1999a). Gobies were marked by hypodermically injecting acrylic paint on each side of the body and sewing a plastic bead (1.5 mm long, 3.0 mm in diameter) with nylon fishing line into the dorsal musculature anterior to the dorsal fin. After marking, the fish were returned to their respective collection sites. We conducted 10-min observations 6.6 times on average for paired females during the egg-tending periods (range, 1–13 times, n = 7) and 14.3 times before and after egg-tending periods (range, 4–44 times, n = 7).

To determine the effect of female mound construction and maintenance on the structure of the mound, mound height was measured daily from the day of spawning until hatching. Mound height was measured by a stainless steel ruler with a level, from the burrow opening to the summit of the mound. We compared any change in mounds maintained by females (n = 26) with those mounds where the female either disappeared or was removed on the day of spawning (n = 9). This investigation was conducted using SCUBA at Nagahama Beach from 14 May–20 July, 1997.

2.5. Mound and female removal experiments

To investigate the relationship between the mound and male egg-tending behavior, we removed both the mound and female just after spawning at Kunri Beach in 1995 and Nagahama Beach in 1996 (n = 18). Removals were made on the day of spawning. We observed males each day after removal to determine if they continued to tend eggs
(usually 2 or 3 days; Takegaki and Nakazono, 1999a). When the males emerged from the burrow before the day or time of hatching and ceased to enter the burrow, we checked the eggs in the burrow by partly breaking the burrow entrance. In our aquarium observations, all four deserting males ate their eggs completely before desertions (Takegaki, unpublished data). Therefore, absence of eggs in those burrows was recorded as egg-desertion by the male. One day after the removals, DO in each spawning burrow was measured (see methods above) between 1 h before and after low tide, when the DO in the burrow drops to the lowest level (Takegaki and Nakazono, 1999c, see Section 3). Moreover, we removed a paired female alone (i.e., burrow left intact) just after spawning to examine female influence on male egg care ($n = 13$).

3. Results

3.1. Effect of the mound on water-exchange

In both egg-tending burrows and vacant burrows with mounds, ink injected into the burrow subsequently appeared primarily from the surface of the mound (Table 1). By comparison, vacant burrows without mounds were less likely to percolate ink from the burrow opening previously covered by the mound (Fisher’s exact probability test, $P < 0.05$; Table 1). In all four cases where the injected ink percolated out from both the mound and another opening, the ink eventually percolated out only from the mound.

3.2. Effect of the mound on DO in the burrow

During the daytime, DO concentrations were always lower within the burrow than outside the burrow (Fig. 3), and DO concentrations increased with flow velocity on the sea floor (Figs. 3 and 4). DO inside the burrow was lowest near the low tide (velocity = 0–1 cm/s), while DO outside of the burrow gradually increased from high tide to low tide (Fig. 3).

DO concentrations in the vacant burrow were significantly higher with an intact mound than after removal of the mound (Fig. 4a: comparison of slopes: $t = 0.36$, NS; $t = 0.36$, NS;

<table>
<thead>
<tr>
<th>Percolating site</th>
<th>Vacant burrows</th>
<th>Egg-tending burrows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>With mound ($n = 17$)</td>
<td>Without mound ($n = 8$)</td>
</tr>
<tr>
<td>Mound</td>
<td>16</td>
<td>4*</td>
</tr>
<tr>
<td>Mound and the other openings</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>The other openings</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Non-percolating</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>

* Percolating from the opening previously covered by the mound.
Fig. 3. Diurnal changes in flow velocity (open square) and DO concentrations in (solid circle) and out (open circle) of a burrow with mound (left) and without mound (right). (a) The burrow after egg hatch (vacant burrow). (b) The burrow during the egg-tending period. H and L with broken line indicate the time of high and low tide, respectively.

comparison of elevations: $t = 2.48, P < 0.05$). DO ratio (in/out) also showed higher values before removal of the mound (Fig. 4b: slopes: $t = 0.21$, NS; elevations: $t = 2.21$, $P < 0.05$): the differences in DO values within the burrow were not affected by DO values outside the burrow.

DO concentrations in the egg-tending burrow showed consistently higher values than those in the vacant burrow, irrespective of the presence of the mound (Fig. 4c). Both DO concentrations and DO ratio in the egg-tending burrow with the mound were higher than in those without the mound (Fig. 4c,d: comparison of slopes: $t = 2.87$ and 1.69, $P < 0.01$ and NS, respectively; comparison of elevations: $t = 8.29$ and 4.93, respectively, both $P < 0.001$).
3.3. Female costs of mound construction

The mound was constructed and maintained from just before spawning until hatching (Fig. 5). During the egg-tending periods, paired females fed less and mended more than at other times (Table 2).

From spawning through day four of egg-tending (i.e., hatching day for six of seven cases) mound height decreased significantly when paired females were either removed or otherwise disappeared on the day of spawning (n = 7 cases which paired males kept on tending the eggs until fourth day) relative to mounds maintained by females (n = 26; ANOVA, F = 11.87, P < 0.01; Fig. 6). In the absence of females, at least two of nine egg-tending males emerged from the burrow to mend the mound (see asterisks, Fig. 6). Both males re-entered the burrow and continued to tend the eggs.

3.4. Egg-desertion by males

When both the mound and the female were removed, eight out of 18 (44%) males...
Fig. 5. Daily changes of mound height through three successive reproductions by a pair (male, 160 mm SL; female, 163 mm). Shaded columns indicate egg-tending periods. The female was removed on 3 July (asterisk).

deserted the eggs before hatching, a significant increase in desertion relative to control males where only 11 out of 138 (8%) deserted (Fisher’s exact probability test, \( P < 0.001 \); Table 3). Furthermore, removal of the female alone also caused higher desertion rates by males (Fisher’s exact probability test, \( P < 0.01 \); Table 3). In nine of these removals, egg-tending males temporarily emerged from the burrows and either mended the mound or carried out the fanning behavior at the burrow entrance. No significant differences in the body size were detected between egg-deserting males and egg-tending males (Mann–Whitney \( U \)-test, \( P > 0.05 \) in all three manipulations), nor between their female partners (all \( P > 0.05 \)).

The day after removal of the mound and female, DO in the burrow ranged from 1.5 to 4.0 ml/l (30.3–80.6% oxygen saturation, mean DO±S.D. = 2.9±0.7 ml/l, \( n = 16 \); two egg-tending males deserted the eggs before measurement). DO concentrations in the burrows deserted by males (measured before desertions) were lower than in those where the males tended their eggs until hatching (Mann–Whitney \( U \)-test, \( U = 11.0, P < 0.05 \); Table 3).

Table 2
Comparisons of feeding and burrowing rates (/10 min) of paired females (\( n = 7 \)) between egg-tending periods and the other periods

<table>
<thead>
<tr>
<th></th>
<th>Egg-tending periods</th>
<th>The other periods</th>
<th>Difference*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Range</td>
<td>Median</td>
</tr>
<tr>
<td>Feeding bites</td>
<td>69.0</td>
<td>30.5–90.2</td>
<td>91.6</td>
</tr>
<tr>
<td>Burrow mending behavior</td>
<td>19.3</td>
<td>9.5–56.0</td>
<td>1.0</td>
</tr>
</tbody>
</table>

* Wilcoxon signed ranks test.
Fig. 6. Daily changes of mound height after spawning when paired females maintained the mound until hatching (thick line, $n = 26$; bar, S.D.), and when females were removed or disappeared on the day of spawning (thin lines, $n = 9$). Asterisks indicate that egg-tending males came out from the spawning burrows temporarily and maintained the mound. Crosses indicate that the males deserted the eggs before hatching.

Table 3
(a) Results of mound and female removal experiments, and (b) DO concentration in the egg-tending burrow on the day after removals of the mound and female

<table>
<thead>
<tr>
<th>Removal (n)</th>
<th>Number of males</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-egg deserting</td>
<td>Egg deserting</td>
<td></td>
</tr>
<tr>
<td>(a) Removal experiments</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>None (138)</td>
<td>127</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Female only (13)</td>
<td>8</td>
<td>5*</td>
<td></td>
</tr>
<tr>
<td>Mound and female (18)</td>
<td>10</td>
<td>8**</td>
<td></td>
</tr>
<tr>
<td>(b) DO concentration (mll/l)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Median</td>
<td>3.2</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>2.7–4.0</td>
<td>1.5–3.4</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>10</td>
<td>6*</td>
<td></td>
</tr>
</tbody>
</table>

*Fisher’s exact probability test were performed between natural condition and each manipulated condition.

Two males deserted the eggs before DO measurement.

* $P < 0.01$; ** $P < 0.001$. 
4. Discussion

4.1. Water-exchange function of the mound

This study revealed that the mound constructed by *Valenciennea longipinnis* promotes water-exchange in the burrow. Ink injected into the burrow percolated out from the mound at a higher rate in burrows with mounds than those without a mound. Although *V. longipinnis* mounds did not have a conspicuous opening typical of mounds built by other animals (black-tailed prairie dog *Cynomys ludovicianus*, Vogel et al., 1973; a thalassinidean prawn *Upogebia africana*, Allanson et al., 1992), the injected ink was percolated from the surface of the mound through the small gaps between the materials that make up the mound. These results were previously observed in preliminary flume experiments (Takegaki et al., 1999). The water-exchange function of the mound is induced mainly by the pressure difference arising from the asymmetry of external flow velocity between the summit of the mound and the other openings (Vogel et al., 1973; Allanson et al., 1992; Vogel, 1994; Ziebis et al., 1996a,b), and may facilitate respiration in the burrow due to an increased oxygen supply.

DO concentration in the vacant burrow of *V. longipinnis* was always lower than outside of the burrow during the day time (see also Takegaki and Nakazono, 1999c). Since the focal burrow was not influenced by underground water (Takegaki unpublished data), the increase of the DO inside the burrow must have been due to the supply of oxygenated sea water from outside into the burrow. DO concentrations in the burrow increased with the flow velocity near the burrow, therefore, the water-exchange between the inside of the burrow and sea water outside appeared to be promoted by the current. At low tide, the exposed reef-edge divided the moat from the outer-reef, and the water in the moat stagnated as in a tidepool. As a result, DO in the burrow showed minimum values near the lowest tide (see also Takegaki and Nakazono, 1999c). The DO concentrations in the vacant burrow after removal of the mound were significantly lower than those before removal, regardless of the DO levels outside the burrow. These results indicated that the mound promotes the flow of oxygenated sea water into the burrow.

*Valenciennea longipinnis* mounds were constructed only on the spawning burrow, and were maintained from just before spawning until hatching occurred. The egg-tending burrow should require more oxygen than usual because eggs as well as the egg-tending male consume oxygen in the burrow. However, the DO concentrations in the egg-tending burrow were consistently higher than those in the vacant burrow. This difference may be attributed to the behavior of male *V. longipinnis* who fan their eggs with their pectoral fins while undulating their body (Takegaki and Nakazono, 1999c). Therefore, male egg-tending behavior may further increase the flow of water in the burrow in addition to the mound. However, the positive correlations between DO levels in the egg-tending burrow and flow velocity indicated that water-exchange depends mainly on the hydrodynamic effect, irrespective of the presence of the mound.

4.2. Ecological role of the mound

During the egg-tending periods, female *V. longipinnis* constructed and maintained the
mound at the expense of their feeding. Why do females perform costly mound construction and maintenance behavior after spawning? Removals of the mound and of the paired female on the day of spawning led to higher rates of egg-desertion by males. Animal brood desertion will partly depend on the costs of parental care affecting future success of the parent (e.g., reduction in feeding and mating opportunities or decline in physical condition, Clutton-Brock, 1991). Removal of the mound induces low DO condition in the burrow (see Section 4.1), and may cause an increase of parental costs of males because frequency and duration of male egg-care (fanning) increases with decreasing DO level in the burrow (Takegaki and Nakazono, 1999c). In fact, on the day after removal, DO values near low tide were significantly lower in the egg-deserted burrows (measured before desertions) than in the burrows without desertion. These results suggest that male egg-desertion after mound removal was caused by the increased parental costs of males. Although our aquarium experiments found that males can temporarily care for eggs under extreme hypoxic conditions (below 1.0 ml l$^{-1}$, Takegaki and Nakazono, 1999c), continued hypoxia led to desertion by some males before hatching (Takegaki, unpublished data). Thus, the egg-desertion in this species seems not to be a simple escape from absolute low DO water in the burrow, but to be a reproductive tactic toward the increase of parental costs. Jones and Reynolds (1999) demonstrated that egg-tending males of the common goby, Pomatoschistus microps, lost more weight in low oxygen treatments than control fish during the first spawning, and were more likely to abandon eggs during the second spawning. Oxygen deprivation by egg-tending V. longipinnis males and/or eggs was also suggested by the changes of fanning style of males. After removal of the mound, some egg-tending males emerged from the burrow and fanned at the burrow entrance, whereas males typically remain within the burrow during the egg-tending period. Similar fanning behavior by male V. longipinnis has been observed under hypoxic conditions in an aquarium (Takegaki and Nakazono, 1999c). Probably, this fanning style may increase ventilation into the burrow and thus DO concentrations inside.

In some animals, parents with a small clutch are more likely to desert than those with a large clutch (Clutton-Brock, 1991), because the costs of caring for a small clutch may exceed the expected reproductive benefits of a small clutch. Since larger female V. longipinnis spawn more eggs and a male tends one clutch at a time, the number of tending eggs depends on female body size (Takegaki and Nakazono, 1999a). However, there was no significant differences in partner size between those males that deserted and those males that tended eggs. Therefore, it is unlikely that egg-desertions in this study were affected by clutch size on the assumption that female body size determine clutch size.

Removals of the female alone also led to higher desertion rate than usual, even though the mound remained over the burrow. After removal of the female, the mound, without the female to maintain it, gradually collapsed by wave action, tidal currents and foraging of benthic fishes. Moreover, the surface of the mound was covered with planktonic material. Due to the striking changes in these mounds in the field, we could easily discriminate between the well-maintained mound typical of an egg-tending burrow versus the non-maintained mounds on a burrow after hatching. Takegaki et al. (1999), using flume experiments, demonstrated that such a lower and silted mound has lower
water-exchange efficiency because of the decrease of flow velocity (pressure) difference between the summit of the mound and another burrow opening, and the decrease of permeability of the mound, respectively (see also Mori et al., 2000). Thus, such a mound of poor quality may do little to promote water-exchange in the burrow and, as a result, lead to egg-desertion of males through the increase of parental costs. In the absence of paired females, some egg-tending males emerged from the burrow temporarily to maintain the mound as females did. These results indicate that the females' mound maintenance behavior during the egg-tending period has an important role in the success of parental care of males. Similar parental style has been reported in other *Valenciennia* species (Shiobara and Tanaka, 1995; Reavis, 1997) and crab-eye goby *Signigobius biocellatus* (Hudson, 1977): a male performs egg care within a burrow and the paired female maintains the egg-tending burrow from outside. However, no adaptive explanation for the female's burrow maintenance behavior was offered in these species.

Most gobiid fishes make burrows using various substrata, and have life-styles based on the burrows. Especially, in the breeding season, burrows are used for spawning and egg tending site. Understanding of function and ecological significance of burrow structure, as shown in this study, may furnish useful clue for behavioral study of gobiid fish.

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