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Density-dependent effect on reproductive behaviour of *Lysmata amboinensis* and *L. boggessi* (Decapoda: Caridea: Hippolytidae)

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We compared the reproductive behaviours of two protandric simultaneous hermaphroditic species (*Lysmata amboinensis* and *L. boggessi*) that belong to two groups of *Lysmata* shrimp with different morphology, geographical distribution, and density. *Lysmata amboinensis* occurs in tropical waters at low population densities, and *L. boggessi* is found in aggregation in sub-tropical and temperate areas. Reproductive behaviour of *L. boggessi* under two densities and *L. amboinensis* in different habitats were compared. Results show that *L. amboinensis* was much less active during mating than *L. boggessi*. Male shrimp of *L. amboinensis* did not display obvious pre-copulation behaviour. They also took significantly longer to transfer spermatophores and lay eggs after mating than *L. boggessi* shrimp did. For *L. boggessi*, moulting time of female shrimp, copulation time and the interval between moulting and mating were significantly shorter when three male shrimp were present than when only one male shrimp was present. Our study suggests that the reproductive behavioural differences in the two shrimp species are possibly the results of density-dependent effect.

INTRODUCTION

It has been well known that behavioural development of a species is determined by both genetic and environmental factors (e.g. reviewed by Alcock, 2001). Density plays a significant role in the evolution of characteristics within populations (reviewed by MacArthur & Wilson, 1967) and affects a number of processes, such as competition (e.g. reviewed by Brown, 1964), population regulation (e.g. Hopper & Crowley, 1996), territoriality (e.g. Elliott, 1994), and behaviour (e.g. Simmons, 1986; Woolbright et al., 1990; Hopper & Crowley, 1996; Moksnes, 2004). Many theoretical studies (e.g. Anderson, 1971; Charlesworth, 1971; Anderson & Arnold, 1983) have predicted, and empirical studies (e.g. Sokolowski et al., 1997) have verified that behavioural polymorphism caused by density-dependent selection is heritable. For example, two types of foraging behaviours in *Drosophila melanogaster* larvae are density-dependently selected (Sokolowski et al., 1997). On the other hand, many density-dependent behaviour changes may be due to phenotypic plasticity (e.g. Greenfield & Shelley, 1985; Woolbright et al., 1990; deRivera et al., 2003). For example, males of woodfrog (*Rana sylvatica*) are less active in the low-density aggregation (Woolbright et al., 1990), and both male and female fiddler crab, *Uca beebei*, alter their search rate for mates in response to density change (deRivera et al., 2003).

A fundamental task in ecology and evolution is to understand the origin and maintenance of biological diversity. Although effect of density on intraspecific behaviour has been well known, information about whether interspecific variation in behaviour is density-related is limited. The primary aim of this study was to investigate whether the reproductive behaviours of two *Lysmata* species that usually occur at different densities is density-associated.

Shrimp in the genus *Lysmata* not only attract the interest of aquarium hobbyists because of their striking colour and functions, but also of biologists because they have a rare and unique reproductive system among the decapod crustaceans, protandric simultaneous hermaphroditism (PSH) (Bauer, 2000). A shrimp matures first as a functional male having male external characteristics and may later change to the euhermaphrodite-phase (EP), termed female-phase by Bauer and colleagues, or simultaneous hermaphrodite by Calado and collaborators) with both male and female functions. Intermoult EP shrimp that functions as a male is able to mate with newly moulted EP shrimp that plays the female role. In *L. wurdemanni* (Gibbes, 1850) and *L. boggessi* (a new species, previously recognized as *L. rathbunae*, ref. Rhyne & Lin, 2006), most male-phase (MP) shrimp pass through four transitional phases (i.e. four transitional moults) to become EP when they reach about 23.0 mm in total length (5.0–6.0 mm in carapace length), as external male characteristics gradually disappear (Zhang & Lin, 2005). *Lysmata amboinensis* is also a PSH species (Fiedler, 1998) that changes from MP to EP at about 36.0 mm total length (8.6 mm carapace length) (D. Zhang, unpublished data).

The *Lysmata* shrimp may be an ideal model to examine whether a difference in reproductive behaviour is associated with density because there is a distinct dichotomy in

Table 1. *Summary of differences in mating behaviour of male shrimp toward female shrimp between* Lysmata amboinensis *and* L. boggessi. *See the text for detail description of the behaviours.*

	Pre-moult female shrimp	Post-moult female shrimp
L. amboinensis		
10-l bucket	No pre-copulation behaviour.	No chase; male and female shrimp may stay close but male shrimp seldom copulated with female shrimp immediately after female moulting.
75-l tank	Followed within 30 min before female moulting. Male shrimp started following 1–5 min after female shrimp moved away. Not always approached and followed female shrimp.	
L. boggessi		
1 male:1 female	Pre-copulatory could be divided into three phases. Pre-copulatory behaviour begins as early as 8 h before the female shrimp moults. Within 30 min before moulting, male always approached, followed and contacted the fe-	Chase or stayed aside female shrimp. Male shrimp copulated with female shrimp as soon as female shrimp completed moulting, and finished copula-
3 male:1 female	male; and chased female 1–2 min before female moulting.	tion sooner when 3 male shrimp were present than when only 1 male shrimp was present.

sociobiology of *Lysmata* species. Low density/pair-living species (e.g. *L. amboinensis* (De Man, 1888), *L. debelius* Bruce, 1983 and *L. grabhami* (Gordon, 1935)) live in tropical waters and are specialized fish cleaners; while group-living species (e.g. *L. boggessi*, *L. seticaudata* (Risso, 1816), and *L. wurdemanni*) live mostly in sub-tropical and temperate areas and are unspecialized, facultative fish cleaners (Wirtz, 1997; Fiedler, 1998; Bauer, 2000). Mating behaviour of *L. wurdemanni* has been well studied (Bauer & Holt, 1998; Bauer, 2002; Zhang & Lin, 2004). Similar behaviour has also been observed in *L. boggessi* (Zhang & Lin, 2006). Male mating tactics in *L. wurdemanni* and *L. boggessi* can be classified as 'pure searching', since they are continuously 'on the prowl' for a receptive female (Correa & Thiel, 2003). When one is encountered, copulation occurs almost immediately after a brief interaction (Bauer & Holt, 1998; Bauer, 2002; Zhang & Lin, 2004). Several pre-copulatory behaviours of *L. amboinensis* have been described based on observations of one pair (Fiedler, 2000). It seems that male-role *L. amboinensis* do not actively search for female-role shrimp as *L. wurdemanni* and *L. boggessi* do. This behavioural difference might be the results of adaptation to their respective social environment (density), i.e. low male competition at low density causes inactive pre-copulatory behaviour. Within species, effects of denstity and/or operational sex ratio on reproductive activities have been demonstrated in many taxa, such as insects (e.g. Greenfield & Shelley, 1985; French & Cade, 1989; Cade & Cade, 1992), and crustaceans (e.g. Debuse et al., 1999; deRivera et al., 2003), and fish (e.g. Jirotkul, 1999a,b).

In this study, two hypotheses were tested: (1) male *Lysmata amboinensis* do not display obvious pre-copulatory behaviour as *L. boggessi* do (approach, follow and chase); (2) reproductive behaviours of *L. boggessi* are different when a female-role shrimp is with three versus one male-role shrimp.

MATERIALS AND METHODS

This study was carried out at the Florida Institute of Technology's Vero Beach Marine Laboratory from December 2004 to April 2005. Juvenile *Lysmata amboinensis* shrimp were purchased from a marine life importer and were originally collected in Bali, Indonesia. The shrimp were kept in pairs in 75-l flow-through maintenance tanks, because the shrimp display aggressive behaviour (Fiedler, 2000) that may lead to mortality when more than two shrimp are housed in a tank without shelter (D. Zhang, personal observation). They were fed with squid and frozen adult *Artemia* sp. once a day. The same water temperature (24.5–25.5 °C), salinity (35 ppt) and photoperiod (14 h light and 10 h dark) were maintained for both *L. amboinensis* and *L. boggessi* (see below). The shrimp were grown to EP before being used for the study. Sizes of EP shrimp used for the observation were 36.0–62.0 mm total length.

Lysmata boggessi shrimp (between 26.0 and 40.0 mm in total length) were collected from the Florida Keys, Florida, USA and housed in 20-l maintenance tanks with flow-through seawater. The shrimp were fed in excess frozen adult *Artemia* sp. twice daily.

Lysmata amboinensis and *L. boggessi* spawn once every 15 and 12 d, respectively, under about 25 °C (D. Zhang, personal observation). Eggs are attached beneath the abdomen of the EP shrimp that usually moult within 24 h after releasing the larvae. Recently moulted EP shrimp are receptive to mating as female for several h. The EP shrimp function as male during inter-moult. To facilitate observation of mating behaviour, moult cycle of individual EP shrimp served as female-role shrimp (simplified as female thereafter; MP or EP shrimp served as male-role shrimp was simplified as male) that was used for mating assay was recorded in advance.

Our preliminary study found that within the size range used in the present study, size difference of male and female shrimp did not affect the mating behaviour. Therefore size effect was not considered in this study.

Identification of mating behaviour

Mating behaviour was identified according to the following criteria (Zhang & Lin, 2004) and analysed. The suitor (male)

Table 2. *Quantitative comparison of reproductive behaviours (mean±SD, N=15) of* Lysmata amboinensis *and* L. boggessi, *and of* L. boggessi *at different densities.*

	MT	CT	IMM	IMS
1. *L. amboinensis* (10-l)	55.9 ±6.5 (t=6.454)[a]	10.8 ±4.8 (t=2.249)[a]	77.0 ±78.8 (t'=3.692)[a]	9.3 ±0.6 (t=31.254)[a]
2. *L. amboinensis* (75-l)	56.8 ±6.1 (t=0.406)[c]	9.3 ±3.7 (t=0.934)[c]	79.6 ±82.8 (t=0.089)[c]	9.4 ±0.5 (t=0.524)[c]
3. *L. boggessi* (1M and 1F)	37.9 ±8.7 (t=3.614)[b]	7.4 ±3.3 (t=2.691)[b]	1.9 ±1.9 (t=2.505)[b]	3.3 ±0.5 (t=0.412)[b]
4. *L. boggessi* (3M and 1F)	27.4 ±7.1	4.8 ±1.7	0.5 ±0.7	3.4 ±0.5

MT (s), moulting time; CT (s), copulation time; IMM (s), interval between moulting and mating; IMS (h), interval between mating and spawning. M refers to euhermaphrodite-phase shrimp functioning as male and F refers to euhermaphrodite-phase shrimp functioning as female. [a], Student's *t*-test values for statistic comparison between *L. amboinensis* and *L. boggessi* (1 and 3) at the same sex ratio (1:1) in 10-l container (IMM were compared using Welch's approximate *t*-test); [b], Student's *t*-test values for statistic comparison between the two densities (1 M:1 F vs 3 M:1 F) within *L. boggessi* (3 and 4); [c], Student's *t*-test values for all parameter comparisons within *L. amboinensis* between 10-l buckets and 75-l tanks (1 and 2). df=28 for all comparisons, compare calculated *t* values with $t_{0.05, 28}$=2.048, $t_{0.01, 28}$=2.763, $t_{0.001, 28}$=3.674 for significance level.

would approach and follow the pre-moult female shrimp. This behaviour begins as early as 8 h before the female shrimp moults, and is the most intense within 2 min of the moulting. A male shrimp would approach the female and explore her (via contact) repeatedly with his head/antennules. The behaviour usually lasts from several seconds to minutes. Some male shrimp stay beside the females and mate with them immediately after the females complete the moulting. Pre-copulatory behaviour of male could be divided into three phases: approach (male approach female, and stay aside and face her for a brief period, usually less than 15 s, but do not follow female if she moves away); approach and follow (male approach, and follow female, but may not follow female every time when she moves away); chase (male follow female closely and consistently, especially when female swim quickly within 2 min prior to moulting).

Male shrimp may follow newly moulted female shrimp consistently after touching the females with antennae/antennules, and grasp the females and bring their ventral surfaces into contact. Normally there is no interaction between male and female shrimp if they encounter each other more than 8 h before the female shrimp moults (Zhang & Lin, 2004).

Mating behaviour of Lysmata amboinensis *and* L. boggessi

For each species, two EP shrimp were housed in a 10-l white bucket with diameter of 23 cm, one about to moult served as female, and the other as male. Mating behaviour in 15 replicate buckets for each species was recorded with a Sony video camcorder using fluorescent illumination and analysed. Behaviour from 10 h before the female moulting to mating completion was recorded. We observed reproductive behaviour under light, because both species can moult and mate during daytime (D. Zhang, personal observation). Also, mating behaviour of a related species, *Lysmata wurdemanni* under light (Zhang & Lin, 2004) does not differ from that observed in the dark under infrared light (Bauer & Holt, 1998). No food was supplied during the observation because

mating shrimp stop feeding several hours before the female moulted (D. Zhang, personal observation).

Effect of density/habitat size

For *Lysmata amboinensis*, because of aggressive behaviour and pair-bonded living (Fiedler, 2000; D. Zhang, personal observation), density effect was not tested. Instead, mating behaviour in the 75-l tank was observed and compared with that in the 10-l bucket to examine the behavioural difference in habitats of different sizes.

For *Lysmata boggessi*, mating behaviour at two densities was observed. Three male were housed with one female shrimp in each of the 15 10-l white buckets. The mating behaviour was taped with a Sony video camcorder using fluorescent illumination and analysed. The results were compared with those of the 1 male:1 female ratio (see above).

Statistics

Moulting time of female shrimp, copulation time, interval between moulting completion and mating initiation, interval between mating completion and spawning, and moult cycle (interval between two complete moultings) were measured (mean±SD). Student's *t*-test was employed to compare these measurements between the two habitats within *Lysmata amboinensis*, and the two densities within *L. boggessi*. All measurements between *L. amboinensis* and *L. boggessi* in 10-l buckets are also compared. If the homogeneity of variance assumption was violated, Welch's approximate *t*-test was used (Sokal & Rohlf, 1995).

RESULTS

Mating behaviour of Lysmata amboinensis

In the 10-l buckets, male shrimp of *Lysmata amboinensis* did not display any obvious searching behaviour (approach, follow and chase) before or after the female shrimp moulted (Table 1). Some male and female shrimp stayed out of reach of each other's antenna/antennule, and some stayed together

without the contact behaviour as shown in *L. boggessi* (male shrimp face female shrimp). Moulting took 45–70 s (55.9 ±6.5 s, N=15) for the female shrimp (Table 2). Copulation lasted 6–20 s (10.8 ±4.8, N=15) (Table 2) and took place within 0–280 s (77.0 ±78.8 s, N=15) after the female shrimp moulted. Of the 15 replicates, only in one case mating took place immediately (<1 second) after the female shrimp moulted; for the rest, mating occurred within 35–280 s after the female shrimp moulted.

In the 75-l tanks, male and female shrimp generally stayed together on the outlet pipe. Within 30 min before the female shrimp moulted, the male shrimp would normally search for the female shrimp if the female shrimp moved away. Male shrimp started searching 1–5 min after the female shrimp moved. After catching up with her, the pair would just stay together. The male shrimp never displayed active approach and followed as *L. boggessi* did (see below) before the female shrimp moulted, and the female shrimp did not flee before moulting. Moulting of the female shrimp took 45–64 s (56.8 ±6.1 s, N=15) (Table 2). Mating took place within 32–292 s (79.6 ±82.8 s, N=15) after the female shrimp moulted. Before copulating, some male shrimp stayed aside the female shrimp for a while, and some even wandered away after antennular contact before coming back. Copulation lasted 5–15 s (9.3 ±3.8 s, N=15) (Table 2). All the reproductive behavioural parameters measured were not significantly (for individual *t* value see Table 2; df=28; *P*>0.05) different from those observed in the 10-l buckets.

Mating behaviour of Lysmata boggessi

Pre-copulatory behaviour of *Lysmata boggessi* could be divided into three phases (approach, follow and chase). Male shrimp might approach and follow the female shrimp as early as 8 h before the female shrimp moulted, but most shrimp did so beginning 2–5 h before the moulting. The male shrimp swam close to the female shrimp, and touched it with antennules/head repeatedly. Within 30 min before the female shrimp moulted, most male shrimp always approach and follow the female shrimp. Within 1–2 min before moulting, the female shrimp actively swam forward or backward to escape the following male shrimp. Some male shrimp caught up with the female shrimp and waited beside them. They would mate as soon as the female shrimp moulted. Sometimes mating took place even before the female shrimp completed the moulting. In addition to approach/ follow, some male shrimp would mount on the dorsum of the female shrimp for a few seconds (perching—Bauer, 2002), as observed in other caridean shrimp (Kamiguchi, 1972; Bauer, 1976). If male shrimp did not catch up with the female shrimp before the female shrimp moulted, they may chase the female shrimp after the moult. After moulting, the female shrimp swam around. Once male shrimp detected the newly moulted female shrimp with antennules/antennae, they immediately swam close to the female shrimp and tried to grasp them to mate. However, some female shrimp fled, followed by the chasing male shrimp. Mating occurred from 0 to 6 s (1.9 ±1.9 s, N=15) after the female shrimp moulted under 1 male:1 female ratio, significantly (*t*=2.505; df=28; *P*<0.05) longer than that under 3 male:1 female ratio (0–2 s, 0.5 ±0.7 s, N=15) (Table 2). Under 1 male:1 female ratio,

most (11/15) male shrimp grasped the female shrimp and turned their body under the female shrimp to position their thoraco-abdominal junction beneath the female shrimp's first abdominal sternite. The other male shrimp (4/15) positioned themselves beside or above the female shrimp. The process of spermatophore transfer took 4–16 s (7.4 ±3.3 s, N=15) under 1 male:1 female ratio, significantly (*t*=2.691; df=28; *P*<0.05) longer than that under 3 male:1 female ratio (4.8 ±1.7 s, N=15) (Table 2).

Some female shrimp actively fled to escape the chasing male shrimp within 2 min before moulting. Under 1 male:1 female, the female shrimp spent 20–52 s (37.9 ±8.7 s, N=15) in moulting, significantly (*t*=3.614; df=28; *P*<0.001) longer than that under 3 male:1 female ratio (range of 19–43 s, 27.4 ±7.1 s, N=15) (Table 2). When the male shrimp were very active or more than one male shrimp interacted with the female shrimp during moulting, the female shrimp often quickly got out of the old exoskeleton by tail-flipping. The female shrimp would refuse to mate more than once, even when multiple male shrimp were presented.

Comparisons of mating behaviours of two species

Major differences of mating behaviour between the two species are summarized in Tables 1 and 2. Male *Lysmata boggessi* displayed the distinct three phases of pre-copulatory behaviour (see Materials and Methods) and chased newly moulted EP shrimp. In contrast, male *Lysmata amboinensis* did not display any obvious pre-copulation behaviour and did not chase newly molted EP shrimp when they were held in the small habitat (10-l bucket). In the large habitat (75-l tank), follow behaviour of the males was only detected within 30 min before female moulting. However, male shrimp did not follow female shrimp immediately after she moved, only started following 1–5 min after female shrimp moved away and not always approached and followed female shrimp.

Post-mating

Female shrimp of *Lysmata amboinensis* had significantly (*t*=31.254; df=28; *P*<0.001) longer intervals from mating to egg laying (9.3 ±0.6 h in 10-l tank, N=15; 9.4 ±0.5 h in 75-l tank, N=15) than those of *L. boggessi* (3.3 ±0.5 h under 1 male:1 female, N=15; 3.4 ±0.5 h under 3 male:1 female, N=15) (Table 2).

DISCUSSION

Results from this study show that *Lysmata amboinensis* and *L. boggessi* displayed different reproductive behaviours. *Lysmata amboinensis* shrimp were much less active during mating than *L. boggessi*. Male *L. amboinensis* did not display obvious pre-copulatory searching behaviour as *L. boggessi* did, and seldom immediately grasped newly moulted female shrimp for copulation even after physical contact by antennules/antennae. *Lysmata boggessi* displayed different reproductive behaviours when one or three male shrimp were present, suggesting that density is a force shaping the reproductive behaviours.

One of the causes for behavioural difference between *Lysmata amboinensis* and *L. boggessi* might be their different living habits and environments. *Lysmata boggessi* and *L.*

wurdemanni, a closely related species which displayed similar mating behaviour to *L. boggessi* (Bauer & Holt, 1998; Bauer, 2002; Zhang & Lin, 2004), aggregate in small tide pools and rock jetties in the wild (Bauer, 2000; D. Zhang, personal observation), and males vigorously search (follow and chase) the pre- and post-moult female shrimp. *Lysmata amboinensis* is often found in isolated pairs in discrete cavities shared with eels and other cleaning hosts in the wild (Fiedler, 2000). Similarly, a closely related species, *L. grabhami*, also live in pairs with sea anemone or moray eel to reduce predation risk (Wirtz, 1997). Male *L. amboinensis* did not display any pre-copulatory behaviour in the 10-l buckets. This may be a reflection of the long-term pair-bonded living in cavities where there is no competition for mate and shrimp are confined in close proximity, thus no need to search for the mate. This may be supported by the behaviour in a larger habitat (75-l tank) in which male *L. amboinensis* did display following behaviour. Moreover, no search or reduced search rate may also be an adaptive response to living at high levels of predation risk. This phenomenon has been demonstrated in the fiddler crab, *Uca beebei*, that reduced their search rate for mate when exposed to high levels of predation risk (deRivera et al., 2003).

Although male *Lysmata amboinensis* in the 75-l tanks did follow the female shrimp within 30 min before the female shrimp moulted, the behaviour differed from that of *L. boggessi*. Male *L. boggessi* always approach and follow the female shrimp, especially within 30 min before the female shrimp moulted (Table 1). Moreover, male-role *L. amboinensis* in both 10-l buckets and 75-l tanks did not mate with newly moulted female shrimp immediately after detecting their presence. This is also different from *L. boggessi* and *L. wurdemanni*. These behavioural differences between the species may be at least partly caused by different social environments. Population density is an important variable that can affect the intensity of competition for resources (e.g. Brown, 1964). Effects of density on reproductive behaviour have been reported in many taxa, such as insects (e.g. Greenfield & Shelley, 1985), decapod crustaceans (e.g. deRivera et al., 2003), frog (Woolbright et al., 1990), and fish (e.g. Jirotkul, 1999b). For example, males of woodfrog are less active in the low-density aggregation (Woolbright et al., 1990). In this study, we found that group size significantly affected the mating behaviour of *L. boggessi*, suggesting that density (therefore competition) has a strong influence on the mating behaviour. The phenotypic plasticity of mating behaviour of *L. boggessi* might predict that mating behaviour of *L. amboinensis* is a result of a long-term enforcement under low density. Even if we do not know whether the mating behaviour of *L. amboinensis* is heritable or phenotypically plastic, and if the ancestors of *Lysmata* shrimp were living at low or high density, our results suggest that interspecific variation in mating behaviour is density-dependent, i.e. density plays a key role in mating behavioural development in *Lysmata* shrimp. Furthermore, these results predict that species of *Lysmata* shrimp living at low density probably diverged from an ancestor living at high density. When a species that originally lives at high density changed to low density living, over time it could be expected that pre-copulatory behaviour of the species gradually changed. It is difficult to imagine that *L. boggessi* comes from a low-density living ancestor like *L. amboinensis* that fights intensively when more than two shrimp live together. The latest molecular evidence supports our suggestions (A. Rhyne, in preparation).

The lack of competition from other males may eliminate the need for pre-copulatory behaviour in *Lysmata amboinensis*. The adaptive value of no pre-copulatory behaviour is significant as the behaviour can be costly. In the simultaneous hermaphroditic pond snail, *Lymnaea stagnalis*, copulation significantly reduces the egg-laying rate (Visser et al., 1994). Pre-mating strugglings (a pre-copulatory behaviour) of the female water striders, *Aquarius remigis*, consume an average 126% more energy compared to non-struggling females (Watson et al., 1998). Aggression and calling is diminished at high population densities in the field cricket *Gryllus bimaculatus*, because males would benefit by silently searching for females (Simmons, 1986).

Pre-copulation behaviour of male *Lysmata wurdemanni* and *L. boggessi* is mediated by distance pheromone (Zhang & Lin, 2006). A similar pheromone may also exist in *L. amboinensis* (Fiedler, 2000). Behavioural difference between *L. boggessi* and *L. amboinensis* may be caused by the difference in olfactory sensitivity. Number of aesthetascs, sensory hair on the outer flagella of the antennules, in *L. amboinensis* is significantly lower than in the high-density species *L. boggessi* (D. Zhang, unpublished data). The number of aesthetascs may be associated with the sensitivity of shrimp to distance pheromone (Beltz et al., 2003). Males of *L. boggessi* with a high number of aesthetascs displayed pre-copulatory behaviour earlier, suggesting that sensitivity of the olfactory system is associated with the number of aesthetascs (D. Zhang, unpublished data).

Behavioural evidences indicate that both distance and contact pheromones are involved in the mating of *Lysmata wurdemanni* (Zhang & Lin, 2006). Mating behaviours of *L. boggessi* are similar to those found in *L. wurdemanni*, suggesting that both pheromones are involved as well. Pre-copulatory behaviour (searching) is triggered by distance pheromone, and male shrimp recognize recently moulted female shrimp by contact pheromone. Contact pheromone may also be present in *L. amboinensis*, although only one male shrimp immediately responded to newly moulted female shrimp after contacting by antennules/antennae. That male shrimp of *L. amboinensis* did not grasp the newly moulted female shrimp to mate immediately after physical contact may also be an adaptive response to low density/competition.

Copulated female shrimp did not spawn immediately, possibly because the egg extrusion requires a calcified exoskeleton. In *Lysmata wurdemanni*, when female shrimp copulated three hours after moulting, the eggs would be extruded immediately (D. Zhang, personal observation). Female shrimp of *L. amboinensis* had significantly (t=31.254; df=28; P<0.001) longer intervals from mating to egg laying than those of *L. boggessi*, suggesting that *L. amboinensis* might take longer to calcify its exoskeleton than *L. boggessi*.

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