Original Article

Behavioural strategy of the ectosymbiotic crab (*Sestrostoma* sp.) during ecdysis of the crab and its upogebiid shrimp host

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Abstract

Moulting is essential for crustacean growth, but is one of the causes of mortality, because a crustacean cannot move during and just after its ecdysis. In the cases of ectosymbiotic crabs, escape from the host's hostile response may also be a problem during its own ecdysis. In this study, *Sestrostoma* sp. (Varunidae), an ectosymbiotic crab which clings to the ventral abdomen of upogebiid shrimps with legs that can walk, was studied to clarify how the crab moults and maintains association with the host. Five cases of crab ecdysis were observed, where the crab moulted with its legs clinging to the host abdomen, without detaching from the host body. Time required for moulting was 14–21 min. Shedding of the old exoskeleton (active phase) took only 40–59 s. *Sestrostoma* sp. detached from the host abdomen and waited in the burrow tube during shrimp ecdysis. The crab then reattached at the same location on the host when shrimp moulting was complete. Our results suggest that *Sestrostoma* sp. are able to maintain a symbiotic relationship with the same shrimp host after its own ecdysis as well after ecdysis of its host.

Introduction

Moulting is an essential behaviour for growth in individuals which are covered with their exoskeleton, such as crustaceans. Body expansion occurs by water absorption during moulting (Philippen *et al.*, 2000). Moulting is composed of two phases: a passive, followed by an active phase (Philippen *et al.*, 2000). In the passive phase, the thoraco–abdominal membrane is ruptured by body expansion. The old exoskeleton is shed in the active phase. During ecdysis, especially in the active phase, crustaceans cannot move (Waddy *et al.*, 1995). In the case of *Homarus americanus*, the lobster loses mobility during the active phase for 10–20 min (Waddy *et al.*, 1995). After moulting, the soft body gradually becomes harder. In the blue swimming crab, *Portunus pelagicus*, the time required for carapace hardening is between 9 and 17 h (Azra *et al.*, 2019).

Ecdysis is one of the causes of crab mortality because of failure to complete, predation or cannibalism (Ryer *et al.*, 1997; Bleakley, 2018; Azra *et al.*, 2019; de la Cruz–Huervana *et al.*, 2019). Crabs cannot move and defend themselves against, or flee from predators, during and after moulting. In general, crabs moult in a safe space such as in burrows or in seagrass beds, which provide a refuge from predation or cannibalism (Ryer *et al.*, 1990; Laidre, 2018; Ortega *et al.*, 2019). In the case of endosymbiotic crabs, the host may provide a safe space for the crab to moult. For example, the pea crab (*Arcotheres* sp.), an endoparasite of the sessile bivalve, *Barbatia virescens*, moults inside the host shell (Watanabe & Henmi, 2009). In the case of ectosymbiotic crabs, the crab usually benefits from the host, obtaining nutrients and protection against predators, but the crab may face the severe risk of dropping off the host's body during the crab's own ecdysis. Ectosymbiotic crabs may therefore have evolved to prevent detachment during their own ecdysis. To the best of our knowledge, however, there has been no research on moulting behaviour of ectosymbiotic crustaceans from this perspective.

The shrimps of the genus *Upogebia* construct typically Y- or U-shape burrows in muddy sediment (Dworschak, 1983; Griffis & Suchanek, 1991; Nickell & Atkinson, 1995). The shrimps create water currents with their rhythmically stroking pleopods so that oxygen-rich seawater and organic substances such as phytoplankton or detritus flow into the burrows (Dworschak, 1987; Dworschak *et al.*, 2012). They feed mainly on suspended matter using the dense setae on the first and second pereiopods (Dworschak, 1987; Nickell & Atkinson, 1995). It is known that various symbionts inhabit upogebiid burrows or bodies (MacGinitie, 1930, 1935; Ross, 1983). Symbionts of upogebiid shrimps can be divided into ectosymbionts and burrow co-habitants (burrow symbionts) (Itani, 2004). In the western Pacific, it is known that ectosymbionts include bopyrid isopods, crabs and bivalves (Kato & Itani, 1995; Itani, 2001, 2004) and burrow symbionts are shrimps, crabs, copepods, phoronids, bivalves, polychaetes and gobies (Miya, 1997; Anker *et al.*, 2001; Itani, 2001; Sato *et al.*, 2001; Kinoshita, 2002; Itoh & Nishida, 2007; Nara *et al.*, 2008; Kinoshita *et al.*, 2010; Henmi & Itani, 2014*a*; Inui *et al.*, 2018).

The varunid crab *Sestrostoma* sp. is an ectosymbiotic crab associated with upogebiid shrimps, clinging on to the host abdomen with legs that can walk. This species is the only

known decapod crustacean symbiotic with another decapod and has a parasitic life cycle because it has been confirmed to feed on host tissue (Itani, 2001). *Sestrostoma* sp. can walk freely and grasp the host again after the crab has become detached from the host; hence, there is no decrease in locomotion ability (Itani, 2001). The crab genus *Sestrostoma* includes both burrow symbionts and an ectosymbiont. A congeneric crab (*S. toriumii*) is a co-habitant in the upogebiid shrimp burrows, where the crab is often expelled from the burrow by the shrimp (Itani, 2001; Henmi & Itani, 2014b). This crab has developed a 'pass-under' (ventral evasion) behaviour to escape the hostile response of the host species (Henmi et al., 2017). Thus, in the case of the ectosymbiotic *Sestrostoma* sp., clinging is an adaptive mechanism to avoid host harassment (Itani, 2001).

As described, *Sestrostoma* sp. should behave appropriately to maintain symbiosis with the host during its own ecdysis. We have three hypotheses about the ecdysis of *Sestrostoma* sp.; (1) *Sestrostoma* sp. moults with its body clinging to the host abdomen; (2) *Sestrostoma* sp. detaches from the host and moults in the burrow; or (3) *Sestrostoma* sp. leaves from the host burrow and moults outside. However, the third hypothesis is improbable because moulting outside will endanger the crab who usually lives inside the burrow. Because of limitations in observation methods, we recorded the moulting behaviour of *Sestrostoma* sp. in an artificial burrow, precluding the possibility of hypothesis (3).

Host ecdysis is also a potential crisis for the ectosymbionts, who can be cast off with the exuviae (Itani et al., 2002). Some symbiotic species have developed adaptive strategies to survive host ecdysis. Examples include the behavioural adaptation of the bivalve *Peregrinamor ohshimai* (Itani et al., 2002) or life cycle adaptation by the cycliophora *Symbion pandra* (Funch & Christensen, 1995). In this study, we recorded the behaviour of *Sestrostoma* sp. during host ecdysis and compared it with behaviour of other ectosymbionts. We will use the term 'symbiotic' literally, in the sense of 'living together' in this paper, after Ross (1983).

Materials and methods

Specimens were collected from the tidal flats in Uranouchi Inlet, Kochi, Japan (33°26′00.1″N 133°26′21.6″E). *Sestrostoma* sp. are symbiotic with *Upogebia sakaii* and *U. yokoyai*, both dominant burrowing species on the tidal flats. Specimens were collected using a yabbie pump (Poseidon) and sieved through a 1 mm meshed sieve. A shrimp was collected together with its symbiotic crab in one collection (one pumping), and was used as the host for subsequent observation in the aquarium. Generally, the burrow of the upogebiid shrimp has spaces for filter-feeding or changing direction, called a turning chamber (Dworschak, 1987; Kinoshita et al., 2010). In the laboratory, PVC pipes with an inner diameter of 13 mm were used as the burrow model, encased with a larger pipe (20 mm diameter) as a turning chamber(s) following Itani et al. (2002). To observe the shrimp and crab behaviour, the pipe was cut longitudinally, and fixed on a transparent acrylic plate with an adhesive. Sand was glued inside the pipe so that *Sestrostoma* sp. could walk freely. The glued pipes were exposed to running water for 24 h before using.

The burrow model was leaned against the glass surface in an aquarium (60 cm width × 30 cm depth × 35 cm height). Seawater was circulated and filtered, and aeration was added. After putting a host shrimp with its *Sestrostoma* sp., both edges of the burrow model were covered with a small net so that only seawater could enter and exit. Water temperature was kept around 25°C with salinity 25–30 psu. Dried fish food was added every 3 days into the burrow using a syringe for feeding. Before the experiment, carapace length of host shrimp (CL) and carapace width of *Sestrostoma* sp. (CW) were measured with callipers (Mitutoyo)

Fig. 1. *Sestrostoma* sp. clinging to ventral abdomen of *Upogebia sakaii*.

to the nearest 0.01 mm as an index of body size. Observations were performed from July to October in 2018 and January to February in 2020. We recorded animal behaviour with a video camera (Canon iVIS HF R21) until the shrimp or the crab moulted. Observation lasted 20.7 ± 8.3 days (mean ± SD) (N = 15).

Results

Ecdysis of the symbiont

Sestrostoma sp. usually clung ventrally to the first abdominal segment of the host (Figure 1) for the whole observation period, except in the cases where the host moulted or died. Five ecdyses of *Sestrostoma* sp. were recorded. In every case, the crab moulted with its legs clinging onto the ventral edges of the first abdominal segment of the host. The sequence of moulting behaviour in the crab was as follows (Figure 2, Supplementary video S1): (1) the thoraco–abdominal membrane was ruptured (passive phase); (2) the exuvia was pushed up diagonally forward and new body extended behind (active phase); (3) after having shed the exoskeleton, the crab still clung to the exuvium, which was still clinging to the ventral abdomen; (4) the crab moved onto the host shrimp abdomen, and clung there, after detaching its exuvium. The time required for moulting was 835–1285 s. Durations of the passive (T_p) and the active phase (T_a) were 794–1237 s and 40–59 s, respectively (N = 5; Table 1). The active phase was 3.7–6.5% of the total moulting time. After moulting, the exuvia remained attached to the host abdomen for 169–1080 s (T_e).

The symbiont at ecdysis of the host

Six ecdyses of the host shrimps were recorded. In every case, the ecdysis of the host shrimps and crabs did not coincide. The moulting of the shrimps (T_m) took 252–392 s (N = 6; Table 2). After moulting, the shrimps wriggled intensely for 445–1394 s (T_w). When the host began moulting, *Sestrostoma* sp. left the host body and stayed nearby (Figure 3, Supplementary Video S2) with one exception where the crab walked from the exuvia to the newly emerged host body, but soon detached upon host wriggling. When the shrimps were quiet and moulting was complete, *Sestrostoma* sp. returned to the ventral abdominal position on the host (Figure 3, Supplementary Video S2).

Discussion

Sestrostoma sp. moults with its body clinging onto the ventral abdominal segment of the host. During moulting, it is crucial for the symbiotic crab not to be detected by the host, because the host shrimp always cleans the burrow and often expels symbiotic animals (Itani, 2001; Henmi & Itani, 2014b; Henmi et al., 2017). The abdomen of the host may be the safest space for the crab, because the host chelipeds and the cleaning legs (fifth legs) do not touch the ventral side of the first abdominal segment
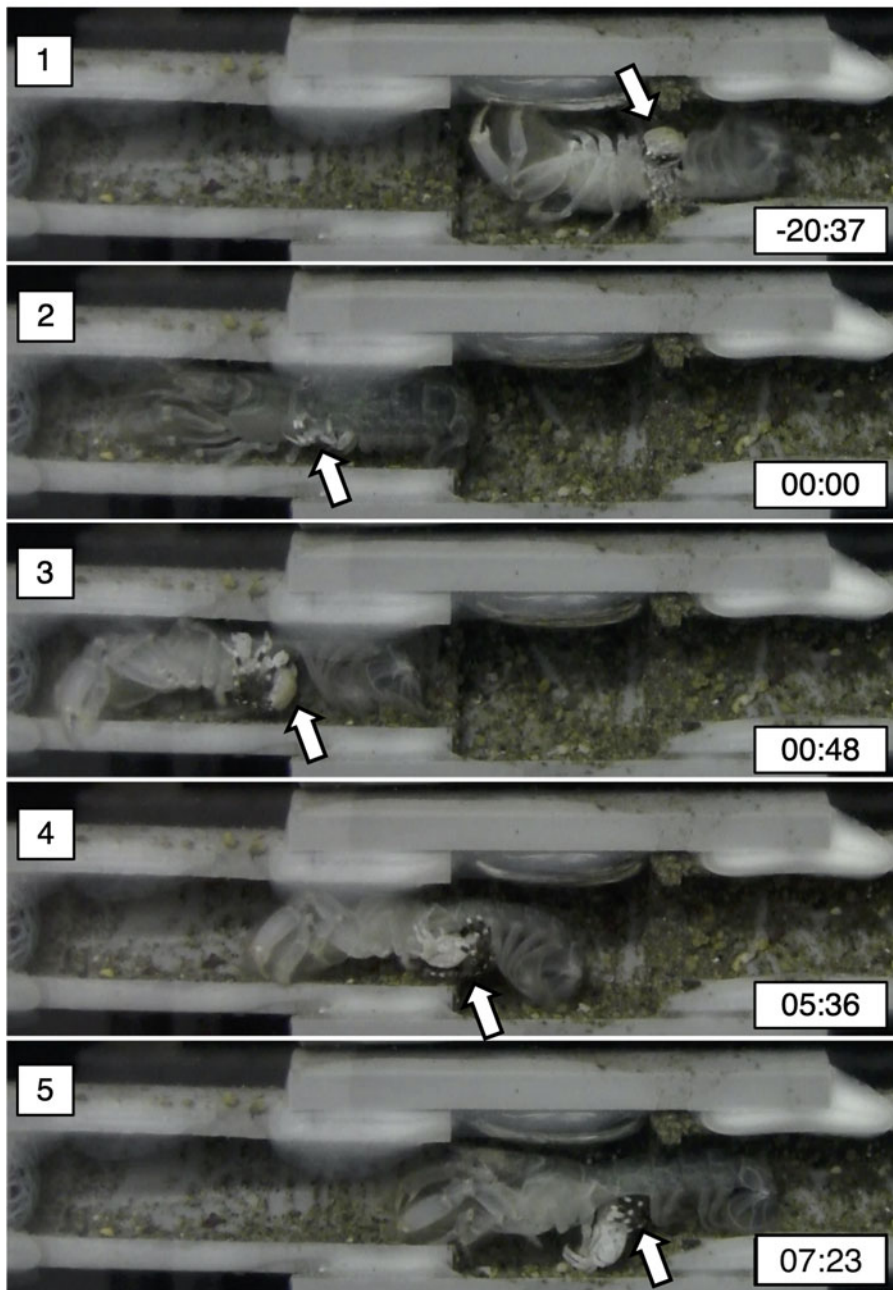
Fig. 2. Moulting behaviour of *Sestrostoma* sp. (No. 4 in Table 1). White arrows indicate *Sestrostoma* sp. (1) The thoraco-abdominal membrane of the crab was ruptured; (2) start of crab moulting (active phase); (3) end of crab moulting; (4) the crab on the exuvium; (5) the crab reattached to the same location on the host after dropping the exuvium.

Table 1. Morphological and behavioural summaries of observed ecdyses of *Sestrostoma* sp.

| No. | Host | | | *Sestrostoma* sp. | | | | | Day of observation |
	Species	Sex	CL (mm)	Sex	CW (mm)	T_p	T_a	T_e	
1	*U. sakaii*	m	8.8	m	3.3	794	41	1080	19 Jul 2018
2	*U. sakaii*	f	9.0	m	3.8	843	59	548	26 Jul 2018
3	*U. sakaii*	f	8.9	f	4.0	879	42	169	24 Aug 2018
4	*U. yokoyai*	m	11.7	f	5.0	1237	48	395	13 Oct 2018
5	*U. sakaii*	f	10.3	m	3.3	1034	40	291	26 Feb 2020
Mean			9.7		3.9	957	46	494	
SD			1.2		0.7	180	8	356	

CL, carapace length of the host shrimp; CW, carapace width of *Sestrostoma* sp.; T_p, duration of passive phase; T_a, duration of active phase; T_e, duration of time the exuvium remained attached to the host abdomen after ecdysis.

Table 2. Morphological and behavioural summaries of observed ecdysis of upogebiid shrimp with *Sestrostoma* sp.

No.	Species	Sex	CL (mm)	T_m	T_w	Sex	CW (mm)	Day of observation
1	*U. sakaii*	m	9.0	298	445	m	3.8	23 Jul 2018
2	*U. sakaii*	m	7.5	329	1081	f	4.1	24 Jul 2018
3	*U. sakaii*	m	10.8	392	1394	f	4.5	12 Aug 2018
4	*U. sakaii*	f	8.9	252	699	f	4.8	3 Sep 2018
5	*U. yokoyai*	m	8.0	261	886	m	3.6	17 Jan 2020
6	*U. sakaii*	f	10.6	315	1061	m	3.3	29 Feb 2020
Mean			9.1	308	928		4.3	
SD			1.3	51	330		0.5	

CL, carapace length of the host shrimp; CW, carapace width of *Sestrostoma* sp.; T_m, duration of shrimp moulting; T_w, duration of shrimp wriggling after ecdysis.
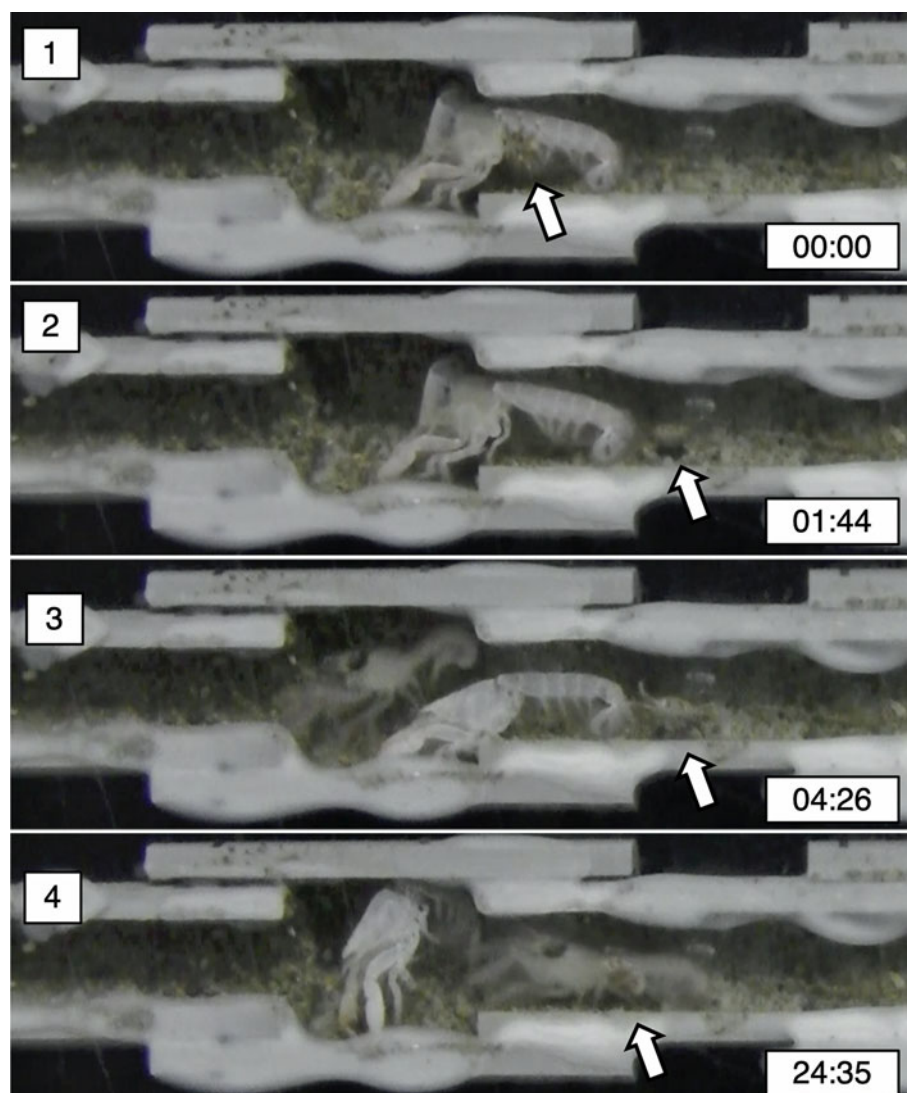
Fig. 3. Moulting behaviour of upogebiid shrimp (No. 3 in Table 2). White arrows indicate *Sestrostoma* sp. (1) At the start of shrimp moulting; (2) *Sestrostoma* sp. detached from the shrimp body; (3) at the end of shrimp moulting; (4) *Sestrostoma* sp. reattached to the same location on the host.

(Itani, 2001). It is reasonable to suggest that moulting while clinging to the host abdomen is an adaptive behaviour for *Sestrosotoma* sp., rather than moulting in the burrow after detaching from the host body.

The moulting process of *Sestrostoma* sp. is almost the same as in other crabs (Phlippen *et al.*, 2000). The time required for moulting (passive and active phase) in adult crabs is known only for *Carcinus maenas*, *Chionoecetes opilio*, *Macrocheira*

kaempferi and *Paralithodes camtschaticus*. In such species, crabs took a longer time to moult than *Sestrostoma* sp. (14–21 min): 45–90 min in *C. maenas*, 2–9 h in *C. opilio*, about 103 min in *M. kaempferi* and 11–32 min in *P. camtschaticus* (Watson, 1971; Phlippen *et al.*, 2000; Stevens, 2002; Okamoto, 2008). Rapid moulting, especially in the active phase where the crab sheds its old exoskeleton, is suitable for *Sestrostoma* sp., because the crab would otherwise be dropped off if the host moved suddenly at

that time. In the case of *C. maenas*, it took 45–50 min in the passive phase, following 5–15 min in the active phase. The active phase was 9–25% of the total moult duration (Phlippen *et al.*, 2000). Time required for the active phase of *Sestrostoma* sp. was 41–59 s (3.7–6.5%), which was much lower than that for *C. maenas*. However, it is not clear whether the length of the active phase of *Sestrostoma* sp. is short as a result of adaptive evolution of symbiosis with the shrimp. Comparing ecdysis in many crabs from a variety of phylogenetic origins is needed. What is unclear is the mechanism and function by which the exuvium of *Sestrostoma* sp. remains attached to the host abdomen after moulting.

Behaviour and strategy of the symbiont in dealing with host ecdyses has been reviewed in Itani *et al.* (2002). Among others, two bivalves show different strategies. *Pseudopythina macrophthalmensis* is a symbiotic galeommatoid bivalve associated with macrophthalmid crabs. Because this bivalve has a high locomotion ability, it is considered that *P. macrophthalmensis* can crawl from the exuvia and reattach to the host crab after host ecdysis (Kosuge & Itani, 1994). Another galeommatoid bivalve, *Peregrinamor ohshimai*, which attaches to the ventral aspect of the cephalothorax of upogebiid shrimps, crawled onto the new body of the host during host ecdysis, without becoming detached. Artificially detached *P. ohshimai* are never able to reattach to the host because of the low locomotion ability of the bivalve, whose shell shape is specialized for symbiotic life (Itani *et al.*, 2002). *Sestrostoma* sp. has a high locomotion ability and can frequently solicit another host (Itani, 2001). In ectosymbiotic animals with a high locomotion ability, host ecdysis is not a problem for their continued association. In this study, once detached from the host, the crab simply reattached to the same host individual. Because of the artificial burrow used in this study, it was not possible to determine whether the crab would change shrimp hosts during host ecdysis under natural circumstances.

This study describes the moulting behaviour of *Sestrostoma* sp. which clings to a ventral abdominal somite of the upogebiid mud shrimp. The crab moults with its legs clinging to the shrimp abdomen, hereby protected from potential hostile behaviour from the host. What is unsolved is the mechanism by which the exuvium remains attached to the abdomen. Many other crabs are ectosymbiotic with other invertebrates, cymothoid isopods attach to fish bodies, and caprellid amphipods are an epibiont associated with algae, all of which lose their host if they are detached during ecdyses. The moulting behaviour of symbiotic and parasitic crustaceans would be an interesting avenue for further research into the symbiotic life cycle of crustaceans.

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