

Host selection by *Synalpheus stimpsoni* (De Man), an ectosymbiotic shrimp of comatulid crinoids, inferred by a field survey and laboratory experiments

D. VandenSpiegel^{a,*}, I. Eeckhaut^a, M. Jangoux^{a,b}

^aLaboratoire de Biologie marine, Université de Mons-Hainaut, 19 ave Maistriau, B-7000 Mons, Belgium

^bLaboratoire de Biologie marine (CP160), 50 ave F.D. Roosevelt, B-1050 Bruxelles, Belgium

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Abstract

During a survey made on symbionts of comatulids in Hansa bay (Bismark Sea, Papua New Guinea), the shrimp *Synalpheus stimpsoni* was observed on 4 species out of the 25 which occur in the bay: *Comaster multibrachiatus* (P.H. Carpenter), *C. multifidus* (Müller), *C. gracilis* (Hartlaub) and *C. alternans* (P.H. Carpenter). Many individuals (ca. 70%) of *C. multifidus*—the most common comatulid of the bay—were infested. The shrimp are ectosymbionts that occur alone or in a pair (one male, one female) under the calyx of their host. While *Synalpheus stimpsoni* has no apparent effect on its host, the comatulid provides, at least, protection against predators. When isolated from its natural host and placed close to different comatulid species, *S. stimpsoni* significantly prefers to reassociate with its natural host. Experiments made for testing the role of vision and olfaction in the recognition and selection of shrimps' hosts show that *S. stimpsoni* is unable to visually distinguish its natural host either from other comatulids or from branched corals. In contrast, *S. stimpsoni* differentiates significantly a water flow carrying the odour of its natural host from any other water flow. It is suggested that vision is the first sense involved, enabling the symbiont to move near any comatulid-like object; olfaction then acts, allowing the shrimp to recognize and select an appropriate comatulid host. © 1998 Elsevier Science B.V.

Keywords: Symbiosis; Comatulid; Shrimp; Host recognition

1. Introduction

Many symbiotic associations between shrimp and echinoderms have been reported from the tropical Indo-West Pacific region. Symbiotic shrimps mainly belong to the

*Corresponding author. Tel./fax.: + 32 65 373434.

families Palaemonidae, Alpheidae and Hippolytidae (Bruce, 1976). Amongst alpheids, most of the comatulid associated species belong to the genus *Synalpheus*, only one species of the genus *Athanas* were found on a comatulid by Fabricius and Dale (1993). *Synalpheus* species are ectosymbionts living under the calyx of their host. Although their systematics has been investigated (Coutière, 1899; Banner and Banner, 1975; Bruce, 1982), little is known about the biology of their association with comatulids, and no data exist on the ethoecology of the symbionts.

This study aimed to investigate the symbiosis between the shrimp *Synalpheus simpsoni* (De Man) and its comatulid hosts. For that purpose, we first determined the comatulids with which these shrimp were associated in a protected site, Hansa Bay (Bismark Sea, Papua New Guinea), where at least 25 species of comatulids occur, some of which were highly infested by shrimp (Eeckhaut et al., in press). We then carried out behavioural experiments to test the fidelity that the symbionts show towards their hosts and to investigate the role of shrimp vision and olfaction in host selection.

2. Materials and methods

2.1. Sampling

Comatulids and their symbiotic shrimps were hand-collected by scuba diving at 6 to 20 m depth in Hansa Bay in July 1994 and July 1995. The specimens were collected on the reef slope around Laing Island, on a reef located North of Laing Island (Durangit reef), and on a Japanese wreck in front of Nubia village (Fig. 1). Each comatulid and its shrimps were put into separate bags during dives and brought to the King Leopold III Biological Station. Special care was taken not to lose the shrimps. They were then fixed in 10% formol and preserved in 70% ethanol to identify the hosts with which the shrimps were associated (July 1994), or kept alive in an openly circulating marine aquarium for behavioural experiments (July 1995). All the *S. simpsoni* used for behavioural experiments were associated with *Comaster multifidus*. Fixed shrimps were measured (rostrum, cephalothorax and abdomen), their sexes determined, and their gut contents analysed.

2.2. Fidelity towards the host

Two experiments were carried out to determine the fidelity of symbionts towards their hosts. First, 20 shrimp were isolated from their comatulids and divided in two lots of 5 heterosexual pairs. Each pair of the first lot was placed on a individual of *Oxycomanthus bennetti* (J. Müller), a species rather similar in size and habitat to *Comaster multifidus* but on which *Synalpheus simpsoni* was never found. The pairs of the second lot were placed on five non-infested *Comaster multifidus* as controls. A set of one experimentally infested *Oxycomanthus bennetti*, one newly infested *Comaster multifidus*, and an additional five non-infested *C. multifidus* were each placed in situ in three separate plastic cages (100 × 50 × 20 cm). The cages were placed close together in the lagoon at 3 m depth. The upper side of each cage was made of a mesh (mesh size: 2 cm/2 cm)

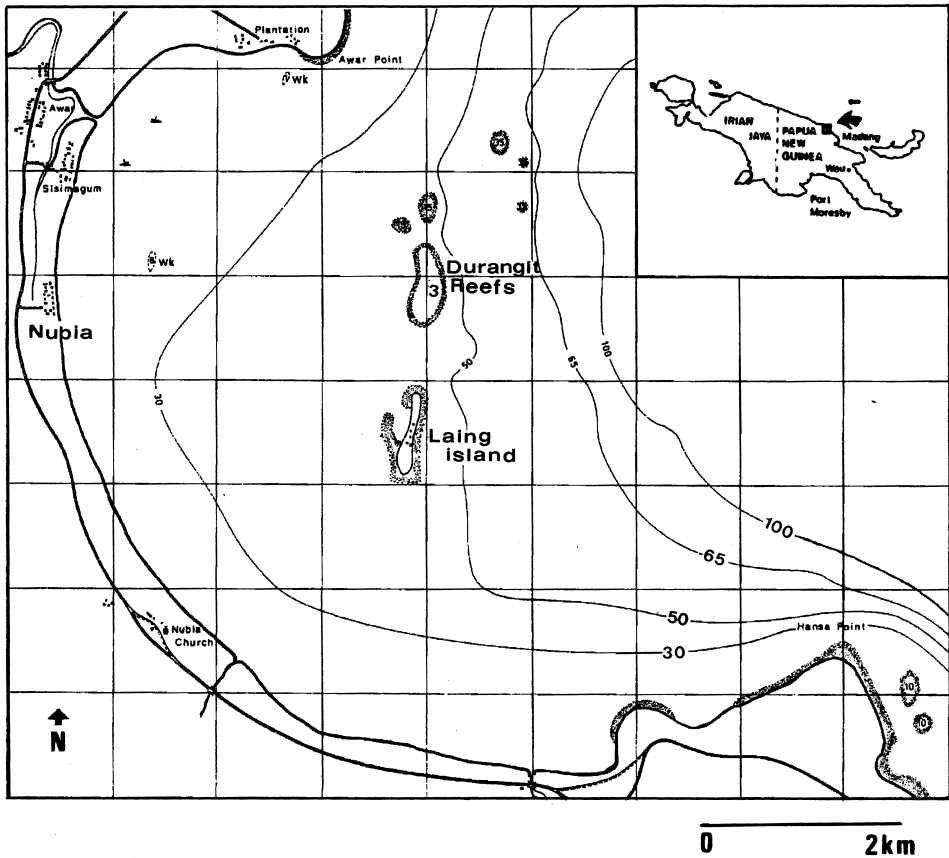


Fig. 1. Map of Hansa Bay.

that allowed the shrimp but not the comatulids to leave or enter it for 15 days. The state of the comatulid-shrimp association was checked every 3 days.

A total of 30 shrimp were used for the second experiment. Each shrimp was placed at the center of an aquarium (100 × 50 × 30 cm), 25 cm from three potential hosts of similar size. One host was always the *C. multifidus* individual on which the tested shrimp was found in situ. The two other potential hosts were either (1) two *C. multifidus* which were not previously infested, (2) two comasterid comatulids that did not belong to the genus *Comaster* or, (3) two non-comasterid comatulids. The choice made by the shrimp was checked after one night. Each of the three series of tests was done 10 times; 5 male and 5 female shrimp were used for each series.

2.3. Visual tests

The role of shrimp vision in host recognition was studied using the system shown in Fig. 2. It consisted of two plastic, transparent aquaria placed 50 cm from each other

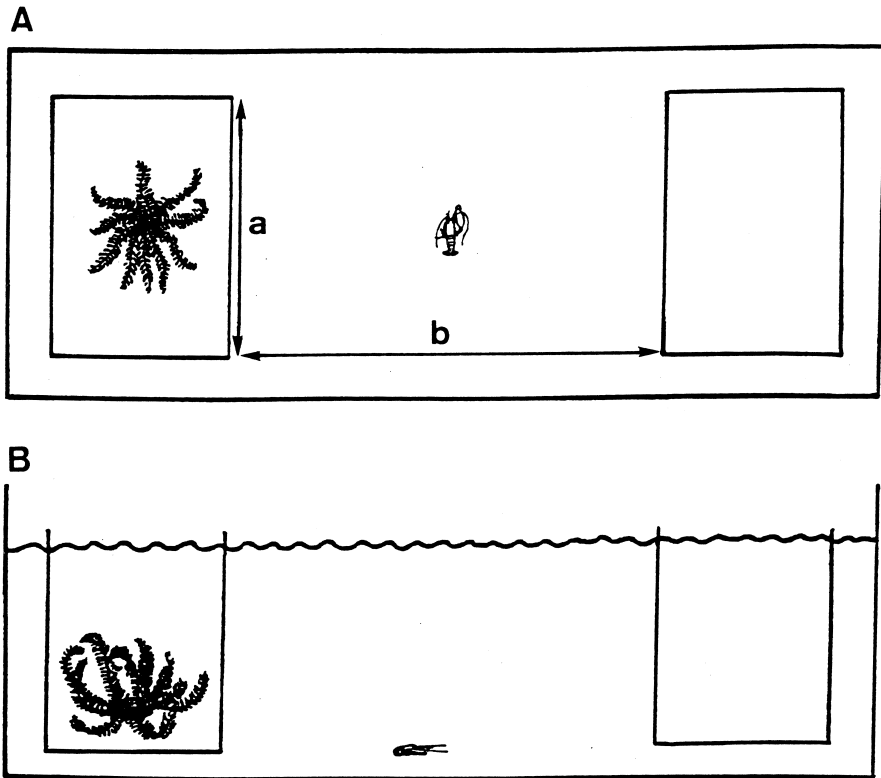


Fig. 2. Diagrammatic representation of the system used to test the role of vision in host recognition. A, upper view; B, profile view ($a = 30$ cm, $b = 50$ cm).

inside a larger aquarium. The system was based on the principle that a symbiont placed at the center of the system will choose between two visual stimuli. Either the shrimp will move towards the aquarium containing the positive stimulus, or it will remain at the center of the system or move randomly. Six different tests were carried out based on what had been placed in the aquaria (see Results). Twenty assays were performed for each type of test using 10 male and 10 female shrimp; each individual shrimp was used for the six types of test. An assay was considered null if the shrimp did not touch the side of any of the experimental aquaria within 5 min. Experimental results were analysed using the Chi-Square test.

2.4. Olfactory tests

The role of shrimp olfaction in host recognition was studied using a Davenport's Y system (Davenport, 1950). The system allowed a symbiont to choose between two chemical stimuli carried by the water flow (Fig. 3). The water flowed from two aquaria (A and B) into the Y-tube, and was evacuated to a bucket through aquarium C. The flow

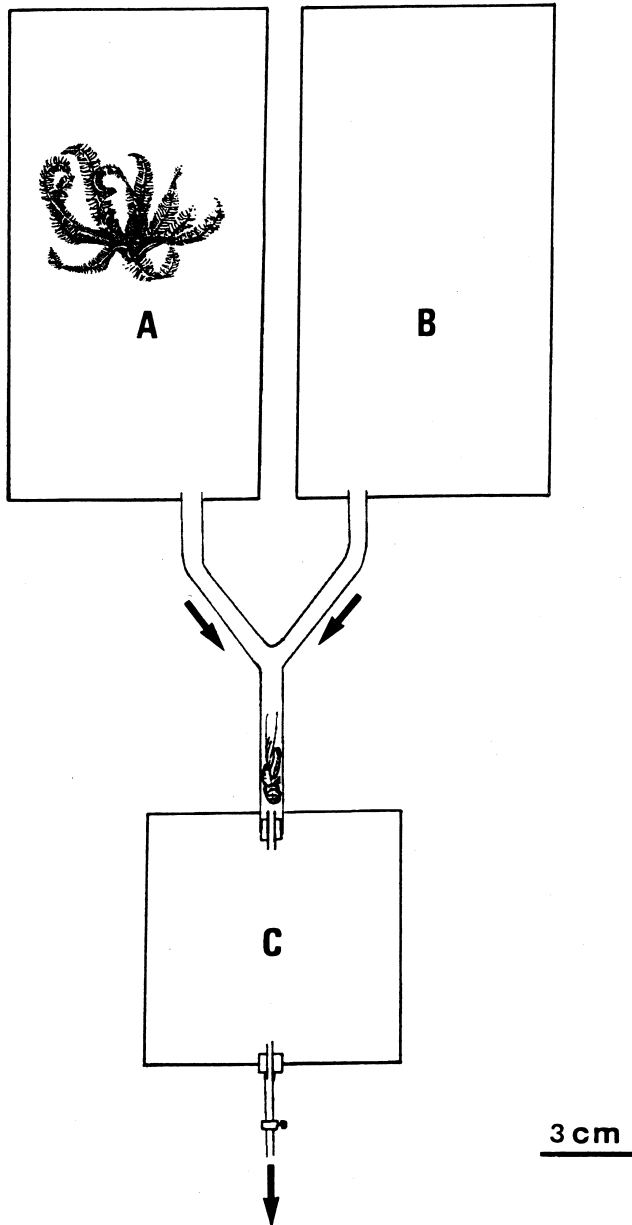


Fig. 3. Diagrammatic representation of Davenport's Y system used to test the role of shrimp olfaction in host recognition.

speed (100 ml min^{-1}) was regulated by a tap. If it is positively stimulated, the symbiont moves into the Y-tube up to the intersection of the paired branches where it is confronted by a choice which will depend on the nature of the stimulus. If it is not stimulated, the symbiont usually remains in the unpaired branch of the Y tube or moves randomly. Nine tests were carried out based on what had been placed in aquaria A and B (see Results). Twenty assays were performed for each type of test with a total of 10 male and 10 female shrimp; each individual shrimp was used for every type of test. Assays were considered null if the shrimp did not reach one of the paired branches within 5 min. Experimental results were analysed using the Chi-Square test.

3. Results

3.1. Occurrence of shrimps on comatulids and feeding strategy

A total of 92 synalpheids were collected from 123 individuals of 12 comatulid species (Table 1). Collected shrimp were either juveniles or adults, but most of them lost some of their appendages during the samplings so that only two species, *Synalpheus demani* and *S. stimpsoni*, were determined without doubt.

Thirty-eight of the 54 *Comaster multifidus* (70%) collected were infested by *Synalpheus stimpsoni*. Seventeen shrimps (five females, three males and nine juveniles) were found alone and 42 were in pairs (19 heterosexual pairs and two undetermined). A comatulid host never harboured more than two *S. stimpsoni* and *S. stimpsoni* was never observed on a comatulid host together with another *Synalpheus* species. However, *S. stimpsoni* may occur together with pontonine shrimps of the genus *Periclimenes*.

Host size was not correlated with shrimp size ($r = 0.03$, $P = 0.9012$; Fig. 4) nor with the number of associated shrimp ($r = 0.33$, $P = 0.3208$). Females (maximum length 31 mm) were generally larger than males (maximum length 23 mm). Most of the females were ovigerous (19 out of 21). The smallest egg-bearing female was 12 mm long, and the difference in size between ovigerous and non-ovigerous females was not significant. One fifth of the *Synalpheus stimpsoni* collected on *Comaster multifidus* were juveniles (nine out of 50).

In situ, individuals of *Synalpheus stimpsoni* usually occurred under the calyx of their host and were never seen to feed upon the host epidermal tissue. Analysis of stomach contents of 20 *S. stimpsoni* revealed that it mostly feeds on seaweeds; no fragment of host was observed in the gut lumen. Non-infested comatulids belonging to host species did not differ morphologically from those infested by *S. stimpsoni*.

3.2. Fidelity shown by the *Synalpheus stimpsoni* towards its hosts

After 3 days, none of the five heterosexual pairs of *S. stimpsoni* put experimentally on *Oxycomanthus bennetti* were found on these comatulids. Two of these pairs infested two of the originally non-infested *Comaster multifidus* which had been placed in a nearby

Table 1
Distribution of symbiotic *Synalpheus* species during a survey of comatulids made in Hansa Bay in Summer 1994

Comatulids				Shrimps		
Family	Species	Number of specimens observed	Number of comatulids infested	<i>Synalpheus</i> species	Number of specimens collected	
Comasteridae	<i>Capillaster multiradiatus</i> (L.)	19	2	<i>S. demani</i>	4	
	<i>Comaster multibrachiatus</i> (P.H. Carpenter)	2	2	<i>S. stimpsoni</i>	2	
	<i>Comaster multifidus</i> (J. Müller)	54	38	<i>Synalpheus spp</i>	2	
	<i>Comaster gracilis</i> (Hartlaub)	4	3	<i>S. stimpsoni</i>	50	
	<i>Comanthina schlegelii</i> (P.H. Carpenter)	3	1	<i>Synalpheus spp</i>	2	
	<i>Clarkcomanthus albinotus</i> (Rowe et al.)	7	1	<i>S. aff.</i>	1	
	<i>Clarkcomanthus littoralis</i> (P.H. Carpenter)	4	1	<i>comatularum</i>	1	
	<i>Comanthus alternans</i> (P.H. Carpenter)	7	1	<i>S. aff.</i>	1	
	<i>Comanthus parvicirrus</i> (J. Müller)	11	6	<i>S. demani</i>	3	
	<i>Comanthus suavius</i> (Rowe et al.)	1	1	<i>Synalpheus spp</i>	8	
				<i>S. aff. tijou</i>	1	
	Colobometridae	<i>Cenometra bella</i> (Hartlaub)	5	1	<i>S. demani</i>	2
		<i>Himerometra robustipinna</i> (P.H. Carpenter)	6	1	<i>S. demani</i>	1

All comatulids listed were collected in 1994 except *Comaster multifidus* of which 45 additional specimens were collected in 1995.

cage. The five *C. multifidus* which were each infested by an heterosexual pair of *Synalpheus stimpsoni* since the first day were still infested after 15 days. Three pairs were thus missing.

When the shrimps were placed in an aquarium with three comatulid species belonging to different families (Colobometridae: *Colobometra perspinosa*; Himerometridae: *Himerometra robustipinna*, and their original host, the comasterid, *Comaster multifidus*), they were always found on *C. multifidus* after one night (test 1, Table 2). When they were placed with three comatulid species belonging to three genera of Comasteridae, one original host (*C. multifidus*), one potential host (*C. alternans*), and one on which *Synalpheus stimpsoni* was never found (*Clarkcomanthus albinotus*), they were always found on *Comaster multifidus* after one night (test 2, Table 2). When the shrimp were placed with three *C. multifidus* (i.e., the original host and two other individuals), they were indifferently found on the original host or another individual after one night (test 3, Table 2).

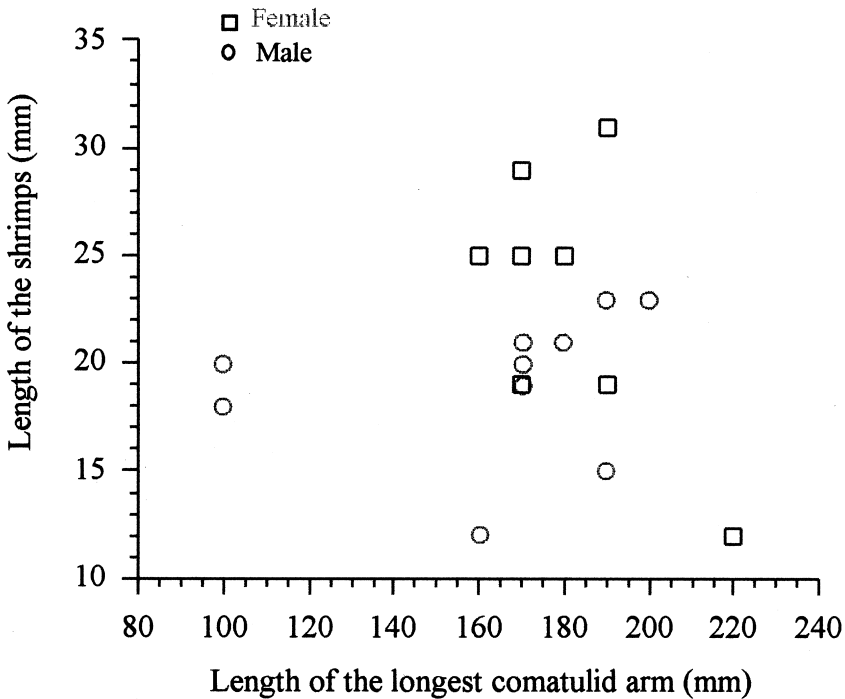


Fig. 4. Relationship between shrimp length (*Synalpheus simpsoni*) and the size of its comatulid host (*Comaster multifidus*).

3.3. Role of vision in host recognition

When both aquaria (Fig. 2) were filled with sea water only, the shrimp was not attracted to either: it turned around itself but most of the time stayed in the middle of the system (test 1; Table 3). When *S. simpsoni* was placed between a tank filled just with sea water and one with either its host, a comatulid on which it never occurs or a branched coral similar in size to *Comaster multifidus*, it was significantly attracted by all three stimuli (tests 2 to 4; Table 3). When it was placed between two comatulids (one

Table 2
Fidelity of *Synalpheus simpsoni* to its host *Comaster multifidus*

Tests	Comatulids presented			P
1	<i>Comaster multifidus</i> * (10)	<i>Colobometra perspinosa</i> (0)	<i>Himerometra robustipinna</i> (0)	0.0001
2	<i>Comaster multifidus</i> * (10)	<i>Comanthus alternans</i> (0)	<i>Clarkcomanthus albinotus</i> (0)	0.0001
3	<i>Comaster multifidus</i> * (4)	<i>Comaster multifidus</i> (4)	<i>Comaster multifidus</i> (2)	0.6673

Numbers in brackets indicate the number of comatulids occupied by shrimp at the end of the 15-day test period. Asterisks refer to the host on which the shrimp was found in situ.

Table 3

Visual attraction of *Synalpheus stimpsoni* by potential hosts in double choice experiments using apparatus described in Fig. 2

Tests	Average time (s) ¹	Aquarium		Results				P
		A	B	Assay	Null	A	B	
1	250	Sea water	Sea water	20	19	1	0	
2	50	<i>Comaster multifidus</i> *	Sea water	20	1	17	2	0.0001
3	100	<i>Oxycomanthus bennetti</i>	Sea water	20	4	16	0	0.0001
4	97	Coral	Sea water	20	0	19	1	0.0001
5	77	<i>Comaster multifidus</i> *	<i>Colobometra perspinosa</i>	20	1	11	8	0.0847
6	98	Coral	<i>Comaster multifidus</i> *	20	1	10	9	0.763
7	54	<i>Comaster multifidus</i> (arm 10 cm)	<i>Comaster multifidus</i> (arm 10 cm)	20	0	3	17	0.0001

¹Average time: time of all experiments/number of assays. *Hosts on which the tested *Synalpheus stimpsoni* were found in situ. P, probabilities from statistical analysis of comparison between the number of times the shrimps touched the side of an aquarium containing a stimulus to the number of times it would have touched it by chance. (The chance that a shrimp would touch the side of the attractive aquarium is equal to the ratio $a/(2b + 2a)$ see Fig. 2).

being its host, the other not) or between its host and a branched coral it showed no significant preference for either of them (tests 5 and 6; Table 3). When it was placed between two *C. multifidus*, a large one (longest arm 22 cm) and a small one (longest arm 10 cm), a significantly greater number of shrimp moved towards the large than the small one (test 7; Table 3).

3.4. Role of olfaction in host recognition

When both aquaria (Fig. 3) were filled with sea water only, *Synalpheus stimpsoni* most often stayed still, whereas it moved up the branch toward the aquarium in which a *Comaster multifidus* was placed for 15 min (tests 1 and 2; Table 4). With a *Himerometra robustipinna* (a himerometrid), or a *Comanthus alternans* (a comasterid on which *Synalpheus stimpsoni* can be found) in one aquarium and sea water alone in the other, the shrimp was not significantly attracted to the comatulids and most often stayed still (tests 3 and 4; Table 4). The result obtained with *Comatella stelligera* (a comasterid on which *S. stimpsoni* was never found) in one aquarium and sea water alone in the other is ambiguous. Indeed, the shrimp start moving when they perceived the odour of *Comaster stelligera*, but were not able to distinguish the water carrying the odour (test 5; Table 4). When the odour of *Himerometra robustipinna*, *Comaster stelligera* or *Comaster alternans* was opposed to that of *C. multifidus*, the shrimp started moving and showed a significant preference for *C. multifidus* (tests 6, 7 and 8; Table 4). When the odour of the *C. multifidus* on which *Synalpheus stimpsoni* was found was opposed to that of another

Table 4

Chemical attraction of *Synalpheus stimpsoni* by comatulid hosts in double choice experiments using apparatus described in Fig. 3

Tests	Average time ^a (s)	Aquarium		Results				P	
		A	B	Assay	Null	A	B	1	2
1	280	Sea water	Sea water	20	17	2	1		
2	77	<i>Comaster multifidus</i>	Sea water	30	6	22	2	0.0001	0.0001
3	260	<i>Himerometra robustipinna</i>	Sea water	20	14	3	3	0.1432	1
4	260	<i>Comanthus alternans</i>	Sea water	20	14	5	1	0.1432	0.0285
5	210	<i>Comatella stelligera</i>	Sea water	20	10	8	2	0.0017	0.0177
6	30	<i>Himerometra robustipinna</i>	<i>Comaster*</i>	20	1	1	18	0.0001	0.0001
7	53	<i>Comatella stelligera</i>	<i>Comaster*</i>	20	0	0	20	0.0001	0.0001
8	40	<i>Comanthus alternans</i>	<i>Comaster*</i>	20	0	5	15	0.0001	0.0098
9	30	<i>Comaster multifidus</i>	<i>Comaster*</i>	20	1	9	10	0.0001	0.8183

^a Average time: time of all experiments/Number of assays. *Hosts on which the tested *Synalpheus stimpsoni* were found in situ. P, probabilities from statistical analysis of 1: comparison between the number of times *S. stimpsoni* starts moving and the number of times it starts moving without chemical stimulation, 2: comparison between the frequency of choices that *S. stimpsoni* makes between the two paired branches of the Y tube and the frequency '50%'.

Comaster multifidus, the shrimp started moving but did not show any marked preference (test 9; Table 4).

4. Discussion

Synalpheus stimpsoni is an ectosymbiont that spends a large part of its post-larval life in close association with a comatulid host. Four hosts, i.e., *Comanthina schlegelii*, *Comanthus parvicirrus*, *Oxycomanthus japonicus* and *Comatula purpurea* have been recorded for it (Bruce, 1982). In Hansa Bay only two of them, *Comaster schlegelii* and *Comaster parvicirrus*, were found but they were never associated with *Synalpheus stimpsoni*. The four *S. stimpsoni*–comatulid associations showed in Table 1 had not previously been reported.

Although more than two specimens of some symbiotic shrimp species occur on a single host (Gherardi, 1991; Guo et al., 1996), *S. stimpsoni* either occurs alone or in heterosexual pairs. Also, the presence of *S. stimpsoni*, either singly or in a pair on a comatulid host appears to prevent infestations by any other shrimp of the same genus.

In the field, to find an appropriate host would be essential for the species. Previous

investigations have indicated a relatively high degree of chemosensory competence in crustaceans: the pinnotherid, *Dissodactylus mellitae*, discriminates its echinoid host, *Mellita quinquesperforata*, from six others species of echinoderms (Gray et al., 1968); the shrimp, *Athanas indicus*, recognizes the odour of its echinoid host from those of two other species of echinoids (Gherardi, 1991); and the porcellanid, *Porcellana sayana*, is attracted chemically to the anemone *Calliactis tricolor* (see Brooks and Rittschof, 1995). Our experiments show that *Synalpheus stimpsoni* is able to discriminate the water flow carrying the odour of its host from that carrying other odours. We also demonstrate that this discrimination is highly specific as *S. stimpsoni* from *Comanthus multifidus* overwhelmingly preferred the odour of *C. multifidus* to the odour of any other comatulids even if the latter are known to be potential hosts for the shrimp. This high specificity is surprising and could indicate that the shrimps learn to recognize the odour of their host species. A *Synalpheus stimpsoni* that undergoes its development in contact with one comatulid may be conditioned to respond positively to its odour. Olfactory conditioning is known in insect partnerships (Thorpe and Jones, 1937) but has not been demonstrated in marine associations. Yet, some authors have suggested that symbionts can be acclimated to a host other than the one on which it normally occurs (Gray et al., 1968; Brooks and Rittschof, 1995).

Synalpheus stimpsoni is highly sensitive to the odour of its hosts. Indeed, it reacts to water in which a host has been immersed for only 15 min. Previous investigations on other symbiotic taxa showed that water must stay in contact with the host for a longer period to be attractive. For instance, asteroid hosts have to be immersed overnight before giving the water an attractive feature for its symbiotic polychaete, *Arctonoe* sp. (Davenport, 1950); water has to be in contact with anemones for at least 3 h before attracting the symbiotic crab *Porcellana sayana* (Brooks and Rittschof, 1995).

Although chemotaxis seems to play a primary role in host location in laboratory experiments, the in water currents that occur close to the comatulids in nature should disrupt the diffusion gradient that is necessary for a chemotactic orientation. Therefore, host location should not be attributed entirely to olfaction. Our results suggest that *Synalpheus stimpsoni* uses both visually and chemically mediated information for recognizing hosts at a distance. Vision would allow the shrimp to be attracted by any object similar in shape to a comatulid. It is the first sense that is involved, enabling the symbiont to move near the comatulid-like object. Olfaction would then function in recognizing and selecting the appropriate host.

In many partnerships, the host plays a role in the nutrition of the symbiont. For instance, the shrimp, *Gnathophylloides mineri*, feeds upon the epidermal tissue (Patton et al., 1985); the crab, *Harrovia albolineata*, probably feeds on its hosts' mucus (Ng and Lim, 1990); the crab, *Echinoecus pentagonus*, uses the host faecal pellet as a food source (Castro, 1971), and the main dietary input for *Athanas indicus* are crumbs from host meals (Gherardi, 1991). *Comaster multifidus* does not seem to participate in the nutrition of *Synalpheus stimpsoni* which appears to feed mostly on seaweeds like most alpheid shrimp associated with echinoderms (Suzuki, 1970). This suggests that *S. stimpsoni* may use the comatulids only as refuges against predators. *S. stimpsoni* has a remarkably cryptic color pattern and prefers, moreover, the underside of comatulids, perhaps to minimize exposure to predators. There is no indication that the comatulid

derives any benefit from the shrimp and we consider the relationship between *S. simpsoni* and *Comaster multifidus* to be simply protective commensalism.

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