

# Symbioses of decapod crustaceans along the coast of Espírito Santo, Brazil

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*Potential host species were searched for decapod crustaceans along the coasts of Espírito Santo State, Brazil. On five species of sea anemones checked, nine species of decapods were encountered. On three species of black coral checked, two decapod species were encountered. On six species of gorgonians checked, three species of decapods were encountered. In nine species of bivalves and one species of gastropod checked, one decapod species was encountered. On three sea urchin species checked, three decapod species were encountered. A further seven potential host species investigated did not have macroscopically visible symbiotic decapods. Four of these 18 symbiotic decapod species represent new records for the State of Espírito Santo, five species represent new records for Brazil, and at least one species (probably three) were new for science. The sea anemone *Condylactis gigantea* harboured the largest number of symbionts (eight species) and the shrimp *Neopontonides* sp. occurred on the largest number of hosts (four different species of gorgonians).*

**Keywords:** marine biodiversity, Actinaria, Gorgonaria, Antipatharia

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## INTRODUCTION

Symbioses are common in the marine environment. Some taxa appear to be particularly prone to be involved in associations. It is the crustaceans that probably form more associations with other classes than any other marine animals (Ross, 1983), crustacean–cnidarian associations being particularly common (Patton, 1967).

Many associations of shrimps and crabs with other animals have been described from the eastern Atlantic (e.g. Wirtz & Diesel, 1983; Wirtz *et al.*, 1988; Wirtz, 1997; Wirtz & d'Udekem d'Acoz, 2001, in press; Calado *et al.*, 2007) and from the Caribbean (e.g. Herrnkind *et al.*, 1976; Criales, 1984; Patton *et al.*, 1985; Spotte & Bubucis, 1996). The crustaceans encountered in these studies often belonged to undescribed species. To date, however, no such studies have been made along the coast of Brazil. Searching potential hosts for associated crustaceans along the coast of Espírito Santo, Brazil, was therefore likely to result in the discovery of new associations, the discovery of crustacean species new for Brazil and the discovery of undescribed species.

## MATERIALS AND METHODS

All observations were made while SCUBA diving (43 dives, 40 during daytime, three during night-time; depth range 0–42 m) or snorkelling during daytime and at night, from March to June 2006, along the coastline of Espírito Santo.

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Potential host species were searched visually and symbionts were collected with the help of a small hand net. The geographical coordinates of the sampling sites are:

Santa Cruz, Aracruz: 20°00'S 40°09'W  
Curva da Jurema, Vitória: 20°18'S 40°17'W  
Ilha do Boi, Vitória: 20°18'S 40°16'W  
Guarapari: 20°39'S 40°30'W  
Ilhas Rasas, Guarapari: 20°40'S 40°22'W  
Baiuana, Guarapari: 20°41'S 40°19'W  
Pedra do Dentão, Guarapari: 20°41'S 40°23'W  
Wreck of 'Victory 8B', Guarapari: 20°41'S 40°23'W  
Ilha Escalvada, Guarapari: 20°42'S 40°24'W  
Piúma: 20°50'S 40°37'W  
Ilha dos Franceses: 20°55'S 40°45'W.

The decapod specimens are deposited in the Museu de Zoologia, Universidade de São Paulo under the numbers MZUSP 17003 to 17017 and 17028 to 17044.

## RESULTS

### SYMBIOSES WITH CNIDARIA

#### (a) Actinaria

##### (1) *Condylactis gigantea* (Weinland, 1860)

Twenty *Condylactis gigantea*, in 9–19 m depth, from 5 to 35 cm diameter, were searched for crustacean symbionts. Only the smallest anemone (5 cm diameter, in 11 m depth) did not harbour crustacean symbionts. The other 19 anemones harboured eight different species of crustaceans.

The most common associate was *Stenorhynchus seticornis* (Herbst, 1788), found at 17 anemones, in group-sizes of one to six. These spider crabs were usually at the outer margin of



Fig. 1. The spider crab *Stenorhynchus seticornis* associated with *Condylactis gigantea*.

the sea anemone but with one or several legs between the anemone's tentacles and touching the tentacles of the anemone (Figure 1). The crab *Mithraculus forceps* (A. Milne-Edwards, 1875) was found at 12 anemones, usually hidden below the tentacles, close to the stem of the anemone. Other decapod species encountered with *Condylactis gigantea* were *Periclimenes yucatanicus* (Ives, 1891) (a single individual in five cases and two individuals in two cases), *Lysmata ankeri* Rhyne & Lin, 2006 (four times a single animal, once five animals; Figure 4), a male–female pair of *Metoporphaphis calcarata* (Say, 1818) (one case; Figure 2), *Periclimenes pedersoni* Chace, 1958 (one case; Figure 3), *Cronius ruber* (Lamarck, 1818) (one case) and an unidentified *Mithrax* sp. (two cases). All these decapod species were in frequent contact with the sea anemones' tentacles.

There were up to four different crustacean species associated with the same individual sea anemone. When the female of the *Metoporphaphis calcarata* pair and the *Periclimenes pedersoni*—collected from the same anemone—were transported to the surface in a plastic bag, the *Metoporphaphis* grabbed the *Periclimenes* and started to feed on it.

**(2) Unidentified aiptasiid, possibly *Bellactis ilkalyseae* Dube, 1983**

In 15 m depth, at Ilha Escalvada, an aiptasiid anemone was hanging over the entrance of a small tunnel. The antennae of



Fig. 2. *Condylactis gigantea* with *Metoporphaphis calcarata*.



Fig. 3. *Condylactis gigantea* with *Periclimenes pedersoni*.

two alpheid shrimps were sticking out from this tunnel, frequently brushing against the anemone's tentacles (Figure 5). The alpheids probably belong to an undescribed species, which has been reported as *Alpheus armatus* Rathbun, 1901 by Coelho *et al.* (1990) from north-east Brazil (A. Anker, personal communication).

**(b) Antipatharia**

**(1) *Tanacetipathes* sp. 1**

A single colony, about 80 cm high, of this bushy black coral was encountered at Ilha Escalvada in 19 m depth (Figure 6). Several specimens of *Periclimenes* sp. 1 were collected from it. This is likely to be an undescribed species of the *Periclimenes iridescens* group but the species cannot be determined, as most pereopods of the specimens are missing. The absence of an apical process on the telson allies it to *Periclimenes antipathophilus* Spotte, Heard & Bubucis, 1994 but the single fifth pereopod available does not have the characteristic rows of comb setae.

**(2) *Tanacetipathes* sp. 2**

A smaller *Tanacetipathes* species, about 40 cm high, was common at Baiuana in 40–42 m depth (Figure 7). A branch of it was sent to an expert at Rio de Janeiro Natural History Museum but never identified. Several specimens of *Periclimenes* sp. 1 were collected from this bushy black coral.



Fig. 4. *Condylactis gigantea* with *Lysmata ankeri*.



Fig. 5. Aiptasiid with *Alpheus* aff. *armatus*.

(3) *Cirripathes (secchini* Echeverría, 2002 ?)

The only whip coral reported from Brazil is *Cirripathes secchini* Echeverría, 2002. About 20 whip corals in 40–42 m depth at Baiuana, were checked visually and by sliding the stem through the fingers of the investigator (Figure 8). A single whip coral had a *Pseudopontonides principes* (Criales, 1980) clinging to it.

(c) *Gorgoniaria*

(1) *Muricea flamma* Marques & Castro, 1995

Many specimens of this common and large gorgonian were wiped with a hand-held aquarium net at Ilha Escalvada in 15–20 m depth. In each case, numerous individuals of two



Fig. 7. *Tanacetipathes* sp. 2 in 40 m depth at Baiuana.

apparently common shrimp species were caught (Figure 9). One of them belongs to the genus *Neopontonides* and is closely related to the species *beaufortensis* (Borradaile, 1920) (and was called *N. beaufortensis* in De Grave, 2008); this is probably an undescribed species. The second, somewhat less-common shrimp on *Muricea flamma* was an (at the time) undescribed species of *Periclimenes*, recently described as *Periclimenes guarapari* De Grave, 2008, currently only known from the Guarapari area. See below for other hosts of these two species. A sample of shrimps collected on 9 April in 15 m depth contained (among numerous *Neopontonides* sp. and *Periclimenes guarapari*) a single specimen of *Latreutes parvulus* (Stimpson, 1866).

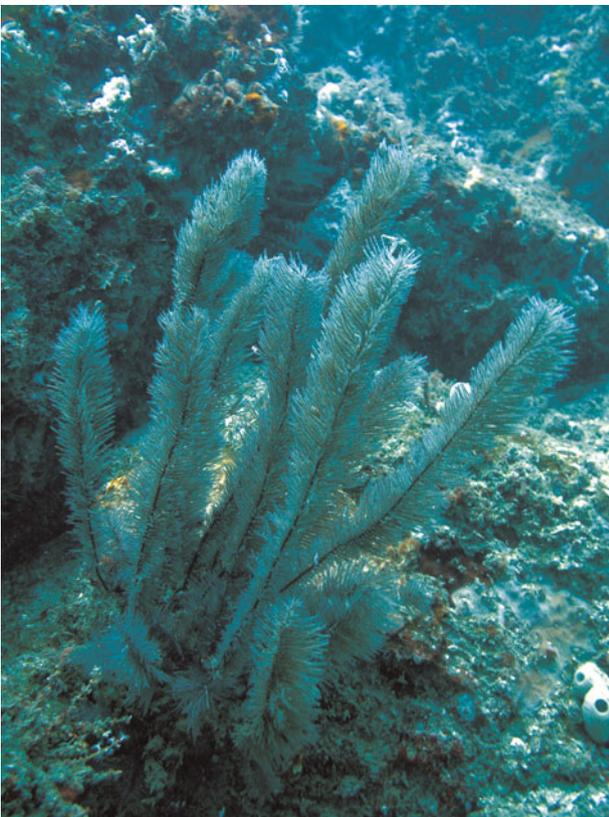


Fig. 6. *Tanacetipathes* sp. 1 in 19 m depth at Ilha Escalvada.



Fig. 8. *Cirripathes (secchini?)* in 42 m depth at Baiuana, host of *Pseudopontonides principes*.

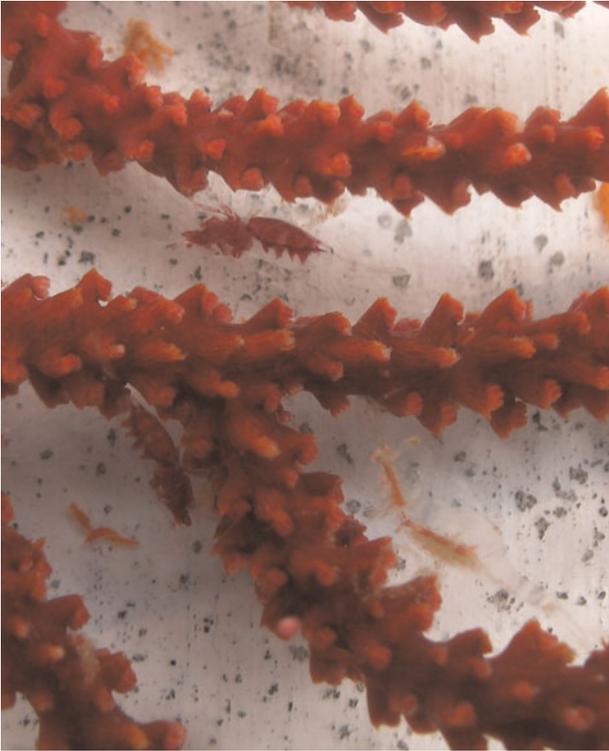


Fig. 9. *Muricea flamma* with *Neopontonides* sp. and *Periclimenes guarapari*.

(2) *Lophogorgia violacea* (Pallas, 1766)

A small colony of this gorgonian (Figure 10) was wiped with a hand-held aquarium net on 6 May, at Baiuana, in 38 m depth,



Fig. 10. The sampled colony of *Lophogorgia violacea* (photograph by Jean-Christophe Joyeux), host of *Pseudocoutierea conchae*.



Fig. 11. The sampled colony of an unidentified white gorgonian (photograph by Jean-Christophe Joyeux), host of *Neopontonides* sp.

and a single shrimp was collected. The gorgonian was sent to the Natural History Museum of Rio de Janeiro. The shrimp turned out to be *Pseudocoutierea conchae* Criales, 1981. This is a new record for Brazil for this species and is the first time that the species has been discovered since its original description from Colombia.

(3) Unidentified small white gorgonian

A small colony of an unidentified white gorgonian (Figure 11) was wiped with a hand-held aquarium net on 6 May, at Baiuana, in 38 m depth, and a single shrimp was collected. This was again *Neopontonides* sp. (cf. the section on the gorgonian *Muricea flamma*).



Fig. 12. *Plexaurella pumila* in the foreground, *P. grandiflora* behind it (Ilha Escalvada, about 10 m depth).



Fig. 13. *Phyllogorgia dilatata*, host of *Neopontonides* sp.

(4) *Plexaurella grandiflora* Verrill, 1912

Colonies of this large, bushy gorgonian (Figure 12) were wiped with an aquarium net, in 10–15 m depth at Ilha Escalvada. Numerous specimens of *Periclimenes guarapari* and *Neopontonides* sp. were caught (cf. section on *Muricea flamma*).

(5) *Plexaurella pumila* Verrill, 1912

Six colonies of this small, bushy gorgonian (Figure 12) were covered with plastic bags and collected *in toto* in 17 m depth at Ilha Escalvada. Two shrimps were encountered in these plastic bags but the sample was lost and the species could not be determined. An additional colony collected in 3 m depth at Ilha dos Franceses had no symbiotic decapods.

(6) *Phyllogorgia dilatata* (Esper, 1806)

Many colonies of this large, broad gorgonian (Figure 13) were wiped with a hand-held aquarium net in 10–18 m depth at Ilha Escalvada and at Piúma. Many specimens of *Neopontonides* sp. were caught in each case (cf. section on *Muricea flamma*).

SYMBIOSES WITH GASTROPODA

*Crepidula* sp.

A gastropod belonging to the genus *Crepidula* was on an *Arca* specimen collected in 11 m depth at Ilhas Rasas.



Fig. 14. *Gnathophylloides mineri* on *Tripneustes ventricosus* (new record for Espírito Santo).



Fig. 15. *Dissodactylus crinitichelis* on unidentified irregular sea urchin.

A small pinnotherid crab was found sheltering underneath it, *Zaops ostreum* (Say, 1817).

SYMBIOSES WITH ECHINODERMATA ECHINOIDEA

(1) *Tripneustes ventricosus* (Lamarck, 1816)

Four large *Tripneustes ventricosus* (diameter about 12 cm) from 10 to 15 m depth at Ilha Escalvada and Ilhas Rasas were visually checked for symbionts. On one of them, four *Gnathophylloides mineri* Schmitt, 1933 could be seen (Figure 14). This sea urchin was collected and soaked in diluted ethanol, whereupon a total of nine shrimps emerged, seven ovigerous females and two (the smallest animals) without eggs. *Gnathophylloides mineri* is known from southeastern Florida as far south as Bahia (Ramos-Porto & Coelho, 1988); thus, to find it in Espírito Santo State slightly extends the known distribution of the species to the south.

(2) *Echinometra lucunter* (Linnaeus, 1758)

About 20 *Echinometra lucunter* were cut out of their boreholes during low tide at Guarapari. The boreholes were visually inspected and the sea urchins were washed in fresh water. A striped gammarid (Crustacea, Amphipoda) was encountered in several cases but no decapods.

(3) Unidentified irregular sea urchin, probably *Meoma ventricosa* (Lamarck, 1816)

This large (about 15 cm long) irregular sea urchin is buried in the sand. A small elevation of the sand betrayed their location in the following cases. One animal from 38 m depth at Baiuana



Fig. 16. *Holothuriophilus tomentosus* on unidentified irregular sea urchin.

had no associated decapods. One of two animals from 15 m depth at Ilhas Rasas had four *Dissodactylus crinitichelis* Moreira, 1901 clinging to its lower side (Figure 15). One animal from 32 m depth at Pedra do Dentão had a *Holothuriophilus tomentosus* (Ortmann, 1894) clinging to its lower side (Figure 16).

#### POTENTIAL HOSTS WITHOUT DECAPOD SYMBIONTS

##### (1) *Bunodosoma caissarum* Corrêa in Belém, 1987

About 20 large specimens of this common intertidal sea anemone were searched for symbionts in shallow water (0–1 m depth); none were encountered.

##### (2) *Stychodactyla duerdeni* (Carlgren, 1900)

Three large specimens (15–20 cm disc diameter) of this sea anemone were seen when snorkelling in tide pools near Santa Cruz. Even though the species is known to harbour shrimps of the genus *Periclimenes* in the Caribbean (e.g. photograph in Human & Deloach, 2002, using the incorrect name *Actinoporus elegans* for the anemone), no symbionts were seen with these three anemones. Carlos Eduardo Ferreira of Niteroi University (personal communication) has seen shrimps with this sea anemone at the Abrolhos Reefs in Bahia State, Brazil.

##### (3) *Actinostella flosculifera* (Le Sueur, 1817)

About ten large specimens of this sea anemone were searched for symbionts in large tide pools and down to 10 m depth; none were encountered.

##### (4) *Palythoa caribaeorum* (Duchassaing de Fonbressin & Michelotti, 1860)

The surface of a large area covered with this encrusting anemone (Cnidaria, Zoantharia) at Ilha dos Franceses, was wiped with a hand-held aquarium net; no crustacean symbionts were encountered.

##### (5) *Carijoa riisei* (Duchassaing & Michelotti, 1860)

The wreck of the 'Victory 8B', in front of Guarapari, is overgrown with many colonies of the telestacean octocoral *Carijoa riisei*. Numerous colonies in 25–30 m depth were checked; no symbiotic decapods were found.

##### (6) *Crassostrea gasar* (Adanson, 1757)

Ten individuals of the bivalve *Crassostrea gasar* (formerly called *C. brasiliiana*) lying on muddy sand at Curva da Jurema, in 1–2 m depth, were collected and opened; no decapods were found inside them.

##### (7) *Crassostrea rhizophorae* (Guilding, 1828)

Ten *Crassostrea rhizophorae*, glued to rock and emerged at low tide at Ilha do Boi, were opened; no decapods were found inside them.

##### (8) *Isognomon* sp.

Twelve of these soft shelled bivalves were opened, in about 15 m depth at Ilha Escalvada; no decapods were found inside them.

##### (9) (*Pseudo*)*chama* sp.

A *Chama* or *Pseudochama* species is commonly attached to the rock, in shallow water in the Guarapari area. Six of these bivalves, from 5 to 10 m depth at Ilhas Rasas and Ilha Escalvada were opened; no decapods were found inside them.

##### (10) *Pinna* sp.

Five small *Pinna* sp., 10–12 cm long, from muddy sand in about 3–6 m depth at Curva da Jurema, were opened; no decapods were found inside these bivalves. Visual inspection (looking into the open valves from above) of a *Pinna* of about 15 cm length, in 8 m depth at Ilha Rasa, did not result in the discovery of symbionts.

##### (11) *Pteria* sp.

Five animals collected in about 3 m depth at Ilhas dos Franceses had no decapods inside them. Two large specimens of this bivalve (about 8 cm long) collected at the wreck of the 'Victory' in 27 m depth had no decapods inside them.

##### (12) *Arca* sp.

A single *Arca*, 8 cm long, was collected in 11 m depth at Ilhas Rasas; no symbionts were found inside this bivalve but see the section on *Crepidula* above.

##### (13) *Spondylus (americanus)* Hermann, 1781?

A large *Spondylus* with long spines was collected in 41 m depth at Baiuana; no decapods were found inside this bivalve.

##### (14) *Spondylus* sp.

A *Spondylus* without spines was collected in 14 m depth at Ilha Escalvada, 14 m; no decapods were found inside it.

##### (15) *Isostichopus badionotus* (Selenka, 1867)

Sixteen large individuals of this common sea cucumber were searched for symbionts at Ilha Escalvada, during daytime, in 10–15 m depth. One to eight individuals of a small undescribed parasitic gastropod of the genus *Melanella* (A. Warén, personal communication) were found on 12 of these sea cucumbers but no crustaceans.

##### (16) Unidentified feather stars

Small red-brown, yellow and white feather stars are common in the Guarapari area. During the day they hide in cracks, at night they come out and unfold their arms. More than 20 feather stars in 10–18 m depth were visually searched for symbionts at night at Ilha Escalvada. No symbionts were seen.

##### (17) Unidentified basket star

More than ten individuals of an unidentified basket star, unfolded at night, were visually surveyed at Ilha Escalvada in 10–18 m depth. No symbionts were seen.

##### (18) *Oreaster reticulatus* (Linnaeus, 1758)

Fifteen individuals of the large starfish *Oreaster reticulatus* were searched for symbionts in the Guarapari area: none were seen.

##### (19) *Styela plicata* (Lesueur, 1823)

Six large (about 8 cm high) specimens of the tunicate *Styela plicata* were collected from 2 m depth at Curva da Jurema and cut open; no symbionts were found.

##### (20) *Microcosmus (exasperatus)* Heller, 1878 ?

Four specimens of this tunicate were collected in 12 m depth at Ilhas Rasas and opened; no symbionts were found inside them.

##### (21) *Phallusia nigra* Savigny, 1816

A single, large tunicate of the species *Phallusia nigra* (about 10 cm high) was collected from 9 m depth at Ilha Escalvada and cut open; no symbionts were found.

## DISCUSSION

## (1) Zoogeography

The two most common species of symbiotic decapods encountered were *Periclimenes guarapari* and *Neopontonides* sp. The first one was undescribed at the time of the study and has since been described on the basis of specimens collected during this study (De Grave, 2008). The latter is probably also an undescribed species and will be dealt with in a separate publication.

The *Periclimenes* species from the two black corals of the genus *Tanacetipathes* is probably also undescribed but the specimens cannot be fully identified.

The finding of *Pseudocoutierea conchae* (associated with *Lophogorgia violacea*) provides the first record of this species from Brazil and the first record since the description of the species. The finding of *Pseudopontonides principis* from whip coral provides the first record of this species for Brazil.

*Periclimenes pedersoni* was recorded from Brazil as *Periclimenes* aff. *pedersoni* by Gasparini *et al.* (2005). The colour pattern of Brazilian animals was compared with those from the Caribbean and no significant difference was found.

*Alpheus* aff. *armatus* has been recorded from north-eastern Brazil (Coelho *et al.*, 1990); the record from Espírito Santo State provides a southward extension of the known range of the species.

Both *Gnathophylloides mineri* and *Periclimenes yucatanicus* have been recorded from Bahia State (Young & Serejo 2006); the current record from Espírito Santo State provides a slight southward extension of their known range.

*Holothuriophilus tomentosus* has only been known from Santa Catarina State and Bahia State (de Melo & Boehs, 2004; Almeida & Coelho, 2008); this is the first record for the State of Espírito Santo.

*Stychodactyla*, *Chama*, *Pinna*, *Spondylus* and *Echinometra* are all known host genera for shrimps or crabs in other areas, such as the Caribbean or the eastern tropical Atlantic (Schoppe & Werding, 1996, references in Introduction); it therefore came as a surprise not to find associated crustaceans with them during the present study. Compared with the Caribbean and the eastern tropical Atlantic, slightly fewer symbionts than expected were found in the present study. This could simply be due to the fact that Espírito Santo is further away from the central tropics and therefore already has a lower species density.

## (2) Host specificity

Table 1 shows which hosts were recorded for the symbiotic decapods of this study.

The host with largest number of symbiotic decapod crustaceans (eight species) was the sea anemone *Condylactis gigantea*. All decapods found in association with this anemone were in contact with the tentacles of the anemone without eliciting a feeding reaction of the anemone (i.e. tentacles adhering to the crustacean). This could be due either to an innate characteristic of these crustacean species or could be individually acquired in an adaptation process to the anemone, the latter suggested by experiments (Levine & Blanchard, 1980; Crawford, 1992; Giese *et al.*, 1996; Melzer & Meyer, in preparation). The crustacean with the largest number of hosts was the shrimp *Neopontonides* sp., encountered on four different species of gorgonians.

Table 1. The symbiotic crustaceans and their host species.

Species	Hosts
<i>Stenorhynchus seticornis</i>	<i>Condylactis gigantea</i>
<i>Mithraculus forceps</i>	<i>Condylactis gigantea</i>
<i>Periclimenes yucatanicus</i>	<i>Condylactis gigantea</i>
<i>Lysmata ankeri</i>	<i>Condylactis gigantea</i>
<i>Metoporphaphis calcarata</i>	<i>Condylactis gigantea</i>
<i>Periclimenes pedersoni</i>	<i>Condylactis gigantea</i>
<i>Cronius ruber</i>	<i>Condylactis gigantea</i>
<i>Mitrax</i> sp.	<i>Condylactis gigantea</i>
<i>Alpheus</i> aff. <i>armatus</i>	Unidentified aiptasiid, possibly <i>Bellactis ilkalyseae</i>
<i>Periclimenes</i> sp. 1	<i>Tanacetipathes</i> sp. 1, <i>Tanacetipathes</i> sp. 2
<i>Pseudopontonides principis</i>	<i>Cirripathes</i> ( <i>secchini</i> ?)
<i>Neopontonides</i> sp.	<i>Muricea flammea</i> , unid. small white gorgonian, <i>Plexaurella grandiflora</i> , <i>Phyllogorgia dilatata</i>
<i>Periclimenes guarapari</i>	<i>Muricea flammea</i> , <i>Plexaurella</i> <i>grandiflora</i>
<i>Latreutes parvulus</i>	<i>Muricea flammea</i>
<i>Pseudocoutierea conchae</i>	<i>Lophogorgia violacea</i>
<i>Zaops ostreum</i>	<i>Crepidula</i> sp.
<i>Gnathophylloides mineri</i>	<i>Tripneustes ventricosus</i>
<i>Dissodactylus crinitichelis</i>	Large irregular sea urchin, probably <i>Meoma ventricosa</i>
<i>Holothuriophilus tomentosus</i>	Large irregular sea urchin, probably <i>Meoma ventricosa</i>

Records of crustaceans with only a single host might represent true monospecific associations but could also be due to low and locally restricted sample size. Indeed, some of the symbionts encountered here with a single host species, e.g. *Thor amboinensis*, are known to live with other host species in other areas (Wirtz, 1997 and references therein).

The pinnotherid crab *Holothuriophilus tomentosus* was known only in association with the bivalve *Anomalocardia brasiliensis* (de Melo & Boehs, 2004); to find it with a sea urchin comes as a surprise. All six known species of the genus *Pseudocoutierea* live in association with gorgonians and antipatharians (De Grave, 2007). The shrimp *Latreutes parvulus* is a seagrass dwelling species but has, on occasion, been recorded on gorgonians (Wirtz & d'Udekem d'Acoz, in press).

## (3) The relation between host species and associated species

The symbiotic decapods probably derive some degree of protection from their host organisms. This is obvious when they manage to live between the tentacles of sea anemones or between the spines of sea urchins. Most gorgonians are unpalatable to predators such as fish (Epifanio *et al.*, 1999 and references therein), and crustaceans living on them may simply profit from the fact that their hosts are avoided; it remains to be tested if the symbiotic crustaceans perhaps even take up unpalatable compounds from their hosts. Many symbiotic decapods are kleptoparasitic, feeding on particles gathered by the host, and occasionally even feed on host tissue (e.g. Telford, 1982; Wirtz & Diesel, 1983; Fautin *et al.*, 1995). Some of them may simply be parasites.

The advantages for the host organisms, if any, are less clear. Smith (1977) observed defence of the anemone *Bartholomea*

*annulata* against the fire worm *Hermodice carunculata* by its symbiotic snapping shrimp *Alpheus armatus*. Spotte (1996) demonstrated elevated levels of ammonia between the tentacles of sea anemones harbouring symbiotic shrimps (presumably due to ammonia excretion by the shrimps); as experimental increase of ammonia concentration has been shown to benefit the zooxanthellae in the sea anemone's tissue, the presence of a symbiotic animal excreting ammonia apparently enhances zooxanthellae production and thus benefits sea anemones that harbour zooxanthellae (Holbrook *et al.*, 2008). See Wirtz (1997) and Goh *et al.* (1999) for a general discussion of possible costs and benefits of hosts and symbionts.

#### (4) The social structure of symbiotic decapods

Symbiotic crustaceans show a great variation in social structures, from solitary and pair-living to living in large groups (e.g. Dellinger *et al.*, 1997; Wirtz, 1997; Thiel *et al.*, 2003a; Baeza & Thiel, 2007; Baeza, 2008, and references therein). The same species may differ in social structure, depending on its host (Dellinger *et al.*, 1997). It appears to be the size and density of the host species that determines the social structure of the symbiont (Dellinger *et al.*, 1997; Thiel & Baeza, 2001; Wirtz & d'Udekem d'Acoz, 2001; Thiel *et al.*, 2003b). Very small hosts harbour single animals, as is the case of *Pontonia* species in *Pseudochama* and in *Spondylus*. Larger but defensible hosts are often occupied by a pair of associates (e.g. Knowlton, 1980; Dellinger *et al.*, 1997; Baeza, 2008), whereas the same species may live in groups of several adult and juvenile animals on still larger organisms (Dellinger *et al.*, 1997; Wirtz & d'Udekem d'Acoz, 2001). When the hosts live in high densities, the symbionts can switch hosts easily (in search of mates, for instance; cf. Diesel, 1986) but this becomes more difficult when host distance increases (cf. Thiel *et al.*, 2003a,b). Another factor determining symbiont group sizes and movement patterns is predation. When predation outside the protecting host is high, symbiont movement between hosts is reduced (Knowlton, 1980; Baeza & Thiel, 2007). In this study, predation between an inachid crab and a shrimp that were initially collected from the same sea anemone was observed. The effect of predation between different symbionts on the same host has not yet been explored.

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