

Crustacean symbionts of the sea anemone *Telmatactis cricoides* at Madeira and the Canary Islands*

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(With 2 figures in the text)

The crustacean symbionts of the club-tipped sea anemone *Telmatactis cricoides* (Duchassaing, 1850) were studied at Madeira ($n=81$ anemones) and the Canary Islands ($n=124$ anemones).

Of all anemones, 86% had crustacean symbionts. Nineteen species of crustaceans were encountered in association with *Telmatactis cricoides*. There were up to 18 individuals of up to four crustacean species associated with the same anemone. Anemone size and number of crustacean symbionts were positively correlated ($P<0.001$) but only weakly so ($r=+0.27$). The most common crustacean symbiont was the shrimp *Thor amboinensis*, encountered with 65% of all anemones.

Frequency and type of association with *Telmatactis cricoides* is described for each of the crustacean symbionts, *Thor amboinensis*, *Lysmata grabhami*, *Lysmata seticaudata*, *Eualus occultus*, *Brachycarpus biunguiculatus*, *Stenorhynchus lanceolatus*, *Homola barbata*, *Pilumnus villosissimus*, *Gnathophyllum elegans*, *Inachus phalangium*, *Heteromysis* sp. nov., *Palaemonella atlantica*, *Herbstia condyliata*, *Stenopus spinosus*, *Athanas nitescens*, *Dromia personata*, *Xantho incisus*, *Galathea* sp., *Liocarcinus* sp.

The shrimp *Lysmata grabhami* appears to live in stable pairs of two simultaneous hermaphrodites, a social structure not previously described for any crustacean species.

Introduction

Symbioses are common in the marine environment. Some taxa appear to be particularly likely 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 are particularly common (e.g. Balss, 1956–57; Patton, 1967).

The club-tipped anemone *Telmatactis cricoides* (Duchassaing, 1850) is the largest and most conspicuous sea anemone in the eastern Atlantic. The species occurs throughout the tropical Atlantic and in the eastern and central Mediterranean Sea; animals at Madeira and the Canary Islands are larger than in the rest of the distributional range, but no other morphological characters that would justify the recognition of a separate species have as yet been found (den Hartog, 1995). *Telmatactis cricoides* is variable in colour (cf. Wirtz, 1995) and is known to harbour crustacean symbionts that live either among the tentacles or on the column of the anemone or within a distance of only a few centimetres from the tips of the tentacles (Criales, 1979, 1984; Pérez Sanchez & Moreno Batet, 1991; Wirtz, 1991, 1995).

Three symbiotic complexes of sea anemones and crustaceans have so far been described in detail. Herrnkind, Stanton & Conklin (1976) characterized the Caribbean sea anemones *Lebrunia danae* and *Bartholomea annulata* and their associates. Six crustaceans, an ophiuroid and a fish were found with

* Dedicated to Prof. Dr Wolfgang Wickler on the occasion of his 65th birthday

Lebrunia danae; nine crustaceans were found with *Bartholomea annulata*. Abel (1961) and Diesel and Wirtz (In prep.) characterized the community living with the Mediterranean sea anemone *Anemonia sulcata*; 40 crustaceans and one fish species were recorded with *Anemonia sulcata*.

In a comparative study, the eastern Atlantic anemone *Telmatactis cricoides* and its crustacean symbionts were studied at Madeira and the Canary Islands. For data on the biology of *Telmatactis cricoides* see Wirtz (In press). The crustacean symbionts and their relation to the anemone are here described.

Material and methods

While SCUBA diving in a depth range of 1–62 m on approximately 400 dives during July 1993–August 1995, I examined every individual of *Telmatactis cricoides* that appeared larger than 3 cm in diameter. On an underwater writing board, that had a scale of 15 cm marked on it, I noted: the depth of the anemone and the presence of any crustaceans visible on or among the tentacles and within less than 5 cm distance from the tentacles. I then pinched one of the tentacle tips, which caused the anemone to contract. Additional crustaceans now visible on the column of the anemone were recorded. Small transparent shrimps of the genera *Eualus* and *Palaemonella* as well as tiny mysidaceans may have been overlooked on occasion; the other species are conspicuous enough to make this unlikely. With the scale on the writing board, the diameter of the column was measured along the longest axis of the ellipsoidally contracted animal.

The number of anemones surveyed at Madeira plus Porto Santo was 78 plus 3. The number of anemones surveyed at Tenerife (Playa Paraiso, south-western coast) was 100, at El Hierro (La Restinga, southern tip) 5, at Gran Canaria (El Cabron, eastern coast) 10, and at Lanzarote (Puerto del Carmen, southern coast) 9, giving a total of 205 anemones surveyed.

Voucher specimens of the crustacean species have been deposited at the Nationaal Natuurhistorisch Museum at Leiden, Netherlands (RMNH) and at the Museu Municipal do Funchal (História Natural) at Madeira (MMF). Colour photos of most of these species can be found in Wirtz (1995).

One subset of the data can be analysed for the frequency of co-occurrence of the symbiotic species (the other data sets are too small or were collected at locations too far apart from each other): 68 *Telmatactis cricoides* were surveyed along a shoreline of a few hundred metres in the area 'Playa Paraiso' at the south-western coast of Tenerife in July 1994. The expected values of co-occurrence of any 2 species are calculated as follows: if species A is encountered at 50% of all anemones and species B at 10% of all anemones, the expected value of co-occurrence is $0.5 \times 0.1 = 0.05$, i.e. 5% of all anemones. Expected and observed frequencies were then compared by chi-square test.

Results

Frequency of association and number of associates

Of the 205 anemones, 86% had crustacean symbionts. The percentage was not significantly different at the Canary Islands and at Madeira (90% vs. 81%, $\chi^2 = 2.37$, $P = 0.13$; Table I). Figure 1 shows the group-size frequency of symbionts, irrespective of species. The most common group size was one, but up to 18 individuals were recorded on an anemone and in the area directly around it. Average number of associates was 1.7.

Associated crustaceans frequently belonged to more than one species: 45% of the anemones with symbionts harboured two to four species at the same time.

Anemone size, anemone depth, and number of associates

All anemones larger than 12 cm diameter ($n = 47$) had crustacean symbionts. The number of associated crustaceans correlated weakly with anemone size, both at Madeira and the Canary Islands

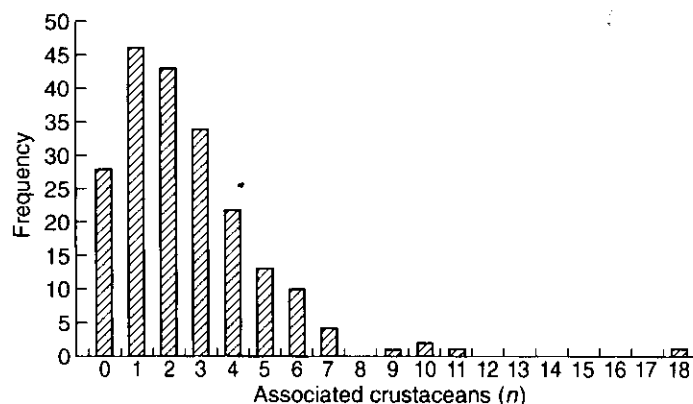


FIG. 1. Number of crustaceans per anemone ($n=205$ anemones at least 3 cm in diameter).

(Madeira $r=+0.47$, $P<0.001$; Canary Islands $r=+0.20$, $P=0.02$; total sample: $r=+0.27$, $P<0.001$). The shrimp *Thor amboinensis* frequently stayed on the substratum close to the anemone but without directly contacting it. Excluding this species, i.e. considering only the species that usually are in direct contact with either the column or the oral disk of the anemone, a much stronger correlation between anemone size and number of associated crustaceans can be detected at the Canary Islands ($r=+0.56$, $P<0.0001$), but not at Madeira ($r=+0.31$, $P<0.005$).

The number of associated crustaceans did not correlate with the depth of the anemone ($r=+0.12$, $P>0.07$).

Species accounts

Table I lists the most commonly associated species and the percentage of anemones harbouring them at Madeira and the Canary Islands.

(a) *Thor amboinensis*

Of the 205 *Telmatactis cricoides*, 59% had one or more *Thor amboinensis* associated with them. The incidence of this species at Madeira (67%) and at the Canaries (54%) did not differ significantly ($\chi^2=3.15$, $P=0.07$).

Figure 2 shows the group-size frequency of *Thor amboinensis* ($n=123$ anemones). Average group size was 2.3 *Thor amboinensis* per *Telmatactis cricoides*. Groups usually contained adult and much smaller individuals. Group size of *Thor amboinensis* associated with *Telmatactis cricoides* was unstable: during re-counts of the associates of the same anemones at intervals of a few days to a few weeks, the numbers of *Thor amboinensis* were never the same as recorded during the previous check.

Thor amboinensis were seen on the substratum in the immediate vicinity of the tentacles of the anemone, on the column of the anemone and occasionally even on the tentacles and on the oral disk of the anemone (cf. photo on page 104 in Wirtz, 1995). Contact between the shrimp and the tentacles did not elicit feeding reactions of the anemone.

At Madeira, *Thor amboinensis* can also be found associated with the snakelocks anemone *Anemonia sulcata* (Wirtz, unpubl.) and in small cracks in the rock face without cnidarian symbionts. *Thor amboinensis* is a circumtropical species that has been recorded with 13 different genera of sea

TABLE I

Associated species and the percentage of anemones with which they were found

Species	No. anemones	
	Madeira (%) (n = 81)	Canary Islands (%) (n = 124)
<i>Thor amboinensis</i>	67	54
<i>Lysmata grabhami</i>	15	33
<i>Lysmata seticaudata</i>	12	26
<i>Eualus occultus</i> and <i>Palaemonella atlantica</i>	12	7
<i>Stenorhynchus lanceolatus</i>	4	14
<i>Brachycarpus biunguiculatus</i>	4	9
<i>Homola barbata</i>	5	2
<i>Pilumnus</i> sp.	4	1
<i>Inachus phalangium</i>	1	0
<i>Stenopus spinosus</i>	0	1
<i>Gnathophyllum elegans</i>	1	0
<i>Herbstia condyliata</i>	1	1
<i>Xantho incisus</i>	0	1
<i>Athanas nitescens</i>	0	1
<i>Galathea</i> sp.	1	0
<i>Liocarcinus</i> sp.	0	1
All species	81	90

anemones (Fransen, 1989). Criales (1984) recorded the occasional association of western Atlantic *Thor amboinensis* and *Telmatactis cricoides* (using the synonym *Telmatactis rufa*).

(b) *Lysmata grabhami*

Of the 205 *Telmatactis cricoides*, 27% had one to three *Lysmata grabhami* associated with them.

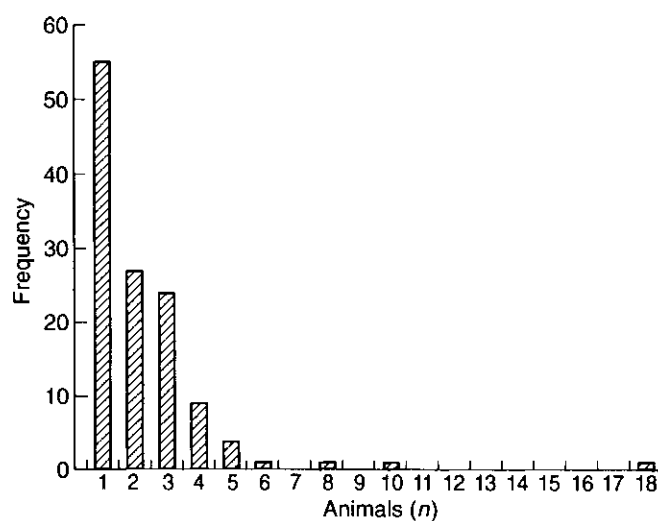


FIG. 2. Group-size frequency of *Thor amboinensis* on *Telmatactis cricoides* (n = 123 anemones).

The incidence of this species was significantly higher at the Canary Islands (33%) than at Madeira (15%): $\chi^2 = 7.58$, $P < 0.006$.

Lysmata grabhami also occurs in rock crevices without *Telmatactis cricoides*; usually then a moray eel inhabited the same crevice. The most common group size of *Lysmata grabhami* was two: 14 singletons, 26 pairs, and one triplet were encountered with *Telmatactis cricoides*, i.e. 52 of the 69 animals seen were in group size two. These pairs are not male-female pairs: almost always both animals carry eggs. Of the 35 pairs encountered (with and without *Telmatactis*), 19 consisted of two ovigerous animals, two consisted of an ovigerous and a much smaller non-ovigerous animal, and in the remaining 14 pairs the state of the animals was not recorded. In the single case of three *L. grabhami* encountered together with a *Telmatactis cricoides*, all three were ovigerous. The 17 singletons were three ovigerous animals, nine much smaller non-ovigerous animals (including juveniles of about 2 cm total length, which is their size at settlement) and five animals whose state was not recorded.

As egg-carrying animals could be either females or simultaneous hermaphrodites, six preserved specimens (three adult-sized and three smaller ones) were sent to Dr R. Bauer at the University of Southwestern Louisiana, who is currently engaged in a study of the sexual system of an American *Lysmata* species. After examining the species, he wrote "The pair of embryo-carrying 'females' you first sent (preserved in Bouin's) both had an ovotestis ... The other larger individual was not carrying embryos, but was otherwise similar ..., i.e. an apparently functional hermaphrodite". From his examination of the three smaller specimens, it appears that small individuals in this species are functional males with an appendix masculina, testis, vasa deferentia, and ejaculatory ducts. Large individuals turn into simultaneous hermaphrodites: the gonad becomes an ovotestis, i.e. with an ovarian part and a testicular part, each with its own set of ducts. As most animals live in pairs of two ovigerous individuals, it appears that the shrimp *Lysmata grabhami* lives in pairs of simultaneous hermaphrodites, a social structure not previously described for any crustacean.

Several pairs of *Lysmata grabhami* have now been observed in stable association with particular anemones for up to 13 months. *Lysmata grabhami* touching the tentacles of *Telmatactis cricoides* do not elicit feeding reactions of the anemone and do not show signs of having been stung by the anemone.

Lysmata grabhami is a cleaner shrimp (Limbaugh, Pedersen & Chace, 1961; Criales, 1979, van Tassel, Brito & Bortone, 1994; photo on page 91 in Wirtz, 1994). The most common "clients" at Madeira are the damselfish *Chromis limbata* and the pufferfish *Canthigaster rostrata*. When cleaning fish, *Lysmata grabhami* leaves the anemone for a distance of up to about 20 cm. Criales (1977, 1979) reported the association of western Atlantic *Lysmata grabhami* with *Telmatactis cricoides* (using the synonym *T. rufa*).

(c) *Lysmata seticaudata*

Of the 205 *Telmatactis cricoides*, 20% had one to six *Lysmata seticaudata*. Most commonly, solitary animals were encountered (20 of the 42 cases), with other group sizes in decreasing frequency (two: six cases, three: three cases, four: two cases, six: one case). The incidence of this species at the Canary Islands (26%) was significantly higher than at Madeira (12%): $\chi^2 = 4.65$, $P < 0.05$. Animals were always seen close to the column of the anemone. When *Lysmata seticaudata* came into contact with the anemone's tentacles, the tentacles did not cling to the shrimp and the shrimp showed no signs of being stung by the cnidocysts.

The association of *Lysmata seticaudata* with *Telmatactis cricoides* is not stable for prolonged periods: during re-counts of the associates of the same anemones at intervals of a few days to a few

months, *Lyssmata seticaudata* was no longer encountered with anemones where they had been recorded before. The species also occurs in cracks and crevices without sea anemones.

(d) *Eualus occultus* and *Palaemonella atlantica*

Nine percent of the 205 *Telmatactis cricoides* had one to three small transparent shrimps. Several samples from Madeiran and Canarian anemones, now deposited at RMNH and MMF, were identified as *Eualus occultus*. All small transparent shrimps associated with *Telmatactis cricoides* at the Canary Islands were initially recorded under this name, but subsequent identification of specimens revealed that, in addition to *Eualus occultus*, another small transparent species, *Palaemonella atlantica*, was also present on the column of *Telmatactis cricoides* at Tenerife, Canary Islands.

The incidence of these species at Madeira (12%) and at the Canary Islands (7%) was not significantly different ($\chi^2 = 0.96$, $P = 0.33$). Because of their nearly transparent body and the small size of the animals, both the frequency of association and the group size of *Eualus occultus* and *Palaemonella atlantica* were probably underestimated.

Animals of these species were seen on the column of the anemone and on the immediate substratum, but not in contact with the anemone's tentacles. Group size of *Eualus occultus* was unstable. During a recount of an anemone at Madeira, where two individuals had been recorded previously, eight were seen two months later.

(e) *Stenorhynchus lanceolatus*

Four percent of *Telmatactis cricoides* at Madeira and 14% of *Telmatactis cricoides* at the Canary Islands had one to four *Stenorhynchus lanceolatus* associated with them. The incidence of this species was significantly higher at the Canary Islands ($\chi^2 = 4.49$, $d.f. = 1$, $P = 0.03$). These large spider crabs were sitting near the anemone, facing outward, and were usually in contact with the anemone, placing one or two of the rear legs between the tentacles of the anemone. The tentacles of *Telmatactis cricoides* did not cling to the legs of *Stenorhynchus lanceolatus*. Figure 2 in Wirtz (1991) shows a *Stenorhynchus lanceolatus* with one of its legs between the tentacles of a *Telmatactis cricoides*.

(f) *Brachycarpus biunguiculatus*

Four percent of *Telmatactis cricoides* at Madeira and 9% of *Telmatactis cricoides* at the Canary Islands had a single *Brachycarpus biunguiculatus* on the substratum directly beside the base of the anemone.

(g) *Homola barbata*

Four times at Madeira and three times at the Canary Islands, a single *Homola barbata* was encountered below the tentacles of *Telmatactis cricoides*, sitting close to the column. Each of them held a small piece of sponge in its rear legs.

(h) *Inachus phalangium*

The only *Inachus phalangium* encountered with a *Telmatactis cricoides* during this survey (at Madeira) was a solitary female. During a re-count a few weeks later, two *Inachus phalangium* were seen at this anemone, a male-female pair (photo of this pair sitting on the oral disk of a white

Telmatactis cricoides on page 119 in Wirtz, 1995). A few days afterwards, the female was alone again. The same female (recognizable individually by the pattern of sponges growing on its carapace) remained on this anemone for four months until it disappeared. This indicates a social structure as described for a Mediterranean population of *Inachus phalangium* (Wirtz & Diesel, 1983; Diesel, 1986, 1988): stationary females are visited by roving males.

(i) *Heteromysis* sp. nov.

A small mysidacean with a light spot on the back was occasionally seen cruising around the column of *Telmatactis cricoides* at Madeira. A careful search of more than 40 anemones at Tenerife did not reveal this species, which may be endemic to Madeira. Because of its small size, the species was noted only some time after the beginning of the survey and its presence was not quantified. A subjective estimate is that about 10% of the *Telmatactis cricoides* at Madeira had this species associated with them. When it was present, there were always several individuals. In contrast to the western Atlantic *Heteromysis actiniae*, associated with the sea anemone *Bartholomea annulata* (see Clarke, 1955), the Madeiran mysids were never seen among the tentacles of the anemone. Prof. Wittmann of Vienna University has informed me that the Madeiran species is an undescribed species of the genus *Heteromysis*, closely related to *Heteromysis actiniae*.

(k) Other species

Single individuals of other species of crustaceans were occasionally encountered at the column of *Telmatactis cricoides* (cf. Table I). These were the following: *Pilumnus* sp. (recorded once at Porto Santo, once at Madeira, and once at Tenerife), *Gnathophyllum elegans* (recorded once at Madeira; when resurveying an anemone already recorded in the main study area, two individuals of *Gnathophyllum elegans* were seen and these two animals continued to be associated with this particular anemone for about two weeks), *Herbstia condyliata* (recorded once each at Madeira and at Tenerife), *Stenopus spinosus* (recorded once at Tenerife), *Xantho incisus* (recorded once at Tenerife), *Athanas nitescens* (recorded once at Lanzarote and recorded once at Madeira during a recount of an anemone), *Galathea* sp. (recorded once at Madeira), *Liocarcinus* sp. (recorded once at Tenerife). During a re-count of an anemone at Madeira, a juvenile *Dromia personata* was seen clinging to the column of the anemone. The *Pilumnus* sp. at Porto Santo was collected and identified as *Pilumnus villosissimus* (C. H. J. M. Fransen, pers. comm.), but it cannot be stated with certainty that all *Pilumnus* seen with *Telmatactis* belonged to this species.

All these species are commonly encountered free-living and are obviously facultative associates of *Telmatactis cricoides* on rare occasions only (*P. villosissimus* has been noted by García Raso & Barrajón (1982) "at the base, below the tentacles of large anemones" at the south coast of Spain, the anemone presumably being *Anemonia sulcata*). As all these occasional associates were found either clinging to the column of the anemone or beside the base of the anemone, it is unknown if they would or would not be stung when coming into contact with the tentacles.

Interrelation of species

Table II gives the expected and the observed values for the co-occurrence of the three most common associates on the same anemone for a population at Playa Paraiso, Tenerife, in July 1994 ($n=68$ anemones surveyed). *Thor amboinensis* and *Lysmata grabhami* occurred together less often than expected from their frequencies, but the difference was not statistically significant (Table II).

TABLE II

Observed and expected frequencies of co-occurrence of the three most common symbionts (Playa Paraiso, Tenerife, July 1994)

Co-occurrences (<i>n</i> anemones):	Obs.	Exp.	χ^2	<i>P</i>
<i>Thor amboinensis</i> – <i>Lysmata grabhami</i>	4	9.8	0.6	0.44
<i>Thor amboinensis</i> – <i>Lysmata seticaudata</i>	11	9.8	0	1
<i>Lysmata grabhami</i> – <i>Lysmata seticaudata</i>	5	6.5	0	1

n anemones surveyed = 68
 with *Thor amboinensis* = 32
 with *Lysmata grabhami* = 21
 with *Lysmata seticaudata* = 21

The size distributions of the anemones harbouring the three most common species of crustacean symbionts differed. Median size of anemones with *Lysmata grabhami* was significantly larger than median size of anemones with *Lysmata seticaudata* (13 cm vs. 10 cm, $P < 0.05$, rank test) and significantly larger than median size of anemones with *Thor amboinensis* (13 cm vs. 9 cm, $P < 0.001$, rank test).

The depth distributions of the three most common crustacean species associated with *Telmatactis cricoides* (*Thor amboinensis*, *Lysmata grabhami* and *Lysmata seticaudata*) did not differ significantly (rank tests, all $P > 0.08$).

Discussion

Crustaceans symbiotic with sea anemones

Three symbiotic complexes of sea anemones and crustaceans have so far been described in detail. Herrnkind *et al.* (1976) characterized the Caribbean sea anemones *Lebrunia danae* and *Bartholomea annulata* and their associates. Abel (1961) and Diesel & Wirtz (In prep.) characterized the community living with the Mediterranean sea anemone *Anemonia sulcata*. Six crustaceans, an ophiuroid and a fish were found with *Lebrunia danae*; nine crustaceans were found with *Bartholomea annulata*; 40 crustaceans and one fish species were recorded with *Anemonia sulcata*. No fish or echinoderms were encountered with *Telmatactis cricoides*. With 19 associated crustacean species, *Telmatactis cricoides* appears to harbour the second largest symbiotic community so far recorded. Respectively, 75% and 84%, of the *Lebrunia danae* and *Bartholomea annulata* harboured at least one crustacean symbiont, values similar to the 86% recorded for *Telmatactis cricoides* in the present study.

Associations of mysid shrimps with sea anemones have so far only been reported from the western Atlantic (Clarke, 1955). The record of an undescribed species of the genus *Heteromysis* associated with a sea anemone is the first such record from another area.

Types of associations

Associations between crustaceans and *Telmatactis cricoides* are either facultative or obligatory, short-term or lasting. Facultative associations are probably the first evolutionary step towards more enduring symbioses. Facultative associates that are already either immune to the stinging action of the anemone, or do not elicit a stinging action of the sea anemone (such as *Sthenorhynchus lanceolatus*,

for instance), are pre-adapted to evolve long-term associations. The observation of facultative associates that constantly have to avoid contact with the anemones' tentacles, lest they be stung, shows a second pathway in the evolution of long-term associations: association first and acquisition of protection against cnidocytes afterwards.

Costs and benefits of the associations

In interspecific associations both organisms may profit (mutualism), or one organism may profit while the other has either no (commensalism) or considerable (parasitism) cost.

For *Inachus phalangium*, Wirtz & Diesel (1983) have shown that the crustacean derives protection from the association with the sea anemone *Anemonia sulcata*: crabs on anemones are protected against predators such as fish and octopuses, while crabs removed from anemones are immediately eaten when detected. Protection against predators is likely to be the main advantage for all crustaceans associated with *Telmatactis cricoides*. Two incidences of predation on *Lysmata grabhami* by *Serranus atricauda* occurred when scuba divers enticed the shrimp to leave the neighbourhood of the anemone: the grouper darted forward and grabbed the shrimp (S. Kärnsch, Tenerife, and T. Baumeister, Madeira, pers. comms).

Fautin, Guo & Hwang (1995) demonstrated that, even in the absence of predators, the growth, longevity and fecundity of *Periclimenes brevicarpalis* are enhanced by living with a sea anemone. When associated with *Anemonia sulcata*, the crab *Inachus phalangium* eats food regurgitated by the anemone and mucus from the surface of the anemone and even crops the tips of the tentacles of the anemone (Wirtz & Diesel, 1983). Similar behaviour was seen by Patton (1979) for the crab *Mithrax cinctimanus*, living in association with the anemone *Stoichactis* in the Caribbean. Mediterranean *Periclimenes* associated with sea anemones also scrape mucus from the surface of their host (Svoboda & Svoboda, 1975) and the Indopacific *Periclimenes brevicarpalis* also tears tentacles from its anemone host and eats them (Fautin *et al.*, 1995 and references therein). No such observations have been made on crustaceans associated with *Telmatactis cricoides*.

A reduction in mobility, leading perhaps to a restriction in food supply and restricted possibilities in mate acquisition, could be the cost of association with a sea anemone in obligate symbionts. For the crab *Inachus phalangium*, Diesel (1986) showed that males rove between anemones at night, even though during daytime both males and females were obligate symbionts of *Anemonia sulcata* in the population studied.

The presence of crustacean symbionts is not obligatory for any of the sea anemones studied. From the anemone's point of view, costs of associated crustaceans could be parasitic behaviour of the symbionts, such as the cropping of tentacles mentioned above. An advantage for the anemone could be defensive behaviour of the crustacean symbiont against predators of the anemone. Smith (1977) observed defence of the anemone *Bartholomea annulata* against the fire worm *Hermodice carunculata* by its symbiotic snapping shrimp *Alpheus armatus*. *Hermodice carunculata* is common at Madeira and the Canary Islands and an act of predation on a *Telmatactis cricoides* (without symbionts) was observed. No encounters between *Hermodice carunculata* and crustacean symbionts of *Telmatactis cricoides* have been observed. Such encounters could be staged in the field or in the aquarium. Herrnkind *et al.* (1976) suggested that the snapping shrimp *Alpheus armatus* keeps its anemone *Bartholomea annulata* from being buried by sediment shifted about by the surge action of large storm swells. Spotte (1996) demonstrated ammonia excretion by symbiotic shrimps and elevated levels of ammonia between the tentacles of sea anemones harbouring shrimps; as experimental increase of ammonia concentration has been shown to benefit the zooxanthellae of sea anemones (references in

Spotte, 1996), the presence of a shrimp probably enhances zooxanthellae production. *Telmatactis cricoides*, however, does not have zooxanthellae (den Hartog, 1995) and Spotte's reasoning therefore does not apply to symbioses with this anemone species.

The borderline between mutualistic and parasitic associations of crustaceans and sea anemones could be very narrow. The same association could well be either parasitic or mutualistic, depending on environmental conditions. A mutualistic association in an environment with many predators of anemones could turn into a parasitic one during periods of food shortage for the crustacean (see also discussion in Fautin *et al.*, 1995).

Mechanism of protection against the anemones' cnidocytes

Obligate relations with stinging sea anemones are an important part of the life history of numerous Indopacific damselfishes (Fautin & Allen, 1992). Several species of the fish families Labridae, Scaridae, Labrisomidae, Apogonidae, Haemulidae, Oxylebidae and Gobiidae enter facultative associations with sea anemones (Abel, 1961; Schlichter, 1970; Hanlon & Kaufmann, 1976; Hanlon, Hixon & Smith, 1983; Fautin & Allen, 1992). As in crustaceans, these fish species fall into two groups: some species can come into contact with the tentacles of the anemone without being stung, others must continuously avoid contact with the tentacles. Despite more than two decades of studies (Mariscal, 1970; Schlichter, 1976; Lubbock, 1980; Miyagawa, 1980, 1989; Murata *et al.*, 1986), it is still not entirely clear why the fish species that can come into contact with tentacles do not elicit a stinging reaction. The reason is probably a combination of innate features of the fish species (Lubbock, 1980; Miyagawa, 1989) and transfer of mucus from the host on to the symbiont (Schlichter, 1976), but the precise mechanism may be different in different species (Miyagawa, 1989; Fautin, 1991) and may even be different at different ages of the fish species.

Little is known about the mechanism protecting crustaceans that can come into contact with the tentacles of sea anemones without being stung. As with anemonefishes, this is likely to be a combination of innate and acquired features of the crustacean symbiont. Acquired protection is indicated by experiments of Levine & Blanchard (1980) and of Crawford (1992): after isolation of several days, the Caribbean shrimps *Periclimenes rathbunae* and *P. anthophilus* elicited stinging behaviour in their host anemone species and needed 1–5 hours to re-acclimatize to their host anemones. In contrast, Fautin *et al.*, (1995) did not see acclimatization behaviour after 30 days of separation of *Periclimenes brevicarpalis* from its anemone host.

An essential difference between fish and crustaceans is moulting in the latter (but note that spider crabs of the family Majidae—a group particularly common among crustacean symbionts of sea anemones—do not moult again after a final moult of puberty (Hartnoll, 1963)). Crustacean species with an innate protection may be able to moult on the anemone, while crustaceans with acquired protection probably will have to leave the anemone for moulting and then will have to re-acquire protection.

A combination of a mechanical and a chemical stimulus is required to set off the discharge of cnidocytes (Thorington & Hessinger, 1988). Shrimps and crabs crawling over the tentacles of anemones provide mechanical stimulation—apparently they do not provide the appropriate chemical stimulus. Crawford (1992) suggests that secretions from the integument of symbiotic shrimps contribute to their protection. Puetz & Buchholz (1991) have shown substantial differences in thickness and composition of the cuticle of various decapod species. A histochemical comparison of the cuticle of crustaceans symbiotic with sea anemones and of their free-living relatives would appear to be a worthwhile study.

Social structure of associated crustaceans

Male-female pairs are commonly encountered in crustaceans associated with invertebrates (e.g. Castro, 1971; Seibt & Wickler, 1979; Knowlton, 1980; Patton, 1994), a situation frequently called 'monogamy' even in the absence of data on the mating patterns of the individuals (Wickler & Seibt, 1981). In other cases, females show a stable association with an invertebrate host, while males visit various females (e.g. Diesel, 1986, 1988). Some species occur in groups of several individuals per host (e.g. Patton, Patton & Barnes, 1985; Nizinski, 1989; Patton, 1994).

The two most common associates of *Telmatactis cricoides* had different social structures. *Thor amboinensis* occurred in unstable groups of up to 18 individuals including juveniles. A related species, *Thor manningi*, is a partial protandric hermaphrodite (Bauer, 1986).

Of the 19 species encountered with *Telmatactis cricoides*, *Lysmata grabhami* was the only crustacean showing a stable association with this sea anemone. *Lysmata grabhami* has a social structure not found in any crustacean species. It is commonly encountered in pairs of simultaneous hermaphrodites. Protandrous hermaphroditism has been observed in a congeneric species and is common in many shrimp species (Dohrn, 1950; Noel, 1973). As small *Lysmata grabhami* are pure males, the individuals of this species apparently retain their male faculties when turning female.

Pair-living of *Lysmata grabhami* had been noted in western Atlantic populations and such pairs were assumed to be male-female pairs (Limbaugh *et al.*, 1961; Criales, 1977, 1979). Simultaneous hermaphrodites have even less need to live in pairs than animals with separate sexes, because any other adult conspecific can serve as a partner for reproduction. Unless the species lives at very low population densities, the evolutionary reason for pair-living in a simultaneous hermaphrodite is likely to be other than reproductive advantages. The only other pair-living simultaneous hermaphrodite reported in the literature is a fish, *Serranus tigrinus*, in which the pair partners hunt co-operatively (Pressley, 1981). A more detailed study of the social system of *Lysmata grabhami* is in progress.

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