Aqaba-Eilat, the Improbable Gulf

Environment, Biodiversity and Preservation

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The Hebrew University of Jerusalem

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14. Biodiversity and behavior of shrimps and fishes symbiotic with sea anemones in the Gulf of Aqaba, northern Red Sea

(color plates pp. 238-239)

Chadwick N.E., Duriš Z. and Horká I.

Introduction

Giant sea anemones are conspicuous members of coral reef communities in both the Indo-West Pacific (IWP) and Atlantic regions, and serve as hosts to a diverse assemblage of symbiotic crustaceans and fish (Bruce, 1976a,b; Hanlon and Kaufman, 1976; Herrnkind et al., 1976; Brolund et al., 2004; Khan et al., 2004). These associations may be ecologically important in that some obligate anemoneshrimps serve as cleaners of ectoparasites from large reef fish (Sargent and Wagenbach, 1975; Nizinski, 1989; Becker and Grutter, 2004).

Most reports of associations between sea anemones and shrimps in the IWP are systematic; little is known concerning quantitative aspects, types of association (commensal, mutualistic, parasitic) in terms of costs and benefits to the associates, or other ecological or behavioral aspects. Costs and benefits of the association between the IWP shrimp Periclimenes brevicarpalis (Schenkel) and the sea anemone Entacmaea quadricolor (Rüppell et Leuckart) were examined by Fautin et al. (1995) who indicated potential parasitism by the obligatory shrimp on the anemone host under conditions of low food availability. That also was reported for the same shrimp and Periclimenes ornatus Bruce by Suzuki and Hayashi (1977), and for the latter by Ono et al. (1994). A survey of host selection by shrimps was presented by Guo et al. (1996), in which P. ornatus was considered a specialist of E. quadricolor, Thor amboinensis (De Man) a general symbiont, and P. brevicarpalis intermediate in specificity. It was observed in the latter study that P. ornatus and P. brevicarpalis formed usually single male-female pairs on 2 or 4 (respectively) different species of anemones, while another shrimp, Periclimenes vemarius Bruce, occurred as at least 25 individuals on each host anemone Heteractis aurora (Quoy et Gaimard), and T. amboinensis as up to 11 individuals per anemone Stichodactyla haddoni (Hemprich et Ehrenberg).

The occasionally parasitic behavior of P. brevicarpalis noted above was confirmed also by Khan et al. (2004) during laboratory studies on spatial distributional patterns of Australian specimens of Periclimenes holthuisi Bruce, P. brevicarpalis, and T. amboinensis on the sea anemone Stichodactyla haddoni (Saville-Kent). All of these shrimps prefer to occupy outer tentacles on the anemone during the daytime, which could

be explained by their feeding practices since these crustaceans clipped and ate parts of the tentacles. *P. holthuisi* moved from the outer tentacles to either the column or off the contracted anemones at night. The spatial and temporal distribution of the shrimps thus depended on their feeding activities and on the degree of anemone expansion.

Studies on symbioses between sea anemones and shrimps in the Red Sea have been only fragmentary (Bruce and Svoboda, 1983), while several studies of fish associations, previously rare (Fishelson, 1965; Fricke, 1974, 1983), have appeared in recent years (Brolund et al., 2004; Porat and Chadwick-Furman, 2004, 2005; Chadwick and Arvedlund, 2005). We quantify here the biodiversity and abundance of shrimps and fish associated with sea anemones in the Gulf of Aqaba, northeastern Red Sea, as well as aspects of their behavior.

**Materials and Methods**

The main study site consisted of coral patch reefs and coral communities on beach rock at 0-30 m depth along approximately 300 meters of shoreline adjacent to the H. Stenitzz Marine Biology Laboratory, Interuniversity Institute (IUI), Eilat, Israel, examined during November 2001 (site description in Chadwick and Arvedlund, 2005). Additional data were recorded from the northern end of the Mashraba coral reef at Dahab, and the coral reef at Ras Mohammad, Egypt, visited in December 2001 and 2002. Divers (ZD and IH) located giant sea anemones by searching for the anemonefish *Amphiprion bicinctus* Rüppell swimming over the reef, and by using (NEC) detailed underwater maps with marked locations of previously numbered anemones. The maximum depth examined at all sites was 30 meters.

The following data were collected on all sea anemones examined at each site: species, outer diameter of oral disc with tentacles (tentacle crown diameter, after Chadwick and Arvedlund, 2005), depth below sea level, number of individuals of each associated species of fish and shrimp, and notes on their behavior and position on or near the host sea anemone. Selected shrimp specimens were collected and transferred to the laboratory at the IUI for closer identification and sex determination. Underwater videos were recorded to document shrimp position, behavior and type of association. A limited series of shrimp specimens was preserved for later taxonomic confirmation of field identifications. Preserved material was deposited in Z. Duris' laboratory at the University of Ostrava, Czech Republic, with final deposition in the Zoological Collections of Tel Aviv University.

**Results**

During field surveys, we collected data on 73 individuals of giant sea anemones belonging to five species (Plate 1 Figs. A-E, color plate p. 238), and associated individuals of nine species of caridean shrimps (Crustacea; Decapoda) (Plate 2, Figs.
A-I, color plate p. 239), one species of opossum shrimp and three fish (Tables 1-3). The sea anemones that hosted the largest numbers of shrimp species were *Heteractis crispa* (Ehrenberg) and *Entacmea quadricolor,* each providing living space to five species of anemone shrimp (Table 1). In addition, *E. quadricolor* frequently was occupied by two species of fishes and was the anemone host to most commonly contain co-occurring fishes and shrimps (Table 2). Six shrimp species occurred with *Cryptodendron adhaerensum* Klunzinger, but at least two of them were accidentally associated, each as one specimen. The number of individual shrimps and fishes to occur on each host anemone varied widely among the anemones examined, mainly due to facultative shrimps such as *Periclimenes longicarpus* Bruce et Svoboda that sometimes occurred in groups of numerous specimens (Figs. 1 and 2). The obligatory-associated shrimps (*P. brevicarpalis,* *P. ornatus*) and fishes (*Amphiprion bicinctus*) usually were present within each host as a pair of heterosexual adults, in some cases

<table>
<thead>
<tr>
<th>Shrimps and fishes</th>
<th>Cryptodendron adhaerensum</th>
<th>Entacmea quadricolor</th>
<th>Heteractis crispa</th>
<th>Megasquilla hirsuta</th>
<th>Sclerodactyla haastioru</th>
<th>Number of sea anemone species</th>
<th>Other types of hosts</th>
<th>Observed leaving sea anemone</th>
<th>Association with sea anemones</th>
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<td>4</td>
<td>6</td>
<td>2</td>
<td>4</td>
<td>Diadema x</td>
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<td></td>
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<tr>
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<td>8</td>
<td>8</td>
<td>2</td>
<td>4</td>
<td>Paragrene x</td>
<td>FR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. ornatus</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
<td>O</td>
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<td></td>
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<tr>
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<td>Idionysis sumati</td>
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<td>Number of shrimp species</td>
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<td>5</td>
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<td>52.2</td>
<td>11.2</td>
<td>80.0</td>
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<tr>
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<td>3.4</td>
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<td>2.4</td>
<td>3.5</td>
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<tr>
<td>Number of fish species</td>
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<td>0</td>
<td>3</td>
<td></td>
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<tr>
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<tr>
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<td>0</td>
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<tr>
<td>SD # fishes per sea anemone</td>
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<td>0.7</td>
<td>0.7</td>
<td>0</td>
<td>0</td>
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</tbody>
</table>

Table 1. Number of sea anemones observed with associated shrimps and fishes at sites in the Gulf of Aqaba, northern Red Sea. Note that some individual sea anemones were occupied by more than one species of shrimp and/or fish. O = obligate, F = facultative, R = regular, A = accidental. N = number of individuals examined of each sea anemone species. *See Debelius (1999, pages 270 and 289).*
with juveniles.

The mysid, or opossum, shrimp (Crustacea: Mysidacea) *Idiomysis tsurunamali* Bacescu was recorded with the sea anemones *Megalaactis hemprichii* Ehrenberg and *C. adhaesivum*, but also with the sea urchin *Diadema setosum* (Leske). This mysid species originally was reported also from the benthic medusa *Cassiopea* (Bacescu, 1973).

Maximal numbers of conspecific shrimps to occur within single anemone hosts (Fig. 2) were observed for *P. longicarpus* (14 specimens), *Kemponia tenipes* (Borradaile) (12), and *Thor amboinensis* (7) on individuals of the anemone *C. adhaesivum*. Next in order was *P. longicarpus* (8 specimens) on *H. crispa*, the same shrimp (7) on *E. quadricolor*, and *T. amboinensis* (8) on *M. hemprichii*. Eight specimens from the 14-specimen group of *P. longicarpus* above were collected to determine sex composition,
of which six were females and two were males. In the eight-specimen group on *H. crispa*, six males and two females were found. Both samples were from depths of 10-11 m.

The shrimp species that occupied the highest percent of individual host anemones were *T. amboinensis* on *C. adhaesivum* (on 90% of all *C. adhaesivum* anemones, n = 10) and on *M. hemprichii* (80%, n = 5), *P. longicarpus* on *E. quadricolor* (35%, n = 23) and on *H. crispa* (24%, n = 34), and *K. tenuiipes* also on *H. crispa* (24%), and on *C. adhaesivum* (50%).

Of the anemones that contained shrimps, the shrimp species that most frequently occurred (the dominant shrimp species) were *P. longicarpus* on *E. quadricolor* (present on 67% of n = 12 *E. quadricolor* anemones that were occupied by shrimps) and on *H. crispa* (58%, n = 14), and *T. amboinensis* on *M. hemprichii* (100%, n = 4) and on *C. adhaesivum* (90%, n = 10). *K. tenuiipes* shrimps occurred with all anemone species except for *Stichodactyla haddoni*, and occurred on occupied hosts in frequencies ranging from 33% on *E. quadricolor* to 57% on *H. crispa*.

The largest shrimp assemblage on a single sea anemone host was of 30 individual shrimps (14 *P. longicarpus*, 12 *K. tenuiipes*, 2 *T. amboinensis*, 2 *Stenopus hispidus* [Olivier]) on *C. adhaesivum* (Eilat, 13 November 2002, depth 11 m). When examined the day before, the same anemone had hosted 23 shrimps (11, 5, 5 and 2 specimens, respectively). In addition, a large individual of the anemone *H. crispa* in close vicinity to the *C. adhaesivum* above it (distance 1 m, depth 10.3 m, recorded on 13 November 2002) hosted 10 shrimps (*P. longicarpus* and 2 *K. tenuiipes*). We observed movement of individuals of *P. longicarpus* between these adjacent anemones, thus an assemblage of 40 shrimps total occurred on this pair of sea anemone hosts of different species.
The depth distributions of associated shrimps and fishes varied with those of their sea anemone hosts (Fig. 3).

Some species of shrimps coexisted on individual anemones with others (Table 3). *K. temnipes* usually co-occurred with *T. amboinensis* or *P. longicarpus*, and *S. hirsuta* was observed in most cases with *T. amboinensis*. Interestingly, the two main anemone-obligate *Periclimenes* shrimps, *P. ornatus* and *P. brevicarpalis*, never co-occurred, and only rarely coexisted with any other shrimp species on individual sea anemones. On the three anemone species that hosted fishes (*E. quadricolor, H. crispa*, and *S. haddont*), the fish often co-occurred with anemoneshrimps (Table 3). The anemonefish *A. bicinctus* most frequently coexisted with the shrimps *P. longicarpus* and *K. temnipes*, while shrimp occurrence with the two-spot damselfish *Dascyllus trimaculatus* (Rüppell) was recorded rarely, and only on the anemone *E. quadricolor*.

We observed signaling behavior in situ by the shrimp *P. longicarpus* - sideward
body swaying and waving of the second pair of legs. In some cases when divers 
examined sea anemones, specimens of *P. longicarpus* swam to approach the diver and 
continued to sway while swimming. Video recordings revealed that they exhibited a 
continuous sideward body swaying in cycles of 1.45 – 2.66 s⁻¹ (Table 4). The swaying 
motion decreased in speed throughout the day; it was more rapid during the morning 
(examined at 10:00 – 10:05) than in the early afternoon (examined at 12:03 – 14:20), 
and evening (examined at 16:03-16:11). The speed also varied among locations; it 
appeared to be faster on the anemone tentacles than when the shrimps were on 
adjacent dead coral or swimming toward divers in open water.

Individuals of *P. longicarpus* also signaled via rapid waving of their large, white-

banded second pericopod legs. These antero-ventrally hanging, claw-bearing legs 
vibrated rapidly from side to side, shortly crossing each other at their innermost 
extent. Analysis of 10 signaling series from *in situ* video recordings showed that the 
duration of these bouts of signaling vibrations ranged from 0.36-2.88 s per bout. The 
cycle length of each vibration approached the resolution speed of the video frames 
(0.04 s), so the exact speed of this rapid vibratory behavior was not estimated.

We also observed individuals of the shrimp *T. ambloinensis* to wave their abdomens 
in the vertical plane when approached. *In situ* and laboratory video records revealed
that the speed of this waving behavior was highly variable and occurred at a rate of at least 2-4 seconds per cycle (Table 4).

Discussion

Our analyses of patterns of association and behavior reveal that two types of true (= frequent) anemone associates occur among shrimps of the genus *Periclimenes* in the northern Red Sea. The first type is represented by the shrimps *P. brevicarpalis* and *P. ornatus*, which form obligate symbioses (Suzuki and Hayashi, 1977; Guo et al., 1996) of one mated pair of shrimps per anemone host, do not leave the body of the anemone, and territorially exclude most other associates. In contrast, the second type

<table>
<thead>
<tr>
<th>Frequency [%], number of co-occurrences (in parentheses)</th>
<th>K. tenuepis</th>
<th>P. brevicarpalis</th>
<th>P. longicarpus</th>
<th>P. ornatus</th>
<th>R. durbanensis</th>
<th>S. marmoratus</th>
<th>S. hispidus</th>
<th>T. ambioensis</th>
<th>U. antrobranui</th>
</tr>
</thead>
<tbody>
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<td>42.1 (8)</td>
<td>5.3 (1)</td>
<td>5.3 (1)</td>
<td>5.3 (1)</td>
<td>5.3 (1)</td>
<td>5.3 (1)</td>
<td>42.1 (8)</td>
</tr>
<tr>
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<td>n</td>
<td>10.5 (2)</td>
<td>10.5 (2)</td>
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<td>10.5 (2)</td>
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<td>10.5 (2)</td>
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<td><em>Periclimenes longicarpus</em></td>
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<td>10.5 (2)</td>
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<td>10.5 (2)</td>
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</table>

Table 3. Co-occurrence among caridean shrimp species associated with sea anemones at sites in the Gulf of Aqaba, northern Red Sea. Black diagonal squares = total number of individuals observed of each shrimp species. Numbers above diagonals = number of co-occurrences (in parentheses), and percent of co-occurrences related to each species in the left column number of occurrences. Numbers below diagonals = percent of co-occurrences related to each species in the top row number of occurrences. n = not calculated, if total number of occurrences was < 5.

<table>
<thead>
<tr>
<th>Periclimenes longicarpus</th>
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<tbody>
<tr>
<td>N of shrimps</td>
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<td>Time of day</td>
</tr>
<tr>
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<td>Afternoon</td>
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<td>Evening</td>
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<table>
<thead>
<tr>
<th>Location relative to host</th>
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</thead>
<tbody>
<tr>
<td>On adjacent dead coral</td>
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<tr>
<td>Swimming in open water</td>
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<tr>
<td>On anemone tentacles</td>
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<table>
<thead>
<tr>
<th>Thor amboinensis</th>
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<tbody>
<tr>
<td>In situ</td>
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<td>In aquaria</td>
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</table>

Table 4. Variation in the speed and duration of lateral body-swaying behavior exhibited by individuals of the shrimp *Periclimenes longicarpus* under different conditions (time of day, location relative to sea anemone host, and species of host), and of abdomen waving behavior by individuals of the shrimp *Thor amboinensis* under field and laboratory conditions in the Gulf of Aqaba, northern Red Sea. Cycle = one complete sway or waving motion; series = a group of behavioral cycles exhibited in continuous sequence; s = time in seconds.
is represented by *P. longicarpus* which regularly occurs with anemones in large social groups but may move nocturnally off the host anemone, co-occurring which some other associates, and exhibits signaling behavior related to fish cleaning.

Individuals of *P. brevicarpalis* and *P. ornatus* belong to the “brevicarpalis” group of closely-related species within the genus *Periclimenes*, which includes at least three other IWP shrimps (Bruce and Svoboda, 1983; Bruce and Coombes, 1997). Our observations here and records from the literature indicate that members of this species group occur as 1-2 adult specimens (male-female pair) per individual anemone host (Fautin et al., 1995; Guo et al., 1996). They are anemone specialists, and never occur on other invertebrates. Members of these species do not, or very rarely, co-occur with one another (*P. brevicarpalis* occurs rather frequently with *P. albolineatus* in Vietnam – I. N. Marin, pers. comm.), but more often with other shrimp species on individual anemone hosts. Infrequently they may share their hosts with anemonefishes. As known for anemonefishes, mutualistic interactions are not expected to promote the coexistence of competitors, because mutualisms produce positive feedbacks on abundances whereas coexistence requires negative feedbacks (Schmitt and Holbrook, 2003). We conclude that individuals of *P. brevicarpalus* and *P. ornatus* are highly territorial, in that the mated pair within each anemone defends this territory against all other conspecific intruders, and, possibly, most other shrimps and fishes, as known for some other obligate crustacean associates of cnidarian hosts (Castro, 1976).

Members of the “brevicarpalis” group of anemoneshrimps restrict their microhabitat use exclusively to the body of the host sea anemone. They locomote by walking or climbing on the host surface, and leave this surface to swim only if they are disturbed (Omori et al., 1994; Khan et al., 2004; ZD, personal observation). We did not observe members of this species group to exhibit swaying of the body or signaling using pereiopods, and no cleaning behavior has been reported for these species. However, individuals of *P. brevicarpalis*, the only markedly-colored shrimp within the group, were reported to swing their bodies (Bruce, 1976b; Bruce and Svoboda, 1983). In some cases, *P. brevicarpalis* were also observed eating the tips of anemone tentacles (Bruce and Svoboda, 1993; Fautin et al. 1995, Khan et al. 2004). Thus, this species may be classified as an obligate commensal or mutualist, but also may facultatively parasitize the anemone host. Relations with anemone hosts of the other shrimps belonging to the “brevicarpalis” group have not been well documented but may be similar.

In contrast, the second type of true anemone associate, the shrimp *P. longicarpus*, forms social groups of up to 14 individuals per anemone host, and may move among the hosts, leading to variation in the number of individuals per host from day to day. This shrimp associates with a wide range of sea anemone host species (Bruce and Svoboda, 1983), and we also observed single specimens on colonies of the bubble coral *Plerogyra* sp. (ZD and IH, personal observation, Elat, November 2002, 3 records, at 19-20.5 m depth; Dahab, December 2002, 1 record, 25 m depth). Individuals of *P. longicarpus* often co-occur with other shrimps, mainly *Kemporia tenipes* and *Thor amboinensis*, and with the anemonefish *Amphiprion bicinctus*. In terms of microhabitat use, during the daytime *P. longicarpus* specimens freely move
on the host tentacles, swim around them, and perch on reef substrate in the vicinity of the anemone. At night they may leave the host, as also reported for the closely-related *P. holthuisi* Bruce (Khan et al., 2004), and may move to other anemones.

The patterns of host specificity for *P. longicarpus* are similar to those reported by Bruce and Svoboda (1983), who initially described this species from the Gulf of Aqaba as associated with the host anemone *Entacmaea quadricolor,* and also reported specimens at Al Ghardaqa from *Heteractis aurora* (Quoy & Gaimard) and *Megalactis hemprichii* at depths to 30 m.

*P. longicarpus* belong to the “aesopus” group of 15 IWP shrimp species within the genus *Periclimenes* (Okuno, 2004; Bruce, 2005; 2008, also termed the “holthuisi” group – e.g. Bruce 2003). Behavioral observations on members of this group are rare. Sideward swinging body movement has been described by Suzuki and Hayashi (1977) for *P. holthuisi,* and later by Okuno and Nomura (2002) for their new species *P. kobayashii.* We (ZD and III) also recently observed this behavior in *P. holthuisi* and *P. magnificus* Bruce in Vietnam. This behavior is not unique to members of the “aesopus” group; it was first reported for *P. pedersoni* Chace by Holthuis and Eibl-Eibesfeldt (1964, as “P. anthophilus”) from the western Atlantic. Similar to members of the “aesopus” group, individuals of *P. pedersoni* occur in large social groups of up to 26 shrimps per anemone, may leave the anemone at night to move among hosts, and are known to be important Caribbean cleaners of fish parasites (Mahken, 1972; Colin, 1978; Humann, 1992; NEC pers. obs.). IWP palaemonine species of *Urocariella* also are cleaner shrimps (Becker and Greutter, 2004) and appear to use body swinging to advertise their cleaning behavior (Becker et al., 2005).

In addition to swaying, Suzuki and Hayashi (1977) recorded that individuals of the shrimp *P. holthuisi* approached divers (some of their reports may belong to *P. speciosus* Okuno – see Okuno, 2004: 874), as indicated here also for *P. longicarpus.* Finally, the rapid vibratory behavior of the markedly-colored second pereiopods in *P. longicarpus* described here also has been reported for other members of the “aesopus” group, *P. kobayashii* Okuno and Nomura (2002) in Japan, and *P. holthuisi* in Vietnam (ZD, personal observation).

We conclude that the *Periclimenes* “aesopus” group represents a complex of closely-related, morphologically similar shrimp species with comparable color patterns that each associate with a variety of anemone hosts as well as certain other cnidarians. Most if not all of these shrimps are facultative but close associates of sea anemones, live in heterosexual social groups, and exhibit color patterns and behaviors that attract fish for cleaning.

Individuals of the hippolytid shrimp *T. aboinensis,* associated predominantly with the anemones *Cryptodendrum adhaesivum* and *M. hemprichii,* exhibit a unique behavioral pattern of slowly waving in a vertical plane the abdomen, which is covered with conspicuous white spots (Bruce, 1976b; Wirtz, 1995). This behavior has not been reported for any other shrimp species that associate with sea anemones. It does not appear to signal readiness to clean, since this shrimp has never been observed to act as a cleaner shrimp. Individuals of *T. aboinensis* appear to initiate this slow
vertical waving of the abdomen only when large moving objects approach the sea anemone host (NEC, pers. obs.). We hypothesize that this behavior functions to lure fish and possibly other visually-oriented mobile prey into contact with tentacles of the host sea anemone. A common host for _T. amboinensis_ is the sticky sea anemone _C. adaexivum_, which possesses highly adhesive tentacles (Dunn 1981). The luring behavior of the shrimp may benefit the host sea anemone and also the shrimp, which could consume some of the trapped prey. Individuals of _T. amboinensis_ are generalists in that they occur with giant actinian sea anemones and also other types of hosts such as cerianthid tube-dwelling anemones (Guo et al., 1996), crinoids (Criasles, 1984) and mantis shrimps (Debelius, 1999). Our observations indicate that some of these associations may be mutualistic in that the shrimps act to lure prey items to the host. Further research is needed to investigate the functions of this unique behavior.

Other hippolytid shrimps observed during the present study included _Saron marmoratus_ (Olivier), which is a free-living shrimp (Bruce, 1976b), here only accidentally found near anemones. The same is true for _Rhynehocinetes durbanensis_ Gordon, _Stenopus hispidus_, and _Urocaridella aff. antonbruuni_ (Bruce), the two latter being known as cleaner shrimps (Spotte, 1998; Becker and Grutter, 2004; Becker et al., 2005) that often associate with moray eels. To some extent, these shrimps may associate with sea anemones in that they utilize the same reef holes for shelter, and if they benefit from anemone presence in these holes, they could form facultative commensalisms with sea anemones. The shrimp _K. tenipes_ also forms this type of association (Bruce, 2004), and here occurred more frequently with sea anemones than did the other three facultative species above. We also observed individuals of _K. tenipes_ to associate with sea urchins _Diadema setosum_, and to occur in reef crevices without any visible host organisms.

In terms of fish symbionts of sea anemones, the patterns of association observed here for the obligate anemonefish _A. bicinctus_, to occur as 1-2 individuals per host individual of the anemones _E. quadricolor_ and _Heteractis crispa_ are similar to those documented previously (reviewed in Brolund et al., 2004; Chadwick and Arvedlund, 2005). Both partners are known to profit from this relation, with the host anemones benefiting in terms of uptake of ammonium excreted by the fish, leading to increased growth of endosymbiotic zooxanthellae and rapid tissue regeneration, and also through protection from butterflyfish predators on the anemone (Porait and Chadwick-Furman, 2004, 2005). Juveniles of the facultative fish symbiont _Dascyllus trimaculatus_ were less often observed in the present survey, only as single specimens on three anemones _E. quadricolor_, but in a large group of 40 juvenile specimens on the anemone _Stichodactyla haddoni_. Mutualistic relations between species of _Amphiprion_ and _Dascyllus_ have been studied by Schmitt and Holbrook (2003).

Our observation that the spottail sand wrasse _Coris caudimacula_ (Quoy & Gaimard) associates with the anemone host _S. haddoni_ is probably rather accidental than specific for the fish. We observed, together with three specimens of the anemonefish _A. bicinctus_, and a large shoal of 40 specimens of _D. trimaculatus_, that 3-4 specimens of _C. caudimacula_ moved immediately over and around the host anemone. The nature
of this association has yet to be studied, but it is likely to be facultative.

Summary

Several types of associations of shrimps and fishes with giant sea anemones occur in the northeastern Red Sea (Gulf of Aqaba), based on our survey and on reports from the literature:

(1) Obligate mutualisms:
Single heterosexual pairs of the anemoneshrims *Periclimenes brevicarpalis* and *P. ornatus*, and the anemonefish *Amphiprion bicinctus* occur with each individual of 1-2 species of host sea anemones (*Entacmaea quadricolor, Heteractis crispa*). Both the sea anemone hosts and the symbionts appear to profit, although occasional parasitism by *P. brevicarpalis* has been reported (see above).

(2) Regular facultative commensalisms:
The shrimps *P. longicarpus* and *Kenponia teniipes*, and juveniles of the damselfish *Dascyllus trimaculatus*, associate with several species of sea anemones that may serve as hosts to groups of these symbionts. The anemones serve as shelters and "fish cleaning stations" for large groups of *P. longicarpus*, which may move to other anemones or leave the host at night. In terms of their highly regular diurnal association with anemones, this latter shrimp species may eventually be re-evaluated as an obligatory commensal. The case of *P. longicarpus* occurring on non-anemone hosts such as the bubble coral *Plerogyra* sp. may be rather accidental. Individuals of *K. teniipes* use a wide number of invertebrate hosts, and also are free-living. Adults of *D. trimaculatus* are free-living, while the juveniles live preferably on a limited number of anemone species, but also on other reef substrata. Costs and benefits of these associations require further study.

(3) Occasional facultative commensalisms:
The shrimps *Stenopus hispidus* and *Urocaridella aff. antonbruuni* rarely associate with sea anemones. Both shrimps are fish cleaners and may use the same crevices for shelter as do sea anemones and moray eels, or be fully free-living. The mysid shrimp *Idiomysis turnamali* (on *Meegalactis hampichii* and *Cryptodendrum adhaesivum*) probably also belongs to this category. These three shrimp associates may profit from association by sheltering near the anemones and gaining protection from predators, without any benefit yet evident for the host.

(4) Occasional association.
The wrasse *Coris cyanorhabdula* is a free-living fish that searches for invertebrate prey on reefs. The single Haddon's anemone found by us on a sea grass meadow off Egyptian Dahab was evidently attractive for several wrasses, possibly as shelter for their potential prey. The true state of the association and benefits to the partners remain to be examined. If the association between anemones and these Red Sea endemic fish is found to be irregular, then they belong to the next category.

(5) Accidental co-occurrence (no association):
The shrimps *Rhyhosphanites durbanensis* and *Saron marmoratus* likely engage in purely accidental associations with sea anemones. The shrimps were found only in one to several cases in the vicinity of anemones. They are free-living and do not display any regular association with the studied hosts.

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**References**


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Plate 1 Sea anemones that host fish and shrimp:

A. Cryptodendron adhaerens (Khunzinger) - Eilat, depth 7 m.
B. Entacmaea quadricolor (Rüppell et Leuckart) (with clownfish Amphiprion bicinctus Rüppell) - Dahab, depth 25 m.
C. Heteractis crispa Ehrenberg - Eilat, depth 4 m.
D. Megalecius horridus (Saville-Kent) - Eilat, depth 22 m.
E. Stichodactyla haddoni (Saville-Kent), with fishes Amphiprion bicinctus Rüppell, juveniles of Dascyllus trimaculatus (Rüppell), and Coris caudigimaculata (Quoy & Gaimard) - Dahab, depth 7 m.
Plate 2. Shrimps associated with sea anemones:
A. Lamponia tenue (Borradaile); B. Percilmenes brevicaudatus (Schmekel); C. Percilmenes longicarpus Bruce et Svoboda; D. Rhynchocinetes durbanensis Gordon; E. Saron marmoratus (Olivi); F. Urocaridella antonibrusi (Bruce); G. Percilmenes armatus Bruce; H. Stenopus hispidus (Olivi); J. Thor amboinensis (De Man).