

Host fidelity of a symbiotic porcellanid crab: the importance of host characteristics

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Abstract

The social behaviour of symbiotic organisms is influenced by the density and distribution pattern of hosts. Herein we examined the host-use behaviour of the anemone-dwelling crab *Allopetrolisthes spinifrons* (Porcellanidae) in which adults usually live as solitary individuals on their hosts. Adults of this crab use two different sea anemone species, one intermediate-sized species that can be found at relatively high densities in the intertidal zone and another large one that occurs at significantly lower densities in the shallow subtidal zone along exposed rocky shores of the south-east Pacific. Mark–recapture experiments demonstrated that crabs in subtidal waters (low abundance of hosts) remained for long time periods on the same hosts while crabs in the intertidal environment (high abundance of hosts) frequently changed hosts. There were no differences in host fidelity between male and female crabs. In an immigration experiment in the intertidal zone, significantly more juveniles immigrated than had been present originally, indicating that host-use behaviour is age dependent. The sex ratio between resident and immigrated individuals did not change. In an additional experiment hosts were planted at two different densities (high and low) both in the shallow subtidal and the intertidal zone to test whether host fidelity of crabs depends on distance between hosts. At the subtidal site, about half the crabs remained on their sea anemones for 14 days while at the intertidal site most crabs disappeared within 1 day in both density treatments. At both sites crabs were seen changing hosts in high density treatments, but no such events could be witnessed at low densities of hosts. Although the results are not fully conclusive, they suggest that host movements are affected by host densities. This relationship may be mediated by host (anemone species, size, distance) and site-specific (predation pressure, exposure time) factors. In general, the present study indicates that host characteristics influence host fidelity of symbiotic organisms and thereby, their social behaviour.

Key words: symbiosis, host-use, host-change, Porcellanidae, Actinia, intertidal, subtidal, *Allopetrolisthes spinifrons*

INTRODUCTION

Refuges represent an important resource for organisms from both terrestrial and aquatic environments. Such refuges may be non-living structures or parts of living organisms. Species that intimately associate with living organisms may obtain important benefits (protection, food) but may also incur substantial costs (defence, restricted mobility) from their symbiotic lifestyle. These costs primarily are owing to the fact that most host organisms cannot satisfy all requirements of their symbiont, and consequently, these may have to leave their

hosts temporarily to fulfil these needs (i.e. obtain food or mating partners). In general, the decision to stay at a specific site (e.g. a host) depends on resources exploitable at this site and the resulting balance between the costs and benefits of staying (see Chmiel, Herberstein & Elgar, 2000).

In the marine environment many organisms live symbiotically with macro-invertebrates. Some of the most typical and common symbionts found in shallow marine waters are crustaceans, which can be found on a variety of invertebrate hosts comprising e.g. hydrozoans, echinoderms, molluscs and polychaetes. Most crustacean symbionts spend considerable parts of their lives on their hosts, and some species remain on the same host individual throughout their lives (e.g. Kropp, 1987; Hamel, Ng &

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Mercier, 1999). Other species, however, frequently move between different host individuals (Bell, 1984; Patton, Patton & Barnes, 1985; Thiel, Zander & Baeza, 2003). These latter species may always be associated with a specific host species, but rarely remain for a long time on the same host individual. Two basic requirements may affect the propensity of a symbiont to move between different host individuals, namely the need to obtain food and to find a mating partner. If food resources are spatially decoupled from hosts, symbionts may regularly have to leave their hosts to obtain food. Similarly, species that feed on host-related resources and deplete those, may occasionally have to leave hosts to locate undepleted hosts (e.g. Stachowicz & Hay, 1999). Other symbionts may feed on ubiquitous resources that are continuously replenished on or under their hosts, such as for example waste products of the hosts themselves or particles suspended in the water column (Castro, 1971; Ng & Goh, 1996). These latter species typically have no need to leave hosts to satisfy their food requirements.

A similar pattern can be expected when considering the reproductive requirements of a symbiont. Many symbionts live in aggregations on their hosts and usually these groups contain members of both sexes (e.g. Patton *et al.*, 1985; Baeza & Thiel, 2000). Other symbiont species inhabit their hosts as heterosexual pairs (Knowlton, 1980; Vannini, 1985). Since in all these cases there is always at least one member of the opposite sex on the host, symbionts have no immediate need to leave hosts in search of mating partners. This is different in symbiont species that lead a solitary lifestyle; during the reproductive period, the members of at least one sex have to leave their hosts in search of mates (e.g. Wirtz & Diesel, 1983; Yanagisawa & Hamaishi, 1986).

Improved nutritional or reproductive conditions may represent important benefits of leaving hosts, but there exist also important costs arising from movements between hosts. These costs are affected by a variety of factors, including tidal stage, sea state, predation pressure and distance between hosts. Predation pressure has been demonstrated to influence the propensity of male snapping shrimp to seek extra-pair matings on neighbouring anemones; when predation pressure is high they reduce their movements (Knowlton, 1980). Based on the analysis of an extensive dataset, it has been suggested that host characteristics (size, abundance) have a strong influence on symbiont movements between individual hosts (Thiel & Baeza, 2001). With increasing host abundance the frequency of movements increased, being expressed in different association patterns of symbionts on their hosts. This analysis was based on a variety of qualitatively different symbiont–host associations and does not explain movement patterns within a species. For example, in many symbiotic crustaceans, there exist intersexual differences in host fidelity with males usually being the more mobile sex, actively searching for female mating partners (Wirtz & Diesel, 1983; Yanagisawa & Hamaishi, 1986; Stachowicz & Hay, 1999). How these intraspecific differences in host fidelity are affected by host characteristics (in particular by distance between

hosts) is not well known at present. In the present study empirical and experimental studies were used to study: (1) whether intraspecific differences in host fidelity of the symbiotic crab *Allopetrolisthes spinifrons* exist; (2) whether host characteristics had an influence on host fidelity.

Our study system consists of the porcellanid crab *A. spinifrons* and its sea anemone hosts. *Allopetrolisthes spinifrons* inhabits the body column of different species of sea anemones both on intertidal and shallow subtidal hard bottoms along the Pacific coast of Peru and Chile (Haig, 1960). While these crabs may occasionally ingest the mucus of their hosts, they primarily feed on suspended materials (Valdivia, 2002), similar to free-living porcellanid crabs (Achituv & Pedrotti, 1999). Large individuals of this crab typically live solitarily on their hosts (at least in the intertidal zone; Baeza, Stotz & Thiel, 2001). Each individual aggressively defends its ‘own’ sea anemone against conspecific intruders of both sexes (Baeza, Stotz & Thiel, 2002). The comparatively low abundance of the host species, and the small size and low morphological complexity of sea anemones may explain the host–resource monopolization behaviour featured by large crabs (Baeza & Thiel, 2003). *Allopetrolisthes spinifrons* reproduces continually throughout the year (Baeza *et al.*, 2001), and females have to re-mate during each reproductive cycle since they cannot store sperm (Zander, 2002). Direct observations of the mating process in *A. spinifrons* have not yet been made.

MATERIAL AND METHODS

Adults of the porcellanid crab *A. spinifrons* occur abundantly on sea anemones in the intertidal and subtidal zone along the Pacific coast of Chile. All experiments were conducted between February and May 2002 at 2 sites near Coquimbo (29°58′30″S, 71°22′30″W), Chile. At the site La Pérgola in the shallow subtidal zone on the northern shore of Bahía La Herradura (Fig. 1), crabs inhabit the large sea anemone *Phymanthea pluvia*, which is the most common and abundant anemone occurring in shallow subtidal waters. At this site, the average pedal disc diameter of *P. pluvia* was 89 ± 25 mm (mean \pm SD, $n = 29$ sea anemones) and the average distance to the nearest neighbour anemone was 264 ± 174 cm ($n = 29$ measurements). In La Pampilla (Fig. 1), crabs inhabit the intermediate-sized anemone *Phymactis clematis*, which is comparatively abundant in the intertidal zone. In the experimental plots, the average pedal disc diameter of *P. clematis* was 44 ± 13 mm ($n = 77$ sea anemones) and the average distance to the nearest neighbour anemone was 10 ± 3 cm ($n = 79$ measurements).

Experiments 1A and 1B: mark–recapture of crabs on sea anemones

To examine host fidelity, crabs were collected from sea anemones, marked individually and returned to the sea anemone host from which they were collected. Thereafter,

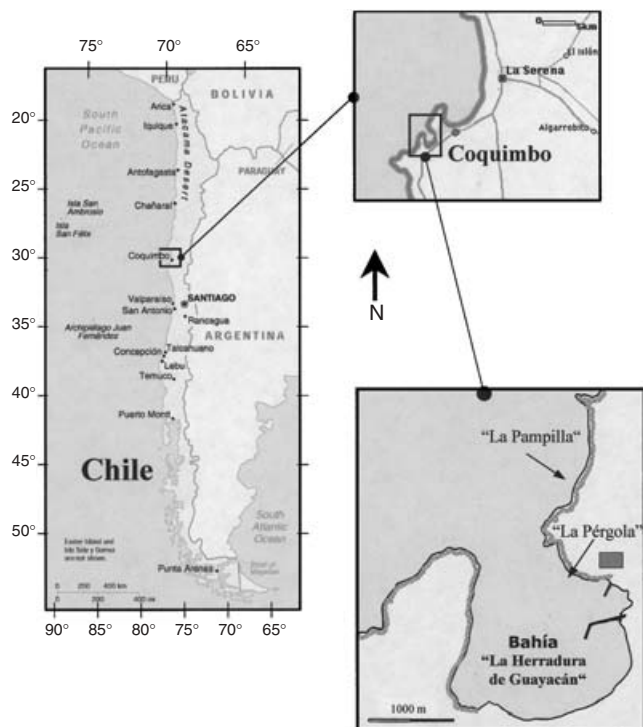


Fig. 1. Study sites La Pégola and La Pampilla near Coquimbo, Chile.

sea anemones were checked at regular intervals for the presence of marked crabs. One experiment was conducted in the shallow subtidal zone at La Pégola (experiment 1A) and one experiment in the intertidal zone at La Pampilla (experiment 1B).

Initially crabs were removed from their sea anemone, and measured (carapace length, CL) and sexed in the field. Following measurements, the crabs were marked with small colour tags that were glued with superglue to their carapace. Laboratory experiments had shown that these colour tags had no effect on the behaviour of the crabs. Each crab obtained a specific combination of up to 3 colour tags that allowed individual recognition of each crab. After marking, crabs were immediately returned to 'their' sea anemones. Newly arriving crabs without a colour tag were marked upon their first observation. Crabs that moulted during the experiment but could be identified safely according to their approximate size and sex were re-marked and treated as a recaptured crab. Recently moulted crabs that could not be identified safely were marked and treated as a newly arriving crab. Sea anemones were characterized individually according to their approximate size, colour pattern, and position, which were marked on a map that was drawn in the field. In the shallow subtidal zone at La Pégola, anemones were additionally marked with buoys attached to boulders to facilitate subsequent relocation. The presence of crabs on sea anemones was monitored for 50 days. The maximum occupation of 1 particular sea anemone for each crab and the number of host changes per observation of an individual crab were evaluated. To calculate the maximum period of continuous occupation of a host, only those days with consecutive

observations of 1 crab on the same sea anemone without interruption were counted. Herein, a host change was considered as only those events where a marked crab was found on a different sea anemone afterwards; temporary absence from a given sea anemone was not taken as a host change when the whereabouts of the crab during the period of absence were unknown.

Experiment 1A (subtidal zone, La Pégola)

An area of $\sim 1000 \text{ m}^2$ was carefully surveyed to identify all sea anemones, which lived attached to boulders or large rock outcrops. All crabs from 29 sea anemones *P. pluvia* were marked and monitored each day during the first 7 days and thereafter at intervals of 1–5 days. Initial and following checks were conducted by semi-autonomous diving. Not all sea anemones in the experimental area were found right at the beginning of the experiment – some, which were hidden in crevices or under large boulders, were found during the progress of the experiment.

Experiment 1B (intertidal zone, La Pampilla)

In 5 patches of $\sim 0.5 \text{ m}^2$ size each, between 7 and 22 sea anemones *P. clematis* were identified. All crabs $> 2 \text{ mm}$ CL found on sea anemones in these patches were marked and monitored each day during low tide for 50 days. Some sea anemones were hidden from direct view on the underside of boulders or in crevices; anemones that were not accessible because of their location in crevices or under boulders were not considered. During the daily surveys each sea anemone was checked visually using a dentist's mirror and a flashlight. If no crab was seen on the anemone, the entire column surface of the sea anemone was carefully touched to verify that no small crabs had been overlooked. Occasionally, waves did not permit the use of the dentist's mirror and crabs had to be removed briefly from the sea anemone to identify their colour tag; this process lasted $\sim 15 \text{ s}$ after which crabs were immediately returned to 'their' sea anemone. During some days, sea conditions were so bad that waves prevented the survey of some patches (3 patches not checked during 2 days, and 1 patch not checked during 1 day).

Experiment 2: immigration of crabs to artificially crab-free sea anemones

In the intertidal zone, a large proportion of sea anemone hosts is usually occupied by crabs (Baeza *et al.*, 2001). Small juveniles are often found on alternative hosts because most sea anemones, the preferred hosts of all life stages of *A. spinifrons*, are occupied (Baeza & Stotz, 2001). The immigration of crabs to experimentally crab-free sea anemones was examined in the intertidal zone at La Pampilla. All crabs we removed from the sea anemones in 5 patches of $\sim 0.5\text{--}1.0 \text{ m}^2$ surface area with 39–51 sea anemones each. Following initial removal of symbiotic crabs, all anemones in a patch were checked each day

Table 1. Numbers and percentages of crabs *Allopetrolisthes spinifrons* marked and recaptured thereafter at the subtidal site La Pérégola and the intertidal site La Pampilla

	La Pérégola subtidal		La Pampilla intertidal	
	<i>n</i>	%	<i>n</i>	%
Crabs marked	13	100	188	100
Crabs not recaptured	0	0.0	73	38.8
Crabs recaptured only once	0	0.0	43	22.9
Crabs recaptured 2–5 times	3	23.1	51	27.1
Crabs recaptured > 5 times	10	76.9	21	11.2
Crabs recaptured that changed host at least once	1	7.7	74	39.4

for the first 7 days, and thereafter every 7 days for new crab immigrants, which were removed during each survey. Occasionally crabs escaped during the surveys, and these crabs were not counted as they probably remained in the patch under boulders or rocks, possibly reappearing on sea anemones over the following days; counting without removing them could have led to an overestimation of the immigration rate. All immigrants were transported to the laboratory and after determination of their sex and CL they were released at the University shore. The immigration rate per day and per sea anemone was calculated. To test whether the sex ratio and the age distribution differed between resident and immigrated individuals, a chi-square test of independence was used (Sokal & Rohlf, 1995). For this purpose, all individuals that immigrated during the course of the experiment were pooled and the resulting frequencies compared with the initial frequencies of resident individuals removed at the start of the experiment.

Experiment 3: host fidelity of crabs at different host abundances

At least 2 qualitatively different factors are likely to influence host fidelity: (1) host density; (2) predation pressure on crabs changing hosts. To explore whether host density affected host fidelity of crabs, the abundance of sea anemones was manipulated in the field. At each site 2 treatments were artificially produced: (1) 'single anemone' in which 1 sea anemone was isolated from the next sea anemone by several metres (2) 'anemone patch' in which several sea anemones occurred in dense patches with distances of < 0.5 m to the nearest neighbour. In both the subtidal zone of La Pérégola and in the intertidal zone of La Pampilla 5 replicate 'single anemones' and 5 replicate 'anemone patches' were produced, and in each replicate 1 anemone was designated to receive an individually marked crab. All designated anemones were marked individually with a thin nylon thread pierced through the column; this treatment had no apparent negative effects on sea anemones. Following placement of the individually marked crabs, their fate was followed for 14 days, and any movements away from the original host were recorded.

In the subtidal zone of La Pérégola, most sea anemones were found as single anemones, and anemone patches had

to be produced by transplanting additional sea anemones to a patch. Anemones were carefully detached from an area ~200 m away from the experimental site, and immediately transferred to the experimental patches, where they were placed between boulders or in crevices such that they were not washed away by currents. Most transplanted anemones attached to the new sites within 1 day. Following first attachment, anemones continuously changed their location for a few days, but then remained at apparently suitable spots. The experiment was started after the newly transplanted sea anemones had reduced their initial movements. Approximately 15 anemones made up a patch and distances between them ranged from 10 to 40 cm. In the intertidal zone of La Pampilla, most sea anemones were found in anemone patches and consequently single anemones had to be produced by removing sea anemones from patches.

RESULTS

Mark–recapture of *A. spinifrons* on sea anemone hosts

Experiment 1A (subtidal zone, La Pérégola)

Most *A. spinifrons* remained for long time periods on their hosts (Fig. 2a). Only one host change was observed during this experiment: one male disappeared the day after it was first marked and was found 16 days later on a sea anemone at ~3 m distance from the original sea anemone. One heterosexual pair was observed to cohabit on one sea anemone for >45 days, during which time the female moulted and produced a new clutch of embryos. The 13 crabs monitored at La Pérégola were recaptured repeatedly (Table 1), and they remained on average for 22.3 ± 15.0 days (mean \pm SD) on the same anemone *P. pluvia* (Fig. 2a). The probability of observing a host change between two consecutive sightings was 0.01 ± 0.03 .

Experiment 1B (intertidal zone, La Pampilla)

Many crabs disappeared after being marked and were never found again during the experiment (Table 1). A relatively high percentage (61.2%) of the marked crabs

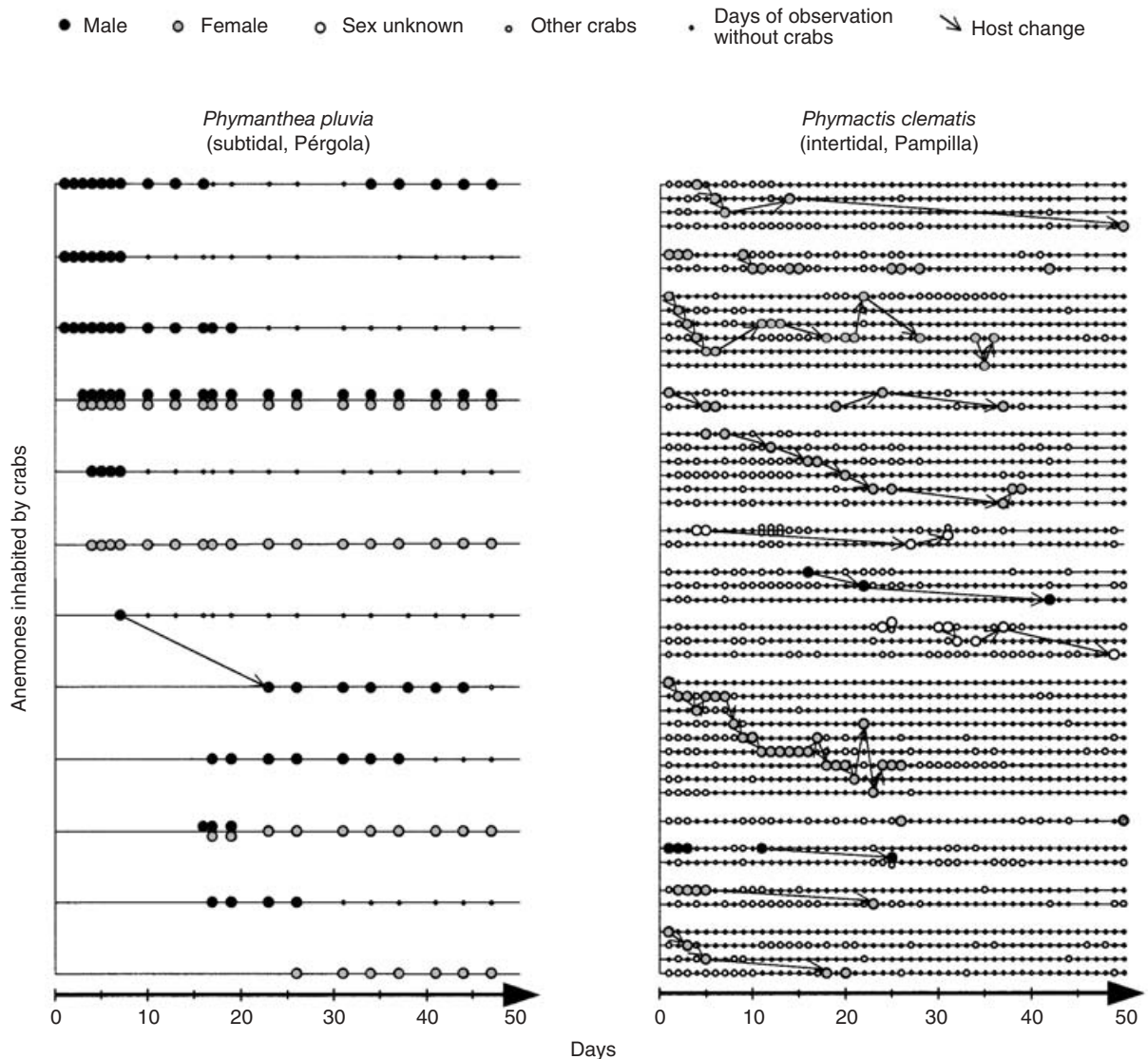


Fig. 2. Host-use pattern of individually marked crabs *Allopetrolisthes spinifrons* on sea anemones *Phymanthea pluvia* in shallow subtidal waters at La Pégola, and *Phymactis clematis* in the low intertidal zone at La Pampilla. At La Pégola sea anemones were monitored every day during the first 7 days of the experiment, and thereafter at intervals of 1–5 days; all observations of all 13 crabs found at the study site are shown; at La Pampilla sea anemones were monitored every day with the exception of a few days during which sea state prohibited access to the patches; only the 13 crabs that were observed for the longest time period and only the sea anemones inhabited by these crabs are shown; for further details see Materials and methods.

was observed at least once following marking, but only 11.2% of all crabs were found on more than five occasions, even though all sea anemones were monitored every day. Occasionally the interval between subsequent recordings of a crab was relatively long (one crab was recaptured after it had not been seen for 36 days). These crabs were probably on sea anemones in the vicinity of the surveyed patches. Of the crabs that were observed at least once after marking, a large proportion changed hosts at least once (Table 1). The 13 crabs that were observed for the most days had an average maximum residence time of 2.4 ± 1.4 days on one particular sea anemone (Fig. 2b). The probability of observing these crabs host change between two consecutive sightings was

0.5 ± 0.3 . For all individuals that were recaptured at least once ($n = 115$) the average maximum residence time was 2.2 ± 1.5 days and the average number of host changes per observation was 0.4 ± 0.4 . Among the sexually mature crabs (> 7 mm CL), females were observed for significantly longer time periods than males (t -test, $t_{0.05(1),30} = 1.974$, $P < 0.05$).

Immigration of *A. spinifrons* to crab-free sea anemones

Following first removal of crabs from the sea anemone patches, many new crabs immigrated to these patches (Fig. 3a). Immigration rates continuously declined and

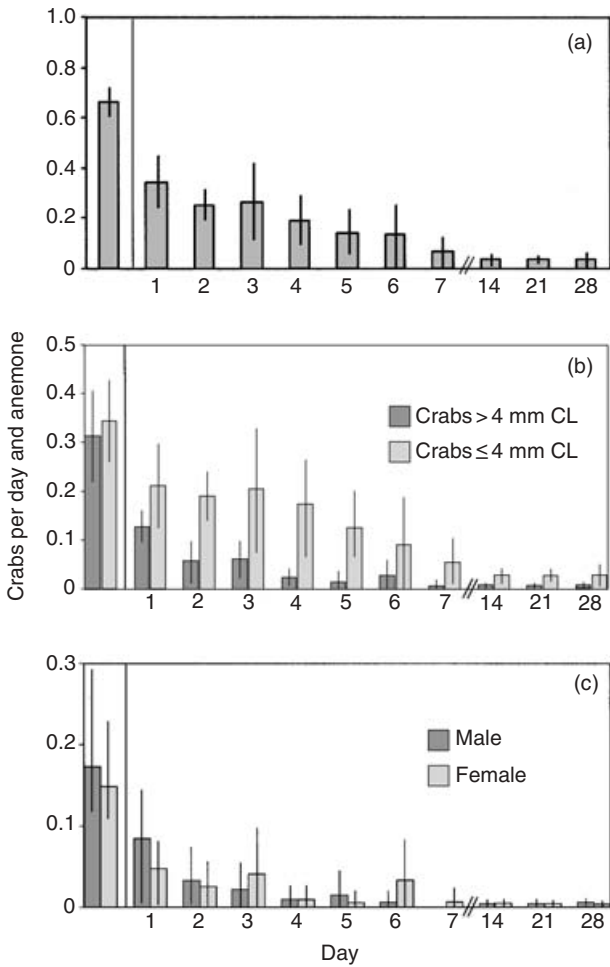


Fig. 3. Immigration rates of crabs *Allopetrolisthes spinifrons* to patches with artificially crab-free sea anemones *Phymactis clematis* in the low intertidal zone at La Pampilla: (a) total immigration; (b) immigration separated by size; (c) immigration separated by sex. All anemones in a patch were checked every day during the first 7 days of the experiment and thereafter at intervals of 7 days; this experiment was conducted in five replicate patches, each of which contained between 39 and 51 sea anemones; columns at day 0 show the natural density of crabs on the first day, i.e. when crabs were first removed from anemones.

reached a minimum of < 0.1 crabs anemone⁻¹ day⁻¹ after 7 days. With increasing duration of the experiment the proportion of small crabs immigrating to the patches increased significantly; after day 7 almost no crabs > 4 mm CL immigrated to the patches (Fig. 3b; $\chi^2 = 12.2$, d.f. = 1, $P < 0.001$). Crabs of both sexes immigrated throughout the duration of the experiment and no significant differences between the sexes were found (Fig. 3b; $\chi^2 = 0.03$, d.f. = 1, $P = 0.874$).

Host fidelity of *A. spinifrons* at different abundances of sea anemones

At both sites many crabs disappeared without ever being found again, even though we intensively searched on the

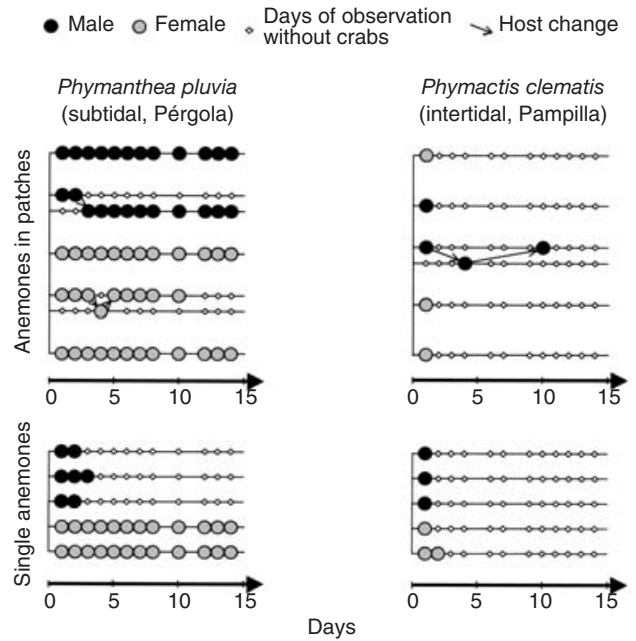


Fig. 4. Host-use pattern of crabs *Allopetrolisthes spinifrons* on sea anemones *Phymanthea pluvia* in the subtidal zone at La Pégola and *Phymactis clematis* in the low intertidal zone at La Pampilla; single anemones occurred naturally at La Pégola, but anemone patches had to be artificially produced there, while anemone patches occurred naturally at La Pampilla, but single anemones had to be artificially produced there (for further details see text); sea anemones that received crabs and in the surrounding area were monitored every day for 14 days after crabs had been placed on the designated anemones.

sea anemones in the surrounding area. This extraordinary high disappearance rate might be caused by the fact that crabs were experimentally placed on host individuals, which they did not select themselves and which therefore did not fully satisfy their needs. Due to the high initial disappearance rate we were not able to perform statistical comparisons regarding host fidelity.

Two trends were observed: (1) symbiotic crabs disappeared more rapidly from sea anemones *Phymactis clematis* in the intertidal zone than from *P. pluvia* in the shallow subtidal zone (Fig. 4); (2) if only those crabs are considered that were observed at least once after they have been released on a host, individuals from patches were more likely to move than individuals from single anemones.

In the subtidal zone at La Pégola, three out of five crabs on single *P. pluvia* disappeared shortly after they had been placed on the sea anemones. These crabs never reappeared during the duration of the experiment (14 days). Most (four out of five) crabs that were placed on a sea anemone in anemone patches remained in these patches for almost the entire experiment. Two of the five crabs were seen on a neighbouring sea anemone during 1 day, but one returned to the original anemone during the following day, while the other remained on the new anemone until the end of the experiment.

In the intertidal zone at La Pampilla, with the exception of one crab that remained on a single sea anemone, all crabs had disappeared the day after they had been placed on the designated sea anemones. The crab from the single anemone disappeared at day 2 and was not seen again during the experiment. On day 3 one marked crab was found on another sea anemone in the anemone patch, but disappeared the following day; this crab was again seen on the original sea anemone on day 10, but during the other days could not be found. These results indicate that in the intertidal zone host density is of minor importance for host fidelity.

DISCUSSION

Host fidelity of the porcellanid crab *A. spinifrons* differed substantially between the two study sites. The general ecology of the two host species also differed substantially. The large sea anemone *P. pluvia* occurred with low abundance in the shallow subtidal zone, while the intermediate-sized anemone *Phymactis clematis* was relatively abundant in the low intertidal zone. Our mark-recapture experiments revealed that crabs showed strong host fidelity in shallow subtidal waters but changed hosts frequently on an intertidal rocky shore. The distinct differences in host characteristics (size and distance) in combination with ecological factors, which influence the costs of moving (subtidal vs intertidal) are likely to explain the differences in host fidelity between the two study sites. To investigate whether the differences in host density or site-specific factors (e.g. different predation risk) explain more of the variation between the two study sites, we conducted an experiment in which host densities at both locations were manipulated. Due to low recovery of marked crabs, these results are not fully conclusive but they support the findings of our other experiments. In the following we will discuss how host characteristics and ecological characteristics influence host fidelity.

Movements in *Allopetrolisthes spinifrons*

In contrast to endosymbiotic species, where members of one or both sexes become trapped within cavities in their hosts, *A. spinifrons* showed a low degree of host fidelity. Movements among host individuals may play several roles in this symbiotic species. Porcellanid crabs are suspension-feeders and water flow conditions affect feeding mechanism (passive vs active; Achituv & Pedrotti, 1999) and probably food intake efficiency in these crabs. Thus, one cause for movements between host individuals in *A. spinifrons* may be searching for 'vantage points' with adequate flow conditions for efficient feeding. Since flow conditions most likely change with tidal height and local sea conditions, crabs may constantly adjust their position in the intertidal and subtidal zone to maximize food uptake. In addition, crabs seem to obtain food directly (i.e. mucus) from their sea anemone hosts (Viviani, 1969; Valdivia, 2002). If mucus

is depleted from a host individual as a result of the feeding activity of crabs, they might have to relocate to other host individuals to fulfil their food requirements. Secondly, sea anemones may offer protection against predators owing to homochromy (Viviani, 1969). While sea anemones vary widely in colour (i.e. *P. clematis* occurs in several colour morphs; red, green, red-green, and blue), *A. spinifrons* crabs invariably present a reddish-green coloration. Thus, crabs may be searching for hosts that permit better food uptake, and simultaneously a high degree of camouflage (protection against visual predators) at least in the intertidal environment (Baeza & Stotz, 2003). Third, because crabs live solitarily on each host individual, as previously reported for the intertidal population (Baeza *et al.*, 2001), they may be forced to search among hosts for mating partners. In the study area, *A. spinifrons* reproduce continuously, and consequently crab movements are expected throughout the year. Searching for mating partners may represent the most important factor explaining movements among hosts in *A. spinifrons*, as has previously been reported for other symbiotic species (Wirtz & Diesel, 1983; Yanagisawa & Hamaishi, 1986).

The observed differences in host fidelity between the two study sites can probably be explained by the trade-off between the potential costs and benefits of travelling between host individuals. This has also been suggested for other species that need to move out of dwellings to obtain resources (Lima, Valone & Caraco, 1985). Predation pressure and physiological stress typically represent the predominant costs, while location of mates and adequate feeding places are considered important benefits. These costs are expected to increase with increasing distances between hosts and consequently movements between hosts are often reduced or cease when hosts are far apart from each other (Knowlton, 1980; Bell, 1984). In the intertidal zone, where sea anemones are close to each other (Table 2), physiological and ecological (e.g. predation risk) costs for *A. spinifrons* are expected to be low, while these costs most likely are high in the subtidal zone where sea anemones are separated over large distances (typically > 100 crab body lengths) (Table 2), and where many fish predators are resident. Varying site fidelity in response to different environmental factors (including host abundance and host size) has also been shown for a variety of other symbiotic organisms (Roughgarden, 1975; Knowlton, 1980; Srinivasan, Jones & Caley, 1999).

In addition to extrinsic factors such as host abundance and predation pressure our results show that host fidelity also depends on intrinsic factors such as the ontogenetic stage of the symbiont. The immigration experiment revealed that relatively more small crabs immigrated to the patches. The sizes of crabs that immigrated during the later phase of the experiment corresponded well to the sizes of crabs that Baeza & Stotz (2001) found on alternative (non-anemone) hosts. These results agree with the idea that small 'floater' crabs roam in search of uninhabited hosts (for other symbiotic crabs see Bell, 1984) where they continue growing to reach sexual maturity and reproduce (Baeza & Stotz, 2001). Apparently, the roaming behaviour

Table 2. A summary of host characteristics and host fidelity of *Allopetrolisthes spinifrons* at the two study sites; only crabs that were recaptured at least once entered analysis; values represent mean \pm SD

	La Pérgola	La Pampilla
Host	<i>Phymanthea pluvia</i>	<i>Phymactis clematis</i>
Habitat	Low rocky subtidal	Shallow rocky intertidal
Distance between individuals (cm)	264 \pm 174 (very high) ($n = 29$)	10 \pm 3 (intermediate) ($n = 79$)
Host diameter (mm)	89 \pm 25 (large) ($n = 29$)	44 \pm 13 (intermediate) ($n = 77$)
Symbiont behaviour		
Average maximum host permanence (days)	22.3 \pm 15.0 ($n = 13$)	2.2 \pm 1.5 ($n = 115$)
Host changes per observation (during 50 days)	0.01 \pm 0.03 ($n = 13$)	0.4 \pm 0.4 ($n = 115$)
Host fidelity	High	Low

of small crabs is because of the limited availability of free hosts, even in the intertidal zone where host abundance is relatively high (see Baeza & Thiel, 2003).

The mating system of *Allopetrolisthes spinifrons*

Adult crabs invariably occurred as solitary individuals on sea anemones in the intertidal zone, while some crabs cohabited with a member of the opposite sex in the subtidal zone. This might be caused by host-related features (host density), ecological features (predation pressure), and traits of the hosts such as its size. If host density is low, crabs may prefer to share hosts with a member of the opposite sex instead of monopolizing a host against members of both sexes (see Baeza *et al.*, 2002). The heterosexual pairs of *A. spinifrons* observed in the subtidal zone may represent socially monogamous pairs, as reported or suggested for other symbiotic species inhabiting environments where the risk of travelling between hosts is high (Knowlton, 1980; Omori, Yanagisawa & Hori, 1994). Strong pair bonding (monogamy) has been proposed to evolve in response to low host density and large distances between host individuals in other associates of macroinvertebrates (i.e. anemone fishes; Barlow, 1986). Cohabitation of heterosexual pairs in the subtidal zone is probably also facilitated by the larger size of sea anemones in the subtidal (*P. pluvia*) compared with the intertidal zone (*P. clematis*), thus offering more space for symbiotic crabs (Table 2). In contrast, in the intertidal zone, where host density is high and hosts are small, *A. spinifrons* display a solitary lifestyle on their sea anemones, and cohabitation of mating partners is apparently brief (Baeza *et al.*, 2001). At high host densities and a high degree of occupancy (as observed herein in the intertidal zone), there are also many potential mating partners in the vicinity. On the sea anemone *P. clematis*, crabs display territorial behaviour (Baeza *et al.*, 2002), but they also move frequently between these hosts (this study). The comparatively small size of *P. clematis* may be primarily responsible for these behaviours as is also suggested by the rapid disappearance of crabs from these anemones at both host densities during the final experiment (Fig. 4). For other symbiotic crabs with a solitary lifestyle,

a polygamous mating system has been described. In the solitary spider crab *Imachus phalangium*, one male seems to patrol various sea anemone hosts with the respective female crabs, effectively exhibiting polygyny (see Diesel, 1986). In this species, females can store sperm and are thus not necessarily dependent on a male during the reproductive moult (Diesel, 1986, 1989). Since females can receive new sperm shortly after moulting, males take the risk of travelling between hosts to achieve copulation (Diesel, 1986). In contrast to *I. phalangium*, females of *A. spinifrons* do not have the ability to store sperm, and thus need to copulate after each reproductive moult, as indicated by laboratory experiments (Zander, 2002). This may explain why female *A. spinifrons* also show relatively high movement frequencies, at least in the intertidal zone. In summary, the present results suggest that the mating behaviour of *A. spinifrons* is a variable trait, most probably being mediated by a combination of host size, distance between hosts and habitat (predation pressure and emersion time). Additional studies are necessary to unveil the interaction between these factors in detail.

Host characteristics and host fidelity in symbiotic organisms

Host fidelity is primarily based on the balance between the costs and benefits of moving between different host individuals (Roughgarden, 1975). If the costs of movements are high, symbionts will show high host fidelity. Extrinsic (predation pressure, physical stress) and intrinsic (sex, stage, size) factors determine the balance between costs and benefits of moving. In symbiotic organisms this balance is affected by host characteristics (Fig. 5). For example, when hosts are close together (at high host abundance), costs of moving are relatively low, resulting in a high frequency of movements. Many observations on symbiotic crustaceans suggest indeed that at low distances between hosts, the frequency of movements is high (Bell, 1984; Nakashima, 1987; Ng & Lim, 1990; Gherardi, 1991). Huber (1987) remarked that inter-host movements probably are limited in a coral-dwelling crab since coral heads are separated by several metres. Moreover, for coral-dwelling gobiid fish it has been suggested that distances between hosts and the

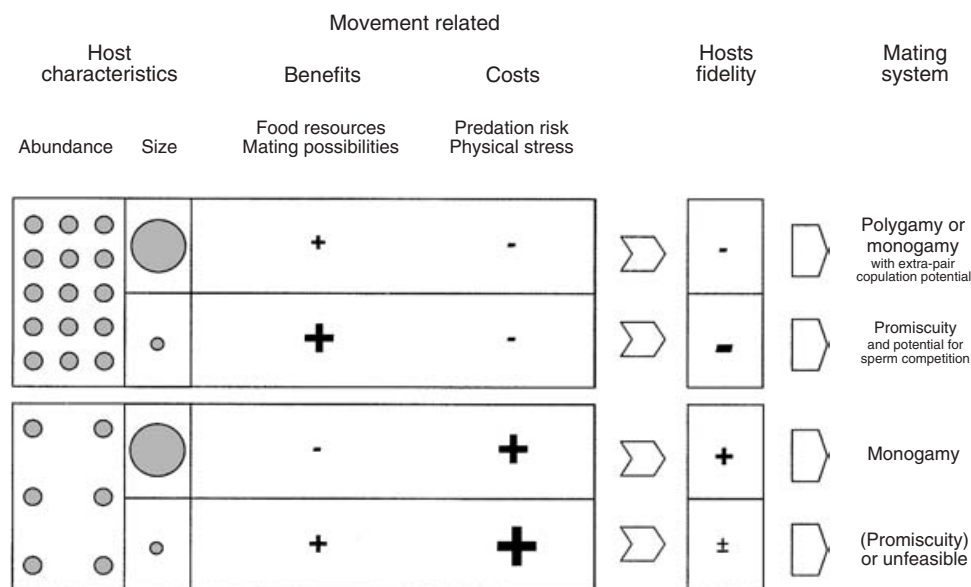


Fig. 5. Relationship between host characteristics and host fidelity of symbionts influenced by the balance of movement-related benefits and costs; host fidelity has direct influence on the mating system of symbionts.

related risk of movement have an effect on host fidelity (Munday, 2002). In general, symbionts show a higher tendency to move between hosts when these are close together.

Besides distances between hosts, their size can also have a strong effect on host fidelity of symbiotic organisms. Small hosts may provide sufficient resources for one symbiont but not for two or more (for crustaceans see Tsuchiya & Yonaha, 1992; for fish see e.g. Fricke, 1980), while large hosts can harbour a heterosexual pair (Tsuchiya & Yonaha, 1992; Munday *et al.*, 2002). Hosts that only sustain single individuals impose restrictions on the host fidelity of symbionts by forcing them to move in search of mating partners. If, in this case, hosts are far apart from each other, then the costs of moving between hosts may be too high and the symbiotic lifestyle not feasible (Fig. 5). In contrast when hosts are large enough to harbour two symbiont individuals, these restrictions disappear and symbionts may adopt a monogamous or even a harem lifestyle (Fig. 5) (e.g. Fricke, 1980), reducing the need to leave hosts in search of mating partners. Finally, if hosts are close together, then either both sexes or males may move in search of mating partners. If hosts are large enough to sustain at least one symbiont for extended time periods, then females may show a higher tendency than males to remain on hosts (Fig. 5). If hosts are comparatively small, then both sexes need to move between hosts in search of food (Fig. 5).

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REFERENCES

- Achituv, J. & Pedrotti, M. L. (1999). Cost and gains of porcelain crab suspension feedings in different flow conditions. *Mar. Ecol. Prog. Ser.* **184**: 161–169.
- Baeza, J. A. & Stotz, W. (2001). Host-use pattern and host selection during ontogeny of the commensal crab *Allopetrolisthes spinifrons* (H. M. Edwards, 1837) (Decapoda: Anomura: Porcellanidae). *J. nat. Hist.* **35**: 341–355.
- Baeza, J. A. & Stotz, W. (2003). Host-use and selection of differently colored sea anemones by the symbiotic crab *Allopetrolisthes spinifrons*. *J. exp. mar. Biol. Ecol.* **284**: 25–39.
- Baeza, J. A., Stotz, W. & Thiel, M. (2001). Life history of *Allopetrolisthes spinifrons*, a crab associate of the sea anemone *Phymactis clematis*. *J. mar. biol. Ass. U.K.* **81**: 69–76.
- Baeza, J. A., Stotz, W. & Thiel, M. (2002). Agonistic behaviour and development of territoriality during ontogeny of the sea anemone dwelling crab *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) (Decapoda: Anomura: Porcellanidae). *Mar. Freshw. Behav. Physiol.* **35**: 189–202.
- Baeza, J. A. & Thiel, M. (2000). Host use pattern and life history of *Liopetrolisthes mitra* (Dana, 1852), an associate of the black sea urchin *Tetrapygus niger* (Molina). *J. mar. biol. Ass. U.K.* **80**: 639–645.
- Baeza, J. A. & Thiel, M. (2003). Predicting territorial behavior in symbiotic crabs using host characteristics: a comparative study and proposal of a model. *Mar. Biol.* **142**: 93–100.
- Barlow, G. W. (1986). A comparison of monogamy among freshwater and coral-reef fishes. In *Indo-Pacific fish biology: proceedings of the second international conference on the Indo-Pacific fishes*: 767–775. Uyeno, T., Ari, R., Taniuchi, T. & Matsuura, K. (Eds). Tokyo: Ichthyological Society of Japan.
- Bell, J. L. (1984). Changing residence: dynamics of the symbiotic relationship between *Dissodactylus mellitae* Rathbun (Pinnotheridae) and *Mellita quinquesperforata* (Leske) (Echinodermata). *J. exp. mar. Biol. Ecol.* **82**: 101–115.
- Castro, P. (1971). Nutritional aspects of the symbiosis between *Echinoecus pentagonus* and its host in Hawaii, *Echinothrix calamaris*. In *Aspects of the biology of symbiosis*: 229–247. Cheng, T. C. (Ed.). Baltimore, MD: University Park Press.

- Chmiel, K., Herberstein, M. E. & Elgar, M. A. (2000). Web damage and feeding experience influence web site tenacity in the orb-web spider *Argiope keyserlingi* Karsch. *Anim. Behav.* **60**: 821–826.
- Diesel, R. (1986). Optimal mate searching strategy in the symbiotic spider crab *Inachus phalangium* (Decapoda). *Ethology* **72**: 311–328.
- Diesel, R. (1989). Structure and function of the reproductive system of the symbiotic spider crab *Inachus phalangium* (Decapoda: Majidae): observations on sperm transfer, sperm storage, and spawning. *J. Crustacean Biol.* **9**: 266–277.
- Fricke, H. W. (1980). Control of different mating systems in a coral reef fish by one environmental factor. *Anim. Behav.* **28**: 561–569.
- Gherardi, F. (1991). Eco-ethological aspects of the symbiosis between the shrimp *Athanas indicus* (Coutière 1903) and the sea urchin *Echinometra mathaei* (de Blainville 1825). *Trop. Zool.* **4**: 107–128.
- Haig, J. (1960). The Crustacea Anomura of Chile. Reports of the Lund University Chile Expedition 1948–49. *Lunds Univ. Arsskr.* **41**: 1–68.
- Hamel, J.-F., Ng, P. K. L. & Mercier, A. (1999). Life cycle of the pea crab *Pinnotheres halingi* sp. nov., an obligate symbiont of the sea cucumber *Holothuria scabra* Jaeger. *Ophelia* **50**: 149–175.
- Huber, M. E. (1987). Aggressive behavior of *Trapezia intermedia* Miers and *T. digitalis* Latreille (Brachyura: Xanthidae). *J. Crustacean Biol.* **7**: 238–248.
- Knowlton, N. (1980). Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. *Evolution* **34**: 161–173.
- Kropp, R. K. (1987). Descriptions of some endolithic habitats for snapping shrimp (Alpheidae) in Micronesia. *Bull. mar. Sci.* **41**: 204–213.
- Lima, S., Valone, T. J. & Caraco, T. (1985). Foraging-efficiency–predation-risk tradeoff in the grey squirrel. *Anim. Behav.* **33**: 155–165.
- Munday, P. L. (2002). Bi-directional sex change: testing the growth-rate advantage model. *Behav. Ecol. Sociobiol.* **52**: 247–254.
- Munday, P. L., Pierce, S. J., Jones, G. P. & Larson H. K. (2002). Habitat use, social organisation and reproductive biology of the seawhip goby, *Bryaninops yongei*. *Mar. Freshwater Res.* **53**: 769–775.
- Nakashima, Y. (1987). Reproductive strategies in a partially protandrous shrimp, *Athanas kominatoensis* (Decapoda: Alpheidae): sex change as the best of a bad situation for subordinates. *J. Ethol.* **5**: 145–159.
- Ng, P. K. L. & Goh, N. K. C. (1996). Notes on the taxonomy and ecology of *Aliaporcellana telestophila* (Johnson, 1958) (Decapoda, Anomura, Porcellanidae), a crab commensal on the gorgonian *Solenocaulon*. *Crustaceana* **69**: 652–661.
- Ng, P. K. L. & Lim, G. S. Y. (1990). On the ecology of *Harrovia albolineata* Adams & White, 1848 (Crustacea: Decapoda: Brachyura: Eumedonidae), a crab symbiotic with crinoids. *Raffles Bull. Zool.* **38**: 257–262.
- Omori, K., Yanagisawa, Y. & Hori, N. (1994). Life history of the caridean shrimp *Periclimenes ornatus* Bruce associated with a sea anemone in southwest Japan. *J. Crustacean Biol.* **14**: 132–145.
- Patton, W. K., Patton, R. J. & Barnes, A. (1985). On the biology of *Gnathophylloides mineri*, a shrimp inhabiting the sea urchin *Triploneustes ventricosus*. *J. Crustacean Biol.* **5**: 616–626.
- Roughgarden, J. (1975). Evolution of marine symbiosis – a simple cost-benefit model. *Ecology* **56**: 1201–1208.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. San Francisco, CA: W. H. Freeman.
- Srinivasan, M., Jones, G. P. & Caley, M. J. (1999). Experimental evaluation of the roles of habitat selection and interspecific competition in determining patterns of host use by two anemonefishes. *Mar. Ecol. Prog. Ser.* **186**: 283–292.
- Stachowicz, J. J. & Hay, M. E. (1999). Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. *Ecology* **80**: 2085–2101.
- Thiel, M. & Baeza, J. A. (2001). Factors affecting the behavioural ecology of crustaceans living symbiotically with other marine invertebrates: a modelling approach. *Symbiosis* **30**: 163–190.
- Thiel, M., Zander, A. & Baeza, J. A. (2003). Movements of the symbiotic crab *Liopetrolisthes mitra* between hosts, black sea urchins *Tetrapygus niger*. *Bull. mar. Sci.* **72**: 89–101.
- Tsuchiya, M. & Yonaha, C. (1992). Community organization of associates of the scleractinian coral *Pocillopora damicornis*: effects of colony size and interactions among the obligate symbionts. *Galaxea* **11**: 29–56.
- Valdivia, N. (2002). *Aspectos alimenticios de Allopsetrolisthes spinifrons* (Decapoda: Anomura: Porcellanidae), simbiote de *Phymactis clematis* (Coelenterata: Anthozoa). Unpublished Honor's thesis, Universidad Católica del Norte, Coquimbo, Chile.
- Vannini, M. (1985). A shrimp that speaks crab-ease. *J. Crustacean Biol.* **5**: 160–167.
- Viviani, C. A. (1969). Los Porcellanidae (Crustacea, Anomura) Chilenos. *Beitr. neotrop. Fauna* **6**: 1–14.
- Wirtz, P. & Diesel, R. (1983). The social structure of *Inachus phalangium*, a spider crab associated with the sea anemone *Anemonia sulcata*. *Z. Tierpsychol.* **62**: 209–234.
- Yanagisawa, Y. & Hamaishi, A. (1986). Mate acquisition by a solitary crab *Zebrida adamsii*, a symbiont of the sea urchin. *J. Ethol.* **4**: 153–162.
- Zander, A. (2002). *Die Lebensgemeinschaft des Porzellankrebses Allopsetrolisthes spinifrons und der Seeanemone Phymactis clematis an der chilenischen Pazifikküste*. Unpublished thesis for Staatsexamen, University of Osnabrück, Germany.