

**AGONISTIC BEHAVIOUR AND DEVELOPMENT OF  
TERRITORIALITY DURING ONTOGENY OF THE  
SEA ANEMONE DWELLING CRAB  
*ALLOPETROLISTHES SPINIFRONS*  
(H. MILNE EDWARDS, 1837)  
(DECAPODA: ANOMURA: PORCELLANIDAE)**

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*Allopetrolisthes spinifrons* is an ectosymbiotic crab of the sea anemone *Phymactis clematis*. As a consequence of low host abundance, these represent a scarce and limited resource for the crab. Additionally, the relatively small size of the sea anemone host suggests that few symbiotic crabs can cohabit on one host individual, forcing crabs to adopt a territorial behaviour. In order to examine the potential presence and ontogenetic development of territoriality, the agonistic behaviour between crabs of various ontogenetic stages (adults, juveniles, and recruits) was studied in the laboratory. Laboratory experiments demonstrated that adult or juvenile crabs aggressively defended their sea anemone hosts against adult or juvenile intruders, respectively, but both adult and juvenile crabs tolerated recruits. Adult crabs behaved indifferently towards juvenile crabs, sometimes tolerating them, sometimes expelling them. Recruits never showed agonistic behaviour among themselves. The agonistic interactions observed in the laboratory and the uniform population distribution pattern on sea anemones recently described for *A. spinifrons* indicate that this species exhibits territorial behaviour, which develops during ontogeny. Territoriality in this species and other symbiotic decapods may function as a density-dependent mechanism of population regulation, being mediated by the availability of hosts. Resource monopolisation behaviours may be common among other symbiotic and free-living marine invertebrates inhabiting discrete habitats that represent a limiting resource.

**Keywords:** Agonistic behaviour; Territoriality; Ontogeny; Symbiosis; Sea anemones; Decapoda

## INTRODUCTION

During the past decades, several studies have described the spacing and dominance system of free-living decapod species. Species, in which a reduced number of large dominant individuals obtain priority in access to resources such as food and/or shelter, have been commonly described (Allee and Douglis, 1945; Warner, 1970;

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Vannini and Sardini, 1971; Salmon, 1983; Salmon and Hyatt, 1983; Jensen and Armstrong, 1991). These socially hierarchical organisations have been observed in lobsters (Fielder, 1965), crayfish (Goessmann *et al.*, 2000), fresh water shrimps (Rubenstein and Hazlett, 1974; Karplus and Harpaz, 1990), and several species of hermit crabs (Dunham and Gilchrist, 1988; Gilchrist, 1991), as well as in terrestrial and marine crabs of several families (Warner, 1970; Vannini and Sardini, 1971; Dunham and Gilchrist, 1988; Jensen and Armstrong, 1991). In a few species, a single individual or a limited number of individuals (e.g. a heterosexual pair) gains exclusive use of a dwelling, which is aggressively monopolised against other conspecifics. In contrast to dominance hierarchies, territorial spacing systems are uncommon in free-living decapods, being recognised or inferred only for certain intertidal crabs (Molenock, 1974; Abele *et al.*, 1986), snapping shrimps (Nolan and Salmon, 1970), and land crabs (Dunham and Gilchrist, 1988). Territoriality has been additionally reported for stomatopods inhabiting self-constructed dwellings or natural shelters (Dingle and Caldwell, 1969). In these territories, males usually monopolise females to mate with them once they become receptive (Seiple and Salmon, 1982; Abele *et al.*, 1986; Dunham and Gilchrist, 1988; van der Meeren, 1994).

Compared to free-living species, studies describing the spacing system of symbiotic decapods are uncommon. The few available studies on symbiotic decapods indicate that most of them inhabit hosts as solitary individuals (Wells and Wells, 1961; Stanton, 1977; Haines *et al.*, 1994; Palmer, 1995) or as heterosexual pairs (Gray, 1961; Castro, 1978; Knowlton, 1980; Gotelli *et al.*, 1985; Omori *et al.*, 1994). However, aggregations of symbiotic individuals on single hosts have also been observed (Mahnken, 1972; Baeza and Thiel, 2000). Only in three symbiotic species a territorial system has been experimentally demonstrated: the snapping shrimp *Alpheus armatus* dwelling on the sea anemone *Bartholomea annulata* (Knowlton, 1980), and the xanthid crabs *Trapezia intermedia* and *Trapezia digitalis* on heads of *Pocillopora* corals inhabit their hosts as heterosexual pairs (Huber, 1987). In other species, the apparent lack of sociality with no distinct spacing system has been recognised, as described for the sea anemone dwelling shrimp *Periclimenes anthophilus* (Nizinski, 1989).

Dwellings of symbiotic decapods feature several characteristics that distinguish them from shelters used by free-living species. Many hosts used by symbiotic decapods may be available in limited numbers, and consequently they represent a scarce resource for symbiotic species. This type of microhabitat usually also features a small size and well-defined boundaries, representing a discrete dwelling. Resource scarcity has been described as one of the main ecological factors determining the development of resource monopolisation behaviours, including territorial systems (Wilson, 1975), in terrestrial and marine invertebrates. Since many symbiotic species inhabit discrete hosts of limited size, they may be capable to defend these without investing much time and energy. Weaponry in many crabs and shrimps is well-developed (e.g., large chelipeds) permitting efficient defence of a dwelling (Thiel and Baeza, 2001). These considerations suggest that territoriality might be more common among symbiotic decapods than previously reported. Territorial behaviour may occur with particular frequency among species that inhabit well-limited hosts such as bivalves, anemones, and echinoderms, which can be easily patrolled and defended.

The porcellanid crab *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) has been described as a common associate of the sea anemones *Phymactis clematis* and *Phymanthea pluvia*, but juveniles have also been found on a variety of other benthic

macro-invertebrates, including sea stars and several gastropod species (Baeza and Stotz, 2001). These crabs apparently feed on debris, waste materials and mucus produced by sea anemones (Viviani, 1969). Protection against visual predation – achieved by homochromy with their hosts – has been suggested as another benefit obtained by crabs when dwelling on sea anemones (Stuardo, 1962; Viviani, 1969). The symbiotic association of *A. spinifrons* appears to be established by active habitat selection behaviour displayed by the crab during larval settlement (Baeza and Stotz, 1998). Habitat restrictions during larval settlement have been suggested to explain the existence of alternative non-anthozoan hosts in the species (Baeza and Stotz, 1998, 2001). All ontogenetic stages prefer sea anemones over alternative hosts (e.g., limpets) (Baeza and Stotz, 2001). *Allopetrolisthes spinifrons* are typically found as solitary individuals on single sea anemones (Baeza *et al.*, 2001). Occasionally, up to 5 symbiotic crabs have been found on a single host, but usually all of them are small. When a large crab is found on sea anemones harbouring two or more crabs, the other(s) inhabitant(s) are small crabs that had recently recruited to the host (Baeza *et al.*, 2001). The frequency of occurrence of *A. spinifrons* on sea anemones is high (*ca.* 70% of sea anemones harbour at least one symbiotic crab throughout the year – Baeza *et al.*, 2001) further suggesting that crabs experience habitat restrictions during their benthic life. In summary, all available information suggests that *A. spinifrons* may develop territorial behaviour during its ontogeny.

The aim of the present study was to examine the possible existence of territorial behaviour in *A. spinifrons*. In the context of this study we rely on Wilson (1975) who defined a territory as ‘an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defence or advertisement.’ We examined whether sea anemones represent a territory for *A. spinifrons* by staging laboratory experiments in which we specifically focused on the description of the agonistic behaviour of the crab during adulthood and the development of territoriality during its ontogeny. For this purpose, we determined the frequency of occurrence of agonistic behaviour and exclusion from host sea anemones between conspecific crabs of various ontogenetic stages under laboratory conditions.

## MATERIAL AND METHODS

### Collection and Maintenance of Crabs and Sea Anemones

Crabs and sea anemones used during the present study were collected from the rocky intertidal of La Pampilla, Coquimbo, Chile (29°57'S, 71°21'W). The rocky intertidal at the collection site is briefly described by Baeza *et al.* (2001). All organisms were maintained for 5–10 days in aquaria (50–100 L) with aerated flowing seawater (15–17°C) before being used in laboratory experiments. During the experiments, all crabs > 7.0 mm carapace length (CL) were considered as adults, crabs of 2.0–7.0 mm CL as juveniles, and crabs < 2.0 mm CL as recruits (see Baeza and Stotz, 2001; Baeza *et al.*, 2001).

### Description of the Agonistic Behaviour of *Allopetrolisthes spinifrons*

In order to describe the agonistic behaviour of *A. spinifrons* in detail, the interaction between a resident – an individual already established on a sea anemone – and an

intruder crab was observed under laboratory conditions. For this purpose, a sea anemone (>45 mm body diameter) attached to a small rock was placed in one of the corners of a glass aquarium (40 cm × 20 cm × 50 cm height) with aerated non-circulating water. After the sea anemone was deposited in the aquarium, an adult crab (resident) was introduced and allowed to colonise the sea anemone. Following an initial acclimatisation period of 30 min for the resident crab, an additional adult crab was introduced to the aquarium. This intruder crab was placed in the vicinity (8–10 cm) of the sea anemone. Most commonly, intruder crabs moved towards the sea anemone soon after their introduction. However, some intruder crabs attempted to find refuge among the surrounding rocks located in the aquarium (see below). If this occurred, the intruders were directed towards the sea anemone by slightly touching their pereopods with a glass rod. Following first contact of the intruder crab with the sea anemone, the behaviour of crabs was observed for 30 min. When crabs interacted (e.g. moving or touching pereopods and/or antennae of conspecifics, see results), the movement patterns displayed by both crabs during the agonistic interaction (sensu Molenock, 1974) and the time transcurring from the beginning of the agonistic interaction until expulsion of one of the crabs from the host was measured. The crab that remained on the sea anemone after agonistic interactions was declared as the winner. Of this experiment, 20 replicates were conducted and each crab was only used once (total *n* of crabs = 40; size range of the crabs varied between 10.2 and 18.5 mm CL). The sex of the interacting crabs was not noted during this first experiment, but care was taken that no receptive females (recently moulted) were used. In order to minimise stress for experimental crabs all replicates were conducted with dim light during the night.

### **Development of Territoriality During Ontogeny of *Allopetrolisthes spinifrons***

A second experiment was designed to examine the development of territoriality during ontogeny of *A. spinifrons*. Our goal was to obtain a measure of the degree of territorial behaviour exhibited by crabs of different ontogenetic stages. In this experiment, we determined the existence of aggressive exclusion between crabs by comparing (1) the probability of a crab of a specific ontogenetic stage to leave its sea anemone in response to a conspecific crab, with (2) the probability of a crab of the same ontogenetic stage to leave its host when alone in an aquarium, i.e. without conspecific crabs. Significant differences between probabilities were determined by an Independence  $\chi^2$  test (Sokal and Rohlf, 1981), which in case of no difference would indicate that factors other than agonistic interactions are responsible for crabs leaving their hosts.

In order to measure the probability of a crab to leave its sea anemone in response to conspecific intruders, one sea anemone and two or three small rocks were distributed in the opposite corners of the aquarium (20 cm × 20 cm × 20 cm). Using the same procedure as in the first experiment, intruder and resident crabs of similar or different ontogenetic stages were allowed to interact. The experiments were started at sunset (*ca.* 18:00–20:00 pm) and lasted until the next morning (8:00–9:00 am). Each possible combination of ontogenetic stages of *A. spinifrons* was tested: (1) adult–adult [where interactions among (1A) and between sexes (1B) were tested], (2) juvenile–juvenile, (3) recruit–recruit, (4) adult–juvenile, (5) adult–recruit, and (6) juvenile–recruit. Of each combination, 20 replicates were conducted, with different crabs each time (40 crabs per replicate, 280 crabs in total). The crabs were observed only for the first

10 min and agonistic interactions occurring during this time period were noted in order to describe the movement patterns preceding the agonistic behaviour of *A. spinifrons*. In case both crabs were found to cohabit on the sea anemone after 12 h darkness, we noted the position of each crab at the end of the experiment (i.e. the next morning).

In order to measure the probability of a crab to leave its sea anemone when alone (without conspecifics in the same aquaria), the presence/absence of a crab initially placed on a sea anemone without a conspecific crab was registered after 12 h of darkness. Twenty replicates of each ontogenetic stage of *A. spinifrons* were conducted.

Following the laboratory experiments, all crabs were released into their natural environment.

## RESULTS

### Description of the Agonistic Behaviour of *Allopetrolisthes spinifrons*

During this first experiment, large (adult) crabs were observed to fight for the monopolisation of their sea anemone hosts employing particular ritualised behaviours. During the first 30 min of acclimatisation, resident crabs most commonly were observed cleaning their antennae with maxillipeds or remaining motionless on the most protected side of the sea anemone (i.e. the side directed towards the walls of the aquarium). These resident crabs held firmly onto their hosts with their pereopods, being always oriented with the anterior part of the body towards the oral disc of the sea anemone (see Fig. 1 in Baeza *et al.* 2001). Upon introduction of an intruder, agonistic behaviour between crabs was observed in 65% of the cases (13 out of 20). Following these agonistic interactions, one of the crabs invariably left the sea anemone. During the interactions, several behaviours were exhibited by the crabs, usually in a particular sequence. After an intruding crab reached the sea anemone with the resident crab, it firmly attached with its pereopods to the outer surface of the sea anemone where it remained motionless. Occasionally, the sea anemone contracted its tentacles upon contact by the intruding crab. Following these movements of the sea anemone, the resident crab usually examined its host, exploring the surface of the sea anemone with the antenna. Consequently, the first interaction between crabs was usually with the antennae culminating in frequent antennal taps (*sensu* Molenock, 1976); crabs moved their antennae repeatedly touching the carapace or antenna of the opponent. In other cases, following initial attachment to the host, intruding crabs attempted to move almost immediately to the most protected part of the sea anemone, where the resident crabs was normally located. During these occasions, first contact between crabs occurred with their pereopods (walking leg contact *sensu* Molenock, 1976). Either the intruding or the resident crab left the sea anemone shortly after this first interaction. If none of the crabs abandoned the sea anemone upon these initial contacts with the pereopods or antennae, one or both crabs displayed the merus of the chelae closest to the opponent subsequently attempting to push this opponent crab away from the host (chela shove *sensu* Molenock, 1976). This movement pattern was maintained by crabs for several seconds and occasionally repeated after short periods of apparent inactivity. If none of the two crabs left the host following these initial contacts, the interactions escalated into wild-fights (4 out of 20 interactions). Both crabs moved across the host in order to maintain themselves in front of the opponent, then grasping

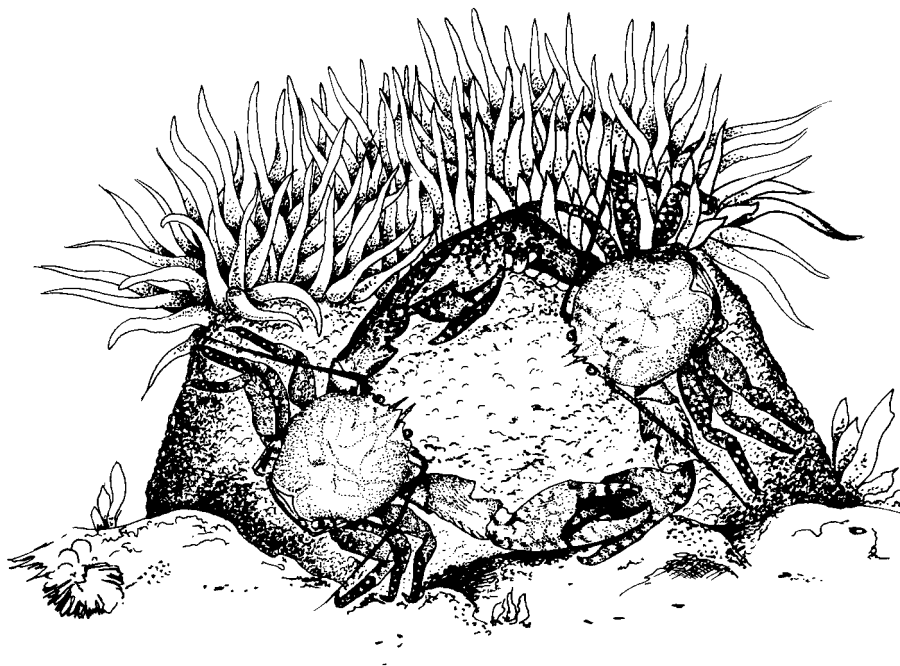


FIGURE 1 Chela shove as observed when intruder and resident crabs of *Allopetrolisthes spinifrons* fought (wild-fight) for sea anemones during the laboratory interactions.

both chelae of the other crab (chela grasp sensu Molenock, 1976) (Fig. 1). In one of these four fights, one of the interacting crabs lost a chela. Antennal lashing (sensu Molenock, 1976) was frequently directed from one crab to the other during this final step of the agonistic behaviour. Invariably, one of the crabs (usually the smaller individual) was excluded from the sea anemone after these aggressive interactions.

#### Development of Territoriality During Ontogeny of *Allopetrolisthes spinifrons*

During this second experiment, crabs showed a strong preference for sea anemones over bare rocks, when alone in an aquarium. In the absence of conspecifics, most symbiotic crabs remained on their sea anemone hosts after 12 h of darkness (90, 95, and 100% of adult, juvenile, and recruit crabs, respectively;  $n = 20$  replicates each).

The results of this second experiment (when two crabs were present in an aquarium) confirmed the presence of territoriality in adult and juvenile crabs. In treatments with two adults or two juveniles, respectively, almost invariably one crab was found in the alternative refuge (bare rock on one of the sides of the aquarium) after 12 h of darkness while the other crab resided on the host (Table I). The percentage of crabs found in alternative refuges in presence of a competitor was significantly higher than in absence of a competitor (72.5 vs. 10%  $\chi^2 = 18.43$ ,  $df = 19$ ,  $p = 0.01$  for adults, and 85 vs. 5%,  $\chi^2 = 22.73$ ,  $df = 19$ ,  $p < 0.01$  for juveniles, respectively, Fig. 2). For the adults, interactions between crabs did not depend on the sex of their opponents (interaction among sexes = 80%, between sexes = 65%, Chi-square test with Yates correction,  $\chi^2 = 0.5$ ,  $df = 1$ ,  $p = 0.4748$ ) (Table I). Furthermore, the percentage of the replicates with agonistic interactions during the first 10 min of the experiment was high

TABLE I Host-use of adult *Allopetrolisthes spinifrons* in experiments (a) with two crabs and (b) with a single crab; (a) Number of cases where two adult crabs *A. spinifrons* cohabited on the sea anemone host compared to the number of cases where one of the two crabs used the alternative refuge rock, and (b) number of cases when a single crab inhabited the sea anemone host or the refuge rock. The percent of the cases with all crabs on the host were taken as "Percent unrestricted host-use". In treatments with one adult crab, male and female crabs were used in equal proportions and the results of these treatments were directly compared with the treatments with two adult crabs. The Chi-square statistic and the *p* value indicating significant differences between frequencies are shown

Interaction	(a) Two adults				(b) One adult				$\chi^2$	<i>p</i>
	Both on host	One on rock	<i>n</i>	Percent unrestricted host-use (%)	On host	On rock	<i>n</i>	Percent unrestricted host-use (%)		
Intra sex	4	16	(20)	20.0	18	2	(20)	90.0	17.1	<0.001
Inter sex	7	13	(20)	35.0	18	2	(20)	90.0	10.7	0.001
Total	11	29	(40)	27.5	36	4	(40)	90.0	18.4	<0.001

TABLE II Frequency of occurrence of agonistic behaviour between crabs of similar or different ontogenetic stages (and sexes) of *Allopetrolisthes spinifrons*. Number and percentage of replicates, in which agonistic behaviour was observed, and the total number of replicates per combination are shown; interactions were observed for 10 min after initiating the experiment

Interaction	Number of replicates aggression /no aggression	Percentage with aggression (%)	<i>n</i>
Adult-Adult	24/16	60	40
Intra sex	12/8	60	20
Inter sex	12/8	60	20
Juvenile-Juvenile	12/8	60	20
Adult-Juvenile	3/17	15	20
Juvenile-Recruit	2/18	10	20
Adult-Recruit	0/20	0	20
Recruit-Recruit	0/20	0	20

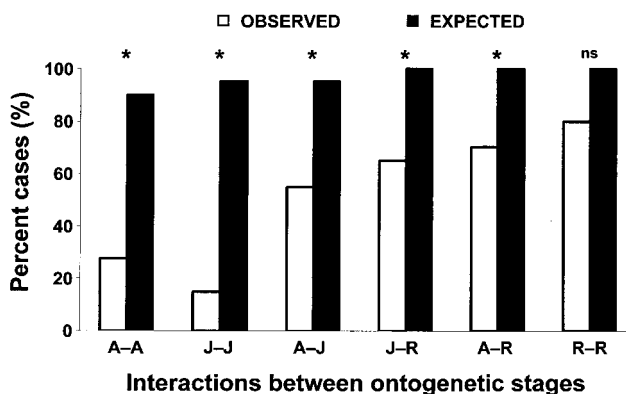


FIGURE 2 Percentage of cases where (1) crabs of a specific ontogenetic stage remained on their sea anemones together with another conspecific crab (open bars) and (2) percentage of cases where crabs of the same ontogenetic stage remained on their hosts when alone in an aquarium (filled bars). Asterisks indicate significant differences between percentages after an  $\chi^2$  test of Independence (see text for details) (A = adults, J = juveniles, R = recruits).

(Table II). The frequency of occurrence of agonistic encounters among adult crabs also did not depend on the sex of the opponents (60% in both inter- and intra-sexual interactions, Table II).

In contrast to adult–adult and juvenile–juvenile interactions, no agonistic behaviour was observed in the interactions between two recruit crabs. Furthermore, in most of the replicates (80%) both crabs were found to cohabit on the single available sea anemone after 12 h of darkness. This percentage did not differ significantly from the percentage of recruit crabs found dwelling on sea anemones when alone in an aquaria (Chi-square test with Yates correction,  $\chi^2 = 2.5$ ,  $df = 19$ ,  $p = 0.1139$ ).

Adult or juvenile crabs of *A. spinifrons* occasionally displayed territorial behaviour towards recruits, although these interactions rarely resulted in agonistic behaviour during the first 10 min of the experiment (0 and 10%, respectively). The percentage of crabs found together dwelling on the sea anemone after 12 h of darkness was high (Fig. 2). However, frequency of occurrence of recruit crabs in alternative refuges in presence of an adult or juvenile crab was significantly higher than in their absence (adult–recruit:  $\chi^2 = 4.9$ , juvenile–recruit:  $\chi^2 = 6.23$ ,  $df = 19$ ,  $0.01 < p < 0.05$  for both assays).

Interactions between adult and juvenile crabs during the first 10 min of the experiment resulted in aggressive behaviour only in 15% of the replicates (Table II). In 45% of the replicates, one of the crabs, invariably the juvenile, was excluded from the sea anemone after 12 h (adult–juvenile:  $\chi^2 = 6.53$ ,  $df = 19$ ,  $p = 0.0106$ ). In the remaining 55% of the replicates, where both crabs cohabited on the sea anemone, the juvenile crab was found on the most exposed area of the anemone while the adult resided on the most protected part of the host (i.e. the side towards the aquarium wall).

Territoriality and aggressive behaviour develop during ontogeny of *A. spinifrons*. The frequency of occurrence of aggression among crabs and the proportion of excluded crabs from sea anemones was higher in interactions between adults or between juveniles than in interactions involving recruits (see Table II).

The size of opponents is an important determinant for the outcome of agonistic interactions, in which one crab is excluded or displaced to the exposed part of the sea anemone. During these interactions, 83.8% of excluded crabs were smaller than their opponents (57 out of 68 interactions, excluding recruit–recruit interactions). In those occasions, in which both crabs were found on the same anemone after 12 h of darkness, almost invariably (94.2%, 49 out of 52 interactions, not considering recruit–recruit interactions) the smaller crab was found on the exposed side of the host while the larger crab resided on the protected part of the sea anemone. This pattern did not depend on ontogenetic stage of crabs, and sex of the opponents when the interactions occurred between adults (Table III).

## DISCUSSION

### Agonistic Behaviour and Development of Territoriality in *Allopetrolisthes spinifrons*

Our results indicate that the porcellanid crab *A. spinifrons* is a territorial species – each large crab attempting to monopolise and defend its hosts aggressively, excluding other large conspecifics. This territorial behaviour explains the low number of crabs observed per sea anemone host in previous studies (Viviani, 1969; Baeza and Stotz, 2001) and the

TABLE III Number of crabs *Allopetrolisthes spinifrons* excluded from sea anemones or found cohabiting with another crab in the single available sea anemone following interactions between resident and intruder conspecifics of similar or different ontogenetic stages (and sexes)

Interaction	Crabs cohabiting but on exposed part		Crabs expelled from sea anemones		n
	Large	Small	Large	Small	
Adult-Adult	3	8	8	21	40
Intra sex	1	3	4	12	20
Inter sex	2	5	4	9	20
Juvenile-Juvenile	0	3	3	14	20
Adult-Juvenile	0	11	0	9	20
Juvenile-Recruit	0	13	0	7	20
Adult-Recruit	0	14	0	6	20
Recruit-Recruit	–	–	–	–	(20)
Total	3	49	11	57	120

uniform population distribution pattern on sea anemones recently described for the species (Baeza *et al.*, 2001). When fighting for hosts, crabs exhibited several movement patterns, all of them already reported for other free-living porcellanid species (see Molenock, 1976). The fact that agonistic behaviours were usually displayed in a specific sequence suggests that individuals transmit information during these interactions, as previously reported for several other decapods, including porcellanid species (Molenock, 1974, 1976; Salmon and Hyatt, 1983). Furthermore, our results also indicate that contests between opponents may escalate, and that this action may be costly for losers – one crab lost a chela during wild-fight. In general, losers are more likely to suffer injuries than winners in other marine decapods (Knowlton and Keller, 1982). Thus, ritualised behaviour during fights, as observed herein for *A. spinifrons*, may help crabs to assess the resource holding potential of their opponents, helping them to make decisions (whether or not to escalate), and respond according to the fighting ability of their opponent in order to reduce the risk of injuries during interactions (see also Huber and Kravitz, 1995).

During the interaction between resident and intruder crabs, the smaller contestant was excluded from the sea anemone in almost 90% of the replicates. In case the small crab was not completely excluded, it was pushed towards the exposed part of the host, while the larger crab remained on the most protected side of the host. Thus, body size apparently plays an important role in determining the outcome of interactions. Several previous studies had shown that body or weapon (i.e. chelae) size determine competitive capability in decapods (Jachowski, 1974; Rubenstein and Hazlett, 1974; Caldwell and Dingle, 1979; Reaka, 1987; Evans and Shehadi-Moacdieh, 1988; Huntingford *et al.*, 1995; Hughes, 1996). However, condition of contestants such as hunger level (Stocker and Huber, 2001), physiological state (Tamm and Cobb, 1978), previous experience (Edwards and Kravitz, 1997), and sex (Knowlton and Keller, 1982) may also affect agonistic behaviours. Thus, ontogenetic changes in competitive capability of *A. spinifrons* may explain why territoriality develops during growth in this species: large crabs with a high resource holding potential (large chelae and body size) are able to compete more effectively than small (juvenile or recruit) crabs with weak competitive capabilities. In addition, the size relationship between symbionts and sea anemone hosts increases during ontogeny of *A. spinifrons*. Thus, for recruit crabs, sea anemones *P. clematis* may be too large to

be efficiently patrolled and defended against intruding conspecifics. In contrast, adult crabs may easily patrol hosts and exclude intruders without much effort. The relationship between the size of a host and its symbiont needs to be considered as one of the factors affecting the capacity to monopolise entire hosts (Thiel and Baeza, 2001). Snapping shrimp that monopolise sea anemones as heterosexual pairs (Knowlton, 1980) are relatively large in comparison to their hosts, while many cleaner shrimp species that live in constantly changing groups on their sea anemone hosts (Nizinski, 1989) are relatively small in comparison to their hosts. *A. spinifrons* apparently feeds on mucus and other waste materials produced by their hosts (Viviani, 1969). Trophic dependence of symbionts on their hosts may also need to be considered in the future as a potential factor determining host-resource monopolisation behaviour in symbiont species (Thiel and Baeza, 2001).

### **The Consequences of Territorial Behaviour in *Allopetrolisthes spinifrons***

Adult and juvenile crabs defend sea anemones aggressively against other adults or juveniles, but they show no aggression towards small recruit crabs. As a consequence, several crabs may cohabit on a sea anemone, but they apparently compete for preferred spots on the sea anemone. This is suggested by the fact that the largest crab (the one with the highest resource holding potential) usually is found on the most protected parts of a sea anemone, while small crabs are found on the exposed parts. This form of resource-sharing may help to explain a frequent and particularly intriguing association pattern (i.e. adults cohabiting with recruits) reported in the field for *A. spinifrons* (Baeza *et al.*, 2001) and other symbiotic decapods (Nakashima, 1987; Lindberg and Stanton, 1988; Tsuchiya and Yonaha, 1992). Presently it is not clear, whether adults overlook small, recruit, crabs or whether they actively tolerate them on their hosts. Since adult crabs are thought to move between hosts in search of mating partners, they require nearby hosts with conspecifics of the opposite sex (Baeza *et al.*, 2001). Tolerance of adult crabs towards small conspecifics on “their” sea anemones may help ensure a high frequency of occupied hosts in their vicinity (Baeza *et al.*, 2001), and subsequently increase the chances to find potential mating partners in the future. Given the importance that adult–juvenile interactions may have for the population dynamics of symbiotic crabs (see below), future studies should focus on these interactions.

Aggressive interactions between adults and growing juveniles have also been reported for several mantis shrimp species (Stomatopoda) and fishes associated to reefs where suitable refuges are limited (Sale, 1983; Reaka, 1987). The influence of these interactions on population structure and recruitment of species may be considerable (see Reaka, 1987). In *A. spinifrons*, adult–juvenile interactions may also play an important role in population-regulating processes since hosts apparently represent a limited resource for this symbiotic crab. Juveniles excluded by an adult from its original sea anemone will need to search for a new host. This may increase their risk of falling victim to fishes and other brachyuran crabs, known to prey upon porcellanid crabs (Varas and Ojeda, 1990; JAB, personal observations). However, if free hosts are available in the vicinity, these predation-induced losses of juvenile *A. spinifrons* most likely will be minimal. Thus, the combination of adult tolerance towards small recruits and the increasing aggression towards growing juveniles will ensure a high prevalence of these (and possibly other) symbiotic crabs on their hosts. Territoriality in combination

with juvenile-tolerance in this and other symbiotic decapods would thus function as a density-dependent mechanism of population regulation, being mediated by host availability.

### The Extent of Territoriality in Other Symbiotic Species

Many symbiotic porcellanid species are found as solitary individuals or in heterosexual pairs on their hosts (Table IV). This is in contrast to free-living porcellanids, which occur in dense aggregations of many individuals in crevices or under rocks (Jensen and Armstrong, 1991; Robinson and Tully, 2000). The highly specific association pattern of symbiotic porcellanids suggests the presence of strong territorial behaviour. A symbiotic organisms needs to secure two major resources during its lifetime, an appropriate host and a mating partner. Fulfilling both these requirements simultaneously is solved best by cohabiting with a member of the opposite sex on one host. It is thus not surprising that most porcellanid species that have adopted a symbiotic life-style inhabit hosts as heterosexual pairs (Table IV). Such heterosexual pairs may represent long-lasting pairs and may include co-operative territorial behaviour of male and female partners that defend their host against intruders. Complex territorial behaviour has been previously demonstrated for the brachyuran crabs *T. intermedia* and *T. digitalis*, symbiotic with *Pocillopora* coral heads, and the caridean shrimp *A. armatus*, associated with the sea anemone *B. annulata* (Knowlton, 1980; Huber, 1987). Each member of these heterosexual pairs excludes conspecifics of the same sex, but tolerates any conspecific of the opposite sex. Similar sex-differential territorial behaviour can also be expected for the symbiotic porcellanid species that inhabit their hosts in heterosexual pairs. In these species, hosts may be sufficiently large to support two (but not more) crabs.

Two symbiotic porcellanid species, *Liopetrolisthes mitra* and *A. spinifrons*, do not live in heterosexual pairs on their hosts (Table IV). In *L. mitra*, the comparatively small crabs (max. size: 10.6 mm CL) occur in aggregations of several individuals (up to 25) on their sea urchin hosts (Baeza and Thiel, 2000). These aggregations are highly variable since crabs move freely between neighbouring sea urchins (Zander, 2000; Thiel *et al.*, in press). The fact that hosts are difficult to monopolise (due to their relatively

TABLE IV Host use pattern of several symbiotic porcellanid crabs (S=single, P=pairs, A=aggregated, ?=no data available)

Species	Host	Habit	Latitude	Author
<i>Allopetrolisthes spinifrons</i>	<i>Phymactis clematis</i> (Actinaria)	S	Temperate	11, 13
<i>Neopetrolisthes maculatus</i> <sup>a</sup>	<i>Stoichactis</i> spp. (Actinaria)	P	Tropical	3
<i>Neopetrolisthes spinatus</i>	<i>Heteractis malu</i> (Actinaria)	P	Tropical	12
<i>Aliaporcellana telestophila</i>	<i>Solenocaulon</i> sp. (Gorgonacea)	P	Tropical	7
<i>Clastoeteuchus vanderhorsti</i>	<i>Echinometra lucunter</i> (Echinoidea)	P	Caribbean	4, 6
<i>Liopetrolisthes mitra</i>	<i>Tetrapygyus niger</i> (Echinoidea)	A	Temperate	10
<i>Minyocerus angustus</i>	<i>Luidia</i> spp. (Asteroidea)	P	Caribbean	2
<i>Polyonyx bella</i>	<i>Chaetopterus variopedatus</i> (Polychaeta)	P	Tropical	8
<i>Polyonyx gibbesi</i>	<i>Chaetopterus variopedatus</i> (Polychaeta)	P	Temperate	1, 5
<i>Polyonyx cometes</i>	<i>Chaetopterus variopedatus</i> (Polychaeta)	?	Temperate	9

(1) Gray, 1961; (2) Gore and Shoup, 1968; (3) Seibt and Wickler, 1971; (4) Werding, 1983; (5) Grove and Woodin, 1996; (6) Schoppe, 1991; (7) Ng and Goh, 1996; (8) Hsueh and Huang, 1998; (9) Ng and Nakasone, 1993; (10) Baeza and Thiel, 2000; (11) Baeza *et al.*, 2001; (12) Osawa and Fujita, 2001; (13) present study.

<sup>a</sup>*N. ohshimai* is considered to be *N. maculatus* (Osawa and Fujita, 2001).

large size and dense aggregation pattern) may primarily be responsible for the apparent lack of territoriality in *L. mitra*. The sea-anemone dwelling *A. spinifrons* is the other exception from the general trend among symbiotic porcellanids in that adults of this species exhibit a solitary life-style characterised by a high degree of territorial behaviour towards adult conspecifics. Juvenile symbionts show less aggressive behaviour than adults (see also Lindberg and Stanton 1988), possibly because they are less restricted by host size than adults. In *A. spinifrons*, one host individual can easily harbour several small juveniles, but few large juveniles and only one adult. Consequently, intraspecific aggressions increase during ontogeny in this symbiotic porcellanid. Adult *A. spinifrons* clearly show a size-differential territorial behaviour, excluding other adults, but tolerating small juveniles. A solitary life-style appears only feasible if hosts with potential mating partners are in the vicinity. Presently, no detailed information, neither on the distances between sea anemone hosts of *A. spinifrons* nor on the sexes of adults on neighbouring sea anemones, is available. This information appears essential in order to fully understand the territorial behaviour of this and other symbiotic crabs, and future studies should also focus on the host distribution in the field.

Based on the comparison of the host use patterns among symbiotic porcellanid species (Table IV), we suggest that territorial behaviour is also common among other symbiotic and free-living marine invertebrates that inhabit dwellings that (a) represent a limited resource, (b) have well-confined borders, (c) are relatively small compared to the symbiont, and (d) are spatially separated, thereby permitting easy monopolisation.

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