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## Predicting territorial behavior in symbiotic crabs using host characteristics: a comparative study and proposal of a model

Received: 15 January 2002 / Accepted: 25 July 2002 / Published online: 24 October 2002  
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**Abstract** Many studies on the social behavior of symbiont species have inferred that besides environmental factors (predation pressure, competition) host-related characteristics (i.e., host abundance and distribution, size, and morphology) have a major influence on the evolution of symbiont behavior. However, in many cases little information is available on host populations and few comparative studies have been conducted to test predictions. Herein, we compare the basic ecology of the sea anemone *Phymactis clematis* and the sea urchin *Tetrapygus niger*, each being host to a different porcellanid crab species, *Allopetrolisthes spinifrons* and *Liopetrolisthes mitra*, respectively. We first provide a description of host abundance and distribution and then test predictions concerning the behavioral ecology of the two crab symbionts to understand how and to what extent host characteristics affect the behavior of symbionts (i.e., host-resource monopolization). In the field, distances between host individuals (~15 cm) were similar for both sea anemones and sea urchins. However, the sea anemones were significantly less abundant than sea urchins. Furthermore, sea anemones represent a relatively small and morphologically simple microhabitat for *A. spinifrons* crabs, whereas sea urchins represent a relatively large and morphologically complex microhabitat for *L. mitra* crabs. The population distri-

bution and size-specific association pattern of the two symbiotic crabs differed substantially, with *A. spinifrons* leading a solitary and *L. mitra* a gregarious life-style. Adults of *A. spinifrons* only cohabited with sexually immature individuals on their host, whereas adult *L. mitra* frequently occurred together with other adult crabs of both sexes on their host. These differences suggest strong territorial behavior for *A. spinifrons* but not for *L. mitra*, which is supported by results from other experimental studies on the intraspecific interactions of the two crab symbionts. The presence or absence of host-resource monopolization behaviors in these crab species appears to be an adaptive behavioral response depending on features of the corresponding host species – particularly host abundance, morphological complexity, and relative size. Based on these results, we developed a conceptual model to predict the probability for a symbiont to monopolize a host successfully, depending on host characteristics. The model predicts that the probability of host-resource monopolization behavior of a symbiont decreases with increasing (1) host abundance, (2) host complexity, and (3) relative host size. The present study is a first attempt to understand how host-resource monopolization behaviors have evolved and developed in symbiotic crustaceans and other marine invertebrates.

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Communicated by O. Kinne, Oldendorf/Luhe

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### Introduction

Resource-guarding behavior is known for a wide variety of marine and terrestrial vertebrate and invertebrate taxa. Guarding behaviors may serve to monopolize shelter, food, offspring, and mating partners from intra- and/or interspecific competitors (Foster 1985; Huber 1987; Shuster 1987; Aoki and Kikuchi 1991). When a single individual or a group of individuals makes exclusive use of a fixed area and potential intruders are excluded by aggressive displays, the term territoriality instead of shelter-guarding behavior is commonly employed

(Wilson 1975). Previous empirical studies and theoretical considerations have suggested that monopolization of resources – including territoriality – evolves when these resources are economically defendable (Emlen and Oring 1977; Grant 1993). The term “economical” implies that resources are monopolized whenever the benefits exceed the costs of defense or when the net benefits of defense exceed those of alternative behaviors (e.g., feeding or nonguarding behaviors instead of guarding; Brown 1964). The abundance and distribution of resources, and the abundance of the individuals exploiting these resources (i.e., intrusion frequency; Chapman and Kramer 1996) have been considered as the main environmental conditions determining resource defensibility (Grant 1993). Overall, resource-guarding behaviors are predicted to evolve when resources are clumped and scarce, and/or when intrusion by intruders is uncommon (i.e., due to low population density; Grant 1993). While the effect of environmental conditions on the expression of resource monopolization behaviors has been examined for various terrestrial taxa or marine vertebrates (see review by Grant 1993), this aspect has been almost neglected in marine invertebrates (for exceptions see Knowlton 1980 and Duffy et al. 2000).

Among marine invertebrates, symbiotic crustaceans feature a wide range of hosts and a wide array of spacing systems and intraspecific association patterns on/in their respective hosts (Thiel and Baeza 2001). Thus, they represent a model system to study the effect of environmental factors on resource-guarding behaviors. Macroinvertebrates used as hosts by symbiotic crustaceans pertain to different phylogenetic groups that differ widely in their ecology (i.e., abundance and distribution pattern) and general biology (i.e., size, morphology, longevity, and nutritive/protective value; see, for example, Ross 1983; Svavarsson et al. 1993; Thiel 2000). These macroinvertebrates represent one of the most important resources for these symbiont species, serving as refuge against predators (e.g., for isopods; Stebbins 1989), a feeding place (for symbiotic crabs; Stimson 1990), and mating arenas (for isopods; Shuster 1987). Symbiotic crustaceans may inhabit hosts in dense unstructured aggregations, apparently lacking any kind of territorial behavior (e.g., palaemonid shrimp; Nizinski 1989). Most commonly, symbiotic species inhabit their hosts as heterosexual pairs (Knowlton 1980; Huber 1987; Omori et al. 1994; Baeza 1999). Polygamous groups, where one male attempts to monopolize reproduction with the females living in “its” host, have also been described (Shuster 1987). Other symbionts live as solitary individuals on a host (Wells and Wells 1961; Diesel 1988), but no studies have been conducted as yet to test for territorial behavior in these species. Several studies suggest that strong predation pressure and limited availability of hosts has favored the evolution of social behavior in some symbiotic species (e.g., snapping shrimp; Knowlton 1980; Knowlton and Keller 1983; Duffy 1996; Duffy et al. 2000).

For symbiotic crustaceans, several other factors besides resource distribution, abundance, and intruder pressure have been proposed to affect their host-resource monopolization behavior and the resulting host-use patterns observed in the field (Thiel and Baeza 2001). Relative size may affect the potential of a species to monopolize a host. An indication of the importance of relative size can be seen in the positive relationship between the size of a host and the number of symbionts inhabiting it – total of individuals as well as of species – or between host size and the size of a single symbiont (Báez and Martínez 1976; Gotelli et al. 1985). Space available and the width of the inhabited spaces in/on a host may affect not only the number but also the life stages or sex of symbionts cohabiting in/on one host individual (e.g., Duffy 1992; Baeza and Stotz 2001). These results provided the first hints that morphological complexity of hosts also affects the monopolization potential of symbiotic crustaceans. In relatively complex hosts, defense against other symbionts may be difficult (i.e., energetically costly) or impossible, whereas relatively simple hosts with limited structural complexity and small access area (e.g., well-defined openings) may be relatively easy to defend against intruders (Thiel and Baeza 2001). Based on the above information, three specific predictions on the behavioral ecology of symbiont species can be made: the probability of host-resource monopolization behavior of symbionts decreases with increasing host abundance ( $P_1$ ), host complexity ( $P_2$ ), and relative host size ( $P_3$ ).

The present study is a first attempt to explore these predictions using information on the biology of two symbiotic porcellanid crabs: *Allopetrolisthes spinifrons* dwelling on the body column of the sea anemone *Phymactis clematis* in the rocky intertidal (Baeza and Stotz 2001), and *Liopetrolisthes mitra*, found among the spines of the sea urchin *Tetrapygus niger* in the shallow rocky subtidal (Baeza and Thiel 2000). The life history and general ecology of both symbiont species have been reported in previous years (Baeza and Thiel 2000; Baeza and Stotz 2001; Baeza et al. 2001, 2002; Thiel et al. 2002).

Herein we first compare the basic ecology (abundance, distribution, size, morphological complexity) of the host species of these two closely related symbionts (see Stillman and Reeb 2001 for phylogenetic relationship). Following this comparison, we examine whether the population distribution and intraspecific association pattern of the symbiont species correspond with the above predictions. We finally test these predictions by comparing them to our present knowledge of the territorial behavior of the two symbiont species. Based on the results of this comparison and on published information on other crustacean symbionts we develop a conceptual model that utilizes basic host characteristics to predict host-resource monopolization behavior of crustacean symbionts.

## Materials and methods

### Study sites

The abundance and distribution of the sea anemone *Phymactis clematis* and the sea urchin *Tetrapygus niger*, the respective hosts to the two studied crabs, were analyzed in the intertidal zone of La Pampilla and in the shallow subtidal zone of La Pergola, Coquimbo (29°57'S, 71°21'W), Chile, respectively. At La Pampilla, a semi-exposed rocky intertidal site, the mid-zone is dominated by green algae *Ulva* spp., and the infra-littoral fringe is characterized by the kelp *Lessonia nigrescens*. The sea anemone *P. clematis* mainly inhabits crevices and spaces among boulders at this site (Baeza and Stotz 1995). Sea urchins *T. niger* occur abundantly at La Pergola in the shallow subtidal zone at a depth of 0–3 m below mean low water (Baeza and Thiel 2000). This study site is characterized by the presence of large and small boulders intermingled with gravel substratum. Crustose coralline algae cover almost the entire surface of boulders on which the sea urchin *T. niger* and the sea anemone *Phymanthea pluvia* can be commonly observed. Near the study site, at Bahía La Herradura, surface water temperature usually varies between 13°C (winter) and 20°C (summer) (Moraga and Olivares 1993).

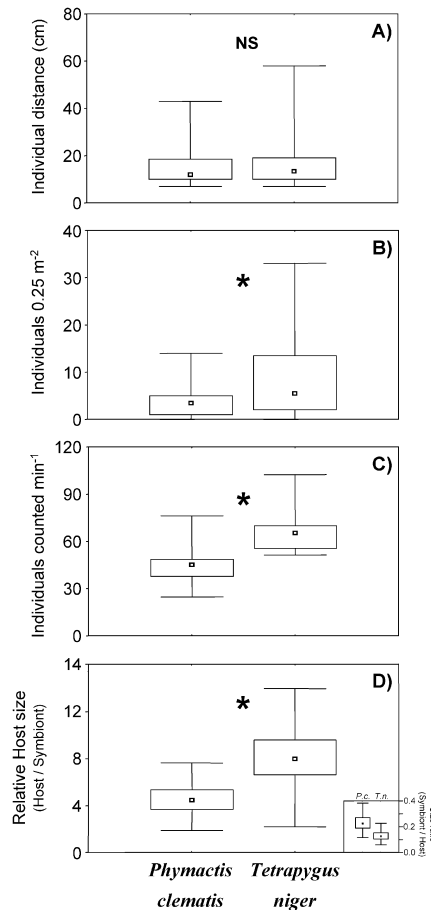
### Host abundance and distribution pattern

Counting and estimating the abundance of organisms in three-dimensional boulder-dominated habitats represents a serious obstacle to ecologists. Herein, we employed several simple and repeatable methods to get objective estimates of the abundance and distribution pattern of the two host species. All measurements of host abundance and distribution were taken in December 2000. We measured the distance from the body center of one host individual to that of the nearest neighbor individual. For each host species, 100 replicate measurements were taken along a stretch of approximately 200 m at each study site. Additionally, we determined the average abundance of each host species based on quadrant counts. Along the same stretch of coastline where we had measured average distances between individual hosts, we placed 0.25-m<sup>2</sup> quadrants at random, counting all hosts within a quadrant. For sea urchins, standard quadrant count procedures on rocky shores were followed (see, for example, Rodríguez and Ojeda 1993). However, for the sea anemones, which often inhabit cavities inaccessible for commonly employed quadrant counts, we adopted a quadrant projection procedure; the quadrant was placed over boulders and cavities, projecting the sides of the quadrant downwards, and then we counted all sea anemones that we could see within the projected area. The mean abundance values ( $n = 50$  replicate counts) obtained this way were considered approximate estimates of host abundance. Our abundance estimates were validated by counting sea urchins and sea anemones in relation to sampling effort. One person counted all host individuals that could be touched with one hand within a given period of time. This exercise was replicated 20 times, and we calculated the mean number of hosts touched per minute. We tested whether host abundance and distribution vary between symbiont species using  $t$ -tests (Sokal and Rohlf 1981). Data transformations (e.g., square root, logarithmic) were conducted whenever necessary to fit the assumptions of each of the tests (Sokal and Rohlf 1981). If assumptions for the  $t$ -tests were not achieved after data transformation, a Mann–Whitney  $U$ -test was conducted to examine for significant differences in abundance and/or distribution between the symbiont species (Sokal and Rohlf 1981).

### Relative host size

This analysis is based on data of host size and crab size available from previous studies (Baeza and Thiel 2000; Baeza et al. 2001). Herein, host diameter – pedal disc diameter in sea anemones and test diameter (not considering the spines) in sea urchins – was taken

as the body measure best suited to describe the size of the two host species and to allow for a direct comparison. The anemone has a more-or-less cylindrical body shape and the sea urchin has a more-or-less spherical body shape (see Fig. 1 in Baeza and Thiel 2000 and Baeza et al. 2001, respectively). Body diameter can be considered as a useful proxy for host surface area, since at a given body diameter, the surface area usable by a symbiont on a sea anemone and on a sea urchin are similar (J.A.B. and M.T., unpublished data). However, sea urchins are substantially more morphologically complex than sea anemones. As a measure of the size of the symbiont, we used the carapace length (CL) of the largest individual crab found on a host. For the analysis, we pooled all hosts that harbored adult crabs (*Liopetrolisthes mitra* > 4.0 mm CL; *Allopetrolisthes spinifrons* > 7.0 mm CL) and we calculated the relative host size (host diameter/CL of largest crab). We tested whether relative host size differed between the two species of interest using a  $t$ -test (Sokal and Rohlf 1981). Data transformation (logarithmic) was conducted whenever necessary to fit the assumptions of the test (Sokal and Rohlf 1981).



**Fig. 1A–D** Basic parameters of the two host species studied during the present study. **A** Host distance; **B** host abundance; **C** hosts encountered per unit time; **D** relative host size. Given are medians, 25th, and 75th percentiles and ranges; \*  $P < 0.05$ , NS not significant. Host distance represents distance to the nearest neighbor ( $n = 100$  measurements for each species); host abundance based on 50 randomly placed quadrant (0.25 m<sup>-2</sup>) counts for each species; hosts encountered per unit time based on 20 replicate counts for each species; relative host size (host/symbiont) is based on 360 individuals of *Phymactis clematis* and 490 individuals of *Tetrapygus niger* (data from Baeza and Thiel 2000, and Baeza et al. 2001), insert shows size ratio symbiont/host for comparative reasons – see Thiel and Baeza 2001; for further details see Materials and methods

## Indication for host-resource monopolization behavior

To examine the presence or intensity of host-resource monopolization in both symbiotic species, we studied the population distribution of both symbionts on their respective hosts, and the size relationship between the largest and the second largest crab on hosts with two or more symbiotic crabs (data for *A. spinifrons* taken from Baeza et al. 2001, data for *L. mitra* taken from Baeza and Thiel 2000). To assess the population distribution of the symbiont species on their respective hosts, we determined the frequency with which crabs occurred in aggregations comprising different numbers of symbionts on their hosts, pooling all available data of hosts that harbored symbiotic crabs. Then, we tested whether the observed frequency distribution differed significantly from random by comparing it with the Poisson distribution. A  $\chi^2$  test of goodness of fit was used to examine for significant differences (Sokal and Rohlf 1981). If distributions differed significantly, we compared specific frequencies (e.g., frequency of hosts harboring a single crab) between the observed and expected distribution by a  $\chi^2$  test of independence (Sokal and Rohlf 1981). We expected that the species displaying host-resource monopolization would show a uniform distribution pattern on their hosts compared to a random or aggregated distribution for the species that does not monopolize its host.

## Results

### Host distribution and abundance

In the rocky intertidal of La Pampilla and in the shallow subtidal of La Pergola, individual sea anemones *Phymactis clematis* as well as sea urchins *Tetrapygus niger* were separated by an average distance of about 14–15 cm. Intraspecific distances to the nearest neighbor did not differ between the two host species (*t*-test:  $t=1.05$ ,  $df=1,198$ ,  $P=0.29$ ; Fig. 1A). The variability was greater in *T. niger* than in *P. clematis*, and some sea urchins were separated from their nearest neighbor by a distance of almost 60 cm (see Fig. 1 in Baeza and Thiel 2000). Although minimal distances between individuals were very similar in sea anemones and sea urchins, the sea urchins usually touched several neighbors with their spines, whereas individual sea anemones never were in direct body contact with conspecifics. Sea urchins were significantly more abundant than sea anemones [Mann–Whitney *U*-test,  $U=928.5$  ( $n=100$ ),  $P<0.05$ ]. The average density of the sea urchins was about 9 individuals  $0.25\text{ m}^{-2}$  (range: 0–33), whereas the density of sea anemones reached only about 4 individuals  $0.25\text{ m}^{-2}$  (range: 0–14; Fig. 1B). The mean number of hosts touched per minute was significantly higher in *T. niger* than in *P. clematis* (*t*-test:  $t=5.67$ ,  $df=1,38$ ,  $P<0.001$ ) underlining the results of the abundance estimate (Fig. 1C). Overall, sea anemone hosts were less abundant than sea urchin hosts, but individuals of both host species were separated by similar distances.

### Relative host size (host/symbiont)

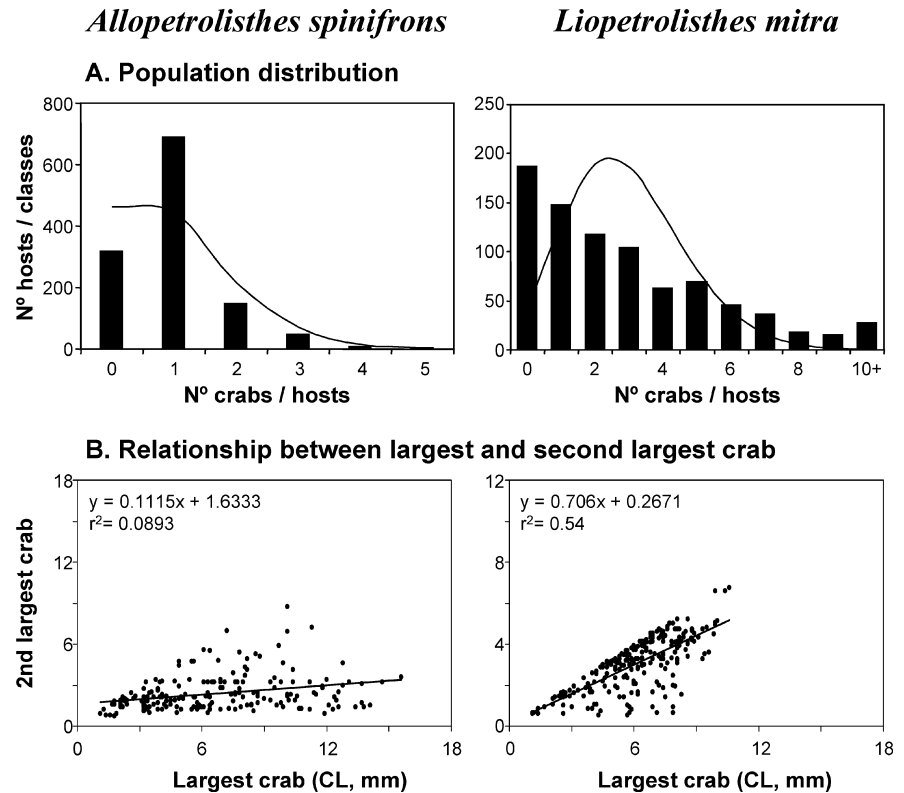
The size ratio between sea anemones *P. clematis* and their symbiotic crab, *Allopetrolisthes spinifrons*, was

significantly smaller than the size ratio between sea urchins *T. niger* and their symbiotic crab, *Liopetrolisthes mitra* (*t*-test after logarithmic transformation:  $t=29.35$ ,  $df=1,848$ ,  $P<0.001$ ; Fig. 1D). For both host–symbiont pairs, there was a high variability in this size ratio, indicating that on various occasions small crabs were found on large hosts and vice versa. This comparison underlines that relative host size in symbiotic crabs *A. spinifrons* was considerably smaller than in *L. mitra*: crabs dwelling on sea anemones are relatively large compared to their host, whereas crabs dwelling on sea urchins are relatively small compared to their hosts.

### Intraspecific association pattern of symbiotic crabs

The intraspecific association pattern of the two symbiotic crabs on their respective hosts differed substantially (Fig. 2A). The population distribution of *A. spinifrons* on sea anemones did not display a random pattern (Chi-square of goodness of fit:  $\chi^2=212.6$ ,  $df=5$ ,  $P<0.001$ ). This was explained by the large number of sea anemones harboring a single commensal crab compared to the number predicted by the Poisson distribution (Chi-square of independence:  $\chi^2=98.49$ ,  $df=2$ ,  $P<0.001$ ; Fig. 2A). Most adults of *A. spinifrons*, regardless of their sex, inhabited their sea anemone hosts as solitary individuals, but on occasion, more than two crabs were found on a single host. The slope and the correlation between the size (CL) of the largest and the second largest crab when more than two crabs were found on a single host were low but significant ( $m=0.112$ ,  $t=4.47$ ,  $P<<0.001$ ;  $r^2=0.089$ ,  $F_{(1,204)}=19.99$ ,  $P<<0.001$ ; Fig. 2B). Thus, small crabs of similar size may be found inhabiting the same host, but medium (juveniles) and large (adults) crabs almost never shared a host with another conspecific of relatively similar size. Occasionally, these large crabs cohabited on a host with other small conspecific crab(s). The population distribution of *L. mitra* did not display a random pattern on sea urchins (Chi-square of goodness of fit:  $\chi^2=1450.3$ ,  $df=10$ ,  $P<0.001$ ; Fig. 2A). This was due to the larger number of hosts without crabs when compared to the number expected by chance (Chi-square of independence:  $\chi^2=104.6$ ,  $df=1$ ,  $P<0.0001$ ) but also due to the relatively large number of hosts harboring nine or more conspecific crabs (Chi-square of independence:  $\chi^2=44.25$ ,  $df=1$ ,  $P<0.0001$ ) compared to the number expected by chance. Aggregations of crabs on sea urchins comprised crabs of similar size classes, regardless of the size or ontogenetic stage of the largest crab in the aggregation. The slope and the correlation between the largest and the second largest crab when more than two crabs were found on a single host were highly significant ( $m=0.706$ ,  $t=16.82$ ,  $P<<0.001$ ;  $r^2=0.54$ ,  $F_{(1,241)}=282.93$ ,  $P<<0.001$ ; Fig. 2B), indicating that the second-largest crab was only slightly smaller than the largest crab found in any given aggregation. Overall, in *L. mitra* most crabs occurred in aggregations of several

**Fig. 2A, B** The population distribution pattern and the relationship between the size of the largest crab and the second largest crab when two or more symbionts were found inhabiting the same host individual (Data from Baeza and Thiel 2000 and Baeza et al. 2001). Data on population distribution and the relationship between the size of the largest crab and the second largest crab of the studied symbiont species are based on a total of 1,214 and 206 hosts of *Allopetrolisthes spinifrons*, and 832 and 243 hosts of *Liopetrolisthes mitra*, respectively. *CL* carapace length



individuals on their sea urchin hosts. These aggregations consisted of individuals of all sizes and life stages. Apparently, they represent unstructured heterosexual groups, because several adults may be found together on the same host as previously reported by Baeza and Thiel (2000). The slopes of the relationship of largest versus second-largest crab (Fig. 2B) differed significantly between the two crab species ( $t = 14.16$ ,  $df = 1,241$ ,  $P < 0.05$ ), supporting the conclusion that the two species differ with respect to their intraspecific association behavior, large *L. mitra* crabs associating with conspecifics of all sizes on their sea urchin and large *A. spinifrons* crabs associating only with small conspecifics on their sea anemone.

## Discussion

The general ecology of sea anemones *Phymactis clematis* and sea urchins *Tetrapygus niger* differ in several aspects. Sea anemones are less abundant and thus represent a limited resource for potential symbionts (Baeza and Stotz 2001) compared to sea urchins that usually occur at high densities (Rodríguez and Ojeda 1993). Furthermore, sea anemones represent a comparatively smaller host for *Allopetrolisthes spinifrons* than sea urchins do for *Liopetrolisthes mitra*. The intraspecific association pattern of the crab symbionts also differed substantially, with *A. spinifrons* leading a solitary (Baeza et al. 2001) and *L. mitra* a gregarious life-style (Baeza and Thiel 2000). These association patterns represent a good

expression of territorial behavior as confirmed by recent experimental studies that demonstrated territorial behavior in *A. spinifrons* (Baeza et al. 2002), but not in *L. mitra* (Thiel et al. 2002). Our results suggest that the differences in the spacing system and host-resource monopolization behaviors between these two symbiont species are related to differences in abundance and defensibility (driven by relative size and also morphology) of the host species as will be discussed below.

The effect of host characteristics on the behavior of symbiont species

Resource (e.g., habitat) limitation has been considered as one of the main selective pressures determining the evolution of resource-guarding behaviors, including territoriality, in several vertebrate and invertebrate taxa (Wilson 1975; Barash 1982; Grant 1993; Chapman and Kramer 1996; Duffy et al. 2000). Thus, territorial behavior in *A. spinifrons* may have developed as a consequence of the limited availability of hosts. In contrast, hosts do not appear to be in limited supply for *L. mitra* symbiotic crabs, and no monopolization behaviors are expected to develop in this species. Sea anemone hosts not only can be considered as small but also as discrete habitat for *A. spinifrons* crabs due to their low morphological complexity. Furthermore, these sea anemones usually occur at moderate densities and maintain minimum distances to neighbors (Rivadeneira and Oliva 2001). Thus, symbiotic crabs on sea anemones

can efficiently patrol and defend a host individual against intruders, since such activities are probably energetically inexpensive (compared to alternative activities). In contrast, sea urchins represent a large and heterogeneous refuge for *L. mitra* crabs, not only because of their large relative size, but also due to their abundant and relatively large spines. Additionally, these sea urchins may occur in dense aggregations with several individuals touching each other (Rodríguez and Ojeda 1993). These host characters may constrain the development of host monopolization behaviors in *L. mitra* because activities allocated to patrolling and exclusion of intruders are expected to be energetically expensive (compared to alternative activities) in these large and structurally complex microhabitats. The expression of host-resource monopolization behaviors in the two studied crab species appears to be an adaptive behavioral response depending on characteristics of their corresponding host species. Our results agree with predictions of resource-defense theory based on the economic defensibility of resources (Brown 1964; Grant 1993). When host monopolization potential is high, symbionts guard their individual hosts, whereas in hosts with low monopolization potential, symbionts exhibit no guarding behavior (Table 1).

Besides host abundance, morphological complexity, and relative size, other host features such as availability of food resources provided by hosts may also affect the social behavior of their crab symbionts. Porcellanid crabs are suspension feeders (Achituv and Pedrotti 1999), which also holds true for the studied species that use their hosts as vantage points for suspension feeding. Observations by Zander (2000) demonstrate that *L. mitra* does not feed on its hosts but depends entirely

on food resources captured directly from the water column; crabs may share hosts without interfering with cohabiting conspecifics. However, sea anemones may provide additional food for *A. spinifrons* (mucus – Viviani 1969, and J.A.B., personal observations). Thus, sea anemone hosts may represent a more valuable resource for *A. spinifrons* (refuge plus food) than sea urchins do for *L. mitra* (refuge only). Increasing food dependence on hosts may also be considered as a selective pressure, promoting host-monopolization behaviors in symbiotic species (see Yanagisawa and Hamaishi 1986).

In contrast to *A. spinifrons* and *L. mitra*, several other porcellanid crabs with a symbiotic life-style inhabit hosts as heterosexual pairs (Baeza et al. 2002). These other species may be able to share their host with one other crab (of the opposite sex) but not more. Their size may allow them to patrol and defend their host individual against intruders of the same sex, resulting in efficient host monopolization. Such heterosexual pairs may also represent long-lasting pairs as previously described or inferred for various other symbiotic decapod species (Knowlton 1980; Huber 1987; Baeza 1999). The different intraspecific association patterns described for symbiotic species further suggests that host ecology (i.e., host abundance) and other host-related characters (i.e., morphological complexity, relative size) not only play an important role in determining the evolution of host-resource monopolization behavior in these symbiotic crustaceans, but structure their mating systems and other complex social behaviors (Thiel and Baeza 2001). Future studies are required to understand the effect of host biology on the mating system of symbiotic marine crustaceans.

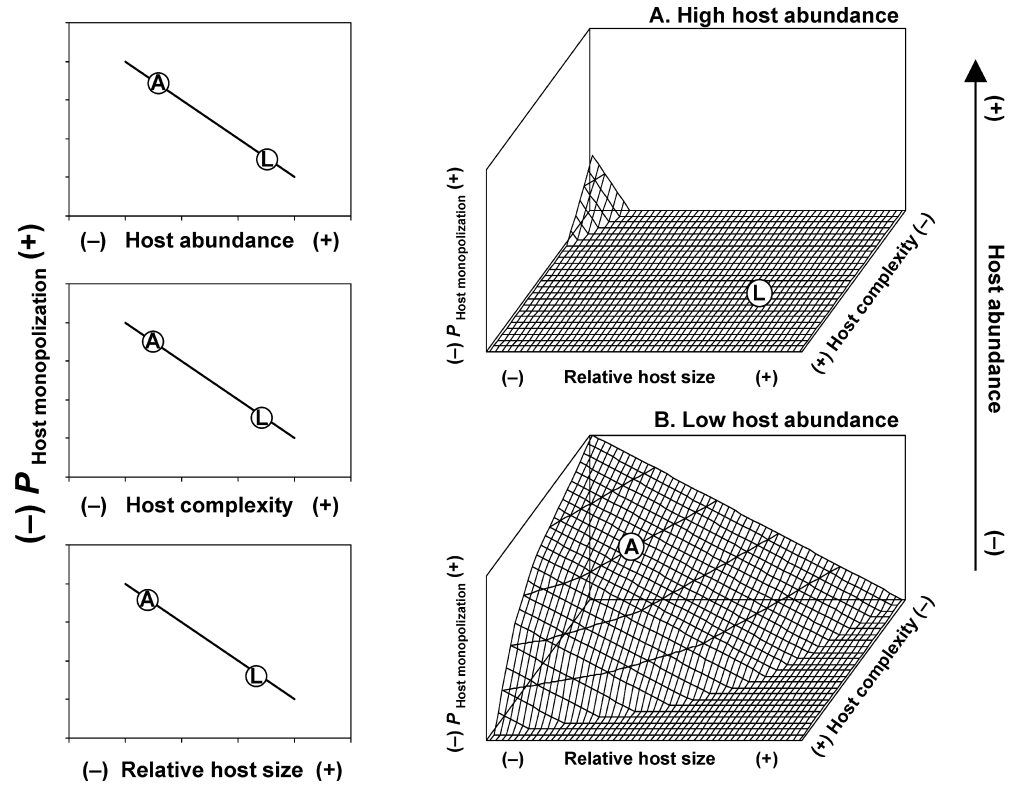
**Table 1** A summary of host characteristics and life-history, ecological, and behavioral characteristics of the two porcellanid crabs examined during the present study and their respective host species; values represent mean  $\pm$  SD

|   | <i>Allopetrolisthes spinifrons</i> | <i>Liopetrolisthes mitra</i> |
|---|------------------------------------|------------------------------|
| Host  | Sea anemones                       | Sea urchins                  |
| Habitat                                       | Low rocky intertidal               | Shallow rocky subtidal       |
| Distance among individuals (cm)               | 14.7 $\pm$ 6.9 (high)              | 15.8 $\pm$ 7.9 (high)        |
| Abundance (individuals 0.25 m <sup>-2</sup> ) | 4.0 $\pm$ 3.6 (low)                | 8.7 $\pm$ 8.8 (high)         |
| Relative host size (host/symbiont)            | 4.5 $\pm$ 1.2 (low)                | 8.1 $\pm$ 2.2 (high)         |
| Morphological complexity                      | Low                                | High                         |
| Potential for monopolization                  | High                               | Low                          |
| Symbiont                                      |                                    |                              |
| Maximum size (L $\infty$ )                    | 20 mm                              | 10.8 mm                      |
| Population distribution                       | Uniform                            | Aggregated                   |
| Tolerance to conspecifics                     | No                                 | Yes                          |
| Host monopolization behavior                  | Yes                                | No                           |
| Territorial behavior                          | Yes                                | No                           |

### Proposal of a conceptual model

Based on the present results and our a priori predictions, herein we develop a conceptual model to explain when and to what extent symbiotic invertebrates (including decapods) exhibit territoriality and/or other host-resource guarding behaviors. Herein we use the term “host resource” to refer to the effective space used by symbionts: for example, in the case of pinnotherid crabs that inhabit the cloaca of echinoderms, the host resource represents the cloaca, but not the entire (nonutilized) surface of the host. In the model, the probability of successful monopolization of the host resource by symbionts decreases with increasing (1) host abundance, (2) host complexity, and (3) relative host size. The interaction among these three factors generates a solid that may be decomposed in layers (areas) representing the potential for host monopolization (Fig. 3). In the model, the probability of successful host-guarding behavior of symbionts decreases stepwise with a gradual increase in host availability. When host abundance is high, the host monopolization potential is low – regardless of relative size or morphological complexity of the host; most likely

**Fig. 3A, B** A conceptual model to explain the development of host-resource monopolization behavior in symbiotic marine invertebrates. The factors are host abundance, host morphological complexity, and relative host size. The interaction between these three factors produce a solid in the space that may be decomposed in several layers (areas) depending on the value of each factor (see discussion for more details). *A* *Allopetrolisthes spinifrons*, *L* *Liopetrolisthes mitra*



this is due to the high costs for symbionts engaging in guarding activities (i.e., intraspecific interference) compared to nonguarding or alternative activities (i.e., food intake for growth optimization). In this first scenario, when host availability is high (Fig. 3A), host-resource guarding behaviors may develop only if hosts are extremely small and simple in shape. On the other hand, when host abundance is low, the potential for host monopolization by symbionts is high because of the low costs of guarding activities compared to nonguarding or alternative activities. In this second scenario, the more simple in shape and smaller a host, the higher the probability of a symbiont to monopolize it: costs of guarding will be low and benefits will be high for symbionts on simple and small hosts as compared to complex and large hosts (Fig. 3B).

When hosts are small and/or simple, thereby allowing for efficient defense against intruders, we predict that symbionts will live on hosts as solitary individuals (e.g. *A. spinifrons*) or heterosexual pairs. When hosts are very large or complex, we predict that symbionts of both sexes and all sizes will be found to cohabit on a single host individual (e.g. *L. mitra*) (Fig. 3). Previously described intraspecific association patterns for symbiotic decapods appear to fit our model predictions: small hosts are usually inhabited by single individuals or heterosexual pairs (e.g. Wells and Wells 1961; Báez and Martínez 1976; Knowlton 1980) whereas large complex hosts appear to be inhabited by unstructured symbiont aggregations (e.g., Mahnken 1972; Nizinski 1989).

The adoption of a symbiotic life-style is one of the main environmental adaptations in marine decapod crustaceans (Ross 1983), and host characteristics have a strong influence on the social behavior of symbiotic crustaceans as shown herein. A main task for the future is to examine to what extent host ecology and the biology of symbiont species (e.g., reproductive traits) affect the social behavior of marine symbiotic organisms. The present study represents a first attempt to understand how host-resource monopolization behaviors have evolved in symbiotic decapods but also intends to provide general guidelines for exploring the reasons for the diversity of social organizations in marine invertebrates.

**Acknowledgements** We are grateful to W. Stotz, D. Lancellotti, and R. Jaeger for their support during our studies on symbiotic crabs and for their comments on the manuscript.

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