Life history of Allopetrolisthes spinifrons, a crab associate of the sea anemone Phymactis clematis

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Allopetrolisthes spinifrons is an ectocommensal crab of the sea anemone Phymactis clematis. The population biology of A. spinifrons in north central Chile was examined between January and December 1996. During 1996, 74% of P. clematis in the rocky intertidal zone hosted at least one commensal crab. In most cases, one sea anemone was inhabited by a single adult crab, either male or female. A few sea anemones hosted two or more crabs, one usually being an adult and the others juveniles or small crabs that had recruited to the host. The sex ratio of adult crabs was ~1:1 during most months. Reproduction occurred with similar intensity throughout the year as indicated by the continuous presence of reproductive females. Similarly, recruitment of A. spinifrons occurred throughout the year with the exception of late winter when no megalopae and small juveniles were found on sea anemones. Fecundity of female crabs varied between 121 and 5661 eggs per female (6.9–19.2 mm carapace length) and was significantly higher during the austral winter (July) than during the summer (December). The fact that most sea anemones were inhabited by a single adult crab indicates that hosts may be monopolized by individual crabs. Resource requirements may prohibit adult crabs from sharing a host individual with another large crab, while adult tolerance towards juveniles may facilitate the maintenance of local populations.

INTRODUCTION

The adoption of a symbiotic life style has important consequences for the life history of decapod crustacean associates. Symbiotic species may be associated with solitary invertebrates, such as polychaetes, echinoids, molluscs, brachiopods, tunicates, sea anemones and echi- noderms or with colonial invertebrates such as sponges or corals (Ross, 1983). All these host species live about as long or much longer, than their associates and thus represent a relatively stable resource. On the other hand, hosts may only be available in limited numbers or offer only limited space or food for associates. As a consequence, the supply of host individuals may have important implications for the population biology of decapod associates. Similarly, availability of space or food resources from individual hosts may have strong effects on the intra (and inter) specific interactions among associates. Furthermore, the size and structural complexity of the host species may have an effect on its defensibility by individuals or groups of associates (Nizinski, 1989; Baeza & Thiel, 2000). Thus, host characteristics (supply, resource value, defensibility) will greatly affect the life history of crustacean associates.

Large sea anemones serve as hosts for a variety of decapod crustaceans (e.g. Mercado & Capriles, 1982; Wirtz, 1997). These associates live attached to the pedal disc of their anemone hosts or dwell under or within the protective tentacle crown (Herrick et al., 1976). Large associates usually live in single individuals or in hetero- sexual pairs on the sea anemones, and they aggressively defend their hosts against conspecific intruders (Seibt & Wickler, 1979; Knowlton, 1980; Diesel, 1986; Omori et al., 1994). Sea anemones have a great protective value for decapod associates, since common predators of these crustaceans are stung by the anemone’s nematocysts. Consequently, associates only leave their hosts when predation pressure is low (Knowlton, 1980), or under the cover of night (Wirtz & Diesel, 1983). Often, a large percentage of available and suitable (i.e. large) sea anemones in a certain location are occupied (Wirtz & Diesel, 1983; Baeza & Stotz, 1995), suggesting that hosts indeed may represent a limited resource, particularly for juvenile crabs. Many decapod associates of sea anemones show high reproductive activity throughout the year and consequently there may always be a considerable proportion of juvenile crabs attempting to establish themselves on suitable hosts. While many previous studies have focused for example on the intraspecific behaviour of adult crabs, few studies have attempted to elucidate the population dynamics of sea anemone associates (for an exception see Diesel, 1986). This information, however, is considered essential in order to gain a thorough understanding of the life history of decapod crustaceans living in association with sea anemones and other macroinvertebrates.

Along the Chilean coast, the porcellanid crab Allopetrolisthes spinifrons (H. Milne Edwards, 1837) has been described as a common associate of the sea anemone Phymactis clematis, but it has also been found on a variety of other benthic macroinvertebrates (Table 1). The commensal association is established by active habitat selection behaviour of the porcellanid crab during larval settlement (Baeza & Stotz, 1998). While post-larvae and small life stages (e.g. recently settled individuals) of
Table 1. Macr(o)invertibrates used as hosts by the commensal crab Allopetrolisthes spinifrons in the rocky intertidal and shallow subtidal of Chile.

<table>
<thead>
<tr>
<th>Species</th>
<th>Taxon</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phymactis clematis (Drayton, 1846)</td>
<td>Actiniaria</td>
<td>1, 2, 3, 4, 5, 6</td>
</tr>
<tr>
<td>Phymanthea pleasia (Drayton, 1846)</td>
<td>Actiniaria</td>
<td>5</td>
</tr>
<tr>
<td>Heliceaster helianthus (Lamarck, 1816)</td>
<td>Asteroidea</td>
<td>1, 5</td>
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<tr>
<td>Stichaster striatus Muller &amp; Troschel, 1840</td>
<td>Asteroidea</td>
<td>1, 7</td>
</tr>
<tr>
<td>Meyenaster gelatinosus (Meyen, 1834)</td>
<td>Asteroidea</td>
<td>1, 7</td>
</tr>
<tr>
<td>Fissurella palcura Sowerby, 1935</td>
<td>Gastropoda</td>
<td>6</td>
</tr>
<tr>
<td>Fissurella eumigrii Reeve, 1849</td>
<td>Gastropoda</td>
<td>6</td>
</tr>
<tr>
<td>Fissurella crassa Lamarck, 1822</td>
<td>Gastropoda</td>
<td>6</td>
</tr>
<tr>
<td>Fissurella nigra Lesson, 1831</td>
<td>Gastropoda</td>
<td>4</td>
</tr>
<tr>
<td>Concholepas concholepas (Brugiere, 1789)</td>
<td>Gastropoda</td>
<td>6</td>
</tr>
</tbody>
</table>


A. spinifrons can be found on all of the reported hosts, adult (mature) crabs exclusively inhabit sea anemones (Baeza & Stotz, 1995, 2000). Habitat restrictions during larval settlement may explain the existence of alternative non-anthozoan hosts in A. spinifrons and the generalist life-style of megalopae compared with the high host-specificity shown by conspecific adult crabs (Baeza & Stotz, 1998, 2000). Adult crabs are only found on sea anemones which appears to be the consequence of an active host-shift behaviour accomplished by small juveniles since all ontogenetic stages of the crab prefer sea anemones over alternative hosts (e.g. limpets) (Baeza & Stotz, 2000). The aim of the present study is to examine the life history of A. spinifrons on one of its most commonly reported hosts, the sea anemone P. clematis. The specific objectives were to examine the population dynamics and reproductive biology of A. spinifrons.

MATERIALS AND METHODS

The study site

The present study was carried out at La Pampilla beach, Coquimbo peninsula (29°57’S 71°21’W), Chile. The intertidal of La Pampilla is a semi-exposed rocky shore, with rock surfaces covered by algal turf, mainly consisting of Ulva spp. and Gelidium spp. during most of the year. The host sea anemone Phymactis clematis inhabits crevices and spaces between boulders at the study site. This sea anemone can be found in four colour morphs; blue, red, green or brown (Sebens & Paine, 1978). In this study, only the last three colour morphs were considered, since in a previous study the commensal crab Allopetrolisthes spinifrons was never found on blue sea anemones (Baeza & Stotz, 1995). Near the collection site, at La Herradura Bay, water temperatures usually vary between 13°C (winter) and 20°C (summer) (Moraga & Olivares, 1993).

Sample processing and data analysis

Between January and December 1996, sea anemones P. clematis were surveyed along a stretch of ~200 m located in the rocky intertidal (mesolitoral and the infralitoral fringe) of La Pampilla beach. Each month, at least 100 P. clematis were randomly selected. The diameter of the pedal disc (PDD) of each sea anemone was measured in the field. Also, the number and size (measured as carapace length, CL) of all crab associates from each host individual was noted. The sex of adult crabs was determined based on gonopore position and pleopod morphology. Measurements of both anemones and crabs were taken with a manual calliper to the nearest 0.05 mm. Megalopa larvae collected from hosts were identified using their external morphology, namely the carapace and rostrum of similar shapes as in the adults, a reddish chromatophore occupying almost the whole cephalothorax length, the abdomen with dense setae on each segment, four pairs of biramous pleopods between the second and fifth abdominal segment, and a rounded telson with long setae along its distal margin (Barrientos, personal communication). Each female crab was classified according to the presence or absence (ovigerous or non-ovigerous) and the developmental stage (I, II & III) of embryos under the abdomen. The embryo mass of each ovigerous female was inspected by eye to allow classification of the developmental stage according to the following characters: stage I, embryo with uniformly distributed yolk and absence of eyes; stage II, embryo with visible but not well developed eyes, and presence of pigments; and stage III, embryo with well developed eyes, chromatophores, and appendages. After taking the measurements, each commensal crab was placed onto the same sea anemone from which it had been collected. In July and December 1996, small samples of ovigerous females (N=32 and N=31, respectively) were removed in order to estimate fecundity (see below).

Host-use pattern of Allopetrolisthes spinifrons

The frequency of occurrence (proportion of hosts that harboured at least one commensal crab) and density (number of crabs per host individual) of A. spinifrons on sea anemones was examined each month during the sampling period. We examined whether the distribution of A. spinifrons on sea anemones differed significantly from random by comparing the observed distribution with the Poisson distribution. A $\chi^2$-goodness-of-fit test was used to inspect for significant differences between distributions (Sokal & Rohlf, 1981). If distributions were observed to
differ significantly, we compared specific frequencies (e.g. frequency of sea anemones harbouring a single commensal crab) between the observed and expected distributions by an Independence $\chi^2$-test (Sokal & Rohlf, 1981).

We investigated whether host size affected the demography of *A. spinifrons* on sea anemones. For this purpose, we monthly examined the relationship between (i) host size and number of crabs per host individual; (ii) host size and size of the largest crab dwelling on each host individual; and (iii) host size and cumulative size of all crabs dwelling on a single host individual. In order to examine the above relationships, only sea anemones harbouring at least one commensal crab were considered.

**Life history of Allopetrolisthes spinifrons**

To examine the population dynamics of *A. spinifrons*, the size–frequency distribution, sex ratio, percentage of ovigerous females, and the developmental stage of embryos were analysed for each month. The fecundity of *A. spinifrons* was determined by counting all embryos carried by individual females in July 1996 ($N=32$) and December 1996 ($N=31$). Direct counts of the embryos were performed on females carrying 300 or fewer embryos. In case females were carrying more than 300 embryos, three subsamples of 100 embryos were isolated from the brood mass and dried for 72 h at 70°C. Similarly, the remaining embryo mass of these females was dried and its weight determined (to the nearest 0.0001g using a Sartorius analytical balance). Fecundity of these females was calculated for each female separately using the equation:

$$N = \frac{dw_{REM}/(dw_{ss} - a + dw_{ss} - b +)}{c/300 + 300}$$

where $N$=total number embryos female$^{-1}$; $REM$=remaining embryo mass after the three subsamples (SS$=a$, SS$=b$ & SS$=-c$) have been taken. The relationship between carapace length and the number of embryos per female was examined, and we tested for differences in fecundity between winter and summer by analysing the data with analysis of covariance (ANCOVA) (Sokal & Rohlf, 1981).

**RESULTS**

**Host use pattern of Allopetrolisthes spinifrons**

Sea anemones *Phymactis clematis* were found in aggregations of a few up to >50 individuals in the rocky intertidal of La Pampilla. A total of 1214 sea anemones were sampled at the study site during 1996. The pedal disc diameter (PDD) of sea anemones varied between 21 and 75 mm with a mean of 42.73 mm (SD = 8.92). Despite seasonal differences of mean sea anemone size (PDD, ANOVA, $F_{[1,1202]} = 6.68, P < 0.0001$) during the collection period, sea anemones of an average size range (40–50 mm disc diameter) were observed year-round in La Pampilla.

*Allopetrolisthes spinifrons* were found on 73.9% ($N=897$ of 1214) of all sea anemones collected during the present study. Large crabs of *A. spinifrons* were firmly attached with their pereiopods to sea anemones, the head always directed towards the oral disc (Figure 1). Smaller crabs were sometimes observed on the oral disc of the sea anemones, hidden between the tentacles. The frequency of occurrence of *A. spinifrons* varied throughout the year. During the austral summer (January–March) and autumn (April–June), the occurrence of the association was relatively high, and during these months always > 70% of the anemones housed crabs. During the austral winter/early spring (July–November), the percentage of occupied anemones decreased slightly (59% in November 1996) but increased again when summer approached (72% in December 1996) (Figure 2). In general, the percentage of sea anemones harbouring *A. spinifrons* crabs was significantly higher during the summer/autumn months than during the winter/early spring months (Independence $\chi^2$-test, $\chi^2=21.46, df=1, P < 0.0001$).

The mean number of crabs per host was approximately one (0.97 ±0.79) throughout the entire sampling period (all sampled sea anemones considered). As was observed for the occurrence of crabs on hosts, the density of *A. spinifrons* on sea anemones was relatively high during summer and fall months (1.09 ±0.84) and relatively low during winter and early spring months (0.78 ±0.69); the

**Figure 1.** The porcellanid crab *Allopetrolisthes spinifrons* on its sea anemone host, *Phymactis clematis*.

**Figure 2.** Average number host$^{-1}$ (±SD) (columns) of crabs *Allopetrolisthes spinifrons* on sea anemones *Phymactis clematis*, and percentage of anemones (open dots) that hosted at least one commensal crab (frequency of occurrence) between January and December 1996.
differences between these two time periods were significant (Oneway analysis of variance (ANOVA), F_{1,122} = 45.6, P<0.0001) (Figure 2). Up to five A. spinifrons were observed on one host individual, but most commonly a single crab, either male or female, was observed on each host (Figure 3). The distribution of A. spinifrons on sea anemones did not show a random pattern throughout the year (observed distribution of crabs on sea anemones differed significantly from the expected random distribution during most of the months, P<0.05). This was explained by the large number of sea anemones harbouring a single commensal crab compared with the number predicted by the Poisson distribution (Independence \( \chi^2 \)-test with Yates’ correction, P<0.05) (Figure 3). Only in February 1996, did the observed distribution of A. spinifrons not differ significantly from random (P>0.05). Nevertheless, the number of sea anemones harbouring a single commensal crab was also higher (albeit not significant) than would have been expected at random during that month.

Only on 206 out of 1214 sea anemones sampled (17%) during 1996, were two or more crabs found (Figure 4). Generally, crabs sharing the same host individual were small (<7.0 mm CL). When a large crab was found on sea anemones harbouring two or more crabs, the other(s) inhabitant(s) were small crabs that had recently recruited to the host. Only three sea anemones hosted two adult crabs, and in all three cases these constituted heterosexual pairs (Figure 4). In general, both sexes of A. spinifrons occurred as solitary individuals on their hosts throughout the year.

The number of crabs harboured by a single host individual was significantly correlated with the size of the sea anemones during 7 out of 12 months (Table 2). A significant relationship between the size of sea anemones and the size of the largest crabs inhabiting them was only observed during three months (3 out of 12 months), while the relationship between the cumulative size of crabs dwelling on a single host and the size of sea anemones was found to be significant during 7 out of 12 months. In general, small sea anemones (PDD<30 mm) could harbour single individuals or small aggregations of two or three commensal crabs while relatively large aggregations (up to five crabs) only occurred on large sea anemones (PDD>50 mm). Also, at the study site, A. spinifrons crabs inhabited a wide range of host sizes, but large sea anemones harboured larger aggregations of commensal crabs than small sea anemones during several months of the year.

**Population dynamics of Allopeltisthes spinifrons**

The size–frequency distribution analysis for crabs A. spinifrons indicated that all sizes of crabs from 0.7 mm (megalopae) to 16.6 mm CL (5.5 ±3.8 mm) utilized the sea anemones throughout the year (Figure 5). The smallest ovigorous female observed during 1996 had a carapace length of 6.9 mm CL. The sex ratio of A. spinifrons found on the sea anemones was close to 1:1 throughout most of the year (Figure 6A). The percentage of ovigorous females was relatively high throughout the year (always >50%) (Figure 6B). Also, the proportion of females carrying mid and late embryos (stages II & III) was

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**Figure 3.** Number of sea anemones *Phymactis clavata* hosting groups of *Allopeltisthes spinifrons* between January and December 1996; all crabs were pooled for each month; nh, number of sea anemones collected per month. Frequency polygon shows the expected Poisson distribution. Asterisks indicate significant differences (P<0.05) of the number of sea anemones harbouring one commensal crab between the observed and Poisson expected distribution.

**Figure 4.** Relationship between the size of the largest crab and the second largest crab when two or more crabs cohabited on a single sea anemone (N=220 sea anemones harbouring two or more crabs during 1996); all months were pooled. Adult–Adult quadrant includes values in which two adult crabs were found on sea anemones established as heterosexual pairs (open circles). The minimum size of adult was established according to the size of the smallest ovigorous female (6.9 mm CL) registered during the present study.
Table 2. Relationship between host size and the number of crabs per host ($N$ crabs host$^{-1}$), the size of the largest crab inhabiting each occupied host and the cumulative size of crabs inhabiting each occupied host. Pearson product-moment statistic ($r$) and $p$-critical ($p$) values are shown for each correlation.

<table>
<thead>
<tr>
<th>Month</th>
<th>N crabs host$^{-1}$</th>
<th>Larger crab</th>
<th>Cumulative size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r$ $p$</td>
<td>$r$ $p$</td>
<td>$r$ $p$ $N$</td>
</tr>
<tr>
<td>January</td>
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<td>0.2674 0.015</td>
<td>0.2767 0.012 82</td>
</tr>
<tr>
<td>February</td>
<td>0.2346 0.040</td>
<td>0.0216 0.852</td>
<td>0.1198 0.299 77</td>
</tr>
<tr>
<td>March</td>
<td>0.2335 0.034</td>
<td>-0.0112 0.920</td>
<td>0.0734 0.510 83</td>
</tr>
<tr>
<td>April</td>
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</tr>
<tr>
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<td>0.3914 0.000 77</td>
</tr>
<tr>
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</tr>
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</tr>
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</tr>
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<td>-0.0160 0.895 71</td>
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<td>October</td>
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<td>December</td>
<td>0.2748 0.019</td>
<td>0.1732 0.146</td>
<td>0.2095 0.021 72</td>
</tr>
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</table>

Figure 5. Number of crabs Allopelastiosthes spinifrons in respective size classes found on sea anemones Phymactis clematis between January and December 1996; all crabs were pooled for each month; nh and nc, number of hosts and crabs collected per month, respectively.

Figure 6. (A) Percentages of male and female crabs Allopelastiosthes spinifrons found on sea anemones Phymactis clematis between January and December 1996; (B) of female crabs A. spinifrons without or with embryos of respective developmental stages; all crabs were pooled for each month; n on top of bars represents (A) number of sexed crabs and (B) number of female crabs collected each month; only crabs > 6.9 mm CL (size of smallest ovigerous female) are included.
relatively high and similar during most months (Figure 6B). Thus, reproduction in *A. spinifrons* is continuous and occurs with similar intensity throughout the year.

Juvenile crabs were also found throughout the year on sea anemones. The relative abundance of the smallest crabs within the population (recently settled crabs or recruits, below 2.0 mm CL) remained high throughout the year. Only during the late austral winter (August and September) were no recently settled crabs observed to dwell on sea anemones (Figure 5). Megalopae were found episodically during the year.

**Fecundity of Allopetrolisthes spinifrons**

Female crabs carried between 121 and 5661 eggs (1872 ±1558, N=32) during the austral winter, and between 132 and 4086 eggs (1430 ±1212, N=31) during the austral summer. The size range of ovigerous females was similar both in winter (smallest and largest ovigerous female=6.9 and 19.1 mm CL, respectively) and summer (smallest and largest ovigerous female=7.9 and 19.2 mm CL, respectively). The fecundity of *A. spinifrons* increased significantly with female size, both during winter (Log N eggs=4.19 Log CL−1.43, r²=0.88, t(30)=14.71, P<0.0001) and summer (Log N eggs=4.05 Log CL−1.48, r²=0.90, t(29)=15.84, P<0.0001) (Figure 7). Fecundity (number of eggs female−1) was significantly higher during winter (July) than during summer (January) of 1996 throughout the size range of females analysed [ANCOVA after log−log transformation, F(1,60)=27.19, P<0.0001].

**DISCUSSION**

Adult crabs, *Allopetrolisthes spinifrons*, regardless of their sex, usually live as solitary individuals on sea anemones. While smaller crabs may occur in aggregations on the anemone hosts, adult crabs almost never shared their hosts with other adults. This could indicate that large adults exclude other adults from their anemones, thus effectively monopolizing their anemone hosts. However, adult *A. spinifrons* were frequently found to share ‘their’ anemone with juveniles which has not been previously reported for other large decapods living on the outer surface of sea anemones. The implications of this tolerance of large adults towards small conspecifics for the population dynamics and life history of *A. spinifrons* is discussed below.

The life history of *Allopetrolisthes spinifrons*

The frequent finding of *A. spinifrons* megalopae larvae on sea anenomes suggests that these settle directly on their hosts, as has also been indicated in previous studies (Baeza & Stotz, 1995, 1998, 2000). The presence of small immature crabs in addition to megalopae throughout the study period also indicated that recruitment occurs throughout the year. Only during two months, in late winter of 1996, did recruitment appear to slow down since no small crabs were observed on sea anenomes. Following recruitment, crabs grow up on the sea anemones where they reach sexual maturity at ~7.0 mm CL. After reaching sexual maturity, crabs reproduce continuously and with similar intensity throughout the year.

In contrast to our results, which indicate continuous reproduction throughout the year, other authors have reported a more seasonal reproductive pattern. For a location about 500 km south of Coquimbo (at 33°S), Antezana et al. (1965) reported a reproductive peak during the austral winter and spring months (July–December), followed by diminishing reproductive activity during the austral summer (January–March) and the complete absence of reproductive crabs during the austral autumn (April–June). Two non-contrasting hypotheses may explain the more seasonal reproductive pattern reported for southern populations of *A. spinifrons*. First, an increase of latitude and the consequent more seasonal conditions may restrict the breeding pattern of *A. spinifrons* (and other porcellanid crabs) as has been previously reported to occur or suggested for other decapods (Jones & Simons, 1983; Hines, 1989). Second, it is likely that the study by Antezana et al. (1965) was conducted during a year with oceanographic conditions drastically different from those that prevailed during our study period. Support for such effects on reproduction may also be found in the fact that we revealed a seasonal change in the fecundity of *A. spinifrons* where females of similar sizes carried more embryos during the austral winter (when waters usually are slightly colder) than during summer. In years with ‘normal’ oceanographic conditions, fast growth and high metabolism during austral summer (or periods with warm waters) may result in less energy going into egg production than during the winter (Diaz, 1980). Previous studies on free-living decapods have shown that reproductive parameters such as size at onset of maturity, eggs produced per brood and egg size (e.g. volume) may also vary at the local scale or with latitude (Jones & Simons, 1983; Hines, 1989; Mashiko, 1990). Both the results and the above considerations suggest that fecundity, at least, in the symbiotic crab *A. spinifrons* may be similarly affected by prevailing oceanographic conditions. Further studies are required to understand whether effects caused by local, latitudinal, seasonal, or interannual variations in oceanic conditions may in symbiotic crabs to some extent be buffered by long-living hosts, which may have stabilizing effects on egg production by female crabs and survival of new recruits.
The host-use pattern of Allopetrolisthes spinifrons

The low densities yet high frequency of occurrence of *A. spinifrons* on sea anemones hosts have been previously noted in several other studies (Stuardo, 1962; Antezana et al., 1965; Viviani, 1969; Baeza & Stotz, 1995, 2000). The fact that many *A. spinifrons*, invariably adult male or females, and in many cases juveniles, occurred as solitary individuals on sea anemones suggests that hosts offer only limited space or food. Sea anemones *Plymactis clematis* are relatively small compared with *A. spinifrons* (maximum size of 19.9 mm CL) (Baeza, unpublished data). The presence of only small crabs on those sea anemones already inhabited by large adult crabs furthermore suggests that sea anemones *P. clematis* are too small to be shared by two large mature crabs. Resident crabs on sea anemones may defend their hosts aggressively against large conspecific intruders but apparently tolerate or overlook small conspecifics, particularly when inhabiting large sea anemones. Similarly, Lindberg & Stanton (1984) found that only one adult male or female of *Pilumnas sayi* and *Thor mannioni* occurred on one brachyuran colony each—adults often shared their host individual with juveniles but never with other adults from the same sex. Tsuchiya & Yonaha (1992) also reported that, almost always, solitary individuals or heterosexual pairs of *Trapesia cymodoce* and *Alpheus lottini* inhabited single coral colonies. However, when colonies were very large, juvenile conspecifics shared hosts with these adults. It thus appears that adults that monopolise a host individual may tolerate juvenile (i.e. non-reproductive) conspecifics on their hosts.

The apparent tolerance of adult crabs towards juveniles permits these crabs to establish themselves on their hosts in a situation where most available hosts are already occupied. It is not clear whether large adults are unable to recognise these small crabs or whether they may even benefit from their presence. Possibly, adults of both sexes tolerate juveniles until these become sexually mature. The maximum size apparently tolerated by adult *A. spinifrons* on their anemone is ~7 mm CL (see Figure 4), i.e. the size at which crabs become reproductive. On reaching ~7 mm CL, crabs are then probably expelled by adult residents, and may have to find a new sea anemone host nearby. In combination with the utilization of alternative hosts by early benthic phases of *A. spinifrons* (Baeza & Stotz, 2000), this tolerance of adult crabs towards juveniles would facilitate the maintenance of local populations.

The occurrence of both sexes of *A. spinifrons* as solitary individuals on their hosts throughout the year and the patchy distribution of the sea anemones *P. clematis* suggests that males (or females) move between hosts in search of mating partners as has been reported for another sea anemone associate, the spider crab *Inachus phalangium* (Wirtz & Diesel, 1983). This form of mating system where members of one sex are visiting neighbouring host individuals in search of mating partners can, however, only function when a sufficient proportion of nearby hosts is occupied by members of the opposite sex. Thus, the tolerance of adult crabs towards small conspecifics on ‘their’ anemones may help ensure a high frequency of occupied hosts in their vicinity.

The possible movements of adult crabs between hosts in search of mating partners may also explain the absence of a relationship between host size and the size of the largest crab inhabiting each sea anemone. Although large sea anemones potentially convey great benefits to a crab associate by offering better protection against predation (e.g. from fish) and more food than small anemones, other factors may be of greater importance during host selection. If commensal crabs indeed move between sea anemones—while searching for mating partners—the establishment on a sea anemone near other hosts with crabs of the opposite sex may compensate for a lower food (i.e. mucus) intake and/or a higher risk of predation. Thus, crabs (particularly males) may prefer hosts in dense sea anemone assemblages irrespective of the size of these hosts. Future studies are required to elucidate how crabs manage to find mating partners in the field, and whether the need to be near potential mating partners affects host selection in *A. spinifrons* and other symbiotic crustaceans.

REFERENCES


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