Host-use and selection of differently colored sea anemones by the symbiotic crab

*Allopetrolisthes spinifrons*

J.A. Baeza a,b,*, W. Stotz b

a Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504-2451, USA
b Universidad Católica del Norte, Sede Coquimbo, Departamento de Biología Marina, Larrondo 1281, Coquimbo, Chile

Received 8 January 2002; received in revised form 19 September 2002; accepted 9 October 2002

Abstract

Adults of the reddish green symbiotic crab *Allopetrolisthes spinifrons* obtain different degrees of camouflage from the red, green, reddish green, and blue sea anemones *Phymactis clematis*, and the orange *Phymanthea pluvia* on which they are commonly found. Previous studies have indicated that the distribution of the crab on sea anemones may be influenced by the host’s coloration. During the present study, we tested whether adult crabs dwell more commonly on those sea anemones that offer a higher degree of camouflage, and whether “behavioral preferences” can explain crab distribution on sea anemone species and color morphs in the field. We examined the frequency of occurrence of adult crabs on 200 sea anemones of each color morph, and crab distribution was compared to that expected by the relative abundance of different anemone hosts in the field. Adult crabs occurred more frequently than expected by chance on sea anemones most similar to their own color (reddish green), and occurred less frequently than expected by chance on sea anemones where homochromy was reduced (e.g. blue). Multiple host selection experiments conducted under laboratory conditions demonstrated that adult crabs avoid blue sea anemones compared to other host color morphs offered for colonization, but no preference was observed among red, green, reddish green, and orange sea anemones. These results suggest that “behavioral preference” play a role in determining the field distribution of *A. spinifrons* adult crabs in the field. The lack of preference for reddish green sea anemones in the laboratory, but its high frequency of occupancy by adult crabs in the intertidal, further suggests that factors other than homochromy-related preferences (e.g. sea anemones habitat) might affect crab distribution in the field. Alternative host selection experiments revealed that the specific host from which crabs were...
collected (source host) affected the host-choice behavior of crabs, indicating that previous experience is important in choice of sea anemone hosts.

© 2002 Elsevier Science B.V. All rights reserved.

Keywords: Behavioral preference; Decapoda; Host selection; Host-use; Porcellanidae; Symbiosis

1. Introduction

Decapod crustaceans often play important roles in rocky intertidal and subtidal marine communities; it has been suggested that they are important keystone predators (Robles et al., 1989; Robles, 1997; Navarrete and Castilla, 1990). Thus, understanding variations in the abundance and distribution of these crustaceans is important in order to understand the processes structuring marine benthic populations and communities. Among those factors thought important in explaining the distribution and abundance of decapods in the field are preferences for one habitat over another (Hedvall et al., 1998). Indeed, habitat selection during larval settlement appears to be a common process among decapods (Botero and Atema, 1982; Jensen, 1989; O’Connor, 1991; Fernández et al., 1994; Hedvall et al., 1998). However, because vulnerability to physical stresses and biotic factors (e.g. predation) often depends on size, the relative importance of such processes may also change throughout the ontogeny of individuals. Whether habitat preference is equally important in decapod adult stages is, however, not known (but see Bell and Westoby, 1986; Hacker and Madin, 1991).

Symbiotic decapod crustaceans, which inhabit sessile marine macro-invertebrates, represent an ideal model for studying preference for habitats. Microhabitats (i.e. sessile hosts) are usually relatively easy to handle and manipulate, making it possible to assess preferences in the laboratory. Previous studies examining the behavior of symbiotic shrimps in shallow tropical communities found that the adults of each species preferred the host species that occurred most commonly in the field (Duffy, 1992; Gwaltney and Brooks, 1994; Guo et al., 1996; VandenSpiegel et al., 1998). Chemical cues are used to recognize and choose among different hosts by these decapod symbionts (Ache and Davenport, 1972; Derby and Atema, 1980; Guo et al., 1996; Brooks and Rittschof, 1995). Such studies highlight the importance of selection in explaining partitioning of habitat by symbiont species among co-occurring host species.

Adults of the porcellanid crab *Allopetrolisthes spinifrons* live only on the sea anemones *Phymactis clematis* (Drayton, 1846) and *Phymanthea pluvia* (Drayton, 1846), while juveniles have been found on a variety of other benthic macro-invertebrates, including sea stars and several gastropod species (Baeza and Stotz, 2001). Previous studies suggest that the symbiotic association of *A. spinifrons* is established by an active habitat selection behavior by the crab during larval settlement (Baeza and Stotz, 1998). Habitat constraints during larval settlement may explain the use of alternative, non-anthozoan hosts, by juvenile *A. spinifrons* (Baeza and Stotz, 2001). Overall, the high host-specificity shown by adult crabs, compared to the generalist life-style of early-life benthic phases, appears to be
the consequence of active movements among hosts accomplished by small juvenile crabs (Baeza and Stotz, 2001).

For adult *A. spinifrons*, the sea anemone hosts act as their reproductive habitat (Baeza et al., 2001), food source (Viviani, 1969), and a refuge against predators, such as fishes and birds (Vásquez, 1993; Bahamondes and Castilla, 1986). Stuardo (1962) and Viviani (1969) suggested that these decapods use homochromy, here defined as matching in coloration between a host and its symbiont, as protection against visual predation. The carapace of *A. spinifrons* invariably has a reddish green coloration, while the different sea anemone species vary widely in their coloration. *P. pluvia* is deep orange and *P. clematis* is found in four color morphs: red, green, reddish green, and blue (Carter, 1965). The camouflage of crabs dwelling on differently colored sea anemones varies widely (i.e. camouflage on reddish green > green ≈ red > blue ≥ orange) and it is likely that the amount of protection offered against visual predators varies accordingly.

Neither adult nor juvenile crabs are found on blue *P. clematis* sea anemones (JAB, personal observations), and adults are less likely to occur on *P. pluvia* than on *P. clematis* sea anemones (Baeza and Stotz, 1995). This suggests that crabs prefer anemones with coloration more similar to their own. If this is true, such a preference may explain the differential distribution of adult crabs on different sea anemone species and color morphs in the field (Baeza and Stotz, 1995).

The aim of the present study is to test the hypothesis that preferences by adult crabs for differently colored sea anemones can explain their observed distribution in the field.

2. Materials and methods

2.1. Study site and field survey

The study was conducted between August and October 1995, at La Pampilla (Peninsula of Coquimbo, 29°57’S–71°21’W, north-central Chile), a semi-exposed rocky intertidal site. The rocky intertidal at the study site is briefly described by Baeza et al. (2001). The anemone hosts *P. clematis* and *P. pluvia*, which mainly inhabit crevices and spaces among boulders in the infralittoral fringe and the mid-intertidal, are the only sea anemones that harbor *A. spinifrons* adult crabs at this site (Baeza and Stotz, 1995). Both sea anemone species are similar in size and morphology and are referred here and thereafter as different color morphs or types. Near the study site, at La Herradura de Guayacán Bay, surface water temperature usually varies between 13 (winter) and 20 °C (summer) (Moraga and Olivares, 1993).

During low tide, each sea anemone encountered along a stretch of approximately 200 m of shore (mesolitoral and the infralittoral fringe) was examined for the presence of symbiotic crabs, until 200 specimens of each color morph (red, green, reddish green, blue, and orange) had been completed. The diameter of the pedal disk (PDD) of each surveyed sea anemone was measured to the nearest 0.5 mm with calipers, and their microhabitat was classified according to the following four categories: (1) among fronds and/or holdfasts of *Lessonia* sp.; (2) among crevices or boulders; (3) beneath rocks or in caverns; and (4) in intertidal pools. The number and body size (measured as carapace length, CL) of all crab
associates in each host individual was noted. After measurements were completed, each crab was returned to the sea anemone from which it was collected. To assess the relative abundance of each sea anemone color morph, the mean number of collected specimens per sampling hour was recorded during seven different surveys regularly performed throughout the sampling period.

2.2. Host-use pattern of the adult *A. spinifrons*

The body size of the smallest ovigerous *A. spinifrons* female examined during this study was 8.0 mm CL, and consequently all individuals >8.0 mm CL were considered to be adults. To quantitatively describe the host-use pattern by adult *A. spinifrons*, we calculated the frequency of occurrence of crabs >8.0 mm CL on each sea anemone color morph as the proportion of examined sea anemones harboring at least one adult crab. Since *A. spinifrons* usually inhabited sea anemones as solitary individuals (Baeza et al., 2001), the frequency of occurrence also reflects the relative abundance of this crab on each sea anemone color morph. To test whether adult crabs more frequently inhabited anemones with a color more similar to their own carapace, we compared the distribution of crabs on the differently colored sea anemones (i.e. host-use pattern) to that expected by the relative abundance of host types in the field. A $\chi^2$ test of goodness-of-fit was used to inspect for significant differences between distributions (Sokal and Rohlf, 1981). The relative abundance of the sea anemone hosts was used as the expected distribution and the power ($1 - \beta$) of the $\chi^2$ test was calculated using the program GPOWER (Faul and Erdfelder, 1992). If a significant nonrandom distribution was observed, we compared specific frequencies between the observed and expected distribution by subdivision of the $\chi^2$ test using the sequential Bonferroni correction (Sokal and Rohlf, 1981; Rice, 1989).

2.3. Laboratory experiments on host preference

Two types of experiments were conducted to determine whether or not adult crabs choose sea anemones of different color morphs. These laboratory assays avoided the potential confounding effect of biotic (e.g. predators) and abiotic factors on crab preferences. In the first experiment, the five sea anemone color morphs were simultaneously offered to crabs for 1 h (i.e. multiple choice experiments). During the second set of experiments, different combinations of only two sea anemone color morphs were offered to crabs for 24 h (i.e. alternative choice experiments). All experimental crabs and sea anemones were collected from the rocky intertidal zone of La Pampilla. All organisms were maintained for 5–10 days in aquaria (50–100 l) with aerated, flowing seawater before being used in laboratory experiments.

2.3.1. Experiment 1: multiple host selection experiments

This experiment was conducted in a large aquarium ($2.0 \times 1.5 \times 0.6$ m) with running seawater. The aquarium was subdivided into 25 sections ($0.12$ m$^2$), with each compartment containing five similarly sized sea anemones (>4.5 mm PDD) of each one of the different color morphs. The sea anemones were randomly distributed at the periphery of each section with regular spacing (ca. 8–10 cm). At the center of each section, a single
adult crab was acclimatized for 30 min inside a white plastic chamber. The number of sea anemones of each type that were colonized by adult crabs was recorded 1 h after the chambers were lifted. The resulting distribution of crabs on sea anemones was compared with the binomial random distribution, which, in the case of no difference, would indicate no preference, by the crabs for a particular color morph (Sokal and Rohlf, 1981). A $\chi^2$ test of goodness-of-fit (Sokal and Rohlf, 1981) was used to examine for significant differences in host choice. The power ($1 - \beta$) of the $\chi^2$ test was calculated using the program GPOWER (Faul and Erdfelder, 1992). When significant differences were observed, we compared specific frequencies between observed and expected distributions by subdivision of the $\chi^2$ test using the sequential Bonferroni correction (Sokal and Rohlf, 1981; Rice, 1989). The experiment was repeated four times, each time using different crabs. Thus, a total of 100 assays were conducted (25 each time), with 100 different crabs and 25 different sea anemones of each color morph. In addition, we estimated the selectivity $C$ index, which has previously been used to estimate the preference of predators for their prey items (Pearre, 1982; Ojeda and Dearborn, 1991). The selectivity $C$ index of adult crabs was calculated using the equation:

$$C = (\chi^2 / N)^{1/2}$$

where $\chi^2$ is the value of the $\chi^2$ statistic of goodness-of-fit previously estimated for each one of the sea anemone color morphs, and $N$ is the total number of replicates conducted during the experiment. The $C$ index varies between $-1$ and $+1$. A negative value indicates avoidance, a value of zero indicates no preference, and a positive value indicates preference (Pearre, 1982).

### 2.3.2. Experiment 2: alternative host selection experiments

This experiment was conducted in cylindrical, acrylic aquaria (45 cm diameter, 50 l volume) with aerated running seawater. In each aquarium, two similarly sized (>4.5 mm PDD) sea anemones of different color morphs were placed opposite to each other, with a distance of ca. 20 cm between them. At the center of each aquarium, a single adult crab of *A. spinifrons* was placed and maintained in a white chamber for at least 30 min, making the distance between the crab and the sea anemones ca. 10 cm. Immediately (0 h), 1 h, and 24 h after the chambers were lifted, we recorded the presence/absence of each symbiotic adult crab on each one of the sea anemones. Different combinations of sea anemone color morphs were offered to the crabs for colonization. Different crabs were used in each color combination, but in some cases, the same crab was used to test more than one color combination. A total of 30 replicates were performed for each combination of sea anemone color morphs, using 30 different crabs per assay, and 60 sea anemones: 30 of each color morph. To determine preference by the crabs, we compared the observed distribution of crabs on the sea anemone hosts offered during the experiment with the binomial random distribution, which, in the case of no difference, indicated no preference (Sokal and Rohlf, 1981). The significance level was established by a two-tailed binomial test (Zar, 1999). The power of each test was calculated as explained in Zar (1999).

To examine the effect of past history (i.e. the sea anemone from where the experimental crab was collected) on host preference, assays were divided into two basic types: (1) crabs
that were offered a sea anemone similar to the host from which it was gathered together
with a different anemone, and (2) crabs that were offered two sea anemones different from
the original host.

2.4. Assumptions when detecting preferences and statistics

The binomial distribution was used as a null hypothesis when testing for crab active
choice of hosts because (1) sea anemones \( P. \text{clematis} \) and \( P. \text{pluvia} \) provided to crabs
during the experiment were identical in size and morphology (see Carter, 1965), and (2)
our previous studies have shown that (2.1) adult crabs prefer sea anemones over any
other marine invertebrate that may potentially be used as host by \( A. \text{spinifrons} \) (Baeza
and Stotz, 2001), and (2.2) when given a choice of sea anemones and rocks (including
crevices), adult crabs almost invariably colonize the sea anemones, regardless of their
coloration (Baeza et al., in press). Thus, differences in accessibility and handling
between sea anemone types are not expected to occur under these experimental
conditions (as occur in other crab species when resource preferences has being
experimentally tested—Liszka and Underwood, 1990). The choice of crabs is not
expected to be driven by host morphology, size or any other unknown factor, besides
host coloration (see Liszka and Underwood, 1990; Olabarria et al., 2002). Based in the
information above, we have no reason to believe that the choice of crabs when offered
sea anemones of the same color should deviate from the random binomial distribution.
We have interpreted departures from this null hypothesis as active choice of crabs for
specific sea anemones color morphs.

We compared the body size and relative abundance of the different sea anemone color
morphs surveyed during the present study. Tests for homocedasticity and normality of the
contrasted data sets (Sokal and Rohlf, 1981) revealed heterogeneity of the variances,
which was not possible to eliminate after transformation (i.e. logarithmic, arcsine) of the
data. Thus, the nonparametric Kruskal–Wallis test was used to compare these measure-
ments between the different host species (Sokal and Rohlf, 1981).

3. Results

3.1. Size, abundance and habitat-use pattern of host sea anemones

Body size of sea anemones in the field varied significantly among color morphs
(Kruskal–Wallis test: \( H(4, \ N=1000) = 21.75, \ p = 0.0002; \) Fig. 1A). The blue, reddish
green, and orange color morphs were similar in size (a posteriori Student–Newman–
Keuls: \( p>0.05 \)), but the blue sea anemones were slightly larger than the red and green
morphs (a posteriori SNK: \( p<0.05 \)). No significant differences were found between the
body size of red, green, reddish green, and orange sea anemones (a posteriori SNK: \( p>0.05 \)).

Relative abundance of anemones varied significantly among color morphs (Kruskal–
Wallis test, \( H(4, \ N=35) = 14.17, \ p = 0.0068 \)). The number of green sea anemones collected
per sampling hour (\( n = 7 \) surveys) was significantly higher than the number of sea anemones
collected per sampling hour of the remaining color morphs (a posteriori SNK: \( p < 0.05 \)), which were similarly abundant (a posteriori SNK: \( p > 0.05 \)) (Fig. 1B).

Microhabitats used by each anemone color morph were observed to be different (Fig. 2). The red morph was most frequently found among fronds or holdfasts of *Lessonia* sp., or in crevices and among boulders, 62% and 37% of sea anemones, respectively. Green and reddish green sea anemones were most commonly found in crevices and among boulders. Orange sea anemones, *P. pluvia*, were commonly observed in crevices and among boulders, secondarily in pools, occasionally among adhesive discs and fronds of *Lessonia nigrescens*, but this color morph was never observed beneath rocks or in caverns, where the blue morph was most frequently found (>75%) (Fig. 2).

### 3.2. Host-use pattern by adults of *A. spinifrons*

A total of 218 adults of *A. spinifrons* were found on the 1000 sea anemones surveyed. The frequency of occurrence of adult crabs on sea anemones was 21% (210
out of 1000 sea anemones harbored at least one adult crab). Of the 210 sea anemones which harbored adult crabs, 202 (96.2%) of them were inhabited by a single male or female crab, while the remaining 8 sea anemones harbored heterosexual ($n=6$) or homosexual pairs ($n=2$) of *A. spinifrons*. Overall, on those sea anemones harboring adult *A. spinifrons* crabs, a single adult male or female was observed, regardless of host color morph. Frequency distribution of adult symbiotic crabs on the different anemones differed significantly from that expected by the relative abundance of host types in the field ($\chi^2$ test of goodness-of-fit: $\chi^2 = 39.53$, $df=4$, $p<0.0001$, $1-\beta=0.9845$) (Fig. 3). Adult crabs were found less frequently than expected by chance on blue anemones (subdivision of $\chi^2$ test of goodness-of-fit with sequential Bonferroni correction: $\chi^2 = 34.06$, $df=1$, $p<0.0001$; Fig. 3), suggesting that crabs avoid blue *P. clematis* or caverns used as microhabitats by these anemones. In contrast, crabs were found more frequently than expected by chance on reddish green anemones (subdivision of $\chi^2$ test of goodness-of-fit with sequential Bonferroni correction: $\chi^2 = 6.82$, $df=1$, $p<0.009$; Fig. 3), suggesting that crabs actively prefer reddish green *P. clematis*. Adult crabs were found on all other anemone types at similar frequencies to those expected by their field abundances (subdivision of $\chi^2$ test of goodness-of-fit with sequential Bonferroni correction: $p>0.05$ in all the cases; Fig. 3), suggesting that crabs did not prefer one anemone over the others.

Fig. 2. Frequency of occurrence (number of sea anemones per habitat) of the different sea anemones (color morphs) in each of the four microhabitats surveyed at the rocky intertidal of La Pampilla, Chile. Habitat categories are as follows: (1) among fronds and/or adhesive discs of *Lessonia* sp., (2) among crevices or boulders, (3) beneath rocks or in caverns, and (4) in tidal pools.

Fig. 3. Observed and expected frequencies of occurrence of *A. spinifrons* adult symbiotic crabs on each of the different sea anemones (color morphs). Observed and expected distributions differed significantly (chi-square of goodness-of-fit: $p<0.05$). Differences of specific frequencies between observed and expected distributions were compared by subdividing the chi-square test of goodness-of-fit with sequential Bonferroni correction (see text); ns = not significant; *$p<0.05$. 

3.3. Multiple and alternative host selection by A. spinifrons adult crabs

When offered multiple hosts, crab colonization pattern differed significantly from the random binomial distribution ($\chi^2 = 10.3$, df = 4, $p < 0.0357$, $1/C_0 = 0.7304$) (Table 1). Adult crabs colonized blue anemones less frequently than expected by chance (subdivision of $\chi^2$ test of goodness-of-fit with sequential Bonferroni correction, $\chi^2 = 9$, df = 1, $p = 0.0027$). In contrast, the remaining sea anemone color morphs were colonized by adult crabs as would be expected by chance ($p > 0.05$; Table 1). Short-term (0 and 1 h) and long-term (24 h) alternative host selection experiments confirmed the results obtained during the multiple host selection experiment. In general, adult A. spinifrons preferred orange and green sea anemones over blue sea anemones (Tables 2–4).

<table>
<thead>
<tr>
<th>Sea anemone, color</th>
<th>Observed (Exp)</th>
<th>$\chi^2$</th>
<th>$P$</th>
<th>C index</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. clematis, red</td>
<td>23 (20)</td>
<td>0.56</td>
<td>0.4533</td>
<td>0.075</td>
</tr>
<tr>
<td>P. clematis, green</td>
<td>22 (20)</td>
<td>0.25</td>
<td>0.6171</td>
<td>0.050</td>
</tr>
<tr>
<td>P. clematis, reddish green</td>
<td>27 (20)</td>
<td>3.06</td>
<td>0.2431</td>
<td>0.175</td>
</tr>
<tr>
<td>P. clematis, blue</td>
<td>8 (20)</td>
<td>9.00</td>
<td>0.0027</td>
<td>−0.300</td>
</tr>
<tr>
<td>P. pluvia, orange</td>
<td>20 (20)</td>
<td>0.00</td>
<td>1.0000</td>
<td>0.000</td>
</tr>
</tbody>
</table>

$N$ = 100, $\chi^2 = 10.30$, $P = 0.0357$, $df = 4$.

The expected random value (according to binomial distribution) is shown between parenthesis. Selectivity $C$ index value indicates preference of symbiotic adult crabs for each one of the different sea anemones.

Table 1

<table>
<thead>
<tr>
<th>Sea anemone, color</th>
<th>Observed (Exp)</th>
<th>$\chi^2$</th>
<th>$P$</th>
<th>C index</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. clematis, red</td>
<td>23 (20)</td>
<td>0.56</td>
<td>0.4533</td>
<td>0.075</td>
</tr>
<tr>
<td>P. clematis, green</td>
<td>22 (20)</td>
<td>0.25</td>
<td>0.6171</td>
<td>0.050</td>
</tr>
<tr>
<td>P. clematis, reddish green</td>
<td>27 (20)</td>
<td>3.06</td>
<td>0.2431</td>
<td>0.175</td>
</tr>
<tr>
<td>P. clematis, blue</td>
<td>8 (20)</td>
<td>9.00</td>
<td>0.0027</td>
<td>−0.300</td>
</tr>
<tr>
<td>P. pluvia, orange</td>
<td>20 (20)</td>
<td>0.00</td>
<td>1.0000</td>
<td>0.000</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$N$</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\chi^2$</td>
<td>10.30</td>
</tr>
<tr>
<td>$P$</td>
<td>0.0357</td>
</tr>
<tr>
<td>$df$</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 2

Alternative host selection experiments after 0 h

<table>
<thead>
<tr>
<th>Source host</th>
<th>Hosts offered</th>
<th>Selection 0 h</th>
<th>Color 1 vs. color 2</th>
<th>$P$</th>
<th>$1 – \beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>-------------</td>
<td>---------------</td>
<td>---------------</td>
<td>---------------------</td>
<td>-----</td>
<td>------------</td>
</tr>
<tr>
<td>P. clematis, green</td>
<td>P. clematis, green/P. pluvia, orange</td>
<td>22/1/7</td>
<td>0.0081</td>
<td>0.5997</td>
<td></td>
</tr>
<tr>
<td>P. clematis, green</td>
<td>P. clematis, green/P. clematis, blue</td>
<td>20/1/9</td>
<td>0.0614</td>
<td>0.5889</td>
<td></td>
</tr>
<tr>
<td>P. pluvia, orange</td>
<td>P. pluvia, orange/P. clematis, green</td>
<td>14/0/16</td>
<td>0.8555</td>
<td>0.8649</td>
<td></td>
</tr>
<tr>
<td>P. pluvia, orange</td>
<td>P. pluvia, orange/P. clematis, blue</td>
<td>19/1/10</td>
<td>0.1360</td>
<td>0.5856</td>
<td></td>
</tr>
<tr>
<td>(a) Source host (color 1) vs. nonsource host (color 2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. clematis, green</td>
<td>P. pluvia, orange/P. clematis, blue</td>
<td>20/1/9</td>
<td>0.0614</td>
<td>0.5889</td>
<td></td>
</tr>
<tr>
<td>P. pluvia, orange</td>
<td>P. clematis, green/P. clematis, blue</td>
<td>16/2/12</td>
<td>0.5715</td>
<td>0.6703</td>
<td></td>
</tr>
<tr>
<td>(b) Nonsource host</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The number of A. spinifrons adult crabs colonizing each host offered during different essays, where different combinations of sea anemone color morphs were offered to crabs for colonization. The $P$ critical value from the binomial test indicates significant differences between the observed distribution of crab on sea anemones and the expected binomial random distribution. The power of each test ($1 – \beta$) is shown.
3.4. The effect of source host on *A. spinifrons* preferences

Adult crabs collected from green sea anemones (*P. clematis*), that were offered a choice between this green morph (i.e. source host) and the orange *P. pluvia*, demonstrated a marked preference for the source host (Tables 2–4). However, when adult crabs collected from orange sea anemones (*P. pluvia*) were offered a choice between orange and the green morph of *P. clematis*, no preference for any color morph was observed. Adult crabs collected from orange *P. pluvia* and allowed to choose between blue and green *P. clematis* showed no preference after 24 h (Table 4). Similarly, crabs collected from orange (*P.

Table 3
Alternative host selection experiments after 1 h

<table>
<thead>
<tr>
<th>Source host</th>
<th>Hosts offered</th>
<th>Selection 1 h</th>
<th>Color 1 vs. color 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Color 1/color 2</td>
<td>Color 1/no selection/color 2</td>
<td>P</td>
</tr>
<tr>
<td>(a) Source host (color 1) vs. nonsource host (color 2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. clematis</em>, green</td>
<td><em>P. clematis</em>, green/<em>P. pluvia</em>, orange</td>
<td>23/1/6</td>
<td>0.0023</td>
</tr>
<tr>
<td><em>P. clematis</em>, green</td>
<td><em>P. clematis</em>, green/<em>P. clematis</em>, blue</td>
<td>21/1/8</td>
<td>0.0121</td>
</tr>
<tr>
<td><em>P. pluvia</em>, orange</td>
<td><em>P. pluvia</em>, orange/<em>P. clematis</em>, green</td>
<td>14/0/16</td>
<td>0.8555</td>
</tr>
<tr>
<td><em>P. pluvia</em>, orange</td>
<td><em>P. pluvia</em>, orange/<em>P. clematis</em>, blue</td>
<td>19/1/10</td>
<td>0.1360</td>
</tr>
<tr>
<td>(b) Nonsource host</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. clematis</em>, green</td>
<td><em>P. pluvia</em>, orange/<em>P. clematis</em>, green</td>
<td>23/0/7</td>
<td>0.0052</td>
</tr>
<tr>
<td><em>P. pluvia</em>, orange</td>
<td><em>P. clematis</em>, green/<em>P. clematis</em>, blue</td>
<td>17/1/12</td>
<td>0.4583</td>
</tr>
</tbody>
</table>

The number of *A. spinifrons* adult crabs colonizing each host offered during different essays, where different combinations of sea anemone color morphs were offered to crabs for colonization. The *P* critical value from the binomial test indicates significant differences between the observed distribution of crab on sea anemones and the expected binomial random distribution. The power of each test (1 – *β*) is shown.

3.4. The effect of source host on *A. spinifrons* preferences

Adult crabs collected from green sea anemones (*P. clematis*), that were offered a choice between this green morph (i.e. source host) and the orange *P. pluvia*, demonstrated a marked preference for the source host (Tables 2–4). However, when adult crabs collected from orange sea anemones (*P. pluvia*) were offered a choice between orange and the green morph of *P. clematis*, no preference for any color morph was observed. Adult crabs collected from orange *P. pluvia* and allowed to choose between blue and green *P. clematis* showed no preference after 24 h (Table 4). Similarly, crabs collected from orange (*P.

Table 4
Alternative host selection experiments after 24 h

<table>
<thead>
<tr>
<th>Source host</th>
<th>Hosts offered</th>
<th>Selection 24 h</th>
<th>Color 1 vs. color 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Color 1/color 2</td>
<td>Color 1/no selection/color 2</td>
<td>P</td>
</tr>
<tr>
<td>(a) Source host (color 1) vs. nonsource host (color 2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. clematis</em>, green</td>
<td><em>P. clematis</em>, green/<em>P. pluvia</em>, orange</td>
<td>21/1/8</td>
<td>0.0121</td>
</tr>
<tr>
<td><em>P. clematis</em>, green</td>
<td><em>P. clematis</em>, green/<em>P. clematis</em>, blue</td>
<td>22/0/8</td>
<td>0.0161</td>
</tr>
<tr>
<td><em>P. pluvia</em>, orange</td>
<td><em>P. pluvia</em>, orange/<em>P. clematis</em>, green</td>
<td>18/0/12</td>
<td>0.3616</td>
</tr>
<tr>
<td><em>P. pluvia</em>, orange</td>
<td><em>P. pluvia</em>, orange/<em>P. clematis</em>, blue</td>
<td>27/1/2</td>
<td>0.000001</td>
</tr>
<tr>
<td>(b) Nonsource host</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. clematis</em>, green</td>
<td><em>P. pluvia</em>, orange/<em>P. clematis</em>, blue</td>
<td>19/3/8</td>
<td>0.0522</td>
</tr>
<tr>
<td><em>P. pluvia</em>, orange</td>
<td><em>P. clematis</em>, green/<em>P. clematis</em>, blue</td>
<td>19/0/11</td>
<td>0.2005</td>
</tr>
</tbody>
</table>

The number of *A. spinifrons* adult crabs colonizing each host offered during different essays, where different combinations of sea anemone color morphs were offered to crabs for colonization. The *P* critical value from the binomial test indicates significant differences between the observed distribution of crab on sea anemones and the expected binomial random distribution. The power of each test (1 – *β*) is shown.
pluvia) and allowed to choose between the source host and blue P. clematis showed a preference for the source host, but only after 24 h (Tables 2–4). Overall, crabs collected from green sea anemones showed a very strong preference for this host, while crabs collected from orange P. pluvia showed no or only a weak preference for their source hosts.

4. Discussion

Adult A. spinifrons crabs occur more frequently than expected by chance on sea anemones which possess a color more similar to their own carapace (reddish green), and occur less frequently than expected by chance on blue sea anemones, where camouflage is reduced. Laboratory experiments demonstrated that adult A. spinifrons crabs avoid blue sea anemones over the rest of the host species and color morphs offered for colonization, although no preference was observed between red, green, reddish green, or orange sea anemones. Thus, the partial agreement between the host-use pattern of crabs in the field, and their preference ranking of different color morphs in laboratory experiments, indicates that host selection behavior by individuals plays a role in determining the field distribution of adult A. spinifrons. However, other factors may explain the distribution of adult crabs in the field, too, as suggested by the occupancy of reddish green sea anemones in the intertidal (higher than expected by chance), but the lack of preference for this color morph by crabs in the laboratory.

Previous studies in free-living decapods and other mobile marine organisms have shown that predation pressure and inter- and intra-specific interactions are the primary factors affecting their abundance and distribution in the field (Navarrete and Castilla, 1990; Wilson et al., 1987). Since A. spinifrons is the only crab species that dwells on sea anemones in the rocky intertidal of north-central Chile (JAB, personal observations), interference from other species can be discarded as a mechanism affecting the host-use pattern by adult life stages in the field. However, predation and abiotic ecological factors may affect the host-use pattern of A. spinifrons. Since homochromy of adults living on blue sea anemones is lower than on the rest of the host species and color morphs (excluding orange sea anemones), an alternative or additional explanation for the lower frequency of crabs on that color morph in the field could be an increased predation rate. Beside fish species reported to prey upon A. spinifrons (Vásquez, 1993), grapsid (Leptograpsus variegatus (Fabricius, 1793)) and xanthid (Gaudichaudia gaudichaudi (H. Milne Edwards, 1834)) crabs were observed attacking crabs on P. clematis sea anemones and when crabs moved away from their hosts during our field collections (JAB, personal observation).

The microhabitat occupied by sea anemones may also affect the host-use pattern of adult A. spinifrons. Blue sea anemones were most frequently found in small caverns or beneath large rocks, and only rarely in crevices or among boulders where most of the other sea anemone species and color morphs live. During field surveys, we observed that the caverns and refuges used by blue sea anemones were more exposed to wave action during high tide, but remained exposed for longer periods during low tide, when compared to the rest of the analyzed microhabitats. These differences may affect the survival of crabs on
blue sea anemones. On the other hand, crevices or spaces among boulders, may represent a more suitable microhabitat for crabs, fact that may explain the high occupancy of reddish green sea anemones by crabs in the intertidal. Further field studies examining mortality experienced by crabs when inhabiting different sea anemone color morphs and its different microhabitats must be conducted to elucidate the relative importance of behavioral mechanisms, and biotic and abiotic processes, in determining the field distribution of *A. spinifrons*.

Our results suggest that habitat selection may be considered as one of the factors explaining the distribution of a single species in different available microhabitats. Behavioral processes may be important in determining the distribution and habitat partitioning of organisms which are capable of high mobility after settlement (e.g. crabs and fishes: Elliott et al., 1995). Visual predation and other host-related factors may be considered the ultimate driving forces in the evolution of avoidance behavior towards blue sea anemones by *A. spinifrons*, as has been proposed for other decapods featuring preferences for habitats where visual predation is less likely to occur (adult shrimps—Bell and Westoby, 1986; Hacker and Madin, 1991; Berggren, 1993; early-life benthic phases of crabs and clawed lobsters—Johns and Mann, 1987; Wilson et al., 1990; Wahle and Steneck, 1992).

When choosing among different host species, symbiotic decapods, including porcelain crabs, use chemicals cues to recognize and discriminate between hosts (Ache and Davenport, 1972; Guo et al., 1996; Brooks and Rittschof, 1995). In *A. spinifrons*, chemical cues may also be involved in host selection, as suggested by the alternative host choice experiments. Crabs whose source host was *P. pluvia* showed a different behavior than those that came from *P. clematis*. It is likely that adult *A. spinifrons* crabs dwelling on *P. clematis* sea anemones in the field became chemically conditioned to the same host, as has previously been suggested for other symbiotic decapods (Gwaltney and Brooks, 1994; Derby and Atema, 1980). *A. spinifrons* adults may also discriminate and choose their preferred host by color cues. Host discrimination by color or other visual cues have been poorly studied in decapods (but see Ache and Davenport, 1972; Guo et al., 1996). Waterman (1961 and references therein) reported that certain decapod species are able to distinguish among colors (e.g. *Carcinus maenas* (Linnaeus, 1758) is able to discriminate between yellow and blue). We also believe *A. spinifrons* represents an interesting biological model for exploring color perception and discrimination as well as the relationship between vision capability and habitat selection in crustaceans.

**Acknowledgements**

We acknowledge Paula Neill, Evie Wieters, Barbara Hasek, Jodi Caskey, Dr. Raymond Bauer, Dr. Martin Thiel, Dr. Rubén Soto, and Dr. Patricio Manríquez whose comments and ideas encouraged the writing of this manuscript. The present study was part of JAB’s thesis to obtain a Master’s Degree (Universidad Católica del Norte, Sede Coquimbo). JAB thanks the Sociedad Chilena de Ciencias del Mar and Compañía Minera La Escondida for a 2-year post-graduate scholarship. This is contribution #88 of the Laboratory for Crustacean Research, University of Louisiana at Lafayette. [AU]
References


