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# Habitat selection by larvae of the symbiotic sponge *Haliclona caerulea* (Hechtel, 1965) (Demospongiae, Haplosclerida)

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**Abstract**
The viviparous sponge *Haliclona caerulea* lives in symbiosis with the calcareous alga *Jania adherens* in shallow rocky ecosystems from the Bay of Mazatlán (Mexican Pacific Ocean). Laboratory and field experiments were carried out with the aim of demonstrating that the symbiosis with this calcareous alga is the result of larval habitat selection. We offered the larvae four different substrates: live fronds of *J. adherens*, loofa (vegetable fiber used to simulate the arborescent form of the alga) and oyster valves as control. In addition, we used loofa impregnated with extract of *J. adherens* to test if the larvae of *H. caerulea* use chemotaxis to locate their host. We also tested the effect of the water flow in the larval settlement using three different current speeds (0, 3.2 and 6.3 cm $s^{-1}$). The settlement was recorded at 24, 48 and 72 h. The percentage of larval settlement was significantly higher in the fronds of *J. adherens* than in the other substrate types, independently of the water flow. However, when movement was applied to the water, most larvae settled during the first 24 h. These results provided direct evidence of habitat selection for the larvae of *H. caerulea*, which showed a high specificity to settle on its association partner.

**Keywords**: Larvae, sponge, symbiosis, settlement, substrate, *Jania adherens*, current speed

## 1. Introduction

The symbiotic association between the sponge *Haliclona caerulea* Hechtel, 1965, and the red macroalga *Jania adherens* Lamouroux, 1816, is one of the most successful organisms in terms of abundance, distribution, and permanence in shallow rocky ecosystems from Mazatlán Bay (eastern tropical Pacific, Mexico) (Ávila and Carballo, 2004). This association forms permanent populations, and it seems obligatory for the sponge, but the aposymbiotic form of *J. adherens* inhabits the intertidal zone, outside of the association's range of distribution (Carballo and Ávila, 2004).

Detailed studies on symbioses involving sponges and macroalgae are scarce (Palumbi, 1985; Rützler, 1990), and most of them deal with population dynamics, distribution, or metabolic relationships between the partners (Trautman et al., 2000; Trautman and Hinde, 2002; Trautman et al., 2003; Ávila and Carballo, 2004; Carballo et al., 2006). To our knowledge, there are no studies about the selection of the algae by the larvae of the sponge. This is an important issue for understanding the population dynamics of these associations, because they need to be reconstituted after sexual reproduction.

Most marine invertebrates have complex life histories in which a dispersive larval phase may alternate with a benthic adult phase. The population dynamics and distribution of such species is highly dependent on larval recruitment to a favorable habitat (Pawlik, 1992). In the life cycle of almost all the sponges there is a planctonick larval stage, which settles on the substratum and becomes a sessile organism (Lindquist and Hay, 1996). One interesting question is how larvae locate an appropriate habitat in which to settle. Settlement can occur randomly (Bergquist, 1978) or through active selection, showing in this case a high specificity for a substrate; for example, the larvae of boring sponges show a high preference for calcareous surfaces (Hartman, 1958; Schönberg, 2003). This active selection of habitat can be considered as advantageous for the persistence of the species, since it allows individuals to find an adequate food supply, avoid competitors, or increase the probability of

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settlement in a suitable physical environment (Martin et al., 1992; Pawlik, 1992; Stoner, 1994; Walters et al., 1997; Maldonado and Uriz, 1998; Carballo and Ávila, 2004).

There is also evidence that the hydrodynamic regime is an important controlling factor that influences the larval settlement (Butman, 1987; Harvey et al., 1995; Pernet et al., 2003). In fact, experimental studies have revealed that in high speed flow the larvae (e.g. the mussel larvae *Mytilus* spp.) can be distributed similarly to passive particles and the exploration phase can be limited (Pernet et al., 2003). However, there are some organisms like the larvae of the bryozoan *Membranipora membranacea*, which are able to explore substrata in flow velocities that are much faster than their locomotion speeds (Abelson, 1997).

The sponge *Haliclona caerulea* liberates parenchymella larvae from May to October in the Bay of Mazatlán (Carballo and Ávila, 2004), which forms part of the plankton for a very short period of time (Maldonado and Young, 1999).

In previous studies, it has been demonstrated that both organisms benefit from the association because both sponge and alga live in an environment where they do not exist in isolation (Ávila and Carballo, 2004; Carballo and Ávila, 2004; Carballo et al., 2006). The strong interdependence between both organisms in order to inhabit a very hydrodynamic environment (shallow rocky ecosystems) suggests that the alga offers a safe substrate for the survival of the sponge larvae.

The aim of this study was to investigate 1) if the larvae of the sponge settle selectively on *Jania adherens*, its partner in the association, and 2) to test if high water movement may affect the larvae's selection of habitat. The work's hypothesis is that the sponge larval behavior may be responsible for the association due to a selective or preferential settlement on the algae. For this, we carried out experiments in the field and laboratory using different substrate types, and different current water speeds, which are inside the range of the speed registered in the association's habitat.

## 2. Material and Methods

*Laboratory experiments*

From May to September 2004, we collected 10 ripe individuals from the Bay of Mazatlán, 23°13'49"N–106°27'43"W (Fig. 1) by SCUBA diving between 3 to 4 m depth, and placing them in a container with seawater. On the boat, larval release was triggered by exposing the adults to the air for a few seconds (Maldonado and Young, 1996). After that, larvae were quickly moved to the laboratory, where they were collected with a Pasteur pipette. The larvae were then placed in previously prepared crystallizing dishes (125 × 65 mm) with 300 ml of 35% salinity filtered seawater. In each crystallizing dish (3 cm diameter), four experimental substrates were placed 5 cm apart from each other. The dishes were placed under an illumination (of ~83 µmol quanta $m^2$ $s^{-1}$, at 12:00 pm) and water temperature (25°C) corresponding to the environmental conditions where the association lives. The irradiance was measured using a cosine corrected underwater light sensor (LI-192SA, Li-Cor, NE, USA) attached to a data-logger (LI-1400, Li-Cor, NE, USA). Half of the water was replaced daily during the experiment.

To test if the larvae of the sponge settled selectively in *Jania adherens*, we provided them with four different substrates simultaneously: (1) The substrate with which the sponge lives in association (fronds of *J. adherens*), (2) a substrate similar in structure to *J. adherens* (*Luffa cylindrica*), (3) *Luffa cylindrica* impregnated with *J. adherens* extract, and (4) oyster valves as control.

*Luffa cylindrica* is a natural vegetable fiber commonly known as loofa or vegetable sponge. We considered it as an experimental substrate because it forms microrefuges similar in size and form to *Jania adherens* (inner spaces 467±87 µm in *J. adherens* vs. 484±35 µm in loofa; [average±SE]). In addition, it can be easily impregnated with natural concentration of *Jania* extract to test if the larvae select sponge by a chemical cue. In order to obtain the extract we used dichloromethane:methanol in a proportion of 1:1 (volume/volume) (Becerro, 1994). The fronds of *J. adherens* used for the extraction were previously measured for volume (ml) to obtain the ratio between dry weight of extract and the volume of fresh alga.

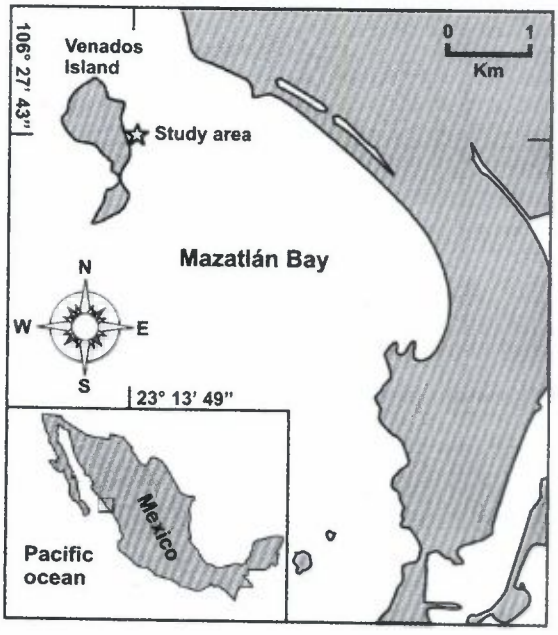


Figure 1. Study area in Bay of Mazatlán (Pacific Ocean, Mexico).

The volume (ml) of the loofa was also obtained to determine the quantity of extract necessary to simulate the natural concentration of the compounds in the alga. The extract was dissolved in acetone (90%), and later concentrated in a small volume to impregnate the loofa with it.

Oyster valves were selected as substrate control because they do not form microrefuges, and to test if the settlement of larvae is at random (no differences with *Jania/Luffa* substrates), or selective. Before using them, the substrates were "aged" by exposing them to running seawater for twenty days (Kaye and Reiswig, 1991).

To investigate the effect of water movement on settlement, we used different current speeds in the laboratory. The flow inside crystallizing dishes was generated with a magnetic stirrer at different speeds in rpm. Magnetic studies on zebra mussels larvae indicated that the magnetic field had no significant impact on the short-term behavior of veliger/post-veliger movement and post-veliger settlement (Smythe et al., 1997).

The rpm equivalence to cm $s^{-1}$ was calculated by measuring the time that a small buoy spent to travel a known distance in the crystallizing dishes ($y = 0.0348x - 0.494$, $R^2 = 0.99$, $p<0.01$). The flows selected were 0 cm $s^{-1}$, 3.2 cm $s^{-1}$ and 6.3 cm $s^{-1}$, which are inside the range of the current speeds registered in the Bay of Mazatlán (between 1.2 and 7.7 cm $s^{-1}$, depending on the tide) (Cabrera, 1988).

We used 20 crystallizing dishes with 10 larvae in each, and we calculated the average number (±SE) of settlements at 24, 48 and 72 h, on each substrate type using a stereoscopic microscope (SZ-ST OLYMPUS, Japan). We counted as a settler the stage at which the larva was irreversibly attached to the substratum by the anterior pole to initiate metamorphosis. We did not consider the larvae that settled on the glass surface of the crystallizing dishes.

*Field experiments*

During the main period of larvae release of *H. caerulea* (from May to October 2004), we carried out a similar experiment in the field. We used the same substrate types as in the laboratory except for the loofa with extract, because in this experiment, the substrates were left in the sea for five months, and the extract would be lost by dilution (Engel and Pawlik, 2000). Using nylon thread, we tied 15 substrata of each type to artificial surfaces (ceramic tiles measuring 10 × 10 cm), which were evenly distributed on a plastic mesh firmly attached to a concrete base (1.0 × 0.6 × 0.1 m). Four bases of concrete with 45 substrates each were placed in the area where the association is more abundant (3 m depth), at a distance of 10 meters from each other. Four other bases were placed at the limit of the distribution area at 6 m depth. We also tried to do the same experiment at 1 m depth, but the high level of water movement made it impossible.

During the experiment, 5 substrates of each type were recovered every 10 days, and kept in covered plastic containers. In the laboratory, a meticulous observation of each substratum was carried out under the stereoscopic microscope to determine the number of settlements.

*Analyses of data*

To test the hypothesis that settlement of larvae depends on (1) the substrate type, (2) current speed and (3) time, the 3 factors were analyzed using a repeated-measure of ANOVA. Substrate type (four levels: fronds of *J. adherens*, loofa with extract, loofa without extract, oyster valves) was a fixed factor, and current speed (three levels: 0, 3.2 and 6.2 cm $s^{-1}$) and time (three levels: 24, 48, 72 hours) were random factors. The assumption of normality was tested using a Kolmogorov-Smirnov test. The assumption of equality of variances was tested using an $F_{max}$ test (Sokal and Rohlf, 1995). Data were transformed as necessary using arcsine function to conform to the assumptions of ANOVA. Analysis of variance was followed by the post hoc test Student-Newman-Keuls (SNK) test on appropriate terms of the model found to be significant.

## 3. Results

Laboratory experiments showed that the larvae of *H. caerulea* settled on the four substrata types (Figs. 2 and 3). However, the three factors tested in the laboratory assay confirmed that larvae of *H. caerulea* presented a high preference to settle on *Jania adherens* (91.6±1.1% of the total of settlements).

Factor 1 (substrate): The highest percentage of larvae settled on the fronds of *J. adherens* (SNK test, $P<0.01$) (Table 1). No significant differences were detected in the number of settlements among the other substrates.

Table 1. Results of the three-way Repeated Measures ANOVA of the number of settlements on each substrate type, current speed and time (time as repetitive measurements). Substrate type (four levels) was a fixed factor, and current speed and time (three levels) were random factors.

| Source | *df* | MS | F | P |
|---|---|---|---|---|
| Current speed | 2 | 235 | 86.5 | <0.001 |
| Substrate | 3 | 1,347 | 495.6 | <0.001 |
| Time | 2 | 29 | 52.7 | <0.001 |
| Current speed × substrate | 6 | 169 | 62.3 | <0.001 |
| Current speed × time | 4 | 2 | 3.3 | 0.01 |
| Substrate × time | 6 | 20 | 35.4 | <0.001 |
| Current speed × substrate × time | 12 | 1 | 2.1 | 0.013 |

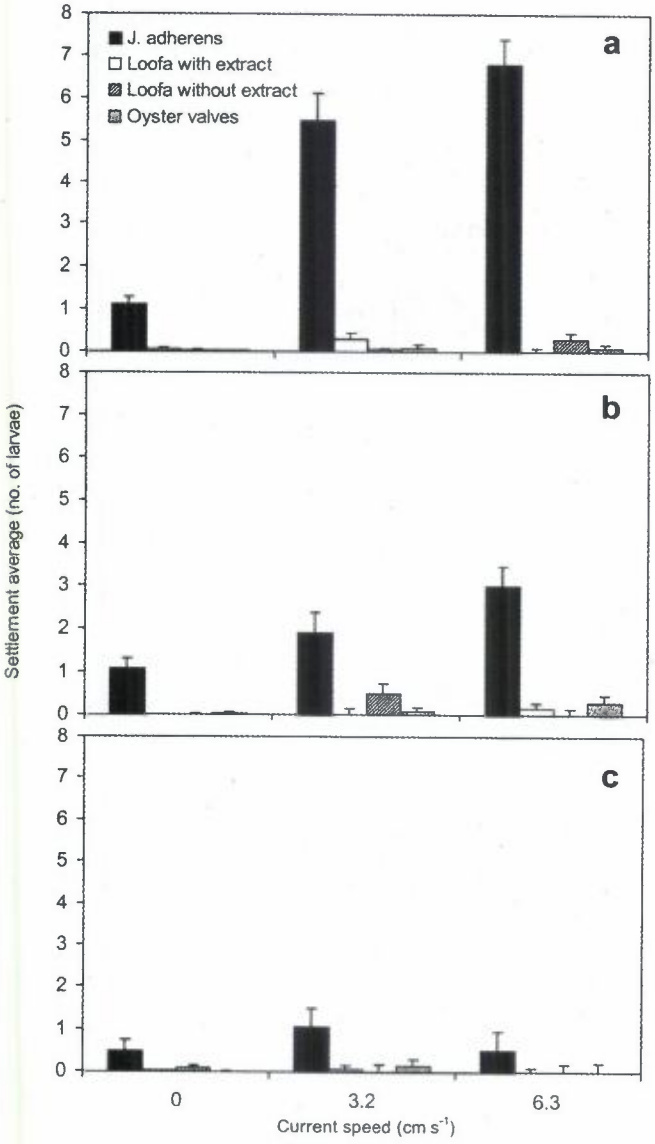


Figure 2. Average number of settlements (± SE) of sponge larvae on all the substrates at different conditions of current and at different time intervals: a) 24 hours, b) 48 hours and c) 72 hours after the beginning of the experiment.

Factor 2 (current speed): The results indicated that settlements on *Jania adherens* were enhanced with increased water speed, but current speed had no significant effect on larvae settlement on the rest of the substrates. For example, the total of settlements increased from 2.6±0.27 larvae at 0 cm $s^{-1}$ to 10.3±0.45 larvae at 6.3 cm $s^{-1}$ (SNK test, $P<0.01$) (Fig. 2), showing that faster current speed induced a faster settlement of larvae on *Jania adherens*.

Factor 3 (time): The number of settlements did not vary significantly over time in the crystallizing dishes without current (SNK test, $P>0.05$). However, when current was applied (3.2 and 6.3 cm $s^{-1}$) most of the larvae settled in the first 24 hours after releasing them (SNK, $P<0.01$) (Fig. 2). This trend was observed only on *Jania adherens*. In the other substrates the number of settlements did not vary significantly through time.

The number of settlement differed between substrates, current speed and time, but this response was not constant through time in each current speed (i.e. a significant Current speed × Substrate × Time interaction; $P<0.013$). For example, the number of settlements on *J. adherens* clearly increases with current speed, but this response was only significant at 24 h.

In the field experiments, we did not find settlements of larvae of *H. caerulea* in any of the substrates during the whole period of study. However, after the first month we found some small sponges in the substrates placed at 3 m depth. The species were *Callyspongia* sp. (3 settlements; 1 on oyster valves and 2 on the surface of the tile), *Mycale magnirhaphidifera* van Soest, 1984 (1 settler on an oyster valve) and calcareous sponges (3 settlements; 1 on the *J. adherens* and 2 on loofa). It is important to note that *J. adherens* did not survive after the first two weeks of the beginning of the experiment.

In summary, the results suggested a high specificity of the sponge larvae to settle on its association partner.

## 4. Discussion

Host location by larvae of marine invertebrates that live in obligatory symbiosis is a critical process for their survival and successful growth (Pasternak et al., 2004).

The results showed that the larvae of *Haliclona caerulea* strongly prefer settling on the fronds of *J. adherens* compared to the other substrates (91.6% of the total of settlements), which suggests a high specificity of the larvae for its partner in the association (Figs. 3A,C). Similar results were obtained with the larvae of the sponge *Halichondria panicea* which lives in association with coralline algae. The laboratory experiments showed that larvae of *H. panicea* settled and metamorphosed faster in the presence of coralline algae than in the presence of natural rocks surfaces (56% vs. 11%) (Palumbi, 1985).

The mechanisms by which marine larvae select a specific substrate could be attributed to a combination of active larval behavior in response to biological, chemical and physical factors (Scheltema, 1986; Butman, 1987; Pawlik, 1992). However, the current view is that hydrodynamic processes dominate at large spatial scales (meters, kilometers), with active habitat selection becoming progressively more important at smaller spatial scales (centimeters, millimeters, micrometers) (Keough and Downes, 1982). Active habitat selection requires that larvae discriminate among potential settlement sites, which is possible through the detection of habitat-specific cues. Thus, the larvae of the parasitic barnacle *Heterosaccus dollfusi* are capable of actively locating their host (the brachyuran crab *Charybdis longicollis*) using chemotaxis

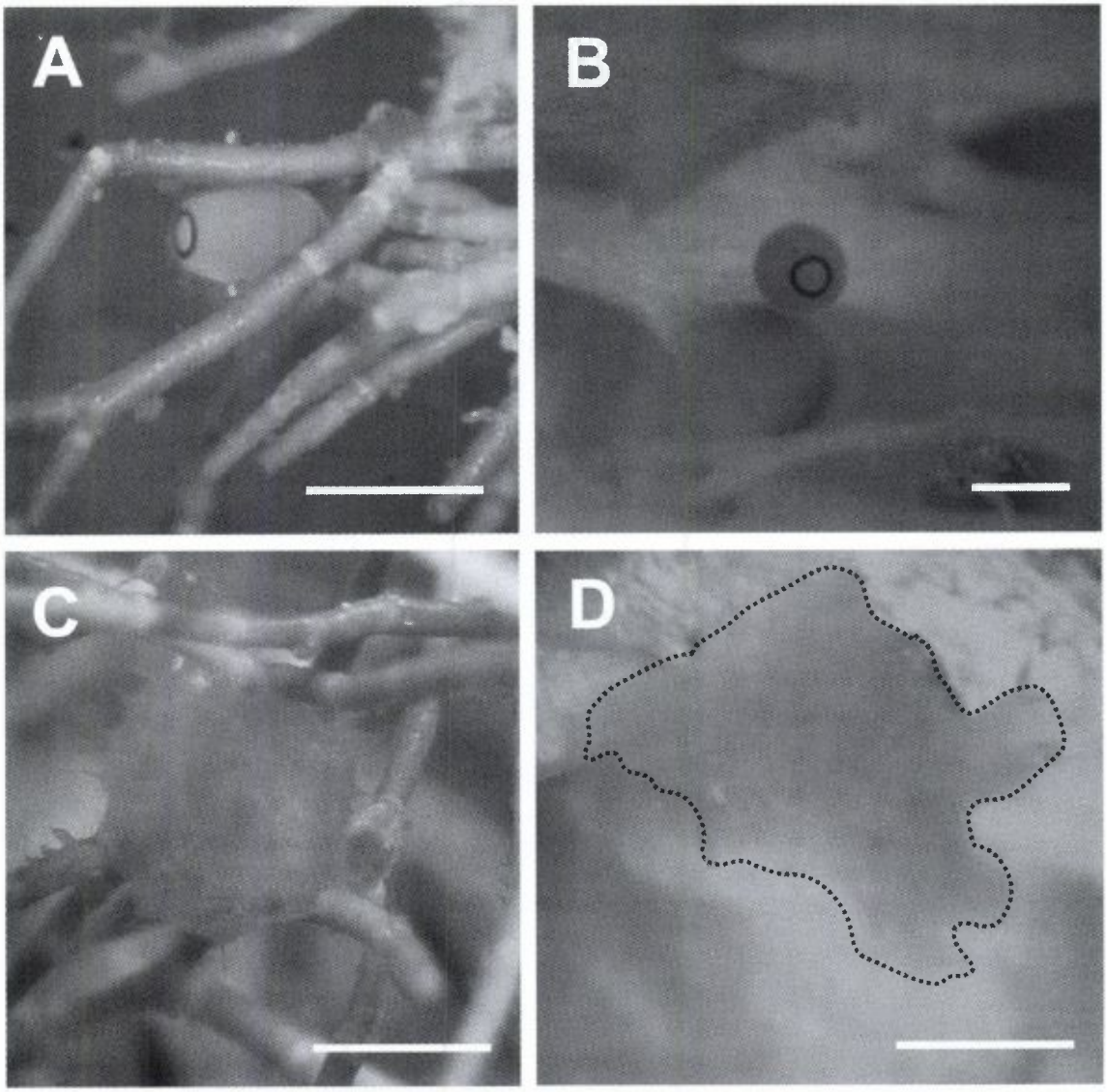


Figure 3. A) *H. caerulea* larva on the fronds of *J. adherens*. B) and on loofa. C) *H. caerulea* post-larval stage of 72 hours old settled on fronds of *J. adherens*, D) The same stage on an oyster valve (dotted line). Scale bar for A, C, D = 500 µm; scale bar for B = 200 µm.

and rheotaxis, and modifying their swimming pattern, direction and velocity (Pasternak et al., 2004). The planktonic larvae of the polychaete *Capitella* sp. are also capable of active sediment selection, settling mainly on a natural, organic-rich muddy sediment (Butman and Grassle, 1992). The larvae of sponges can also respond to chemical cues (Sará, 1984; Burke, 1986; Pawlik, 1992), and it has been shown that organic compounds isolated from marine sponges have induced settlement of ascidian larvae (Tsukamoto et al., 1994, 1995). Some physical factors including the light (Maida et al., 1994; Maldonado and Young, 1996) and physical microrefuges (Carleton and Sammarco, 1987; Maldonado and Uriz, 1998) have also been shown to induce settlement in sponge larvae.

The settlements recorded on the loofa with the extract of *J. adherens* (Fig. 3B), were significantly fewer than on the fronds of the alga, which suggest that the larvae of *H. caerulea* do not use a chemoreception mechanism to locate their host. The selection of the fronds of *J. adherens* is probably based on the search for a shady microrefuge, which may increase the survival post-settlement (Buss, 1979). This is supported by the fact that the larvae of *H. caerulea* show negative phototaxis during their free-swimming period (Maldonado and Young, 1996), and in general, larvae that possess negative phototaxis settle mostly in places that offer microrefuges with low illumination, which has been documented for the larvae of the sponges *Crambe crambe* and *Scopalina lophyropoda* (Maldonado and Uriz, 1998).

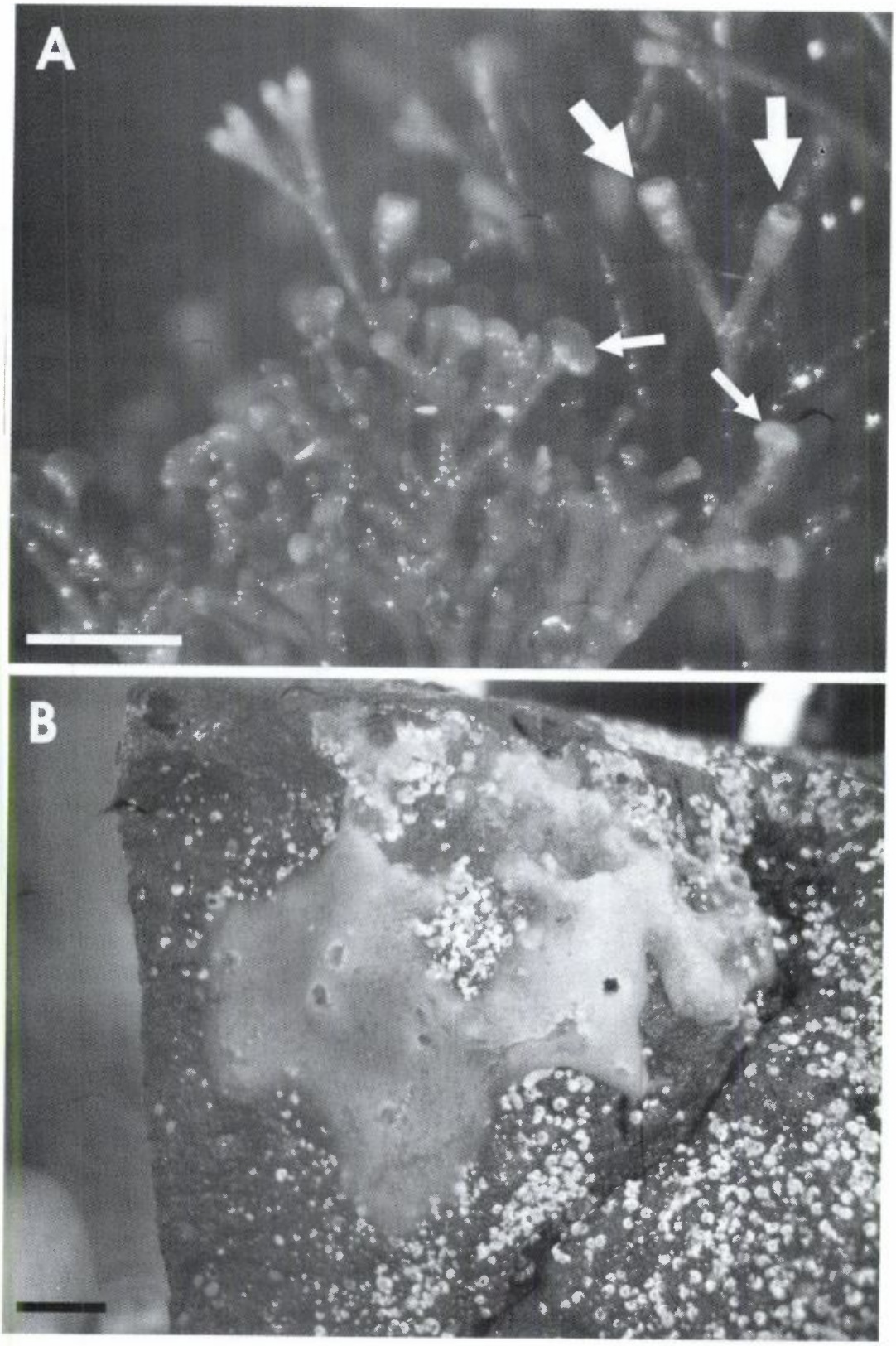


Figure 4. A) *J. adherens* from the intertidal zone. Thick arrows show the axial conceptacles for the sexual reproduction, and thin arrows show the fixation discs used for asexual propagation. Scale bar = 1 mm. B) Specimen of *H. caerulea* living in isolation under a boulder from the intertidal zone, scale bar = 1 cm.

It is important to note that although the loofa could offer a multitude of similar microrefuges to *J. adherens*, it was not selected as a settlement surface by the larvae. Possible reasons to explain these differences could be due to the different nature of the two substrates (calcareous vs. vegetal), and different level of shading since loofa fibers are not as opaque as the branches of *J. adherens*. Another possible reason that might explain the differences in the larval settlement between loofa and *J. adherens* could be their different branch diameter (loofa = 267±26.7 μm vs. *Jania* = 208±21.9 μm), since it has been demonstrated that the larval settlement of some bivalves is bigger on filamentous substrates with a smaller branch diameter and heterogeneity (Harvey et al., 1995).

It is also important to note that the settlements on *J. adherens* were faster when the current was higher. Similar results were obtained with larvae of polychaetes that live in habitats subjected to waves as adults (as are *H. caerulea*) (Butman, 1987).

The faster settlement with high-speed current could be explained by passive settlement because the circular movement in the dishes would concentrate larvae in the central part where they would be trapped by the structure of *J. adherens*. However, there are two strong arguments against this supposition: 1) The substrates were placed in the periphery of the crystallizing dish, thus the centrifugal force would be not the cause of the faster settlement on *J. adherens*. 2) If this were the main reason, they would be equally trapped into the loofa tangle when turbulence increased. Thus, the results suggest that the reduction of free-swimming time in high flow conditions is an active response of the larvae of *H. caerulea* against the increase of the water's movement. The same behavior has been documented for the larvae of the parasitic barnacle *Heterosaccus dollfusi* and the polychaete *Capitella* sp. (Pasternak et al., 2004; Butman and Grassle, 1992). In previous studies it has been documented that the positive correlation between settlement success and main flow velocity might also result from the enhanced contact rate of larvae with the substratum in fast flow (Mullineaux and Butman, 1991; Mullineaux and Garland, 1993).

In contrast with the laboratory experiments, we did not find any settlements of larvae of *H. caerulea* on any of the experimental substrates in the field, despite other sponges settling on them. The lack of recruitment on the experimental substrates during the time of larval production suggests that the larvae are unable to survive on a substrate other than *J. adherens*. This is also supported by the fact that other coralline algae such as *Amphiroa* sp., or red algae such as *Gelidiopsis* sp. live in the same range of the association, but *Haliclona caerulea* associated with these species very sporadically (Carballo and Ávila, 2004).

Field experiments are also important to support our previous hypothesis that the population of this association in the Bay of Mazatlán uses fragmentation as the main form of recruitment (Ávila and Carballo, 2004), and for understanding the population dynamics of this sponge/alga association because they need to be reconstituted after sexual reproduction. It is possible that the larvae settled on *J. adherens* from the intertidal zone. This hypothesis could be supported by the fact that juveniles of the association have been sporadically found in small intertidal pools (unpublished data) (Fig. 4B). This alga has the capacity to suffer fragmentation (Woelkerling, 1996) (Fig. 4A), and some of the fragments could have young juveniles of the sponge, which could drift to the area where the association lives.

In summary, this study had the aim of demonstrating that the symbiosis with the calcareous alga *J. adherens* is the result of larval habitat selection. Although selective settlement in a suitable habitat may be advantageous for the survival of the species, the current evidence for its importance is in many cases indirect (Carballo, 2000). The laboratory experiments showed that the larva has a high specificity for its partner in the association, which could offer it a better substrate for its survival in this highly hydrodynamic environment, where the sponge is not able to live in isolation (Ávila and Carballo, 2004; Carballo and Ávila, 2004).

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