Population dynamics of a mutualistic interaction between the sponge *Haliclona caerulea* and the red alga *Jania adherens*

José Luis Carballo*, Enrique Ávila

Laboratorio de Ecología del Bentos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apartado Postal 811, Mazatlán 82000, Mexico

ABSTRACT: A population of the association between the haplosclerid sponge *Haliclona caerulea* and the red algae *Jania adherens* was studied in the Bay of Mazatlán (east tropical Pacific Ocean, Mexico), along a spatial gradient (from 1 to 5 m depth) and over time (from February 2001 to September 2003). No clear seasonality was found in the abundance (from 0.5 to 17 ind. 25 m^{-2}), volume (from 741 to 7241 cm^3 25 m^{-2}), recruitment (up to 9 new ind. 25 m^2 mo^{-1}) and mortality (50% loss mo^{-1} average). The population was capable of recovering after 50% of the specimens were lost; abundance and volume recovered after 7 and 17 mo, respectively. Recruitment was determined in part by asexual propagation through fragmentation, and the relationship with abundance suggested that the population was self-sustaining. Seasonality was only evident in the sexual reproduction of the sponge, which occurred when water temperature increased: from May to September in 2001, from March to July in 2002, and from April to October in 2003. An important feature was that axial conceptacles of *J. adherens* living in association with the sponge were never found. The association was permanent over time and the interaction affected the abundance, survival and distribution of the 2 partners in the association. *J. adherens* was found growing independently in the intertidal zone, which is out of the range of distribution for the association, but we did not find any evidence of sponge living in isolation, although in association it is one of the dominant members of the shallow rocky ecosystem in the Bay of Mazatlán. The association was very highly specific; other coralline algae such as *Amphiroa* spp. were found in the same habitat, but *H. caerulea* only associated with *Amphiroa* spp. in less than 3% of the samples studied. The advantages for *J. adherens* can be deduced from the fact that it spreads and persists below 1 m thanks to its association with the sponge. The sponge benefits from the fact that it can persist and colonize shallower zones by living in association with the alga. Thus, we conclude that this association is mutualistic.

KEY WORDS: *Haliclona caerulea* · Sponge · *Jania adherens* · Coralline algae · Associations · Mutualism · Abundance · Recruitment · Mortality · Reproduction · Depth · Distribution

INTRODUCTION

Sponges are organisms with a high morphological plasticity. Among their abilities is the capacity to establish a multitude of associations with a large variety of organisms. Some of these associations include prokaryote organisms such as cyanobacteria (Wilkinson 1978), bacteria (Reiswig 1981), ammonium-oxidizing bacteria (Díaz 1997) and archaebacteria (Preston et al. 1997); eukaryotes such as zooxanthellae (Rosell & Uriz 1992); as well as zoochlorellae (Gilbert & Allen 1973, Saller 1989), cryptophytes (Duclaux 1973), diatoms (Cox & Larkum 1983), scyphozoans (Uriz et al. 1992, Meroz & Ilan 1995a), zoanthids (West 1976, Hill 1998), corals (Wulff & Buss 1979), scallops (Forester 1979, Pond 1992), ophiuroids (Hendler 1984, Turón et al. 2000), other sponges (Wulff 1997a, Wilcox et al. 2002), mangroves (Ellison & Farnsworth 1992) and macroalgae (Rützler 1990).

Some of these associations seem to be mutually beneficial, but the benefits for the organisms that take part

in the association are not clear in the majority of cases. Mutualism between scyphozoans and horny sponges (Uriz et al. 1992), between sponges of different species (Wulff 1997a, Wilcox et al. 2002), and between sponges and photosynthetic symbionts has been suggested (Arillo et al. 1993). The benefits of photosynthetic symbionts for the sponge include involvement in the nutritional process, either by intracellular digestion or by translocation of metabolites in the form of glycerol and other small organic phosphates (Wilkinson & Garrone 1980, Arillo et al. 1993). Data have been published on the transfer of dissolved inorganic nitrogen from sponges to mangrove roots, and carbon from mangrove roots to sponges (Ellison & Farnsworth 1992). The participation of some microorganisms in the host's chemical defense system against predators and biofouling has also been documented (Bakus et al. 1986, Paul 1992). Recently, a symbiosis between a massive and an epibiont encrusting sponge has provided clues suggesting that the epibiont benefits from a stable attachment site for larval settlement. In return, the massive sponge obtains a chemical defense system against predators (Wilcox et al. 2002).

Most of the previous work was aimed at understanding the putative benefits for the organisms involved in the relationship. However, the evolution and ecological stability of these relationships as well as the spatial and temporal scales over which the ecological relationships varied were largely unexplored (Palumbi 1985, Wilcox et al. 2002). Only a few papers dealing with this matter have been published so far (Palumbi 1985, Trautman et al. 2000, 2003, Ávila & Carballo 2004), most of them concerning relationships between sponges and macroalgae.

Associations between sponges and macroalgae have been described in the literature since the last century (Weber Van Bosse 1890, Scott et al. 1984, Palumbi 1985). One of the most common associations is the one constituted by the haplosclerid sponge *Haliclona cymiformis* (Esper) (formerly *Sigmadocia symbiotica* Berquist & Tizard) and the red macroalga *Ceratodictyon spongiosum* Zanardini, which appears on shallow coral reefs of the Indo-West Pacific (Vacelet 1981, Price et al. 1984). This association seems to be an obligatory relationship, as neither sponge nor alga has ever been identified growing independently or in association with other species in the study area (Trautman et al. 2000). Recent findings have revealed that the sponge-alga symbioses may not only be autotrophic but may also benefit from the transfer of nitrogen between the symbiotic partners. The nitrogen required for algae growth can be provided by sponge catabolism and alternatively, the compounds translocated to the sponge may be important (Davy et al. 2002). More recently, the role of habitat in determining the distrib-

ution of this association was also addressed (Trautman et al. 2003).

Haliclona caerulea (described as *Sigmadocia caerulea*) is common throughout the Caribbean and the Pacific coast of Panama (Wulff 1997b), where it has sometimes been reported to grow in association with articulated coralline algae (Zea 1987, Rützler 1990). Recently, a very important population of *H. caerulea* growing in association with *Jania adherens* (an articulated coralline alga) was found in the Bay of Mazatlán, at the entrance of the Sea of Cortez (Ávila 2002). The use of the calcified thallus of Rhodophyta algae as a substitute for skeletal fibers in sponges has been previously documented in the species *Dysidea janiae* and *Strongylacidon osburnensis*, which substitute or reinforce their own skeleton by living in association with calcified Rhodophyta algae of the genus *Jania* (de Laubenfels 1950, Sará & Vacelet 1973).

An intensive survey was carried out in more than 100 localities (2000 km apart) along the coast of the Sea of Cortez during the last 5 yr. The main objective of this research was to study the sponge fauna of the Mexican Pacific coast, one of the least studied zones in the Pacific Ocean and in the world for sponges. The preliminary results (Gómez et al. 2002, Carballo et al. 2003, 2004, J. L. Carballo pers. comm.) showed that the *Haliclona caerulea–Jania adherens* association only appears in the Bay of Mazatlán, where it is locally abundant in shallow rocky ecosystems. The association consists of a massive and compact form of up to 40 cm in diameter and 13 cm in height, where the sponge completely fills the spaces between the algal branches (Fig. 1). The sponge generally covers the alga, and the algal branches very rarely protrude beyond the association surface. The alga is also common living in isolation in the intertidal zone, but the sponge growing
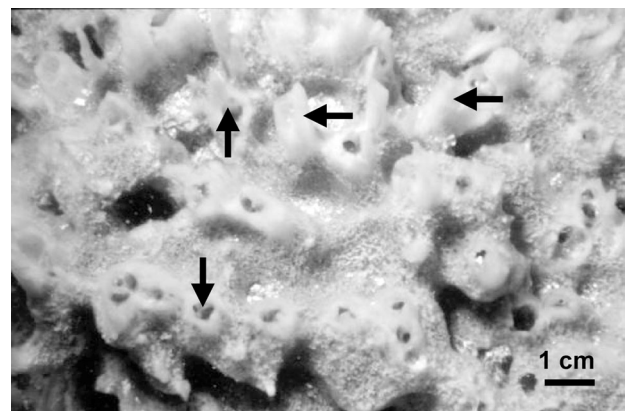

Fig. 1. *Haliclona caerulea* in association with *Jania adherens* photographed at a depth of 3 m (top view). Arrows indicate the oscules and small erect processes of the sponge rising from the surface of the association. Scale bar = 1 cm

independently from the alga has only been found spo-radically in rocky ecosystems below 7 to 8 m.

This study is part of more extensive research work on the association of *Haliclona caerulea* and *Jania ad-herens*, which seeks to answer 2 main questions: (1) What are the benefits for the 2 partners of living in association? and (2) Why is the association so abundant in the Bay of Mazatlán? The main objectives of this first study were to analyze the dynamics of the association with respect to time and depth, to determine the timing of sexual reproduction and recruitment, and to deter-mine the role of habitat in the distribution of this asso-ciation. Once these objectives are obtained, it will be possible to determine if the association is persistent across a temporal and spatial scale, as well as to gather clues about the nature of the relationship.

MATERIALS AND METHODS

Study area and meteorological conditions. A prelim-inary survey along the Bay of Mazatlán determined that the association was distributed in shallow rocky substrates at approximately 2 to 5 m in depth. We did not find any zone where the 3 components existed simultaneously: alga living alone, alga in association with the sponge, and sponge living without alga. The alga only lives alone in the intertidal zone and some specimens of the sponge were occasionally found growing in isolation in rocky ecosystems below 7 to 8 m depth. However, no studies on sponges lacking the association could be performed because no populations of *Haliclona caerula* alone existed anywhere. Once we studied the distribution of the sponge–alga association,

a representative area in Venados Island in the centre of the Bay of Mazatlán was selected (Mexico, eastern Pacific Ocean) (see Fig. 2). The area was selected because at least 2 of the components were found along the same depth gradient (alga and alga living in associ-ation with the sponge). The shallower zone (1 to 2 m) is mainly composed of large and medium-size boulders on a rocky bottom; between 2 and 5 m, the bottom con-sists of a gently sloping mosaic of relatively flat boul-ders between patches of sediment, which increase until the rocks disappear almost completely at 7 to 8 m.

The climate is tropical/sub-tropical, with 2 contrast-ing seasons in the year. The average annual air tem-perature is 25°C and the average annual rainfall is 800 mm, occurring mainly during the rainy season from June to October (data provided by the National Water Commission 2002) (see Fig. 3).

Water temperature. Water temperature was mea-sured monthly with a maximum/minimum thermome-ter permanently placed at a depth of 4 m on the seafloor in the area of study.

Sampling methodology, abundance and recruitment of the association. Two permanent parallel rows of sta-tions were set 20 m apart at depths of 2, 3, 4, and 5 m off the coast of Venados Island (Fig. 2). The original design also included a sampling station at a depth of 1 m. How-ever, the absence of the association and difficulties in sampling, due mainly to wave action, forced us to leave this station. Each station (5 m wide × 5 m long) was sur-rounded by plastic lines and conveniently labeled to ensure its location in subsequent samplings.

The abundance was determined monthly by SCUBA dives from February 2001 to June 2003, counting all specimens found within each of the 8 permanent sta-tions (non-destructive sample). The total area sampled monthly was 200 m^2 (8 sampling sta-tions of 25 m^2) and the abundance was repre-sented as numbers 25 m^{-2}.

The size of the sponge–alga complex was determined by the following *in situ* proce-dure: the height and the perimeter from the base, from the middle, and from the upper part of 4 specimens per sampling station were determined bimonthly from February 2001 to June 2002. The size in cm^3 was calculated by estimating the shape as a cylinder (Fig. 4). The mean size per sampling station was used to calculate the volume as cm^3 25 m^{-2}.

Underwater measurements for volume were evaluated by comparing data to correspond-ing measurements determined by fluid dis-placement (Rützler 1978). For this, 40 speci-mens of the association were collected in the study site outside the sampling stations and were moved to the laboratory, where the vol-
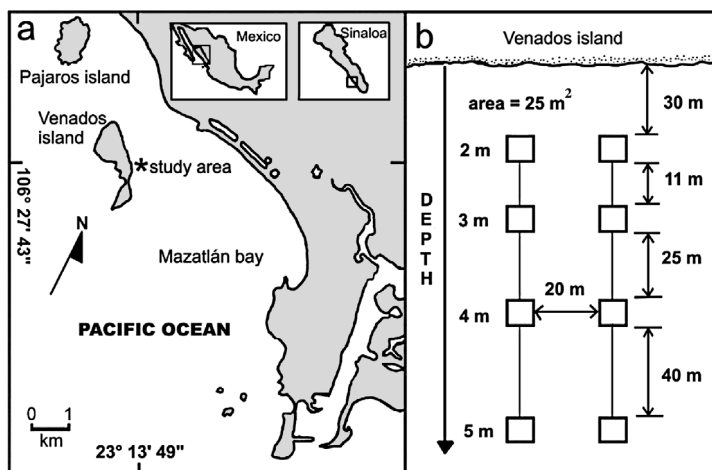

Fig. 2. (a) Location of study area in the Bay of Mazatlán. (b) Sampling stations in front of Venados Island (23° 13′ 49′′ N, 106° 27′ 43′′ W). Depth and distance from the shore line indicated at the side of each sampling station
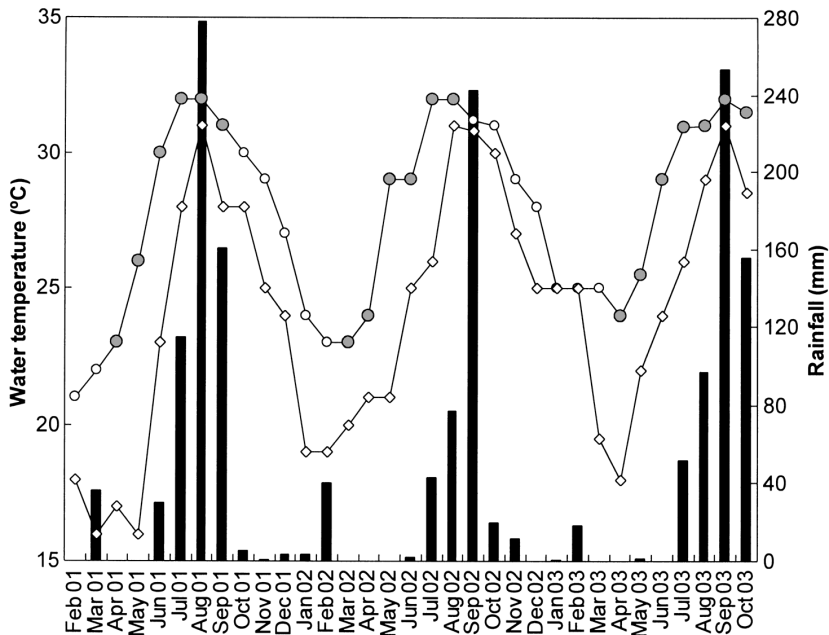
Fig. 3. Mean monthly maximum (o,●) and minimum (◇) water temperature (—, left axis) and precipitation (■, right axis) from February 2001 to October 2003. Periods of sexual reproduction in *Haliclona caerulea* indicated by bigger shaded circles (●) in the maximum water temperature series

ume was determined by the previously described procedure (cm³) and by fluid displacement (ml). The line on the graph was fitted by linear regression analysis (Fig. 5). The regression was highly significant and it indicated a parallel trend of increasing volumes using both methods. However, the results showed that the volume measured by the fluid displacement method was lower than the *in situ* measurements because fluid displacement does not consider the internal volume of the association, while the *in situ* measurements do. However, the latter procedure provides reproducible measurements easy to measure *in situ* and gives a basis for comparisons, since variations in size would affect these measurements simultaneously.

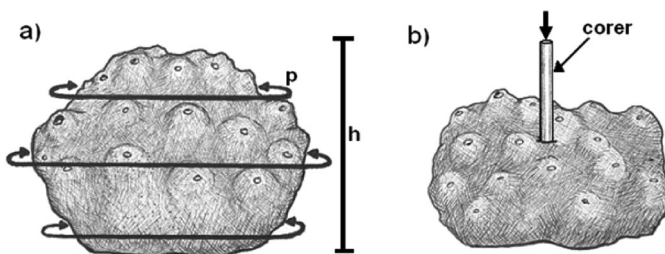**Mortality and recruitment.** The recruitment of the

Fig. 4. (a) Different measurements taken *in situ* to estimate the size of the association (p = perimeter of the association at different levels, h = height of the association). (b) Corer steel used to obtain a representative sample of the association

sponge–alga complex was monitored over 16 mo (from February 2001 to April 2002) to ascertain its relation to abundance and timing of sexual reproduction. Each individual inside the sampling stations was labeled with numbered plastic tags set into the rock bottom beside it in February 2001 and in the following months all the new recruitments were also labeled and counted (Ayling 1980, Meroz & Ilan 1995b). Recruitment was considered as the appearance of new individuals adhered to the substrate in each permanent sampling station. The results were expressed as recruitment 25 m⁻² ($25\ m^{-2}$).

The mortality was recorded monthly as the difference between the number of initial and final labeled specimens (Meroz & Ilan 1995b). We considered specimens as lost if we found the mark attached but the specimens missing. However, this method would over-report mortality because specimens could occasionally detach from the substrate and reattach outside the study area.

Timing of sexual reproduction. To determine reproductive seasonality, 10 individuals of the sponge–alga complex were collected monthly outside the permanent sampling stations from February 2001 to September 2003. They were cut into small pieces with a razor blade in the laboratory and the fleshy cut surface was examined under a stereoscopic microscope for the presence of embryos or larvae in the sponge, both of which are large enough (at maturity) to be seen under low magnification (10×). The numbers of reproductive elements were then related to the sponge–alga complex volume (Ayling 1980). The volume of the sponge-alga complex was previously measured in the laboratory by volumetric displacement. This sampling method allows for the quantification of the proportion of the population involved in reproduction as the number of embryos or larvae per sponge–alga complex volume.

Abundance and reproduction of the macroalgae living in association with the sponge. The frequency of the appearance of the different algae living in association with the sponge (*Jania adherens*, *Gelidiopsis* spp. and *Amphiroa* spp.) was examined in almost 2000 small samples collected bimonthly from February 2001 to April 2002 (Ávila 2002, Ávila & Carballo 2004 in press). To determine whether the distribution and abundance of some of these algae living in isolation were correlated to the abundance and distribution of the association, a grid of 25 × 25 cm with meshes of 1 cm² was randomly placed 4 times on the bottom of each sampling
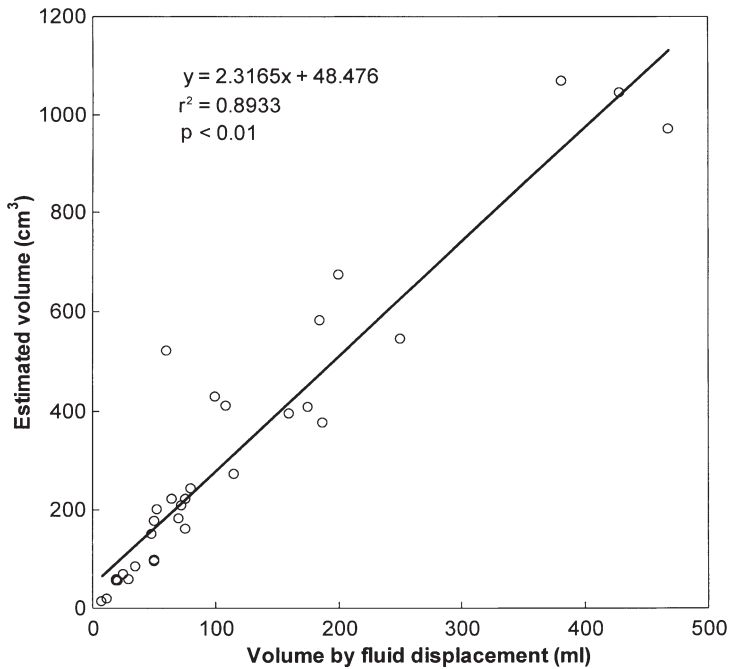
Fig. 5. Relationship between volume estimated (cm³) by the procedure in Fig. 4 and by fluid displacement (ml). Regression lines, significant level and their equation are shown in the plot

Fig. 6. Monthly abundances (ind. 25 m⁻²) of the association by depth. The mean abundances (···○···) and mean volume (⊠) are also represented. Note that only the period from February 2001 to June 2002 has been represented for the volume (see 'Materials and methods'). Vertical lines indicate standard error

station. It was very difficult to sample at a depth of 1 m and only visual observations could be made. The abundance of the alga growing alone was estimated as the percentage of the grid occupied by the alga.

The presence of axial conceptacles of the main algae associated with the sponge was used to determine the timing of sexual reproduction.

Data analysis. To test the hypothesis that the abundance of the association varies with depth and time, a 2-way model ANOVA was performed (time × depth were random factors), followed by a Newman-Keuls multiple range test (Underwood 1997). After verifying normality (Kolmogorov-Smirnov test) and variance homogeneity (Barlett test), there were no significant departures from homogeneity.

RESULTS

Water temperature

Water temperature differed greatly over time and a seasonal pattern was evident, with high temperature values in summer and low temperature values in winter (Fig. 3). The temperature varied from 16°C (March) to 32°C (August) in 2001, from 19°C (January) to 32°C (July/August) in 2002 and from 18°C (April) to 32°C (September) in 2003. The most important feature was the wide range between maximum and minimum temperatures detected in May 2001 (10°C), May 2002 (8°C) and April 2003 (6°C). In contrast, the range of these fluctuations generally decreased in summer/autumn. The increase in the water temperature preceded the rainy season each year, which generally lasted from June to October.
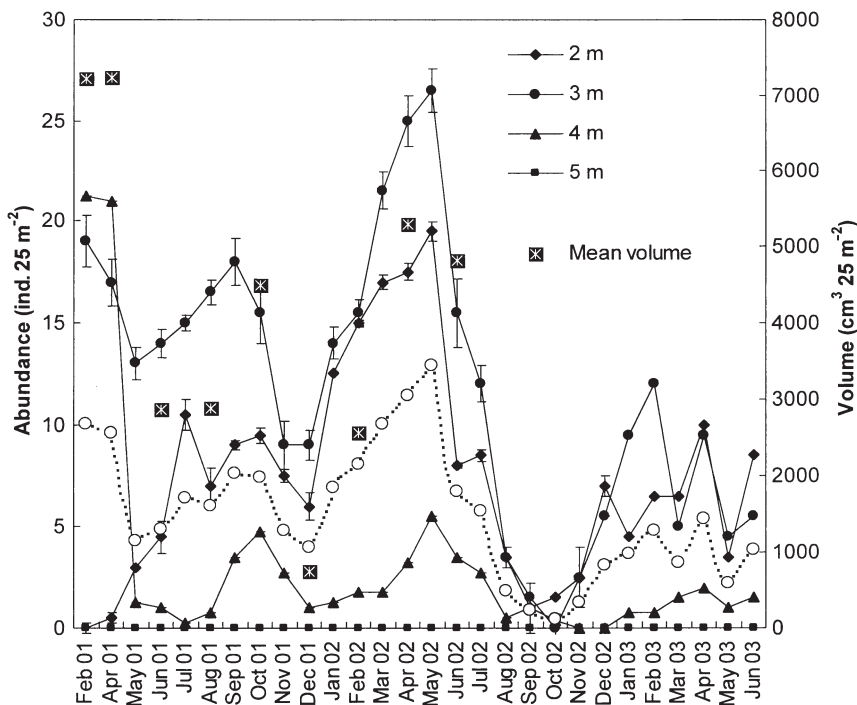
Variation of the abundance of the association

The mean abundance changed significantly over time (F = 93.2, p < 0.0001), peaking at a similar time each year: 9.6 to 10 ind. 25 m⁻² (February–April 2001), 11.4 to 12.8 ind. 25 m⁻² (April–May 2002) and 4.8 to 5.3 ind. 25 m⁻² (February to April 2003). Two important features were an ample range of variation over time (from 0.5 to 26.5 ind. 25 m⁻²) and frequent short-term fluctuations. Moreover, a high spatial heterogeneity was found over time (F = 9.6, p < 0.0001) (Fig. 6). At the
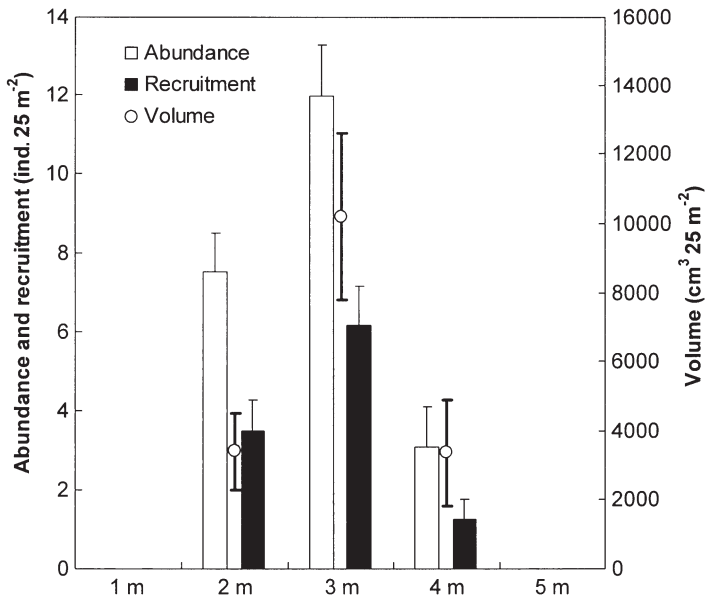
Fig. 7. Mean abundance (□), recruitment (■, both left axis) and volume (○, right axis) of the association by depth

beginning of the study (from February to April 2001), the maximum abundance was registered at 4 m, but later the association disappeared from this depth, decreasing from 21 to 1 ind. 25 m^{-2}. After April 2001, there was a very clear shift of the distribution to more shallow waters. In contrast, the population at 2 m started to increase from 0 ind. 25 m^{-2} (February 2001) to 20 ind. 25 m^{-2} (May 2002).

The volume fluctuated in a similar manner as the abundance over most of the study, ranging from 741 to 7241 cm^3 25 m^{-2}, with lowest values in December (2001 and 2002) and highest values from February to April (2001 and 2002), when the highest abundances were also registered.

It is important to note 2 declines in population that occurred after the peaks in May 2001 and June 2002 (Fig. 6). Abundance recovered 7 mo after the May declines, but the volume was not completely recovered after 17 mo.

A clear pattern was found relative to depth. The abundance typically had a unimodal response, ranging between a depth of 2 and 4 m with a peak at 3 m (Fig. 7). The volume followed the same distribution as abundance, with a peak at a depth of 3 m (605 cm^3 25 m^{-2}). At 2 and 4 m, the values were very similar: 400 and 315 cm^3 25 m^{-2}, respectively (Fig. 7). The abundance/volume relationship showed that the population at 2 m was composed of smaller specimens than those found at 4 m.

The most important feature was that the association was persistent during the whole period of

study and sponge or alga growing alone were never found.

Sexual reproduction in *Haliclona caerulea*

The species presented one sexual reproduction period per year, which occurred in the warm months of spring and summer, or from spring to autumn (Fig. 3). This period lasted from May to September in 2001, from March to July in 2002 and from April to October in 2003 (Fig. 8). The maximum number of reproductive elements (embryos and larvae) was detected in May 2001, March 2002 and June 2003, with 3, 6 and 7 elements ml^{-1}, respectively, and they increased progressively with the size of the association, up to 200–300 ml, when the maximum density of elements appeared (Fig. 9). Similar results have been reported for the sponge *Halichondria* spp. (Lewandrowski & Fell 1981). However, a high dispersion was observed in the relationship between size and number of reproductive elements in the association. This could be because the association is not only composed of sponge and it seems evident that different proportions of sponge in the association could explain these results. The proportion of the population in sexual reproduction also varied over time, but the maximum always occurred in June/July (100% of the population).
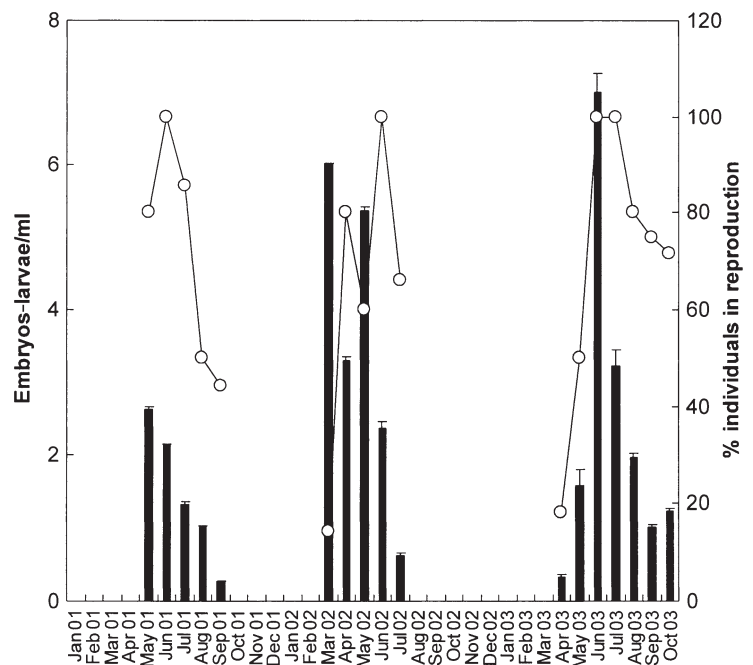

Fig. 8. *Haliclona caerulea*. Variation of the numbers of reproductive elements over time (■, left axis) and percentage of individuals in reproduction (—○—, right axis). Vertical lines indicate standard error
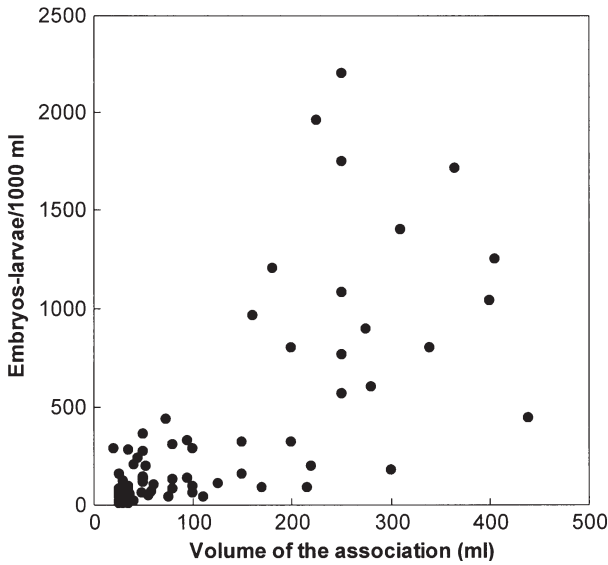
Fig. 9. Relationship between the numbers of reproductive elements and volume of the association

Recruitment and mortality

Recruitment was continuous with the exception of November 2001, when new individuals were not found (Figs. 10 & 11). Maximum recruitment was detected from June to July in 2001 (9 ind. 25 m^{-2}) and from February to March in 2002 (8 ind. 25 m^{-2}), but there was no clear seasonal pattern. It was not determined how much recruitment resulted from larvae vs. fragmenta-
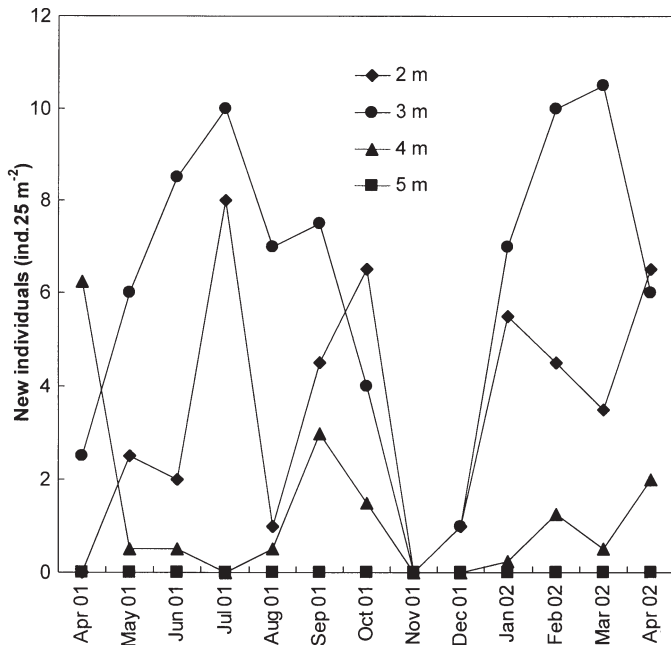

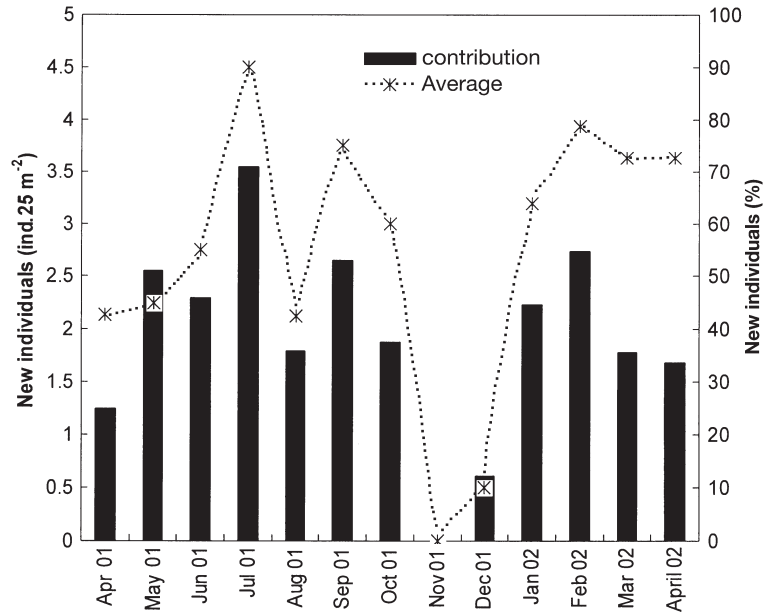Fig. 10. Monthly number of new individuals of the association over time by depth

Fig. 11. Mean monthly number of new individuals of the association (···✳···, left axis) and percentage of new individuals of the association (contribution) in relation to the total population (■, right axis)

tion; however, the new individuals always measured more than 86 cm^3 in size (Ávila & Carballo 2004), suggesting that they probably originated from fragmentation. In fact, the appearance of new individuals outside of the sexual period showed that fragmentation was important in the life history of the association. The percentage of new individuals in the total population was very high in July 2001 and February 2002, when the population was composed of 71 and 55% of new individuals, respectively (Fig. 11).

Recruitment also showed a high spatial heterogeneity (Fig. 10), but as with abundance, a similar pattern relative to depth was found, with maximum recruitment at 3 m (6 ind. 25 m^{-2}) (Fig. 7).

Mortality was high and constant, but without a clear temporal pattern (Fig. 12). The rate of loss was close to 50% after 1 mo, between 50 to 75% after 2 mo and more than 75% after 3 mo. Less than 3% of the initially labeled specimens survived until the end of the experiment in April 2002. Most notable was the very high mortality detected in May, when 75% of all the specimens labeled in April (95) were lost.

Distribution, abundance and reproduction of algae living in isolation

The prime algae associated with *Haliclona caerulea* were *Jania adherens* (≈90% of the specimens studied), *Gelidiopsis* spp. (≈7%), and *Amphiroa* spp. (≈3%). The
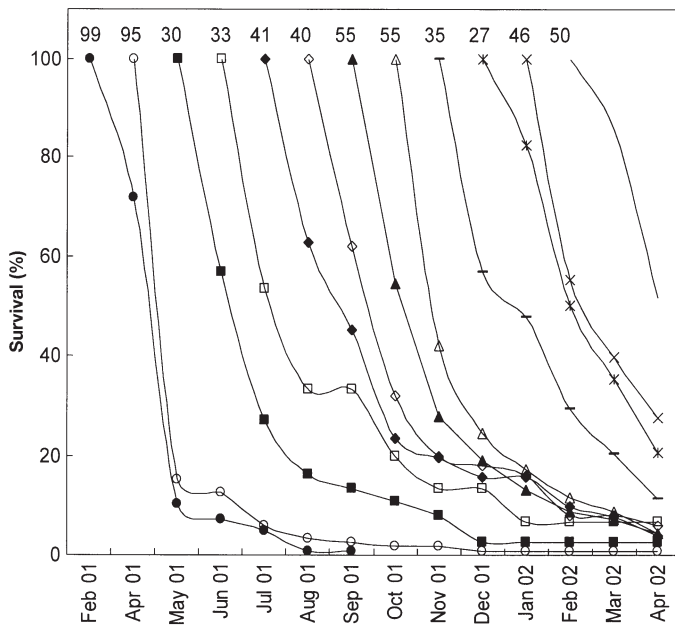
Fig. 12. Percentages of labeled specimens of the *Haliclona caerulea*–*Jania adherens* association surviving over time. Each series shows the mean variation of the survival percentage of the initially labeled specimens over time. The initial numbers of labeled specimens in each sampling are indicated at the top of the graph and the numbers in the subsequent samplings are represented by the different symbols. The initial number is different because all the specimens were labeled in the sampling area during each sampling

Fig. 13. Mean abundance of the association (—●—, left axis) and of *Amphiroa* spp. (■, ▨, right axis) by depth. The absence of the association and the presence of *Jania adherens* and *Amphiroa* spp. at a depth of 1 m were registered by visual observation (see 'Materials and methods'). The height of both bars is only representative in order to show their presence at this depth. Vertical lines indicate standard error

most important feature was the absence of *J. adherens* from the area of distribution of the association. The distribution of *J. adherens* was always in the shallowest water and in the intertidal zone, where no individuals of the association were found. Another important feature was the lack of axial conceptacles in all of the algae samples. These observations were always made for *J. adherens* living in association. The only alga that was distributed along the same depth range as the association was *Amphiroa* spp., which had maximum abundance at a depth of 1 to 2 m. The low contribution of this genus to the association leads us to conclude that its presence in the association (like *Gelidiopsis*) was accidental (Fig. 13) and that the relationship between *J. adherens* and *H. caerulea* is highly specific.

DISCUSSION

Spatio-temporal variation and life history of the association

Seasonality has been described in different sponge populations, where the highest abundances, biomass, growth, etc., are generally detected at the time of high-
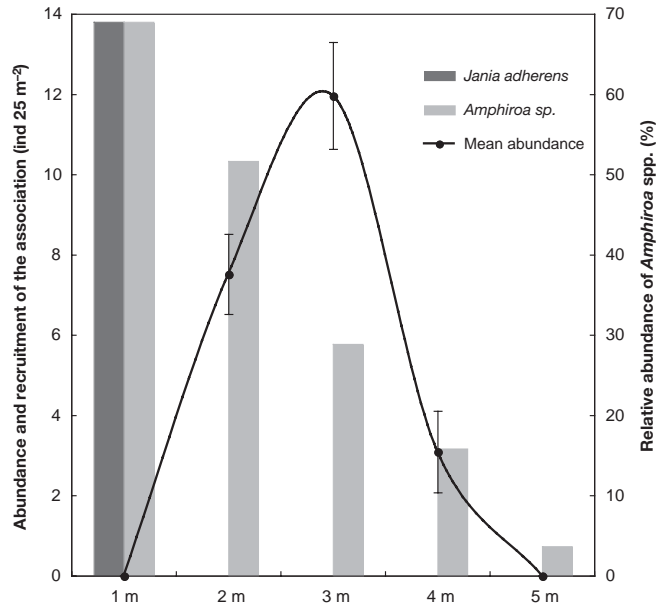
est water temperature (Rader & Winget 1985, Barthel 1991, Meroz & Ilan 1995b, Turon et al. 1998). However, although the abundance of the association changed significantly over time, with a peak in late winter or early spring each year, there were also significant short-term fluctuations and no clear seasonal tendency was found.

Unlike temporal variation, a clear pattern was found in relation to depth. The abundance, volume and recruitment followed a unimodal distribution with a peak at a depth of 3 m (Fig. 7). When gradients are studied long enough, species typically have unimodal (1 peak) responses to gradient. What environmental factors could explain this distribution? The absence of the association in the shallowest water (1 m depth) could be attributed to high energy by wave stress, which is known to affect morphology and survival of invertebrates such as sponges (Meroz & Ilan 1995b, Carballo et al. 1996, Bell & Barnes 2000a,b). On the other hand, the lack of a rocky substrate below 5 to 6 m could also explain the differences observed, as has been reported for other sponges (Meroz & Ilan 1995b). The *Haliclona cymiformis*–*Ceratodictyon spongiosum* association is distributed at a similar depth (between 1 and 4 m), with maximum biomass at a depth of 3 m and recent studies suggest that this association is absent from determined habitats because of the lack of solid substrata for attachment (Trautman et al. 2000, 2003).

The sexual reproduction of *Haliclona caerulea* occurred seasonally during a few months each year, as has been previously reported (Maldonado & Young 1999). The sponge incubates embryos and releases lecithotrophic free-swimming parenchymella larvae during the summer/autumn, and the water temperature appears to have an important role in the reproductive behavior of the sponge. We never found axial conceptacles in the alga living in association. In contrast, sexual reproduction is rare in the sponge *H. cymiformis*, but the sporangia were found in the alga *Ceratodictyon spongiosum* (Trautman et al. 2000). We do not know if the same situation exists in the alga living in isolation, but the lack of reproduction in *Jania adherens* is very interesting with respect to the fact that the association needs to be reconstituted after sexual reproduction. This leads to further interesting questions such as: (1) At which stage of the sponge cycle is the association established? (2) Do larvae recruit on the alga and then overgrow it? or (3) Do algal fragments recruit on the sponge? These are important questions for understanding the population dynamics of the association and will be addressed in subsequent studies.

Recruitment was correlated to abundance and the study showed that the population remains in the zone due to the continuous settlement of recruits (in some months recruits were between 50 and 70% of the total population). The origin of these new recruits is not clear; recruitment occurred during larval production but it also occurred outside the period of sexual reproduction (Fig. 14), which suggests that the role of fragmentation is to maintain the association. In fact, fragmentation could exist throughout the entire period of monitoring and even though we could not separate it from those specimens produced by sexual reproduction, the size of the recruits suggest they were generated mainly by fragmentation. These results agree well with Trautman et al. (2000), who showed that fragmentation was the most important form of reproduction in the association of *Haliclona cymiformis* and the red macroalgae *Ceratodictyon spongiosum*. This was confirmed by fusion experiments between individuals collected from different sites, which showed that all the existing populations of *H. cymiformis–C. spongiosum* may have originated, via fragmentation, from the same parent population (Trautman et al. 2003). This does not seem to be an exception in sponge populations. Several papers describe fragmentation as the main form of reproduction. For example, in the sponge *Hymeniacidon perleve*, sexually derived recruitment was not observed in a 3 yr study (Stone 1970). The causes that may produce fragmentation of individuals in the association are not clear, but the influence of storms, as occasionally occurred in the Bay of Mazatlán, has been considered an important factor (Christopher & Bergquist 1990). The mortality for the encrusting sponge *Crambe crambe* after 24 mo was about 31 to 62% (Turon etal. 1998) and the rate of mortality for *Mycale* spp. in Jamaica was 34% yr^{-1}, and was largely attributable to winter storms (Reiswig 1973). However, the continuous recruitment suggests that fragmentation also occurred due to other factors such as water movement from wave action. Perhaps the population in the shallowest zone was the main source of recruitment that finally settled at 3 or 4 m.

The labeled specimens confirmed a short life expectancy for the association and the almost constant loss of specimens over time could really reflect a high rate of turnover due to fragmentation. The monthly rate of loss was between 25 to 50% and less than 3% of the sponges labeled stayed in the place of origin after 1 yr. However, viable pieces of the association were found during dives (Ávila 2002); thus, the results could also reflect an internal migration by detachment and subsequent reattachment of fragments (or even complete individuals) in a different place within the same population. It is also important to mention the ability of the population to recover after impor-
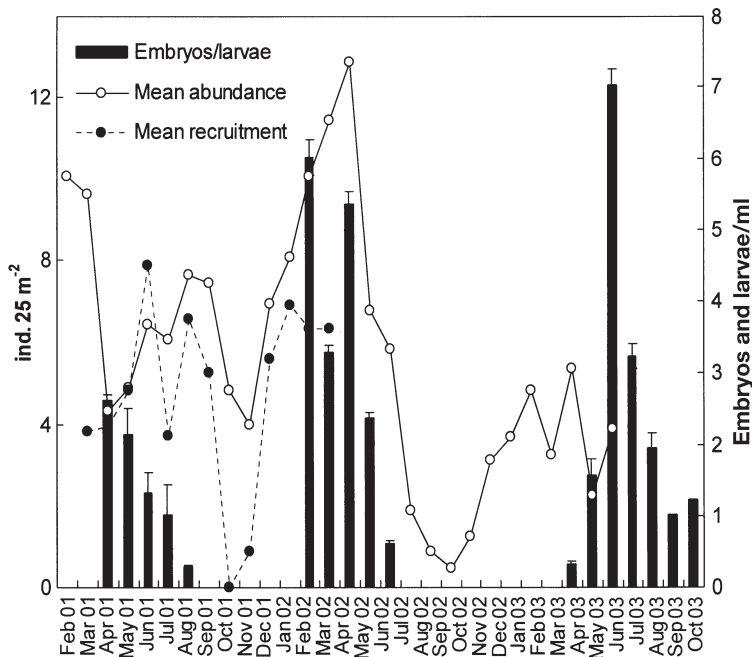

Fig. 14. *Haliclona caerulea*. Relationship between the variation in the mean abundance and recruitment of the association (—○—, – –●– –, left axis), and number of reproductive elements over time (■, right axis). Vertical lines indicate standard error

tant declines, when more than 50% of the population disappeared. The recovery of the numbers of individuals occurred after approximately 7 mo, but the recovery of the volume (cm^3 m^{-2}) only after 17 mo. Wulff (1995) showed that the loss of about 25% of the biomass of free-living sponges during a hurricane took at least 2 yr to recover. This ability to recover so slowly contrasts with that of the *Haliclona cymiformis–Ceratodictyon spongiosum* association, which recovered approximately 7 mo after more than 50% of the standing stock was lost during 2 severe storms (Trautman et al. 2000).

Finding the cause of this ecological interaction

Most symbioses between plants and animals are considered to be mutualistic associations (Trench 1979). It is not completely known whether the sponge and alga derive mutual metabolic benefit from living in this particular partnership; however, given the distribution and abundance of this association, it is clear that the interaction is stable, very specific and most likely positive in nature. We did not find evidence of sponges living in isolation, although in association it is one of the dominant members of the shallow rocky ecosystem in the Bay of Mazatlán. Positive interactions among sessile organisms, such as we have shown here, seem to be common predictable forces in harsh environments or under marginal ecological conditions (Bertness & Hacker 1994). In fact, studies from a range of plant and animal communities have suggested a strong
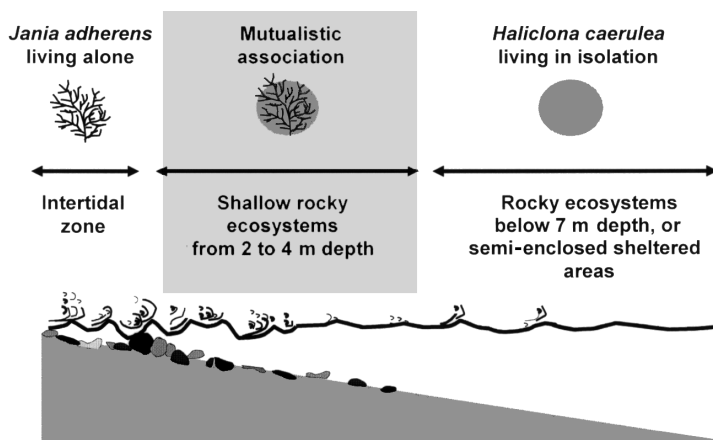

Fig. 15. Schematic distribution of the mutualistic association between *Jania adherens* and *Haliclona caerulea*. The zone where the association is always obligatory and the zones where each partner lives independently are shown. In the area of study, only alga growing in isolation and sponge in association with alga appeared. However, sponge growing independently of the alga is included in the figure because of its presence in other rocky deeper zones (see 'Materials and methods' for more information)

association between physical stress and positive interactions (Bertness & Hacker 1994). The Bay of Mazatlán is a natural disturbed zone subject to strong wind-wave action during the summer and affected by SW waves caused by tropical storms. Some of the most severe physical aspects of the environment of the zone are water turbulence, sand abrasion and deposition of sediment in the shallow rocky ecosystem (Carballo et al. 2002). This association seems to be the most conspicuous organism in this environment, where few other species of large, sessile organisms are able to survive. In fact, the sponge community in this area is largely composed of encrusting sponges (Wilson 2002). In shallow water, or wherever strong water movement occurs, sponges should have a substrate stable enough to permit their development until sexual maturity is reached (Rützler 1970); thus, the availability of a suitable substrate could be a limiting resource for this sponge to live in shallow water where potential stable attachment sites for larval sponges may be few. The abundance of *Halichondria* spp. was enhanced by the co-occurrence of the erect coralline alga *Corallina vancouveriensis* in areas of high wave action, which also provided the sponge with physical protection from desiccation (Palumbi 1985). Thus, the association of *Haliclona caerulea* with *Jania adherens* could provide a mechanism to remain in this stressful area and to offer resistance to heavy flow, as it has been reported for the *Haliclona cymiformis–Ceratodictyon spongiosum* association (Davy et al. 2002). This can also be supported by the fact that the sponge appears to be able to live without the alga in more sheltered habitats, such as on mangrove roots in San Blas Island (J. L. Wulff pers. comm.), in a semi-enclosed coastal lagoon near the Bay of Mazatlán or in deeper rocky ecosystems (J. L. Carballo pers. obs.).

The association has also been suggested to offer resistance to predators (Wulff 1997b). Associational defenses are positive interactions that arise when consumers drive palatable organisms into interactions with less palatable organisms (Wilcox et al. 2002). However, the data exposed here and in other studies (Camacho-Cruz 2004) do not support resistance to predation as the main cause of the association in the Bay of Mazatlán.

In summary, that advantages are gained by the alga and the sponge from an association can be deduced from the fact that all specimens of *Jania adherens* were associated with the sponges below 1 m and the sponge was never found alone in this habitat (Fig. 15). Moreover, previous studies showed that *J. adherens* is seasonal in the zone, appearing from winter to spring or from early spring to autumn (Garza 1999, Carballo et

al. 2002), but thanks to its association with the sponge, it remains in the zone all year round, even when it does not exist in the intertidal zone. We conclude that this stable mutualistic association between *Haliclona caerulea* and *J. adherens* is maintained by ecological factors unique to their habitat.

Associations of sponges with microorganisms probably date back to Precambrian times, about 500 million yr ago (Wilkinson 1984), but the age of associations like these is unknown. It is very interesting to note that the 2 associations (in Australia and in Mexico) share similar ecological characteristics, namely that the sponge species are of the same genera (previously *Sigmadocia*) and that the alga partner is a red macroalga.

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