Growth and Standing Stock Biomass of a Mutualistic Association between the Sponge *Haliclona caerulea* and the Red Alga *Jania adherens*

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Abstract

The association of the sponge *Haliclona caerulea* and the red macroalga *Jania adherens* is one of the most conspicuous organisms on shallow rocky ecosystems of the Bay of Mazatlán (eastern tropical Pacific, Mexico). The variations in size, growth rate and biomass were studied along a temporal and a spatial gradient. The association was persistent during the period of study. Size and growth varied with the seasons, and peaked during spring in both years (785 cm^3 and 1342 cm^3 month^{-1}, respectively). After that, the association started to shrink in size until December (from -505 cm^3 to -1063 cm^3 month^{-1}). The biomass of *Jania adherens* (as g CaCO$_3$ m^{-2}) was enhanced by the association with *Haliclona caerulea*, and the evidence showed that the ability of these species to utilize space was affected by mutualism. *Jania adherens* was living in isolation only in the intertidal zone, but in association with the sponge, it spreads to deeper zones. However, its contribution to the association (as ratio CaCO$_3$ to Si) decreased from 0.29 at 2 m depth to 0.12 at 4 m depth showing that the mutualistic relationship decreases with depth. *Haliclona caerulea* was never found living in isolation; thus, it is concluded that the association increased the amount of space that the two partners can cover and hold.

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1. Introduction

Sponges are one of the major phyla found in hard-substrate marine ecosystems (Sarà and Vacelet, 1973). In some of these ecosystems, they are a major component of the animal biota (Reiswig, 1973), and can contribute significantly to net primary productivity through photosynthetic symbionts (Wilkinson, 1983). These symbiont organisms are mainly microscopic prokaryotic and eukaryotic organisms, such as cyanobacteria, dinoflagellates and microalgae (Duclaux, 1973; Vacelet, 1981; Cox and Larkum, 1983), and some studies on their ecology (Wilkinson, 1978a,b), and about their contribution to sponge energy requirements, have been published in the last decades (Wilkinson, 1987).

Moreover, other photosynthetic symbionts, like macroalgae, occur in sponges (Price et al., 1984; Rützler, 1990), but unlike the associations with microorganisms, very little is known about them (Palumbi, 1985). One such association is the one constituted by the haplosclerid sponge *Haliclona cymiformis* (Esper) and the red macroalgae *Ceratodictyon spongiosum* Zanardini (Vacelet, 1981). The population dynamics of this association (Trautman et al., 2000), and the role of the habitat in determining its distribution, have been reported recently on shallow coral reefs of the Indo-West Pacific (Trautman et al., 2003). Another of these associations is the one constituted by the sponge *Haliclona caerulea* (Hechtel, 1965) and the red algae *Jania adherens* Lamouroux, which is common throughout the Caribbean and on the Pacific coast of Panama (Wulff, 1997). *Haliclona caerulea* is the most persistent sponge in the Bay of Mazatlán, which lives in association with the red seaweed *Jania adherens*. The sponge, which also lives between the algal filaments, generally covers the alga and the algal branches very rarely protrude beyond the association surface (Fig. 1). This association is locally abundant in shallow rocky ecosystems, and despite a large sampling program to study the diversity of sponges along the Sea of Cortez in the last five years (Gómez et al., 2002; Carballo et al., 2003; Carballo et al., 2004; among others), the association was found only in the Bay of Mazatlán.

The possible benefits for the partners of this association are not yet clear. However, one of the main hypotheses to explain this association between *Haliclona* and *Jania* is that it is not inquilinistic, but mutualistic. Mutualism is an interaction in which two species positively affect each other's abundance, survival or distribution (Vance, 1978; Margalef, 1982). It seems that the alga offers a stable structure for the sponge to live in shallow exposed ecosystems, and the alga in return spreads to deeper zones thanks to its association with the sponge (unpublished data).

This research is part of a more ample study on the ecology of the association of *Haliclona caerulea* and *Jania adherens*, which pursues the following: (1) to

determine which are the possible benefits of the partners living in association, and (2) to determine which are the factors that control this association.
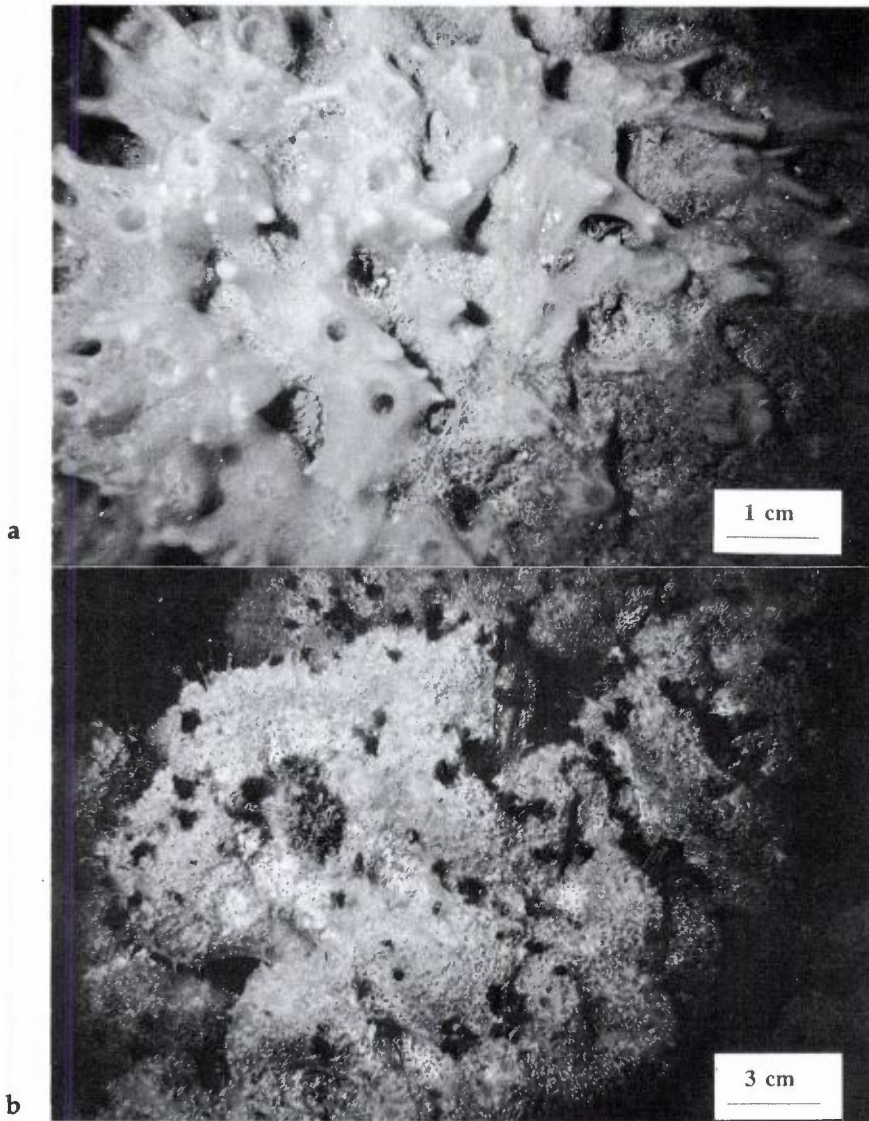

Figure 1. Underwater images of the association *Haliclona caerulea* and *Jania adherens* taken at 3 m depth. a) Photograph taken in February, when the environment is more stable. The sponge protruding beyond the association surface (see the vertical projections). b) Photograph taken during the summer.
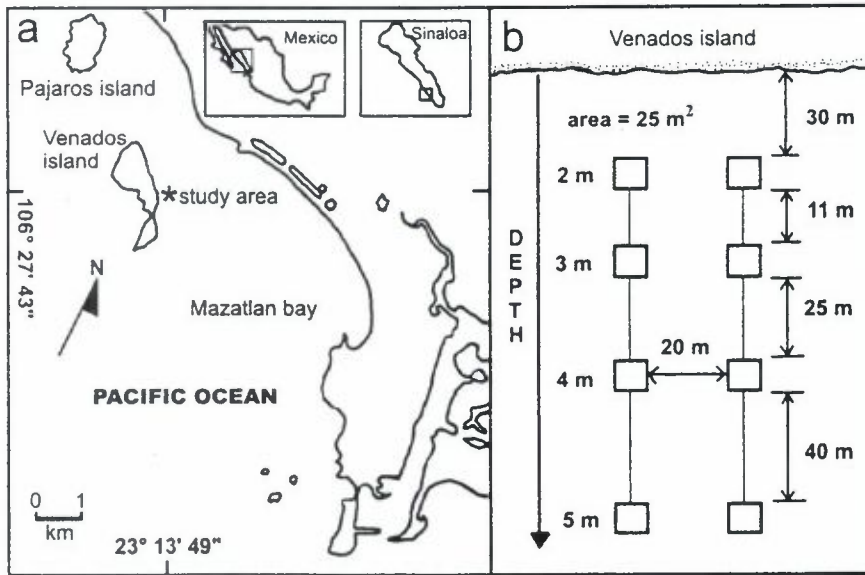
Figure 2. Location of study area at Bay of Mazatlán showing the eight sampling stations in front of Venados Island (23°13'49"N–106°27'43"W). The depth and the distance from the shoreline are indicated at the side of each sampling station.

The main objective of the present work was to contribute to the knowledge of this particular association by analyzing the variation of its size, growth and biomass, as well as the contribution of each partner to the association over time and along depth.

2. Material and Methods

Study area and meteorological conditions

A preliminary survey along the Bay of Mazatlán (eastern Pacific Ocean, Mexico) determined that the association was distributed only in shallow rocky substrates at a depth of 2 to 5 m (Fig. 2). We did not find any zone where the three components existed simultaneously: alga, alga in association with the sponge, and sponge. The sponge was occasionally found living in isolation in rocky ecosystems below 7–8 m depth; however, no studies on sponges lacking the association could be run because no populations of *Haliclona caerulea* existed anywhere. *Jania adherens* only exists in isolation in the intertidal zone.
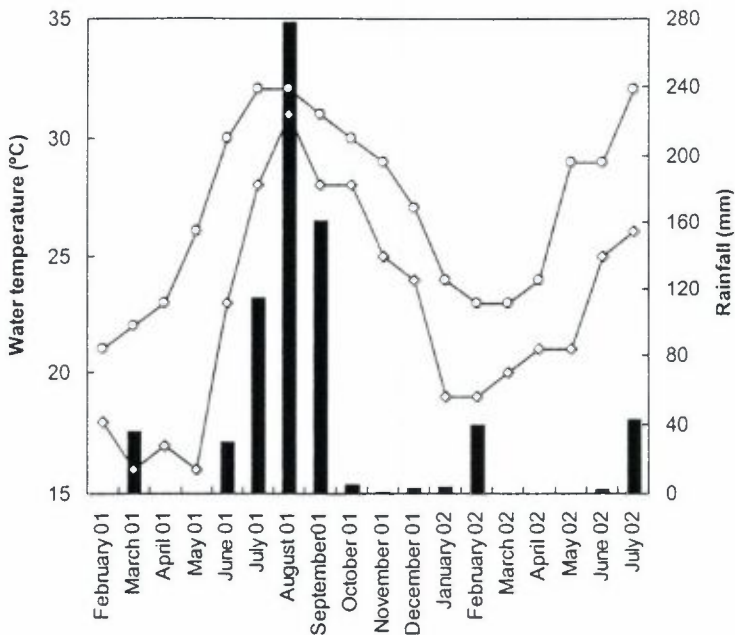
Figure 3.   Mean monthly water temperature (lines, left axis) and precipitation (bars, right axis) from February 2001 to July 2002.

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 (Fig. 2) because at least populations of two of the components were found along the same gradient in depth (alga and alga/sponge). At shallower depths (1–2 m) there are mainly large and medium size boulders on a rocky bottom. From 2 to 5 m the bottom consists of a gently sloping mosaic of relatively flat boulders between patches of sediment. Below this depth, the patches of sediment increase until the rocks disappear completely at 7–8 m.

The climate in the zone is tropical/sub-tropical, with two contrasting seasons in the year. The average annual air temperature 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) (Fig. 3). The Bay of Mazatlán is a naturally disturbed zone subject to strong wind-wave action during the summer, affected by SW waves caused by tropical storms. Some of the most severe aspects of the physical environment of the zone are water turbulence, sand abrasion, and deposition of sediment (Carballo et al., 2002).
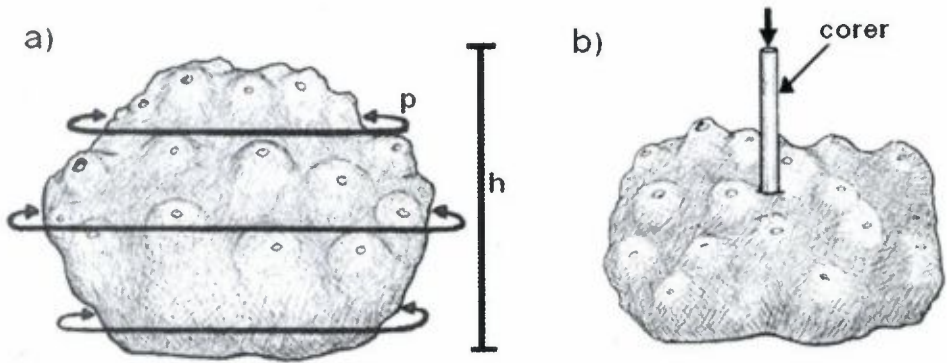
Figure 4.   a) Different measurements taken *in situ* to estimate the size of the association
            (p = perimeter of the sponge at different levels; h = height of the sponge). b) Corer
            steel used to obtain a representative sample of the association.

Water temperature

Water temperature was measured monthly with a maximum/minimum
thermometer permanently placed at a depth of 4 m on the seafloor in the area
of study. Spearman rank correlation and cross-correlation analyses were used to
assess relationships between mean size, growth rate, and water temperature.

Sampling methodology

Two permanent parallel rows of stations 20 m apart were set at 2, 3, 4, and 5 m
depth (Fig. 2). The original design also included a sampling station at 1 m
depth. However, the absence of the association and the difficulties for
sampling due mainly to wave action, forced us to leave this station. Each
station (5 m wide × 5 m long) was delimited by plastic lines, and conveniently
marked to ensure its location in subsequent samplings. Each specimen inside the
sampling stations was labelled with numbered plastic tags set into the rock
bottom beside the sponge in February 2001 (Ayling, 1980). The total area
sampled monthly was 200 m^2 (8 sampling stations of 25 m^2).

Size, biomass and growth rates of the association

The size of the association (in cm^3) was determined *in situ* by non-destructive
sampling following this procedure: the height and the perimeter from the base,
from the middle and from the upper part of four specimens per sampling station,
were measured. The volume in cm^3 was calculated by estimating the shape of
the specimens as a cylinder (Fig. 4). Thirty-two specimens were measured bi-

monthly from February 2001 to June 2002 for this procedure. The same specimens were measured through time using the plastic tags, and the difference between volumes from one date to another in a growth period provided the net growth rate in cm^3 $time^{-1}$. The numbers of the specimens were previously selected at random in the laboratory, and later located in the sampling stations with the numbered plastic tags (see Sampling methodology).

To determine association weight, the size measured *in situ* by the procedure previously explained (in cm^3) was compared to corresponding measurements of wet weight (WW) and dry weight (DW) in the laboratory. For this, 40 specimens of the association were collected in the study site outside the sampling station, and they were moved to the laboratory where the WW (g) was determined using an analytical scale. The volume was determined by the previously commented procedure. Later, the samples were washed with distilled water, and dried at 100°C for 24 h to determine the dry weight (DW). Line was fitted by linear regression analysis, and the resulting model was used to estimate the wet and dry weight from the *in situ* measurements. Significant size vs WW ($y = 0.315x + 2.1831$; $r^2 = 0.96$; $p<0.01$), and size vs DW ($y = 0.0532x - 0.6779$; $r^2 = 0.98$; $p<0.01$) correlations were determined. Using the first model, the mean WW per individual from the underwater size measurements was obtained. Later, the biomass (g WW 25 m^{-2}) was estimated by multiplying the mean WW by the number of individuals in each sampling station.

Tests of the null hypothesis of no significant difference between depths and along time were done for size, using a Kruskal-Wallis analysis by ranks (data departure from normality). This analyzes the effect of a classification factor for a balanced or unbalanced one-way design (Sokal and Rohlf, 1981).

Contribution of the sponge and the alga to the association

To determine the contribution of the sponge and the alga to the association, five circular core samples were taken, with a diameter of 0.6 mm from the surface to the basal part of each measured specimen. The first core was placed in the centre of the association, and the remaining four at the margins so that they would be equally distant from the central core (Fig. 4). This procedure was followed bi-monthly in four specimens per sampling station from February 2001 to June 2002. In order to determine if the species of algae in association with *Haliclona caerulea* could change through time, the core samples were checked for alga species.

The samples were washed with distilled water in the laboratory, and dried at 100°C for 24 h to determine the dry weight (DW). 1 g of DW was burned during 24 h in a muffle furnace at 550°C to obtain the ash weight (AW), and the organic substances were expressed as ash-free dry weight (AFDW). AW

represents the inorganic fraction and is commonly used to describe the amount of siliceous skeleton in sponges (Schönberg and Barthel, 1997). However, in our case, the inorganic fraction also included the $CaCO_3$ from the alga. Thus, to obtain the ash-free $CaCO_3$ fraction ($AFCaCO_3$), the carbonate was burned at 1000°C during 24 h. The carbonate content was estimated by calculating the difference between the two dry weights ($AW-AFCaCO_3$). The amounts were converted to $CaCO_3$ and silica per g DW of the association, and these amounts were used to estimate the contribution of alga and sponge, respectively, in the association. The sponge-alga variation in the association along depth or through time was expressed as g of $CaCO_3$ and silica m^{-2}.

3. Results

Species of algae in association with Haliclona caerulea

The frequency of appearance of the different algae living in association with the sponge was examined in more than 2000 small samples of the specimens measured from February 2001 to March 2002. Three different species appeared with different frequency, with *Jania adherens* as the preferred substrata of *Haliclona caerulea* (about 90% of the samples studied). The other two species in the association (*Gelidiopsis* sp. and *Amphiroa* sp.) can be considered as incidental, due to the low proportion of their appearance (7% and 3%, respectively).

Variation in size of the association

The size increased progressively from winter to spring (when the largest size was registered), and decreased from late summer to autumn (test statistic = 22.42; p = 0.004) (Fig. 5). The mean monthly size varied from 231 cm^3 to 785 cm^3, and it covaried positively with water temperature from the preceding month (r = 0.99, p = 0.01), showing that the variation in size was in part governed by season. The mean variation in the size of the association through depth showed no clear differences (plot in the small box) (test statistic = 2.96; p = 0.22; using the entire data by depth pulled together) (Fig. 6). However, the variation in size was very heterogeneous along depth, and the association could be simultaneously increasing their size at one a depth, and decreasing at another depth. For example, from August to October 2001, the size of the association at 3 m significantly increased from 297 cm^3 to 1036 cm^3, and at 2 m it decreased from 1623 cm^3 to 114 cm^3 (test statistic = 2.96; p = 0.02) (Fig. 6), when a mean negative growth rate was detected (Fig. 7). Neither the association nor sponge living in isolation were found at a depth of 5 m.
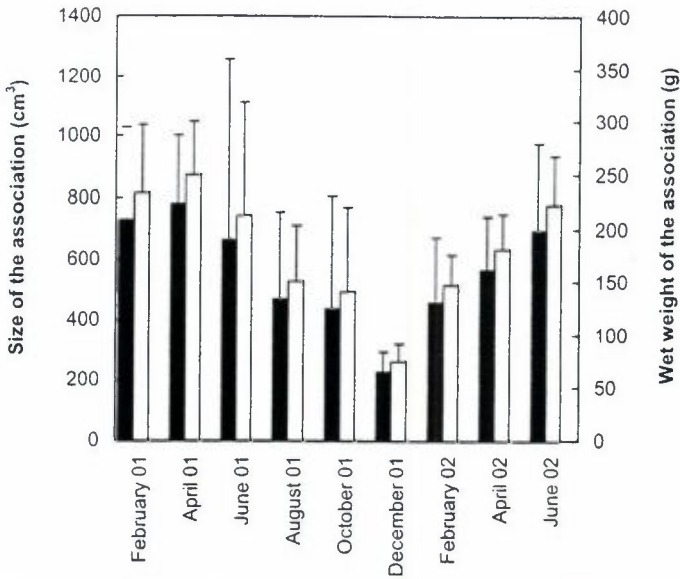
Figure 5.   Mean size (left axis), and wet weight (right axis) of the association throughout time. The underwater measurements of size were converted to weight wet using the regression obtained (see Material and Methods). The lines represent the standard error.
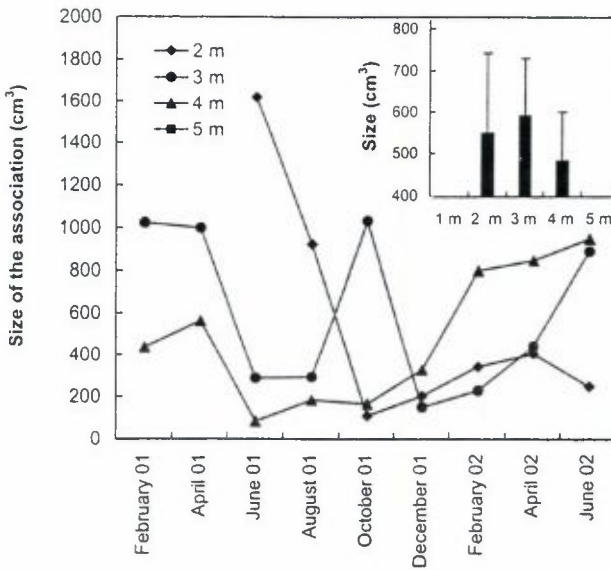

Figure 6.   Temporal variation of the size of the association for each depth. The small upper box represents the spatial variation (the values by depth are the averages of all the specimens measured during the study at each depth). The association was never found at 5 m depth. The lines represent the standard error.
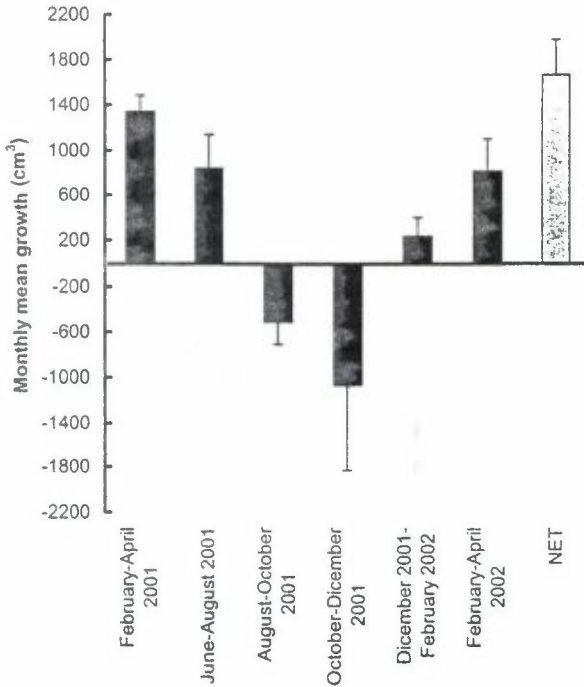
Figure 7. Monthly mean growth rate (in cm^3) of the association through time. The lines represent the standard error.
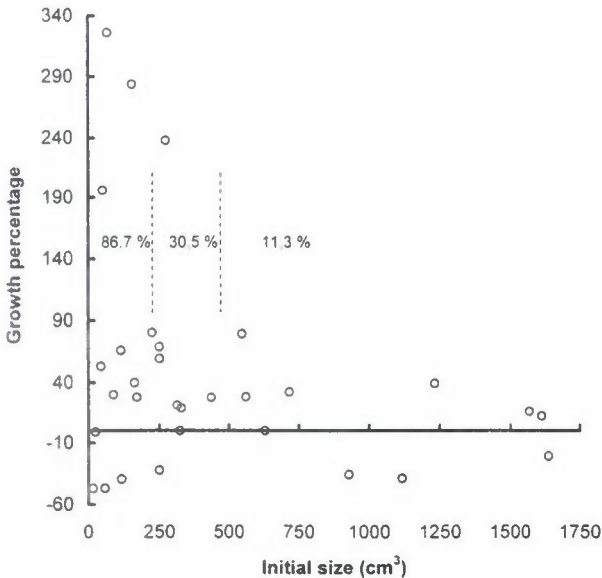

Figure 8. Plot showing specimen percentage of growth by a comparison of the initial size against the size after one month. The numbers between the dashed lines show the mean growth for different ranges in size (0–250 cm^3; 250–500 cm^3; >500 cm^3).
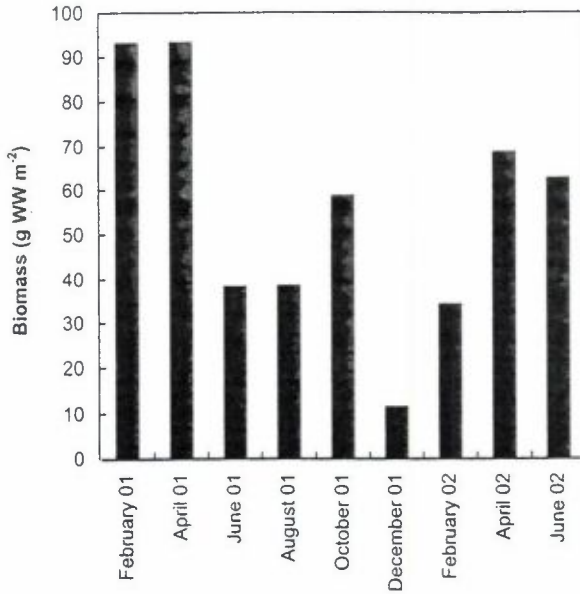
Figure 9.   Temporal variation of the mean biomass during the period of study.
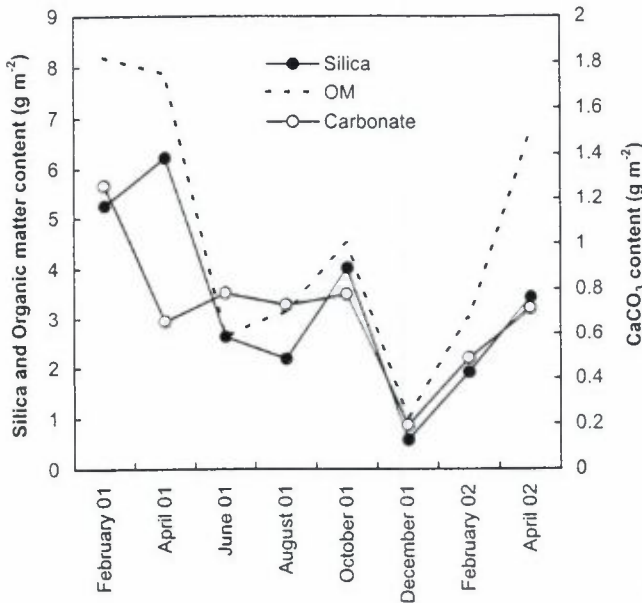

Figure 10.   Temporal variation of silica, carbonate ($CaCO_3$), and organic matter (OM) per m^{-2} through time.
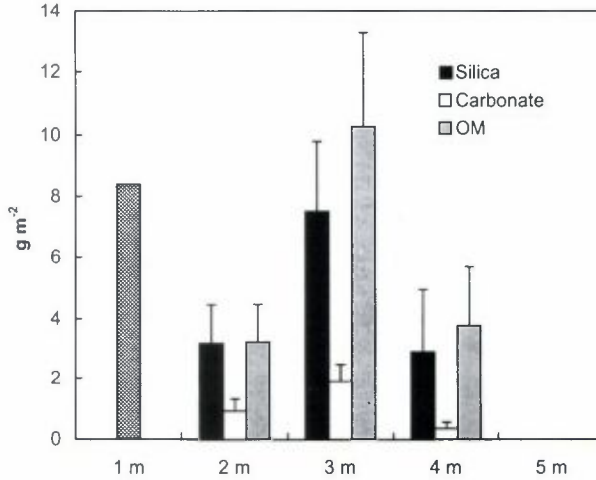
Figure 11.   Spatial variation of silica, carbonate (CaCO3), and organic matter (OM) per
m^{-2}. The bar at 1 m depth shows the carbonate content (g CaCO3 m^{-2}) of *Jania
adherens* living in isolation (from Garza, 1999).

Figure 12.   Variation in the contribution of the sponge and the alga to the association
through depth. The contribution of *Jania adherens* as ratio of CaCO3 to Si (solid
bar, left axis), and *Haliclona caerulea* as ratio of Si to CaCO3 (white bar, right
axis) are shown in the main plot. The variation in the contribution of organic
matter (OM) is represented in the small box, upper left.

Growth rate of the association

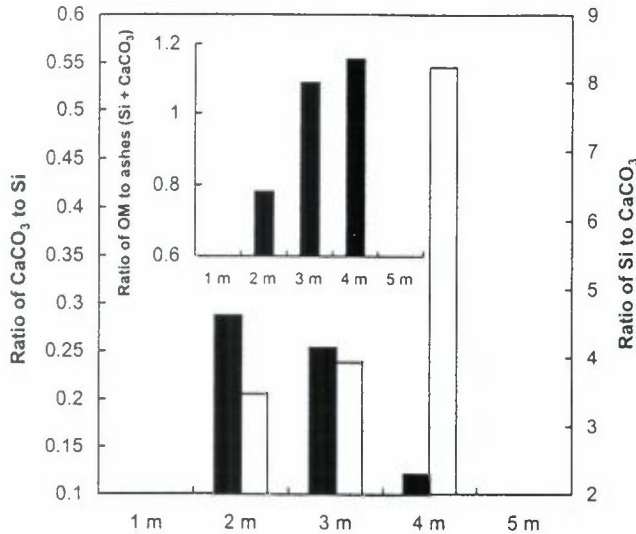A high mortality limited the number of measurements that could be made on each specimen (unpublished data); of the 32 specimens initially selected in each period to obtain data on their growth, it was only possible to measure a maximum of 11 specimens per sampling. The monthly mean growth varied from -1062 cm^3 to 1342 cm^3 (Fig. 7) according to the size ($r = 0.96$, $p = 0.008$). Specimens began to grow in early spring (up to 1342 cm^3 per month), but growth rate decreased towards late summer (842 cm^3 per month). From August to December 2001, there was a negative growth (from -505 cm^3 to -1062 cm^3 per month), but specimens started to grow again with the onset of spring, and from February to April 2002, the specimens grew at a rate of 814 cm^3 per month. At this time, the sponge frequently protruded the surface of the association (Fig. 1a). The population had a mean increase of 127% at the end of the study, ranging from -31.4% to 117% per month.

An inter-specimen variation was observed where large specimens grew more slowly than smaller ones (Fig. 8). The growth rate for the specimens up to 250 cm^3 in size was from -46 cm^3 to 326 cm^3 per month (a mean monthly increase of 86.7%); for the specimens between 250 cm^3 and 500 cm^3 the growth rate was -32 cm^3 to 80.2 cm^3 per month (30.5% on average); specimens greater than 500 cm^3 grew from -38 cm^3 to 79 cm^3 per month (11.3% on average). However, it is important to note that a higher growth rate in the smaller specimens does not necessarily represent higher biomass: if a large specimen (for example of 1000 cm^3) increases its size by 11.3%, it would represent a higher increase in biomass than a smaller specimen (100 cm^3) that increases by 86.7%.

Biomass and contribution of the partners (sponge and alga) to the association

The biomass of the association ranged from 11.5 g to 93 g WW 25 m^{-2}, and although it peaked in spring each year, no clear seasonal pattern was found (Fig. 9). Large specimens contributed most of the biomass from February to June 2001 and from April to June 2002, and during the period of the lowest standing stock biomass, small specimens of the association predominated within the population.

The association consists of a massive and compact form where the sponge fills the spaces between the algal branches completely, making the separation of both partners impossible. However, the variation of each partner was estimated as amount of silica and CaCO$_3$ per m^{-2} (Fig. 10). The two periods of growth detected in the association (Fig. 7) matched with a high increase in organic matter (from February to April 2001, and 2002), and with the moment when the sponge protrudes the surface of the association (Fig. 1a). We do not know what the exact contribution was from each component to the organic

matter, but it seems evident that the sponge supplied most of this organic matter because the alga is mostly $CaCO_3$. From February to April 2001, the contribution of *Jania adherens* decreased considerably; however, the biomass of the association did not vary, probably due to the growth of *Haliclona caerulea*. Later, from April to August 2001 the component that most reduced its contribution to the association was the sponge. This can be easily observed when we compare the period of decrease in size and biomass (from April to August 2001) with the variation in the Si and $CaCO_3$ m^{-2} at the same time. This moment also matched with a negative growth period, suggesting that the association was starting to shrink in size, or losing biomass through fragmentation. From December to April 2002, an important increase in the mean size and in the biomass matched with the increase in organic matter, silica, and $CaCO_3$ m^{-2}.

The silica, $CaCO_3$ and organic matter per m^{-2} peaked at 3 m depth (Fig. 11), However, the contribution of the alga (as ratio of $CaCO_3$ to Si) decreased progressively with depth, from 0.20 g to 0.12 g, and the variation of Si (as ratio of Si to $CaCO_3$) did the opposite (from 3.4 to 8.2) (Fig. 12). This clearly shows that each partner contributes to the association in a different proportion through depth, and that the mutualistic relationship decreases with depth.

4. Discussion

Temporal patterns

The association showed seasonal growth, indicating that it responded to the seasonal changes in the environment. This seasonal pattern seems to be common in sponge populations, and water temperature is the most important factor controlling this variation (Stone, 1970; Elvin, 1976; Fell and Lewandroski, 1983; Barthel, 1989; Turon et al., 1998; Garrabou and Zabala, 2001). In fact, in our study, size and growth covaried with water temperature, which was determined by the two contrasting drought and rainy seasons (see Fig. 3). This seasonal growth pattern may determine the seasonal resource allocation to different processes of the association's life cycle.

No data on the reproduction of *Jania adherens* are available; however, the sponge reproduces mainly during summer/autumn (unpublished data). This could indicate that the *Haliclona caerulea* could have a trade-off between somatic growth and reproduction, which peaked in winter/spring and summer/autumn, respectively. At the end of the study, the size increased 127%, in a consistent manner with data previously reported for other sponges, which varied between 60% and 150% per year (Reiswig, 1973; Wilkinson and Vacelet 1979; Wilkinson and Cheshire, 1988; Barthel, 1989). Growth dynamics is one of

the most important parameters when trying to understand the life history of a species.

However, processes of degrowth (recession from a formerly occupied space), such as partial mortality, fusion, fission or fragmentation, also affect the size of the specimen (Garrabou, 1998). Some of these processes are denoted by negative growth rates (Reiswig, 1973; Barthel, 1986; Barthel, 1989; Turon et al., 1998; Garrabou and Zabala, 2001; among others) as shown in our study (from -505 cm^3 to -1063 cm^3 per month). The differences in mean growth (233–1342 cm^3 per month) and shrinkage (from -505 cm^3 to -1063 cm^3 per month) were in the same order of magnitude. However, at the end of the study, the association increased 127% because the period of positive growth was longer than the period of negative growth. Moreover, the association had the ability to become fragmented (pers. obs.), and this negative growth could show the effect of fragmentation on the large specimens. This seems a very important mechanism to maintain the population, because of large specimens formed at 2 and at 3 m depth during the favorable drought season could be an important source of asexual recruits during the rainy season. These results agree well with Trautman et al. (2000), who showed that fragmentation was the most important form of reproduction in the association *Haliclona cymiformis* and the red macroalgae *Ceratodictyon spongiosum*.

The growth also varied according to the initial size, with higher growth rates in small specimens than in larger ones. This has been indicated for other sponges (Dayton, 1979; Barthel, 1989; Turon et al., 1998), but it does not seem a generality (Fell and Lewandroski, 1981). Moreover, there was a high variability in growth among specimens of a similar size, which could be explained in part by microhabitat conditions (Garrabou and Zabala, 2001). It can be concluded that water temperature and initial size (age) are important factors governing growth of the association.

No clear seasonal pattern was found in the variation of the biomass, probably due to the stochastic nature of factors responsible for biomass. Fluctuations in sponge populations not related to seasonality or reproductive cycles have been found (Ayling, 1983), showing that other environmental parameters or biological processes are involved. During the drought season, the biomass of the association progressively increased, and later, the loss of biomass in the rainy season was consistent with extreme physical disturbance, mainly from high water movement and resuspension (Wilson, 2002). The mean monthly biomass of this association (ranging from 11.5 g to 93.2 g WW m^{-2}) was lower than that reported for the association *Haliclona cymiformis* and *Ceratodictyon spongiosum*, which can reach up to 270 g WW m^{-2} (Trautman et al., 2000). In fact, the biomass reported for sponges living in association with photosynthetic symbiosis are considerably higher than the one obtained for the association *Haliclona caerulea* and *Jania adherens*. Some representative

examples are *Halichondria panicea* living with microalgae (up to 500 g WW m^{-2}) (Barthel, 1988), and foliaceous sponges in Australia living with microorganism symbionts (up to 1225 g WW m^{-2}) (Wilkinson and Cheshire, 1989).

Spatial patterns

Haliclona caerulea was never living in isolation, and *Jania adherens* was living in isolation only in the intertidal zone (up to 8.4 g CaCO$_3$ m^{-2} in Garza, 1999), but it was able to extend its distribution to deeper zones in association with the sponge (up to 1.9 g CaCO$_3$ m^{-2} at 3 m depth). Moreover, the proportion of alga in the association decreased towards deeper water in contrast to the proportion of the sponge, showing that the mutualistic relationship decreases with depth. In a similar way, the abundance of *Halichondria panicea* was enhanced by the co-occurrence of an erect coraline alga, and the sponge-alga relationship varied over remarkably small spatial scales (Palumbi, 1985). These results could result from a combination of different factors such as water movement, silting or resuspension (Wilkinson and Cheshire, 1989). It is known that sponges exposed to high mechanical stress contain more spicules than sponges from habitats with less water movement (Palumbi, 1984; 1986), and they can use different organisms as a substitute for skeletal fibers (Uriz et al., 1992). The species *Dysidea janiae* and *Strongylacidon osburnensis* substitute or reinforce their own skeleton by association with calcified *Rhodophyta* algae of the genus *Jania* (Rützler, 1990). Thus, *Haliclona caerulea* at a depth of 2 and 3 m would need to reinforce their body to stay in this energetic habitat. The only way for the sponge to do this would be in association with *Jania adherens*, since sponges living in isolation were never found in the study area.

However, an important question that needs to be solved is why the alga is not able to live alone beyond the intertidal zone. The availability of light, along with the previously mentioned water movement, could be another important factor to explain these questions, and its absence could be related to the irradiance from high turbidity and silting. The reduction in the proportion of the alga to sponge along depth is consistent with this hypothesis, and is currently addressed in another study.

The association between *Haliclona cymiformis* (Esper) and the red macroalga *Ceratodictyon spongiosum* is very common on shallow coral reefs of the Indo-West Pacific, where it has been described as one of the most conspicuous organisms in these areas (Vacelet, 1981; Price et al., 1984). The nitrogen required for alga growth can be provided by sponge catabolism (as ammonium), and alternately, the organic compounds as amino acids translocated to the sponge could be important (Davy et al., 2002). We do not

know if any metabolic relationships exist between *Haliclona caerulea* and *Jania adherens*. However, it seems evident that the association improves the survival of both species, and increases the amount of space that they can cover and hold. The evidence also shows that the ability of these species to utilize space is strongly affected, if not determined by mutualism. Thus, we conclude that the interaction between *Haliclona caerulea* and *Jania adherens* is a facultative mutualistic relationship influenced by the environment.

Acknowledgements

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