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Boring sponges and the modeling of coral reefs in the east Pacific Ocean

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ABSTRACT: A total of 900 coral fragments collected across 2 fringing reefs located southwest of Mexico, La Entrega (LE) and San Agustín (SA), were examined for the presence of boring sponges. Of all samples, 43% were invaded by boring sponges, and 7 species belonging to 5 genera (*Aka*, *Cliona*, *Pione*, *Cliothosa* and *Thoosa*) were identified. The most abundant species were *Cliona vermifera* (17.9%), *Cliona* sp. (10.8%), *A. cryptica* (7.8%) and *P. carpenteri* (6.0%). The distribution and abundance of the species varied considerably throughout the reef area (margin and platform) and displayed certain selectivity for specific calcareous substrata. *C. vermifera*, *Cliona* sp., *A. cryptica* and *P. carpenteri* were most common on the reef margins, while *T. calpulli* was common on the central platform. *A. cryptica*, *P. carpenteri*, and *Cliothosa hancocki* were frequently found living in the immediate vicinity of live coral tissue, contrary to *C. vermifera*, *T. calpulli* and *Cliona mucronata*, which preferentially bored coral rubble. The results showed that reef margins had a significantly higher infestation level than the platforms (mean infestations of 60.6 and 26.2%, respectively). There were also differences between reefs. The infestation was higher on LE than on SA (48.6 and 38.2%, respectively), and these differences were larger between the platforms of the 2 reefs (41.3 and 11.1%, respectively). In general, the results of the present study have demonstrated that the diversity and abundance of species, as well as the infestation of coral frameworks by sponges, was significantly higher in the margin at both reefs studied and on the platform of LE, where the availability of exposed carbonate substrate was higher. In the margin of these reefs, the consequences of boring went far beyond the mere hollowing out of a few cavities, since by weakening the coral's attachment to the substrate, the sponges accelerated coral loss and restructured the reef edge. This pattern may have important implications for the preservation of the reef framework.

KEY WORDS: Bioerosion · Boring sponges · Fringing coral reefs · Reef margin · Reef flat · Mexican Pacific

INTRODUCTION

Coral reefs are diverse and productive biological communities that form massive biogenic structures and serve as a refuge for a multitude of sessile and mobile organisms (Richmond 1993). In the Atlantic and Indo-Pacific Oceans, coral reefs show typical zonation patterns (lagoon, back-reef and fore-reef) (Stoddart 1973). In contrast, in the East Pacific Ocean the reef framework is narrow and does not form a crest or a lagoon between the crest and the shoreline (Carriquiry & Reyes-Bonilla 1997, Reyes-Bonilla 2003). This general structure, constructed mainly by coral of the genus *Pocillopora*, can be frequently observed from the Gulf of California to Central America (Glynn & Leyte-Morales 1997, Glynn & Ault 2000, Reyes-Bonilla 2003). In this region, some studies have examined reef growth (Cortés et al. 1994) and the effects on their structure from climatic events like the El Niño Southern Oscillation (ENSO) (Reyes-Bonilla et al. 2002), but there are very few data on the destruction and bioerosion of these reefs (Londoño-Cruz et al. 2003).

Bioerosion is an essential, and often overlooked, aspect of reef ecology, and it is perhaps the most important destructive force on coral reefs (Zubia & Peyrot-Clausade 2001). Bioeroding species of many

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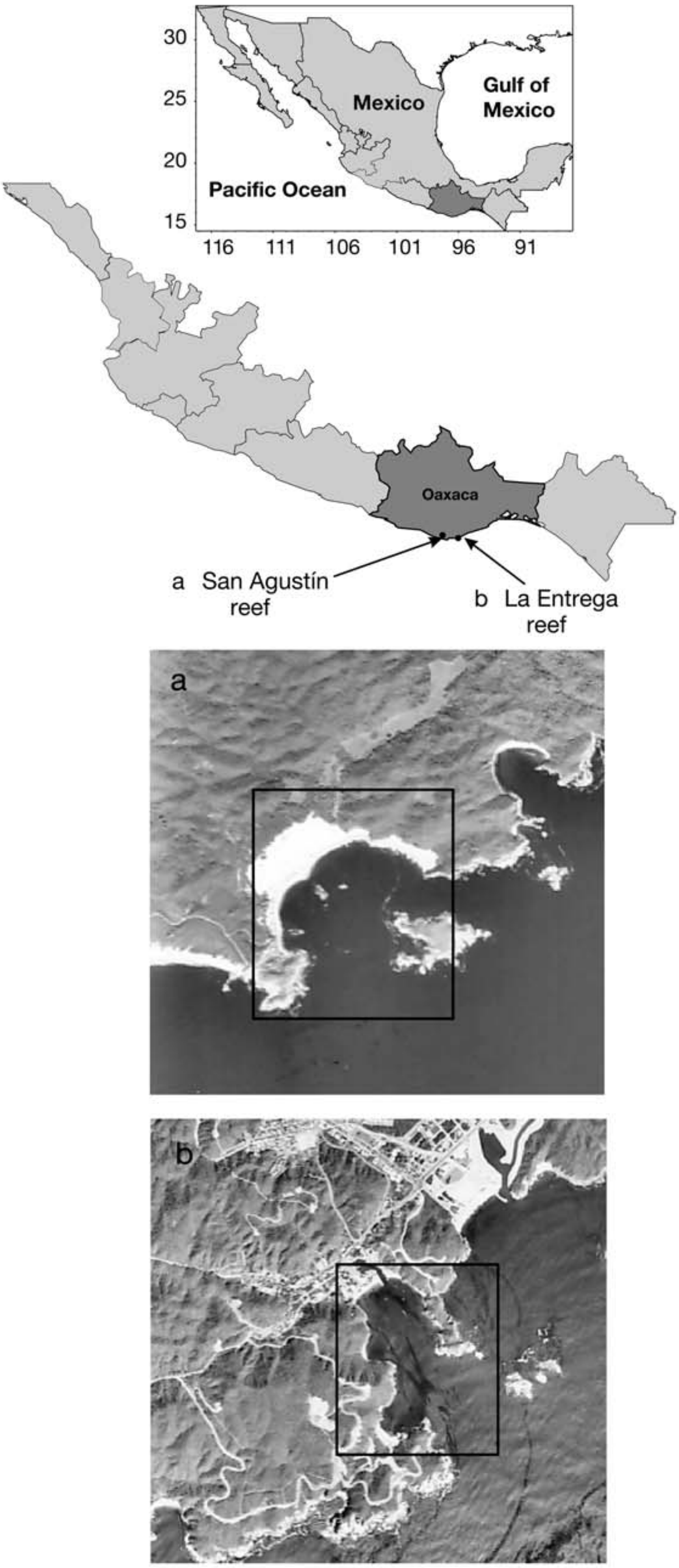

Fig. 1. Reef locations: (a) San Agustín and (b) La Entrega

different types of organisms, which act on the environment in a wide variety of ways, interact with the ecosystem and with each other as part of the cycle of reef growth and degradation (Macdonald & Perry 2003). Amongst these, the boring sponges are considered one of the main agents that modify coral reef ecosystems (Goreau & Hartman 1963, MacGeachy 1977). Globally, they are the most common type of macroendolith and are responsible for more internal degradation of coral than any other group of organisms, internally (Perry 1998). They can accelerate the erosion of the reef framework (Tunnicliffe 1979) and cause a shift in the carbonate balance (Rose & Risk 1985). Sponges obviously play one of the most important roles in bioerosion worldwide. However, they have been omitted in most studies because of their complex taxonomy and cryptic habitat that makes their quantification difficult (Schönberg 2001a,b).

In the Mexican Pacific Ocean most studies have focused on the taxonomic description of sponge species living in coral and other carbonate substrates (Carballo et al. 2004, 2007). Thus, there are very few data on the spatial distribution, diversity, abundance and effects that these sponges have on the reef framework.

The present study assesses the composition of boring sponge species, their abundance, substrata preference and the degree of framework infestation across 2 fringing coral reefs in the Mexican Pacific Ocean. One interesting feature of these fringing-reef corals is that 2 contrasting zones can be identified: (1) the margin or reef edge, with a higher quantity of exposed carbonate substrate, and (2) the central platform or reef flat, where live coral colonies form a more compact structure, increasing live surface area and decreasing the area of exposed carbonate substrate. We tested the hypothesis that abundance and diversity of boring sponges will be higher on the margin than on the central platform.

MATERIALS AND METHODS

Study location. The Huatulco reefs (Huatulco bays, Oaxaca, southwestern Mexico, Fig. 1) are fringing reefs constructed predominantly by branching pocilloporid corals (Glynn & Leyte-Morales 1997), but some massive species of the genus *Porites* and *Pavona* also occur (Reyes-Bonilla 2003). These coral reefs are located in bays, and usually extend down to 14 m. This research was conducted on La Entrega (LE) and San Agustín (SA) reefs (7.3 and 2.5 ha respectively), which were chosen because of their similar frameworks. Both reefs are constructed by interlocking branches of species of the genus *Pocillopora* that stabilize a continuous platform (Fig. 2b), surrounded by wide zones of exposed carbonate substrate that form the borders of the reef (1 to 3 m wide) (Fig. 2a). Sandy bottoms, with patches of coral fragments and calcareous algae, surround the framework of both reefs, and their general structure corresponds to that normally observed on coral reefs in the east-central Pacific (Carriquiry & Reyes-Bonilla 1997, Reyes-Bonilla 2003). Glynn & Leyte-Morales (1997) give more detailed information on these reefs including bathymetry, cover and conservation.

Characterization of the reef environment. A set of environmental variables was measured on the reef flat of both reefs, including suspended particulate matter (SPM) concentration, chlorophyll a (chl *a*) concentration, water transparency, sediment deposition, water movement and water temperature. The data were collected twice, during the wet season (July) and the dry season (April). SPM was calculated by filtering 3 l of seawater, with the filter subsequently oven-dried and weighed. Chlorophyll sampling and analysis followed the methods described by Holm-Hansen (1978). Irradiance (µmol quanta m^2 s^2) was evaluated using a LI-COR data logger at 1 m intervals to a depth of 5 m. Irradiance was used to calculate the attenuation coefficient (kd). Water transparency was estimated horizontally with a Secchi disc. Sediment deposition was measured using a trap system, consisting of 2 sets of cylindrical plastic bottles (1 l), positioned with their mouths (2.9 cm in diameter) at 60 cm above the reef platform. Each bottle was held in position in a vertical PVC cylindrical tube that was attached to the bottom for 1 wk each sampled season. The collected material was rinsed with distilled water to remove salts and dried at 60°C for 24 h before weighing. To estimate the water movement, we used the 'plaster dissolution' method, consisting of 2 sets of plaster spheres 5 cm in diameter (Naranjo et al. 1996). Deployment and retrieval of the plaster spheres were done every 3 d during each sampling period (10 d). The effect of water temperature on dissolution rates of the plaster spheres was corrected through a regression model previously calculated in the laboratory. Water temperature was measured daily during every sampling period with a HOBO water temperature data logger placed at a depth of 6 m.

Quantification of boring sponge infestation frequency. Branches of coral colonies (*Pocillopora damicornis*) of 3 different categories were collected by SCUBA diving in April 2004. The classification of the coral colonies was based on a modification of the methodology described by Peyrot-Clausade et al. (1992): (1) live coral colonies of *P. damicornis* attached to the substrate (Fig. 2c), (2) colonies partially alive and

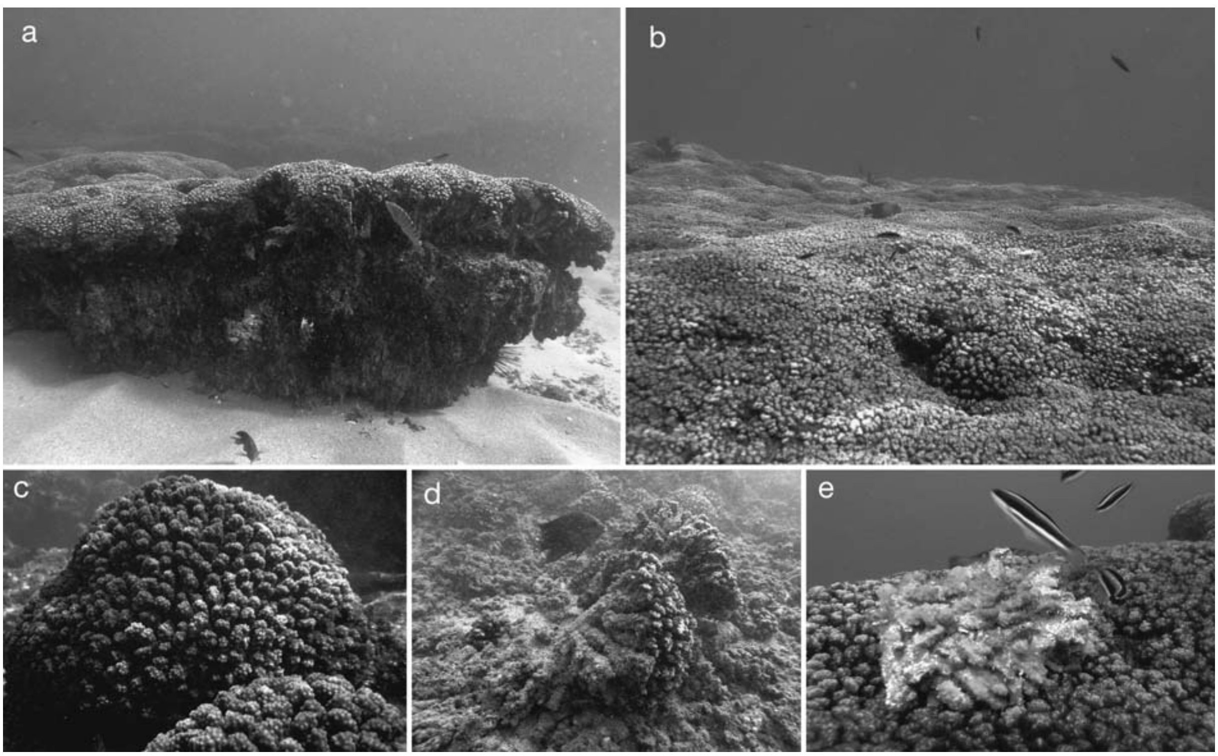

Fig. 2. San Agustín reef: (a) margin, (b) central platform, and classification substrata used in the present study: (c) attached live coral colony, (d) detached live coral colony, (e) coral rubble

detached from the substrate (Fig. 2d), and (3) fragments of dead coral commonly called 'rubble' (Fig. 2e).

On each reef, 3 line transects 50 m long were run along the central platform, and 3 more transects were run around the margin of the reef edge. Along each transect, a complete branch (Category 1 and 2) and rubble (Category 3) were collected at random every 2 m (25 samples for each category), yielding 75 samples per transect. For Category 1 a complete branch (from the tip to the stem) was collected from the colony closest to the transect. Thus, a total of 225 branches were collected from the central platform and 225 from the margin in each reef (450 branches per reef).

In the laboratory the coral branches were cut into parallel slices at right angles to the axis and examined for the presence of boring sponges. Identification of boring sponges was based mainly on Carballo et al. (2004) and Carballo et al. (2007). Spicule preparation followed the techniques described by Rützler (1974) for light and scanning electron microscopy (SEM). The material has been deposited in the Colección de Esponjas del Pacífico (LEB-ICML-UNAM) of the Instituto de Ciencias del Mar y Limnología, UNAM, in Mazatlán, México.

The occurrence/non-occurrence of boring sponges in each sample collected was expressed as percentage of infestation per category (1, 2, 3), per reef zone (central platform and margin), and per reef (LE and SA). The average of the 6 transects on each reef (3 from the central platform and 3 from the margin) was used to determine the total percentage of infestation by boring sponges per reef.

Data analysis. Using the environmental parameters, a correlation-based principal components analysis (PCA) was applied to characterize the environment of both reefs. A series of 2-way ANOVAs were carried out separately to study the variation of environmental variables between seasons and reefs. Where necessary, data were log transformed.

The percentage of infestation was compared between reefs using a 3-way ANOVA with the factors Locality (2 levels), Zone (2 levels) and Coral Colony Category (3 levels). Separate means of Coral Colony Category were compared using the Student-Newman-Keuls (SNK) post hoc test (Zar 1984) to determine which of the means were significantly different. The statistical package STATISTIC v. 7.1 was used for ANOVA analyses.

RESULTS

Reef environment

The ordination of environmental factors of the reefs by PCA (Fig. 3, cumulative percent variation explained 83.2%) showed a difference between the wet and dry seasons, irrespective of the reef (temporal variation, first principal component [PC1], 61.3% of the total variance explained). Chl *a* concentration, phosphate and total N were higher in April, the dry season ($p < 0.0001$, $p = 0.0212$ and $p = 0.0002$, respectively, separate 2-way ANOVAs), while water transparency and suspended solids in the water column had higher values in July, the wet season ($p = 0.0002$ and $p = 0.0179$, respectively, separate 2-way ANOVAs). The second principle component (PC2) (spatial variation, 21.9% of variation explained) showed that there were also differences between the reefs themselves, largely independent of the sampling season. LE was richer in organic matter and had a higher chl *a* concentration and sedimentation rate ($p = 0.0235$, $p < 0.0001$ and $p < 0.0001$, respectively, separate 2-way ANOVAs), with sedimentation rates at 340 g/m^{-2} d^{-1} for April and 199 g/m^{-2} d^{-1} for July, respectively. In contrast, water movement was significantly higher at SA ($p < 0.0001$, separate 2-way ANOVA). There were no significant differences in water temperature or irradiance between localities and seasons.

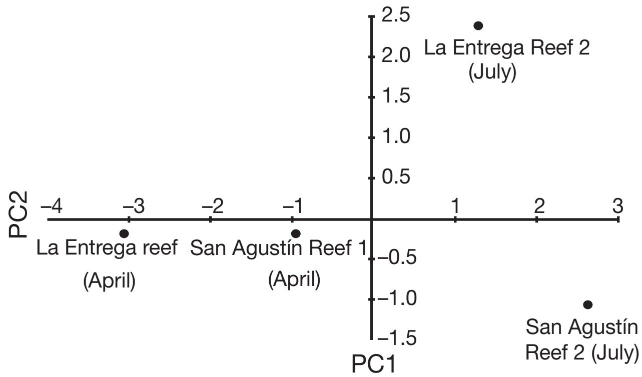

Fig. 3. Principal components analysis (PCA) ordination of coral reefs based on environmental parameters (as listed in 'Materials and methods')

Boring sponge species richness

Nine hundred coral branches from LE and SA were collected and analyzed. Boring sponges invaded 43%, and 7 species belonging to 5 genera were identified (*Cliona*, *Pione*, *Cliothosa*, *Aka*, and *Thoosa*). Of the 7 species identified, 5 were found on LE: *Cliona vermifera*, *Cliona* sp., *P. carpenteri*, *A. cryptica* and *T. calpulli*, and 7 in SA: *C. vermifera*, *Cliona mucronata*, *Cliona* sp., *P. carpenteri*, *A. cryptica*, *T. calpulli* and *Cliothosa hancocki*. The most abundant species were *C. vermifera* (17.9% of all samples), *Cliona* sp.

(10.8%), *A. cryptica* (7.8%) and *P. carpenteri* (6.0%). *C. hancocki* and *C. mucronata* were uncommon at the sample sites.

Cliona sp., the second most common sponge, is an undescribed species, and a brief diagnosis is necessary to make its identification easy. This is a bright yellow sponge in alpha form, i.e. superficially showing only circular or oval-shaped papillae 0.5 to 1.9 mm in diameter (4 to 8 papillae cm^{-2}). The tylostyles are slender, with the shaft slightly bent in the upper third, with a mean length and width of 193.4 and 5 µm, respectively (N = 50). The spirasters are straight, slightly curved or spiral-shaped, with 2 to 5 turns (mean length 25 µm, N = 50), and possess very fine short thorns generally terminating in branches.

Spatial patterns of boring sponge occurrence

Considering all samples, sponge infestation differed significantly between reefs (Table 1): 38.2% of the fragments were affected at SA versus 48.6% at LE (Fig. 4). This difference was more pronounced when comparing only the platforms of the 2 reefs (11.1 and 41.3%, respectively, Fig. 4). Regardless of the respective reef, sponges were more common on the margins than on the platforms (Fig. 4).

On LE all 5 species found occurred both on the reef margin and on the central platform, except for *Aka cryptica*, which was exclusively found on the margin. *Cliona vermifera* (69.3%), *Cliona* sp. (64%) and *Pione carpenteri* (32%) were the most abundant species on the margin (Fig. 5a). This same pattern of dominance was observed on the central platform, although the frequency for each species was lower; 51, 47 and 21%, respectively (Fig. 5b).

Aka cryptica was found exclusively in branches of detached live colonies, but the rest of the species did not show a clear specificity for any of the coral colony categories. However, *Cliona vermifera* occurred mainly in coral rubble, while *Cliona* sp. was more common in branches of attached and detached live colonies (Fig. 5d).

Table 1. ANOVA comparing the frequency of infestation in the reefs of La Entrega and San Agustín. Factors: locality (2 levels: La Entrega and San Agustín), zone (2 levels: margin and central platform) and coral colony category (3 levels: 1, 2 and 3). *Significant ($p < 0.05$)

Factor	df	MS	*F*	p
Frequency of infestation				
Locality	1	61.36	11.32	0.0026*
Zone	1	667.36	123.20	<0.0001*
Colony category	2	6.02	1.11	0.3450
Locality × Zone	1	220.02	40.62	<0.0001*
Locality × Colony category	2	0.52	0.09	0.9075
Zone × Colony category	2	35.02	6.46	0.0056*
Locality × Col. cat. × Zone	2	20.19	3.73	0.0389*
Residual	24	5.41		

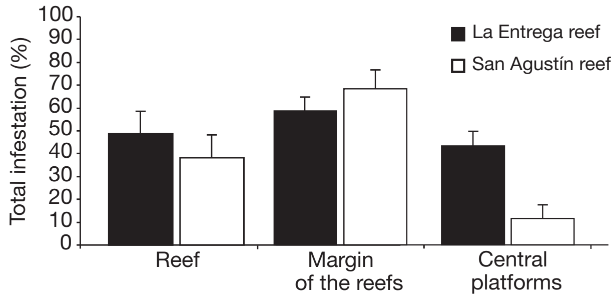

Fig. 4. Percentage of boring sponge infestation by reef and reef zone (+SD)

Sponge infestation of all substrate categories together was significantly higher on the margin (56%) than on the central platform of LE (41.3%) (Fig. 4). However, this pattern was not consistent when considering the categories separately, since rubble was more infested on the central platform (58.6%) that on the margin (46.6%) (Fig. 5c). Infestation was higher in the rubble (53%), followed by detached and attached live coral (both 47%) (Fig. 5d).

Species were evenly distributed among the zones on SA, except for *Cliothosa hancocki* and *Cliona mucronata*, which were exclusively found on the margin. The most abundant species on the margin were *Aka cryptica* (81%) and *Cliona vermifera* (77%, Fig. 6a). On the central platform this pattern was the same, but the frequency of all species was lower, with *C. vermifera* found in 17% of all fragments (Fig. 6b). In this reef some species, such as *A. cryptica* (19.3%) and *Pione carpenteri* (4.7%), were frequently found in branches of unattached live coral; *Cliona* sp. was found in branches of attached live coral (6.7%). In contrast, *C. vermifera* was more frequent in coral rubble (27.7%). The frequency of infestation was similar in the 3 categories considered: 40% in rubble (Coral category 3), 38% in attached coral (Category 1) and 36% in detached live coral colonies (Category 2) (Fig. 6d). As at LE, the sponge infestation was significantly higher on the margin (65.3%) than on the central platform (11.1%, Fig. 4, Fig. 6c).

Abundances and distribution patterns of all the species are summarised in Table 2. *Cliona vermifera*, *Cliona* sp., *Aka cryptica* and *Pione carpenteri* were most commonly found on the reef margins, and only *Thoosa calpulli* was observed to occur commonly on the central platforms. *Cliothosa hancocki* and *Cliona mucronata* were found only on the reef margins.

Substrate effects on sponge infestation

Regardless of reef origin, no significant difference was found in sponge infestation of the 3 coral colony categories representing substrate attributes (Table 1). Including samples from both reefs, the average value of infestation was 46.6% in rubble (Coral Category 3), 42.3% in attached live coral (Category 1) and 41.3% in

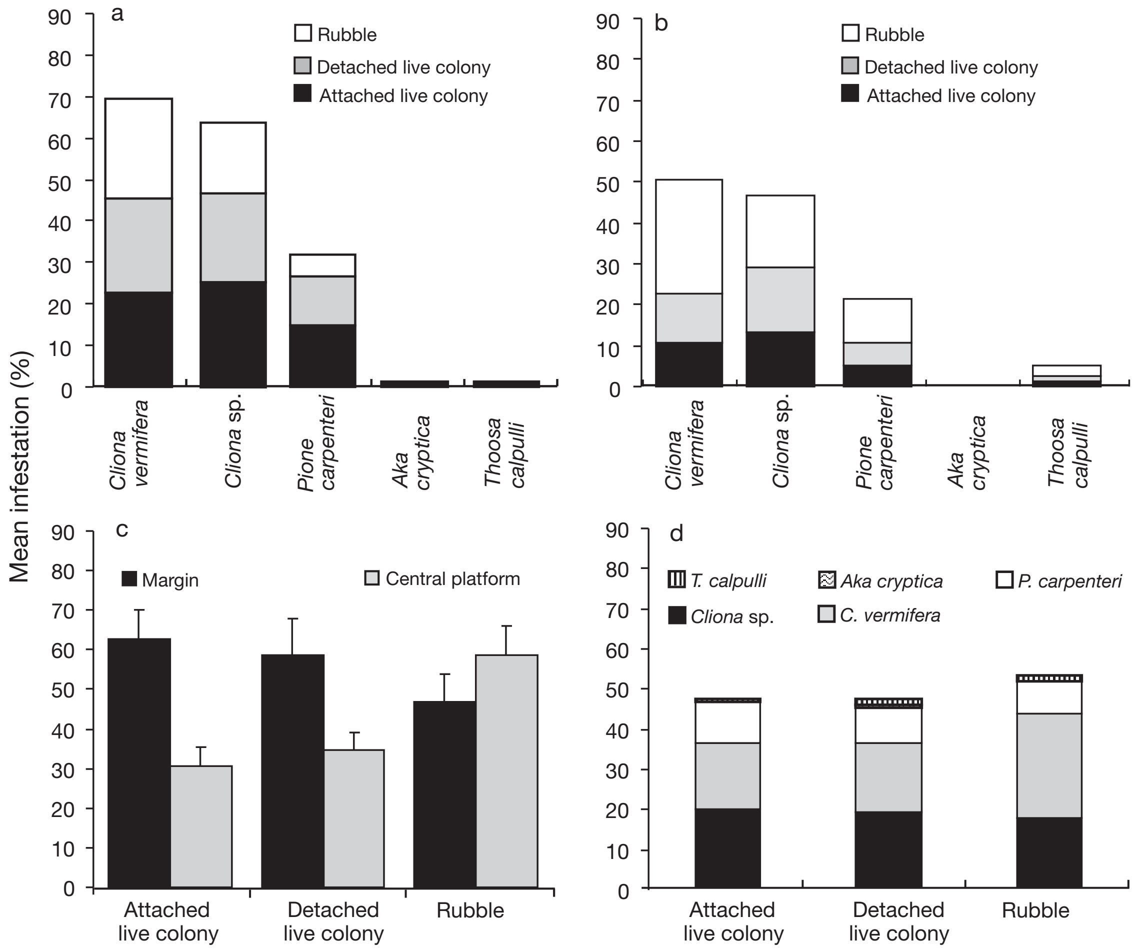

Fig. 5. Boring sponge infestation at La Entrega (LE) reef. Mean percentage of infestation by species (a) in the margin and (b) in the central platform, and by substrata category. (c) Comparison of the percentage of infestation between the margin and central platform. (d) Percentage of infestation by substrata category

Table 2. Number of samples collected (N) and number of these invaded (N_{inv}), percentage of infestation and relative abundance of boring sponge species by reef zone and coral colony category. The abundance of boring sponges was estimated from the number of samples invaded. CP: central platform; AL: attached live; DL: detached live; *Cv*: *Cliona vermifera*; *C*sp: *Cliona* sp.; *Ac*: *Aka cryptica*; *Pc*: *Pione carpenteri*; *Tc*: *Thoosa calpulli*; *Ch*: *Cliothosa hancocki*; *Cm*: *Cliona mucronata*

	N	N_{inv}	Mean infestation (%)	Relative abundance *Cv*	*C*sp	*Ac*	*Pc*	*Tc*	*Ch*	*Cm*
Reef zones										
Margin	450	273	60.6	68.3	61.9	88.6	68.5	28.6	100	100
CP	450	118	26.2	31.3	38.1	11.4	31.5	71.4	0.0	0.0
Colony category										
AL	300	127	42.3	26.1	33.0	41.4	40.7	14.3	100	0.0
DL	300	124	41.3	24.8	39.2	37.1	33.3	28.6	0.0	0.0
Rubble	300	140	46.6	49.1	27.8	21.4	25.9	57.1	0.0	100

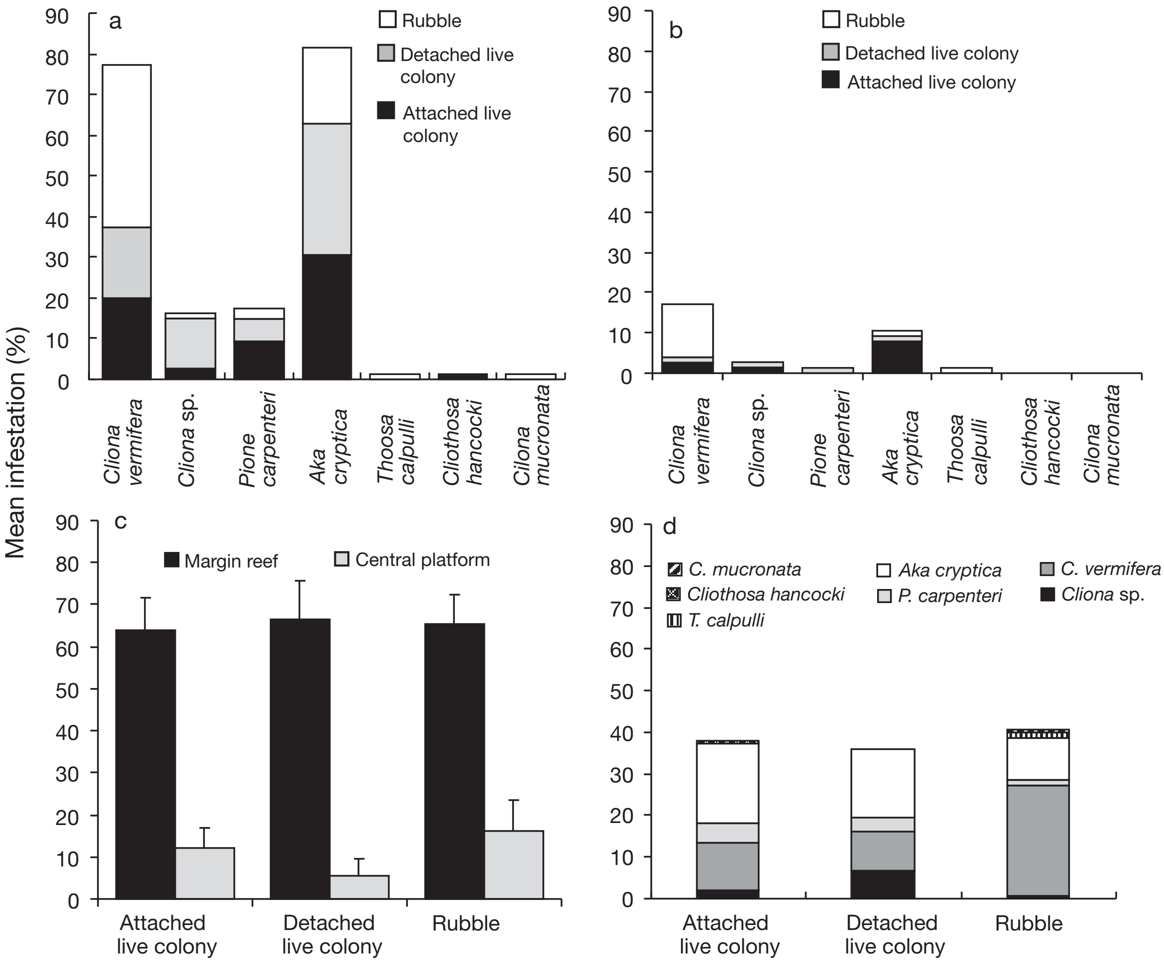

Fig. 6. Boring sponge infestation at San Agustín (SA) reef. Mean percentage of infestation by species (a) in the margin and (b) in the central platform, and by substrata category. (c) Comparison of the percentage of infestation between the margin and central platform. (d) Percentage of infestation by substrata category

detached live coral (Category 2) (Table 2). However, the significant interaction between zone and colony category showed that infestation per category could vary between reef zones. On the central platform of the reefs, rubble was more infected than the other 2 categories, with 37.3% in rubble versus 21% in attached coral and 20% in detached live coral.

Sponge species did not show a strict preference for any of the coral colony categories. *Cliona* sp. was common in the 3 coral categories, but more common in branches of attached and detached live colonies than in rubble (Table 2), while *Cliona vermifera* occurred mainly in coral rubble and less frequently in attached and detached live coral colonies. *Cliona* sp., *Aka cryptica* and *Pione carpenteri* were mostly found invading the dead parts of both detached and attached live colonies, but also inhabited a small quantity of rubble (Table 2). In contrast, *Thoosa calpulli* mainly invaded rubble and was less common in attached and detached live coral colonies. *Cliothosa hancocki* only occupied dead parts of attached live coral colonies, whereas the few specimens of *Cliona mucronata* found during the present study occurred exclusively in rubble (Table 2).

DISCUSSION

In recent years, boring sponges have been profusely studied on the Mexican Pacific coast, although most of these studies have focused on taxonomic descriptions (Carballo et al. 2004, 2007). Thus, the present study is the first to provide data about distribution, abundance, infestation and substrate preferences of boring sponges on 2 different coral reefs from the Pacific coast of Mexico.

The number of boring sponges found on the Huatulco reefs is comparable to that registered for other coral-dominated areas. For example, at Orpheus

Island, Great Central Great Barrier Reef, Australia, Schönberg (2001a) distinguished more than 8 different species of boring sponges, and at Discovery Bay (Jamaica), Perry (1998) reported a dominance of boring sponges in the fore-reef, with a total of 10 species. Other authors like Buznego & Alcolado (1987) reported 12 species of boring sponges in scleractinian corals in the southern and northwest regions of Cuba.

One of the most important results of the present study was that the highest sponge infestation was registered on the margins of both reefs (60.6% vs. 26.2% on the central platform). We attributed this difference to the extensive areas of exposed carbonate substrate on the reef margins, which is easily colonized by boring sponges. Substrate availability for larval settlement is one of the most important factors that control the establishment, distribution and abundance of boring sponges (Kiene & Hutchings 1994, Schönberg 2001a, Schönberg & Wilkinson 2001). The present results highlight the marked effect of the availability of calcareous substrata free of live coral on boring sponge occurrence.

In the Caribbean reefs the effects of sponge boring are also most obvious on deep slopes, where the density of living coral is already low and large areas of bare substrate are available for sponge larval settlement (Goreau & Hartman 1963). However, zone-dependent occurrence may also be related to the different levels of environmental factors to which habitats are subjected, such as wave energy and sedimentation (Macdonald & Perry 2003). Intense sedimentation incurs the risk of burial and is an important factor influencing distribution patterns of boring sponges. Species of the genus *Aka* are well adapted to survive burial and are common in shallow depths and in sandy bays (Rützler 1971). The present study showed that *Aka cryptica* was very abundant on SA, where we registered the highest rate of sedimentation (340 g m^{-2} d^{-1}). At Barbados, rubble collected from the back reef contained significantly fewer clionaid sponges than rubble collected from other reef zones (Holmes 2000). The constant wave action, scour, high sedimentation and occasional burial made this zone comparatively inhospitable to boring sponges. In contrast, the subtidal part of the reef margin usually represents an advantageous habitat for bioeroding sponges due to the low risk of extreme temperatures, exposure and desiccation, such as on the reef flat (Schönberg 2001a), good water circulation and comparatively high concentrations of nutrients (e.g. Wild et al. 2005).

We also found distribution patterns related to the occupied substrata that may also be related to survival abilities and competitive advantages. For example, while *Cliothosa hancocki* can exist at a relatively close distance to live coral tissue, *Cliona mucronata* was only found in dead pieces of rubble. Some species of *Cliona* are able to live in the immediate vicinity of live coral tissue but kill it (e.g. Schönberg & Wilkinson 2001) with the production of toxic mucus (Rützler 1971). The availability of dead substrate per reef or zone will affect spatial distribution patterns.

The presence of bioeroders has been considered a key factor that contributes to the weakening of reef framework (Glynn & Colgan 1992). The pattern reported in the present study may have important implications for the preservation of the reef framework, since it suggests that the destruction of these fringing coral reefs could begin from the outer areas and move toward the interior. In fact, the consequences of long-term boring activity of the sponges were more obvious in the reef margins than in the central platforms, where a high percentage of complete detached live coral heads infected by boring sponges (41.3%) was frequently found. Thus, in the reef margins the consequences of boring go far beyond the mere hollowing out of a few cavities, since by weakening the coral's attachment to the substrate, the sponges accelerate coral loss and deteriorate the reef edge structure. After they are dislodged, the fate of corals depends on the extent of injury suffered when turned over and the possibility of burial (e.g. Goreau & Hartman 1963). But in some cases the effect on the corals may be positive and support asexual propagation (Tunnicliffe 1979). In the Caribbean, it was noted that borers basally broke 87% of the live colonies of *Acropora cervicornis,* mainly by *Cliona aprica*, aiding to the asexual propagation of the coral (Tunnicliffe 1979). We do not know if the same positive effect occurs in *Pocillopora damicornis* branches dislodged from the reef matrix; however, the loss of reef framework in LE during recent years seems to suggest the opposite (Lirman et al. 2001).

Boring sponge abundances have previously been linked to disturbance events on reefs (e.g. Rose & Risk 1985). The present study yielded values (up to 50%) that more closely match boring sponge occurrences previously found on impacted or stressed reefs (Holmes 2000, Macdonald & Perry 2003). In contrast, in well-conserved Caribbean reefs much lower values are reported than those for non-impacted reefs, for example: from 0.8 to 23% in Barbados (MacGeachy 1977), from 13 to 14% in Belize (Highsmith et al. 1983), from 7.7 to 19.4% in Colombia (López-Victoria & Zea 2004) and 14.2% in Cuba (Buznego & Alcolado 1987). It seems that the infestation frequency of boring sponges is always lower than 23% on Caribbean coral reefs considered healthy (MacGeachy 1977, Highsmith et al. 1983, Buznego & Alcolado 1987, López-Victoria & Zea 2004). Thus, it can be argued that the present 2 reefs are, or were, severely disturbed. However, environmental data obtained for LE and SA were incongruent with organic enrichment or eutrophication, factors that are considered highly influential in the increase of boring sponge abundances (Rose & Risk 1985, Holmes 2000, Macdonald & Perry 2003).

Although in general we could consider both reefs unpolluted, important differences between the 2 reefs exist. SA presents a more compact and homogeneous structure (Leyte-Morales 2001), but LE, with the highest frequency of infestation by boring sponges, is currently subjected to intensive tourist activities and unregulated fishing. Moreover, incidents of natural perturbations, such as storms and hurricanes that have had catastrophic effects, have resulted in the deterioration of LE, weakening its structure and causing the detachment of massive corals and big blocks (ca. 1 m^3) (Lirman et al. 2001). Losses of coral cover in LE exacerbated the numerous depressions that cross and interrupt its framework, making it more heterogeneous. An increase in heterogeneity and the area of exposed carbonate surface on the central platform may have promoted bioeroders and may in part explain the differences found between LE and SA, with sponge infestation rates of 41.3 and 11.1%, respectively.

A healthy reef exists in a state of dynamic balance between growth and the coupled effects of bioerosion and wave shock. In healthy non-impacted reefs the rates of reef growth and destruction are generally in balance (Hutchings 1986), but in impacted reefs, the rates of bioerosion greatly exceed the rates of growth (Kiene 1988, Peyrot-Clausade et al. 1995). Thus, the combined effects of natural phenomena and constant anthropogenic impact on LE promote fragmentation, breakage and transportation of big coral colonies, which considerably decrease the coverage of live coral tissue and increase its susceptibility to destruction during hurricanes and storms (Glynn et al. 1998, Lirman et al. 2001). These events lead to increasing amounts of exposed carbonate substrate available, favouring infestation and abundance from boring sponges and other micro- and macroborers, thereby accelerating the natural process of reef degradation.

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