ORIGINAL ARTICLE

Parrotfish mediation in coral mortality and bioerosion by the encrusting, excavating sponge *Cliona tenuis*

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Abstract

The parrotfish *Sparisoma viride* often grazes live coral from edges undermined by the Caribbean encrusting and excavating sponge *Cliona tenuis*. To test whether parrotfish biting action has an effect on the dynamics of the sponge–coral interaction, we manipulated access of parrotfishes to the sponge–coral border in two species of massive corals. When parrotfish had access to the border, *C. tenuis* advanced significantly more slowly into the coral *Siderastrea siderea* than into the coral *Diploria strigosa*. When fish bites were prevented, sponge spread into *S. siderea* was further slowed down but remained the same for *D. strigosa*. Additionally, a thinner layer of the outer coral skeleton was removed by bioerosion when fish were excluded, a condition more pronounced in *D. strigosa* than in *S. siderea*. Thus, the speed of sponge-spread and the extent of bioerosion by parrotfish was coral species-dependent. It is hypothesized that coral skeleton architecture is the main variable associated with such dependency. *Cliona tenuis* spread is slow when undermining live *S. siderea* owing to the coral's compact skeleton. The coral's smooth and hard surface promotes a wide and shallow parrotfish bite morphology, which allows the sponge to overgrow the denuded area and thus advance slightly faster. On the less compact skeleton of the brain coral, *D. strigosa*, sponge spread is more rapid. This coral's rather uneven surface sustains narrower and deeper parrotfish bites which do not facilitate the already fast sponge progress. Parrotfish corallivory thus acts synergistically with *C. tenuis* to further harm corals whose skeletal architecture slows sponge lateral spread. In addition, *C. tenuis* also appears to mediate the predator–prey fish–coral interaction by attracting parrotfish biting.

Introduction

Excavating sponges encrust the reef substratum and aggressively compete for space with sessile reef organisms by overgrowth (Vicente 1978) or by undermining (Schönberg & Wilkinson 2001; Rützler 2002; López-Victoria et al. 2003, 2006). Those that undermine completely eliminate the first few millimeters of the upper portion of substratum, forming a shallow encrusted valley; the edge of the substratum is continually eroded as these sponges spread laterally (for details see Ward & Risk 1977; Acker & Risk 1985; Schönberg & Wilkinson 2001; Rützler 2002;

López-Victoria et al. 2003; Chaves-Fonnegra & Zea 2007). Coral tissue is killed and displaced by an as yet incompletely understood mechanism (Chaves-Fonnegra et al. 2008) at rates that can reach several centimeters per year (Rützler 2002; López-Victoria et al. 2003, 2006).

The lateral growth rates of encrusting, excavating sponges vary between and within sponge and coral species (McKenna 1997; Schönberg 2003; López-Victoria et al. 2006). For example, *Cliona albimarginata* has different boring patterns and rates of advance depending on the substrates it excavates (Calcinai et al. 2007, 2008). Extraneous factors may also influence the rate of advance.

Temperature increase may indirectly accelerate sponge spread by putting stress on the coral (Rützler 2002; but see Márquez *et al.* 2006). Corallivorous fish may also indirectly increase the sponge's rate of advance by biting the coral at the sponge–coral interface (Rützler 2002; López-Victoria *et al.* 2003, 2006). Conversely, spongivorous fish can delay or prevent the sponge's advance over the coral (Hill 1998; Wulff 2006). Also, the abundance of excavating sponges has been positively correlated to grazing activities (Cebrian 2010). Predators often indirectly modify competitive interaction between their prey and other organisms. Fish are leading actors in modifying interactions in marine systems, especially among benthic organisms (Wootton 1993, 1994). There are many examples from coral reefs where fish mediate competition for bottom space between stony corals and macroalgae, usually favoring corals (Lewis 1986; Coye 1993; McCook & Price 1996; Lirman 2001; Mumby *et al.* 2006; Burkepile & Hay 2008; Mumby 2009). Sponge–coral space competitive interactions were demonstrated by Hill (1998), who found that overgrowth of corals by an encrusting sponge could be controlled by angelfish spongivory. The mediating role of fish in sponge–coral interactions has not been widely reported (see Wulff 2006), but must be more common than assumed given the impact fish have on sponge distribution and the frequency of sponge–coral interactions (Dunlap & Pawlik 1996; Pawlik 1998; Wulff 2006). On the other hand, fish mediation via predation does not always benefit corals, as some fish bite them when feeding on adjacent algae, removing live coral tissue or coral recruits and favoring algal recruitment (Miller & Hay 1998). Likewise, herbivorous fish like parrotfish regularly feed on corals, although at lower frequency (Bruggemann *et al.* 1994, 1996), leaving scars on them. When these scars are too large to be regenerated they provide unoccupied space for the colonization of algae and invertebrates (Bruckner *et al.* 2000). The role of parrotfish as incidental yet strong reef bioeroders while feeding on the reef has also been highlighted (Bruggemann *et al.* 1996).

The Caribbean encrusting and excavating sponge, *Cliona tenuis* Zea & Weil 2003, is one of the most effective species at rapidly displacing and killing coral tissue (Zea & Weil 2003; López-Victoria *et al.* 2003, 2006). A mediating effect of fish in *C. tenuis*–coral interactions has been presumed from a few correlative and casual observations. Rützler (2002) mentioned that fish bites on corals may accelerate the speed of sponge spread over it. In previous work (López-Victoria *et al.* 2006), fish corallivory was often observed at the *C. tenuis*–coral boundary. This observation led us to suggest that parrotfish corallivory would (1) favor sponge spread by removing the live coral in front of the advancing sponge and (2) contribute to the bioerosion of the outer coral skeleton, helping form the depression in which the sponge sits. To test these hypotheses, a series of observations and fish exclusion experiments were undertaken in *C. tenuis* colonizing massive reef coral species.

Material and Methods

Study area

This study was carried out in the Islas del Rosario, an emerged coralline archipelago located SW of the city of Cartagena off the continental coast of Colombia (10°7′–10°14′ N; 75°37′–75°52′ W) in the Caribbean Sea. Observations and experiments were carried out at the Pajarales northern fringing reef, at the windward fore-reef (4–6 m depth) where massive corals *Montastraea* spp., *Diploria* spp., and *Siderastrea siderea* (Ellis & Solander, 1786) are interspersed among dense dead thickets and collapsed branches of *Acropora palmata* (Lamarck, 1816). These dead branches are now profusely covered by *Cliona tenuis*. Massive corals are also being colonized by this sponge (López-Victoria & Zea 2004).

Experimental set-up

Fish were experimentally excluded from *Cliona tenuis*-live coral boundaries to determine whether they had an effect on (i) sponge–coral boundary dynamics (lateral advance or retreat) and (ii) the bioerosion of the upper layer of the coral skeleton. *Cliona tenuis*-colonized coral colonies of the massive starlet coral *Siderastrea siderea* (n = 14) and the symmetric brain coral *Diploria strigosa* (Dana 1846; n = 12) were located and tagged in August 2004. Care was taken to only choose cases in which *C. tenuis* and its host coral colony were confronting each other at an angle ≥180°. At this confronting angle, simultaneous sponge advance and coral retreat is most likely. It is only in this configuration that the excavating tissue filaments of the sponge can reach the basal portion of the coral polyps and elicit coral retreat (López-Victoria *et al.* 2006).

Fish access to the sponge–coral boundary was prevented by a rectangular piece (up to 10 × 20 cm) of hard, 3-cm mesh Vexar plastic net fastened with plastic cable ties to four 2.5–3″-long steel nails (Fig. 1A). The net was tied horizontally (tangentially to the surface) approximately 2–3 cm above the surface to prevent contact with live tissue and to allow water circulation. Net-supporting nails driven into the sponge side (hereafter called enclosed nails) were used as a reference for measuring *C. tenuis* and coral lateral advance or retreat when fish were excluded (see below). Two to three additional nails were driven in the sponge tissue on a free portion of the sponge–coral boundary, usually adjacent to the enclosing net. These nails (hereafter called open nails) were used to
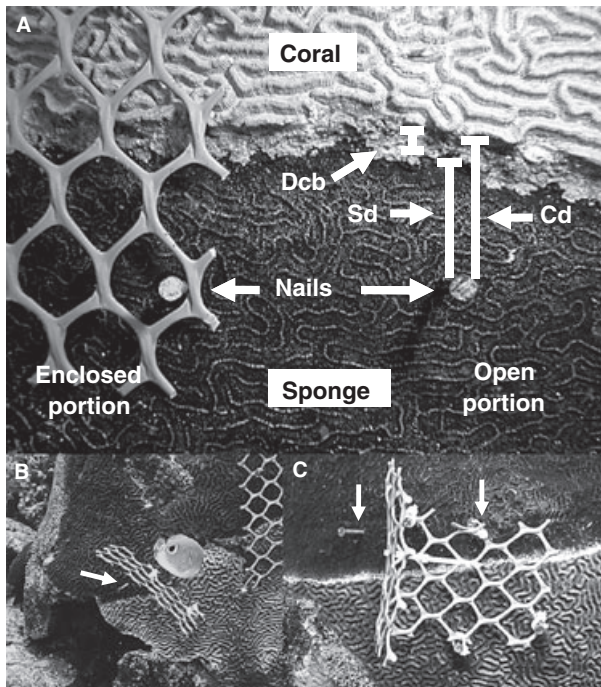
Fig. 1. Experimental fish exclusion net placed on the encrusting, excavating sponge *Cliona tenuis*–coral boundary. The coral is *Diploria strigosa*. (A) Measurements taken from the reference nails to establish sponge and coral lateral advance or retreat speed in the enclosed and open portions. Cd, distance to the coral; Sd, distance to the sponge; Dcb, dead coral band width. (B,C) Control nets for quantitative measurements of sponge and coral advance or retreat, placed vertically (in relation to the colony surface) at the boundary. Scale: plastic net internal mesh size was 3 cm.

measure sponge and coral lateral advance or retreat in the natural situation (fish not excluded, open boundary). Both enclosed and open nails were driven into the sponge approximately 3–5 cm away from the coral boundary to avoid interference with sponge–coral interactions.

We chose this method of localized, small-scale fish exclusion instead of the typical complete coral colony enclosure (Tanner 1995; Hill 1998; Miller & Hay 1998) for two reasons. First, large nets and structures would be easily lost to strong surge and to local fishermen and divers. Second, the lateral advance of *C. tenuis* is known to vary a great deal between coral colonies (López-Victoria *et al.* 2006; Márquez *et al.* 2006) so that comparing open *versus* enclosed boundaries would be more effective within the same sponge–coral pair, and preferably on adjacent portions of substratum.

Two different types of control were used for testing for unwanted net effects, one qualitative and the other quantitative. Qualitative controls consisted of square pieces of net placed above coral and sponge tissue some distance away from the interacting boundary in all sponge–coral pairs (Fig. 2C,D). These were used for assessing how
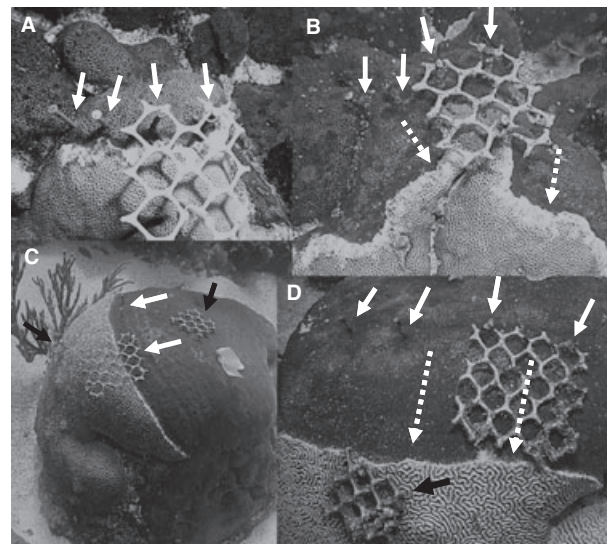

Fig. 2. Examples of the effect of fish exclusion on the lateral advance of the sponge *Cliona tenuis* into the corals *Siderastrea siderea* (A: initial; B: 13 months after exclusion) and *Diploria strigosa* (C: initial; D: 13 months after exclusion). Solid white arrows show the reference nails; hatched white arrows show the distance advanced by the sponge and retreated by the coral in 13 months; black arrows mark the position of qualitative control nets placed inside coral and sponge tissue, horizontally in relation to the surface. Notice little or no sponge advance and coral retreat under the net in *S. siderea* and similarly large advance and retreat under and off the net in *D. strigosa*.

shading and modification of currents and local conditions affected sponge or coral tissue underneath enclosure nets. Quantitative controls consisted of square pieces of net placed vertically (perpendicular to the coral surface) across the sponge–coral boundary; one to two nails (hereafter called control nails) were driven into the sponge tissue adjacent to each net to measure sponge and coral advance or retreat under the influence of these control nets (Fig. 1B,C). These nets allowed fish access while presumably generating the physical effects of a horizontally orientated net (*e.g.* partial shading, change in currents). They were only installed on six of the *Siderastrea siderea* and four of the *Diploria strigosa* marked colonies.

Nets and nails were left in place for 13 months, with one visit after 6 months to take measurements and for maintenance. Qualitative controls were installed at the beginning of the experiment and quantitative controls were deployed at 6 months. Nets and nails placed in coral tissue were removed at the end of the experiment, but nails in sponge tissue were left for future monitoring.

Sponge–coral boundary dynamics

The width of the dead coral band (Dcb) between the sponge and coral tissues often varies in excavating

sponge–coral interactions (Chaves-Fonnegra *et al.* 2005; López-Victoria *et al.* 2006; Chaves-Fonnegra & Zea 2007, in press). Distance from reference nails (enclosed, open, control) to the edge of the sponge (Sd) and to the live coral (Cd; Fig. 1A) were measured with plastic calipers (0.5 mm precision) at the beginning, after 6 months and then after 13 months to estimate sponge and coral advance or retreat rates and changes in dead coral band Dcb width. Differences between final (13th month) and initial distances were used for calculating annual (365-day) sponge and coral tissue lateral advance or retreat rates. In several cases, measurements were only available for the first 6 months or only for the last 7 months. In these cases, rates were calculated for the measurement interval and then extrapolated to 1 year. The difference between Sd and Cd was used for calculating Dcb width at each visit (Fig. 1). Notes were taken regarding Dcb characteristics during each visit (presence of organisms, sediment and parrotfish bite marks).

Bioerosion of the upper layer of the coral skeleton

The difference in height between coral tissue and sponge tissue at the sponge–coral border was measured in open and enclosed portions to determine how much fish biting could be aiding the sponge in removing the outer layer of the coral skeleton. These measurements were made at the end of the experiment by placing the butt of the caliper vertically on the coral border and lowering the shaft down to the sponge level. The height of the open portion provided a measurement of the combined bioerosion from fish and sponge, whereas the difference in height between open and enclosed portions reflected that of the sponge alone.

Data analysis

A single datum was obtained for each fish exclusion treatment (open, enclosed, control) for each sponge–coral pair by averaging the measurements taken for the reference nails (one to three nails per treatment per sponge–coral interaction). Mean annual rates of lateral sponge and coral advance or retreat, Dcb, width and coral–sponge tissue height difference were separately compared between exclusion levels (open, enclosed) using a completely randomized block ANOVA (blocked by sponge–coral pairs). This analysis was done separately for those cases in which perpendicular control nets were added, resulting in three levels of fish exclusion factor (open, enclosed, control) with least significant difference (LSD) *a posteriori* multiple comparisons between level means. The above tests were performed separately for each coral species because assumptions were never met when coral species were

added as a factor in more complex ANOVA (factors: coral species, sponge–coral pairs nested within coral species, exclusion; see Milliken & Johnson 1992), even after several standard transformations. Mann–Whitney non-parametric tests were carried out to compare lateral advance or retreat rates between coral species in the natural situation (portions open to fish). Student *t*-tests were used to test for differences among species in the heights of coral and sponge tissues at the interface (Sokal & Rohlf 1981).

Results

Qualitative effect of nets

Locally abundant herbivorous fish kept most nets continually clean of macroalgae at the study site, with only crustose and filamentous algae colonizing them (Fig. 2B,D). A few enclosure nets were fouled by macroalgae, a situation that had deleterious effects on the underlying sponge or coral tissue. Measurements for those interactions were excluded from the analyses. In some cases, macroalgae became established on nails, bleaching and smothering the surrounding sponge tissue. However, as adjacent tissue remained healthy, it was almost always possible to measure accurately the distances advanced or retreated. There was only a slight darkening of coral tissue under a few qualitative control nets placed horizontally over coral tissue (Fig. 2C,D) and there was no discernible effect under those placed over sponge tissue.

Effect of fish on sponge–coral boundary dynamics

All coral margins of marked sponge–coral boundaries showed evidence of fish bites. In fact, parrotfish (*Sparisoma viride* Bonnaterre, 1788, *Scarus* spp.) and wrasses (*Thalassoma bifasciatum* Bloch, 1791) were repeatedly observed biting at the substratum between the sponge and the coral as well as at the coral margin adjoining the sponge. This behavior was observed in both coral species, but was seen more frequently in *Diploria strigosa*. The butterflyfish, *Chaetodon capistratus* Linnaeus, 1758, was also seen consuming boundary coral polyps of *D. strigosa*. However, only *Sparisoma viride* produced clear bite scars on corals, so the observed fish bites could be attributed to this species. It is also likely that this parrotfish was the only fish completely excluded given the mesh size of the net. It was thus assumed that any discernible influence on sponge or coral advance or retreat rates or Dcb width was exclusively the result of *S. viride* corallivory. Corroborating this assumption, *S. viride* was seen foraging on the previously inaccessible coral border within minutes of the final removal of experimental nets at the conclusion of

the experiment; an activity that left wide white scars. Clearly, the sponge-undermined coral margin attracted this parrotfish species.

The natural rate of advance (fish not excluded, open nails) for *Cliona tenuis* was, on average, significantly greater in *D. strigosa* (8.0 ± 1.7 cm·year^{-1}, n = 9) than in *S. siderea* (3.5 ± 0.6 cm·year^{-1}, n = 12; Kruskal–Wallis, P = 0.02). Regarding fish exclusion, the results are presented separately below for each coral species, as its effect on *C. tenuis* advance rates varied between these two corals.

Cliona tenuis versus Siderastrea siderea

Parrotfish biting at the margin between *Siderastrea siderea* and *Cliona tenuis* left a rasped, slightly dipped band a few cm wide. This Dcb was either white (recently rasped) or already slightly colonized by filamentous algae (see Figs 2A,B and 5C). Two of the 14 marked sponge–coral pairs were disregarded (one could not be found and one had its net fouled by macroalgae). Annual lateral advance or retreat rates by *C. tenuis* into *S. siderea* varied significantly between fish exclusion treatments (completely randomized block ANOVA with coral colonies as blocks, data $\log_{10}[x + 100]$ transformed; $F_{1,11} = 26.1$, P = 0.0003 for the sponge; $F_{1,11} = 31.0$, P = 0.0002 for the coral, n = 12). *Cliona tenuis* advanced an average of 3.4 cm·year^{-1} in the open portion [notice that this mean was different from that given above for comparing coral species because it was back-transformed from logarithms; 2.2–4.7 cm·year^{-1} confidence limits (CL)], whereas *S. siderea* retreated 2.2 cm·year^{-1} on average (CL 1.3– 3.2 cm·year^{-1}; Fig. 3). The parrotfish-rasped coral margin was present during the three visits in all but three colonies, which were seen rasped during only one visit. By contrast, the sponge only advanced an average of 0.6 cm· year^{-1} in the enclosed portion (CL 0.1–1.1 cm·year^{-1}) and the coral recovered an average of 0.5 cm·year^{-1} (mean retreat −0.5 cm·year^{-1}, CL −0.9 to 0.1 cm·year^{-1}; note that negative coral retreat values implied recovery; Figs 2A,B and 3). The coral recovered part of its former extent in eight of the 12 enclosed portions and the sponge either partially advanced into the rasped band or even receded. The sponge spread into the previously bitten coral in the remaining four enclosed areas and advanced slightly further against live coral. Concomitant to all the above, the Dcb between live sponge and coral tissue in the open portion remained rather wide throughout the duration of the experiment (mean ± 1 SE: 1.8 ± 0.4 cm, n = 7 at the beginning *versus* 1.0 ± 0.3 cm, n = 9 at the end), whereas it narrowed greatly in the enclosed portion (mean changed from 1.3 ± 0.2 cm, n = 7, to 0.2 ± 0.1 cm, n = 9), being significantly narrower than
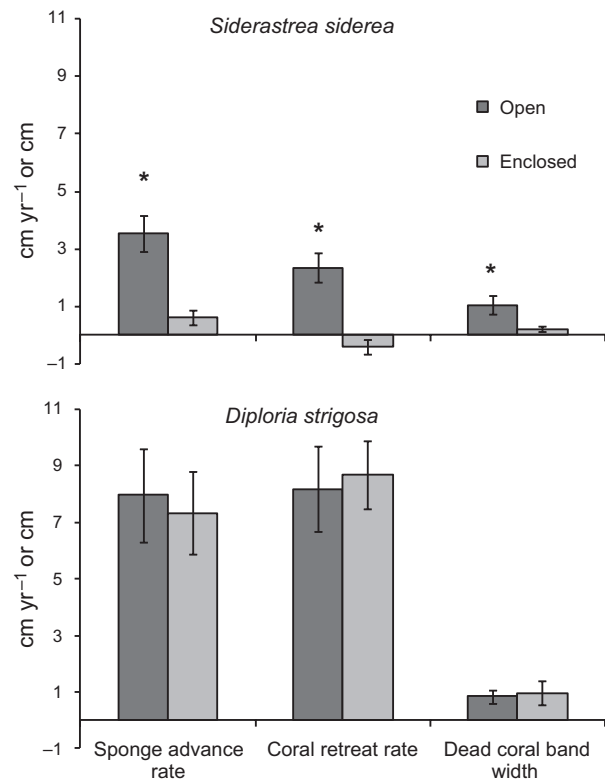

Fig. 3. Mean sponge lateral advance and co-occurring coral retreat and dead coral band width (at the end of the experiment) in *Cliona tenuis*–coral interactions (*Siderastrea siderea*, *Diploria strigosa*) comparing enclosed *versus* open portions. Error bars are ±1 SE. Asterisks represent significant differences between open *versus* enclosed portions (completely randomized block ANOVA, coral colonies being blocks, P < 0.05).

the open portion at the end of the experiment (randomized block ANOVA, $\log_{10}$ transformed data, $F_{1,7} = 9.3$, P = 0.018, n = 9, Fig. 3). Whereas incipient algal turfs developed at the Dcb in open portions wherever parrotfish rasping receded, the closing of the Dcb by sponge growth under enclosure nets generally prevented algae establishment. *Cliona tenuis* thus significantly advanced into *S. siderea* thanks to fairly continuous fish corallivory. The gap between the sponge and the coral closed in the absence of fish and sponge spread slowed down.

Cliona tenuis advanced significantly faster into *S. side-rea* next to vertical control nets (5.7 ± 0.7 cm·year^{-1}) than in open (3.0 ± 0.9 cm·year^{-1}) and enclosed boundaries (0.0 ± 0.6 cm·year^{-1}; randomized block ANOVA, $F_{2,5} = 15.8$, P = 0.0008, n = 6; LSD multiple range test; Fig. 4). The coral retreated or recovered in parallel to the sponge (control 6.4 ± 1.0 cm·year^{-1}, open 2.1 ± 0.9 cm·year^{-1}, enclosed -0.3 ± 0.5 cm·year^{-1}; randomized block ANOVA, $F_{2,5} = 14.9$, P = 0.001, n = 6), although open and enclosed portions were statistically similar to
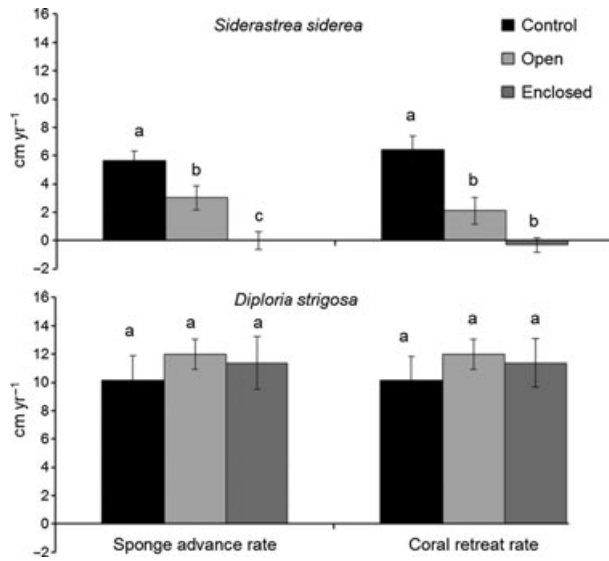
Fig. 4. Mean sponge lateral advance and concomitant coral retreat in *Cliona tenuis*-coral (*Siderastrea siderea*, *Diploria strigosa*) pairs in open, enclosed and control portions. Error bars are ±1 SE. Bars sharing the same letter are not significantly different (completely randomized block ANOVA, coral colonies being blocks, and LSD multiple range test, carried out separately for sponge advance and coral retreat, $P < 0.05$).

each other (LSD multiple range test, Fig. 4). Faster sponge advance and coral retreat beside control nets would indicate that enclosure nets had additional positive effects on sponges and deleterious effects on corals. However, since corals tended to recover from fish bites and sponges slowed down under enclosure nets, it can be concluded that enclosure did not have any discernible effect, other than preventing parrotfish from entering the sponge–coral boundary.

Cliona tenuis versus Diploria strigosa

Parrotfish bites at the *Diploria strigosa* coral margin confronting the sponge removed the upper skeletal ridges in chunks, flattening them completely and leaving an irregular and often discontinuous dead band about 0.5–1 cm wide. The band was either bare or already colonized by incipient turf algae and filled with sediments (Figs 1, 2C,D and 5B). Three of the 12 experimental sponge–coral pairs were disregarded (one with net fouled by macroalgae, one in which the sponge advanced to the outer edge of the coral and thus the time frame was unknown, and one in which the coral escaped the sponge, growing upwards). In contrast to *Siderastrea siderea*, *C. tenuis* advanced into *D. strigosa* at a similar average speed in open (8.0 ± 1.7 cm·year^{-1}) and enclosed (7.3 ± 1.4 cm·year^{-1}) portions (randomized block ANOVA, $F_{1,8} = 0.32$,
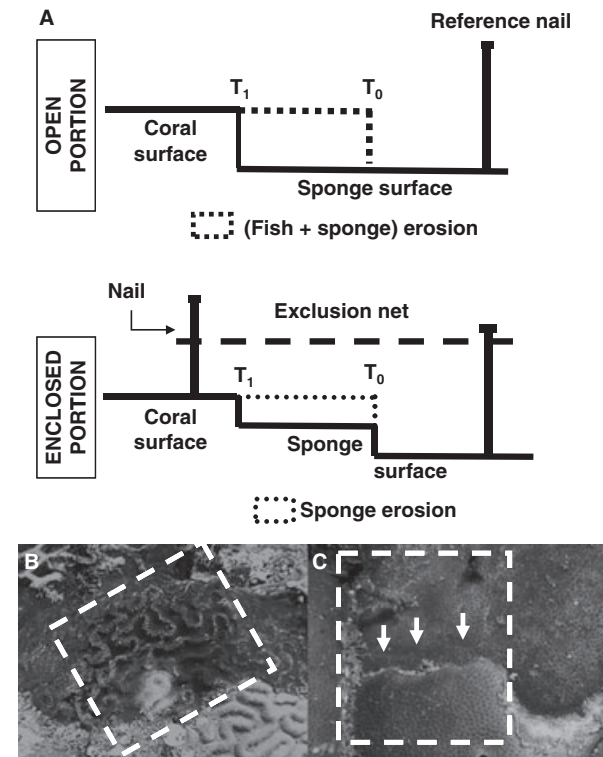

Fig. 5. (A) Schematic drawing comparing the relative level of the outer surface of *Cliona tenuis* in a coral when fish had access to the sponge–coral boundary (upper drawing) to its level when fish access was prevented by the experimental net (lower drawing). T_0 = time of initial marking and placement of net; T_1 = end of the experiment. Dotted areas show the fraction of the totally removed superficial coral skeleton. There was a portion of coral skeleton (1–2 cm deep) under the sponge which had been partially eroded by the sponge (not shown). (B,C) Advance of *C. tenuis* under enclosure nets (removed to take the photo, the original placement is shown by the hatched frames) for (B) *Diploria strigosa* (the bleached spot in the sponge was produced by algae attached to the net-supporting nail) and (C) *Siderastrea siderea* [the original boundary is marked by white arrows; only a slight difference in height between the initial and final sponge level was seen; notice coral has grown upwards under the net (left side of picture) and has retreated by fish corallivory in the open portion (right side of the picture)].

$P = 0.58$, $n = 9$). Coral retreat followed sponge advance (enclosed 8.7 ± 1.2 cm·year^{-1}, open 8.2 ± 1.5 cm·year^{-1}; ANOVA $F_{1,8} = 0.3$, $P = 0.60$, $n = 9$, Figs 2B,C and 3). There was a great deal of variability in advance or retreat rates between sponge–coral pairs, but rates within pairs were similar for enclosed and open portions, showing that fish exclusion did not have a consistent effect. The width of the boundary between the live sponge and coral tissue remained constantly narrow throughout the study period in both the excluded portion (from 0.5 ± 0.2 to 1.0 ± 0.4 cm, $n = 8$) and the open portion (from 0.7 ± 0.3 to

0.8 ± 0.3 cm, n = 8), being not significantly different at the end of the experiment in either portion (randomized block ANOVA $F_{1,7}$ = 0.20, P = 0.67, n = 8, Fig. 3). Bare skeleton could often be seen under the enclosure nets where the coral polyps had become detached, although in some cases, *C. tenuis* closed the gap and was almost touching live coral. In other cases, turfs of algae had become established at the enclosed boundary but they had been overrun thereafter by the sponge. The experimental prevention of fish corallivory at the margin of *D. strigosa* confronting *C. tenuis* thus did not change the speed at which the sponge spread.

Sponge advance and coral retreat next to vertical control nets were not significantly different in enclosed and open portions (sponge advance: 10.1 ± 1.7 cm·year^{-1}; randomized block ANOVA, $F_{2,6}$ = 0.70, P = 0.53, n = 4, coral retreat: 10.5 ± 1.7 cm·year^{-1}; $F_{2,6}$ = 0.49, P = 0.63, n = 4, Fig. 4). Thus, any deleterious or positive effects of the enclosure nets on *C. tenuis* and *D. strigosa* rates of advance or retreat were dismissed.

Effect of fish on removal of the outer coral skeleton layer

At the end of the experiment it became obvious that in cases where the sponge had advanced, the level of the new sponge tissue was higher in the enclosed portions than in those portions to which fish had access (Fig. 5A). This was especially conspicuous in *Diploria strigosa* where the new sponge tissue segment under the net overgrew intact ridges of the coral skeleton, whereas these structures were completely flattened in the open portions (Fig. 5B, a previously enclosed portion of *D. strigosa* showing the most extreme case). Indeed, the sponge excavation level was significantly shallower in enclosed portions of this coral species (enclosed 4 ± 1 mm *versus* open 6 ± 1 mm, randomized block ANOVA, $F_{1,9}$ = 10.0, P = 0.011). Thus, without the aid of fish, *Cliona tenuis* removed approximately the upper 4 mm of *D. strigosa* skeleton on average, whereas the upper 6 mm was removed when fish bit at the coral margin.

New growth of *C. tenuis* to a higher level in *Siderastrea siderea* enclosed portions, although occurring, was less frequently apparent because the sponge advanced very little under the net (Fig. 5C). Furthermore, the coral's frequent recovery at the border in the enclosed portion, which included slight upward growth, made the measurement of differences in height between coral and sponge tissue an unreliable estimator of sponge growth level in the absence of fish. Indeed, measurements of coral height in relation to sponge level in the enclosed border were not significantly different from those in open portions (5 ± 0.4 mm *versus* 6 ± 0.4 mm, $F_{1,14}$ = 0.42, P = 0.529). Unfortunately, we were not aware of this fact when we

carried out measurements, it only became evident after detailed analysis of photographs. Measuring the difference in sponge height at the end of the experiment at the point at which the sponge was originally located when the enclosure was made would have been more appropriate (in Fig. 5A, measuring at time T_1 the height of the step located at point T_0).

Discussion

Our fish exclusion experiments revealed a role of parrotfish predation in mediating spatial competitive interactions between the encrusting, excavating sponge *Cliona tenuis* and reef corals. However, this role was coral species-dependent. By biting coral at the sponge–coral interface, the parrotfish, *Sparisoma viride,* indirectly facilitated the lateral advance of *C. tenuis* into the coral *Siderastrea siderea*, but not into the coral *Diploria strigosa*.

Even with facilitation by parrotfish, *C. tenuis* advance into *S. siderea* was still significantly slower than into *D. strigosa* (see also López-Victoria *et al.* 2006). There thus seemed to be a correlation between mediation by parrotfish corallivory and the difficulty with which *C. tenuis* advanced into a given coral species. The intrinsic properties of coral species responsible for enhancing or inhibiting sponge lateral advance speed could be defensive abilities or skeletal characteristics. As coral defensive abilities are greater in *D. strigosa* than in *S. siderea* (when tested against each other and other corals, see Logan 1984) they cannot explain *C. tenuis* speed of advance (López-Victoria *et al.* 2006).

Regarding coral skeleton internal properties, Calcinai *et al.* (2007, 2008) observed that *Cliona albimarginata* growth rate and excavation patterns are different depending on the mineralogical and microtexture characteristics of the calcareous substrata it excavates. Also, sponge bioerosion rates and tissue volume growth have been positively correlated to coral skeletal density and porosity. *Cliona orientalis* Thiele 1900, an Indopacific sponge very similar in habit to *C. tenuis*, causes greater bioerosion and increases its tissue volume faster in corals having denser, less porous skeletons and with more structural barriers than in less dense, more porous ones (Schönberg 2002, 2003). However, it is not clear whether overall tissue volume growth or bioerosion rates, as measured by Schönberg (2002, 2003), are positively correlated to lateral tissue spread, as measured here. If they are, one would expect a slightly faster lateral growth in *S. siderea* with its slightly greater skeletal density than *D. strigosa* (1.61 g·cm^{-3} *versus* 1.57 g·cm^{-3}, see Hughes 1987), which was not the case. Detailed studies of sponge excavation progress have shown that sponges tend to first occupy the most porous areas of the substratum such as coral calices

and then widen them by erosion (Ward & Risk 1977; see review in Schönberg 2003). It is therefore possible that in corals of about the same skeletal density, such as *S. siderea* and *D. strigosa*, the rate of lateral advance by an encrusting and excavating sponge depends more on differences in skeletal architecture, *e.g.* how large and continuous skeletal pores are and how thick and continuous skeletal barriers are. Indeed, *S. siderea* calices and thecae have many but rather small pores (Ogilvie 1896; pers. obs. by S.Z. in ground and polished histological sections), while *D. strigosa* skeleton is more open and labyrinthine (Helmle *et al.* 2000; pers. obs. by S.Z. in ground and polished sections). *Cliona tenuis* would thus have difficulty in filling such small spaces in *S. siderea* and would need to erode more to advance within the skeleton, whereas it would be much easier to advance relatively unimpeded through the wider spaces of *D. strigosa*.

With reference to the external properties of coral skeletons, it was found that parrotfish bites leave different marks on both studied coral species in a clear relation to their outer skeleton's texture and compactness. Concentrated and recurrent or focused biting by parrotfish in coral colony margins or crests is a common phenomenon in coral reefs (Bruckner & Bruckner 1998; Bruckner *et al.* 2000). This focused biting also occurred at most, if not all, margins of corals being actively undermined by *C. tenuis* (*e.g.* in confronting angles ≥180°) in the study area. The cerioid colony morphology of *S. siderea*, having a rather even and more compact surface, is widely rasped by parrotfish, whereas portions of the brittle ridges in the meandroid surface of *D. strigosa* are removed in chunks that are narrower and deeper. Our previous studies have shown that lateral advance rates of *C. tenuis* and other encrusting and excavating sponges are greater in denuded coral or in clean blocks of coral skeletons than when directly confronting live coral tissue or heavily fouled substrata (López-Victoria *et al.* 2003, 2006; Chaves-Fonnegra & Zea 2011). Thus, when fish corallivory on *S. siderea* removes the upper live coral layer, *C. tenuis* can spread faster than when there is no corallivory, probably because it can overgrow the coral tissue-free skeletal surface. In the latter situation, it can fill spaces and widen galleries from above, achieving a greater lateral speed than when it has to undermine and displace live coral from below in the absence of fish corallivory. By contrast, fish biting the surface in *D. strigosa* is usually not wide enough to help increase (on the surface) the presumably already fast spread of *C. tenuis* tissues inside the coral skeleton.

Apart from the mediation by parrotfishes in the advance of *C. tenuis*, our experimental results confirm a previous suggestion by López-Victoria *et al.* (2006) that fish corallivory contributes to the removal (bioerosion) of the coral skeleton's external layer, which would otherwise have been entirely attributed to the spreading excavating sponges themselves. Parrotfish, such as *Sparisoma viride*, leave rather deep feeding scars in corals and calcareous substrata (Bellwood & Choat 1990; Bruggemann *et al.* 1996; Bruckner *et al.* 2000). In this case, parrotfish clearly contribute to the bioerosion of the outer coral skeleton by removing the coral in front of the advancing *C. tenuis*. Indeed, whenever fish were excluded from the sponge–coral boundary, *C. tenuis* grew in a shallower depression than when fish had access. The qualitative observation of deeper biting by parrotfish in *D. strigosa* than in *S. siderea* (our data was unreliable for quantitative comparison of the depth of parrotfish bioerosion between coral species) suggested that differences in architecture and compactness of the coral skeletons mentioned above also play a role in determining the extent of parrotfish bioerosion effects, as they do in sponge advance. Accordingly, Littler *et al.* (1989) found that *S. viride* bites were deeper on *Porites porites* than on *Porites astreoides,* a fact that they correlated to a harder corallum at the subsurface level in the latter species.

Corallivory in Caribbean reef corals is not intensive, occurring in both even and ridged portions of coral colonies (Bruggemann *et al.* 1994; Reyes-Nivia *et al.* 2004). Interestingly, in the study area, parrotfish seemed to prefer feeding on the coral margins adjacent to *C. tenuis*. This preference was further demonstrated at the end of our experiments when, immediately upon the retrieval of nets, parrotfish actively fed on the coral at the previously excluded margin. Biting is perhaps encouraged by the presence of a step at the margin or because the polyps have their skeletal support partially undermined by the sponge (López-Victoria *et al.* 2006). The sponge is thus indirectly modifying the predator–prey fish–coral interaction by attracting the fish. Whatever the reason for this attraction, *C. tenuis* and parrotfish corallivory are acting synergistically against live coral, at least in corals such as *S. siderea*, whose skeletons make sponge advance more difficult.

Conclusions

The mediating role of fish corallivory in the competitive interaction between encrusting and excavating sponges and reef corals seems to occur in two complementary ways. First, the speed at which the sponge advances laterally, displacing live coral, may be influenced by fish corallivory. Second, by preferentially biting the coral edge adjoining the sponge, corallivorous fish are responsible for part of the coral outer skeleton's bioerosion. Both vary with coral species. We hypothesized that the extent of the influence of fish corallivory on both sponge spread and bioerosion depends on coral skeleton architecture

and compactness. In the coral *Siderastrea siderea*, parrotfish scraped with wide, shallow bites on the relatively even coral surface, allowing the sponge to overgrow the denuded area. *Cliona tenuis* thus advances faster than when live coral is not removed and the sponge has to directly erode the more compact skeleton. In the brain coral *Diploria strigosa*, with its uneven surface and a much more open and labyrinthine skeleton, parrotfish biting is deeper and narrower, not being wide enough to enhance or facilitate the already fast progress of the sponge inside the skeleton's looser arrangement.

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