Storm-mediated coral colonization by an excavating Caribbean sponge

Mateo López-Victoria[1,2], Sven Zea[2,*]

[1]Instituto de Investigaciones Marinas y Costeras–INVEMAR, Cerro Punta de Betín, A.A.1016, Santa Marta, Colombia

[2]Departamento de Biología and Centro de Estudios en Ciencias del Mar–CECIMAR, Universidad Nacional de Colombia, INVEMAR, Cerro Punta de Betín, A.A. 10–16, Santa Marta, Colombia

ABSTRACT: The broken, dead stands of the Caribbean elkhorn coral *Acropora palmata*, which suffered massive mortalities from disease and bleaching during the early 1980s, are now widely covered by *Cliona tenuis*, an encrusting and excavating brown sponge (Hadromerida, Clionaidae). This sponge displaces live coral tissue by undermining the polypal skeletal support. On the windward fringing reef of Islas del Rosario (Colombian Caribbean), 26% of *C. tenuis* individuals currently dwelling on live corals had colonized their host from sponge-carrying branches of *A. palmata* thrown against the corals during storms. Times of initial colonization were traced back from sponge growth rates in a few marked massive coral colonies and found to coincide approximately with hurricanes that had affected the area. Transplantation experiments confirmed that *C. tenuis* is able to spread to new coral hosts from attached fragments. The extent of *C. tenuis* dispersion via branching coral fragments and further massive coral colonization is now evident and, given that *C. tenuis*-encrusted *A. palmata* fragments are becoming progressively smaller, the phenomenon is likely to increase. *C. tenuis* was also found undermining encrusting and foliose corals settled on dead *A. palmata* branches, thus also retarding the process of reef recovery to an unknown degree.

KEY WORDS: *Cliona tenuis* · *Acropora palmata* · Excavating sponge · Dispersion · Colonization · Coral · Storms

1. INTRODUCTION

Tropical storms and hurricanes are among the many forces that control coral reef community structure (Birkeland 1997), frequently causing upturning and fragmentation of sessile invertebrates (e.g. Rogers et al. 1982, Rützler & Macintyre 1982, Edmunds & Witman 1991, Wulff 1995). The dominant species composition in Caribbean shallow reef zones has changed dramatically since the early 1980s, after the massive mortality of acroporid corals from disease and bleaching (Hughes 1994). *Cliona tenuis*, a brown encrusting and excavating, zooxanthellate-bearing sponge (Porifera, Demospongiae, Hadromerida, Clionaidae, see taxonomy in Zea & Weil 2003), progressively occupied the newly available substratum (Cortés et al. 1984, Williams et al. 1999, López-Victoria et al. in press). This and other encrusting sponges of the genus *Cliona* are able to erode and spread laterally even when the adjacent space is covered with live tissue of several other organisms. By sending out pioneering excavating tissue filaments just beneath the surface, these sponges undermine the skeletal support of coral polyps, inducing their retraction and death despite their above-substratum defense mechanisms (Schönberg & Wilkinson 2001, Rützler 2002, López-Victoria et al. in press). Thus, in addition to the traditional role of bioerosion of reef framework and sediment production attributed to excavating sponges (Rützler 1975, Wilkinson 1983), their role in substratum monopolization has also become evident (e.g. McKenna 1997, Schönberg & Wilkinson 2001, Rützler 2002).

Cliona tenuis is widely distributed on shallow Caribbean reefs, and each individual can encrust up to several square meters of light-exposed substratum with a thin veneer of brownish tissue, excavating and filling

the upper 1 to 2 cm (see Acker & Risk 1985, Williams et al. 1999, Rützler 2002 [*C. caribbaea* or *C. langae*], Zea & Weil 2003). During a study of coral-encrusting *C. tenuis* interaction mechanisms (López-Victoria 2003, López-Victoria et al. in press), we noticed that several massive coral colonies which had *C. tenuis* spreading on them had sponge-carrying loose branches of dead *Acropora palmata* leaning against them. We hypothesized that the corals had been initially colonized by *C. tenuis* from the branch. From their size (up to 1–2 m in the largest dimension), we assumed that these branches had been shifted during major storms. We then re-interpreted previously obtained data in light of these findings, and undertook new observations and experiments to: (1) determine if the current direction of sponge growth was away from the leaning branch; (2) carry out a retrospective analysis of sponge growth to determine if estimated dates of initial colonization of corals with leaning sponge-colonized branches were concurrent with past major storms; (3) determine experimentally the likelihood of sponge colonization from fragments and the subsequent advance against live coral tissue; (4) establish the relative importance of various means of apparent colonization of corals by the sponge; and (5) ascertain some current and future effects of sponge dispersion and coral colonization mechanisms on the reef community.

2. MATERIALS AND METHODS

The phenomenon was studied at 2 sites on the northern, windward fringing reef of Islas de Rosario, Colom-

bia, in the Pajarales Islands sector (Fig. 1). The sites were flat sand troughs (5 to 6 m deep) with massive coral heads, surrounded and interspersed by still-standing thickets and loose branches of dead *Acropora palmata*. At the study sites, 56 individuals of *Cliona tenuis* dwelling on corals and interacting directly with live coral tissue had been previously marked to measure their lateral advance (see López-Victoria 2003). However, only 5 of them were on corals which each had a leaning branch of sponge-carrying *A. palmata* from which the sponge had apparently started colonization of the coral host (Fig. 2). The direction and rate of lateral advance of these 5 marked sponges were thus used to ascertain the origin of the sponge, to calculate an approximate date of contact, and to relate it with major storms. Coral-sponge boundaries had been marked with steel nails in June 2001, and the linear lateral advance of each sponge was measured after 6 and 13 mo (see Fig. 2). To further demonstrate the colonization capabilities of encrusting excavating sponges which had fallen against corals (see also Schönberg & Wilkinson 2001, Schönberg 2002, 2003, López-Victoria 2003, López-Victoria et al. in press), fragments (ca. 5 cm on one side) and cores (2.8 cm diameter by 1 to 2 cm thickness) of *A. palmata* containing *C. tenuis* were obtained with a hammer and chisel or an impact corer, allowed to heal, and attached to corals. Fragments were tied with copper wire to nails and cores were implanted in new holes made with a corer. Two sets each of 6 transplants (4 fragments and 2 cores) were located in dead parts (one set) and in live tissue (another set) of massive coral colonies. To establish the proportion of various means of coral coloniza-
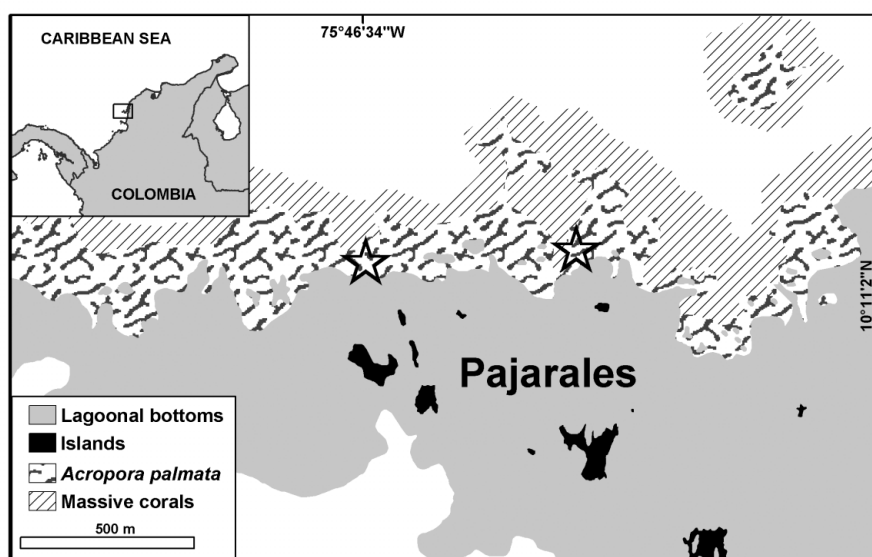

Fig. 1. The study area showing main bottom features and sampling sites (stars). The *Acropora palmata* zone is now composed of broken and collapsed dead branches and fragments, mixed with massive corals in sand troughs and reef depressions. White areas are deep basins off the insular shelf
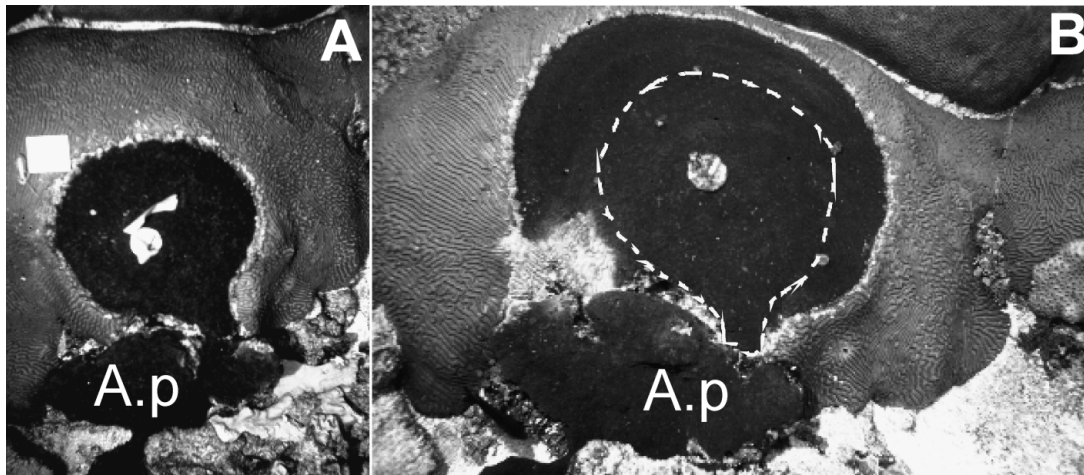
Fig. 2. *Cliona tenuis* encrusting and undermining *Diploria strigosa*. Underwater photographs of sponge individual #1898 (A) at marking, June 2001 and (B) after 13 mo, July 2002. Broken line in (B) represents the outline of the sponge at initial marking. Diameter of the white plastic square in (A) is 5 cm, and of the circular metal tag at the center of the sponge (A,B) is 3.8 cm. The original sponge-carrying *Acropora palmata* (A.p) fragment is visible in the lower foreground

tion utilized by the studied sponge, a 560 m^2 area was searched in 4-m-wide band transects, successively deploying 20 m tape measures as a guide. Transects were not intended to be replicates, but to cover as much area as possible in the sand troughs. All *C. tenuis* individuals dwelling on live coral colonies were counted in the transects, and their apparent means of colonization noted. Four categories of sponge colonization of live corals were defined: (D) direct contact, when a sponge-carrying *A. palmata* fragment was found still leaning against the coral, and the sponge had apparently colonized and spread from the contact point; (P) previous possible contact, when there was a sponge-carrying *A. palmata* fragment lying close (usually at or near the base), but not currently touching the coral on which the sponge was living; (U) unknown, when the sponge-colonized coral colony did not have any sponge-carrying *A. palmata* fragment lying close by; (S) from the substratum, when a coral colony that had settled on an *A. palmata* dead branch had been

reached and colonized by the spread of a sponge already present on the branch. This last category was clearly not the result of dispersion of the sponge via movement of coral skeletal fragments, but it was included, together with (U), to cover all instances of sponge coral colonization found and to determine their proportion.

3. RESULTS

Overall advance rates of the sponges on the 5 marked coral heads that had sponge-carrying *Acropora palmata* branches leaning against them are given in Table 1. Sponges were advancing on the corals away from the branch point of contact, further confirming the likely origin of colonization. None of the leaning branches had moved from its original location during the 13 mo of study. Since rates were similar in the 2 sets of measurements made in each sponge after 6 and

Table 1. *Cliona tenuis*. Retrospective analysis of sponge growth on massive corals colonized through direct contact with a sponge-encrusted dead *Acropora palmata* branch, in relation to hurricanes that affected the area. Sponge rates of advance measured between June 2001 and July 2002

Sponge no.	Coral	Rate of advance (cm yr^{-1})	Distance from contact to edge (cm)	Estimated time since initial colonization (yr)	Closest hurricane	Time lag vs hurricane
1895	*Siderastrea siderea*	4.8	22	4.6	Mitch (Oct–Nov 1998)	−10 mo
1919	*Siderastrea siderea*	5.1	55	10.8	Joan (Oct 1988)	+3.1 yr
1904A	*Diploria strigosa*	19.7	55	2.8	Lenny (Nov 1999)	+8.4 mo
1904B	*Diploria strigosa*	4.2	50	11.9	Joan (Oct 1988)	+2.0 yr
1898	*Diploria strigosa*	15.3	42	2.7	Lenny (Nov 1999)	+9.6 mo

Table 2. *Cliona tenuis.* Number and percentage of individuals found colonizing coral colonies either by direct contact (D) or from the substratum (S)

Coral species	Direct contact (D)		From the substratum (S)	
	Total count	% of total	Total count	% of total
Acropora palmata (live)			1	5.9
Agaricia agaricites			2	11.8
Colpophyllia natans	2	3.8		
Diploria clivosa	2	3.8		
D. labyrinthiformis	1	1.9		
D. strigosa	12	23.1		
Millepora spp.			2	11.8
Montastraea annularis	7	13.5		
M. cavernosa	1	1.9		
M. faveolata	13	25		
Porites astreoides	1	1.9	10	58.8
Siderastrea siderea	13	25	2	11.8
Total	52	100	17	100

after 13 mo (data not shown), and sponges were spreading over the light-exposed coral surface, rates were assumed to be constant through time. Estimated times of initial coral colonization varied from 10 mo before (1 case, ind. 1895) to about 8 mo to 3 yr after (4 cases) the last 3 hurricanes that had passed close to the study area, i.e. Joan, Mitch and Lenny. The 2 most recently colonized colonies (1904A, 1898) yielded similar estimated times, ca. 8 to 10 mo respectively after Lenny. Estimated times for the 2 earliest (1919, 1904B) colonization events were also relatively similar to each other, but much later, ca. 3 and 2 yr respectively after Joan.

In the 2 implanted cores surrounded by live coral tissue, death of sponge tissue occurred within days, through progressive necrosis starting from the outer edge; corals were not affected, and at night their defensive appendages were seen contacting the sponge. In contrast, in tied fragments, which shaded and pressed live tissue, bleaching of both coral and sponge tissue was evident after a few days; after 13 mo, 2 of the 3 remaining fragments (1 lost) still retained some live sponge tissue on top, and the coral tissue below the fragment was dead. In dead coral, the 2 cores, and 2 out of 4 fragments successfully took root and spread laterally to maximum distances of 0.5 to 8.3 cm in 13 mo. The 2 fragments which did not take root had lost all their sponge tissue by the end of the experiment. One core, which had been implanted some 2 cm away from the live edge of a *Montastraea faveolata* colony, advanced the farthest and had already penetrated 6.3 cm into the live coral tissue after 13 mo.

Colonization of live corals by *Cliona tenuis* through direct contact (D) with a sponge-carrying *Acropora palmata* dead coral fragment accounted for 25.7% of the total 202 sponges found dwelling on live coral colonies (both sites and all transects combined) (Table 2). The upper surface of the leaning branches was generally entirely covered by the sponge, and the leading sponge edge on the coral host had the looks of an actively undermining and growing front (for details see López-Victoria 2003, López-Victoria et al. in press). Sponge tissue bridges in the intervening space between the fallen fragment and the coral host were evident in most cases; in a few, the gap was colonized by turf and crustose algae. Sponges colonizing coral heads with fallen sponge-encrusted branches lying near by (former possible contact) (P) constituted 13.4%, while in 52.5% of the sponges colonizing coral colonies the origin of the sponge was unknown (U).

An 8.4% of the live coral-dwelling sponges had colonized their corals from the substratum (S), as both sponges and corals were living on dead *Acropora palmata*; sponge tissue bridges joining the substrata and the coral were also evident, the sponge tissue almost always forming a continuous veneer. The direction of sponge growth from the substratum to the coral was evident.

There were 12 coral species which had been colonized by *Cliona tenuis* through direct contact (D) or from the substratum (S), the most frequent being *Siderastrea siderea*, *Montastraea faveolata*, *M. annularis*, *Diploria strigosa*, and *Porites astreoides* (Table 2). Most colonization through direct contact (D) occurred on large, massive-growing species, while laminar, encrusting, low mound, branching or foliose species now living on the dead *Acropora palmata* branches, such as *Agaricia agaricites*, *Millepora* spp. and *Porites astreoides*, were found to have been mainly invaded by *C. tenuis* from the substratum (S).

4. DISCUSSION

Estimated times of initial colonization of marked coral heads were reasonably close to hurricanes that could have generated a surge heavy enough to break, lift and move around (e.g. Denny 1988) large branches of *Acropora palmata* previously colonized by the sponge. This association in time with hurricanes, although not conclusive for the role of a particular one, further supports the assumption that these branches were dispersed during storms. The normal surge of the wind-exposed study sites was not strong

enough to move marked branches. Although *Cliona tenuis* rates of lateral advance may vary seasonally (Rützler 2002), its spread is more or less steady while the sponge is encrusting and undermining the upper portion of a massive coral, and usually halts or diminishes once the vertical or overhanging sides are reached (Rützler 2002, López-Victoria et al. in press). Thus, the assumption of constancy of growth was appropriate for the calculation of initial contact time, as all sponges were spreading upwards from a lateral point of contact (see Fig. 2). Indeed, despite known coral species and individual variation in *C. tenuis* rates of advance (presented in López-Victoria 2003), estimated times of initial colonization were similar between branches assumed to have been moved by the same hurricane. A longer delay between the estimated dates of contact for Joan, the earliest hurricane, than for Lenny, the latest, may indicate that sponge lateral growth may be slowing with age even though the sponge is still actively spreading. Bioerosion of experimental blocks by this sponge is known to slow with time (Rützler 1975, *C. aprica*). The overestimation of time from contact in the case of hurricane Mitch, indicative of a current faster growth rate by the sponge, cannot be explained at the moment. From the transplantation experiments and previous work (Rützler 1975, 2002, McKenna 1997, Schönberg & Wilkinson 2001, Schönberg 2002, 2003, López-Victoria 2003), it can be assumed that upon extended contact, both coral and sponge tissue die from smothering; the initial impact itself may crush contacting tissues. But any surviving exposed sponge tissue develops bridges that reach the coral at the contact zone, then takes root and starts its undermining process. The delay between the occurrence of the heavy surge and the date of initial colonization may thus be the time needed for the sponge to bridge the gap and initiate growth in the new substrata. In contrast, sponge cores inserted in holes made inside live coral are killed by the coral's defense mechanisms before they can send out pioneering excavating tissue filaments.

Most colonization through direct contact occurred on massive corals. This is the logical consequence of branches falling on top of or in narrow depressions between coral heads, thus unavoidably leaning against them. As strong storms and hurricanes have progressively been breaking apart the dead colonies of *Acropora palmata*, there are increasingly more and smaller branches to be moved around (S. Zea pers. obs.). The sponge itself is excavating the branches, thus weakening them (Tunnicliffe 1979, López-Victoria et al. in press). Hence, we speculate that the phenomenon of sponge dispersion via coral fragments and colonization of massive corals is likely to be on the increase. Proba-

bly, as coral fragments become smaller, they will be transported farther, although fragments may progressively fuse to the reef framework via crustose algae and other sponges (Wulff 1984, S. Zea pers. obs.). However, data to distinguish whether there was more sponge dispersion and colonization in recent than in earlier events are not available. For future comparisons, by 2002, cover of *Cliona tenuis* at the study sites had reached 7.7% of the hard substratum, and a density of about 1.3 ind. m^{-2} (López-Victoria 2003).

The extent of storm-induced dispersion and subsequent colonization of new corals depends on local topography. In the study area, *Cliona tenuis* is present only throughout the *Acropora palmata* reef zone in the windward side of the islands; the massive coral heads of the slopes beyond the *A. palmata* zone, and those at the leeward side reef are virtually devoid of the sponge (López-Victoria 2003). The wide depressions in between coral heads in these zones are sandy or carpeted by branching or lettuce corals overgrown by foliose algae, probably trapping loose coral branches and hindering sponge lateral spread. Larvae of *C. viridis*, a closely related sponge from the Mediterranean, are oviparous and disperse over short distances (Mariani et al. 2000). The absence of *C. tenuis* in neighboring reef zones may thus also be the result of a similar pattern of short distance dispersal by its larvae. We also observed cases of *C. tenuis* and *C. aprica* living in *A. palmata* which had colonized massive corals by direct contact in other reef areas, such as the spur-and-groove system and the shallow fore-reef terrace of the windward barrier and peripheral reefs of the San Andrés and Old Providence Archipelago in the SW Caribbean.

Encrusting, platy and foliose corals (e.g. *Porites astreoides*, *Millepora* spp., *Agaricia agaricites*) which are currently re-colonizing the dead *A. palmata* reef framework (Cendales et al. 2002, authors' pers. obs.) are prone to be invaded by adjacent *Cliona tenuis*. We also had marked 14 colonies of these corals living on *A. palmata* and having neighboring *C. tenuis* (authors' unpubl. obs., see also López-Victoria, 2003). Two of these (1 *A. agaricites*, 1 *P. astreoides*, both <10 cm in diameter) were completely lost to the sponge in less than 6 mo. They were either detached from the substratum after erosion of their basal support, or were completely covered by the sponge tissue. Of the remaining 12 colonies (2 *A. agaricites*, 4 *Millepora* spp., 6 *P. astreoides*), 6 lost tissue to the sponge (at rates of 0.2 to 7.9 cm yr^{-1}), 3 gained (0.1 to 1 cm yr^{-1}), while 3 others remained unscathed. Thus, besides being dispersed by storms and colonizing massive coral heads, *C. tenuis* is also slowing down the current process of coral species replacement to an unknown degree.

LITERATURE CITED

Acker KL, Risk M (1985) Substrate destruction and sediment production by the boring sponge *Cliona caribbaea* on Grand Caiman Island. J Sediment Petrol 55 (5):705–711

Birkeland C (1997) Life and death of coral reefs. Chapman & Hall, New York

Cendales MH, Zea S, Díaz JM (2002) Geomorfología y unidades ecológicas del complejo arrecifal de Islas del Rosario e Isla Barú (Mar Caribe, Colombia). Rev Acad Colomb Cienc 26(101):497–510

Cortés J, Murillo MM, Guzmán HM, Acuña J (1984) Pérdida de zooxantelas y muerte de corales y otros organismos arrecifales en el Caribe y Pacífico de Costa Rica. Rev Biol Trop 32(2):227–231

Denny MW (1988) Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, NJ

Edmunds PJ, Witman JD (1991) Effect of hurricane Hugo on the primary reef framework of a reef along the south shore of St. John, US Virgin Islands. Mar Ecol Prog Ser 78: 210–204

Hughes T (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551

López-Victoria M (2003) Interacciones entre esponjas excavadoras del complejo *Cliona aprica*–*C. langae*–*C. caribbaea* y corales pétreos en el Caribe colombiano. MS thesis, Universidad Nacional de Colombia, Bogotá

López-Victoria M, Zea S, Weil E (in press) New aspects on the biology of the excavating sponge complex *Cliona caribbaea*–*C. langae*–*C. aprica*. Boll Mus Ist Biol Univ Genova 68

Mariani S, Uriz MJ, Turon X (2000) Larval bloom of the oviparous sponge *Cliona viridis*: coupling of larval abundance and adult distribution. Mar Biol 137:783–790

McKenna SA (1997) Interactions between the boring sponge, *Cliona lampa* and two hermatypic corals from Bermuda. In: Lessios HA, Macintyre IG (eds) Proc 8th Int Coral Reef Symp, Panamá 2:1369–1374

Rogers CS, Suchanek TH, Pecora FA (1982) Effects of hurricanes David and Frederic (1979) on shallow *Acropora palmate* reef communities: St. Croix, U.S. Virgin Islands. Bull Mar Sci 32(2):532–548

Rützler K (1975) The role of burrowing sponges in bioerosion. Oecologia 19:203–216

Rützler K (2002) Impact of crustose clionid sponges on Caribbean reef corals. Acta Geol Hisp 37(1):61–72

Rützler K, Macintyre IG (1982) The habitat distribution and community structure of the Barrier Reef Complex at Carrie Bow Cay, Belize. Smith Contr Mar Sci 12:9–45

Schönberg CHL (2002) Substrate effects on the bioeroding Demosponge *Cliona orientalis*. 1. Bioerosion rates. PSZN I: Mar Ecol 23(4):313–326

Schönberg CHL (2003) Substrate effects on the bioeroding Demosponge *Cliona orientalis*. 2. Substrate colonization and tissue growth. PSZN I: Mar Ecol 24(1):59–74

Schönberg CHL, Wilkinson CR (2001) Induced colonization of corals by a clionid bioeroding sponge. Coral Reefs 20: 69–76

Tunnicliffe V (1979) The role of boring sponges in coral fracture. In: Levi C, Boury-Esnault N (eds) Biologie des spongiaires. Colloques Internationaux CNRS 291, Paris, p 309–315

Wilkinson CR (1983) Role of sponges in coral reef structural processes. In: Barnes DJ (ed) Perspectives on coral reefs. Brian Clouston Publisher, Manuka, p 263–274

Williams EH, Bartels PJ, Bunkley-Williams L (1999) Predicted disappearance of coral-reef ramparts: a direct result of major ecological disturbances. Global Change Biol 5: 839–845

Wulff JL (1984) Sponge-mediated coral reef growth and rejuvenation. Coral Reefs 3:157–163

Wulff JL (1995) Effects of a hurricane on survival and orientation of large erect coral reef sponges. Coral Reefs 14: 55–61

Zea S, Weil E (2003) Taxonomy of the Caribbean excavating sponge species complex *Cliona caribbaea*–*C. aprica*–*C. langae* (Porifera, Hadromerida, Clionaidae). Caribb J Sci 39(3):348–370