Impact of Crustose Clionid Sponges on Caribbean Reef Corals

K. RÜTZLER (1)

(1) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0163, U.S.A. Fax: 202 357 3043. E-mail: ruetzler.klaus@nmnh.si.edu

ABSTRACT

Some species of limestone-excavating Porifera (Clionidae, Hadromerida) cover their substrate as a thin, continuous, veneer-like crust (beta stage). This film of tissue is the result of fusion of the initially discrete incident and excipient papilla (alpha stage) that are the common and lifelong morphological feature of most other representatives of the family. In the tropical and subtropical western Atlantic, at least four species of clionids encrust reef-coral skeletons (Scleractinia, Hydrozoa): Cliona caribbaea CARTER (including C. aprica PANG and C. longae PANG), C. delitrix PANG, C. lampa de LAUBENFELS, and C. varians (DUCHASSAING and MICHEL-ELOTTI) (=Anthosigmella varians of authors). One conspicuous feature of these encrusting sponges is that many border live coral or cover recently dead coral as indicated by the clear outline of the coral calicular structure under the thin sponge veneer. Field experiments and histological study conducted on Cliona caribbaea in Belize and Cliona lampa in Bermuda indicate that the sponges overpower stressed coral which they overgrow at a fast rate. Stress parameters include extended periods of above-average water warming or below-average water cooling, excess of suspended sediments, organic pollution, and physical damage inflicted by fish bites, anchor polyps. Overgrowth is accomplished by excavating coral calices from below the surface, thus depriving the polyps of their support, or by covering skeletons of dying coral. Overpowering corals by bioerosion is a successful competitive mechanism that works alike on ungrounded coral, albeit at a much slower pace. On the other hand, also non-boring encrusting sponges may overgrow coral by lateral spreading, for instance the symbiotic (with cyanobacteria) species of Chondrilla and Terepios, particularly if sponge growth is stimulated and coral resistance weakened by elevated levels of pollution. There are indications that encrusting clionids and other sponges may dramatically change the community structure and physical stability of shallow reefs that are readily compromised by natural or anthropogenic pressures.

LOCATIONS, MATERIAL AND METHODS

The principal location for this study is the Smithsonian Institution’s Carrie Bow Marine Field Station on the barrier reef of Belize. Observations from Bermuda (without experimental support at this time) are included for comparison because they point to a similar phenomenon of space competition between sponge and coral but involve a different sponge species (not found in Belize) and a cooler climatic regime.

Belize

A shallow section (<5 m) of the Belize barrier reef fringing the southern tip of Carrie Bow Cay (16°48'N, 88°05'W; Rützler and Macintyre, 1982: figs. 2, 3) is the focus of this study; it was first surveyed in May 1979 (Fig. 1a). Cliona caribbaea is presently the most abundant sponge there, encrusting many square meters of recently dead coral (Fig. 2). The other clionids with beta growth in the area are C. varians on nearby back reefs and C. delitrix on the fore reef below 15 m; neither appears to have recently increased in dominance.

The study reef covers about 3,000 m² and ranges in depth from 0.5 m to 8 m. It is primarily composed of the stony corals Acropora palmata, Montastraea annularis, Diploria labyrinthiformis, D. strigosa, and Agaricia tenuifolia, and the hydrocoral Millepora complanata. Associated large demosponges in this high-energy environment are Chondrilla cf. nucula, an extensively encrusting, non-boring species, massive and tough Ircinia felix, and tubular, flexible Callyspongia vaginalis.

Bermuda

Cliona lampa is an abundant and conspicuous sponge in Bermuda and was studied in the field during October 1969 and January 1973, and re-surveyed in December.
Figure 3. *Cliona caribbaea*, surface structure and excavation. (a) Perpendicular view of surface showing incipient pores and protruding spicule bundles; (b) magnified view of outer cell layer (exopinacoderm), spicule brushes, and pores (background); (c) pits left in coral rock from chemical coring; (d) coral chip removed by coring (among siliceous tyoostyle sponge spicules).

...illustrated by Rützler (1974:5, figs. 2-4). Another modern author, Pang (1973: p. 22) described a sponge by that name from Jamaica but it lacks the characteristics of the holotype: it agrees with another clionid, *C. flavifodina* RÜTZLER, first established for specimens from Bermuda but since found elsewhere in the Caribbean (including Belize). Nonetheless, in the same paper, Pang (1973) established two new encrusting Clionidae, *Cliona langae* PANG (p. 34) and *C. aprica* PANG (p. 42). These two forms are very similar to each other and agree well with *C. caribbaea* CARTER. All share the same range in morphology, size and shape of spicules, and type of zooxanthellae. A survey of growth forms and depth distribution of this species (0.5-40 m) on the Carrie Bow fore-reef revealed a variance of taxonomic characters (color, extent of papillar fusion to fully encrusting; spicule shape and size) that suggests including *C. langae* and *C. aprica* as junior synonyms of *C. caribbaea* unless other convincing arguments to the contrary, for instance molecular data, can be found. The species is encrusting (Fig. 3 a, b); (young specimens start as papillate stage), may cover a square meter or more of carbonate rock, and is dark olive to brown, to almost black in color (from zooxanthellae). It penetrates the substrate by chemical coring (Fig. 3 c, d) and permeates it with small, yellow-brown, tissue-filled chambers to about 10 mm depth. Spicules are robust tyoostyles and delicate, double-bent or undulating thin spirasters with slender spines (Fig. 4).

*Cliona lampa* de LAUBENFELS, 1950a (holotype from Bermuda) is extremely common on the shallow Bermuda platform where it thinly encrusts and excavates calcium carbonate sandstone and coral skeletons (Fig. 5a). Outside these islands it is has only been found in the subtropical waters of Florida and part of the Bahamas. Rützler (1974: p. 21; figs. 17-20) re-described the species and named a papillate (alpha-stage) forma *occulta* which was considered conspecific, based on spicule type and shape, although the tyoostyles are larger and the tiny papillae never fuse and are dark red in color, in con-
Taстраea annularis were marked by nails driven into the corals at the sponge-coral tissue boundary (Fig. 6 a). Measurement of sponge spreading that took place at the expense of the coral during the 127-day period until August 1997 showed linear growth of 0.13-0.31 mm/day (mean 0.25±0.10 s.d.; n=23). In the following observation period, August 1997-March 1998 (230 days), spreading rate slowed to 0.09-0.14 mm/day (0.11±0.04; n=25). In March 2000 the sites were revisited and it was found that although some of the recorded boundary points had advanced by 57-124 mm, many others had reached the end of available substrate, making comparison with previous data impossible. Another thinly encrusting sponge, but without excavating capacity, *Chondrilla* cf. *mucula* (*Chondrillidae*, Hadromerida) bordering live *Diploria labyrinthiformis* was also tagged and mapped during the observation period but although it dramatically took over bleached and dying *Agaricia* corals in the Pelican Cays, just 20 km away (MacIntyre et al., 2000), it did not further invade this coral.

An experiment was conducted (starting in March 2000) to determine whether *Cliona caribbaea* is capable of harming a healthy coral on contact, for instance, by toxic substances such as secondary metabolites. Sponge-infested coral disks were implanted on healthy *Diploria labyrinthiformis*, *Montastraea annularis*, and *Acropora palmata*. During the following 10-day period, the coral tissue around the implant remained healthy and coral mucus appeared to affect the sponge which retreated from the outer margin of its substrate disk in six of the eight trials. The controls (attached to dead rock) remained healthy. By November 2000, all experimental corals and the sponge controls remained healthy, one *Montastraea implant* was lost, the other two had reduced sponge volume to an estimated 25% and 45%; in *Diploria*, one implant sponge was dead, the others were reduced to 50% and 80%; in *Acropora*, both implants were healthy and occupied 100% of the exposed substrate but had not spread to the coral.

**Micro-anatomical Findings**

The smooth crust of *Cliona caribbaea* is 1-2 mm thick and bears scattered oscula of 1-4 mm diameter, with raised rims. The ectsosome is dark brown from intracellular zooxanthellae (8-10 μm diameter) which decrease in density toward the base of the sponge, which is yellowish. Tissue-filled chambers (ca. 2x4 mm) reach 8-10 mm into the substratum. The megascleres (tylostyles) are arranged in radiating tracks in the choanosome, as diverging bundles (en bouquet) at the sponge surface. Microscleres (spirasters) are dispersed without orientation.

Close examination of the live coral-sponge tissue interface reveals a narrow barren zone (1-3 mm) with fine sediments possibly agglutinated by coral mucus. There is never a situation where sponge material touches directly any of the coral polyps, at least not during the day when they are retracted.

The sponge excavates the calcareous substrate in the usual manner, by chemical coring (Rützler and Rieger, 1973), liberating small (25-60 μm) carbonate chips that are expelled through the oscula (Fig. 3 b, c). Examination
demonstrated by many infested dead skeletons, are readily overwhelmed when stressed. In Bermuda, McKenna (1997) tested Cliona lampa against an aggressive Montastraea cavernosa and a non-aggressive Porites astreoides and found Montastraea successful in its defense against the sponge. This is probably the typical result in healthy corals, whereas sponge-infested Montastraea and Diploria specimens may reflect the consequence of environmental stress. However, it is likely that none of the corals are able to resist invasion by an aggressive clionid through bioerosion from below the live tissue, a slow but effective process as demonstrated in the current study.

Water temperature is an important factor in the well-being of corals. During 1976-1980, about the time of our original abundance estimates for Cliona caribbaea, the surface temperature over the study reef in Belize ranged from 25° C in February to 30° C in August. Measurements recorded nearby during periods in 1997-2000 indicate an average increase of 2° C or more for the warmest months, May-August (K. Koltes, personal communication), with coral bleaching and death reported for the first time from several locations on the barrier reef. A similar observation was made in Caribbean Costa Rica where temperature peaks of 33-35° C caused massive coral bleaching and death but apparently provided an opportunity of territorial expansion for Cliona caribbaea (Cortés et al., 1984). For the Pacific too, observations are available showing that elevated temperature near a power-plant effluent (averaging nearly 34° C) caused coral mortality and enhanced growth of clionid sponges (Siegrist et al., 1992). High-temperature stress may weaken the coral defense system and allow encrusting clionids with rapid spreading capacity to take over the gradually exposed skeleton. Extended periods of water warming are known to encourage other coral pests as well, such as black band disease (Rützler et al., 1983). In contrast, low-temperature extremes may be a factor in a place like Bermuda where recently dead, still identifiable corals coated by the thin vermilion veneer of Cliona lampa are a common sight. This oceanic island is the northern outpost (32°20' N) of the West Indian fauna, including reef corals. Sea temperatures ranging from 18° C (February) to 29° C (August) despite the northern latitude are due to the effect of the Gulf Stream. Nevertheless, corals and other warm-adapted invertebrates may become severely stressed or killed during unusually cold winters, particularly in the shallow lagoons which cool more rapidly that the deep offshore water mass (de Laubenfels, 1950b).

Another aspect of coral stress favoring spectacular takeover of large Diploria coral boulders by Cliona lampa in Bermuda was historically reconstructed and experimentally confirmed by McKenna and Ritter (1999). In the early 1940s, airport construction in Castle Harbour caused changes in water flow patterns and led to increased silting and high turbidity, stressing and killing the venerable coral heads. Large areas of these substrates are still covered by Cliona lampa which seems to resist the high rate of sedimentation and benefits from increased nutrients and lack of predators. Sponges in general resist increased sedimentation better than corals, and even algae, particularly when turbidity values are also elevated (Zea, 1994).

A number of additional stresses of corals that may in turn benefit clionid and other sponges should be mentioned although they were not in evidence during the current study in Belize. Because sponges feed primarily on bacterioplankton, organic pollution (sewage discharge) promotes sponge growth through elevated bacterial biomass until toxic effects of eutrophication takes effect. Corals are particularly adapted to low-nutrient environments and among the first to become victim to pollution. For instance, an increase of infestation of Montastraea cavernosa by the Caribbean encrusting Cliona deltirix on a Grand Cayman fringing reef was linked to the discharge of untreated sewage (Rose and Risk, 1985). In Barbados, clionid abundance and a significant increase of bioerosion rates could be related to a coastal pollution gradient, even though no direct effect of the sponges on coral health was determined, except for the predictable increase of fine sediments and weakening of the reef framework (Holmes, 2000). Also the Great Barrier Reef of Australia is not immune to these kinds of disturbances. Growth and bioerosion rates of Cliona orientalis THIELE, an encrusting clionid with close taxonomic relation to C. caribbaea and playing an almost identical ecological role as its West Indian counterpart, was shown to be enhanced by elevated nutrient levels although pollution became detrimental beyond a certain measure (Schönberg, 2000). Physical damage to coral colonies, such as lesions caused by fish bites, anchors, or divers, may be considered a small-scale or local problem but it impacts competitive interaction, usually in favor of the sponge (Aerts, 2000).

The energetic and ecological efficiency of thin sponge crusts rapidly taking over stressed or recently dead coral before other settlers, such as algal turfs, are able to take hold is also exemplified by non-boring, thinly encrusting species of Chondrilla and Terpios, both “bacteriosponges” containing symbiotic cyanobacteria as substantial part of their biomass. In Belize, an extended calm period with high temperatures was asso-
Third International Coral Reef Symposium, 2. Miami, Rosenstiel School of Marine and Atmospheric Science, 617-623.


Balboa, Panamá, Smithsonian Tropical Research Institute, 1369-1374.


