

Impact of Crustose Clionid Sponges on Caribbean Reef Corals

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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 incurrent and excurrent papillae (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. langae* PANG), *C. delitrix* PANG, *C. lampa* de LAUBENFELS, and *C. varians* (DUCHASSAING and MICHELOTTI) (= *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, anchors, and other means. Clionids do not seem to produce toxic compounds that affect virile coral colonies and are repelled by healthy coral polyps. Overgrowth is accomplished by excavating coral calyces 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 also on unstressed 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 *Terpios*, 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.

Keywords: Sponges. Clionidae. Corals. Competition. Bioerosion. Reefs. Caribbean.

RESUMEN

Algunas especies de esponjas perforantes de carbonatos (Clionidae, Hadromerida) cubren el substrato calcáreo como una costra delgada y continua, similar a un revestimiento (estadio beta). Esta película de tejido es el resultado de la fusión de las inicialmente aisladas papilas incurrentes y excurrentes que son la característica morfológica común y de mayor longevidad de muchas otras representantes de la familia. En el Atlántico occidental tropical y subtropical, por lo menos cuatro especies de cliónidas incrustan los esqueletos del coral arrecifal (Scleractinia, Hydrozoa): *Cliona caribbaea* CARTER (incluyendo *C. aprica* PANG y *C. langae* PANG), *C. delitrix* PANG, *C. lampa* de LAUBENFELS, y *C. varians* (DUCHASSAING y MICHELOTTI) (= *Anthosigmella varians* de los autores). Un carácter conspicuo de estas esponjas incrustantes es que muchas ribetean el coral vivo o cubren el coral recién muerto, como queda indicado por el contorno claro de la estructura de coral calicular bajo el fino revestimiento de la esponja. Los experimentos de campo y el estudio histológico sobre *Cliona caribbaea* en Belize y *Cliona lampa* en Bermudas muestran que las esponjas dominan el coral que se encuentra bajo estrés, creciendo sobre él a una velocidad rápida. Los parámetros de estrés incluyen periodos amplios de aguas con temperaturas tanto por encima como por debajo de la media, exceso de sedimentos en suspensión, contaminación orgánica, y lesiones físicas infligidas por mordiscos de peces, anclas u otros medios. No parece que las cliónidas produzcan componentes tóxicos que afecten las colonias coralinas vigorosas y los pólipos coralinos sanos las repelen. El sobrecrecimiento se lleva a cabo mediante la excavación en los cálices coralinos desde debajo de la superficie, privando de esta manera a los pólipos de su soporte, o cubriendo los esqueletos de coral muerto. El ataque a los corales mediante bioerosión es un mecanismo competitivo eficaz que funciona también en corales no estresados, si bien a un ritmo mucho más lento. Por otra parte, las esponjas no perforantes también pueden sobrecrecer el coral por expansión lateral, como hacen por ejemplo las especies simbiotas (con cianobacterias) de *Chondrilla* y *Terpios*, en especial si los niveles de contaminación altos estimulan el crecimiento de la esponja y reducen la resistencia del coral. Existen indicios de que las cliónidas incrustantes y otras esponjas pueden cambiar drásticamente la estructura de la comunidad y la estabilidad física de arrecifes someros que fácilmente se ven comprometidos por presiones naturales o antropogénicas.

Palabras clave: Esponjas. Clionidae. Corales. Competición. Bioerosión. Arrecifes. Caribe.

INTRODUCTION

Sponges are an important component of coral-reef communities, particularly in the Caribbean Sea where their diversity is estimated at about 600 species (Rützler, 1978; Diaz and Rützler, 2001). On many reefs, sponges exceed hermatypic corals (including Milleporina, Scleractinia, and Octocorallia) also in biomass (ashless dry weight; see Rützler, 2001) although many surveys using point-count or projected-area measurements underestimate their abundance. Among them is a large number of limestone-excavating sponges (Goreau and Hartman, 1963), the majority belonging to the family Clionidae (Hadromerida), which are easily overlooked by divers because they have a cryptic habit, filling chambered tunnels that they excavate in limestone rock with only small incurrent and excurrent papillae (<1-5 mm diameter, depending on species) showing at the substratum surface.

It is a well-known fact that some species of Clionidae exhibit encrusting (beta stage) and massive (gamma stage) growth forms (the papillate form is termed alpha stage) (Vosmaer, 1933). The beta stage is the result of laminar growth that starts with the fusion of papillae; it appears to be genetically induced as it is not evident but in a small number of Atlantic species, such as *Cliona caribbaea*

CARTER [Pang, 1973 (as *C. langae*, *C. aprica*); Rützler, 1974]; Mediterranean *C. nigricans* (SCHMIDT) (Rützler, 1973; Bavastrello et al., 1996); *C. delitrix* PANG (Pang, 1973; Rose and Risk, 1985); *C. lampa* de LAUBENFELS (de Laubenfels, 1950a, b; Neumann, 1966; Rützler, 1975); and *C. varians* (DUCHASSAING and MICHELOTTI) (Wiedenmayer, 1977; as *Anthosigmella varians* forma *incrustans*; Vicente, 1978; as *A. varians*). A few species, for instance *Cliona celata* GRANT and *C. nigricans* (often referred to as massive *C. viridis* SCHMIDT) exhibit the massive (and often very large) gamma stage, particularly in specimens found on volcanic bottoms after the originally bored piece of calcium carbonate substrate is destroyed (Sarà and Vacelet, 1973).

During past surveys of Bermuda and Belize reefs I made several studies on systematics, biology, and ecology of clionid sponges (e.g., Rützler, 1974; Rützler, 1975; Rützler and Macintyre, 1982) which led to the observation of a substantial recent increase of encrusting forms and of its detrimental effect on large reef-building corals. The present contribution analyzes the available information on encrusting Clionidae and examines excavation mechanisms, growth rates, and environmental conditions that affect space competition between these sponges and corals on shallow Caribbean reefs.

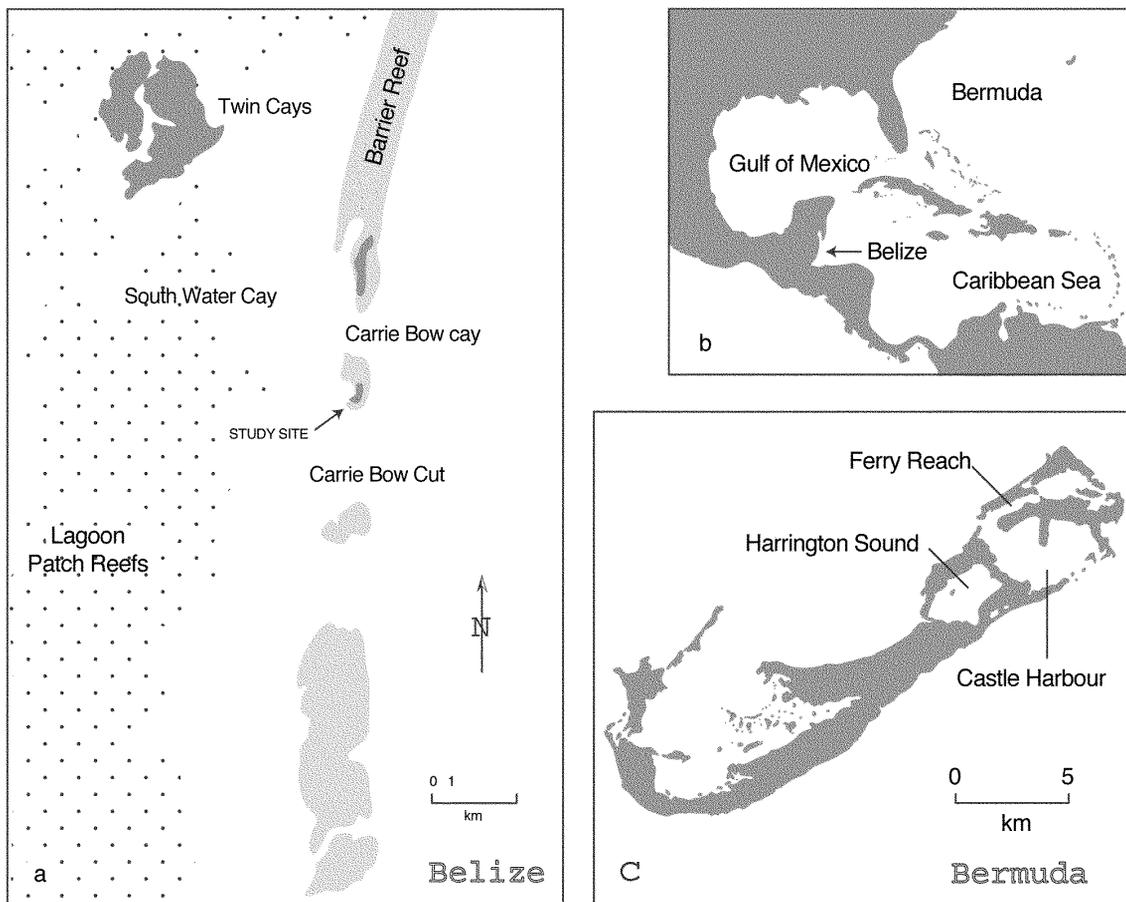


Figure 1. Study locations in Belize and Bermuda. (a) Carrie Bow Cay on the barrier reef of Belize; (b) locator map; (c) Bermuda inshore waters.

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 re-

cently 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 vaginialis*.

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 2. *Cliona caribbaea* encrusting recently dead coral, *Acropora palmata*, on Belize barrier reef, 3 m depth (August 1999).

1998. The species is particularly common in shallow lagoons (in-shore waters with few and narrow passages to the surrounding ocean), such as Ferry Reach, Castle Harbour, and Harrington Sound (Rützler, 1974: p. 4, fig. 1; Fig. 1c).

Cliona lampa is the only Bermudian clionid species that covers more than a few square centimeters of substrate. *C. caribbaea* too is very common and its papillae have the tendency to fuse into small crusts but its coverage did not exceed 3 cm². The two other Caribbean crustose excavating sponges, *C. delitrix* and *C. varians* do not occur in Bermuda.

Field Surveys and Experiments

Estimates of abundance are based on frame-counting (0.5 m² frame subdivided into 100 cm²-mesh grid) along transect lines of 20 m length, with random starting point and orientation (May 1979; March 1998). The frame was placed every 2 m along the transect and sponge-area cover estimated to the nearest 25 cm².

Spreading rate of *Cliona caribbaea* was measured on projected transparencies of periodically taken underwater photographs of known scale. The camera used was a Nikonos V with 28 mm or 35 mm lens, Nikon close-up lens attachment with image framer (5:1 at 35 mm; 6.5:1 at 28 mm focal length), and two small strobes (Ikelite M) at 45° angle to the picture axis. Each series was started by hammering masonry nails along the sponge margin where it was in contact with live coral (March 1997). The species

Diploria labyrinthiformis and *Montastraea annularis* were used because they are both abundant and represented by large specimens (1-2 m² average live surface area). Elkhorn coral, *Acropora palmata*, is also abundant and greatly affected by *Cliona caribbaea* but most specimens were dead in the area when the study began. Re-surveys were made in August 1997, March 1998, and May 2000.

To determine if *Cliona caribbaea* is able to kill healthy coral tissue, disks of sponge-infested coral (*Acropora*) were cut (ca. 35 mm diameter, 15 mm thick) and left in situ for 3 days to heal (May 2000). The disks were then mounted rigidly (by one central stainless-steel deck screw each) on live coral surface of the three common species (3 each on *Diploria* and *Montastraea*, 2 on *Acropora*, and 3 controls on dead coral rock). The results were monitored daily for 10 days and re-examined after 6 months.

Laboratory Techniques

Sponges and sponge-coral tissue interactions were studied histologically after fixation in buffered 1.5% glutaraldehyde, dehydration (alcohol series) and embedding in epoxy resin, grinding-polishing to 50 µm thickness, and staining by methylene blue (more about the method in Rützler, 1978). Scanning electron micrographs (SEM) were made on critical-point-dried tissue, nitric-acid treated siliceous spicules, and sodium hypochloride-cleaned limestone coral skeletons. Samples were gold-coated and photographed by an Amray 1810 microscope with digital camera at 500-2000x primary magnification.

For measurements of sponge biomass and calcium carbonate loss from coral by sponge erosion, samples were measured (surface cover, penetration depth, displacement volume) and weighed before and after treatment with sodium hypochloride, after drying to constant weight at 60° C.

RESULTS

Systematic Position of the Sponges

Both sponge species studied in this contribution are subject to some taxonomic controversy. Although this is not the place for a revision, some clarification is considered necessary.

Cliona caribbaea CARTER, 1882 (holotype from St. Vincent, West Indies) is a common species with Caribbean-wide distribution). It was re-described and il-

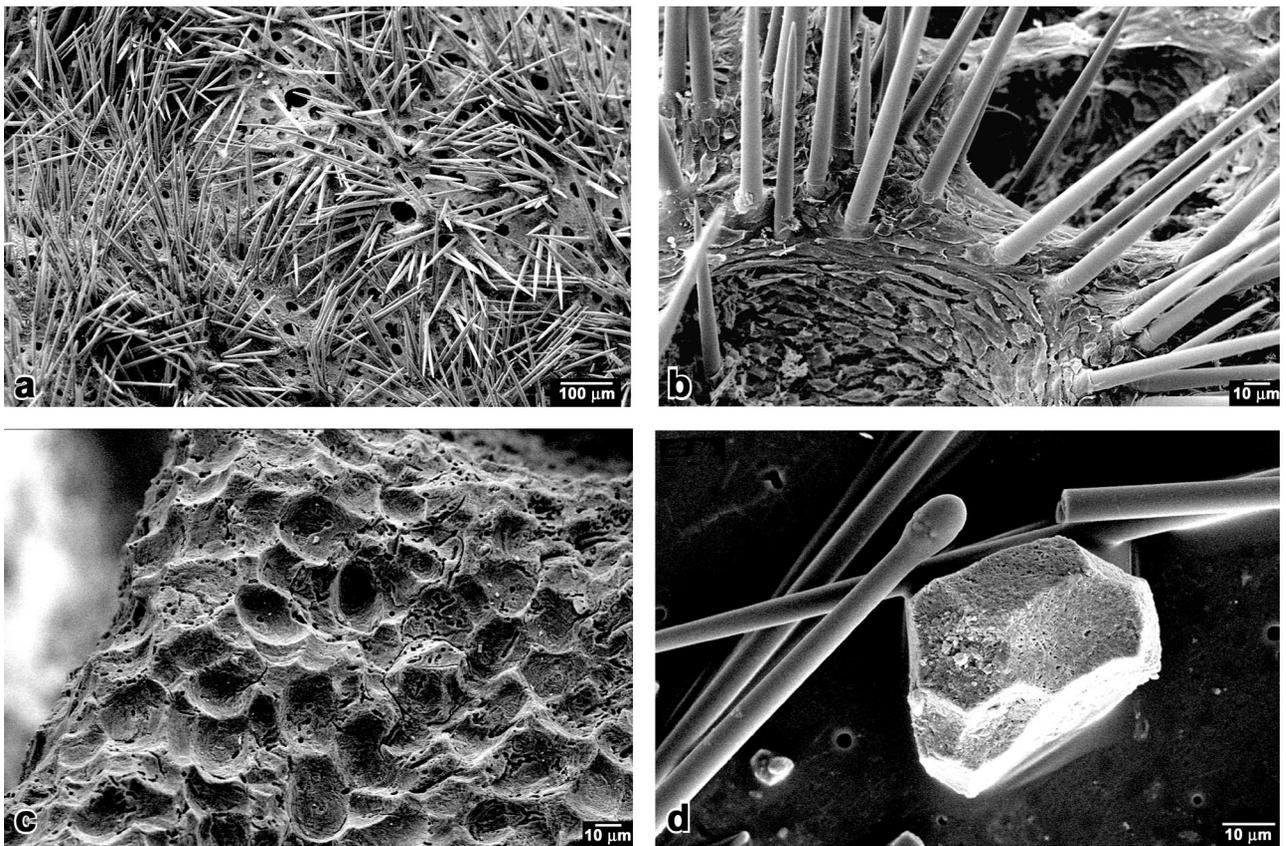


Figure 3. *Cliona caribbaea*, surface structure and excavation. (a) Perpendicular view of surface showing incurrent pores and protruding spicule bundles; (b) magnified view of outer cell layer (exopinacoderm), spicule brushes, and pores (background); (c) pits left in coral rock from chemical coring; (d) coral chip removed by coring (among siliceous tylostyle 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 papillary 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 tylostyles 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 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 tylostyles are larger and the tiny papillae never fuse and are dark red in color, in con-

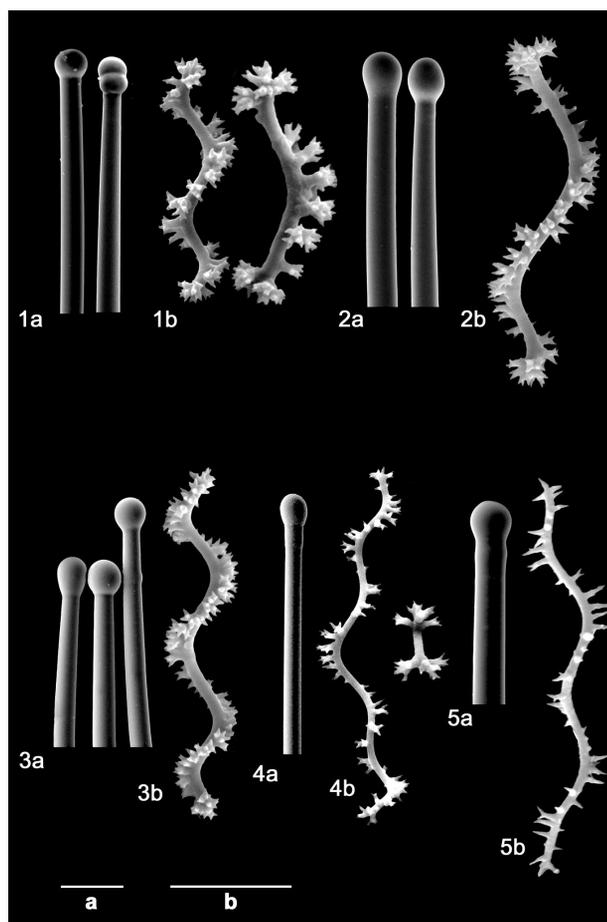


Figure 4. *Cliona caribbaea*, spicule variation in specimens of different growth form, depth, and location (a=tylostyle head portions, b=spirasters and derivative). (1) Papillate form (alpha-stage), Carrie Bow lagoon, 0.5 m; (2) Encrusting form (beta stage), Carrie Bow fore reef, 2 m; (3) Encrusting form, Curlew bank (1.2 km south of Carrie Bow) fore reef, 9 m; (4) Encrusting form, fringing reef, San Salvador, Bahamas; (5) Encrusting form (beta stage), Carrie Bow fore reef, 25 m. (Scales: a=20 μ m; b= 10 μ m.)

trast to the bright vermilion of the forma *typica* incrustations. Curiously, the papillate form can be found throughout the Caribbean where crustose *C. lampa* is absent (e.g., Pang, 1973: p.18). In July 1982, during unrelated work in Bermuda, several specimens were found that undoubtedly represented early papillate growth stages of *C. lampa* (Fig. 5 b). Compared to forma *occulta*, the papillae are relatively large, their color is the typical vermilion rather than dull red, and papillary fusion is already evident in very small specimens. This observation is considered proof that *C. lampa* is distinct from forma *occulta* which agrees in morphology with the cos-

opolitan species *C. vastifica* HANCOCK, a common oyster pest. New material of *C. lampa* collected in the Red Sea (J. Vacelet, Marseille, personal communication) suggests that the species is a recent invader to Bermuda, which would explain why this conspicuous species was not described or mentioned from these islands until 1950. Both, *C. lampa* and *C. vastifica* possess tylostyles for megascleres and microspined oxeas and microstrongyles. This spicule complement prompted Rosell and Uriz (1997) in their cladistic analysis to re-erect the genus *Pione* GRAY. This view is not adopted here but will be subject to further analysis in a forthcoming revision (Rützler, in preparation).

Growth Rate and Competitive Strategy of *Cliona caribbaea*

Sponge Abundance

At Carrie Bow Cay, the beta-form of this sponge is common on dead and live coral of the fore reef, including the shallow study reef (<10 m) that wraps around the south tip of the island and is exposed to open-ocean water because of a wide break (channel) through the barrier reef. Alpha-stage specimens are most abundant in coral rubble and dead conch shells among sand and seagrass of the back reef and lagoon where stable substrates are lacking. In May, 1979, estimates of *Cliona caribbaea* cover on the study reef ranged 1.8-2.3% of suitable substrate, depending on reef zone; live coral covered 21-35% surface area although many coral heads showed infection by black band disease (Antonius, 1977; Rützler, et al., 1983). In a March 1998 re-survey, sponge cover had about doubled, to 2.7-6.8%, whereas only 11-17% of coral was alive. Many recently dead *Acropora palmata* corals were entirely covered by the blackish sponge crusts and numerous heads of live *Diploria labyrinthiformis*, and *Montastraea annularis* were in various stages of infection.

Mass comparison of coral samples with and without clionid infestation showed a loss of 31.9% to bioerosion. Further calculation determined that each 1 m² coral rock covered by *Cliona caribbaea* (9 mm penetration), lost about 3.9 kg of its mass.

Spreading Rate

In March 1997, a number of sponge patches that were established on live *Diploria labyrinthiformis* and *Mon-*

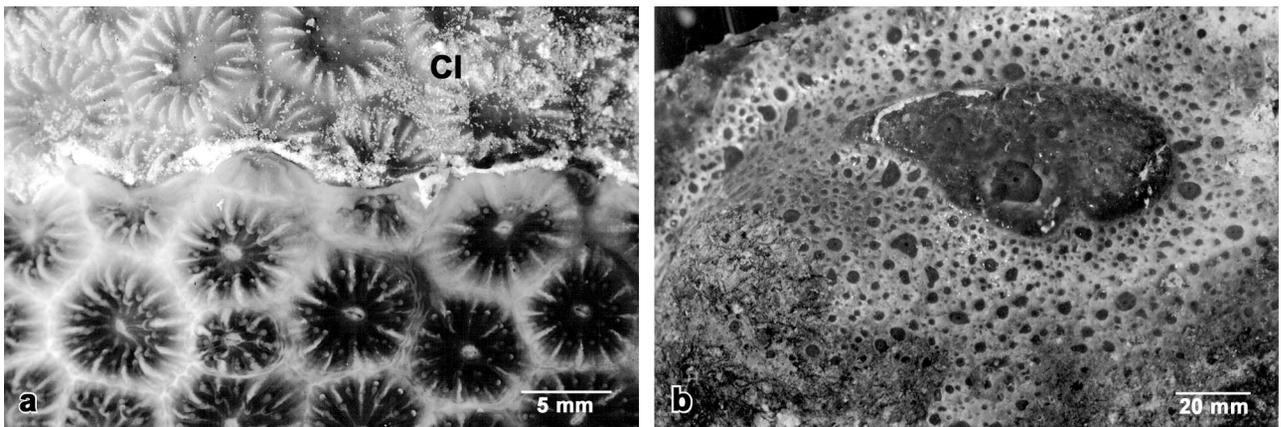


Figure 5. *Cliona lampa*, Bermuda. (a) Underwater close-up of sponge crust (CI) displacing live coral tissue without changing the skeleton structure (calyces) of the dead, overgrown coral (January, 1973); (b) papillate (alpha) stage, fusion toward encrusting (beta) stage starting in the center of the sponge.

tastraea 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. *nucula* (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*, *Montastrea 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 *Montastrea* 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 ectosome is dark brown from intracellular zooxanthellae (8-10 μ m 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 μ m) carbonate chips that are expelled through the oscula (Fig. 3 b, c). Examination

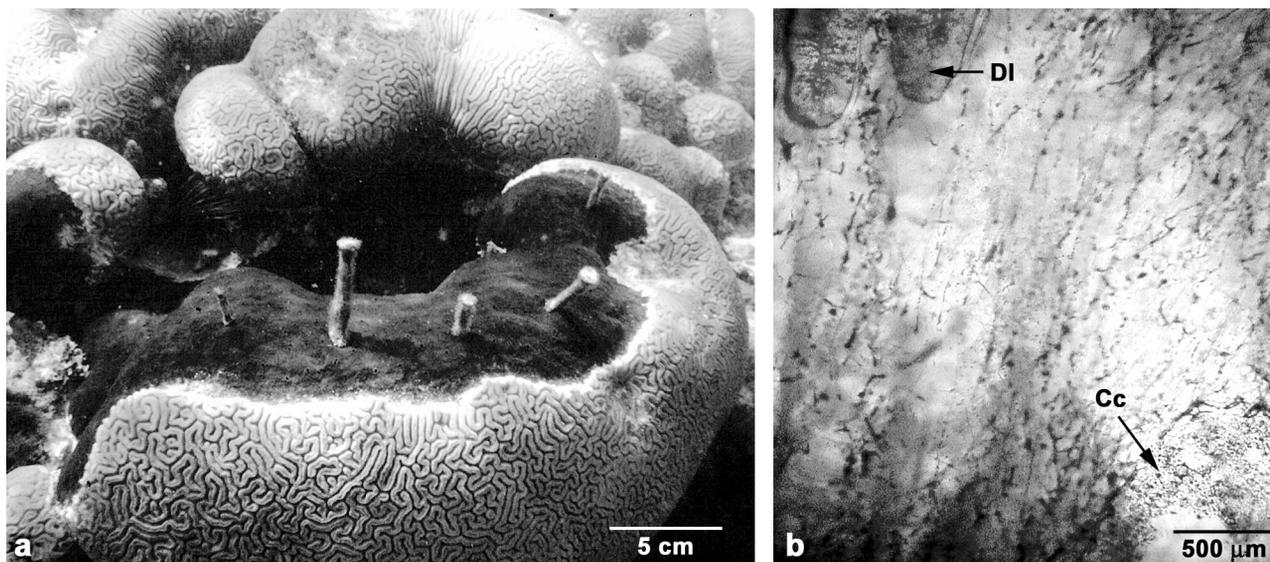


Figure 6. *Cliona caribbaea* overpowering the coral *Diploria labyrinthiformis*. (a) Underwater view with reference markers in place, showing one year of progress; (b) Section perpendicular to coral surface showing invasion of sponge (Cc) toward polyp base (DI) from below (the central area in the photomicrograph is coral rock riddled by boring microalgae).

of consecutive sponge (with substratum) sections approaching the live coral reveals that the sponge is advancing below the live coral and is able to destroy the coral skeleton from under the polyps (Fig. 6 b). Coral tissue, robbed of its support, recedes and allows the sponge to spread further without getting exposed to defensive nematocysts and mucus.

DISCUSSION

Cliona caribbaea, dull blackish brown, with zooxanthellae, and *C. lampa*, brilliant vermillion, without symbionts, are highly distinctive excavating sponges but from the ecologist's point of view they play a very similar role on Caribbean coral reefs. Both may spread rapidly when favored by environmental conditions, covering areas the size of one or more square meters, and both have the potential to overpower a variety of large reef corals. The two species also share the property of coating their substrate with a thin, veneer-like tissue layer so that the nature and condition of the underlying substratum at the time of overgrowth (for instance, recently dead coral, versus rock already "aged" by erosion or other settlers) can be readily seen. Many more data and experiments will be needed to arrive at iron-clad conclusions but there is no lack of evidence that corals and coral reefs worldwide are stressed or endangered (Sebens, 1994) and that a number of environmental parameters that are not af-

fecting sponge vitality are causing the weakening of coral defense against aggressive competitors.

Over 20 years ago, concern was expressed about *Cliona varians* forma *incrustans* (Wiedenmayer, 1977; as *Anthosigmella*) which overgrew and killed corals in some parts of the Caribbean. Vicente (1978) determined 11 species of reef corals (among other sessile invertebrates) that were affected, including those involved in the present study. However, during his extensive (1976-1977) surveys along the Puerto Rican coastline and at remote Desecheo island, he encountered just 37 encrusted specimens of hermatypic scleractinians and milleporids, about the same number as occur on our tiny Belizean study reef alone. At the same time, *Cliona varians* f. *incrustans* was also fairly conspicuous in the Carrie Bow back-reef zone, but even then much less than *C. caribbaea* and it has not increased in abundance since then. Vicente (1978) considered the competitive superiority of the sponge an "ecological disturbance", not a genuine threat to reefs.

The nature of competitive success of *Cliona caribbaea* versus coral has yet to be tested. It has long been determined that coral species display a distinctive hierarchy of aggressive capabilities, against each other (Lang, 1973) as well as against sponges (Vicente, 1990; Porter and Targett, 1988; McKenna, 1997). In Belize, all three corals (*Acropora*, *Diploria*, *Montastraea*) were successful in their defense against sponge-tissue invasion when healthy but, as

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 than 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 exper-

imentally 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 delitrix* 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-

ciated with hurricane Mitch in October 1998 and led, among other problems, to bleaching and death of large populations of *Agaricia tenuifolia* in the Pelican Cays, south of the Carrie Bow laboratory (Macintyre et al., 2000). These corals are now overgrown by extensive crusts of the non-excavating encrusting sponge *Chondrilla* cf. *nucula* (possibly an undescribed species) which, however, did not conquer substrate on the Carrie Bow study reef where a large crust abutting *Diploria* was monitored. This stand-off may have been owed to superior water flushing at the high-energy barrier-reef site. (Regrettably, no usable *Cliona* growth measurements are available for the Hurricane Mitch aftermath because an accidental fire destroyed the Carrie Bow laboratory in December 1997 and most tagged sponges had run out of new substratum to colonize when the study resumed.) A study of the interactions of *Chondrilla* cf. *nucula* with reef corals in Puerto Rico indicates that the sponge is an aggressive competitor which, under suitable conditions, may overpower most reef corals (Vicente, 1990). In Guam and Japan, another encrusting hadromerid sponge, *Terpios hoshinota* (Suberitidae), became known as a highly successful competitor of reef corals, particularly in stressed near-shore habitats (Bryan, 1973; Rützler and Muzik, 1993).

It is interesting to note that many aggressive encrusting sponges contain high densities of photosynthetic symbionts: *Cliona caribbaea* and *C. varians* are each associated with a different species of dinoflycean zooxanthellae, *Chondrilla* cf. *nucula* and *Terpios hoshinota* contain different cyanobacteria (zoocyanellae) (Rützler, 1990; Rützler and Muzik, 1993). Sponge workers have long speculated that clionid zooxanthellae enhance excavating capacity (a reversal of the catalytic function of coral xanthellae in CaCO₃ deposition) and Hill (1996) has demonstrated that possibility for *C. varians*. And it is possible that cyanellae contribute to the allelopathic action of the non-borers. Nevertheless, the assumption that plant associates are needed for competitive superiority is weakened by the fact that highly successful competitors such as *C. lampa* and *C. delitrix* are without symbionts.

CONCLUSIONS

Cliona caribbaea and *C. lampa* are distinctive members of the sponge family Clionidae and common inhabitants of Caribbean reef communities. Although taxonomically distant, they share a thinly encrusting habit (beta stage) as their adult growth form. *C. caribbaea* occurs throughout the Caribbean region whereas *C. lampa* is restricted to Bermuda and the subtropical northern portion of

the area although it may be an Indo-Pacific invader with the potential to spread throughout tropical America.

Encrusting Clionidae are among the most efficient space competitors of Caribbean reef corals. Like other thinly crustose sponges, they can spread rapidly as adjacent substrate occupants, such as corals, recede during periods of stress. Unlike other sponges, clionids may kill coral polyps by undermining and eroding their skeletal base, thus avoiding contact with defensive mucus and nematocysts.

In recent years, many Caribbean reefs have become stressed and increasingly victim to less delicate competitors, including sponges. Extended high or low water temperature extremes, pollution, sedimentation, turbidity, and physical damage by fish bites or anchors are factors that cause bleaching or otherwise stress or kill hermatypic corals. A decrease of live coral area and increase of abundance and excavation rates of *Cliona caribbaea* on a study reef in Belize over the past 20 years is attributed to water warming, either by catastrophic events, such as hurricanes, or as a long-term trend.

If the process of bioerosion of limestone on reefs is accelerated and carbonate deposition by corals and other delicate organisms is slowed we can expect large-scale breakdown of the reef framework and increase of coastal erosion, silting, and other parameters that will prevent reef recovery. The results of this study should be yet another encouragement for legislators and coastal resource managers to keep environmental degradation under control.

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