NEW ASPECTS ON THE BIOLOGY OF THE ENCRUSTING EXCAVATING SPONGES *CLIONA APRICA, CLIONA CARIBBAEA* AND *CLIONA* SP.

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ABSTRACT

In order to understand the mechanisms of interaction with corals in three species of encrusting and excavating sponges (*Cliona aprica; Cliona caribbaea=Cliona langae; Cliona* sp.) that actively undermine live coral tissue, detailed observations and follow-up of marked individuals were carried out in reefs of two coralline areas of the Colombian Caribbean. A not previously described final growth stage was found, in which tissue of older individuals thickens and becomes infested by epibiotic zoanthids. An agglutinating stage occurred in one species when growing on rubble. Maximum rates of lateral advance against live coral in 13 months were 19.7 cm *Cliona* sp., 8.3 cm for *C. aprica*, and 6.5 cm for *C. caribbaea*. By sending excavating tissue threads underneath live coral tissue, these sponges weaken the skeletal support of the polyps, resulting in their retraction or detachment. Fish bites and growth of turf algae and accumulation of sediment at the boundary produce further coral death. The sponge then advances, excavating and encrusting the freed substratum. This undermining mechanism is thus a highly effective competitive strategy that explains partly the ability of these sponges to gain and monopolize reef space.

KEY WORDS

Cliona, growth stages, excavating, competition, corals.

INTRODUCTION

Excavating sponges burrow into calcium carbonate skeletons and limestone substrata. During their growth, some excavating sponges may pass through three stages, alpha (α), beta (β) and gamma (γ) (VOSMAER, 1933). In the α stage, most of the living tissue is concealed in tunnels and galleries within the substratum and only inhalant (ostial) and exhalant (oscular) papillae are visible. In the β stage, through extensive papillary fusion, the sponge encrusts the surface of the excavated substratum. In the γ stage, the sponge becomes massive (see RÜTZLER, 2002). But some species always remain in the α stage, others start as encrusting (β) and remain as such, and very few become γ. There also seem to exist alternative growth stages. Whether growth stages are genetically fixed and/or environmentally controlled is not well known.

In the Caribbean Sea, there is a group of brown to brown-black, zooxanthellate sponge species which excavate and encrust calcium carbonate substrata, forming as they grow sideward, a shallow depression covered extensively or completely with their tissue. *Cliona aprica* PANG, 1973 appears as groups of small, dark brown to black papillae, usually fused extensively, but rarely covering completely the substratum. *Cliona caribbaea* CARTER, 1882 (junior synonym *Cliona langae* PANG, 1973) covers completely the excavated substratum with a thicker (up to 1 mm), amber brown or gray brown tissue. *Cliona* sp. encrusts the entire excavated substratum with a thin veneer of tissue, clay to dark grayish brown in color, through which the underlying excavated carbonate structures can usually be seen. Detailed descriptions of the three sponges are forthcoming (ZEA & WEIL, unpubl. data). At any given time, only about the upper 1 cm of substrate beneath the surface of these sponges is excavated, and the galleries are completely filled with dark yellow tissue. Upon encounter with live coral, they are able to continue their lateral excavation progress, generally resulting in relatively fast (in the order of cm yr^{-1}) and extensive death of coral tissue. They have recently brought considerable attention from the marine scientific community, owing to an apparent population boom of *Cliona* sp. (variably called *C. aprica*, *C. caribbaea* or *C. langae*) which has been gaining ample reef space in several localities since the early 1980´s, killing in the process many colonies of the most common reef-building corals (ANTONIUS & BALLESTEROS, 1998; WILLIAMS *et al.,* 1999; RÜTZLER, 2002; WEIL, 2002). The purpose of this paper is to summarize some known and add new aspects of the biology of these sponges, of their growth stages, and of their ability to monopolize reef space. Other papers regarding their taxonomy, ecology, and impact on coral reefs are under elaboration.

MATERIALS AND METHODS

The study was carried out at the oceanic reef complex of San Andrés Island, and at the continental shelf Archipelago of Rosario islands, Colombian Caribbean (Fig. 1).

One hundred and eighty sponge individuals were marked in seven stations throughout the two studied areas in May-June 2001. Steel nails were driven in the sponge boundaries, and lateral advance was measured after 6 and 13 months. Nail height was also measured to determine if the excavated substratum depression is increased further. The sponges, their neighbors and the boundaries were observed in detail.

Fragments of sponges, substrata and neighbors were collected with hammer and chisel or core borer, and fixed in 96 % ethanol or in buffered formalin. In the laboratory, fragments were cut with a circular diamond saw, to be embedded in resin, cut, mounted on slides, and ground and polished, for observation under transmitted light (see RÜTZLER, 1974; WILLENZ & POMPONI, 1996). Measurements of vertical penetration of excavating tissue inside the substratum were obtained from most fragments sampled. Cores of the three *Cliona* species with their substratum were obtained with a 2.8 cm diameter core borer. They were allowed to heal for a few days, and transplanted into similarly sized holes made in live and dead corals, or in blocks cut from coral skeletons and mollusk shells; their fate was followed after 6 and 13 months.

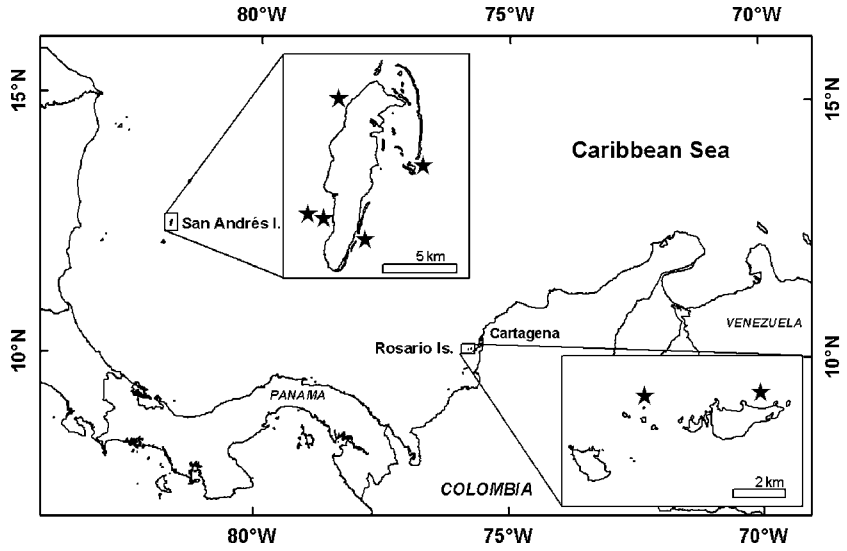

Fig. 1. Study areas and sampling stations (stars).

RESULTS

Cliona aprica was widespread throughout all reefs at San Andrés, and occurred in growth stages from purely papillated (α), to partly, to almost completely fused (β). At Rosario islands this species was found in rubble and in the base of branching live corals in lagoon environments. There, it occurred only in papillated stages with a small degree of papillary fusion. Transplanted fragments always grew papillated (Figs 2a, b).

At San Andrés, *Cliona caribbaea* was found in the leeward reef terraces from ca. 3 m to the outer reef edge (ca. 30 m). In the windward side the species occurred from 15 to ca. 30 m. It was rarely papillated (α), and predominantly fully encrusting (β). In contrast, in continental reefs (Rosario islands), this species was uncommon, apparently restricted to deeper parts of the reef (> 15 m), and only papillated (α). Transplanted cores of β individuals of this species grew both continuous and papillated (Fig. 2a), the latter more evident in harder substrata (*e.g., Acropora palmata* blocks and mollusk shells).

In both *C. caribbaea* and *Cliona aprica*, an additional final growth stage was found. In this stage, once the sponge had encrusted (and slightly depressed) the entire exposed surface of its substratum, not being able to further advance laterally, its tissue thickened (up to ca. 2 mm) and frequently its surface was colonized by epibiotic zoanthids (probably *Parazoanthus parasiticus*) (Figs 2c, d). Apart from the thickening, they did not grow upwards and became massive. In rubble (shallow and calm waters < 1 m), papillated *C. aprica* grew fleshy tissue extensions, 1 - 2 mm thick, up to 5 mm long, that bound substratum fragments across several centimeters, conforming an agglutinating growth stage (Fig. 2e).

Cliona sp. was found in shallow (1 - 8 m) pavement of wave-exposed reef terraces of San Andrés, and restricted to the *A. palmata* zone (now almost totally dead, 3 - 6 m in depth) in the continental reefs of Rosario islands. In contrast to the other two species, *Cliona* sp. always grew as a smooth, continuously encrusting, β stage, both at San Andrés and at Rosario islands, even when small or in transplants (Fig. 2b). The growing edges could have small tissue extensions that did not resemble ordinary papillae. In Colombia, we seldom found it with epibiotic zoanthids.

The three species were found on a wide variety of substrata, including several coral species (at least 22), rubble, pavement of reef terraces and mollusk shells. In those marked coral-sponge boundaries in which there was advance by the sponges against live coral tissue, the greatest advance measured for *Cliona* sp. (Rosario islands) was 19.7 cm in 13 months (0.50 mm d^{-1}). For *C. caribbaea* (San Andrés), it was 6.5 cm in 13 months (0.16 mm d^{-1}), and for *C. aprica,* 8.3 cm in 13 months (0.21 mm d^{-1}). After settlement on dead portions of corals, these species start to excavate downwards and laterally, forming a shallow, ca. 3 - 10 mm, usually sharp-edged depression in the substratum. Interestingly, from the lack of change in height of the nails driven into the sponges, it was evident that the depression made in the substratum did not increase in depth during the 13 months of observation. In fact, these species did not continue the vertical penetration, the excavated portion being restricted to the uppermost 0.7 - 1.5 cm of the substratum. As they encounter live coral, they excavate the coral skeleton immediately below the neighboring coral tissue, sending tissue extensions in the shape of dendritic filaments, called pioneer tissue threads (see SCHÖNBERG & WILKINSON, 2001), which were found to be about 1 - 2 mm in diameter and to reach 4 cm in length (Figs 2f, g). In cross sections of branching corals (*e.g., Acropora, Porites*), pioneering filaments were seen to be sent downwards from one surface to the other; downwards directed filaments were seen in just one massive corals (*Porites astreoides*). When growing horizontally, the filaments weaken (undermine) the skeletal polyp support. As a result, coral tissue retracts and is often sloughed or bitten off by corallivorous fishes, allowing further advance by the sponge (Fig. 2h). In all 23 marked sponge-coral boundaries in which clear fish bite marks were found in the live coral at the boundary, there was advance of the sponge at that point, often greater than at points with no bites (data analysis in progress). We casually observed parrotfish scraping and butterflyfish sucking at the coral polyps in and near the boundary. In some corals with projected and brittle calices (*e.g., Diploria, Colpophyllia*), it appears that the parrotfish themselves had helped with the erosion at the boundary, as sometimes there was a band of bitten, leveled skeleton in front of the advancing sponge. In contrast, in other corals with non-projected calices (*e.g., Siderastrea*), fish seem to help less in the erosive process as bite marks were located in and beyond the step of coral skeleton in front of the advancing sponge (Fig. 2h). Apart from fish bites, coral tissue death and further sponge advance seems to be favored by the smothering action of the turf algae, coral mucus and silt that commonly occur at the sponge coral boundary. Evidence of this phenomenon was the frequent occurrence at the boundary of sharply-cut polyps, missing part of their former tissue (Fig. 2i). This turf belt is continuously displaced by the advancing sponge, being renewed constantly. On the other hand, we observed that in non-advancing coral-sponge boundaries, corals had been able to outgrow the

reach of the excavating filaments, thus preventing the loss of polyps and stopping the sponge advance.

DISCUSSION AND CONCLUSIONS

The growth stages of the *Cliona* species here studied differ from other congeners. Comparing with the final γ stage of species such as *Cliona varians* or *Cliona nigricans* (see VICENTE, 1978; CALCINAI *et al.,* 1999), the final thickly encrusting stage found in this study lacks a significant three-dimensional growth below and above the substratum. Indeed, penetration towards the interior of the carbonate substratum in the studied species is limited to the first 1.5 cm, in contrast to the deeper excavations (10 cm or more) of species such as *Cliona delitrix* (see PANG, 1973; ZEA, unpubl. data), limiting their ability of becoming massive. Considering that the main direction of growth in these species is towards the sides, the final thick stage could be consider equivalent to the massive γ stage of other species. For the agglutinating growth stage found in *Cliona aprica*, by virtue of bridging coral rubble with tissue extensions, this sponge becomes a consolidating agent, in addition to its traditional role as bioeroder. *C. nigricans* also actively agglutinates substratum fragments during its massive γ stage (CALCINAI *et al.,* 1999). Far from diminishing the available carbonate substratum, these two species create new habitat for multiple organisms.

Although papillae were absent in *Cliona* sp. in Colombia, fields of papillae off the margins of fully encrusting specimens were rather frequent in Belize. But these resulted from a secondary regeneration reaction in areas where the tissue had been smothered by sand or crustose algae, or bitten by fish (ZEA, unpubl. data). Epibiotic zoanthids were rare in this species in Colombia, but present in several deep-water (20 m) individuals in Puerto Rico (ZEA & WEIL, unpubl. data). This lack of zoanthids in most specimens of this sponge could be related to the typically strong turbulence in the shallow and windward environments that this species prefers.

Our findings of pioneering sponge tissue threads penetrating beneath live coral tissue agree with those recently found by SCHÖNBERG & WILKINSON (2001) in *Cliona orientalis*, a Great Barrier Reef sponge of similar habit to our *Cliona* sp., and by RÜTZLER (2002) who is currently working with the latter species in Belize (as *Cliona caribbaea*). While the sponge is out of the reach of the aggressive coral tentacles, digestive filaments and of mucus, pioneering sponge tissue filaments are able to penetrate and erode the skeleton directly beneath the coral polyps, weakening their support and resulting in their retraction or detachment. The weakening, retraction and loss of coral tissue often induce the biting by fish and the settlement of filamentous algae and accumulation of silt, which in turn result in further coral tissue loss. The fish also aid in the bioerosion of the upper part of the skeletons. The process culminates with overgrowth and occupation (excavation + filling) by the sponge of the upper layer of the freed substratum, in what is left of the coral skeleton. The supplementary effect of fish and turfs make the sponge's undermining mechanism a highly effective competitive strategy that explains partly the ability of these sponges to gain and monopolize reef space. The aggressive mechanism of undermining would be the sponge's equivalent to extracoelenteric digestion by corals (see LANG & CHORNESKY, 1990), or the use of allelopathic secondary metabolites by any organism, to weaken the resistance of its neighbor. Direct growth over live

tissue of a neighbor (overgrowth in a more strict sense), with the consequent smothering, acts in the opposed side to undermining; this mechanism is used by encrusting, sheet-like sponges such as *Terpios hoshinota* (RÜTZLER & MUZIK, 1993) and *Chondrilla nucula* (VICENTE, 1990). Undermining appears to be widespread, since some other Clionaidae, such as *Cliona lampa* (RÜTZLER, 2002), and *C. delitrix* use it (ZEA, unpubl. data). *C. varians* is known to directly overgrow live coral tissue (VICENTE, 1978; AERTS & KOOISTRA, unpubl. data), but whether this species also undermines the live coral polyp support remains to be determined.

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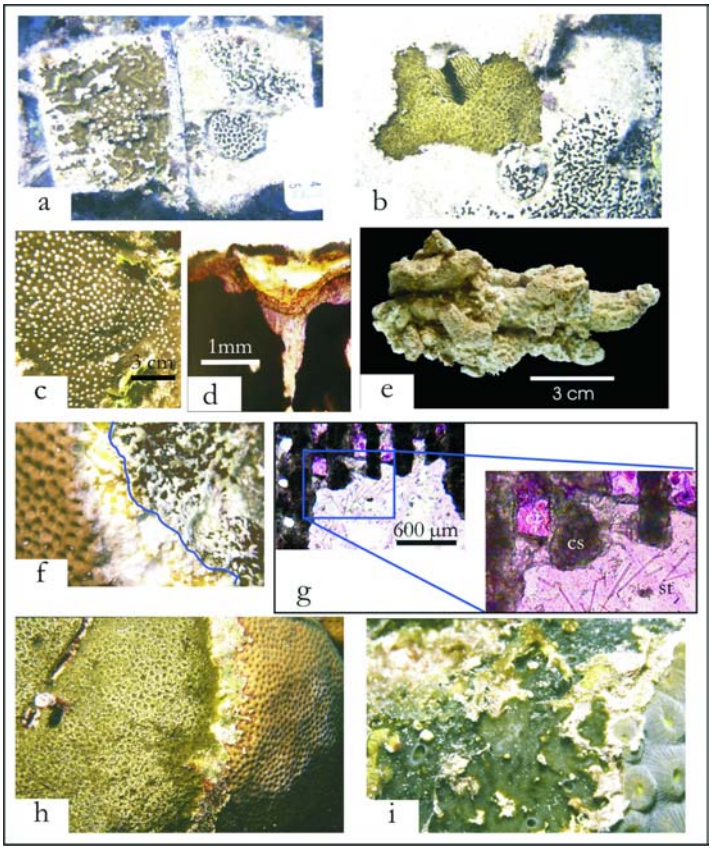

Fig. 2. a, Growth after 6 months of implanted *Cliona caribbaea* (left) and *Cliona aprica* (right) 28 mm diameter cores into a dead coral block. **b,** Same as in a but for *Cliona* sp. (left) and *C. aprica* (right). **c,** *Cliona caribbaea* at the final growth stage, incrusted by zoanthids. **d,** Ground and polished cross section of *Cliona caribbaea* showing a portion of a zoanthid (under light microscopy). **e,** Agglutinating stage of *Cliona aprica*. **f,** Filament-like sponge tissue growing underneath live coral tissue (the blue line indicates the original sponge-coral boundary; frame width 7.2 cm). **g,** Cross section of *Cliona aprica-Siderastrea siderea* border, showing sponge tissue (st) filament excavating coral skeleton (cs) underneath live coral tissue (ct). **h,** Typical scene of a sponge-coral boundary bitten by fish (the steel nail marks the location of the boundary 6 months before; frame width 16.4 cm). **i,** Sponge-coral boundary with turf algae, mucus and sediments (frame width 7.2 cm).