Observations on reef coral undermining by the Caribbean excavating sponge *Cliona delitrix* (Demospongiae, Hadromerida)

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Abstract: Sponges which simultaneously encrust and excavate calcareous substratum are strong space competitors in coral reefs, actively undermining and displacing live coral tissue. On Caribbean reefs, *Cliona delitrix* colonizes massive corals, encrusting, deeply excavating and aggressively killing entire coral heads. To establish the details of the process of colonization, excavation, undermining and death of corals by this sponge, we carried out observations on sponge-colonized corals at San Andrés Island (SW Caribbean Colombia), and obtained samples for microscopical observation. As it spreads sideward, *C. delitrix* removed the upper few mm of the coral skeleton, maintaining its surface slightly lower than the surrounding coral, following the curved outline of the coral head. Internal excavation resulted in a solid outer supporting frame and a strongly eroded lace-like internal network. The outer frame was perforated below inhalant papillae by narrow vertical tunnels and below the large oscules by wide and deep spaces. A band of dying or dead coral surrounded the sponge. The sponge sent out a front of tissue using pioneering filaments projecting underneath the coral polyps. Long filaments may surface farther off, forming new bodies that later fuse. From microscopical observations, physical detachment of polyps was ruled out as the cause of coral death, because coral tissue displacement occurred before significant erosion of the polypar skeletal support had taken place. When sponge tissue reached underneath coral tissue, the latter remained healthy when still separated by thin skeletal barriers, but appeared as debris when barriers were broken. Live sponge and coral tissue could occur in direct contact, in which case there was accumulation of granulous cells in the coral tissue. We hypothesize that the mechanism of coral death involves close-range tissue, cell and/or biochemical interactions rather than fluid- or mucus-borne allelochemicals.

Keywords: *Cliona delitrix*, excavation, corals, colonization, cell-cell interactions, Caribbean reefs.

Introduction

Sessile colonial organisms living on hard substrata often compete for space by overtopping or directly overgrowing their neighbors. Takeover of space could be achieved by fast lateral growth that smothers and kills the overgrown tissue, but the neighbor’s tissue death could precede or parallel space takeover through deployment of aggressive appendages at the boundary and/or release of allelochemical substances (Jackson and Buss 1975, Suchanek and Green 1981, Lang and Chornesky 1990). Upright growing organisms with a limited holdfast area avoid competing for space with more massive or encrusting ones. Similarly, organisms able to penetrate and excavate into the substratum limit competition with organisms dwelling over the surface of the substratum to those points of their body that are exposed (Jackson 1979, Woodin and Jackson 1979).

Excavating (burrowing, boring) sponges live in cavities that they themselves bore into calcium carbonate (corals and coralline substratum, mollusk shells, polychaete tubes, calcareous algae) (Goreau and Hartman 1963, Rützler 1975). Excavation is achieved by both mechanical and chemical etching and removal of coarsesilt-size grains through filopodial extensions of the basal epithelium cellular membrane (see Rützler and Rieger 1973, Pomponi 1977). Many species only expose papillae and oscula through which food and oxygen are taken and wastes eliminated. However, several species also encrust the excavated substratum and aggressively compete for space with corals and other reef organisms. Some may overgrow live tissue of neighboring organisms (e.g. Vicente 1978). Others, however, avoiding external defense mechanisms of their neighbors, bore directly under them, sending excavating tissue fronts preceded by pioneering tissue filaments, making neighbors detach, apparently by eroding their support (Ward and Risk 1977, Schönberg and Wilkinson 2001, Rützler 2002, López-Victoria et al. 2003, 2006). Some papillated sponges also kill surrounding coral tissue by releasing mucus presumably laden with allelopatic compounds (Sullivan et al. 1983, Sullivan and Faulkner 1990).

The encrusting and excavating sponge *Cliona delitrix* Pang, 1973 (lat. *delitrix*: a destroyer; Hadromera: Clionaidae) is considered one of the most destructive bioeroders in reef corals. It appears as an encrusting layer of bright scarlet tissue of closely spaced papillae and interspersed large, high collared oscules in which deep exhalant canals open (Pang 1973). It
penetrates deeply (down to 10-12 cm or more) into the coral skeleton, filling existing and newly eroded spaces with tissue. The lateral and vertical expansion of the sponge eventually leads to the overpowering of entire coral heads, sometimes as large as 1 m in diameter (Pang 1973, Rose and Risk 1985). The sponge is often surrounded by a band of dead coral from where live coral tissue has been eliminated (Pang 1973, Rose and Risk 1985), but the exact mechanism by which this is achieved is not known. *Cliona delitrix* has been reported to increase in abundance in recent decades, at the expense of live corals, in various reef areas subjected to nutrient runoff and organic pollution (Rose and Risk 1985, Ward-Paige *et al.* 2005, Chaves-Fonnegra *et al.* in press).

With the aim of obtaining a better understanding how encrusting excavating sponges in general, and *C. delitrix* in particular, confront, erode, and kill reef corals, we undertook detailed field observations on the sponge and its host corals at San Andrés Island (SW Caribbean, Colombia), and histological analyses of samples from the sponge-coral boundary, to establish: (1) substratum preferences and growth forms, (2) overall excavation processes and, (3) details on the undermining and killing of live coral tissue.

**Materials and methods**

San Andrés (12°32’N, 81°43’W) is an oceanic island of coralline origin, located in the SW Caribbean and surrounded by a calcareous platform with a windward barrier reef, a lagoon with patch reefs, and leeward and windward fore reef terraces with coral carpets (Díaz *et al.* 1995, 1996). Observation and sampling took place throughout the leeward, western margin of the island. There, individuals of *Cliona delitrix* were photographed and observed in detail, noting its host coral species or substratum (pavement, old dead coral), surface characteristics, aspect of the zone of interaction with live coral, etc.

To understand why *Cliona delitrix* tended to grow at a slightly deeper level than the surrounding substratum, we made detailed observations and measured the depth of the sponge at the boundary step using the butt of a caliper (Fig. 1). To study excavation patterns, several live sponges were fragmented with hammer and chisel. By bathing in commercial bleach remains of dead sponges and small coral heads completely colonized by a live sponge, intact clean skeletons were obtained. To obtain a crude estimate of the depth of sponge excavation inside the coral skeleton, a bicycle steel ray was forcefully driven perpendicularly through one sponge papilla, approximately at the center of the sponge (Fig. 1). This was done only in sponges whose host coral was still alive. The ray was then retrieved and the depth of penetration measured with a caliper. The size of the sponge, measured as projected surface area, was statistically correlated to the depth of the ray penetration using Pierson’s product-moment correlation coefficient (Sokal and Rohlf 1981). Surface area was obtained from digital photos using the Coral Count Point Program with Excel extension (NCRI-NOVA).

To understand the way in which *Cliona delitrix* excavates under live coral tissue, portions of the coral at the sponge border were detached with hammer and chisel. Structures were measured with a caliper and sketches of the sections were made. Some fragments were fixed for histology in seawater 10% formalin neutralized with methenamine (20 g L\(^{-1}\)) for three days, after which they were stored in 70% ethanol. In the laboratory samples were trimmed and cut into 2 mm thick slabs with a petrographic low speed circular diamond saw (Isomet®, Buehler, Chicago). They were then dehydrated, stained (acid fucsin and crystal violet), and embedded in Spurr’s low viscosity resin (ERL 4206, Electron Microscopy Sciences). Resin blocks were cut in two and each cut section was glued onto microscope slides using fresh resin. Each section was then ground in a low speed Polisher/Grinder (Minimet 1000®, Buehler, Chicago) with diamond-coated grinding paper of increasingly finer grain (79-9 μm), and then polished by hand with car burendum 1500 grit paper and metal polishing paste (for details see Rützler 1974, Willenz and Pomponi 1996, López-Victoria 2003).

**Results**

**Substratum preferences and growth forms**

Most individuals of *Cliona delitrix* were found growing on live massive corals or on elevated substratum (old dead coral); none were colonizing branching or thin foliaceous corals and only a few were dwelling directly on the flat calcareous pavement (Fig. 2A, B). There was no mucus on the surface nor was it produced when the sponge was handled. The few small sponge individuals seen were always on dead areas of corals, and consisted generally of an oscule with surrounding papillae, separated or fused (Fig. 2C); individuals larger than 3-5 cm always completely encrusted the surface of the excavated area (Fig. 2D). Sponges had inhalant papillae throughout their surfaces (Fig. 3A), but often the external border of a given colony was comprised of a belt of smooth and level tissue, lacking papillae (Fig. 3B).

**General observations on the excavation process**

The surface of *Cliona delitrix* colonies was 0.1 to 1.7 cm lower than the surrounding substratum (from 164 measuring
points in 30 sponges), being variable within coral species (mean±1 standard deviation; *Diploria labyrinthiformis* 0.5±0.2 cm, n=4; *Porites astreoides* 0.9±0.8 cm, n=2; *Siderastrea siderea* 0.5±0.5 cm, n=24; statistical tests were not carried out because of low sample sizes of all but one coral species). The surfaces of the sponges that were found within about 0.5-1 cm of live coral tissue were only a few mm deeper than that of the coral (Fig. 2D). At greater distances the surrounding substratum could be higher, forming a step, because while the sponge eroded the outer coral skeleton to about the same elevation, the surrounding live coral (or dead coral covered by crustose coralline algae) had grown further upwards (Fig. 3B, C). As the sponge spread, it apparently carved the wall of the step by undermining its base, often with tissue fingers and papillae appearing beyond the wall margin (Fig. 3B, 4A, D). When live coral was at some distance from the sponge, its new upward growth formed a second step (Fig. 3B). Apart from oscular collars and papillae, the sponge did not elevate its tissue above the initial level.

A single individual of *Cliona delitrix* could overtake and completely encrust a medium size (up to ca. 30-50 cm in diameter) coral head (Fig. 3D). In larger coral heads the sponge was frequently characterized by several contiguous mounds, which we assumed were formerly surviving islands of coral that grew upward until the sponge covered them (Fig. 3C, E). Fragmentation of a few whole coral colonies revealed that the sponge could send tissue filaments of about 1 mm in diameter that would extend into the coral skeleton as far as 10 cm from the main sponge body, surfacing to form new sponge bodies, which would later fuse with the main body.

From inspection of dead sponges and bleached fragments we found that just below the dermis of the sponge there remained a rather solid frame, 3 to 6 mm thick, perforated by vertical tunnels located below each papilla, and by ample and deep cavities below oscules (Fig. 3F). Vertical tunnels were made directly into each coral calyx, eroding continuously downwards (allowing the insertion of bicycle rays to measure approximate depth of excavation). Below the frame, the skeleton was strongly eroded to a lace-like thinner network, thicker towards the periphery of the sponge, thinner towards the center, traversed by tunnels of the exhalant canals, which converged into oscular cavities. The bicycle rays penetrated...
up to 10.1 cm inside sponges that had not yet covered a given coral head. For these sponges, penetration depth was rather similar between coral species: Diploria labyrinthiformis, 3.7±1.4 cm, n=3; Montastraea faveolata, 4.7±2.1 cm, n=2; Porites astreoides, 5.2±1.0 cm; n=2; Siderastrea siderea, 4.7±1.6 cm, n=30 (again, no statistical comparisons were carried out because of small sample sizes in most corals). Sponge surface tissue area did not correlate statistically with depth of bicycle ray penetration in Siderastrea siderea (r=0.36, p=0.063, n=28). For sponges larger than 25 cm, depth of ray penetration varied between 3.5 cm and 6.8 cm, while in smaller sponges it varied between 2 and 3.5 cm. In S. siderea colonies of about 30 cm in diameter by 20-25 cm in height, completely overtaken by C. delitrix, we noticed (but did not measure) that they were excavated almost to their base.

**Undermining by the sponge vs. coral tissue death**

Every Cliona delitrix confronting a live coral, regardless of its size, was surrounded by a band of dead or dying coral. When coral tissue was dead, the calices appeared clean (coral tissue was just removed), or already colonized by turf, frondose or crustose algae. Often the band of dead coral appeared rasped by the long-spined urchin Diadema antillarum Philippi 1845, algae being partly removed and coral calices leveled further. Fish bite marks were rare on the edge of coral tissue confronting the sponge. In coral tissue close ≤5 mm to the sponge, 1-2 mm to 1-2 cm-wide unhealthy or dead strips of coral tissue were sometimes seen spreading radially outwards from the sponge border (Fig. 3A). Dislodging of coral tissue with hammer and chisel showed that these affected coral areas were undermined by shallow excavating sponge pioneering tissue filaments, apparently involved in coral
death. In relatively narrow bands of dead coral (<2.5 cm), an excavating tissue front 1-3 cm thick advanced 0.5-2 cm below the surface, often penetrating beyond the edge of live coral tissue, preceded by tissue filaments, reaching upwards towards coral polyps or extending horizontally farther ahead (Fig. 4A, B, C). In wider bands of dead coral, the front of sponge tissue reached only a few mm beyond the edge of the sponge, but filaments advanced several cm ahead, sometimes into live coral (Fig. 4D). Thick tissue bridges extended beneath adjacent sponge bodies of the same individual (Fig. 4E).

The etching marks characteristic of excavating sponge erosion were evident in ground and polished sections of the coral skeletons inhabited by *Cliona delitrix*, including the encrusted surface. Beneath live coral tissue, sponge tissue filaments penetrated through existing skeletal spaces, expanding them, proceeding upwards through the columnellar space of the calices, breaking through dissepiments, until reaching the base of the polyp. Throughout the filaments there were abundant granulous, naturally pigmented golden-brown cells of varied shapes, 12-15 µm in diameter (Fig. 5), also common in the outer surface tissue and reminiscent of spherulous cells (see Pang 1973). In several places healthy sponge and coral tissue were separated by still intact dissepiments or walls. But empty calyx spaces where the sponge had partially penetrated often contained what appeared to be dead coral tissue debris. In the few instances where actual sponge and coral tissue contact was seen, coral granulous cells accumulated (Fig. 5, pers. comm. by Esther Peters, July 27 2005).

**Discussion**

Our observations have confirmed that *Cliona delitrix* is a highly aggressive and destructive reef sponge, and added details about its growth form and how it confronts live coral, allowing us to formulate hypotheses on the mechanism by which it kills coral tissue.

The few small, young *Cliona delitrix* observed were growing on dead coral substratum, indicating that the larva, possibly planktonic (see Mariani *et al*. 2000) settles preferentially on old dead coral. This behavior has been described for several excavating sponges (see reviews by Goreau and Hartman 1963, McKenna 1997, Schönberg and Wilkinson 2001). But for slightly larger individuals, which were completely surrounded by live coral tissue, one may wonder if larval settlement could have occurred directly on live coral tissue. In fact, Rützler (1971) hypothesized that

![Fig. 4: Schematic drawings showing how *Cliona delitrix* excavating tissue fronts and pioneering filaments reach out below live coral (A to D), and how two bodies of the same individual are connected under the surface (E). The leftover coral skeleton within the sponge tissue was not drawn.](image-url)
mucus-laden larva of the excavating sponges of the genus *Aka* (as *Siphonodictyon*), which release abundant mucus, might be able to smother and kill live coral polyps, then taking root and expanding. But *C. delitrix* does not release mucus, and recent studies have shown that healthy corals prevent settlement of other organisms on them (Díaz-Pulido and McCook 2004), perhaps through the use of allelochemicals (Fearon and Cameron 1997).

As most other encrusting and excavating sponges, *Cliona delitrix* tends to grow at a level slightly lower than the surrounding substratum (see Acker and Risk 1985, Schönberg and Wilkinson 2001, Rützler 2002, López-Victoria et al. 2003; but see Vicente 1978 for an exception). Rather than directly overgrowing the adjacent substratum, the lateral undermining by these sponges tends to remove its upper layer (elevated septa in corals, crustose and turf algae in fouled substratum). Differences in height between *C. delitrix* and the surrounding substratum were quite variable within a coral species, showing that other factors apart from the density and texture of the outer skeleton play a role. By biting the edge of the live coral that confronts other encrusting and excavating sponges, corallivorous fish may sometimes be responsible for initiating and maintaining the difference (see López-Victoria et al. 2006). But fish bite marks were rare on coral tissue confronting *C. delitrix* in San Andrés. Perhaps grazing of the band of dead coral by sea urchins plays a similar role, but we could not clearly ascertain this. Overall, for *C. delitrix* we believe that two opposing factors are responsible: (1) while the sponge maintains its curved surface at the same level of the coral skeleton, upward growth of adjacent coral tissue or of crustose coralline algae increases the height of the substratum around it and, (2) rasping of the dead coral area by sea-urchins decreases the height of dead coral areas. Further shrinkage of the substratum under the live sponge by bioerosion and subsequent lowering of the sponge surface may also occur (Acker and Risk 1985). Microscopical observations on shallow excavating species (Rützler 1971, Zea and Weil 2003) and in *C. delitrix* (this study) revealed characteristic etching marks on the surface of the external skeleton, showing that some vertical reduction of the substrate level indeed occurs. However, significant substratum shrinking is unlikely to exist in the case of *C. delitrix*, because its outer skeletal frame remains uniformly thick throughout the sponge. Further substratum shrinkage would occur only if directly eaten and scoured by fish or urchins, which does not seem to be happening, or from mechanical abrasion during storms. In fact, marked individuals and fragments of shallow excavating sponges did not shrink within 1 to 5 years of observation (López-Victoria et al. 2003, S.Z. pers. observations 2005).

The curved surface of *Cliona delitrix* may be maintained as it grows, when the lateral erosion and advance is made preferentially following the same coral skeletal growth bands, which are laid cyclically in different densities in various coral species (e.g., Macintyre and Smith 1974, Huston 1985). Unfortunately, from our skeletal fragments and skeletal sections we could not ascertain whether this was the case. The extent of vertical penetration of *Cliona delitrix* into a coral while the sponge is still spreading does not seem to be affected by density or texture of the host coral species’ skeleton, and does not increase significantly as the sponge increases in size. Perhaps it penetrates only deeper once it has taken over the entire colony. Similar values for vertical extension of *C. delitrix* have been reported in other studies (5 cm, Rose and Risk 1985; 10-12 cm, Pang 1973; vs. 10 cm in our study). Vertical penetrations of the substratum as deep as 8 cm occur in other species as well: in *Pione lampa*...
de Laubenfels 1950 (see Rützler 1974, as *Cliona*) and in *Aka corralliphaga* (Rützler, 1971) (see Glynn 1997).

The outer advancing tissue front of *Cliona delitrix* in massive cerioid corals is similar to the “string of beads” morphology of excavating tissues in non-encrusting excavating sponges such as *Cliona vermifera*, in which vertical lobes of tissue located within coral calices are interconnected by horizontal excavating filaments of varying diameters; smaller filaments penetrate through the thecal wall, invading another calyx; the calyx is then filled with tissue and eroded vertically and horizontally cutting dissepiments and septae (Ward and Risk 1977). This may be a general way by which excavating sponges erode corals, first filling existing spaces and then eroding walls and obstacles (see review en Schönberg 2003), subsequently varying widely within and among species in further erosion of the coral skeleton. The vertical component of calyx erosion is emphasized in *C. delitrix* in comparison to other shallow excavating encrusting sponges.

When they become large enough, some excavating sponge species add tissue and supporting siliceous skeleton above the substratum, becoming massive, and often erode all skeletal connections to the substratum, becoming free-living, in both cases conforming what is called a gamma stage (e.g., Topsent 1888, Vosmaer 1933, Rützler 1971, Vicente 1978, Calcinaí et al. 1999). Even shallow excavating excavating species that spread horizontally in the upper few cm of substratum slightly thicken their tissue when they run out of space (López-Victoria et al. 2003). Owing to its rather soft tissue *Cliona delitrix* is perhaps not able to grow further upwards. It may compensate its lack of upward growth with deep vertical penetration into the substratum. Its excavation pattern of an outer solid shell and an inner cavernous core provides enough space for the tissue and water-circulation system, while giving stability and support to the sponge.

The growth of *Cliona delitrix* with far-reaching ramifications inside the coral skeleton allows it to simultaneously weaken coral tissue in various portions of the colony. In a similar way, but from a completely eroded central chamber filled with tissue, some species of the genus *Aka* erode tunnels that reach out to several separated places of the surface of a coral; further expansion of the outgrowths and the central chamber ends up taking over the entire coral head (Rützler 1971). Not penetrating deeply, shallow excavating and excavating sponges resort to shallow-lying tissue fronts and closer-range pioneering filaments that penetrate directly beneath live tissue coral at their borders (Ward and Risk 1977, Schönberg and Wilkinson 2001, Schönberg 2001, Rützler 2002, López-Victoria et al. 2003, 2006).

Our histological observations of the zone of interaction between *Cliona delitrix* and coral tissues show that coral tissue death occurs before erosion of the calyces is enough to induce coral polyp detachment. Indeed, coral tissue and its skeletal support are so strongly interwoven that polyp detachment seems hardly possible if the skeleton is not thoroughly eroded. This purely physical detachment has been assumed in other works with encrusting and excavating sponges (e.g., López-Victoria et al. 2003, 2006). Coral death in close vicinity of *C. delitrix* could be the consequences of the release of allelochemicals that can kill coral tissue, and which are known to be present in its organic extract (Chaves-Fonnegra et al. 2005). Similar effects have been observed in the fistulate excavating sponges of the genus *Aka* (Rützler 1971), and have been attributed to the release of abundant mucus assumed to be carrying known allelopathic compounds (Sullivan et al. 1983, Sullivan and Faulkner 1990). The mucus is a medium that helps spreading and retaining compounds on the surface of corals, facilitating their entrance into tissue (Hay et al. 1998). However, as *C. delitrix* does not produce mucus, there must be some other means, if any, for the deployment of the potentially harmful substances it produces. Whether they are exuded directly to the water remains to be determined. At any rate, our histological observations show healthy sponge and coral tissues within the coral skeleton just separated by thin carbonate walls, as well as sites of direct contact where the two tissues are still alive. This appears to indicate that chemical substances are not being released into the fluids contained in the coral skeleton. Moreover, the observed accumulation of cells in coral tissue in direct contact with sponge tissue points towards close-range cellular or biochemical processes involved in coral tissue death, which require further study.

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