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LAGOON SPONGES FROM CARRIE BOW CAY (BELIZE): ECOLOGICAL BENEFITS OF SELECTIVE SEDIMENT INCORPORATION

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ABSTRACT

Sponges living in tropical lagoons on mobile substrata face many challenges. The most important requirement is stable anchoring allowing the sponge to grow with defined polarity. We determined the anchoring ability for thirteen common species in the lagoon of Carrie Bow Cay (Belize) by evaluating the type and amount of incorporated sediments and comparing them with the nearby substrate components. In the example of *Tectitethya crypta,* sediment is not merely utilised as substratum but serves also the sponge's structural organisation. Sand is transported into the body where it is organised in patterns that are determined by granulometry and sponge size. The transport is performed by an unusual type of cell characterized by its size (between 40 and 150 μm) and the presence of inclusions. Sediment incorporation processes strongly affect sponge ontogeny.

KEY WORDS

Psammobiontic sponges, stability, soft bottom, *Tectitethya,* Caribbean.

INTRODUCTION

In recent years the interaction between sponges and environmental sediments was subject of several studies. In many cases foreign material is selectively incorporated and used to reinforce spongin skeletons (TERAGAWA, 1986a, b; BAVESTRELLO *et al.,* 1995, 1996). This phenomenon was studied on few species (ILAN & ABELSON, 1995; TERAGAWA, 1986a, b; SIM & LEE, 1999) and little is known about sediment selectivity (CERRANO *et al.,* 1999, 2002).

Sponges generally live on hard substrates where they can firmly attach but a few species are able to flourish on soft bottoms in shallow lagoons. As suggested by ILAN & ABELSON (1995), the main problem for a psammobiontic sponge is to avoid clogging of the aquiferous system by sediment and ensuring stable anchoring at the same time. The ability to anchor is essential in shallow waters that are subject to strong water movement, at least during certain periods of the year. Several sponge species living on sedimentary bottoms are able to incorporate sand, thus improving stability. The role of psammobiontic sponges in the reef community was investigated by RÜTZLER (1997) in the Caribbean and by CERRANO *et al.* (2002): which, studying an Indonesian lagoon, described how these sponges deeply penetrate the bottom and at the same time select and partially incorporate large fragments of shell and coral to enhance stabilisation.

The aim of this paper is to describe sediment incorporation in sponges living on soft bottoms of the barrier-reef lagoon between Carrie Bow Cay and Twin Cays, Belize, and to evaluate i) the number of species with this ability, ii) the kind and amount of sediments incorporated in the tissue, iii) the selectivity of each species in respect to nearby sediments and iv) the role these foreign bodies may play during different developmental phases, using the species *Tectitethya crypta* (Demospongiae, Hadromerida) as an example.

MATERIALS AND METHODS

The lagoon leeward of Carrie Bow Cay (16º48' N, 88º05' W) is mainly composed of a sandy bottom covered by turtle grass *Thalassia testudinum,* interspersed with sparse stands of *Syringodium filiforme* and *Halimeda* spp. The seagrass beds adjacent to Twin Cays lie on a shallow shelf that slopes gradually from the shoreline to the lagoon bottom (approximately 7 m) about 300 m offshore and are broken up by rubble fields, reef patches, and sponges (RÜTZLER & MACINTYRE, 1982). Bottom sediments to a depth of at least 1 m consist primarily of *Halimeda* sand mixed with fine clay, but coral and shell fragments are also present. For our surveys we chose an area between Carrie Bow Cay and Twin Cays (Fig. 1) where we collected all sponge species encountered during a series of 100-minute dives. Among 13 species sampled, four were represented by only one specimen each (Tab. I).

The foreign mineral material incorporated in each sample was assessed and compared with ambient sediments (paired t-test, Cluster Analysis with the Nearest Neighbour method), to determine particle selectivity by the sponges. Specimens were dried and weighed and sediments were extracted by dissolving each sample in 130 vol. hydrogen peroxide (H_2O_2). After rinsing twice in distilled water to dissolve precipitated salts, the remaining inorganic matter was dried at 60° C for 24 hours and weighed. Three granulometric fractions were separated by sieving: > 5 mm, 1 - 5 mm, and < 1 mm. To compensate for weight of the siliceous spicules proper to the sponges, the calcareous fraction was determined after exposure to 5 % hydrochloric acid (HCl) solution overnight (only negligible terrigenous silica is present at this location, RÜTZLER & MACINTYRE, 1978).

Particular emphasis was placed on studying sand incorporation in *Tectitethya crypta*, a massive shallow-water demosponge common in the Caribbean and known for being mostly covered by sediment. In lagoon environments this sponge can occur either loose or attached and accordingly displays different morphologies. For 50 specimens of this species, the pattern of distribution of incorporated sediments was analysed and sediment utilisation by the two morphological types evaluated. For this extended study we included one finer size fraction (< 500 μm) in addition to the ones stated above. Fine and coarse sediments were separately investigated to determine possible selective processes during incorporation of foreign materials by the sponge. Particles smaller than 500 μm were qualitatively characterised from microscope slide preparations, three from each of five specimens. Composition and size frequency distribution of sediments from sponges and their habitats were thus compared. On each preparation the diameter of 100 sand grains was measured using a Graphtec KD digitizer. The coarse fraction was compared to ambient sediment using the same procedure described above for the other species. For histological analysis portions of sponge tissue were fixed underwater *in situ*, in 2.5 % glutaraldehyde buffered by artificial seawater (pH = 7.6) for two hours. After rinsing in the same buffer, the samples were dehydrated in an ethanol gradient. Sections were made after embedding in Technovit 8100 (Kulzer). Sections, 3 μm thick, were collected on slides, stained in toluidine blue, and mounted in resin (Eukitt).

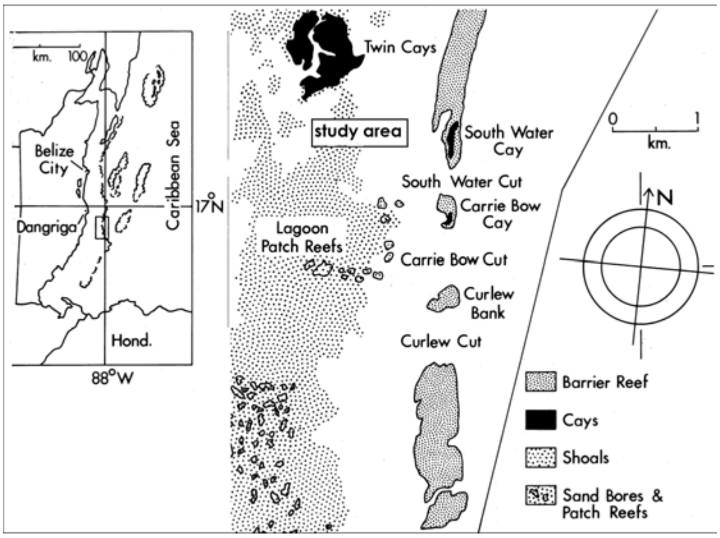

Fig. 1. Location of the study area in the *Thalassia* meadow between Carrie Bow Cay and Twin Cays (map after K. Rützler & I. McIntyre, 1982, modified).

RESULTS

In the Carrie Bow lagoon, we have recorded 13 sponge species and their different ways of sediment incorporation. Some species accumulate a conspicuous lump of sediment in the basal part of the body, while others cover the surface or distribute grains throughout their bodies.

Among the collected species, *Phorbas amaranthus*, *Aplysina lacunosa* and *Clathria (Microciona) spinosa* were previously recorded only from reef environments, never from lagoons.

The comparison between ambient sediments and sand incorporated by sponges shows that eight species [*Aplysina lacunosa, Lissodendoryx strongylata, Amphimedon viridis, Clathria (Microciona) spinosa, Phorbas amaranthus, Clathria (Thalysias) schoenus, Amphimedon compressa* and *Xestospongia carbonaria*] select for the fraction larger than 5 mm (Fig. 2), while the five remaining species [*Haliclona (Soestella) coerulea, Cliona varians, Aplysilla longispina, Clathria (Wilsonella)* sp. and *Tectitethya crypta*] utilize the same size fractions found covering the habitat bottom (Fig. 3). The cluster analysis supports these patterns (Fig. 4). Among the selective species, *Amphimedon compressa* and *Aplysina lacunosa* incorporate quite exclusively fragments larger than 5 mm while the others may utilise also the smaller sizes. Among the non-selective species it is important to consider that *Cliona varians* is an excavating species, at least in its younger stages, and that the granulometry of the sediments it incorporates may be affected by its boring activity, which reduces the size of large fragments and increases the amount of the fine fraction.

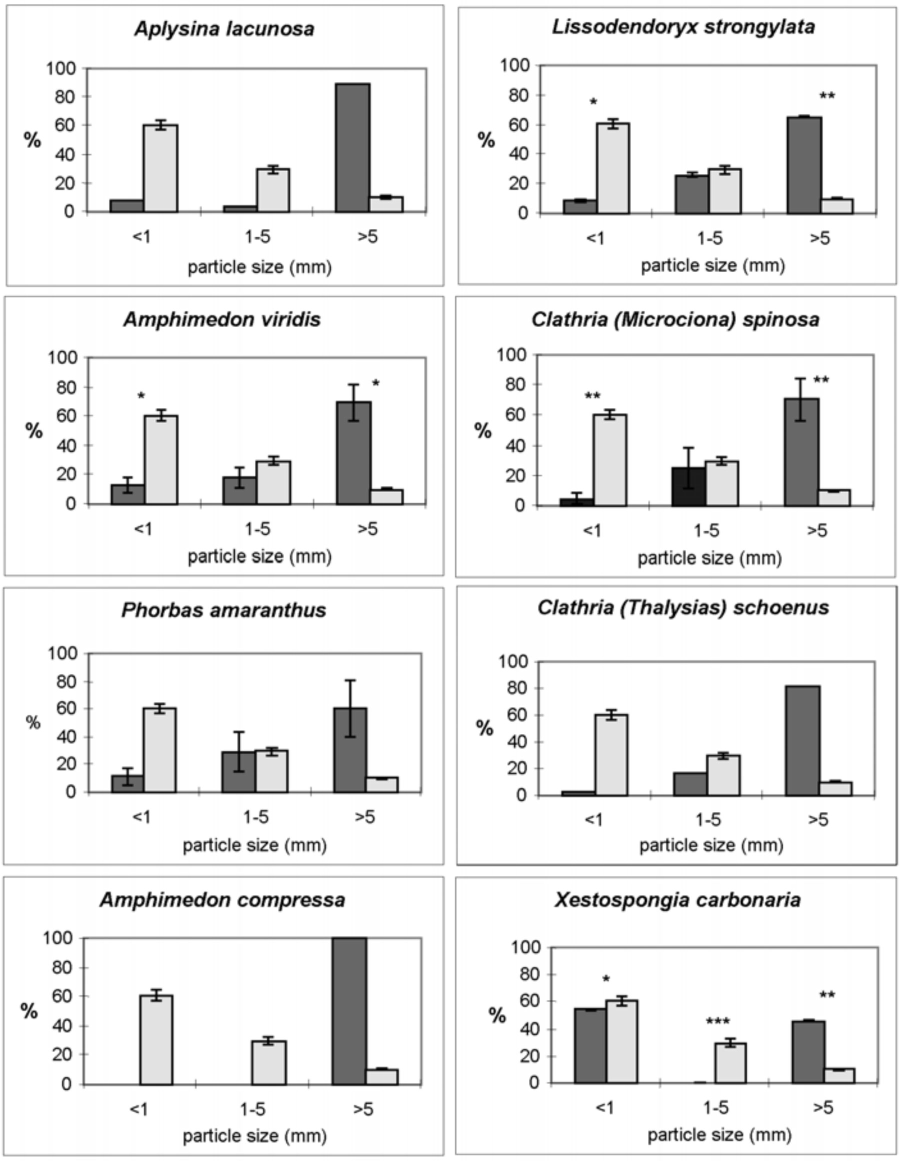

Fig. 2. Selective species. They incorporate mainly the fraction of sediment bigger than 5 mm (* = significant $P < 0.05$; ** = very significant $P < 0.01$; *** = very much significant $P < 0.001$).

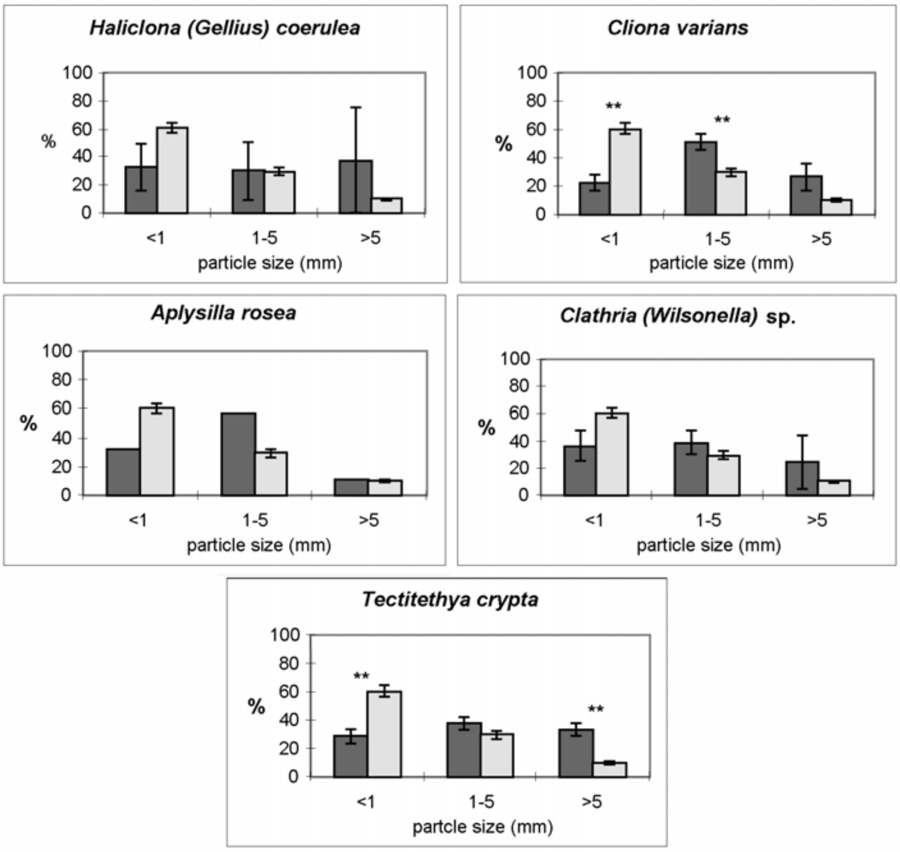

Fig. 3. Not selective species. In the case of *C. varians* and probably of *T. crypta* the corrosive ability of the sponge can modify the initial sediment features (* = significant P < 0.05; ** = very significant P < 0.01; *** = very much significant P < 0.001).

Tab. I. List of species collected, their typical habitats (R = reef, L = lagoon), weight-percent (± SE) of incorporated sediments, and number of specimens (n) examined. References indicated by letters are (a) HOOPER & VAN SOEST, 2002; (b) WIEDENMAYER, 1977; (c) ZEA, 1987; (d) VAN SOEST, 1980; (e) VAN SOEST, 1984; (f) HECHTEL, 1965.

Species	habitat	% Incorporated sediments	n
Amphimedon compressa Duchassaing & Michelotti, 1864	R-L (d)	5.1	1
Haliclona (Soestella) coerulea (Hechtel, 1965)	L (f)	25.85±8.26	2
Aplysilla longispina George & Wilson, 1919	R-L (a)	33.04	1
Tectitethya crypta (de Laubenfels, 1949)	R-L (a)	35.35±8.04	5
Amphimedon viridis Duchassaing & Michelotti, 1864	L (c)	36.94±13.05	3
Phorbas amaranthus Duchassaing & Michelotti, 1864	R (a)	42.18±6.75	2
Xestospongia carbonaria (Lamarck, 1814)	R-L (c)	45.46±9.39	2
Clathria (Thalysias) schoenus (de Laubenfels, 1936)	L (e)	46.94	1
Aplysina lacunosa (Lamarck, 1814)	R (c)	50.31	1
Clathria (Microciona) spinosa (Wilson, 1902)	R (e)	50.43±8.15	4
Lissodendoryx strongylata van Soest, 1984	L (e)	63.92±7.35	2
Cliona varians (Duchassaing & Michelotti, 1864)	R-L (b)	64.53±5.38	5
Clathria (Wilsonella) sp.	L	96.76±1.09	2

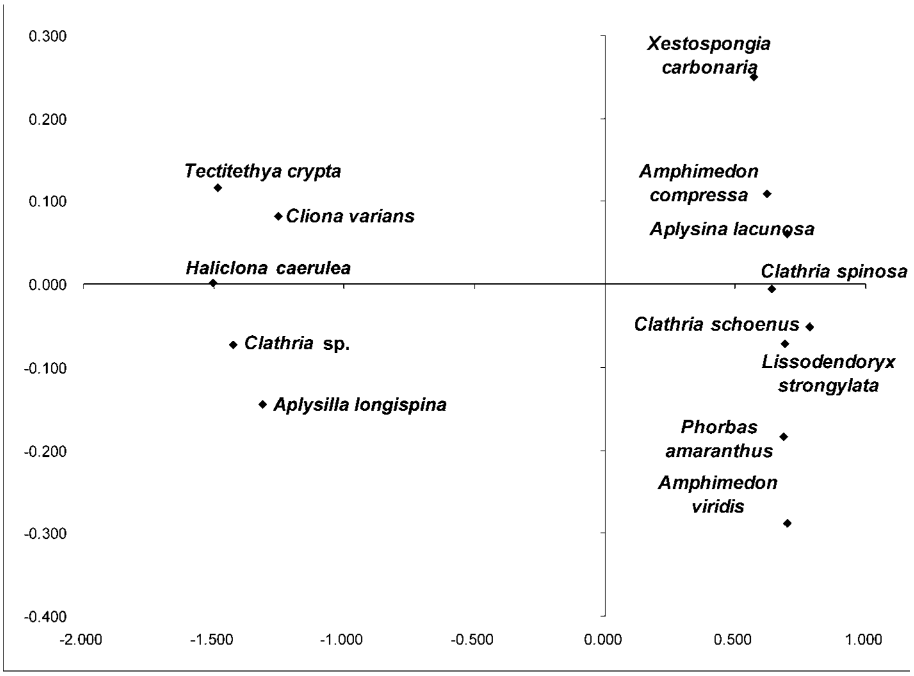

Fig. 4. Cluster analysis (Nearest Neighbour) of the investigated species and ambient sediments. Non-selective species group on the left and selective species on the right.

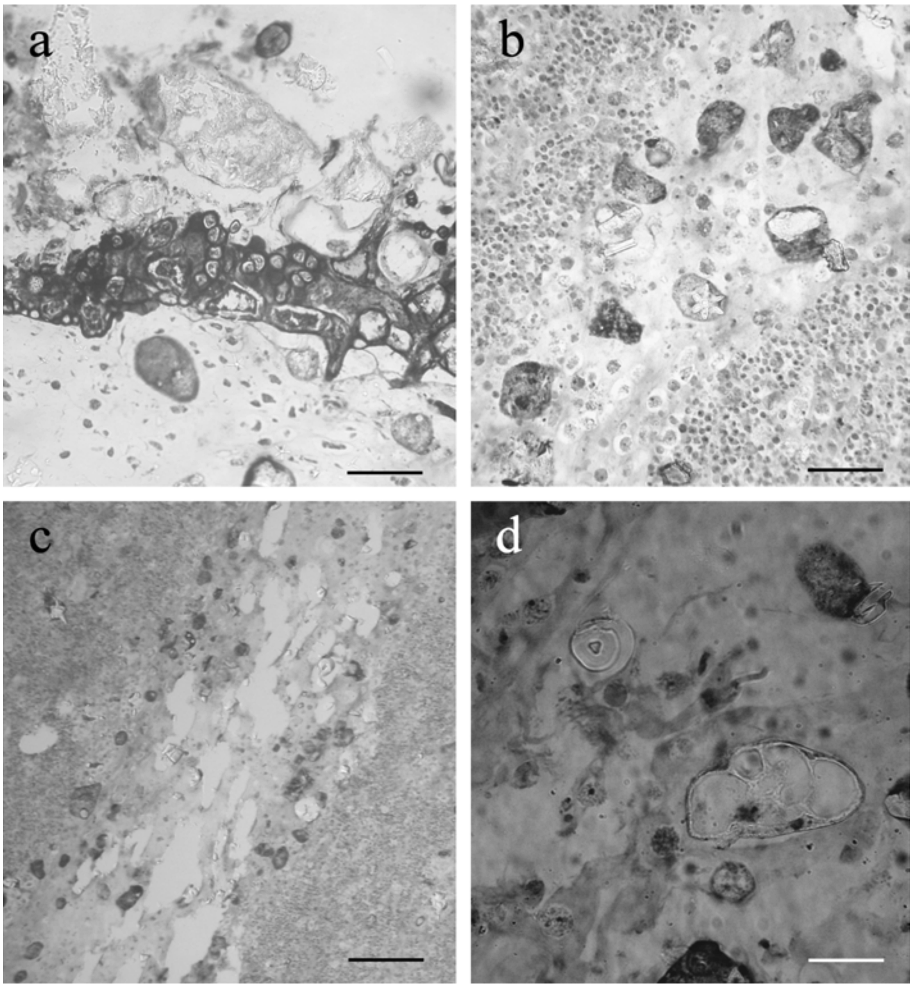

Fig 5. *Tectitethya crypta.* **a,** Ectosome with algal thalli on the upper part. Immediately below, numerous big cells with exogenous inclusions are evident (Scale bar = 30 μm). **b,** Cells involved in the transport of exogenous material are frequent in collagenous scarcely organized areas and **c,** along spicular tracts (Scale bars = 30 and 100 μm respectively). **d,** A detail of a big cell containing a phoraminifer (Scale bar = 13 μm).

Tectitethya crypta is a common species in the lagoon and specimens are found in considerable size range. The largest, with 1.5 - 10 liter volume, represent 7.5 % of the studied population and are usually found attached. The smaller sponges, with 0.5 - 1.5 liter volume, are always unattached, resting free on the bottom.

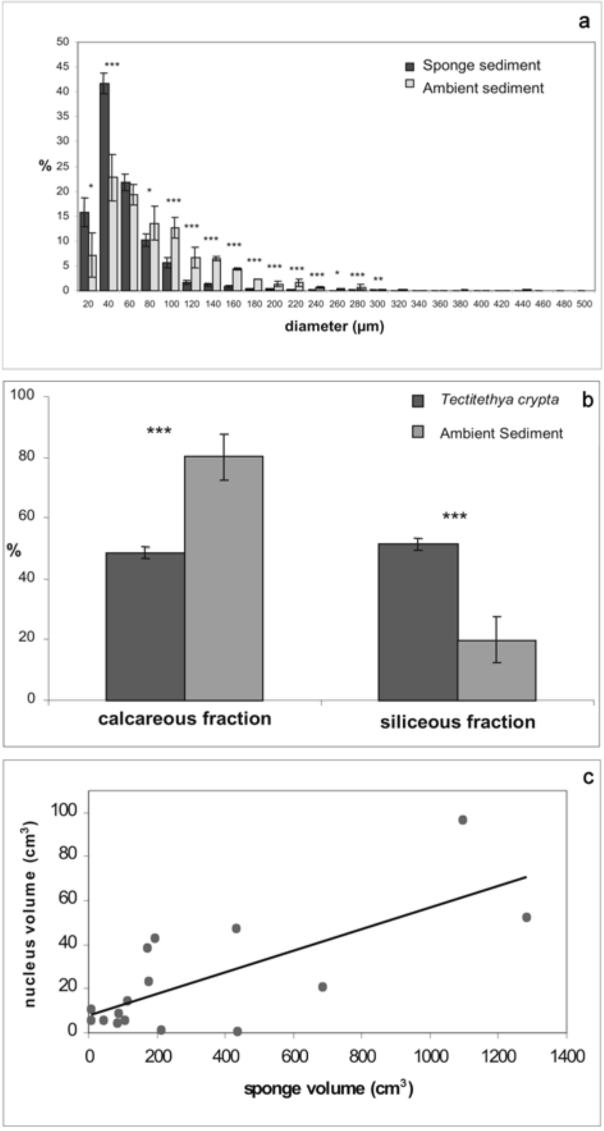

Fig. 6. *Tectitethya crypta.* **a,** Granulometric analysis of the sediment fine fraction (< 500 µm) recorded in the sponge tissues and in the surrounding environment. **b,** Comparison between the calcareous and the siliceous fractions of sediment in *T. crypta* and in the environment (* = significant P < 0.05; ** = very significant P < 0.01; *** = very much significant P< 0.001). **c,** Pearson correlation (r = 0.73) between the sponge sizes and the volume of coarse sediment nuclei.

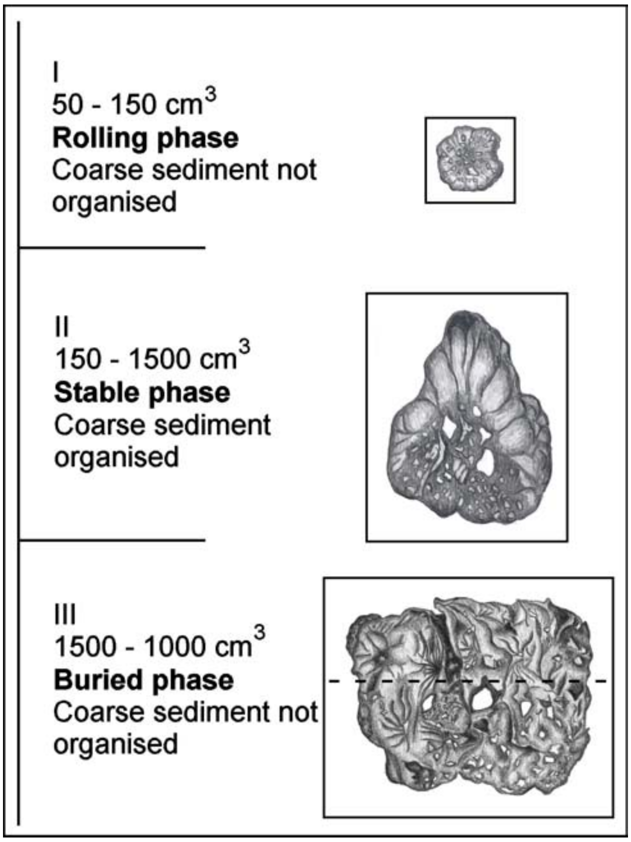

Fig. 7. *Tectitethya crypta* specimens, undergoing three different growth phases, gradually change their life habit, together with the embedded sediment organization. Choanosomal nuclei of fine sediment are drawn in white and the dashed line represents the sea floor.

Tectitethya crypta is characteristically covered by a layer of sand and algae (Fig. 5a) and it incorporates all the granulometric classes of nearby bottom sediments using them in different ways. In the choanosome, sediments are sorted and distributed according to their size: fine sediments (< 500 µm) always accumulate in clusters (nuclei), whereas coarse particles are more evenly distributed throughout the body. The volumes of these nuclei of fine sediment are not correlated with sponge size. Compared to ambient fine sediments (< 500 µm), the sponge seems to select for the smaller grains, in particular the 40 - 60 µm range (Fig. 6a). Qualitatively, the choanosomal nuclei of fine sediments contain more siliceous material than the ambient sediment of the same size class (Fig. 6b). Microscopical analysis of the particles shows that this species selects allocthonous sponge spicules, radiolarians and diatoms. Histological sections reveal also an unusually large type of cell: they are larger (40 - 150 µm) than most other sponge cells and often contain exogenous material (Figs 5b-d). Further studies on this cell type are in progress.

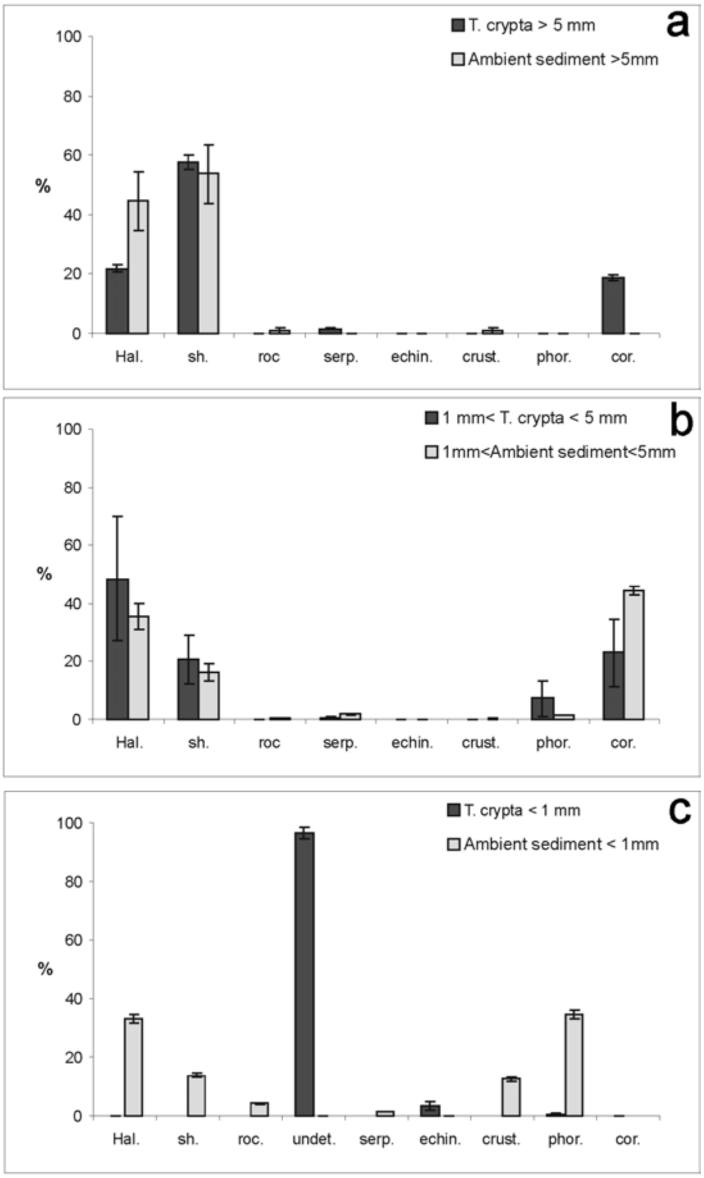

Fig. 8. *Tectitethya crypta*. Qualitative analysis of the incorporated sediment. **a, b,** No differences arise from the comparison between the fractions bigger than 1 mm. **c,** Considering the fraction smaller than 1 mm, is possible to evidence a high amount of unrecognisable material in the sponge. Hal.: *Halimeda* thalli; echin.: echinoderms; sh.: shells; crust.: crustaceans; roc.: rocks; phor.: phoraminiferans; serp.: serpulids; cor.: corals; undet.: not recognizable material.

Sponge size and localization of coarse sediment inside the body, allow to identify at least three developmental phases. Small sponges (50 - 150 cm^3 volume) spherical and with evenly dispersed coarse sediment; medium- sized sponges (150 - 1500 cm^3 volume) conical and with sediments concentrated near the base and large, massive and irregular specimens (1500 - 10000 cm^3 volume) which again contain evenly distributed sediments (Fig. 7). These three types reflect different life habits of the sponges. Small *Tectitethya* specimens are unattached and rest or roll freely on the bottom. Medium sized specimens are still unattached but because of shape and sediment concentration tend to be more stable. Large, massive sponges become attached to the bottom, with two thirds of their body buried in sand. The size of coarse sediment clusters in the second phase is correlated with the sponge size, suggesting continuous transport of particles towards these accumulation areas (Fig. 6c).

The coarse, sponge-incorporated sand fraction is generally composed of carbonate chips from *Halimeda* thalli and shell and coral fragments, all among the most abundant components of the ambient bottom sediments (Figs 8b-c). Fine particles in the 500 µm - 1 mm range, on the other hand, seem to be derived from different sources as they are not all present in the ambient sediment (Fig. 8a).

DISCUSSION AND CONCLUSIONS

Many sponges can reproduce asexually by fragmentation. Fragments may derive from breakage of sponge branches during storms, localized infections by pathogens, or predator bites (WULFF, 1985; BATTERSHILL & BERGQUIST, 1990; CERRANO *et al.,* 2000). The survival of unattached fragments depends on their ability to re-settle. If fragments do not re-attach rapidly, their healing potential suffers and they may become smothered by sediments before they recover from the distress. If they anchor themselves within a short time, however, they will soon reorganize their aquiferous system and resume feeding and ability to clear passages from fine sediments. In lagoon environments, where the bottom is generally sedimentary and unstable, sponges have a better chance to proliferate through asexual propagules than through sexually produced larvae which have a poor chance of encountering a substratum stable enough for settlement and metamorphosis into a functional individual (HIGHSMITH, 1980; BOTHWELL, 1981).

All species collected in the lagoon incorporate sediments to some degree and 66 % of them clearly select coarse fragments, larger than 5 mm in diameter. Sediment incorporation appears to be a necessity for sponges living on or in soft bottom because even specimens that start unattached as rollers become stabilized by the weight of a cluster (nucleus) of accumulated sand. For this purpose, it is more important to incorporate coarse than fine particles. During the rolling phase, sponges generally show irregular shapes whereas in stabilised condition they develop a more distinctive, polarised morphology. Under some circumstances, the aggregation of specimens from different species may stop the rolling phase. Two species in the study area, *Xestospongia carbonaria* and *Lissodendoryx strongylata,* were found to readily attach to each other, but many more examples were previously recorded (BERGQUIST, 1978).

Although anchoring is probably the most important role of sediment incorporation in lagoon sponges, in some species the sand intake may lead to more complex utilisation. In the example of *Tectitethya crypta,* we noticed that this species utilises coarse and fine sediments differently. Sediments do not serve as mere substratum or for reinforcing the skeleton, but take part in the morphogenesis of the sponge. By forming several clusters (nuclei) of embedded coarse sediments to stabilise its body, this species can shift its skeleton structure from initially radial to branched (characteristic of the genus), a configuration that allows development into a massive form. The coarse fraction is not selected in each size range we considered. The largest sand grains (fraction > 5 mm) found inside the sponge match the kinds that occur in the nearby bottom sediments. Many smaller limestone particles (fraction < 1 mm) were not encountered in the habitat They were not readily identifiable, possibly because they were broken down inside the sponge, a corrosive ability common to many members of the order Hadromerida (*e.g.,* Clionaidae and *Suberites* spp.).

Tectitethya crypta is more selective in its uptake of fine than coarse sediments; it prefers the 60 and 40 µm size class of siliceous particles, such as allochtonous siliceous sponge spicules, and radiolarian and diatom tests. As to fine sediments, if *T. crypta* has a corrosive ability, an accumulation of siliceous material and a size reduction of the calcareous sediments, more than a true selectivity, may be hypothesized. Histological examination reveals the existence of a cellular track along the skeleton tracts that facilitates the transport of sediment particles from the ectosome to the accumulation nuclei. These strands remind the cords of cells described by LEYS & REISWIG (1998) for a species of *Aplysina* but an unusual large type of yet unstudied cell is involved in this process in *Tectitethya crypya*. These cells are very common in a loosely organized subectosomal tissue zone and along the spicule tracts. They differ from those described by LEYS & REISWIG (1998) because they are larger in size (till 150 µm in diameter) and never elongated. Morover these cells are not involved in the transport of food but sediment only.

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