

Do sponges help hold coral reefs together?

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The growth and form of coral reefs is the result of a complex balance between rates of carbonate accretion and carbonate loss. Reef organisms have traditionally been classified, with respect to their role in this balance, as primary frame-builders, frame-cementers, biological eroders or sediment producers^{1,2}. Scleractinian corals are the primary frame-building organisms in most modern reef environments. The growth of many such corals generates large volumes of unoccupied cryptic space. Successful reef construction occurs if this space is infilled with sediment, this sediment is cemented by frame-cementing organisms, and the resulting complex is subsequently lithified³⁻⁵. As this lithification process may be slow, frame material is highly susceptible to becoming separated from the reef framework due to the action of physical disturbance (such as wave shock) before permanent consolidation⁶⁻¹⁰. We present here experimental evidence that demosponges (which may be second only to scleractinian corals in space occupancy on many Caribbean reefs) play an important role as interim binders of unconsolidated frame material, a process which is expected to increase rates of carbonate accretion.

Although sponges may bind carbonate to the reef frame in several reef zones (for example, interstices of ramose corals and carbonate rubble), our investigations have focused on Caribbean deep fore-reef environments. Deep fore-reef zones are characterised by steeply sloping sand plains dotted with small patch reefs or larger reef pinnacles and are bounded to the seaward by vertical rock walls which drop to considerable

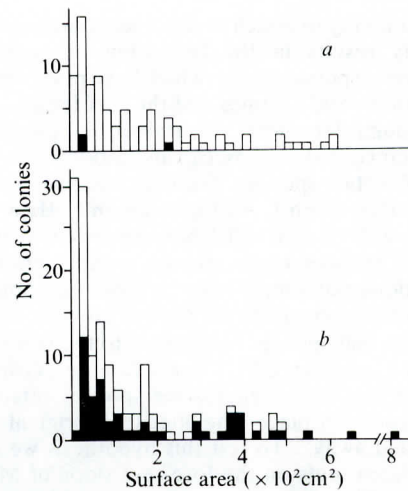


Fig. 1 Size against frequency distribution of foliaceous corals originally extant on *a*, unmanipulated reefs and on *b*, manipulated reefs. Shaded histograms represent those corals which became separated from the reefs. Patch reefs selected were comparable in size and sponge-coral faunal development. Specific data on patch morphology, sponge-coral distributions, and sponge-coral identifications are available from the authors. Coral surface area measurements were made by approximation to regular polyhedrons. Corals which immediately fell off the manipulated reefs when sponges were removed constituted <2% of the total corals manipulated (and are not included in the analysis) indicating that any disturbance to the reefs involved in removal of sponges was minimal. Data presented are clumped for all patches over the two observation periods. There was negligible sponge regrowth on manipulated reefs over the experimental period.

depths. Scleractinian corals growing in this zone generally exhibit a foliaceous growth morphology. Such forms are especially susceptible to disengagement from the reef since their attachment zones are small; their undersurfaces are largely devoid of live coral tissue, leaving them open to recruitment of boring organisms; and they extend off the reef rather than resting on it, making them unstable once their attachment zone is weakened¹¹. Foliaceous corals have become separated from the reef frame by the forces exerted by a feeding parrotfish, by the actions of storm-induced wave shock⁶⁻¹⁰, by the fins of a careless scuba diver, or simply due to collapse under their own weight¹¹. Once separated from the reef, corals cannot reattach and are rarely consolidated.

Non-burrowing sponges characteristic of deep fore-reef environments are of two general types: those which inhabit the holes and crevices in the reef frame and those which inhabit exposed reef substrata. Cryptic sponges (such as *Agelas clathrodes* (Schmidt)) commonly have zones of attachment which include both the undersurface of foliaceous corals and the reef frame itself. The porosity of the reef frame allows many of these sponges to extend from one attachment spot on the undersurface of a coral, through the reef frame to an attachment zone on another coral.

Sponges, including those which inhabit open reef substrata, have been observed to attach to one another without harm to either side^{12,13}. Experiments performed on the barrier reef of Belize show that several such sponges may also kill small patches of coral tissue on contact and bind to the exposed coral skeleton. Growing tips of at least five individuals of each of 12 sponge species were severed with a diving knife and attached to living agariciid corals with cotton twine. As controls, pieces of commercial bath sponge were attached to living corals. The contacts were examined after one week for evidence of coral tissue death and sponge-coral binding. Of the 12 species, 10 killed a small patch of coral tissue and bound to the skeleton (Table 1). The two remaining species killed small patches of coral. The bath sponge had no observable effect. The morphological flexibility of sponges, their ability to attach to other living sponges and

Table 1 Sponge-coral binding experiment

Sponge species	Total no. of individuals tested	Total no. killing tissue	Total no. binding to coral
<i>Agelas clathrodes</i> (Schmidt)	5	5	0
<i>Agelas conifera</i> (Schmidt)	5	5	5
<i>Agelas scepstrum</i> (Lam.)	5	5	5
<i>Aplysina cauliformis</i> (Carter)	5	5	5
<i>Callyspongia</i> sp.	7	7	7
<i>Ectyoplasia ferox</i> (D & M)	10	8	8
<i>Haliclona rubens</i> (Palles)	30	25	15
<i>Iotrochota birotulata</i> (Higgin)	5	5	5
<i>Niphates erecta</i> D & M	10	5	0
<i>Smenospongia aurea</i> (Hyatt)	5	3	3
<i>Thalysias juniperina</i> (Lam.)	5	2	2
Unidentified	7	7	5
Control	5	0	0

Experiments were performed while operating from the RV Alpha Helix. Two locations, one each in the lee of Glovers and Lighthouse Atolls at depths of 20-30 m, were studied. The Lighthouse Atoll site is 1 mile south of Long Cay and the Glovers site on the reef pinnacle, Movie Mountain, located on the southwestern extreme of the atoll. The experiment does not provide any understanding of the mechanism (for example, allelopathy and abrasion) by which sponges kill coral tissue. As these results represent the number of individuals binding to corals in only 1 week, they probably underestimate the actual capacity of these sponges to bind to corals.

corals, and their ability to attach to clean substrata with any part of their colony results in the formation of anastomosing networks of several sponge species which have many attachment points on different coral colonies and the reef frame.

Corals, although far more constrained in morphological flexibility by their rigid skeletons, can also modify their forms in the presence of certain sponges. We have observed colonies of *Agaricia agaricities* (Linn.), *Agaricia lamarcki* (E & H), and *Helioserius cucullata* (E & S) which have encircled the tissue and even attachment zones of nearby sponges with skeletal material. These observations may simply reflect a passive response of the coral to any obstruction within the path of growth.

The hypothesis that sponges bind corals to the reef frame has previously been suggested¹⁴⁻¹⁷: for example, Goreau and Hartman stated that "large encrusting sponges often support and hold such corals in place long after their original holdfasts have been eroded away". To test this hypothesis we removed sponges from patch reefs on the fore-reef slope of Marsagantupo Island, San Blas, Panama, and monitored how the coral survived. The experiments were performed on the leeward side of the island at depths ranging from 13 to 20 m. Marsagantupo Island is exposed directly to the Caribbean Sea. The first 3 months of the experimental period correspond to the dry season in Panama, the period of greatest swell. Although physical data are scant for this region, the Caribbean coast of Panama is regularly exposed to seas up to 10 ft (ref. 18). Eight small patch reefs were selected and all corals mapped as to their position on the patch. All sponges, with the exception of borers and surface encrusters of <1 cm vertical relief, were carefully removed by hand or with a diving knife from half of the reefs. The patches were revisited at three and six months after the removal and all corals remapped.

Figure 1a shows the size (surface area live tissue) frequency distribution of foliaceous corals originally extant on unmanipulated reefs and Fig. 1b shows that for manipulated reefs. Control reefs lost 2% of their colonies (2% surface area) within three months and 4% of their colonies (3% surface area) after six

months; whereas manipulated reefs lost 26% of their colonies (29% surface area) within the first three months and a total of 40% of their colonies (46% surface area) after six months. The high mortality of small colonies, many of which had no direct contact with any sponge, reflects the need of juvenile corals for stable substrata on which to grow. Those small corals which have been asexually reproduced (or which have settled) on top of larger colonies are clearly as dependent on sponge binding as their older counterparts.

The traditional interpretation of the role of sponges in the reef carbonate balance has emphasised the destructive influence of a small group of biological eroders. Although the influence of bioerosion should not be underestimated, neither should the binding capacities of other reef sponges. Demosponges clearly require several terms in the reef carbonate balance equation.

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