

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Sclerosponges: Primary framework constructors on the Jamaican deep fore-reef

by Judith C. Lang¹, Willard D. Hartman² and Lynton S. Land¹

ABSTRACT

Sclerosponges grow on hard substrates in areas protected from high rates of sediment accumulation to depths of about 200 m at Discovery Bay, Jamaica. Here they are primary framework builders on the deep fore-reef between 70 m and 105 m.

1. Introduction

In Jamaica, coralline sponges of the class Sclerospongiae are part of the coral reef cryptofauna (Hartman and Goreau, 1970; Jackson et al., 1971). Sclerosponges grow in tunnels and in caverns within the framework of coral buttresses and fore-reefs (10 m to 30 m), and on the undersides of reef corals and coral talus on fore-reef slopes (25 m to 55 m). Below 55 m, they are also found on steep, well-drained surfaces of the deep fore-reef³. The largest Jamaican sclerosponge, *Ceratoporella nicholsoni* (Hickson), has been thought to replace hermatypic (reef-building) corals between 70 m and 95 m as a primary reef framebuilder (Goreau and Land, 1974), but to achieve its maximum size and density at less than 30 m in sub-reef tunnels and caves (Hartman and Goreau, 1970). In exploratory dives with the General Oceanographics' submersible NEKTON "Gamma", at Discovery Bay on the northern coast of Jamaica in August 1972, we confirmed that sclerosponges, particularly *C. nicholsoni*, actually *construct* reef framework to a depth of 105 m on the deep fore-reef, and can survive to a depth of at least 303 m. Observations with SCUBA and NEKTON "Beta" indicate that sclerosponges are comparatively scarce at similar depths on some southern reefs in Belize (British Honduras), where they are probably only minor contributors of calcium carbonate to the basal reef framework.

2. The deep fore-reef

A. Jamaica. At Discovery Bay, the vertical to overhanging escarpment called the deep fore-reef extends from 55 m to between 115 m and 145 m as a series of pro-

1. Dept. of Geological Sciences, The University of Texas at Austin, Austin, Texas 78712, U.S.A.

2. Dept. of Biology and Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520, U.S.A.

3. Reef zone terminology according to Goreau and Goreau (1973) and Goreau and Land (1974).

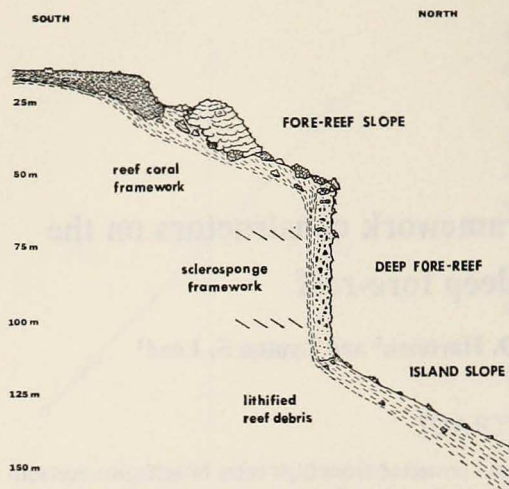


Figure 1. Sketch of the Discovery Bay reef and island slope between 15 m and 150 m. The fore-reef terrace (above 15 m) and fore-reef escarpment (15 m–26 m) are seen above the fore-reef slope at the upper left. Above 70–75 m, reef corals are the predominant framework constructors in all reef zones. Sclerosponges form primary reef framework on promontories of the deep fore-reef between 70 m and 105 m. Sand channels transport reef-derived sediment downslope between reef lobes of the fore-reef terrace and fore-reef escarpment and between pinnacle reefs and coral outcrops on the fore-reef slope, and empty sediment into near-vertical re-entrants that alternate with the promontories of the deep fore-reef. Sclerosponges are less common at the base of the deep fore-reef (below 105 m) and on outcrops of lithified reef debris on the island slope. The horizontal distance from the fore-reef escarpment on the left at 25 m depth to the top of the deep fore-reef escarpment at 60 m depth is approximately 125 m.

A few erect demosponges grow alongside reef corals on upward-facing ledges. However, most of the sessile organisms of the deep fore-reef are restricted to the downward-facing surfaces of overhangs, the vertical surfaces which extend between ledges, and the walls and ceilings of depressions and caves. These areas are relatively protected from the sediment which we frequently observed cascading down the face of this escarpment (Meaney, 1973, has estimated that in this area the rate of sediment transport into the re-entrants is about $1-4 \times 10^6$ gm sediment per meter of re-entrant front per year). At all depths on the promontories, the predominant cover on vertical

montories alternating with re-entrants (Figure 1). Numerous crevices, caverns up to 12 m deep, fissures at least 10 m high, and projecting ledges up to several meters wide occur at various depths on the promontories, and a zone of maximum cavern development is located between about 82 m and 91 m. In contrast, sand channels which actively transport sediment downslope from shallower reef zones empty into the near-vertical re-entrants, where sediment descends onto the island slope below. Fine sediment also settles out on all horizontal and sloping surfaces on the promontories.

Near the tops of the promontories, reef corals are relatively abundant, and form up to 95% of the cover at 60 m. On horizontal and oblique surfaces they form massive-flattened or foliose colonies, commonly tilted seaward, presumably to aid sediment drainage. Reef corals also encrust open vertical surfaces, but do not occur beneath overhanging ledges. Previous work has shown that above 70–75 m, these promontories are constructed of coral skeletons and of lithified, reef-derived sediment (Goreau and Goreau, 1973; Goreau and Land, 1974). Hermatypic corals are only infrequently found below 70 m, but occur as deep as 98 m.



Figure 2. Small specimens of *Ceratoporella nicholsoni*, which are alive only on their downward-facing surfaces, are constructing a ledge at 77 m on the deep fore-reef (across top of photo). Beneath the ledge (center and lower left), larger individuals of *C. nicholsoni* are protected from falling sediments. Both on and under the ledge, the nodular skeletons of dead sclerosponges (particularly *C. nicholsoni*) are being overgrown by encrusting demosponges and by crustose coralline algae. The distance across the bottom of the photo is approximately 1 meter.

surfaces consists of species of erect and encrusting demosponges (20% to 80%) and of crustose coralline algae (2% to 15%). Calcareous green algae of the genus *Halimeda* occur here to a maximum depth of about 98 m, but, with the exception of *H. cryptica* Colinvaux and Graham in certain localities, are rare below 70 m. Several genera of whip and fan gorgonians and antipatharians also grown on these open vertical surfaces.

Under ledges and corals, and in crevices and caverns, the demosponge and crustose coralline algal cover is reduced, whereas sclerosponges, whip antipatharians and ahermatypic (lacking zooxanthellae) corals are very abundant. All six sclerosponges listed from Jamaica (Hartman, 1969; Hartman and Goreau, 1970) were collected on the deep fore-reef. The largest, and most conspicuous is *Ceratoporella nicholsoni*. Between 74 m and 98 m, the cover of living *C. nicholsoni* was estimated to be as high as 25–50% beneath ledges and on the walls and ceilings of large caves (see Hartman and Goreau, 1970, Figure 19, p. 233), where they grow downward and laterally outward. Interspersed between these living specimens, and often filling much of the remaining space, encrusting sponges, crustose coralline algae and other sessile organisms overgrow dead *Ceratoporella* skeletons (Figure 2). Here population densities, and individual sizes in excess of 1 m in diameter are as great as in the relatively shallow (less than 30 m) caverns and tunnels at Runaway Bay, where conditions were previously thought to be optimal for sclerosponge growth (Hartman



Figure 3. *Ceratoporella nicholsoni* (approximately 0.25 m wide) growing above a small ledge on the deep fore-reef at 91 m. Only the tissues on the lower half of this sclerosponge are alive. The upper part of its skeleton is covered with sediment, small hydroids, worm tubes and encrusting sponges. Photo by H. M. Reisiwig.

and Goreau, 1970). Below about 105 m, the cover of *C. nicholsoni* is greatly reduced, and rarely exceeds 10%.

Stromatospongia vermicola Hartman also grows under ledges and in caves. At Runaway Bay, individuals grow up to 40 cm in diameter and 10 cm in height, but the largest specimen collected on the Discovery Bay deep fore-reef (at 92 m) was 11 cm in diameter and 6 cm high. *S. vermicola* was seen at all depths on the deep fore-reef, and appeared to be most common above 83 m. It was estimated to be locally more abundant than *C. nicholsoni* between 60 m and 70 m, and to form as much as 15–40% of the total sclerosponge cover between 74 m and 83 m. Occasionally *S. vermicola* occurs on exposed, vertical surfaces, suggesting that it may be more tolerant of sediment than other Jamaican sclerosponges⁴. In such areas, *C. nicholsoni* is invariably covered with living tissues only on the undersurfaces (Figure 3), where sediment cannot accumulate.

The remaining species of Jamaican sclerosponges are relatively small (usually less than 10 cm across) and were difficult to recognize from the submersible. Nonetheless, individuals of *Hispidopetra miniana*, which Hartman and Goreau (1970) list as being relatively abundant below 60 m were found under a number of ledges

4. However, M. J. DeNiro (pers. comm.) who subsequently studied sclerosponges on the Discovery Bay fore reefs, has estimated that between 15 m and 50 m, *Hispidopetra miniana* Hartman is more likely to occur in areas of rapid sediment accumulation.

Table 1. Distribution of sclerosponges on the deep fore-reef and upper island slope (55 m to 303 m) at Discovery Bay, Jamaica.

Species	Deep fore-reef			Island slope		
	(meters)	(meters)		(meters)	(meters)	
	Depth Range ¹	Greatest Abundance	Location	Depth Range	Greatest Abundance	Location
<i>C. nicholsoni</i>	55	75	Under ledges and in caves, undersurfaces of reef corals	115	115	On rock outcrops, undersurfaces of fallen <i>Agaricia</i>
	to 115	105		to 203; 303?	to 155	
<i>S. vermicola</i>	55	60	Under ledges and in caves, undersurfaces of reef corals	115	?	On rock outcrops
	to 115	83		to 126		
<i>S. norae</i>	55	?	In holes, ?deep in crevices and caverns	115	?	On the "cliff", undersurfaces of fallen <i>Agaricia</i>
	to 115			to 170; 176?		
<i>H. miniana</i>	55	?	Under ledges	129	?	?on a rock in sediment, undersurface of fallen <i>Agaricia</i>
	to 115			to 130		
<i>G. auriculata</i>	55	?	Under ledges, ?deep in crevices and caverns	129	?	Undersurfaces of fallen <i>Agaricia</i>
	to 97; 106?					
<i>Merlia</i> sp.	83	?	Undersurface of <i>Agaricia grahamae</i> , under a ledge	?	?	?
	to 91					

¹ Calculated from visual observation in NEKTON "Gamma", from collected samples, and from SCUBA observations above 80 m at the Buoy Reef, Discovery Bay, where the depth of the base of the deep fore-reef is about 115 m.

between 74 m and 115 m. Specimens of *Stromatospongia norae* Hartman were noted at about 90 m growing in a small hole, and others were believed to have been identified at 98 m and at 106 m. One individual of *Goreauia auriculata* Hartman was seen under a ledge at a depth of about 94 m. Numerous specimens of these three species were collected on rock samples brought up from the excavation sites between 85 m and 97 m. *H. miniana* and *S. norae* were also taken at 120 m. In shallower Jamaican reef habitats, large populations of *S. norae* and *G. auriculata* live on the sides and ceilings of deep caves and tunnels under conditions of extremely low light (Hartman and Goreau, 1970). These two species probably occupy similar recessed habitats deep in caverns and crevices on the deep fore-reef, sites that were inaccessible from the submersible. A specimen of the smallest and, to date, rarest Jamaican sclerosponge, *Merlia* sp., was found encrusting the undersurface of a foliaceous *Agaricia grahamae* Wells from 83 m. Another *Merlia* was discovered growing on a dead *Ceratoporella* removed from under a ledge at 91 m. The living tissue of these

Merlia were colored orange, similar to those described from 25 m at Rio Bueno (Hartman and Goreau, 1970).

We did not observe contact between living sclerosponges, but the available samples indicate that their skeletons do form a substrate for the growth of other sclerosponges. In addition to the *Merlia* described above, individuals of *H. miniana*, *S. norae* and *G. auriculata* were found encrusting *C. nicholsoni* skeletons.

The outward and downward growth of *Ceratoporella nicholsoni* is clearly contributing to the formation of small ledges (Figure 2) on the middle portion of the deep fore-reef (approximately 70–105 m). Samples of the reef rock excavated between 85 m and 105 m are largely composed of aragonitic sclerosponge skeletons surrounded by lithified sediment. Thus earlier impressions with SCUBA that sclerosponges actually replace scleractinian corals as the framework constructors of the deep fore-reef at these depths are confirmed. One of these sclerosponge reef rocks, blasted from approximately $\frac{1}{2}$ m behind the nearly vertical reef-water interface at 105 m, gave a modern C^{14} age (200 ± 60 yrs.). This zone of the deep fore-reef therefore appears to be rapidly prograding seaward.

Except for the change of primary framework, the sclerosponge reef rocks being formed on the deep fore-reef are similar to those that Land and Goreau (1970) described from shallower reef zones. The internal sediments of these rocks are composed of sand- and silt-sized skeletal debris, and abundant Mg-calcite pellets. These sediments fill, or partly fill, natural cavities, and cavities that have been produced by bioerosion. This complex rock is massively cemented with Mg-calcite. In contrast, rock samples collected at the base of the deep fore-reef consist primarily of lithified reef debris, and are lacking in any primary framework component. Massive Mg-calcite cementation is again characteristic of these "debris piles" (Land and Moore, 1975).

B. Belize (British Honduras). Our SCUBA surveys in Belize suggested that sclerosponges are uncommon on the southern part of the barrier reef and on one of the outer atoll-like banks. We did find one group of *C. nicholsoni* on a pinnacle reef at 38 m on the fore-reef slope on the southwestern, leeward side of Glovers Reef. NEKTON "Beta" explorations undertaken in 1971 and 1972 (Ginsburg and James, 1973) revealed that sclerosponges are nowhere as abundant in that region as they are on the north coast of Jamaica. Both *C. nicholsoni* and *S. vermicola* occur on the deep fore-reef escarpment of the barrier reef off Tobacco Cay from 60 m to 111 m in depth; *C. nicholsoni* is found beneath ledges and is most abundant between 78 m and 83 m. *C. nicholsoni* was also observed off Queen Cay between 75 m and 95 m. At both these localities the sclerosponge cover seldom exceeds 10%. One *G. auriculata* was seen at 111 m off Tobacco Cay. *G. auriculata*, *H. miniana* and *S. norae* were brought up on rock samples from 115 m off Tobacco Cay.

Sclerosponges are particularly scarce on the windward side of Glovers Reef. Only one specimen of *C. nicholsoni* was observed off South Water Cay at 100 m. Off North East Cay, one *C. nicholsoni* was seen under an overhang at 98 m, and

several others were noted in a crevice at 130 m. Rock samples excavated on the deep fore-reefs of Belize consist of fragments of coral and *Halimeda* skeletons cemented with Mg-calcite and aragonite (Ginsburg and James, 1973). Sclerosponges do not appear to be primary framework constructors at any depth on these deep fore-reefs.

3. The slopes below the deep fore-reefs

A. *Jamaica*. The island slope in the vicinity of Discovery Bay was explored to 306 m, the maximum working depth of NEKTON 'Gamma'. The angle of this slope varies from about 45° between 115 m and 145 m, where reef-derived debris is piled up below the re-entrants, to about 30° below about 260 m. Above approximately 200 m, a hard substrate of lithified reef talus is overlain in many areas by a thin layer of reef-derived sediment, through which many small outcrops protrude. Sediment grain size tends to decrease rapidly with increasing depth, as unconsolidated pelagic sediment becomes more abundant. Between 155 m and 203 m, cliffs composed of lithified reef debris extend for a horizontal distance of about 200 m, and a group of huge, rounded limestone blocks of unknown origin are located below 210 m in the axis of the Discovery Bay submarine canyon. There appears to be intense biological erosion of all these rock surfaces, which are predominantly covered with a diverse sponge, coelenterate and echinoderm fauna, many species of which are found in the deep fore-reef or shallower reef zones.

Sclerosponges are less abundant here. Living *C. nicholsoni*, *S. norae*, *H. miniana* and *G. auriculata* were found on the undersides of fallen *Agaricia* plates removed from talus piles between 120 m and 136 m. *S. vermicola* was observed at 126 m on the seaward sides of rock outcrops. At least one *H. miniana* was noted sitting upright in the sediment at 130 m. A specimen of *S. norae* was taken from an excavation of one of the cliffs at 170 m. *C. nicholsoni* was fairly common between 120 m and 155 m, and was occasionally seen on the cliff and small outcrops to about 203 m. The deepest living sclerosponges observed were two small *C. nicholsoni* on a piece of rock found at 303 m by H. M. Reising. Unfortunately we do not know whether these had attached and grown *in situ*, or if they had been transported downslope from a shallower location.

B. *Belize*. Sclerosponges are extremely rare on the upper part of the continental slope off Tobacco Cay. One *G. auriculata* was seen at 124 m growing on a rock outcrop, and specimens of *S. norae* were found on a rock sample collected at 138 m. *S. norae* was also collected on rock samples from 125 m and 177 m off North East Cay, Glovers Reef.

4. Discussion

At present we can only speculate about factors which might cause the relative scarcity of sclerosponges towards the base of the deep fore-reef and on the slopes

below. The shallower reef zones may be the source of much of the organic matter consumed by sclerosponges. Reiswig (1971, 1972) has described abundant, quasi-particulate organic material which is unresolvable by direct microscopy, and which is thought to originate on Jamaican reefs. At Discovery Bay the top of the thermocline layer is located at about 105 m, and it may not be coincidental that sclerosponge framework construction was rarely observed below this depth. We should expect that the increase in water density below about 105 m, caused by decreasing temperature and by a layer of highly saline water (Wüst, 1964; J. D. Cochrane, pers. comm.), would retard the sinking of organic matter. Available food materials may simply decrease with increasing depth (Hartman, 1973). If skeletal calcification rates (Lang, 1974) or larval settling vary as a function of ambient temperature, sclerosponges may also be limited by the sudden decrease in water temperature.

The factors that determine the relative paucity and smaller individual sizes of sclerosponges on the southern Belize reefs as compared to those off the northern coast of Jamaica are equally obscure at present. Of possible significance are the strong northerly and southerly currents that pass along the windward sides of the barrier reef and Glovers Reef. These may lead to a rapid dispersal of particulate organic matter produced on the fore reefs, depriving sclerosponges of what is probably their chief source of nutrition. At the same time the thermocline layer is up to 50 m closer to the surface in the waters off Belize (R. L. Molinari and R. Starr, pers. comm.). The combined effect of these two phenomena perhaps narrows considerably the zone favorable for settling and growth of sclerosponges on the Belize deep fore-reef.

Acknowledgments. We should like to acknowledge the financial support of the National Science Foundation (Grant No. GA-35111 to L. S. Land) for the Jamaican submersible study. We are grateful for the logistical assistance which we received in Jamaica from General Oceanographics, Inc., D. C. Tretzyl of the Kaiser Bauxite Company and the staff of the Discovery Bay Marine Laboratory. We are specially indebted to our colleagues who contributed to the observations reported here, and who provided the personnel support for much of the NEKTON "Gamma" operation. We thank R. N. Ginsburg for the opportunity to extend our observations to the Belize area, and National Science Foundation Grant No. GX-28676 to the Smithsonian Institution for additional support for one of us (JCL) at Glovers Reef.

REFERENCES

- Ginsburg, R. N and N. P. James. 1973. British Honduras by submarine. *Geotimes*, 18: 23-24.
- Goreau, T. F. and N. I. Goreau. 1973. The ecology of Jamaican coral reefs. II. Geomorphology, zonation and sedimentary phases. *Bull. Mar. Sci.*, 23: 399-464.
- Goreau, T. F. and L. S. Land. 1974. Fore-reef morphology and depositional processes, north Jamaica. *In*, *Reefs in Time and Space*, pp. 77-89. L. F. Laporte, Editor. *Soc. Economic Paleontologists and Mineralogists, Spec. Pub. 18, Tulsa, Oklahoma* iv + 256 pp.

- Hartman, W. D. 1969. New genera and species of coralline sponges (Porifera) from Jamaica. *Postilla*, 137: 1-39.
- Hartman, W. D. 1973. Beneath Caribbean reefs. *Discovery*, 9: 13-26.
- Hartman, W. D. and T. F. Goreau. 1970. Jamaican coralline sponges: their morphology, ecology and fossil relatives. *Symp. zool. Soc. Lond.*, 25: 205-243.
- Jackson, J. B. C., T. F. Goreau and W. D. Hartman. 1971. Recent brachiopod-coralline sponge communities and their paleoecological significance. *Science*, 173: 623-625.
- Land, L. S. and T. F. Goreau. 1970. Submarine lithification of Jamaican reefs. *Jour. Sed. Petrology*, 40: 457-462.
- Land, L. S. and C. H. Moore, Jr. 1975. The deep fore-reef and upper island slope (55 to 305 m), north Jamaica. *Geol. Soc. America Bull.*, in press.
- Lang, J. C. 1974. Biological zonation at the base of a reef. *American Scientist*, 62: 272-281.
- Meaney, W. R. 1973. Sediment transport and sediment budget in the fore-reef zone of a fringing coral reef, Discovery Bay, Jamaica. M.S. thesis, Louisiana State University, Baton Rouge, La.
- Reiswig, H. M. 1971. Particle feeding in natural populations of three marine demosponges. *Biol. Bull.*, 141: 568-591.
- Reiswig, H. M. 1972. The spectrum of particulate organic matter of shallow-bottom boundary waters of Jamaica. *Limnol. Oceanogr.*, 17: 341-348.
- Wüst, G. 1964. Stratification and circulation in the Antillean-Caribbean basins. Columbia University Press, New York, 201 p.