

# Sponge-Mediated Coral Reef Growth and Rejuvenation

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Accepted 13 August 1984

**Abstract.** Sponges mediate consolidation of *Porites furcata* rubble on shallow Caribbean reefs by quickly adhering to rubble and stabilizing it until carbonate secreting organisms can grow and consolidate it to the reef. Experimental investigations demonstrate that the entire cycle from (1) temporary binding of rubble by sponges, through (2) rubble consolidation by encrusting coralline algae, to (3) colonization of consolidated rubble by corals, can be completed within 10 months. Bound rubble both adds to vertical reef growth and also provides stable substrata for colonization by corals. Corals that colonize stabilized rubble are damaged less and survive better than on unstable rubble. Rubble that is not temporarily stabilized by sponges does not become bound to the reef, because continuous movement disturbs the consolidation process, and does not provide suitable substrata for settlement and growth of corals. Sponge-mediated consolidation of rubble may increase rates of reef growth and enhance reef recovery after damage. This new role for sponges in reef growth is not obvious from examination of the internal fabric of a reef frame. Sponge-mediated consolidation may help to explain geographic and temporal differences in growth and morphology among shallow reefs of ramose corals.

## Introduction

Growth of a coral reef is not a simple accretion process, but the result of a complex cycle involving growth of live reef building organisms, accumulation of their dead and broken skeletons, break down and loss of carbonate, infilling of interstices and lithification, and the recruitment and growth of new reef builders (e.g., Goreau and Hartman 1963; Ginsburg et al. 1967; Land and Goreau 1970; Zankl and Schroeder 1972; Schroeder and Zankl 1974; Goreau and Land 1974; James et al. 1976; Macintyre

1977; Glynn and Macintyre 1977; Stearn and Scoffin 1977).

The biological production and reworking of carbonate is linked with the geological processes which consolidate and shape that carbonate into a permanent structure by intermediate processes that temporarily bind broken pieces of carbonate to the reef. Temporary binding of large pieces of carbonate, ensuring that they are not lost from the reef before consolidation can occur, has not been examined in detail. In reef habitats where temporary binding enhances consolidation, this process may strongly affect rates of reef growth and repair after damage.

Coral skeletons may be disengaged from the reef frame by activities of boring and scraping organisms and water action. Although live fragments of some corals (e.g. *Acropora*) are able to reattach themselves, detached dead corals can only become reattached to the reef if they are bound to it by carbonate secreting organisms, such as coralline algae, or by submarine lithification. To become bound in this way, a coral skeleton must remain fixed in position until carbonate secreting organisms grow, binding it to the reef. Unless the coral skeleton is sufficiently large to remain stationary in spite of water movement and activities of burrowing and grazing organisms, the binding process will be disturbed repeatedly.

Sponges, diverse and abundant on most Caribbean coral reefs, may mediate consolidation by temporarily holding coral pieces stationary. Sponges may adhere firmly to carbonate substrata after only a few days of contact, and serve as "glue" between loose rubble and the reef, until growth of carbonate secreting organisms binds them more permanently. This adds coral skeletons, which might otherwise be lost, to the reef frame. It also provides stable substrata onto which coral larvae can settle, rejuvenating the reef.

The hypothesized stages of sponge-mediated consolidation and rejuvenation are:

1. sponges enter piles of rubble by growing into them from crevices in the reef or by migrating in as errant frag-

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ments, and some of these sponges adhere to rubble within a few days of contact;

2. sponge-stabilized rubble is colonized by carbonate secreting organisms, such as encrusting coralline algae and bryozoans, which bind the pieces of rubble together and to the reef;

3. corals that colonize consolidated, rather than loose, rubble are more likely to survive and grow.

Using experiments and observations, I investigate temporary binding by sponges, and illustrate the rates and frequencies at which it can occur on shallow reefs of ramose corals in the Caribbean. I then discuss this process with respect to: (a) its possible importance in other habitats and situations, (b) biogeographic differences in reef morphology and recovery from disturbance, and (c) historical interpretations of coral reef growth.

## Materials and Methods

### Study Areas and Species

Dense growth of the ramose coral *Porites furcata* Lamarck crowns many shallow reefs of the San Blas Islands, Panama (Glynn 1973; Robertson and Glynn 1977). A characteristic assortment of associated corals includes clusters of *Agaricia* and *Millepora* on shallow windward edges and occasional massive heads of *Siderastrea*, *Porites*, *Diploria*, and *Colpophyllia*. Where the bases of the reefs, which may be from 1 to more than 10 m deep, are deeper than several meters, they are often surrounded by small thickets of *Acropora cervicornis* or large *Montastrea annularis*. The tops of the reefs are 0.5 to 3 m deep and their largest areal dimensions from 5 to over 100 m. The observations and experiments reported here were conducted primarily on two representative *Porites furcata* reefs, Ukkup Tupo and Guigala Tupo, near the San Blas Field Station of the Smithsonian Tropical Research Institute.

*Porites furcata* branches are narrow (1–1.5 cm in diameter) and also tend to be cored by excavating sponges. These traits make shallow stands of this coral especially susceptible to high rates of damage due to water movement in the dry season (December–April), collisions of boats and drift logs, and excavation and transport of the coral by the Kuna Indians, who use it to expand their islands. Consequently each *Porites* bank is a mosaic of standing live coral, loose and eroding dead coral, and consolidated rubble.

The hypothesized sequence of stabilization, consolidation, and colonization of coral skeletons was initially thought to take many years and was, therefore, divided into experimentally tractable stages. Experiments were designed to imitate each of these stages in order to determine if sponge-mediated consolidation of rubble occurs, and to estimate the rate of completion of each stage and frequently of successful passage from each stage to next.

Shallow reefs of ramose corals are also found on the Pacific side of the Isthmus of Panama, in the Gulf of Chiriqui (Glynn 1976). Infrequent access to these reefs precluded experimentation, but observations were made for comparison where possible. The Pacific reefs, of primarily *Pocillopora* spp., differ from the Caribbean reefs in their conspicuous lack of sponges on open surfaces.

### Binding of Coral Skeletons to the Reef by Sponges

Two types of sponges may bind rubble together and to the reef: erect sponges, which stand above the reef surface; and cryptic sponges, which are confined to spaces within the reef and rubble.

Erect sponges may be broken off their bases and rolled about by water currents and the activities of fishes and echinoderms until they reattach. The frequency of rubble binding by errant sponges was estimated from their rate of immigration into a cleared area. All erect sponges were cleared from a shallow (–2 m) 3 m by 2.5 m quadrat of

coral rubble, small corals, and carbonate sediment on Guigala Tupo reef. For 2.5 years, the cleared area was examined for sponge immigrants that had reattached to carbonate substrata there.

Rubble that falls onto a cryptic sponge can be immobilized as the sponge grows up and adheres to the under surface of the rubble. The probability of rubble falling or rolling onto a cryptic sponge was estimated as the percentage of 90 points, at 0.5 m intervals along 3 randomly located transects, which fell over cryptic sponges with visible access to the reef surface.

Estimates of the time required for erect sponges to bind rubble were made by cutting 64 pieces (4 cm long) of several common species of erect sponges [*Iotrochota birotulata* Higgin, *Haliclona rubens* (Pallas), *Niphathe erecta* Duchassaing and Michelotti, *Aplysina* (= *Verongia*) *fulva* (Pallas), and *Desmapsamma anchorata* (Carter)] and tying them onto small (3 cm long) pieces of coral rubble with cotton string. These sponges were examined daily until all had become attached to the rubble to which they were tied. They were then scattered over the top of a *Porites* bank on Guigala Tupo reef. The movements of these sponges and the rates at which they bound rubble together and to the reef were recorded for 4 months.

To understand the dynamics of binding rubble to the reef by cryptic sponges, piles of 50–60 pieces of sun-bleached *Porites furcata* rubble were heaped over cryptic sponges. The most abundant sponges included *Mycale laevis* Carter and *Halichondria* cf. *melanodocia* de Laubenfels. The progress of stabilization, as cryptic sponges grew up and adhered to the rubble, was followed for 5 months.

### Consolidation of Sponge-Bound Rubble by Carbonate Secreting Organisms

If sponge binding of rubble is important relative to other factors influencing vertical reef growth, then a positive association is predicted among sponges, consolidated rubble, and relative height of the reef surface. To document this association, the 90 points which were examined for sponge presence were also examined for consolidation of rubble and relative height of the reef surface.

Experimental piles of rubble were constructed on Ukkup Tupo reef out of sun-bleached *Porites furcata* rubble, marked, for future identification, with small dabs of epoxy paint. Sun bleaching and drying of the rubble killed all inhabitants, allowing clear enumeration of colonizing organisms. Each pile included 35 pieces of rubble and initially measured approximately 25 cm in diameter and 15 cm in height. Included in each of eight rubble piles were 5 pieces, each approximately 5 by 1.5 cm, of common shallow water reef sponges [one each of *Iotrochota birotulata*, *Haliclona rubens*, *H. erina* de Laubenfels, *Niphathe erecta*, and *Callyspongia vaginalis* (Lamarck)]. Eight other rubble piles were constructed without sponges. The rubble was examined 6 times over 10 months to see if it became buried, scattered, or bound to the reef.

### Recruitment and Survival of Corals on Stable and Unstable Substrata

The rubble used in the preceding experiment was examined at intervals for coral recruits in order to compare recruitment onto stable and unstable rubble of known history.

To test the hypothesis that small corals survive better on stable than on unstable substrata, 275 small individuals (most between 1 and 4 cm in largest dimension) of 1 hydrozoan and 6 scleractinian coral genera (*Millepora*, *Acropora*, *Agaricia*, *Diploria*, *Favia*, *Porites*, and *Siderastrea*) were collected and attached to stable substrata (clay bricks) or unstable substrata (lengths of waxed twine). The corals were attached to the bricks and twine with "Sea-go-in' Poxxy Putty", which was allowed minimal contact with live coral tissue. Throughout the operation, the corals remained immersed in sea water. The bricks and lines were placed on the two study reefs and examined for coral growth and survival for 4 years.

Consolidated and loose rubble was examined for in situ association of coral recruits and substratum stability. A ¼ square meter quadrat was randomly placed in an area of *Porites furcata* rubble on Ukkup Tupo reef that was consolidated to various degrees by encrusting coralline red



algae. The rubble in each  $1/16$  square meter was judged to be bound, partly bound, or loose, and the live corals counted. In the eastern Pacific these same data were collected on Uva reef, also a shallow reef of ramose corals, in the Gulf of Chiriqui, Panama.

## Results

### *Binding of Coral Skeletons to the Reef by Sponges*

Fragments of erect sponges repopulated the cleared quadrat at a rate of 2.6 sponges/m<sup>2</sup>/year (49 immigrants/7.5 m<sup>2</sup>/2.5 years).

Cryptic sponges had visible access to the reef surface over about half of the area (49/90 transect points) on the top of Guigala Tupo reef (from data in Table 1).

All pieces of erect sponges became attached to rubble, such that they could only be removed by tearing sponge tissue, within five days. One month after these sponges were scattered on top of a *Porites* bank, 23% (15/64) had attached to the reef, rubble, and to pieces of live coral. Up to six pieces of rubble and one live coral were bound together by a single piece of sponge. After four months, 31% (20/64) of the sponges had attached to rubble, the reef, or both; and by this time all unattached sponges had been swept off the reef top by water movement.

Cryptic sponges had grown up and adhered to under-surfaces of the fresh rubble in 25/45 of the rubble piles within one month. After 5 months, 33/45 of the experimental rubble piles were tightly bound together and clearly raised above the reef surface.

Various species of stoloniferous macroalgae (mostly *Dictyota*, *Caulerpa*, and *Halimeda*) grew over 28/45 of the rubble piles. These algae bound rubble rapidly and securely, but they deteriorated, and disappeared altogether from 10 of the 28 piles, by the end of the dry season (March; 4 months after the experiment began). Boring sponges also bound rubble within a month. However, these sponges bind carbonate by invading it, and they were able to penetrate through *Porites furcata* rubble completely in 6 weeks.

### *Consolidation of Sponge-Bound Rubble by Carbonate Secreting Organisms*

The predicted positive associations were found between (1) presence of sponges and consolidation of rubble, (2) consolidation of rubble and relative height of the reef surface, and (3) presence of sponges and relative height of the reef surface (Table 1; Chi-square test statistics are 43.1, 23.6, and 24.2; all significant at  $P < 0.001$ ).

Heights of experimental rubble piles without sponges had diminished to an average of 4.5 cm, versus 8.6 cm for those with sponges (difference significant by the Wilcoxon-Mann-Whitney test,  $P < 0.007$ ), after 2 weeks. After 7 weeks, those piles that had not included sponges were no longer raised above the surface of the reef, and the pieces of marked rubble had become widely scattered and buried (Table 2).

Encrusting coralline algae had colonized rubble in sponge-bound piles by 7 weeks. Five months after the

**Table 1.** Associations, at 90 points, among consolidation of rubble, presence of sponges, and relative height of the reef surface on a shallow *Porites furcata* reef, Guigala Tupo, San Blas Islands

	Sponges associated	No sponges
Rubble consolidated	40	5
Rubble not consolidated	9	36
	Rubble consolidated	Rubble not consolidated
Reef height above median	33	10
Reef height below median	12	35
	Sponges associated	No sponges
Reef height above median	35	8
Reef height below median	14	33

**Table 2.** Progress of consolidation of coral rubble in 8 experimental rubble piles which included sponges and 8 without sponges on Ukkup Tupo reef, San Blas Islands

	Rubble piles	
	With sponges	Without sponges
Average height of rubble piles above reef surface after 7 weeks	8.6 cm (SD = 3)	4.5 cm (SD = 1.1)
Configuration of rubble in piles after 5 months	Hummocks, raised above reef surface	Scattered, buried, not raised
Encrusting bryozoans per piece of rubble after 12 weeks	0.44	0.08
Total number of hermatypic coral recruits in 10 months	4	0
Time after which rubble was tightly bound together by encrusting coralline algae	7 months	Never

start of the experiment, the algae had almost completely covered rubble in these piles; and after 7 months, the rubble was firmly bound together with thick coralline algae. After 10 months, the rubble was joined together and to the reef by the growth of encrusting coralline algae, such that individual pieces of rubble could no longer be distinguished clearly. Coralline algae settled onto and grew around rubble that wasn't bound by sponges, but this rubble remained loose and mobile. Rubble in sponge-bound piles remained in consolidated hummocks, raised above the loose rubble (Table 2).

While the coralline algae bound the pieces of rubble together from the top and sides, other carbonate secreting organisms, especially encrusting bryozoans, bound from within. After 12 weeks, 52 encrusting bryozoan recruits were found on 118 pieces of bound rubble; whereas







## Discussion

Rubble generated by damage to the ramose coral *Porites furcata* may be bound by cryptic sponges, which have access to the reef surface over about half its area, or by errant pieces of erect sponges, which reattach to rubble at a rate of about 2.6 per square meter per year. As cryptic sponges grow, they adhere to rubble above them, binding it within a month. Pieces of erect sponges may adhere to rubble in less than 5 days, and nearly a third (31%) of the errant erect sponges which pass through an area may remain, binding rubble. The sponges temporarily stabilize the rubble until carbonate secreting organisms, especially encrusting coralline red algae and bryozoans, settle on the rubble and grow. Within 10 months, the carbonate secreting organisms can grow sufficiently to tightly bind pieces of rubble to each other and to the reef. This produces hummocks of stable, consolidated rubble onto which coral larvae can settle.

Small corals on stable rubble are only half as likely to be damaged as those on rubble that is free to be jostled (34% versus 65% damaged in 4 months). Survival of corals on stabilized rubble is better by an order of magnitude (13% versus 1%), over 4 years.

On these shallow reefs of ramose corals, rubble that is not temporarily stabilized by sponges does not become bound to the reef and does not provide favorable substrata for colonization by corals.

The role that sponges play in stabilization of *Porites* rubble is especially significant for carbonate accretion because it allows a sequence of growth and damage to cycle through repair and recruitment stages. Carbonate which might otherwise be lost is added to the reef frame, extending the reef and also providing suitable substrata for colonization by corals.

Entrapment and stabilization of organically generated carbonate by mats of microorganisms, algae, and marine grasses has been described (Ginsburg and Lowenstam 1958; Neumann et al. 1970; Scoffin 1970; Basan 1973). Stabilization by these organisms ranges from ephemeral (green algae) to sufficiently permanent to build up significant differences in accumulation between stabilized and unstabilized areas (*Thalassia*). A sponge has been described (*Bubaris ammosclera* Hechtel 1969) that can bind carbonate sands and rubble by growing as a mat over them. Macintyre et al. (1968) suggested that the sponge mat stabilizes the sediments until they can become chemically cemented.

In these examples, the carbonate bound was dominantly sand-size or finer, rather than rubble. Unless cementation occurs, binding of sands does not produce hard substrata suitable for colonization by corals. Mats also restrict colonization of carbonate secreting organisms by covering bound sediments. Stoloniferous macroalgae were found to stabilize *Porites furcata* rubble temporarily, but they may inhibit recruitment of the encrusting coralline algae which bind rubble more permanently (Vine 1974). In contrast, rubble binding sponges

leave recruitment surfaces open. Cryptic sponges appear to be restricted to living in spaces within the reef and do not engulf the tops of the rubble they bind. Pieces of erect sponges tend to remain true to their normal growth forms, and also bind rubble without covering all potential recruitment surfaces.

### *Limitations and Extensions of Sponge Binding*

Sponge-mediated cycling from rubble to live reef can be limited by lack of opportunities for sponges to contact and bind rubble, or by lack of settlement and growth of carbonate secreting organisms to bind rubble more permanently.

Sponges are abundant on *Porites furcata* banks and in most other habitats on Caribbean reefs. The combined biomass of non-excavating demosponges can equal or exceed that of the scleractinians in many reef zones (e.g., Bonem and Stanley 1977; Hartman 1977; Wulff, unpublished data).

Benthic topography may limit the situations in which sponges can bind carbonate rubble. Broken coral skeletons may remain on flat topped banks of *Porites furcata* or other ramose corals until sponges contact and hold them, but coral which breaks off a vertical cliff is more likely to add its skeleton to talus heaps at the cliff base. It has been suggested (Goreau and Hartman 1963) that sponges also bind talus, providing stable substrata upon which deep water scleractinians [e.g. *Agaricia undata* (Ellis and Solander)] can settle and grow.

Size of the rubble generated when corals break may also limit the role of sponges as intermediaries in binding. *Porites furcata* breaks into small pieces, easily retained by small sponges. Larger rubble can only be retained by large and tenacious sponges. Very large blocks of carbonate, generated by the demise of massive and tabular corals, remain stable without temporary binding by sponges.

Temporary binding of rubble is probably most important in shallow water, and where bioturbation keeps unbound rubble in motion (e.g. Glynn et al. 1972). Rubble not influenced by water movement and bioturbation may become consolidated by submarine lithification, without temporary binding by sponges, producing stable recruitment surfaces within a year (Goreau and Land 1974).

Reef organisms that affect recruitment and growth of carbonate secreting organisms may stall or aid the binding process. The thick mats of algae guarded by benthic pomacentrid damselfishes appear to inhibit the settlement and growth of coralline algae, and rubble can be noticeably looser within their territories (Vine 1974). Conversely, where growth of encrusting coralline algae is enhanced by herbivory (e.g., Paine 1980; Steneck 1983), high densities of grazing gastropods and echinoderms may speed consolidation of sponge-bound rubble.

The role of sponges as mediators in consolidation of rubble may be extended to other habitats and situations.



Panama is outside the hurricane belt, but the San Blas reefs do receive heavy swell during the dry season (Glynn 1973), causing chronic small scale damage. During these months, rapid binding by sponges is of daily importance on shallow reefs. Sponges may also be important in aiding recovery of reefs which receive massive and sporadic damage. In addition to shallow *Porites* banks, common habitats on Caribbean reefs which may benefit from sponge aided rubble consolidation after large storms include deep talus heaps, *Acropora cervicornis* "buttresses", fore-reef escarpments, and shallow mounds of *Agaricia* or *Madracis*. Rejuvenation of damaged reefs will be hastened where sponges aid consolidation of storm generated rubble, quickly providing suitable substrata for recolonization by coral larvae.

#### *Interpretation of Biogeographic Differences*

If temporary binding by sponges is an important mediator of rubble consolidation, reefs without sponges might be characterized by abundant unconsolidated rubble. The paucity of sponges on shallow reefs of ramose *Pocillopora* in the Gulf of Chiriqui (eastern Pacific) may be reflected in this way.

Where live *Pocillopora* colonies grow in an interlocking mass, growth rates of the eastern Pacific reefs can equal those determined in the Caribbean and Western Pacific (Glynn and Macintyre 1977). Glynn (1976) has been able to trace branches of live *Pocillopora* in dense stands back through centuries of uninterrupted growth. Where integrity of the interlocking mass is maintained, rapid growth is achieved because the cycle of breakage, consolidation, and recolonization is avoided altogether.

Consolidated rubble is found only on the reef tops, which become emersed on very low tides. Although densities of small corals on this stabilized substratum are strikingly similar to those on *Porites furcata* rubble (Table 5), restriction to occasionally emersed substrata prevents these corals from ever contributing substantially to reef growth.

The live *Pocillopora* is flanked by aprons of unconsolidated rubble, especially where exposed to high energy water movements (Glynn et al. 1972). Once a piece is broken from the interlocking mass of *Pocillopora*, it remains loose. The rubble aprons are subject to high levels of bioturbation (Glynn et al. 1972; Glynn 1974) by fishes, gastropods, and echinoderms. Small corals living in the loose rubble may have only  $\frac{1}{3}$  the average linear growth rate of those on stable substrata (Glynn 1974); and massive corals in deeper water may be damaged by slumping of the unconsolidated debris generated in shallow zones (Glynn 1976). Seaward development and recovery from damage of these reefs may be slowed by lack of rubble binders, such as sponges.

Geographic differences in reef development and recovery from damage may depend as much on organisms auxiliary to the cycle of carbonate generation and consolidation as on conditions affecting coral growth directly.

#### *Historical Interpretations of Coral Reef Growth*

Demosponges are infrequently represented in reef sections except as disarticulated spicules (Hartman et al. 1980). When most demosponges die, the spongin fibers, which give their skeletons integrity in the absence of live tissue, soon deteriorate.

Non-excavating demosponges have been demonstrated to enhance survival of corals on fore-reef slopes in the Caribbean. Mortality of corals on patch reefs from which non-excavating sponges were removed was an order of magnitude higher (40% versus 4%, than for corals on control reefs (Wulff and Buss 1979). Although presence or absence of sponges can affect coral survival so dramatically, and this result had been suggested by Goreau and Hartman (1963) from observations of living reefs; clues implicating sponges in coral survival are lacking within the framework of living or fossil reefs. The only suggestions of places occupied in life by non-excavating sponges may be found in the form of rare coral skeletons which became molded to the shapes of neighboring sponges (Goreau and Hartman 1966; Wulff and Buss 1979; personal observation). Likewise, clear evidence for sponge mediation of carbonate consolidation may not exist, even where this process has been important. Different rates of carbonate accretion, interpreted as evidence for environmental differences affecting corals, may actually have depended on differences in sponge fauna.

Possibility for misinterpretation of paleoenvironmental variables from the fossil record was also stressed by Neumann et al. (1970) and by Bathurst (1967) with respect to carbonate sediments stabilized by mats. Because the mats leave no obvious or direct record, mat-stabilized sediments appear later to have been deposited in very low energy environments instead of in areas of high water agitation.

Conditions favorable for growth of corals, and other producers of frame-building materials, may not be favorable for auxiliary mediators of carbonate accretion. Sponges, or other soft-bodied creatures that could temporarily bind coral rubble, may help cause the frequent lack of correlation between growth of individual corals and growth of entire reefs (review in Stoddart 1969).

During times of rapid sea level change, consolidation of rubble to the reef frame instead of loss to surrounding sediments, may have been critical for continued provision of suitable habitat for light-requiring organisms living on hard substrata. Sponges that mediate consolidation of coral rubble may have played, as they now play, an important role in building and shaping coral reefs.

*Acknowledgements.* I am indebted to Peter W. Glynn, Egbert G. Leigh, and Ross Robertson for their help and encouragement throughout my field work. Peter Glynn, Willard Hartman, Ian Macintyre, and Clive Wilkinson generously provided many helpful comments on the manuscript. I thank the Kuna Indians of the Comarca de San Blas for allowing me to study their coral reefs. This research was supported primarily by Short Term Assistantships from the Smithsonian Tropical Research In-



stitute, and by the Lerner Fund for Marine Research (American Museum).

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stitute, and by the Lerner Fund for Marine Research (American Museum).

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