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Animal-Sediment Relations in a Tropical Lagoon: Discovery Bay, Jamaica

Robert C. Aller
Yale University

Richard E. Dodge
Yale University, dodge@nova.edu

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Animal-Sediment Relations in a Tropical Lagoon Discovery Bay, Jamaica[1]

Robert C. Aller and Richard E. Dodge

Department of Geology and Geophysics
Yale University
New Haven, Connecticut 06520

ABSTRACT

The distribution of many macrobenthic species in the back-reef lagoon of Discovery Bay, Jamaica can be related to a gradient in bottom stability. This gradient is defined by increasing rates of biogenic reworking and sediment resuspension in the western part of the lagoon. Infaunal diversity and coral growth decrease in the western, unstable areas. The infauna of the carbonate sand consists mainly of deposit feeders. In the western lagoon, the feeding activities of this group result in high biogenic reworking rates (up to 6–7 cm/week) producing loose surface sediment easily resuspended by waves. A maximum, mean resuspension rate of 19 mg/cm^2/day was measured. Instability of the lagoon floor, resulting in high water turbidity, inhibits settlement and growth of most suspension feeders and reduces infaunal diversity and coral growth. Because stability of the soft-bottom is significantly influenced by deposit feeders, our observations represent an extension of the trophic group amensalism principle to tropical nearshore environments.

1. INTRODUCTION. In temperate marine environments the reworking of muddy sediments by deposit-feeding organisms may result in an unstable bottom whose properties are not suitable for suspension feeders. This kind of exclusion or inhibition of one trophic group as a consequence of the activities of another is termed trophic group amensalism (Rhoads and Young, 1970). The amensalism principle has recently been applied to the distribution of tropical benthos in a Florida estuary (Bloom, Simon, and Hunter, 1972). In this study, we investigated the tropical benthos of a typical back-reef lagoon, Discovery Bay, Jamaica. Emphasis was placed on the different animal-sediment relations, the stability of bottom sediments and the possibility of amensalistic interaction between different groups of bottom organisms. The results of this study and their implications for the reef community are discussed here, and are compared with examples from the temperate benthic environment.

[1] Received: *12 November 1973*; revised: *24 January 1974*.

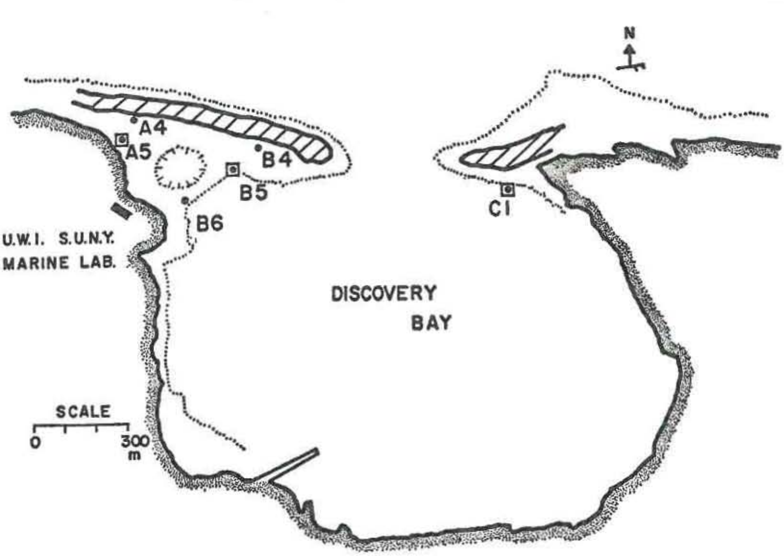

Figure 1. Map of Discovery Bay showing station numbers and positions. Reef top is hatched. Dotted line = 3 m contour. A small basin can be seen in the western shelf area between stations A and B. Squares indicate stations where resuspension and biogenic reworking were measured.

2. STUDY AREA. Discovery Bay is located on the north coast of Jamaica. The bay is approximately 1.0 by 1.5 km in dimension and can be readily broken into two bathymetric provinces: shallow lagoonal shelf regions (0–8 m) behind the reef in the east and western areas, and a basin (8–53 m) (Fig. 1). Bottom types in the shallow shelf areas range from bare limestone to loose or plant-bound calcareous sand. Deeper parts of the bay act as a sink for fine-grained sediment (Reiswig, 1971). Beds of the angiosperm *Thalassia* are common near shore and benthic algae are found in varying abundance on the lagoon floor.

The N. E. Trade Winds, which blow daily, set up a slow clockwise surface current during the day; at night this current ceases (Reiswig, 1971; Jackson, 1972). The wind produces a daily cycle of wave activity which interacts with the bottom in shallow areas. Tidal range is small (~ 30 cm).

On the basis of variations in annual water temperature and storm wave stress in the bay, the year can be divided into a warmer, calm summer (April–October) and a cooler, stormy winter (November–March) (Reiswig, 1971). The months on either end of these periods are transitional. The yearly ranges of average monthly temperature and salinity are 26–30°C and 34–36‰ respectively (Reiswig, 1971; Jackson, 1972). The major environmental stresses in the bay are winter storms which cause severe scour and resuspension of sediments in the shallow areas including the *Thalassia* beds (Jackson, 1972).

Table I. Station descriptions and depths.

Station #	Description	Depth (m)
A4	White, mound-covered with loose sand and intermixed coral debris.	1.7
A5	White, mound-covered with loose sand.	2.0
B4	Gravel and sand. Reef rubble zone. Limestone base ∼10 cm depth.	1.0
B5	Sand bottom bound by the filamentous alga *Lyngbia* and other benthic algae. A diversity of burrows and mounds are present.	2.1
B6	White, mound-covered with loose sand. Some intermixed coral debris. Small coral patches present.	2.1
C1	Thin veneer of white sand over limestone rubble. Sediment patchy. Loose rock and coral patches.	4.0

3. SAMPLING. A preliminary study of the soft and hard-bottom benthos was made during the period March 10–16, 1973. Based on data from this reconnaissance study, a program of quantitative and semi-quantitative sampling of the lagoon was begun on March 16 and extended through March 24, 1973. This sampling involved three major goals: 1) determination of the distribution and type of soft-bottom fauna, 2) measurement of coral growth rates in different areas of the lagoon, and 3) quantitative investigation of biologically and physically controlled bottom processes.

Six stations were established in the shallow lagoon areas behind the reef (Fig. 1) A short description of bottom type and water depth at each station is given in Table I. Faunal samples were collected at five stations: A4, A5, B4, B5, and B6 (Fig. 1). Biogenic reworking and resuspension rate measurements were made at A5 and B5 (March 16–23, 1973) and C1 (March 17–24, 1973). Specimens of the coral *Montastrea annularis* 20–30 cm in height were collected within 50 m of stations A4, A5, B5, and C1. *M. annularis* is the major reef forming coral of the Caribbean (Goreau, 1959). No storms occurred during our sampling and weather conditions were identical throughout the sampling period. The data given in this study are therefore more representative of the summer period than winter.

4. METHODS. *a. Fauna.* At each station a 1/10 m^2 grid was thrown to the bottom. The number of burrows lying within the grid and thought to be inhabited by the deep-burrowing (to about 1 m depth) shrimp, *Callianassa*, were counted. The area was then rapidly excavated to a depth of 20–25 cm by use of a wide mouth ∼ 3 l can. Excavated sediment was placed in a large plastic trash can which had been laid on its side next to the sampling site. Following

excavation, the can was carefully turned upright, sediment allowed to settle to the bottom, and then slowly raised to the surface. All samples were taken by the same diver.

Each bulk sample was fixed in 30% formalin and living tissue stained with Rose Bengal for 24 hours. The sediment was then sieved through a 1.0 mm sieve. Retained organisms were preserved in 50% ethanol and later separated and identified. Taxonomic keys for the region were not available for most animals. We followed the example of Wade (1972) (Kingston Harbor study) and separated many animals as "form species". Samples were sorted several times by different people.

The rarefaction method of Hurlbert (1971) and the Brillouin index Hb (Pielou, 1966) are used to measure sample diversity. The formulas for these indices are: Hurlbert rarefaction,

$$E(S_n) = \sum_i \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right] =$$

number of expected species in a sample of n individuals selected at random from a collection containing N individuals, S species, and N_i individuals in the ith species; and Brillouin diversity, $Hb = 1/N \log_2 (N!/N_1!\, N_2!\, N_3! \ldots N_s!)$ where N = total number of individuals, s = the number of species, and N_i = the number of individuals of the ith species.

Stomach contents were used to determine trophic types of organisms whose food preference was not already known. The criteria for trophic classification of unfamiliar animals are as follows: Cnidarians and nemerteans are termed carnivores. Syllids are classified as browsers (Neumann, Gebelein, and Scoffin, 1970). Brachyurans and hermit crabs are classified as scavengers. If an animal possessed obvious filtering structures and had small amounts of sediment in its stomach it was termed a suspension feeder (e.g., sabellids). If an animal possessed or lacked filtering structures and the stomach was heavily packed with sorted or unsorted sediment, the animal was termed a deposit feeder (e.g., some amphipods, maldanids). If an animal lacked filtering apparatus and had either an empty stomach or one with small amounts of sediment it was not classified (e.g., most sipunculids). Some additional species were left as uncertain (e.g., some amphipods). This is an operational classification and animals which might be facultative with respect to trophic type are classified as only one type under this scheme. Species that process large amounts of sediment are emphasized.

Hemispherical specimens of the coral *Montastrea annularis* were sectioned with a rock saw along a plane which intersected the point of highest relief on the growing surface and the midpoint of the base. An approximately 0.5 cm slab was obtained by a second saw cut parallel to the section face. Slabs were

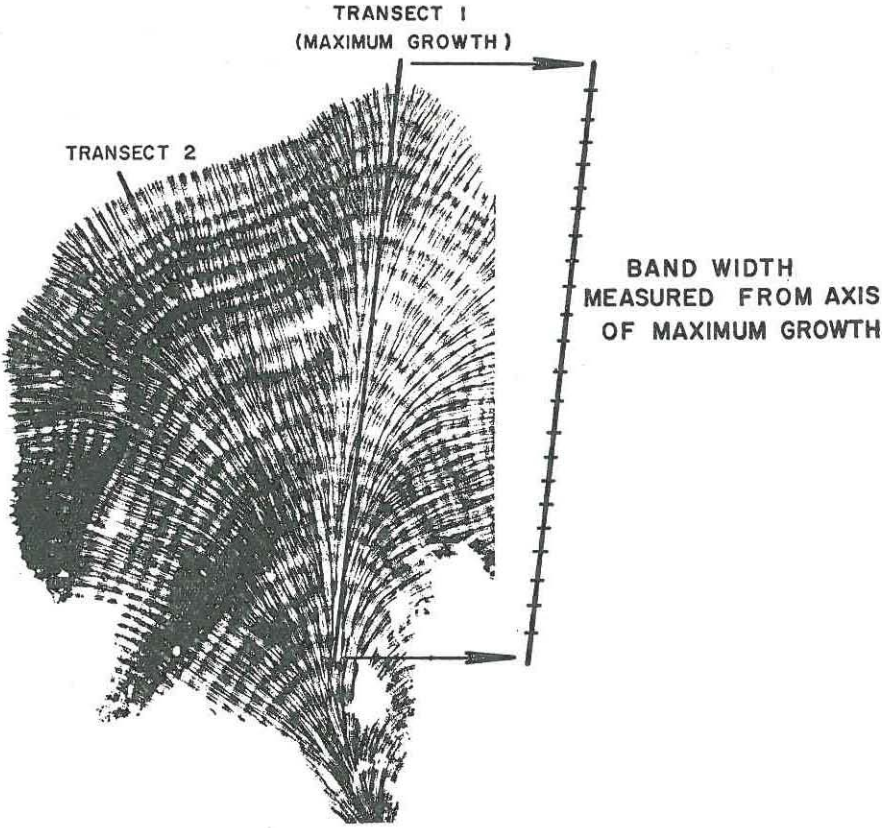

Figure 2. *X*-ray positive of *Montastrea annularis* section showing method of band width measurement.

X-radiographed using Kodak AA X-ray film. As previously reported in Dodge, Aller, and Thomson (1974), annual skeletal density bands are revealed in X-radiographs of these slabs. Because specimens were never perfectly hemispherical, it was decided to measure the average band width (i.e., linear upward growth) along two or three transects drawn on the X-radiograph. One transect was always drawn to intersect the axis of maximum growth (Fig. 2). By taking a weighted mean of all transect band width averages in an individual head, we obtained the "average" upward growth for that coral. This value was always slightly lower than the axis of maximum growth transect average. Coral growth rates for a station are presented in two ways: (1) maximum growth rate is the weighted mean of the band width averages from the maximum growth transects of all corals at that station; and (2) "average" growth rate is the weighted mean of all transect averages of every coral at that station.

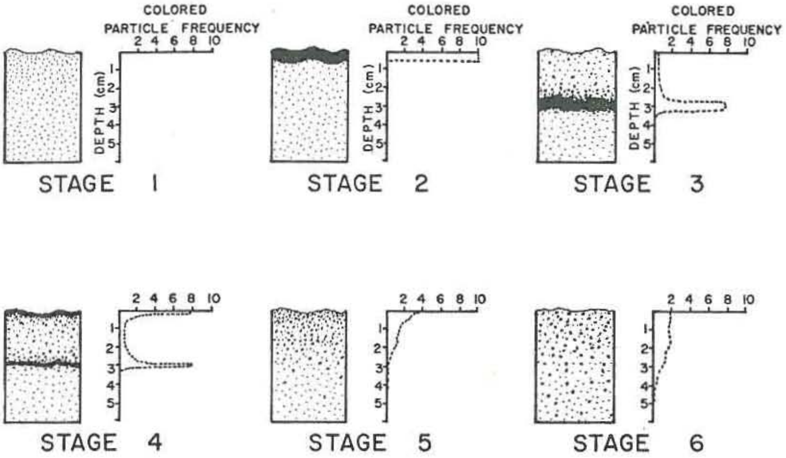

Figure 3. Idealized stages in biogenic reworking of a colored layer by vertically oriented deposit feeders. A schematic cross-section of the sediment and the relative abundance (arbitrary scale) of colored particles with depth is shown for each stage. Stage 1: sediment prior to deposition of colored layer. Stage 2: colored layer deposited on surface. Stage 3: feces and excavated sediment are placed on top of layer. Layer sinks. Stage 4: layer reaches depth at which dominant reworking animals are feeding and if particles in layer are of ingestable size, begins to be recycled to surface. If particles are not of ingestable or suitable size, parts or all of the layer will become a lag deposit at depth of feeding and remain intact. Stage 5: equivalent to stage 2 but after approximately two cycles. Stage 6: after many cycles, layer is homogeneously mixed to depth of feeding by dominate reworking animals and tails off as animal abundance or residence time decreases with depth. (After: Aller (unpublished work), see also Darwin (1837); Haven and Morales-Alamo (1966), and Clifton and Hunter (1973)). Our measurements were made mostly during stage 3, and correspond to the average rate of sinking.

5. Water and Sediment. The temperature of the sediment and surface water at each station was measured by a diver using a thermometer accurate to 0.1°C. Bottom salinity was measured by use of a hydrometer. Sediment samples for particle size analysis were collected concurrently with faunal samples at each station. These were wet sieved within 72 hours of collection.

Resuspension rates of sediments were measured with sediment traps placed at various heights above the bottom. Duplicate measurements were made at 50 cm above the bottom at A5, B5, and C1. One liter plastic containers with a mouth opening of 63.6 cm^2 were used at A5 and B5; metal traps having openings of 74 cm^2 were used at C1. Traps were wired to metal rods (1 cm diameter) which had been driven into the bottom. Differences in opening size does not significantly affect results (Young and Rhoads, 1971). At B5 and A5 three standard petri dish traps (62 cm^2) were placed atop cans ~ 7 cm above bottom. Resuspended sediment collected in these traps was dried and weighed. Some samples were wet-sieved for grain size determination.

To measure *in situ* reworking of sediments by the infauna, colored sediment layers were laid down at stations A5, B5, and C1. The volume of sediment

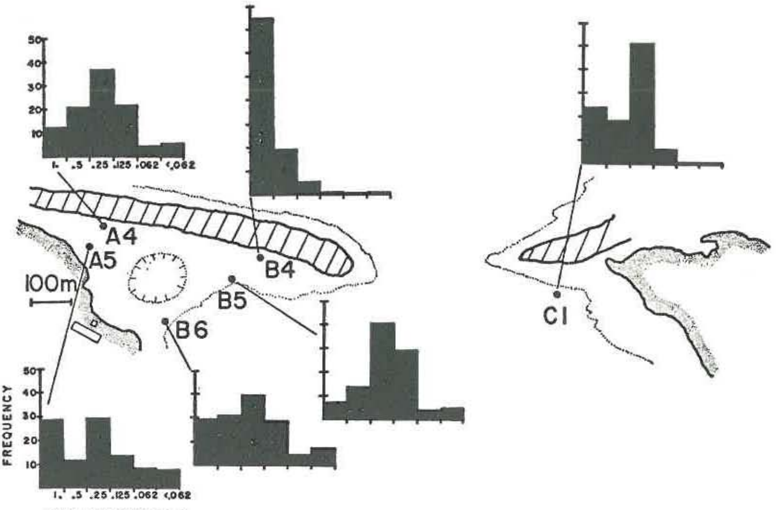

Figure 4. Sediment size-frequency distributions by weight percent. Sizes in mm.

placed on top of this layer by organisms and the vertical displacement of colored particles over time was noted. The colored marker layer consisted of carbonate sand painted with Fiesta Red, Berger Master Emulsion paint (non-toxic). Particles were allowed to dry and then thoroughly washed to eliminate free paint and fines. A layer of this sediment 1–2 mm thick was spread over the bottom ($\sim 0.5\ m^2$) at each station (Stage 2, Fig. 3). Deposit feeders which place feces, pseudofeces, or excavated sediment on the sediment-water interface cause the layer to move down (Stage 3, Fig. 3). The layer eventually reaches the level at which either most animals or the dominant reworking animals are feeding, at which time particles of easily excavated size are passed to the surface (Stage 4, Fig. 3). By measuring the approximate volume of sediment placed on the layer and the average vertical displacement of the layer before it is recycled to the interface, an approximate average depth of sediment placed on the interface per unit time can be calculated. From the reference frame of the sediment-water interface this is a measure of the biogenic sedimentation rate or the reworking rate in one dimension. This method is a reasonably accurate measure of sediment recycling when deposit feeders are mostly vertically oriented or when one or two deep-burrowing species of deposit feeders dominate the reworking cycle. Both these conditions are met in Discovery Bay. The method is valid only for time periods that are short relative to the mixing rate because the marker layer will disperse over long periods (Stages 5, 6; Fig. 3).

6. Results. Sediment size distributions for each station are given in Figure 4. Sorting is moderate at B5, B6, C1, and A4, poor at A5, and could not be

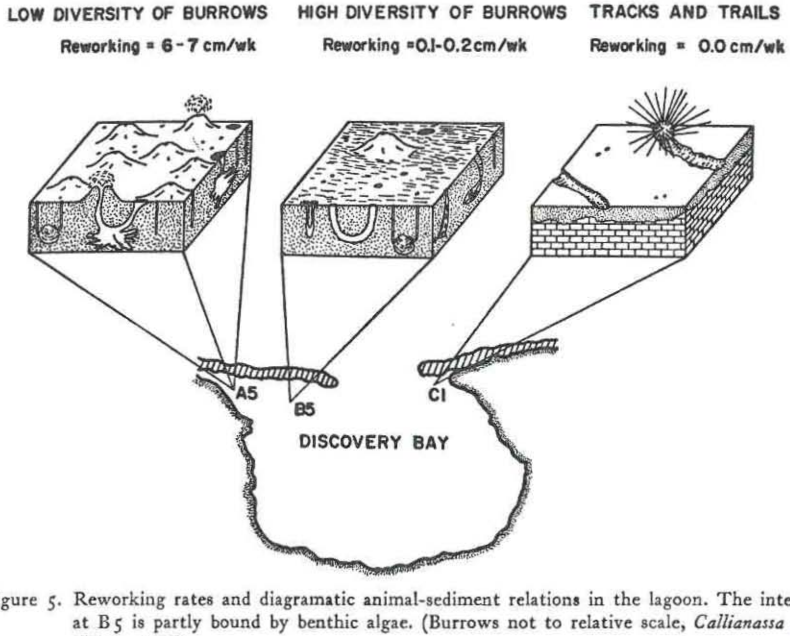

Figure 5. Reworking rates and diagramatic animal-sediment relations in the lagoon. The interface at B5 is partly bound by benthic algae. (Burrows not to relative scale, *Callianassa* after Shinn, 1968).

evaluated at B4. The weight percentage of fines increases from east to west behind the reef. Pieces of *Halimeda* are a major sedimentary component. The ≥ 1 mm fraction at station A5 is formed of large (mostly molluscan) bioclastic material contributed from *Thalassia* beds nearer shore. The increase in the bioclastic coarse fraction at B4 and C1 is derived from destruction of the reef. The contribution of reef material to the lagoon can be observed as an increase in abundance of pieces of red colored *Lithothamnion* in sediments as the reef is approached.

Bottom and surface water temperatures ranged from 27.1–27.8°C, and bottom salinities from 33.8–34.9‰. Values showed no consistent trends between stations.

The biogenic reworking experiment showed that the colored marker layer was covered by an average of 6–7 cm of sediment at station A5. The layer cropped out in valleys at the base of large *Callianassa* mounds. At B5 the layer was partially covered by mounds but was not covered at all in places. The average depth of sediment deposited on the layer, as calculated by assuming the mound sediment was spread evenly over the surface of the marker, was 0.1–0.2 cm/week. The layer at C1 was traversed by urchin trails and other tracks but not otherwise disturbed; the reworking rate at this station is taken as 0.0 cm/week (Fig. 5).

The *Callianassa* mounds are easily dispersed and resuspended by wave action.

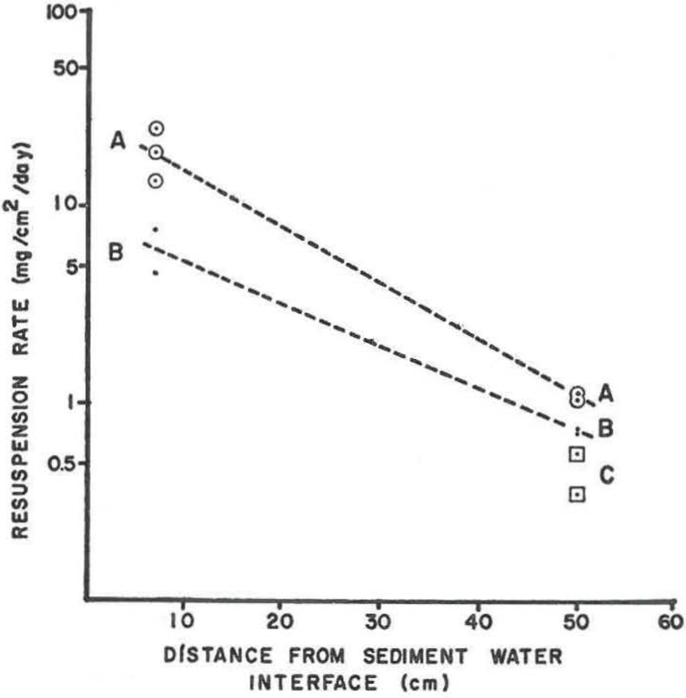

Figure 6. Resuspension rates versus distance above the bottom. Dotted line joins measurements at same station.

During one afternoon of the preliminary study period the N.E. Trade Winds were slightly stronger than usual. Mounds present in the area between A5 and B5 were leveled and rebuilt by the next day. During the period of measurement of bioturbation and resuspension no marked differences in wind-wave action were noticed. These observations suggest that the measured reworking rates are below the maximum possible.

Mean bottom resuspension rates at 7 cm are ~ 19 mg/cm^2/day at A5 and ~ 6 mg/cm^2/day at B5 (Fig. 6). Only two of the three traps at B5 7 cm were successfully recovered. Mean rates at 50 cm are 1.10, 0.73, and 0.45 mg/cm^2/day at A5, B5, and C1, respectively (Fig. 6). Because of burrowing activity, which results in changes of bottom relief, the heights above bottom are only approximate. It is possible that currents scoured sediment from the petri dishes, thereby making rates at 7 cm conservative; but the abundance of fines in the size distributions for resuspended sediment at this level suggest that scouring is probably not important. Laboratory experiments indicate that sediment inside these shallow traps is stable when horizontal currents pass over the traps up to at least 25 cm/sec.

Particle size distributions of resuspended sediment show a rapid increase in

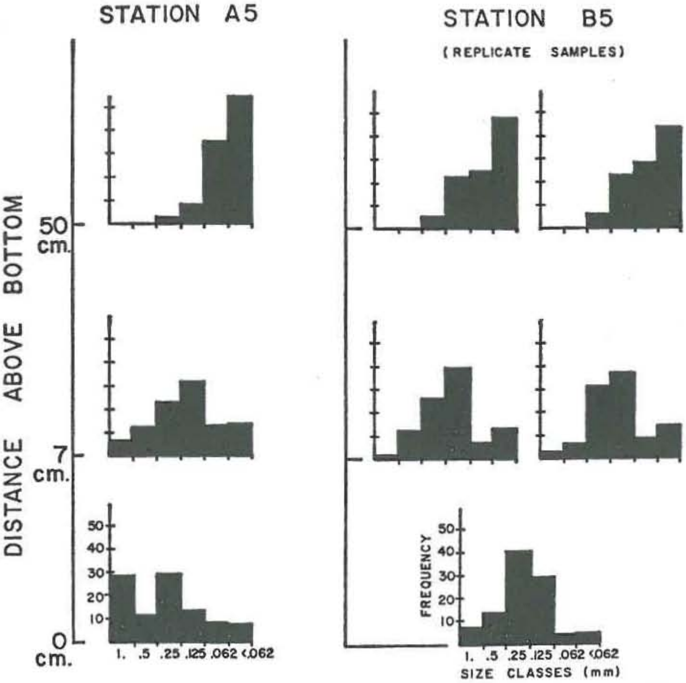

Figure 7. Particle size-frequency distributions (weight %) of bottom and resuspended sediments at A5 and B5. Replicate samples are from different traps.

fine particles with height above bottom (Fig. 7). The mean sediment size shifts regularly with height and the abundance of the different size classes reflects the relative abundances in the bottom sediment at each station (Fig. 7). Given these facts, resuspended sediments could be either locally derived or transported from another area.

There are several reasons to believe that the resuspended sediments are locally derived: (1) Wind-waves move southwest so that any transported sediment would move over two basins (Fig. 4). These basins should act as sediment traps and not sources for the shallow shelf. (2) If our trap experiments measured a net sedimentation or transport rate and not the recycling flux of the upper sediment surface, the "sedimentation rate" would be orders of magnitude higher than other carbonate environments. This can be shown by a simple calculation. Assuming an average sediment density of approximately 1 g carbonate/cm^3, the sedimentation rate at A5 and B5 would be approximately 7 cm/year and 2 cm/year, respectively. At these rates the lagoon would fill in after a short time. A typical net sedimentation rate in a shallow carbonate environment might be ~ 0.5 mm/year (Bahama Bank near Andros Island, based on Broecker and Takahashi, 1966). We conclude that the resuspended sediments are predominantly locally derived.

Table II. Faunal listings (see Table III for abbreviations).

Note: Polychaete morphotype species are not necessarily equivalent *between* stations.

Faunal List	Stations				
	B4	B5	B6	A4	A5
Annelida					
Nereidae a	1	4	3	1	1 D.F.
Nereidae b	1	–	1 D.F.	3	2
Nereidae c	8 D.F.	–	–	–	–
Glycera sp.	8 C.	2 C.	2 C.	1 C.	–
Typosyllis sp.	31 B.	1 B.	2 B.	15 B.	1 B.
Syllidae b	1 B.	1 B.	–	2 B.	–
Syllidae c	1 B.	1 B.	–	1 B.	–
Exogone sp.	22 B.	–	2 B.	–	11 B.
Syllidae e	1 B.	–	1 B.	–	–
Spionidae a	5 D.F.	2 D.F.	2 D.F.	1 D.F.	–
Prionospio sp.	2 D.F.	1 D.F.	2 D.F.	3 D.F.	1 D.F.
Spionidae c	1 D.F.	–	2 D.F.	1 D.F.	–
Spionidae ?	–	–	–	–	1
Polymastia sp.	4 D.F.	–	1 D.F.	1 D.F.	–
Terebellidae b	1 D.F.	–	3 D.F.	4 D.F.	–
Terebellidae c	–	–	2 D.F.	–	–
Lumbrineris sp.	1 D.F.	–	2 D.F.	17 D.F.	3 D.F.
Capitellidae a	–	–	1 D.F.	5 D.F.	1 D.F.
Capitellidae b	–	3 D.F.	1 D.F.	1 D.F.	4 D.F.
Capitellidae c	–	4 D.F.	1 D.F.	–	1 D.F.
Capitellidae d	–	–	3 D.F.	–	1 D.F.
Scyphoproctus sp.	–	1 D.F.	4 D.F.	–	–
Notomastus sp.	–	–	10 D.F.	–	–
Sabellidae a	–	5 S.F.	41 S.F.	10 S.F.	13 S.F.
Maldanidae a	–	–	2 D.F.	5 D.F.	6 D.F.
Opheliidae a	–	–	–	1 D.F.	–
Myriochele sp.	–	1 S.F. ?	1 S.F. ?	–	–
Cirratulidae a	1	1	2	–	–
Chrysopetalidae a	1	1	–	–	–
Scalibregmidae ?	–	–	–	–	1
Magelona sp.	–	1	–	–	–
Dorvilleidae a	–	–	–	–	1
Orbiniidae a	–	–	1 D.F.	1 D.F.	1 D.F.
Orbiniidae b	–	–	–	1 D.F.	3 D.F.
Naineris sp.	–	1	1	–	1
Arabellidae a	–	–	1	–	–

(To be continued.)

Table II (continued).

Faunal List	Stations				
	B4	B5	B6	A4	A5
Paraonidae a	–	–	–	1 D.F.	2 D.F.
Aricidea sp.	–	–	–	2 D.F.	–
Sthenolepis sp.	–	–	–	1	–
Polychaeta a	1	1 S.F.	1	–	1 D.F.
Polychaeta b	1	1 D.F.	–	–	–
Polychaeta c	1	1	–	–	–
Polychaeta d	1 D.F.	1	–	–	–
Polychaeta e	1	–	–	–	–
Oligochaeta a	1 D.F.	1 D.F.	11 D.F.	7 D.F.	2 D.F.
Oligochaeta b	44 D.F.	4 D.F.	2 D.F.	–	–
Oligochaeta c	1 D.F.	–	1 D.F.	–	–
Nemertea					
Nemertea a	5 C.	1 C.	16 C.	1 C.	2 C.
Nemertea b	1 C.	2 C.	9 C.	–	–
Nemertea c	–	4 C.	–	–	–
Sipunculida					
Sipunculida a	–	2 D.F.	1	–	–
Sipunculida b	3	–	4	–	–
Sipunculida c	–	–	3	–	–
Sipunculida d	–	–	4	–	–
Echiuroidea					
Echiuroidea a	5	–	–	–	–
Echiuroidea b	2	–	–	–	–
Arthropoda					
Decapod shrimp a	1	–	2	–	–
Decapod shrimp b	–	1	–	–	–
Callianassa sp.	–	1 D.F.	2 D.F.	2 D.F.	3 D.F.
Brachyura a	–	1 S.	–	–	–
Isopoda a	–	6 D.F.	3 D.F.	–	–
Isopoda b	–	–	2	–	–
Amphipod a	4	1	–	–	1
Amphipod b	–	8	1	–	–
Amphipod c	1 D.F.	2 D.F.	1 D.F.	–	–
Amphipod d	5 D.F.	1 D.F.	–	–	–
Amphipod e	5 D.F.	–	–	–	–
Amphipod f	3 D.F.	–	–	–	–
Amphipod g	4 D.F.	–	–	–	–
Amphipod h	1	–	–	–	–
Amphipod i	1 D.F.	–	–	–	–
Amphipod j	–	1 D.F.	–	–	1 D.F.
Amphipod k	–	–	1	–	–

Table II (continued).

Faunal List	Stations				
	B4	B5	B6	A4	A5
Anomura a	–	–	1 S.	–	–
Calanus tibicen	1 S.	–	–	–	–
Porifera					
Porifera a	1 S.F.	–	–	–	–
Cnidaria					
Anemone a	5 C.	–	–	–	–
Anemone b	–	–	1 C.	–	–
Anemone c	–	–	1 C.	–	–
Gastropoda					
Persicula sp.	1	–	–	–	–
Olivella sp.	1 C.	2 C.	–	–	–
Scaphopoda					
Dentalium sp.	–	1 D.F.	–	–	–
Bivalvia					
Tellina sp.	–	2 D.F.	–	–	–
Tagelus sp.	–	–	–	–	1 D.F.
Macoma sp.	–	–	1 D.F.	–	–
Codakia sp.	–	–	1 S.F.	–	–
Codakia cf. *pectinella*	–	–	1 S.F.	–	–
Codakia orbicularis	–	–	–	–	1 S.F.
Diplodonta cf. *nucleifm.*	–	1 S.F.	–	–	1 S.F.
Divaricella sp.	–	–	–	7 S.F.	–
Echinodermata					
Ophiuroidea	1	–	–	–	–
Cephalochordata					
Branchiostoma sp.	1 S.F.	–	–	–	1 S.F.
Hemichordata					
Hemichordata a	–	–	1	–	–
Ptychodera sp.	7 D.F.	–	–	–	–
TOTAL					
INDIVIDUALS:	200	76	164	96	69
SPECIES:	47	39	50	26	29

The animals found at each station are listed in Table II. Most animals were extremely small with representative lengths of ~ 0.2–2.0 cm. Only one individual of *Callianassa* sp. was captured (Station A4); all other *Callianassa* listed in the table correspond to the number of *Callianassa* burrows at each station. It is only recently that the deep (up to 1 m) and highly characteristic burrows

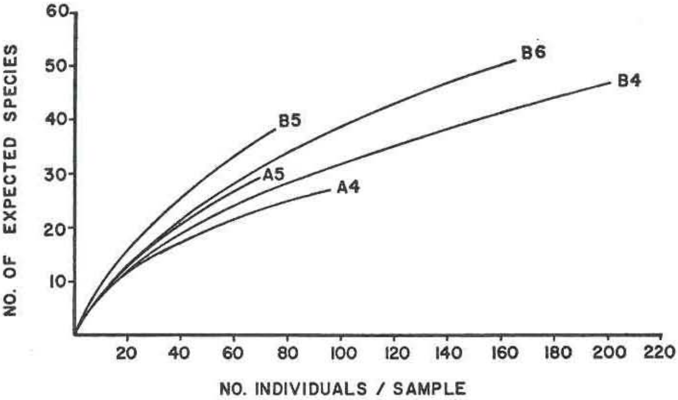

Figure 8. Diversity at each station plotted as Hurlbert's rarefaction curves. B4 has a sizeable gravel fraction, all other stations are from medium sand.

formed by this animal could be attributed to members of the genus *Callianassa* (Shinn, 1968). The distinctive mound (Fig. 5, Fig. 13) and fecal pellet morphology, (Shinn, 1968) allowed identification in Discovery Bay where specimens were not collected.

The Brillouin diversity indexes for each station are: B4 = 3.90, B5 = 4.13, B6 = 4.06, A4 = 3.48, and A5 = 3.55. Fig. 8 gives the results of the diversity plots using Hurlbert's rarefaction. The trends are: Diversity decreases from east to west behind the reef and also decreases towards the reef at B4 (rubble zone). Diversity calculations include only those animals found in the top 25 cm and *Callianassa*; other deep-burrowing animals are ignored. The rarefaction curves for the more diverse, somewhat deeper water stations at B5 and B6 are comparable to those found by Wade (1972) in Kingston Harbor, Jamaica. On the other hand, population densities (no. individuals/m^2) in this study are 5–10 times that reported by Wade (1972).

The per cent abundance of each trophic type has been listed for each station (Table III). In order to clarify trophic dominance, species were first ranked by abundance and the 8–13 top-ranked species separated. The ratio of the number of deposit feeding species within this highly ranked group to the total number of top-ranked species is given in Table III. The ratios of the number of suspension-feeding species and those of uncertain trophic type to the total number of top-ranked species are also given. Deposit feeders are numerically dominant.

Annual growth values for *Montastrea annularis* are presented in Table IV. Weighted means have been used to favor individuals that show more even growth. Both the average and maximum coral growth rates for each station were plotted against resuspension rates at 50 cm (Fig. 9). There is an inverse relationship between resuspension values and coral growth. Associated with

Table III. Distribution of trophic types * at sampled stations.

Station #	% Unknown	% D.F.	% S.F.	% C.	% B.	% S.
A4.......	5.2	56.3	17.7	2.1	18.8	0.0
A5.......	10.1	46.4	23.2	2.9	17.4	0.0
B4........	13.0	47.5	1.0	10.0	28.0	0.5
B5........	27.6	42.1	10.5	14.5	3.9	1.3
B6........	16.5	35.4	26.8	17.7	3.0	0.6

	# D.F. species / # Top Ranked	# S.F. species / # Top Ranked	# Unknown / # Top Ranked
A4.......	8/13	2/13	1/13
A5.......	7/11	1/11	1/11
B4........	6/12	0/12	1/12
B5........	4/8	1/8	2/8
B6........	6/13	1/13	4/13

* D.F. = Deposit Feeder
S.F. = Suspension Feeder
B. = Browser on grains
C. = Carnivore
S. = Scavenger

Table III: The ratios at the bottom of the table were made by first ranking all species at a station by abundance and then separating the 8–13 top-ranked species. The ratio of the number of deposit-feeding species within this highly ranked group to the total number of top-ranked species was taken. The ratios of the number of species of suspension-feeding or uncertain trophic types within the group to the total number of species are also given.

decreasing growth is decreasing standard deviation of the growth rate indicating that not only does high resuspension decrease coral growth but that it might also suppress growth variability.

In order to determine whether an increase in wave stress might be responsible for the decrease in coral growth, two specimens of *M. annularis* from the buttress zone of adjacent Runaway Bay, Jamaica were analyzed. Loose, easily resuspended sediment is not present in this buttress zone due to the sill reef and lagoon acting as sediment traps. *M. annularis* was collected from 7 m and 12 m and their maximum, 0.85 and 0.80 cm/year, and average, 0.84 and 0.78 cm/year, growth fall within the error limits of stations B and C.

7. Discussion.

The results show that decreasing bottom stability, represented by increasing biogenic reworking and resuspension rates, parallels decreases in infaunal diversity and coral growth. Infaunal trophic distributions may also change. Deposit feeders predominate at most stations and make up a higher percentage of the most abundant species in the western lagoonal area. No corresponding correlations with temperature or salinity were found.

a. Factors Influencing Bottom Stability. Unstable sediments can be roughly defined as those sediments which are highly mobile and have low cohesion or shear strength. Resuspension rate is a measure of the mobilization and rede-

Table IV. Coral growth measurements.

Corals and Stations	Number of Transects	Average number of Bands/transect	Growth Rate (Band width in cm/yr) Weighted mean ± weighted σ
Coral			
A1	2	16	0.50 ± 0.059
A1	2	21	0.60 ± 0.082
A3	2	6	0.72 ± 0.055
Station			
A maximum	–	–	0.65 ± 0.050
A average	–	–	0.62 ± 0.036
Coral			
B2	3	6	0.82 ± 0.055
B4	3	6	0.83 ± 0.077
Station			
B maximum	–	–	0.90 ± 0.063
B average	–	–	0.82 ± 0.047
Coral			
C2	3	4	1.06 ± 0.085
C3	2	12	0.58 ± 0.108
C7	3	10	0.88 ± 0.075
Station			
C maximum	–	–	1.00 ± 0.082
C average	–	–	0.88 ± 0.050

position of surface sediment by current action and therefore one index of the stability of a deposit. Sediments having high water content and low cohesion are more readily entrained and resuspended by currents than those of low water content (Postma, 1967). Biogenic reworking increases the water content of sediments (Young, 1971). This increase and the associated production of biogenic microtopography resulting in a hydrodynamically-rough surface facilitate resuspension of bottom sediments by currents (Rhoads, 1970; Young, 1971). Resuspension rates therefore reflect both mass properties of the bottom, as controlled by organisms, and water motion. As shown in the results section, resuspended sediments in the western lagoon are predominantly locally derived. This means that even if currents significantly increase to the west (unlikely from qualitative observations) localized bottom properties are very important in determining bottom mobility in the lagoon.

In Discovery Bay, the deposit-feeding crustacean *Callianassa* is mainly responsible for the high reworking rates in the western lagoon and for the building of mound structures easily dispersed by wave action. Bathurst (1971, p. 128) has observed that *Callianassa* mounds often act as sources of mobile sediments in otherwise stable bottom areas. When the activities of this animal and other

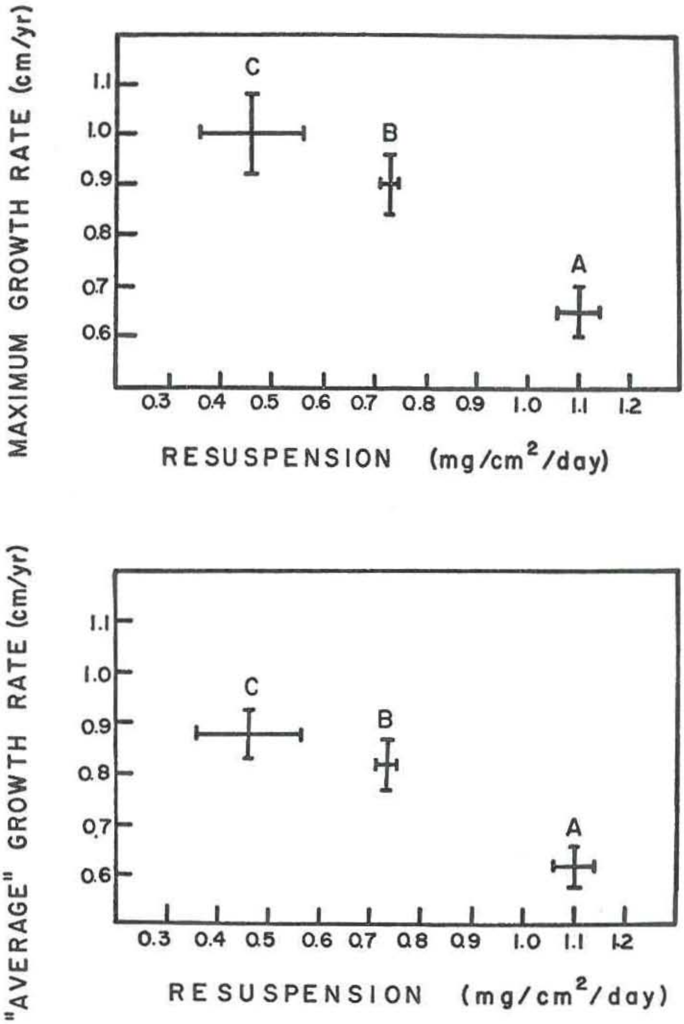

Figure 9. Maximum and average upward coral growth (error bars = 2σ) versus ranges of resuspension values at 50 cm above bottom for each station.

deposit feeders are coupled with wind-produced wave motion, an increase in bottom resuspension results.

Although the activities of deposit feeders promote instability, other organisms in the lagoon promote stability. Both corals and benthic algae tend to stabilize sediments, the former by dispersing wave energy and the latter by binding particles (Ginsberg and Lowenstom, 1958; Scoffin, 1970; Neumann *et al.*, 1970). In the strictest sense, bottom stability in Discovery Bay is controlled by the relative dominance of the four functional types: deposit feeders (destabilizers), algae and other plants (binders), herbivores (destabilizers), and corals (current dissipators). For example, when algal mats are present sediment mobility is damped. But, because burrowing organisms may punch holes in the mat and lower its "peeling threshold", mats can be easily destroyed (Scoffin, 1970; Neumann *et al.*, 1970). Herbivores may graze back sediment-binding plants exposing bare sediment (Ogden, Brown, and Salesky, 1973). In the lee of coral patches, even with deposit feeders and exposed sediment present, the bottom should be more stable than in open areas. An example of change in this association of functional types is recorded in bottom photographs (Figs. 10, 11, and 12). These photos were taken while moving successively farther westward from a coral-covered, karst jetty in the western lagoon. Algal-bound sediment with mixed trophic groupings (suspension and deposit feeders, Fig. 10) grade into increasingly less stable areas (Fig. 11) with an occasional large suspension feeder (sabellid). Finally an unstable area is reached (Fig. 12) where the fauna is dominated by the ghost-shrimp *Callianassa*.

b. *The Effect of Bottom Stability on Growth and Distribution of Fauna*. The effect of bottom stability in determining the distribution of benthos is well established in both tropical (e.g., Newell *et al.*, 1959; Purdy, 1964; Jackson, 1972) and temperate regions (e.g., Sanders, 1958; Rhoads and Young, 1970; Johnson, 1970; Levinton and Bambach, 1970). Shifting, unstable bottoms of high water content cause high larval mortality for settled suspension-feeding larvae (Levinton and Bambach, 1970), and probably coral planulae. High fluxes of resuspended sediment may clog filtering mechanisms of suspension feeders and prevent efficient feeding (Loosanoff, 1962). When given a stable substratum above the bottom some suspension feeders may actually show higher growth in turbid environments than in their normal habitat (Rhoads, 1973); but animals living on or within unstable bottoms are often stunted (Hallam, 1965). An unstable bottom may maintain community development in an immature state and reduce diversity (Margelef, 1968) and may require constant recolonization by organisms as a result of high mortality. Our results agree with Margelef's theory: Infaunal diversity (upper 25 cm) in the lagoon decreases as bottom stability, represented by resuspension and biogenic reworking, decreases.

Possibly as a result of the inability of coral planulae to establish themselves, the extent of "living coral cover" may be reduced in turbid environments (see data of Roy and Smith, 1971). Special adaptations are required to withstand sediment influx onto the adult coral polyps and many corals, including *Montastrea annularis*, have the ability to clean themselves (Yonge, 1935; Marshall and Orr, 1931; Goreau and Goreau, 1960; Goreau and Yonge, 1960; Hubbard and Pocock, 1972). Hermatypic corals depend on light for skeletal growth (Goreau, 1961). Constant energy expenditure by corals for removal of sediment particles as well as reduction of light by suspended particles might be

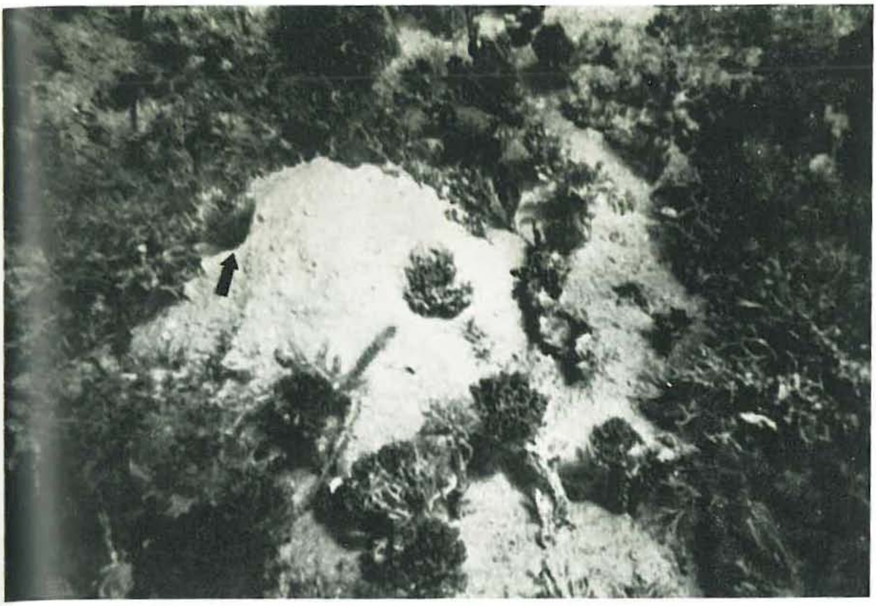

Figure 10. Well-bound sediment in lee of coral patch (location∼150 m SE of A 5). Arrow indicates suspension-feeding sabellid on the side of deposit feeder mound (sabellid∼4 cm across).

Figure 11. Decrease in sediment binding related to increasing distance away from a coral patch (location∼140 m SE of A 5). Occasional suspension-feeding sabellid (lower center) present. Mound building increases, (sabellid∼5 cm across).

Figure 12. Exposed lagoon floor (station A 5). Deposit feeders (*Callianassa*) dominate. Sediment is unbound and mobile (center mound ~ 14 cm high).

expected to decrease growth rate. The inverse relation between the growth rate of *M. annularis* and resuspension of bottom sediments (Fig. 9) supports this hypothesis. The growth rates of *M. annularis* taken from the buttress zone of adjacent Runaway Bay are comparable to low resuspension areas B and C of Discovery Bay. The buttress zone exhibits high wave stress but low turbidity. We conclude from these data that resuspension of sediments, not increase of current activity, is causing reduction in growth.

For comparative purposes it should be noted that the resuspension rates for western parts of Discovery Bay are similar to those found in certain temperate embayments where bottom stability is thought to be important for faunal distribution. For example, over a muddy bottom (~ 20 m depth) in Buzzards Bay and Cape Cod Bay, Massachusetts, values of ~ 21–35 mg/cm^2/day and ~ 80–100 mg/cm^2/day, respectively, have been found (Young, 1971; Rhoads, 1970; Young and Rhoads, 1971). In comparison, values of ~ 3.5 mg/cm^2/day above a sandy bottom (~ 10 m depth) were measured in Cape Cod Bay (Young and Rhoads, 1971). These resuspension rates are from open regions of deeper water, smaller median grain size, and higher tidal current velocities than in Discovery Bay. The next section shows that sediment instability as measured by resuspension rates has a comparable effect on the distribution of trophic types and rate of skeletal growth in these two environments.

c. *Community Amensalism.* The exclusion or inhibition of one trophic group as a result of the activities of another is termed trophic group amensalism (Rhoads and Young, 1970). Suspension-feeding groups experience increased larval mortality and lowered growth in the presence of deposit feeders. The latter group ingests larvae directly or promotes bottom instability by its feeding activities. In Discovery Bay many species of suspension-feeding eulamellibranch bivalves are found in *Thalassia* beds (Jackson, 1972) and as borers in corals (Carter, 1974). At the stations examined in this study, all epifaunal and infaunal bivalves, except eurytopic lucinids and deposit-feeding tellinids, were absent. In addition to the lucinid bivalves small tubiculous sabellids were the only other major suspension feeders present. These polychaetes and bivalves are able to live in the presence of deposit feeders (Rhoads and Young, 1971). Figs. 10, 11, and 12 show that large, fragile sabellids can also live in close association with deposit feeders but only in the presence of binding algae or protective corals.

We conclude that the absence of many suspension-feeding types from large areas of the lagoon floor is a result of bottom instability. It was shown that resuspended sediments in the lagoon are locally derived and that resuspension rates correlate with biogenic reworking rates and the construction by deposit feeders of easily dispersed mounds. The feeding activities of deposit feeders therefore aid in producing bottom instability. The trophic group amensalism principle apparently holds in the areas of the lagoon which were studied; but, because of the additional biological factors which influence bottom stability in a tropical lagoon, the amensalistic interactions are more complex than in subtidal temperate regions.

If the correlation between coral growth and resuspension rate is causative then by promoting resuspension of sediments the activities of deposit feeders also affect more than suspension feeders. The decrease in coral growth with increase in resuspension appears to represent an indirect coupling of the soft-bottom benthos with the hard-substrate benthos. This feedback of the soft-bottom dwellers on the corals represents a possible extension of the trophic group amensalism principle of the temperate environments to one of community amensalism in tropical lagoons. By indirectly inhibiting coral growth and larval settlement, deposit feeders, once established, may aid in creating, maintaining, or enlarging the lagoonal environment.

8. SUMMARY. (1) Six stations were studied in carbonate sands behind the reef (lagoon) in Discovery Bay, Jamaica.

(2) Mean resuspension rates increase from east to west in the lagoon and are comparable in magnitude (19 mg/cm^2/day) to larger and deeper temperate embayments having smaller median grain size and stronger tidal currents.

(3) Biogenic reworking rates increase from east to west and reach 6–7 cm/week in the western part of the lagoon. The deposit-feeding shrimp *Callianassa*

is largely responsible for these high values and its mound building facilitates bottom resuspension. Other taxa, algae and corals, stabilize the bottom.

(4) Infaunal diversity was measured at 5 stations and decreases in the western end of the lagoon. Diversity varies directly with bottom stability. High stability was defined by low resuspension and biogenic reworking rates.

(5) Deposit feeders numerically dominate in the western lagoon. All epifaunal and infaunal bivalves, except eurytopic lucinids and deposit-feeding tellinids, were absent.

(6) The growth of the coral *Montastrea annularis* parallels changes in bottom stability; growth decreases in areas of high resuspension.

(7) Because coral growth inhibition and the general paucity of suspension feeders can be correlated to the activities of deposit feeders, our results represent an extension of the trophic group amensalism principle.

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