The influence of deposit-feeding organisms on sediment stability and community trophic structure
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The Influence of Deposit-feeding Organisms on Sediment Stability and Community Trophic Structure[1]

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ABSTRACT

Deposit-feeding and suspension-feeding benthos in Buzzards Bay, Massachusetts, show marked spatial separation; suspension feeders are largely confined to sandy or firm mud bottoms while deposit feeders attain high densities on soft muddy substrata. Food source and bottom stability have been investigated as potential factors effecting this trophic-group separation.

Between October 4, 1967 and August 22, 1969, observations were made at 11 stations in Buzzards Bay, Massachusetts, along two widely separated transects over bottoms ranging in texture from silt to fine and medium sand. Water depths at these stations ranged from 3 m to 20 m. SCUBA divers made many of the field observations and collected most of the samples. This study included sampling of benthic macrofauna, taking bottom photographs, analyzing sedimentary structures, texture, organic content and water content of the sediments, and measuring both water currents and suspended sediment above the bottom. Laboratory experiments were also carried out to determine differential resuspension between burrowed and unburrowed muds.

Intensive reworking of the upper few centimeters of a mud bottom by deposit feeders produces a fluid fecal-rich surface that is easily resuspended by low-velocity tidal currents. We suggest that the physical instability of this fecal surface tends to: (i) clog the filtering structures of suspension-feeding organisms, (ii) bury newly settled larvae or discourage the settling of suspension-feeding larvae, and (iii) prevent sessile epifauna from attaching to an

unstable mud bottom. Thus suspension feeders are unable to successfully populate all areas of the bottom where a suspended food source is available, especially in areas where mud bottoms are intensively reworked by deposit feeders. Modification of the benthic environment by deposit feeders, resulting in the exclusion of many suspension feeders and sessile epifauna, is an example of trophic group amensalism. This biotic relationship appears to be important in shaping trophic-group distributions in embayments and basins on continental shelves.

Introduction. Heterotrophic benthic marine organisms are predominantly either suspension feeders or deposit feeders, with the exception of a few species that are facultative feeders. Most of these species feed primarily on either a suspended or deposited food supply. Divisions of these types may be based on (i) the degree of food selectivity among deposit feeders and (ii) the level of feeding above the bottom by suspension feeders (Turpaeva 1959). Organisms that feed exclusively on deposited food would, *a priori*, be expected to reach maximum diversity and biomass on fine-grained organic muds containing an abundant food supply. A population that feeds on suspended material may, however, be less influenced in its distribution by the type of substratum than by the quantity and quality of the suspended material in the water column. It has been shown that benthic suspension feeders and deposit feeders exhibit distributions where zones of high diversity and abundance of deposit feeders are commonly accompanied by low diversity and biomass of infaunal and epifaunal suspension feeders. This trophic group[2] relationship has been reported for Buzzards Bay by Sanders (1960). Trophic group segregation has been reported in benthic studies representing a broad latitudinal range [i.e., Adriatic Sea (Gamulin-Brida 1967), Mediterranean Sea (Pérès and Picard 1964), Okhotsk Sea (Savilov 1959), Gulf of Mexico (Parker 1956), and Gulf of California (Parker 1963)].

Turpaeva (1959) has indicated that the trophic composition of benthic communities closely reflects the availability of the food supply; this correlation suggests that low diversity and biomass of suspension feeders on silt-clay facies result from a limiting food supply in the water above such bottoms. Sanders (1958) and Driscoll (1967) have suggested that a limiting supply of suspended food may be a controlling factor in the distribution of suspension feeders in Buzzard's Bay. However, Young (1968b) has shown, for Buzzards Bay, an abundance of particulate organic-rich material in the water over bottoms that are low in numbers and biomass of suspension feeders. In addition, the ecotone between bottoms dominated by suspension feeders and bottoms dominated by deposit feeders is frequently abrupt, without correspondingly sharp gradients in the suspended food supply. It is well known that solid objects (anchors, bottles, etc.) projecting above a soft mud bottom soon become fouled with barnacles, hydroids, and epifaunal molluscs, indicating that a suspended food

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2. The term trophic group refers to the general mode of feeding, i.e., deposit-feeding or suspension-feeding. This term does not imply a particular position within the food chain.

supply is present to support settlement and growth. Thus we seem to be confronted with a paradox.

It seems likely that there are operative factors that discourage suspension feeders and attached epifauna from populating certain types of mud bottoms, even though a potential food supply is present in the water. The intensive feeding activities of deposit feeders in muds may provide an explanation for this paradox. It is well known that deposit feeders produce significant changes in the benthic environment, the most important changes being production of a fecal surface and a decrease in compaction of the reworked sediment surface (Moore 1931, Brinkmann 1932, Schwartz 1932, Schäfer 1952, Rhoads 1963, 1967, McMaster 1967, Young 1968b).

This study has been undertaken to investigate the ecologic importance of biogenic reworking of bottom sediments in limiting the distribution of suspension-feeding organisms. Emphasis has been placed on detailed features of the environment immediately above and below the sediment-water interface because it is the quality of the bottom surface that attracts or discourages settling larvae; the physical stability of this surface may also be important for the survival of early juvenile stages of sedentary or sessile suspension-feeding species.

Study Area. Buzzards Bay, Massachusetts, is approximately 35 km long and 13 km wide. The average depth in the axis of the Bay is 13 m to 16 m. The salinity throughout a year ranges from 29.5 % to 32.0 %. Bottom-water temperatures range from 22°C in summer to 0°C in winter. The summer thermocline disappears in October and reappears in April (Anraku 1962).

Sediment distribution studies by Hough (1940) and Moore (1963) have defined the major lithofacies of the Bay (Fig. 1). The central part of the Bay, a silt-clay facies, is surrounded by sand and gravel bottoms.

The greatest biomass of suspension feeders in Buzzards Bay occurs where the bottom sediment is sandy and largely free of silt and clay; these same bottom types also support a high biomass of epifauna (Sanders 1958, 1960). Sanders named this biofacies the *Ampelisca* community for the dominance of suspension-feeding amphipods. The silt-clay facies in the axis of Buzzards Bay is, in contrast, dominated by deposit feeders; this community has been defined as the *Nucula proxima-Nephtys incisa* assemblage (Sanders 1958). These two major biofacies are present in both Buzzards Bay and Long Island Sound. The distribution of trophic types at our sampling stations is summarized in Fig. 2.

Sampling. Fig. 1 shows the locations of our sampling transects. The Quissett Harbor transect (Sts. 1–8) was first used in this study. The Pasque Island transect (Sts. P, Q, R) was established earlier by Sanders (1958, 1960). These stations were sampled to relate the distribution of organisms to food avail-
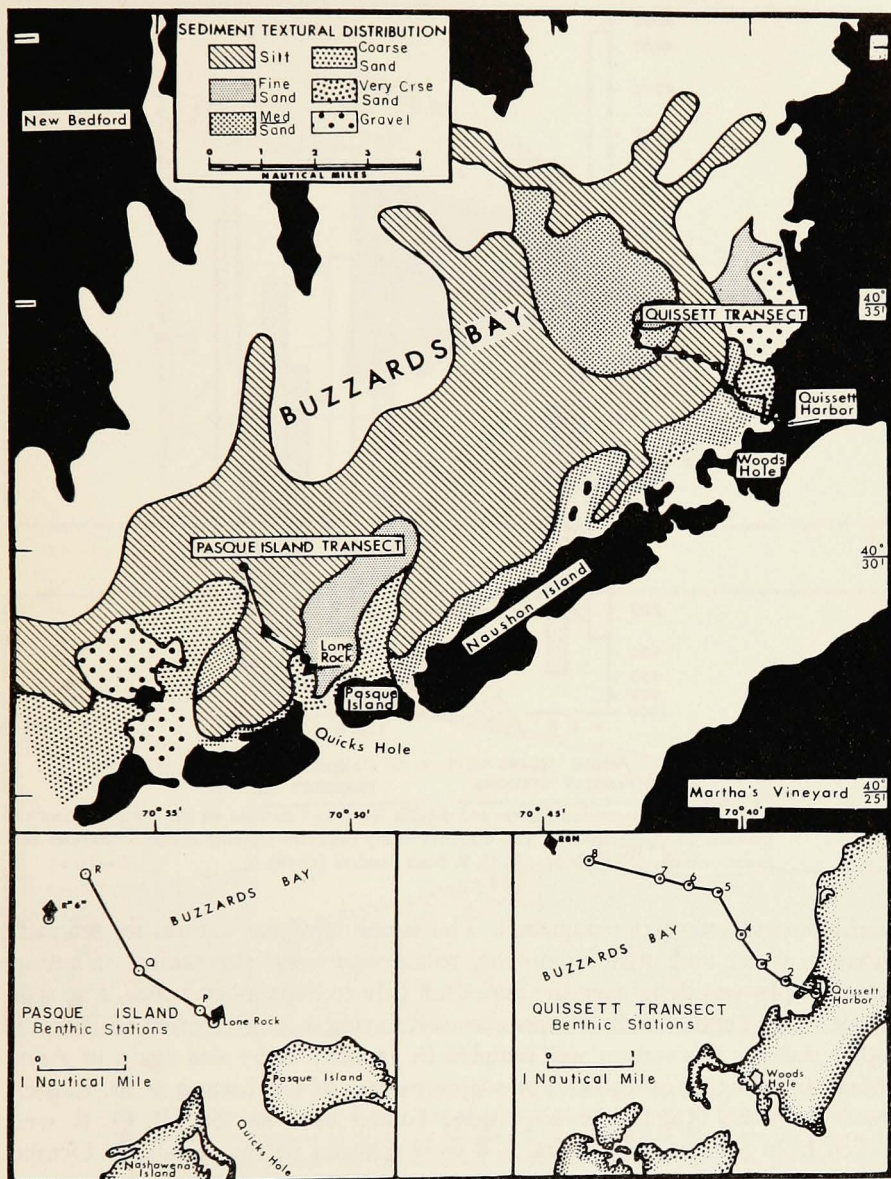
Figure 1. Location of the two sampling transects in Buzzards Bay, Massachusetts. The Pasque Island transect stations were established by Sanders (1958). The Quissett Harbor transect, with eight additional stations, was added for this study. The sediment-distribution data are from Moore (1963).
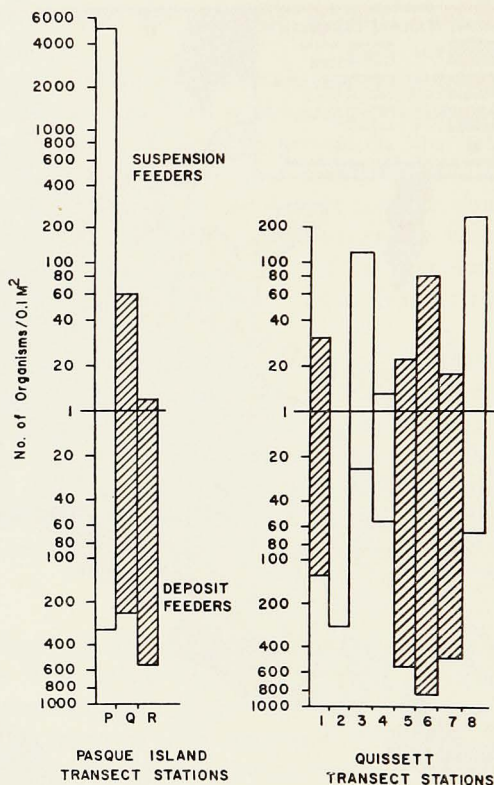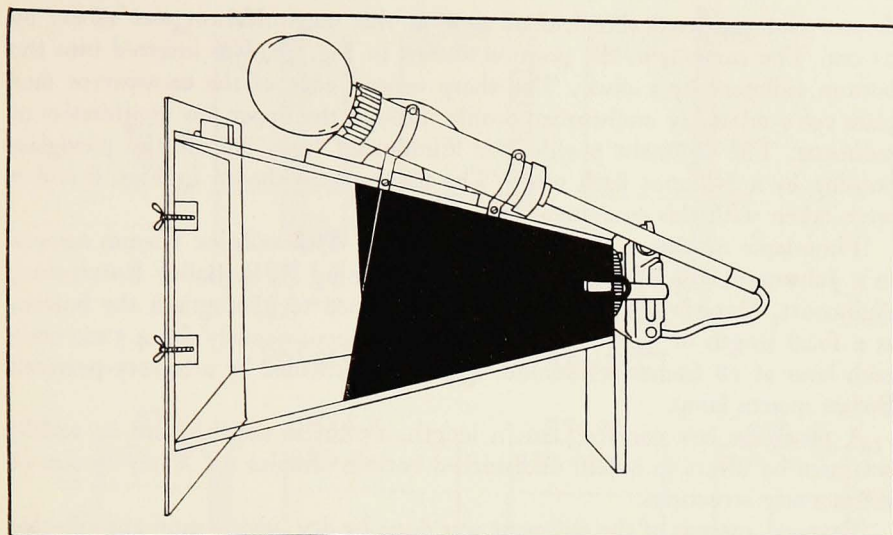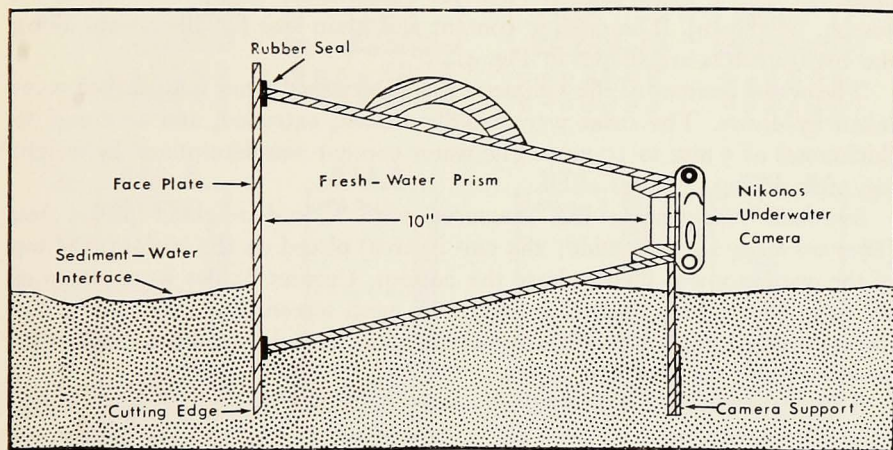
Figure 2. Abundance of suspension feeders and deposit feeders at stations on the Pasque Island and Quissett Harbor transects. The diagonal ruling indicates stations having a granular burrowed surface. Data for Sts. P, Q, R from Sanders (1958).

ability and sedimentary parameters. The sampling of the stations for sediment texture, water and organic content, resuspension and the taking of bottom photographs was done over the period of July to September 1968. The sediment water content at St. R was observed during a longer period than at any other station; this station was sampled in January 1967 and again in April, May, and August of 1968. Time-lapse movies of the bottom at St. R. were made between August 20–22, 1969. Faunal data for Sts. P. Q, R were taken from Sanders (1958). Sts. 1–8 were sampled by the authors in October 1968.

Methods and Apparatus. A study of the undisturbed structure of the sediment-water interface requires techniques of observation and collection that are not possible by shipboard sampling. Therefore Scuba divers were used for most of the sampling and field observations.

Figure 3. Sediment-water interface camera. (A) Lateral view showing the plexiglas pyramid attached to a Nikonos underwater camera, the apical part of the fresh-water prism, painted black to decrease backscatter of light, and Nikonos flash unit used to illuminate the sediment-water interface profile. (B) Cross-section showing the camera placed in position (by a diver) to photograph the sediment surface in profile.

In situ photographs of the sediment-water interface were taken in profile with a specially designed camera (Fig. 3). A Nikonos underwater camera was fitted onto the apex of a truncated plexiglass pyramid filled with clear water. A focal length of 25.4 cm was obtained by fitting the camera with a 6 X

diopter close-up lens; the field of view at this magnification was 18 cm by 21 cm. The camera, in the position shown in Fig. 3b, was inserted into the bottom sediment by a diver. The sharp ventral edge of the transparent face plate cut a relatively undisturbed profile through the upper few centimeters of sediment. The sediment profile was illuminated from outside the plexiglass housing by a Nikonos flash unit. (The photographs shown in Figs. 6 and 7 were taken with this equipment.)

Time-lapse movies of the bottom were made with a Bolex 16-mm camera in a Jubamarine 16 Mark IV underwater housing (J. R. Bailey Enterprises, Agincourt, Ontario). The camera was positioned to photograph the bottom at a focal length of 34.5 cm. The camera ran continuously for 4.5 sec once each hour at 18 frames per second. Light was provided by a battery-powered BoSun quartz lamp.

A plexiglass box core (43 cm in length, 15 cm in depth, 5 cm in width) was used by divers to obtain undisturbed bottom samples for X-ray studies of sedimentary structures.

Textural analysis of the sediment was done by dry sieving sand and silt-clay fractions through an Udden-Wentworth sieve series. The organic content was measured with a Leco Carbon Analyzer (Laboratory Equipment Corp., St. Joseph, Michigan). The organic content and grain size for all stations along the two transects are shown in Fig. 4.

The water content of the sediment was determined from undisturbed cores taken by divers. The cores were rapidly frozen, extruded, and sectioned to thicknesses of 5 mm to 10 mm. The water content was determined by weight loss after drying.

Sediment resuspension was measured with a lead-weighted plastic box (19.9 cm long, 14.3 cm wide; 285 cm^2 in area) placed on the bottom; the top of the open box was 10 cm above the bottom. Current baffles were placed in the opening to retain trapped sediment. A mesh screen (mesh 12 mm in diameter) covered the box to exclude mobile epifauna and fish. These traps were positioned and recovered by divers.

The current direction and velocity were measured with a Geodyne A-100 Film-recording Current Meter for 5 days at St. 7 (Fig. 1). The meter was moored in 16 m of water, with the rotors and vane approximately 60 cm above the bottom.

Faunal samples, obtained with a 0.1-m^2 Smith-McIntyre grab, were washed on 1.0 mm and 0.5 mm mesh, as were those used in Sanders' (1958) benthic survey in Buzzards Bay.

Experiments. The following experiments and observations were made to determine the influence of deposit feeders on bottom-sediment stability and the effect of turbidity on growth of suspension-feeding bivalves living on an unstable mud bottom.
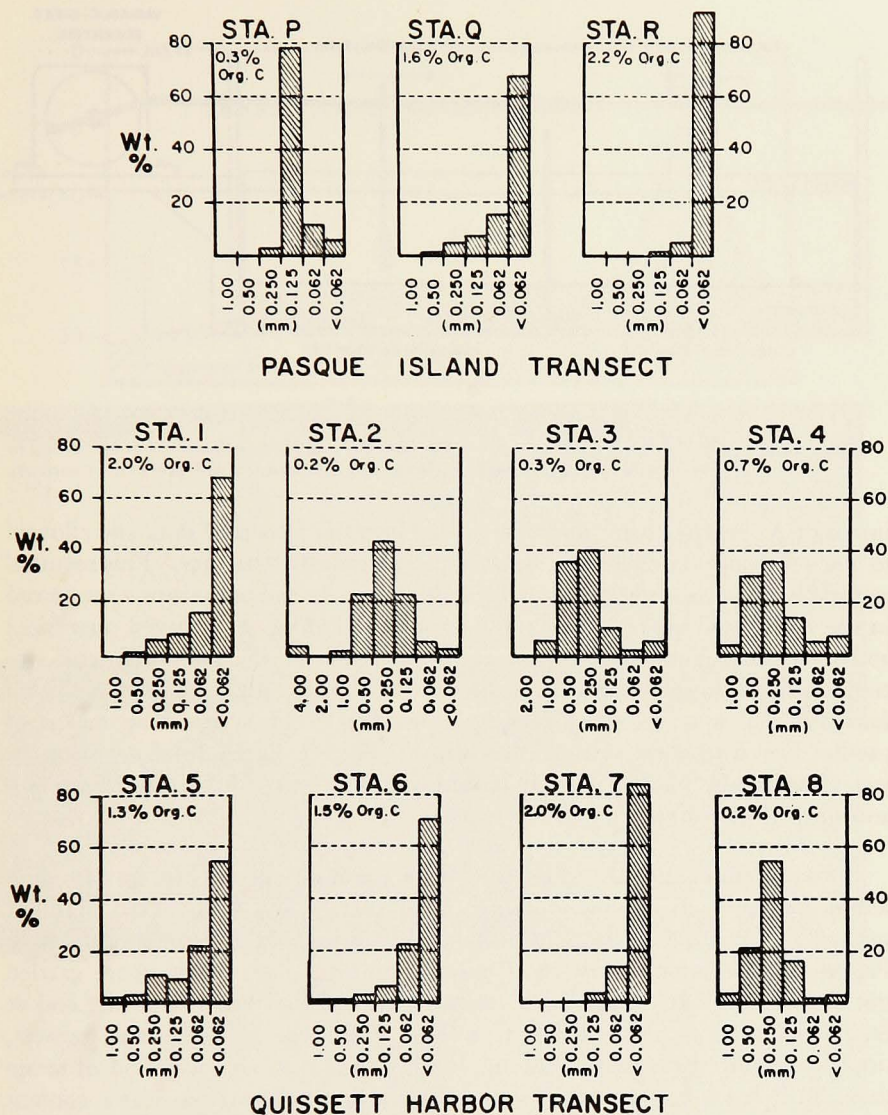
Figure 4. Size-frequency distribution and organic-carbon content of sediment from the Pasque Island and Quissett Harbor transects.

DIFFERENTIAL EROSION. The effects that deposit-feeding organisms have on the physical stability of muds was determined with this experiment. A mud sample from St. R was sieved, and all macrofaunal invertebrates were removed. Equal volumes of this sample were introduced to a depth of 6 cm into right-hand and left-hand tanks of the erosion apparatus (Fig. 5). Several hundred spec-
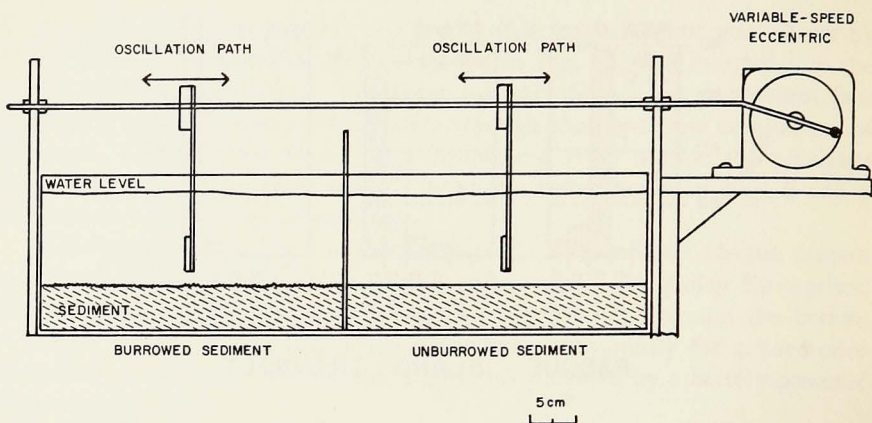
Figure 5. Differential erosion apparatus used in the laboratory to observe the effect of burrowing by *N. proxima* on the physical stability of the sediment surface in the presence of currents.

imens of *N. proxima* were then introduced into the left-hand tank and allowed to work the upper surface until it developed a granular structure.[3] This required approximately 10 days at 21°C to 23°C. No macrofaunal organisms were placed in the right-hand tank, so that the near-surface sediment remained unworked and featureless. When burrowing of the sediment in the left-hand tank was completed, the water above the sediment surface in both tanks was oscillated for 30 minutes at velocities ranging from 1.3 to 13.0 cm/sec by means of paddles linked to a variable-speed eccentric (Fig. 5). Differential resuspension was measured by photometrically monitoring water turbidity over the worked and unworked sediments.

OBSERVATIONS ON RESUSPENSION. The effect of currents in resuspending sediments above an unworked nongranular surface and a reworked granular surface was measured at stations on both the Quissett Harbor transect and the Pasque Island transect. On the Quissett transect, observations were carried out for five days at St. 6, which has a well-developed granular zone, and at St. 4, which has an unworked surface (Fig. 7). On the Pasque Island transect, similar measurements were made at all three stations over a period of seven days. St. P has a bottom of fine sand with a low near-surface water content whereas Sts. Q and R have a granular structure (Fig. 6).

TRANSPLANTING *Mercenaria mercenaria*. The relationship between sediment-water interface stability and the growth of suspension feeders was determined by transplanting juvenile *Mercenaria mercenaria* from laboratory holding

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3. The term granular structure is used here to describe the presence of biogenically produced sand-size pellets as well as sand-size mud clasts at the surface of a reworked sediment. As the term 'granular' has been used to describe a variety of petrographic and textural features of sediments and crystalline rocks, it is necessary to define this word as used in the present context.
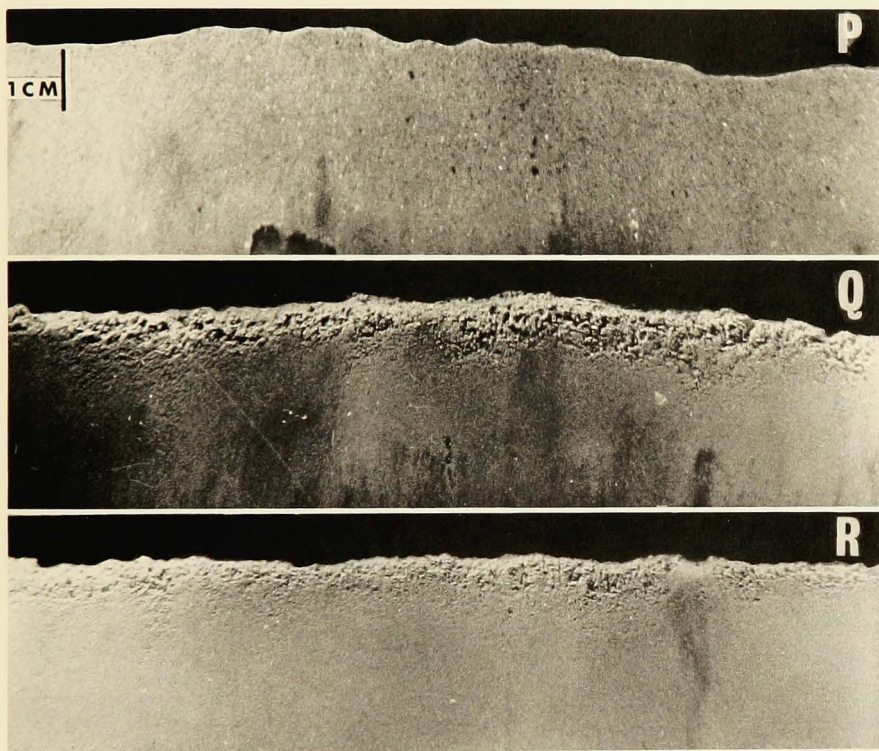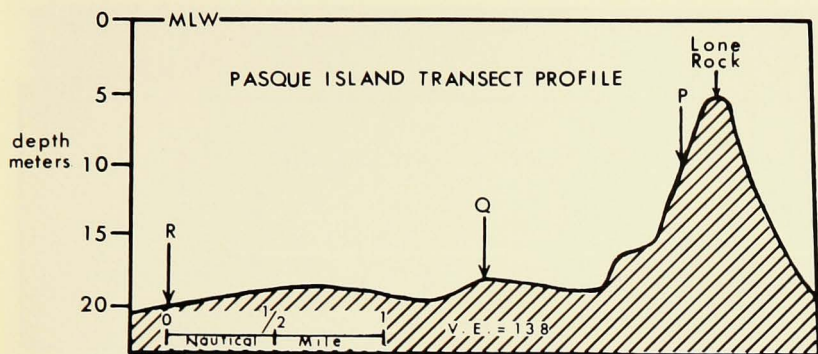
Figure 6. Diagrammatic profile of the Pasque Island transect and *in situ* surface sediment photographs taken at Sts. P, Q, and R. Sts. Q and R, which are populated by deposit-feeding bivalves, show a granular burrowed surface.
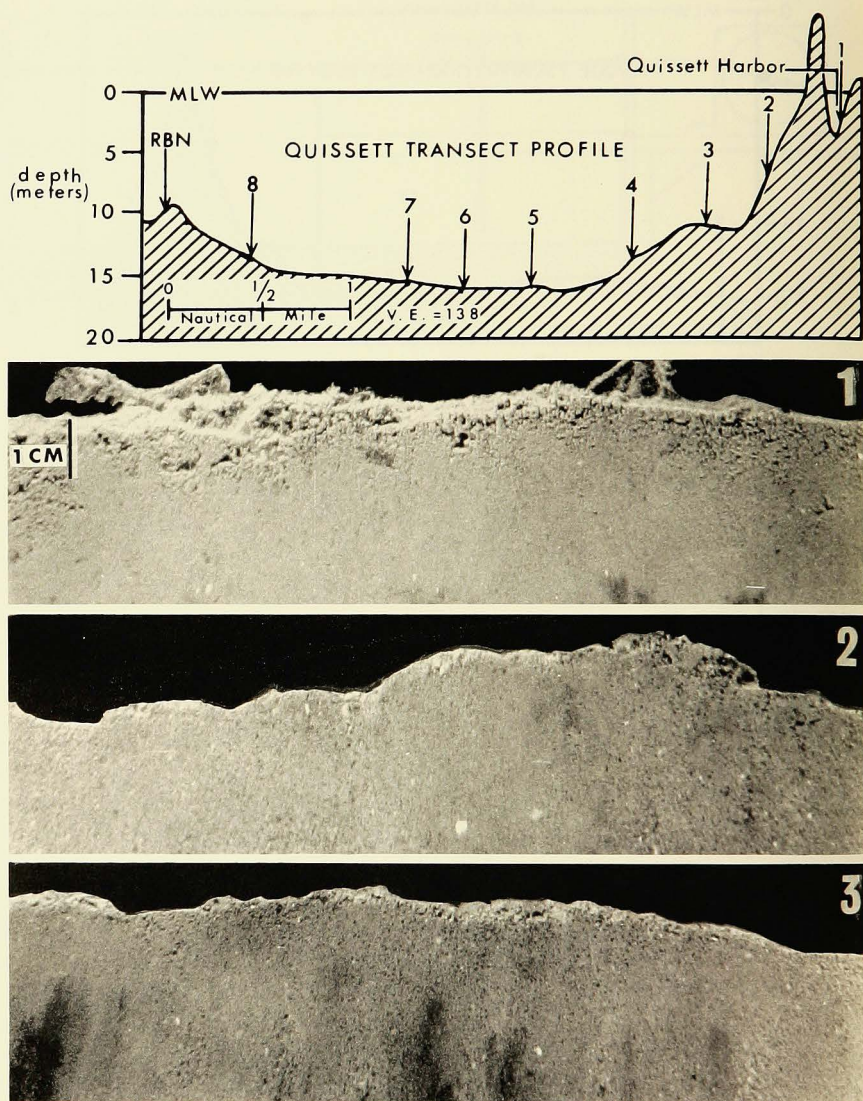
Figure 7a. Diagrammatic profile of the Quissett Harbor transect and *in situ* surface sediment photographs taken at Sts. 1-3. St. 1, numerically dominated by deposit feeders, exhibits a granular burrowed surface, which is absent at Sts. 2 and 3. See Fig. 7b for similar photographs of Sts. 4-8.
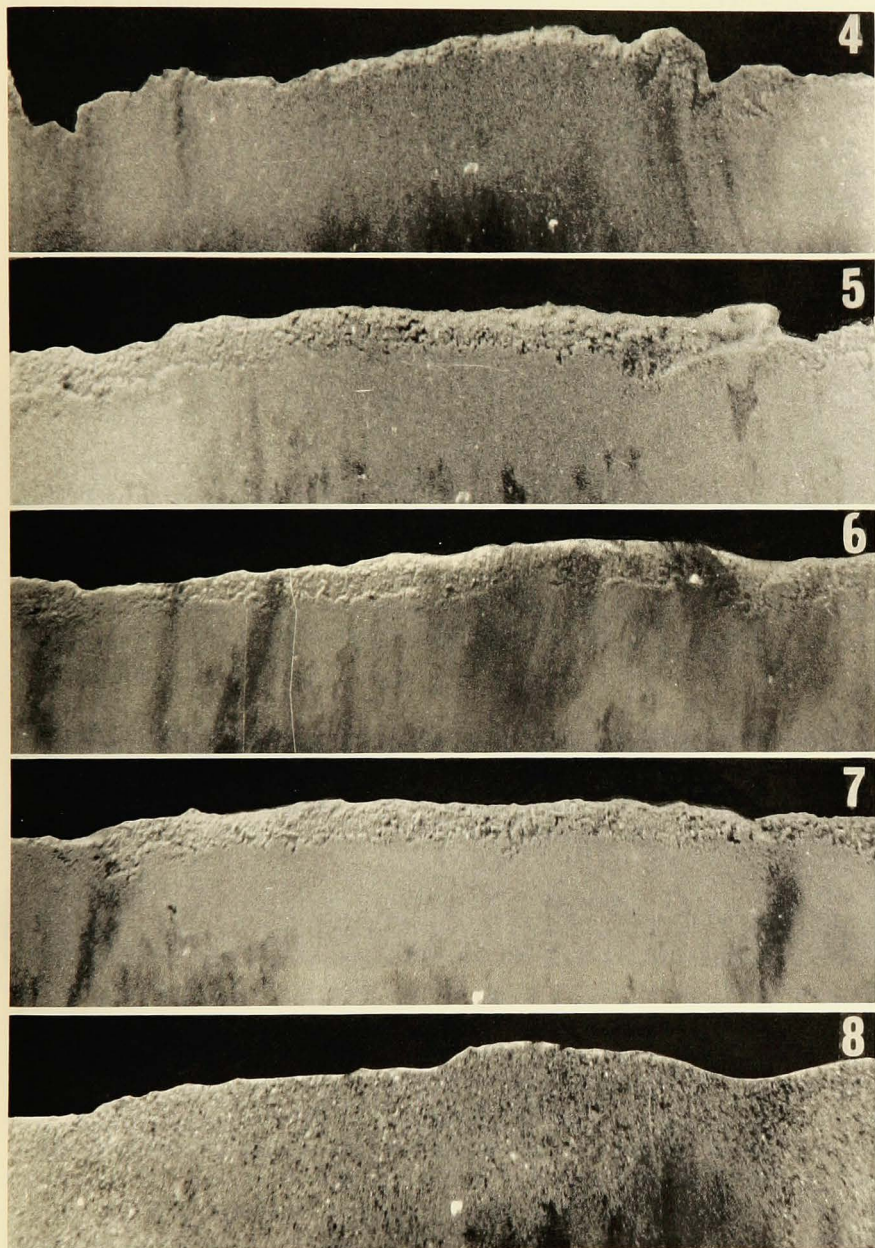
Figure 7b. *In situ* interface photographs taken at Sts. 4-8 on the Quissett Harbor transect. Sts. 5-7, numerically dominated by deposit feeders, exhibit a granular burrowed surface.

Figure 8. Development of a granular surface by the near-surface burrowing activities of *Nucula proxima*. *In situ* profile of the granular surface at (A) St. R and (B) in an aquarium.
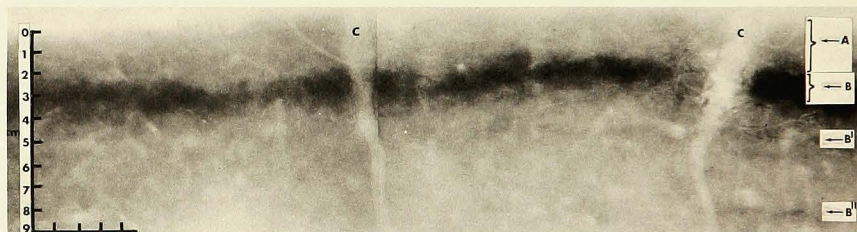

Figure 9. Radiograph of a box core from St. R. A laterally continuous X-ray opaque zone (B) below 2-3 cm of the burrowed zone (A), resulting from differential settling of the quartz-rich fraction caused by the burrowing of organisms. The concentration of detrital silicate minerals at the base of this unstable zone produces an X-ray opaque region. Older partially preserved X-ray opaque zones (B' and B'') have been largely destroyed by deep-burrowing polychaetes (?); *Cerianthus* (Anemone) tubes (C) are formed by the only deep burrowing organism at this station.

trays to a subtidal station having an extensively reworked muddy bottom populated predominantly by deposit feeders. Specimens one summer old were obtained at the Biological Laboratory, Bureau of Commercial Fisheries, Milford, Connecticut, on October 4, 1967. The specimens were notched for growth reference and then placed in plastic trays (27 cm wide, 30 cm long) containing mud and sand to a depth of 6 cm. Each of the four trays contained 32 specimens. On October 23, 1967, three of these trays were transplanted to water having a depth of 20 m, at St. R (Fig. 1). One tray, kept in the intertidal zone at Milford, provided a comparative population. The three trays were arranged vertically above the bottom on a three-tiered platform; the bottom of the lowermost tray was 10 cm above the silt-clay bottom. The second and third trays were, respectively, 45 cm and 75 cm above the bottom. After 66 days (October 23 to December 7, 1967), the top and middle trays at St. R and the Milford control tray were recovered. The specimens were killed and measured for new shell growth beyond the reference notch. The bottom tray was recovered 117 days following placement, on January 29, 1968.

Differential growth in this experiment was estimated from shell growth. Feeding takes place only when the valves are open, and it is only during periods of valve separation that shell deposition takes place. For this reason, hard-tissue growth reflects metabolic activity. During extended periods of starvation, soft-tissue growth may be negative while net hard-tissue growth, although small, is positive.

Results. The relationship between trophic-group distribution and structure of the sediment-water interface is apparent when the faunal data in Fig. 2 are compared with the *in situ* sediment-profile photographs in Figs. 6 and 7. All sampling stations in the silt-clay facies (Sts. Q, R, 1, 5, 6, 7) were densely populated with deposit feeders, especially tellinid or protobranch bivalves. The surface layers of the sediment at these stations had a reworked structure. This granular zone is present at the sediment surface whenever *Nucula proxima* is efficient in reworking this stratum (Fig. 8). Aquarium observations indicate that this granular structure results when *N. proxima* reworks the silt-size and clay-size particles into sand-sized fecal pellets. Frequent lateral movements of *N. proxima* in the sediment also displace the mud, producing sand-sized and larger clasts of semiconsolidated sediment. *Yoldia limatula* and *Macoma tenta* also play a role in producing a loose uncompacted surface.

The bottoms at Sts. 3, 4, and 8 were sandy, were low in organic content, and had a low density of deposit feeders. Consequently the bottom at these stations lacked a reworked granular surface. The relatively high densities of deposit feeders appear anomalous at Sts. 2 and P, where there was no evidence of a well-developed granular surface. Unlike other stations dominated by deposit-feeding bivalves, Sts. 2 and P were largely populated by tubicolous deposit-feeding polychaetes, which are less efficient in reworking sediment

than are mobile deposit-feeding bivalves. Also, Sts. 2 and P had a low organic content and were sandy in texture (Fig. 4). It is difficult for organisms to produce a reworked pelletal surface in this type of sediment.

The phenomenon of intensive sediment reworking is recorded in the sedimentary structures at St. R. X-radiographs show an opaque zone 2 to 3 cm below the surface (Fig. 9). This zone, which consists of a concentration of detrital quartz, feldspar, and other minerals that are relatively opaque to X-rays, is relatively poor in organic matter compared with the sediment above and below it. The lateral continuity of this zone has been determined with additional radiographs of other box cores taken at St. R. The base of this zone corresponds closely to the zone of maximum reworking by macrofaunal deposit feeders (Fig. 10). If Postma (personal communication) is correct in suggesting that this "opaque layer" is produced by the downward reworking of heavier minerals by the deposit feeders, then the upper 2–3-cm layer of sediment represents a biogenically graded layer.
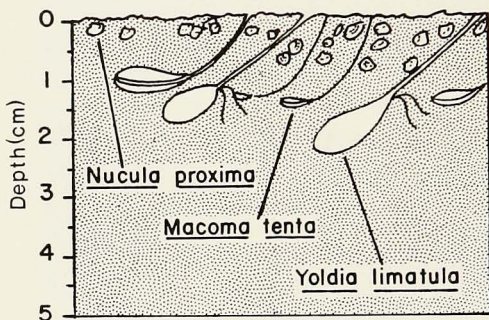

Figure 10. Vertical distribution of three deposit-feeding bivalves. The feeding activities of these bivalves are largely responsible for the reworked appearance of the uppermost 2–3 cm of sediment. Positions of organisms in the sediment based on data from X-rays of bivalves in aquaria.

The water content of samples from the Quissett Harbor transect is given in Fig. 11. The uppermost part of all cores (0 to 5 mm) was highest in water content. At a depth of about 1 cm, the water content was sharply reduced. Below 1 cm, there was less reduction in the water content with depth. Reversals in water content at depth, shown for St. 4 (Fig. 11), probably reflect compositional or textural differences within the core. A decrease in water content at depth, in most cores, reflects increased grain packing and loss of pore water. As compaction is greatly modified by biologic activity, the water content in the uppermost sediment largely reflects the degree of bioturbation at these stations. At stations dominated by bivalve deposit feeders (Sts. 1, 5, 6, 7), the water content in the uppermost sediment was greater than 60% (by wgt.); at stations with fewer deposit feeders (Sts. 2, 3, 4, 8), the water content was between 30% and 50% (by wgt.). Although the bimodal distribution of sediment-water content largely reflects the intensity of biogenic reworking, it is also a function of compositional and textural differences. At Sts. 2, 3, 4, and 8 the sediment was sandy and contained less organic matter (and water) than the sediment at Sts. 1, 5, 6, and 7, where the silt-clay sediment contained a large amount of organic matter. However, removal of bot-
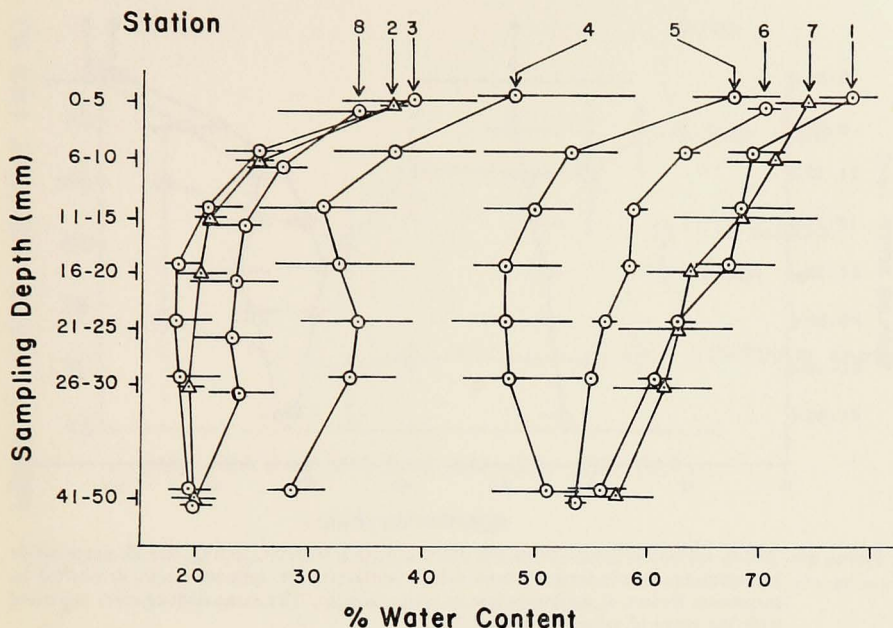
Figure 11. Water content of cores from the Quissett Harbor transect. Sts. 1, 5, 6, and 7—bottoms extensively burrowed by deposit feeders—have a high surface-water content. Sts. 2, 3, 4, and 8—less intensively burrowed—have a lower water content. The mean of four cores is plotted with the range of values (horizontal bar).

tom organisms from muds in the laboratory resulted in a decrease of approximately 10% in the water content of the uppermost sediment, indicating a strong biogenic control of compaction. Sanders' Sts. P, Q, and R showed a similar relationship between high sediment turnover and high water content (Fig. 12). St. P lacked a surface maximum in water content; this station also lacked a granular surface (Fig. 6). Sts. Q and R had a well-developed reworked granular surface and are comparable in water content and trophic structure to Sts. 5, 6, and 7 on the Quissett Harbor transect.

Mixed trophic groupings were encountered in this study at Sts. 1, P, and Q. Although the highly reworked mud bottom at St. 1 is capable of being resuspended by weak bottom currents, the stabilizing effect of beds of *Zostera* at this station prevents frequent resuspension. This stability permits the co-occurrence of deposit feeders and suspension feeders. Similarly, St. Q has a highly reworked sediment, yet this station shows little resuspension activity when compared with other reworked bottoms; marine grasses are absent, so we infer that tidal-current velocities are very low at this station. At St. P, also populated by a mixed trophic group, deposit feeders are not efficient in producing a granular reworked sediment; although some resuspension does take place, the clean hard-packed sand is sufficiently stable to support a prolific
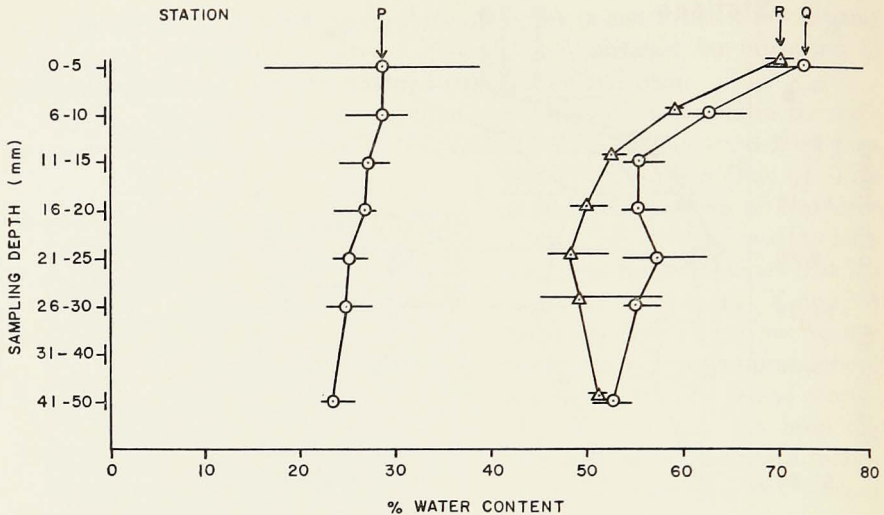
Figure 12. Water content of cores from the Pasque Island transect. Sts. Q and R—extensively burrowed by deposit feeders—have a high surface-water content. St. P, dominated by suspension feeders, is uniformly low in water content. The mean of four cores is plotted with the range of values (horizontal bar).

epifaunal population of suspension feeders. All of the unstable reworked stations in the open Bay (Sts. R, 5, 6, 7) are primarily homogeneous trophic groups of deposit feeders. The only suspension feeder that is significantly abundant at St. 6 is *Mulinia lateralis*. This mactrid bivalve occasionally reaches high densities on mud bottoms, but the numbers in such a population appear to be highly variable from year to year.

The water-content values shown in Figs. 11 and 12 were obtained during July and August. We might expect a seasonal change in the water content of sediment as the biologic activity fluctuates with changes in water temperature (Fig. 13). A maximal water content in the uppermost sediment was observed in late August and early September at the time of maximum bottom-water temperatures. A minimal water content and the lowest bottom-water temperatures were observed in late winter.

Although the maximal macrofaunal reworking activity was confined to the uppermost 2 to 3 cm of the sediment, the water content at depths of 3 to 5 cm also showed a change, but it was considerably less. Surface photographs taken concurrently with the coring show that the thickness of the granular zone is maximal in late summer; this granular surface is still present in January but is much less apparent in April.

Fig. 14 summarizes the results of three differential-erosion experiments. Little turbidity was developed in either tank at velocities up to 3 and 4 cm/sec. But at velocities greater than 4 cm/sec, there was greater resuspension of sedi-
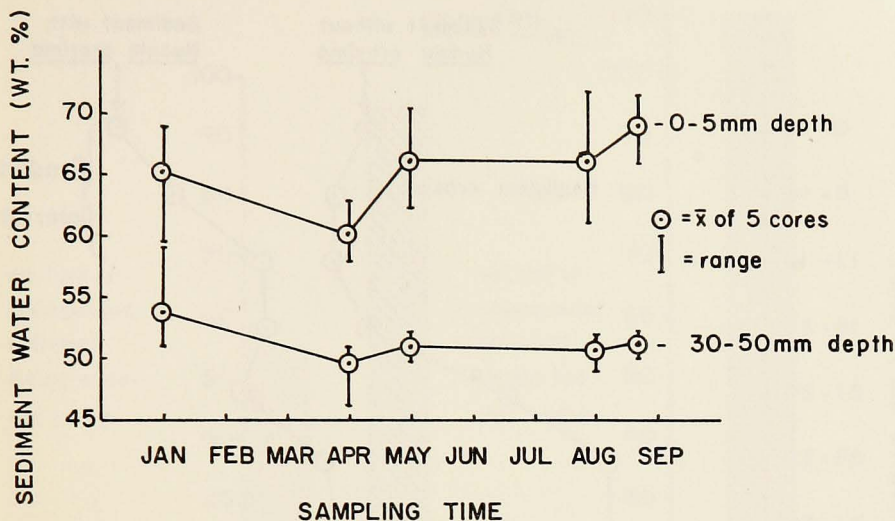
Figure 13. Seasonal change in the sediment water content at St. R at depths of 0–5 mm and 30–50 mm. Periods of minimum and maximum water content correspond to times of minimum and maximum water temperature and benthic activity.

ment and greater turbidity above the burrowed sediment than over the unburrowed sediment. Fecal pellets and mud clasts in the burrowed sediment were preferentially eroded and suspended at velocities greater than 4 cm/sec. These particles soon disintergrated into silt-size and clay-size grains, producing high turbidity. During erosion of the loose granular sediment, the roughness
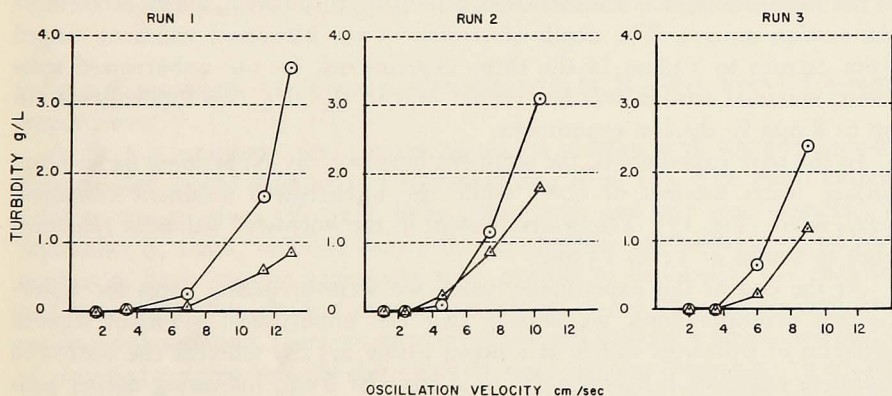

Figure 14. Differential erosion of muds burrowed and unburrowed by *Nucula proxima*. The results of three experiments are plotted. Each datum point represents the cumulative turbidity generated in the water over the bottom at a given oscillation velocity. Oscillation velocities were maintained for 30 minutes before turbidity was measured. Triangle indicates sediment without *N. proxima*; circle indicates sediment with *N. proxima*.
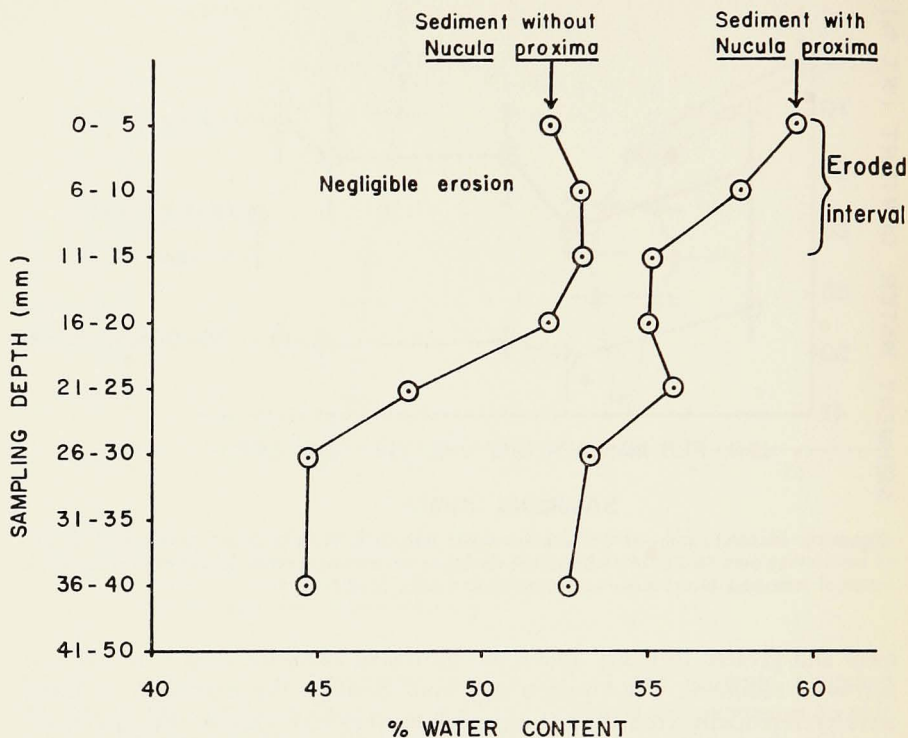
Figure 15. Difference in water content between sediment that has been burrowed and unburrowed by *N. proxima*. Data from cores obtained in the differential-erosion experiment.

of the sediment surface was increased, producing turbulence, which accelerated the erosion process. The depth of erosion in the burrowed sediment ranged from 10 mm to 13 mm in the three experiments. In the unburrowed sediment, maximal erosion was less than 1 mm in the first two experiments but up to 8 mm in the last experiment.

In the tank experiments, the sediment burrowed by *N. proxima* had a near-surface water content of 60% while the unburrowed sediment contained 52% water (Fig. 15). The water content in the burrowed sediment remained high to depths of 11 to 15 mm.

At the end of this experiment, when we were preparing cores for water-content determinations, we noticed that the unburrowed sediment showed evidence of hydrogen sulfide at a depth below 2.5 cm whereas the burrowed sediment exhibited a lighter color to a depth of 6 cm, indicating deeper penetration of oxygen in the reworked sediment.

In the experiments on resuspension at various stations, the volume of sediment trapped over St. 6 on the Quissett Harbor transect was more than seven times the amout trapped over St. 4. On the Pasque Island transect, the greatest
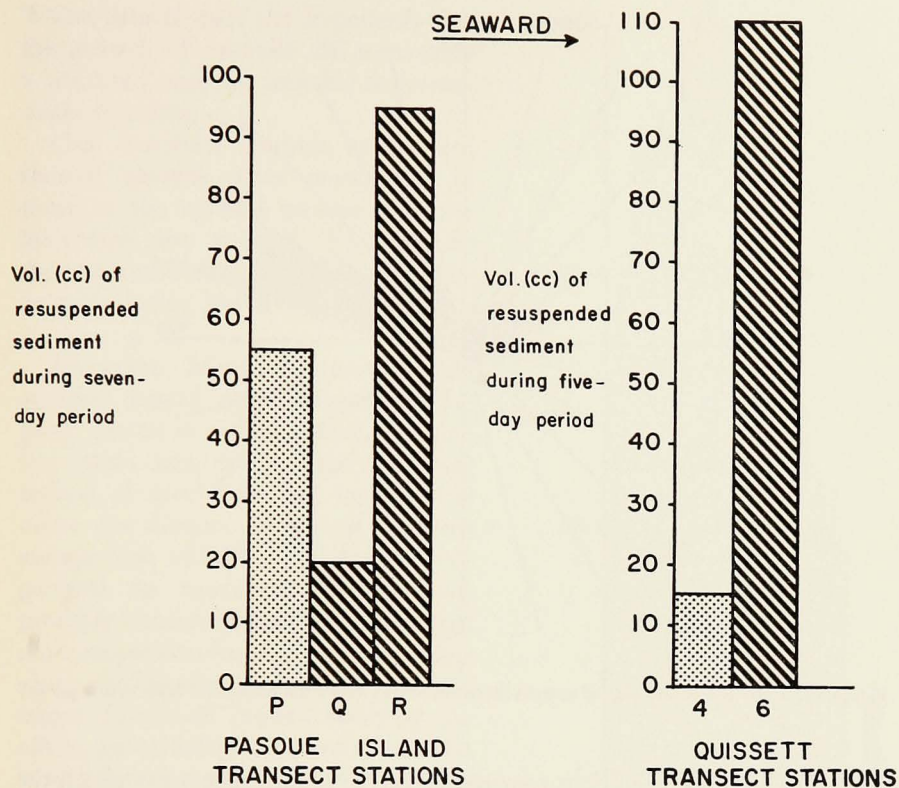
Figure 16. Differential resuspension of sediment at selected stations on the two sampling transects in Buzzards Bay. Maximum resuspension was measured over muds burrowed by deposit feeders (Sts. R and 6). Diagonal lines indicate stations with a granular surface.

volume of resuspended sediment was trapped over St. R—five times the volume trapped over St. Q (Fig. 16).

At St. 7 a rotational tidal-current pattern is present, with the predominant flow parallel to the long axis of Buzzards Bay (Fig. 17). The mean current velocity was 5 cm/sec (Fig. 18). When the meter and trap were installed on September 4, 1968, visibility below the thermocline was about 2 m; on September 5, large organic aggregates were present in the water, the visability had been reduced to about 1 m, and the bottom of the trap was covered with resuspended sediment. Current data for this period indicate a 20-minute period of maximal current velocity during flood tide, ranging from 5 to 10 cm/sec. During the 5.5 days of measurement, the total cumulative time of current velocities approaching 10 cm/sec was 109 minutes; these periods were related to both flooding and ebbing tides. A total volume of 80 cc of sediment was trapped, representing a flux of 15 mg/cm²/day.
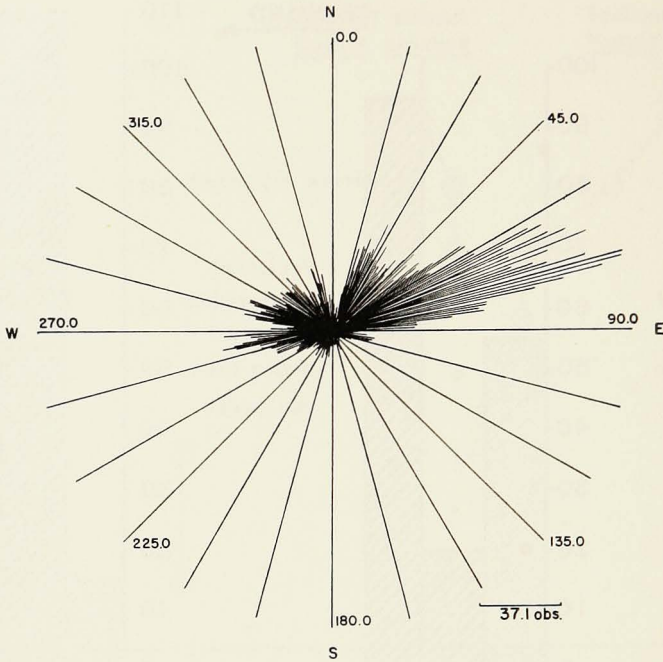
Figure 17. Polar coordinate plot of current direction 60 cm above the bottom at St. 7 over a 5.5-day period.

The type of flow conditions responsible for the resuspension of muds on the bottom was observed photographically at St. R over a 26-hour period by means of time-lapse movies of the bottom. Tidal flow was observed by following the motion of suspended particles near the bottom. Most of the photographic records show a rotational motion of some of the particles. This type of motion is probably related to turbulent eddies generated during tidal flow. This turbulence is most likely the primary agent in the erosion and resuspension of bottom muds. Relative turbidity of the near-bottom water changed dramatically from hour to hour. A watch placed on the bottom in the camera's field of view was covered and uncovered with mud several times over the 26-hour period of observation.

The transplant experiment at St. R was designed to determine whether near-bottom turbidity limits suspension-feeder growth in the bottom tray relative to the two upper trays (Fig. 19). The mean growth in the bottom tray (0.6 mm/117 days) was significantly less than that in the middle tray (1.2 mm/ 66 days) at the 0.95 level of confidence (two-tailed student's t test). The mean growth in the bottom tray was also significantly less than that in the uppermost tray at the 0.99 level of confidence. Mean growth in the middle and uppermost trays (1.3 mm/66 days) did not differ significantly at the 0.95 level.

These data support the hypothesis that the growth of juvenile *M. mercenaria* is inhibited near the unstable sediment-water interface.

Our intertidal controls at Milford showed growth rates comparable to those of the subtidal specimens in the lowermost tray at St. R. This may be the result of little shell deposition by the controls during low tide.

Discussion. Many suspension feeders actually depend upon resuspended organic matter as a food source (Jørgensen 1966; 252, 263). This is characteristic of species feeding immediately above the bottom. However, frequent resuspension of both sediments and organisms on reworked mud bottoms probably exceeds the silting tolerance of most suspension-feeding benthos, especially during the larval and juvenile stages. Loosanoff (1962), studying the effects of turbidity on larval and adult bivalves, concluded that suspension feeders generally feed most effectively in relatively clear water. However, a wide range of tolerance to turbidity does exist among some filtering bivalves (Maurer 1967). Factors other than turbidity must be considered as limiting for suspension feeders in reworked muds. Reduced permeability in fine-grain sediments may inhibit siphonal water exchange across the sediment-water interface, or inhibitory chemical substances may accumulate in muddy substrata (Pratt and Campbell 1956). Tenore et al. (1968) have suggested that fine-grain sediments that are high in organic content and phosphate concentration may inhibit growth in *Rangia cuneata*. The chemical and sedimentologic conditions that have been proposed as limiting for filter-feeding bivalve growth may also be important in discouraging the larvae of suspension feeders from settling on soft reworked mud. The possibility also exists that settled larvae are eaten at the surface by deposit feeders (Thorson 1966). The resuspension of sediment and the subsequent burial of juveniles may be an even greater limiting factor. Deposit-feeding bivalves show remarkable morphologic and
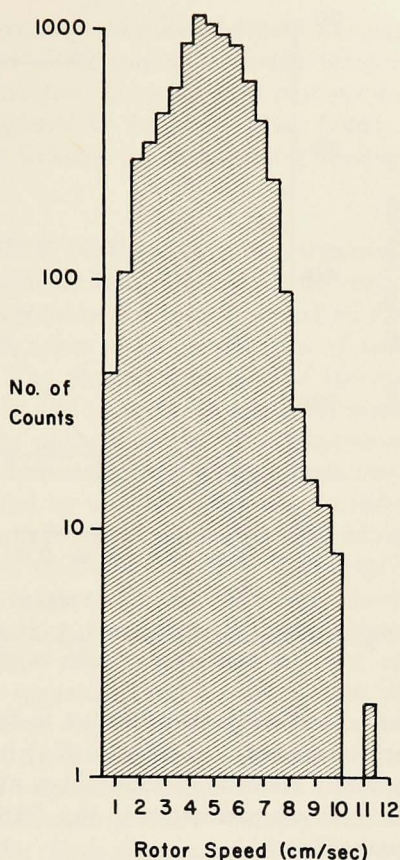

Figure 18. Velocity histogram of currents 60 cm above the bottom at St. 7 over a 5.5-day period.
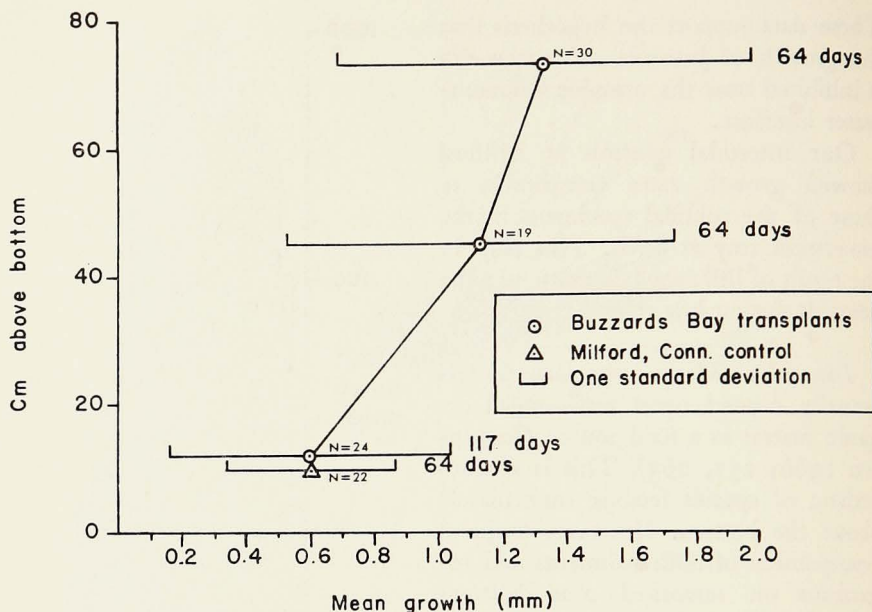
Figure 19. Differential growth of transplanted juvenile *Mercenaria mercenaria* at three elevations at St. R above a mud bottom burrowed by deposit feeders.

behavioral adaptations relative to the physical instability of their muddy biotope. Harrison and Wass (1965) have found that sediment-water content is a major controlling factor in a multiple-regression analysis relating several sedimentary parameters to the distribution of three benthic species in Chesapeake Bay.

The deposit-feeding bivalves encountered in this study (*Nucula proxima, Yoldia limatula,* and *Macoma tenta*) are low in bulk density, which facilitates flotation in a noncompacted mud with high water content; these species are also rapid burrowers (Stanley 1970). Time-lapse radiography has revealed that these three species, buried in aquaria with several centimeters of artificially introduced sediment, are capable of sensing the location of the new surface. Burial was accompanied by rapid movement to the new surface (negative geotaxis). Glude (1954) found that the survival of artificially buried *Mya arenaria* was inversely proportional to the depth of burial, that the juveniles were more adversely affected than the adults, and that mortality increased with increasing silt content. Carriker (1961) has shown that there is a high vertical mobility in juvenile *Mercenaria* in unstable sandy substrata.

Bottoms populated by dense concentrations of suspension feeders may become increasingly fine-grained and enriched with organic matter as the feces produced by suspension feeders accumulate (Verwey 1952, Van Straaten and Kuenen 1958, and Haven and Morales-Alamo 1966, 1968). Resuspension of

these fecal muds (perhaps facilitated by reworking activities of deposit feeders) may, in turn, result in the local extinction of the suspension feeder biotope through the generation of high bottom turbidity. Unstable mud bottoms do not affect all feeding types equally, as suggested by McNulty et al. (1962). These bottom types are clearly the most limiting for a suspension-feeding benthos.

An Hypothesis of Trophic Group Amensalism. Amensalism is an interaction between two populations in which one population is inhibited while the other is not (Odum and Odum 1959). This relationship was initially described for the interactions of two species, but here it refers to the interactions of two trophic groups composed of several taxa. The physical instability of the reworked environment of a deposit feeder, in the presence of relatively weak bottom currents, may discourage the settling of the larvae of many suspension feeders on this type of bottom. If settling does occur, early growth stages may subsequently be inhibited in growth or killed by unstable sedimentary conditions. The inhibitors (deposit feeders) are unaffected in this relationship while the amensals (suspension feeders and sessile epifauna) are either discouraged from settling or are killed during early benthonic stages. Although many larvae of suspension feeders show high settling descrimination, some larvae settle and metamorphose in sediments where adult populations are rare or absent (Muus 1966). Holme (1961) has suggested that the distribution of some benthic groups is determined to a lesser degree by the extent of larval dispersal than by conditions encountered at the bottom during metamorphosis and early juvenile growth. The settling of suspension feeders on the unstable muds occupied by deposit feeders may lead to mass juvenile mortality such as that described by Harrison et al. (1964) for *Ensis directus*, which settled on a bottom in Chesapeake Bay that was found to be highly reworked (Young 1968a). In cases where the instability of the interface is not totally lethal to a population, surviving individuals may exhibit stunted growth (Hallam 1965). The problem of attachment and stability of suspension-feeding epifauna on soft muds has been recognized as a limiting factor in the Okhotsk Sea (Savilov 1959) and on "vaseau molles" in the Mediterranean (Pérès and Picard 1964).

Limitations of the Hypothesis. The hypothesis of amensalism does not adequately describe the factors that separate deposit-feeding and suspension-feeding trophic groups where food is actually limiting to suspension feeders. These two feeding types are found separated in the deep sea, but the distribution of suspension feeders in such a case is related to the presence or absence of a small amount of suspended food above the bottom (Sokolova 1959). The hypothesis of amensalism is limited, then, to areas of high primary productivity on the continental shelves where food is not limiting to suspension feeders.

The production of unstable and reworked mud bottoms is largely limited to the deeper subtidal bottoms, for intertidal and shallow subtidal muds tend to be stabilized by the binding properties of marsh grass, benthic diatoms (Van Straaten and Kuenen 1958), and shallow-water algal mats and grasses (Ginsburg and Lowenstam 1958). High densities of tube-dwelling polychaetes may also bind sediments in subtidal areas (Fager 1964).

Epifaunal filter feeders have commonly been reported as occurring on soft mud bottoms that have received, or are continuing to receive, ice-rafted erratics. The presence of these erratics on the mud surface provides a firm surface for the attachment of epifauna on an otherwise unstable bottom.

Summary. The intensive near-surface reworking by infaunal deposit feeders (especially protobranch bivalves) has been shown to produce the following changes in sediments dominated by this trophic group: (i) an uncompacted granular surface consisting of fecal pellets and reworked clasts of semiconsolidated mud, (ii) a surface of biogenic sand-size particles of low bulk density, and (iii) a water content greater than 60% at the surface of highly reworked sediments. The compaction of reworked sediments fluctuates with water temperature, reflecting seasonal change in metabolic activity of benthic organisms.

Biogenic modification of fine-grained deposits affects the physical stability of the bottom by increasing surface-water content and interface roughness, thereby lowering the critical erosion velocity. This physical instability is manifested by: (i) high turnover rate of bottom muds by a process of resuspension driven by weak tidal currents, (ii) high turbidity at the sediment-water interface, and (iii) production of textural and compositional grading in reworked sediments corresponding to the maximal depth of biologic reworking (x-ray-opaque zone).

Physical instability of the reworked surface is proposed to be stressful for suspension feeding benthos by: (i) clogging filtering structures, (ii) resuspending and burying newly settled larvae, and (iii) discouraging the settlement of suspension-feeding larvae. Instability at the interface also limits the ability of sessile epifauna to maintain a firm connection with the unstable bottom.

This study suggests that the trophic group distribution in Buzzards Bay may be related to the following biotic and sedimentologic features: (i) *Homogeneous suspension-feeder trophic groups.* These groups result when deposit feeders are largely excluded from the suspension-feeder biotope by an inadequate food source in the sediment. (ii) *Homogeneous deposit-feeder trophic groups.* These groups result when suspension feeders are largely excluded from the deposit-feeder biotope by frequent resuspension of biogenically reworked sediments containing fine particles. It is suggested that this sediment instability and water turbidity is limiting for most suspension feeders. (iii) *Mixed trophic groups.* The occurrence of a diverse suspension-feeder population on a mud

bottom reworked by deposit feeders indicates physical stability of the bottom. A reworked mud surface is effective in limiting suspension feeders only when the surface becomes mobile.

Future near-shore benthic surveys should consider the sedimentary features of the sediment-water interface structure and the sediment water content. Placement of sediment traps on the bottom of faunal sampling stations should reveal the relative stability of the bottom. Correlation of the benthic trophic structure with the sediment-water interface stability in the region of subtidal muds may be one of the most important but neglected parameters of benthic ecology.

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