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Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments¹

by G. A. Brenchley²

ABSTRACT

Bioturbators alter the sediment surface in the following ways: by depositing sediment on the surface in the form of feces or in the process of tunnelling, and by transporting sediment about the surface while feeding or while burrowing. Two questions, i) whether these different kinds of bioturbation will similarly effect an assemblage of macrofauna, and ii) whether one bioturbator will alter several assemblages in comparable ways, were addressed by a series of field and laboratory experiments involving intertidal assemblages in False Bay, Washington (USA). Densities of tube-builders, both surface deposit feeders and herbivores (6 polychaetes, 2 crustaceans), were significantly reduced following the addition of infaunal burrowers (*Upogebia pugettensis* and *Abarenicola pacifica*) or an epifaunal burrower (*Dendraster excentricus* or *Parastichopus californicus*). As a result, proportions of suspension feeders and subsurface-deposit feeders rose in the disturbed assemblages. Rates of mortality were greatest among juvenile and small tube-builders in treatments compared to controls. Adult-juvenile interactions were documented for the tanaid *Leptochelia dubia*. These general results had been predicted a priori by exposing 3 assemblages to moderate levels of sediment deposition (80 mg/cm²/d) for 7-8 d. Thus, physical events appear to be important to these interactions. Because the results were not characterized by trophic group and the bioturbators were deposit feeders and suspension feeders, the results emphasize a need to shift attention from trophic group to categories of relative mobility (sedentary or tubicolous, mobile or burrowing) in hypotheses relating bioturbation to benthic community structure.

1. Introduction

Marine benthic organisms influence the physical character of their habitat and thus they influence the surrounding community (Rhoads and Young, 1970; Woodin and Jackson, 1979). An important and taxonomically diverse class of benthic organisms are the "bioturbators," organisms that loosen the sedimentary fabric by burrowing through the sediment or by ingesting and defecating it elsewhere (reviewed by Rhoads, 1974). The biology and abundance of benthic organisms inter-

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Table 1. Selected life habits of the bioturbators used in this study.

| Species | Feeding mode | Life position | Nature of disturbance | Reference |
|---|--------------|---------------|--|-----------------------------|
| <i>Abarenicola pacifica</i> (lug worm) | Deposit | Infaunal | Transports sediment to the surface as unconsolidated feces | Hobson (1967) |
| <i>Upogebia pugettensis</i> (mud shrimp) | Suspension | Infaunal | Transports sediment to the surface while tunnelling | MacGinitie (1935) |
| <i>Callianassa californiensis</i> (mud shrimp) | Deposit | Infaunal | (as above) | MacGinitie (1934) |
| <i>Dendraster excentricus</i> (sand dollar) | Suspension | Semi-infaunal | Transports sediment about the surface during burrowing | Chia (1969) Timko (1976) |
| <i>Parastichopus californicus</i> (sea cucumber) | Deposit | Epifaunal | Transports sediments about the surface during process of feeding, feces bound in mucus | |

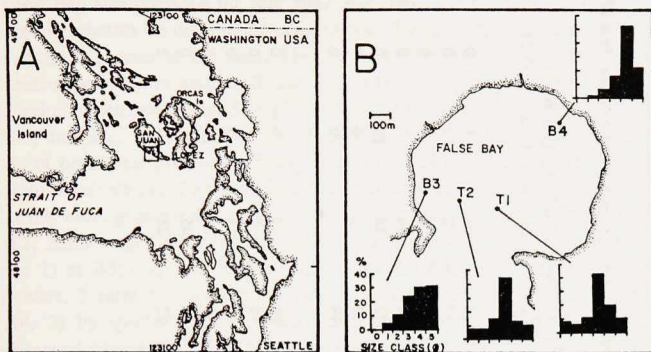


Figure 1. Locations of study sites in False Bay (B) on San Juan Island (A) off the northwest coast of Washington, U.S.A. ($48^{\circ}29' N$; $123^{\circ}04' W$). Shown are size classes (% in ϕ units) of the upper 10 cm of sediment, analyzed as per Emery, 1938.

act with the physical character of the habitat in ways sufficiently complex (see Ginsberg and Lowenstam, 1958; Rhoads, 1974; Rhoads *et al.*, 1978; Yingst and Rhoads, 1978; Baumfalk, 1979; Nowell *et al.*, 1981) to question whether i) one bioturbator in different habitats and ii) different species of bioturbators in the same habitat, will influence community composition in a similar fashion. No quantitative data adequately distinguish between these two phenomena. Caging studies that have addressed the importance of co-occurring species of sediment-disturbers (e.g., Orth, 1977; Virnstein, 1977; Young *et al.*, 1976) are complicated by predatory activities of the organisms and artifacts of the cages. The present study offers quantitative evidence that a variety of bioturbators alter community composition in a comparable manner despite large differences in their life habits.

Bioturbators redistribute marine sediments in several ways: by transporting sediment to the surface in the form of feces (subsurface deposit feeders), or in the process of tunnelling (any feeding mode); and by transporting sediment about the surface during feeding activities (surface deposit feeders), or during burrowing activities (any feeding mode). A representative species of each of these general types was selected for this study (Table 1) from False Bay, San Juan Island, Washington (Fig. 1). The list includes a polychaete (*Abarenicola pacifica*), thalassinid crustaceans (*Upogebia pugettensis* and *Callianassa californiensis*), an echinoid (*Dendraster excentricus*), and a holothurian (*Parastichopus californicus*). Each species is relatively large and thus likely to play an important role in structuring macrofaunal communities. Note that both deposit feeders and suspension feeders are included in the list.

Table 2. Life habits of common species present in field and laboratory experiments. Depth distributions are percentages of total numbers of individuals from 3 cores sectioned in the field.

| Species ¹ | Mobility ² | Feeding ³ | Reprod. | Depth distribution (%), in cm | | | |
|---------------------------------------|-----------------------|----------------------|---------|-------------------------------|-----|------|-------|
| | | | | 0-2 | 2-6 | 6-10 | 10-14 |
| Group I | | | | | | | |
| (P) <i>Rhynchospio arenicola</i> | Tubicolous | surface DF | Broods | 78 | 21 | 1 | 0 |
| (P) <i>Pygospio elegans</i> | Tubicolous | surface DF | Broods | 98 | 2 | 0 | 0 |
| (P) <i>Pseudopolydora kemp</i> | Tubicolous | surface DF | Broods | 95 | 5 | 0 | 0 |
| (P) <i>Onuphis stigmatis</i> | Tubicolous | surface DF | | 54 | 44 | 1 | 0 |
| (P) <i>Platynereis bicanaliculata</i> | Tubicolous | herbivore | | 72 | 18 | 10 | 0 |
| (C) <i>Leptochelia dubia</i> | Tubicolous | surface DF | Broods | 97 | 3 | 0 | 0 |
| (C) <i>Corophium</i> sp. | Tubicolous | epistratic | Broods | 99 | 1 | 0 | 0 |
| Group II | | | | | | | |
| (B) <i>Transennella tantilla</i> | Burr. Epi. | Susp. F. | Broods | 96 | 4 | 0 | 0 |
| (C) <i>Paraphoxus</i> spp. | Burr. Epi. | Susp. F. | Broods | 98 | 2 | 0 | 0 |
| (H) <i>Leptosynapta clarkii</i> | Burr. Inf. | DF | | 87 | 13 | 0 | 0 |
| (B) <i>Macoma nasuta</i> | Burr. Inf. | DF | | 30 | 46 | 16 | 8 |
| (P) Capitellidae | Burr. Inf. | DF | | 44 | 45 | 11 | 0 |
| Oligochaeta | Burr. Inf. | DF | | 62 | 28 | 8 | 2 |

¹ B, bivalve; C, crustacean; H, holothurian; P, polychaete

² Mobility: Tubicolous, Burrowing semi-infauna or epifauna, Burrowing infauna

³ Feeding: DF, deposit feeder; Susp. F., suspension feeder; Herbivore; Epistratic feeder

False Bay also provided the four sites (Fig. 1B) used to study the effects of the above bioturbators on community composition. Table 2 lists pertinent life habits of the common species at the sites. The dominant organisms were shallow-dwelling tubicolous polychaetes and small crustaceans (Group I), and mobile forms (Group II), including surface-oriented amphipods and a small bivalve, and subsurface bivalves, annelids, and a holothurian. The surface texture at the sites reflected the kinds of organisms present: a tightly bound mat of tube-builders (notably *Rhynchospio arenicola* and *Leptochelia dubia*) and seagrass (*Zostera marina*) at T1; a relatively even, granular surface bound by tube-builders (*R. arenicola* and *L. dubia*) at T2; holes ringed with pebbles formed by burrowing mud shrimp (*Upogebia*, Table 1) at B3; and fecal castings of lug worms (*Abarenicola*, Table 1) at B4. Hereafter, I refer to bioturbators (Table 1) by genus and benthic macrofauna (Table 2) by species. Both protected and more exposed sites were chosen for purposes of comparison. The two more exposed sites, T1 and T2, were centrally located about 150 m apart at +0.2 m tidal elevation (0 m = MLLW), and were composed of sands (median grain, 0.19 mm) with 10% silt-clay (Fig. 1B). The two more protected sites, B3, along the edge of the bay about 150 m from T2 at +1.0 m, and B4, in the high intertidal zone at +2.5 m, were composed of finer grades of sand (median, 0.10 and 0.09 mm, respectively) with a greater proportion of silt and clay (29-31%).

Thus, the physical and biological attributes of the 4 sites are sufficiently diverse, as are the bioturbators (Table 1), to address the two questions raised above. Short-term experiments were performed in the laboratory using intact cores of sediment. To separate the importance of physical disturbance from other biological activities (e.g., predation; see Highsmith, 1977), small quantities of sediment were added in different intensities and frequencies, generating results used to predict the effects of the bioturbators. Field experiments, also of short duration, were performed at several sites in order to compare the effects of one bioturbator, *Dendraster*, on assemblages of different composition.

2. Methods

For laboratory studies, undisturbed cores of sediment ($400 \text{ cm}^2 \times 14 \text{ cm}$ deep) were collected during low tide and placed into empty aquaria. Each aquarium had two water-tight compartments ($400 \text{ cm}^2 \times 30 \text{ cm}$ deep) with separate seawater inputs and drains. These cores were maintained at the Friday Harbor Laboratories for a maximum of 10 d in running seawater. Experiments (see below) began 1-2 d following collection. Cores from each site were maintained concurrently in the laboratory without further manipulation to serve as controls.

Samples of sediment were gathered in the field and from the above aquaria within $100 \text{ cm}^2 \times 14 \text{ cm}$ deep frames for faunal analysis. Field samples were

collected at the same time and in the same locale as experimental cores and were sacrificed to document initial densities in experimental cores. At the termination of each set of experiments, four samples were extracted from each control and experimental core to document changes in faunal abundances. Samples were fixed in formalin and washed 1-2 d later on 0.5 mm screens. Preliminary field samples washed on 0.5 and 0.25 mm screens (stacked sieves) showed that the average loss from the 0.5 mm screen was 5% for tube-builders, 6% for burrowing infauna, and 4% for mobile epifauna (listed by species in Brenchley, 1978). The samples were stained with rose bengal, stored in glycerine-alcohol, and sorted under a dissecting microscope. Blades of *Zostera* were removed prior to sampling and discarded to avoid contamination by blade epifauna. Animals with heads were counted. Organisms were classified as tube-builders, burrowing infauna, or burrowing semi-infauna or epifauna, and as suspension feeders, deposit feeders, herbivores, or predators, based on direct observations of the species and on descriptions in the literature.

a. Sediment deposition experiments. Because my purpose was to identify those animals of several assemblages which were most sensitive to sediment deposition, I added sediment in the laboratory to cores in May 1977. I did not attempt to re-create the conditions of False Bay. Rhoads and Young (1971) estimated a sediment flux of about 80 mg/cm²/day in Cape Cod Bay. Their estimate is a conservative amount for subtidal environments since in Long Island Sound, for example, summer rates often exceed 250 mg/cm²/day (McCall, 1977). This estimated value is also considered to be a conservative amount for more intensely reworked sites in False Bay, where worms daily deposit 2.6 g of unconsolidated sediment on the surface (Hobson, 1967). See Cadée (1976) for a summary of sediment reworking rates.

After removing the macrofauna, B4 sediment (median grain, 0.09; sorting coefficient, 0.47; silt-clay, 29%; 1.6 g wet weight = 1 cc) was slowly ejected from a syringe throughout the aquaria near the water line, 16 cm above the bottom. Sea-water flow was stopped for 30 min to allow the sediment to settle. Three treatments were performed: 6.6 cm³ of sediment added every 8 hr, abbreviated 6.6 cc @ 8 hr, 20 cc added every 8 hr, and 20 cc added daily between 7 and 8 o'clock. The addition of 6.6 or 20 cc each 8 hr tested the effects of sediment quantity. The daily addition of 20 cc (equivalent to Rhoads and Young's estimate of sediment flux), in one large or three smaller doses tested the effects of frequency of deposition, i.e., sudden deposition of sediment versus more chronic conditions of sedimentation. Sediment was added for 7 or 8 consecutive days, accumulating a surface layer 5 to 10 mm thick. No sediment was added to the control aquaria. Both experimental and control aquaria were then sampled for fauna.

b. Laboratory studies of bioturbators. Several infaunal burrowers that deposit

sediment on the surface were added in June, 1976 to a T1 core to determine which organisms are inhibited by this form of bioturbation. The introduction of organisms proceeded as follows:

- Day 1: 20 *Abarenicola pacifica*, 25-35 mm length
4 *Upogebia pugettensis*, 40-55 mm carapace length
- Day 2: 2 *Callianassa californiensis*, 75-85 mm carapace length

Tunnel formation by *Upogebia* and fecal mound production by *Abarenicola* indicated that the individuals of both species were behaving normally, for no individuals were seen above the surface again. In contrast, neither of the 2 *Callianassa* had penetrated the surface after 24 hr when they were removed. The aquarium and a control—no burrowers added—were sampled for infauna on day 8. During the first three days of this experiment, small plastic funnels (6 cm dia) were suspended by threads 7 cm above the bottom in the control and experimental tanks. Sediment accumulating in these 6 traps was removed every 12 hr, washed with distilled water, and oven dried at 60°C for dry weight determinations.

To compare the effects of infaunal burrowers (above) with surface-oriented forms, I collected sand-dollars, *Dendraster excentricus*, from False Bay. *Dendraster*, suspension feeders (Chia, 1969; Timko, 1976), were most common in subtidal areas of the bay but also inhabited troughs that separated the 3 lower study sites (see Fig. 1B). Two specimens (test dia. 80-90 mm) were added to aquaria containing T1 or T2 cores in mid-May, 1977. Changes in the position of the sand-dollars were noted daily. Their position was never seen elevated which is the position they often assume when suspension feeding in strong currents. These and control T1 and T2 aquaria—no *Dendraster* added—were sampled 9 d later for fauna. The effect of *Dendraster* on surface stability was also studied in the laboratory using a crude method developed by Rhoads and Young (1970). A paddle (21 cm²) was driven back and forth 2 cm above the bottom for 3 min by an eccentric motor. Three funnels (6 cm dia) were suspended by threads 7 cm above the bottom to trap sediment. The funnels were removed after 30 min and their contents washed, dried, and weighed.

To compare the effects of a semi-infaunal suspension feeder (*Dendraster*) with those of an epifaunal deposit feeder, the holothurian *Parastichopus californicus* was dredged from offshore in May, 1977. Although most individual *Parastichopus* exceed 1 kg (and thus were too large for the aquaria), a small specimen, wet weight 80-95 g, was added to a T1 core after it had ceased to produce feces in the holding tank. Feeding on the sediment surface by this holothurian did occur during the experiments. Since this experiment ran concurrently with the *Dendraster* additions, the same T1 control core was used for both experiments.

c. *Field manipulations.* Again in May, 1977, *Dendraster* were added to four sites in False Bay (Fig. 1) to determine whether this bioturbator affects different assemblages of infauna in comparable ways. Two cages, each 0.25 m² with sides and tops constructed of a heavy plastic mesh (4 mm openings), were installed at each site to enclose *Dendraster*. The sides were pressed 8 cm into the sediment, projected 10 cm above the substrate, and were secured by 50 cm corner stakes driven 40 cm into the sediment. Similar stakes marked locations of unmanipulated 0.25 m² control areas. Cages installed at site T1 could not be pressed 8 cm into the eelgrass root-mat and were later lost during a storm. Eight *Dendraster* were added to each cage. This density of sand-dollars (32/m²) is greater than that found in the intertidal zone of False Bay (Smith, 1980), but is less than that found nearby in intertidal (Smith, 1980) and subtidal areas (Chia, 1969; Birkeland and Chia, 1971). Individuals remained buried at all sites. To test for possible cage effects, I installed two identical cages at each site but added no sand-dollars. So with laboratory experiments, the field experiments were of short duration, lasting 7-8 d. Upon sampling the sites for infauna, two 0.01 m² samples were taken from each 0.25 m² area.

3. Results

The relative abundances of infauna in initial field samples were compared to the corresponding laboratory controls, held 7-10 d in running seawater before sampling, using Kendall's coefficient of rank correlation: at no site were differences significant at $P \leq 0.05$. Densities of infauna were similarly compared by means of the Mann-Whitney U test, again with $P \leq 0.05$ as the critical level for significance. The only difference which was significant involved the tanaid *Leptochelia dubia*, more abundant in the laboratory because broods were released during the experimental period and the young settled within the aquarium. Spionid polychaetes were consistently less dense in the laboratory cores, but none of the differences were significant. Therefore, differences in densities between controls (reflecting field densities) and experimental cores cannot be attributed to the effects of simply maintaining the cores in the laboratory for 7-10 d.

Densities of species in control cores were compared to those in experimental cores using Mann-Whitney U tests. To identify age-specific patterns of mortality, size frequency distributions (10 size classes, each 9-12% of controls) were compared using Chi-square tests. The critical level for significance was 0.05 throughout the study. Animals were measured under a microscope using an ocular micrometer.

a. *Sediment deposition experiments.* Because the results of the three sets of experiments (T1, T2, B3) are similar, detailed results of T2 only are presented (Table 3). A summary of T1 and B3 experiments is given in Table 4. Small amounts of sediment added to cores from these 3 sites consistently reduced densities of the two

Table 3. Effects of sediment deposition on fauna of site T2. Mean density per 100 cm² (n = 3) is listed. Sediment treatments abbreviated as in text. Treatments that differ significantly from controls, and from one another, are indicated: *, densities different by Mann-Whitney U tests (* P < 0.05); +, size frequencies different by Chi square tests (+ P < 0.05); n.s. P > 0.05.

| Species | Control | A | B | C | A vs B | B vs C |
|-------------------------------------|---------|----------------|----------------|---------------|------------------|-----------------|
| | | 20cc @ 24hr | 6.6cc @ 8hr | 20cc @ 8hr | (fre- quency) | (quan- tity) |
| Tube-Builders | | | | | | |
| <i>Rhynchospio arenicola</i> | 531.0 | 415.7* | 506.3 | 276.0** | * | * |
| <i>Leptochelia dubia</i> | 2600.0 | 1210.3** | 1293.0* | 489.7** | n.s. | ** |
| <i>Axiothella rubrocincta</i> | 6.7 | 5.0 | 4.3 | 11.3 | n.s. | n.s. |
| Burrowers & Mobile Forms | | | | | | |
| <i>Paraphoxus spinosus</i> | 105.7 | 72.0 | 79.3 | 87.7 | n.s. | n.s. |
| <i>Leptosynapta clarkii</i> | 65.7 | 62.7 | 58.0 | 41.7 | n.s. | n.s. |
| Nematoda | 37.0 | 49.7 | 46.7 | 38.7 | n.s. | n.s. |
| <i>Transennella tantilla</i> | 73.0 | 85.7 | 88.3 | 86.7 | n.s. | n.s. |
| <i>Macoma nasuta</i> | 10.0 | 9.3 | 10.3 | 13.3 | n.s. | n.s. |
| <i>Lumbrineris zonata</i> | 7.0 | 2.7* | 5.3 | 6.0 | * | n.s. |

most numerous tube-builders: the spionid polychaete *Rhynchospio arenicola* and the tanaid crustacean *Leptochelia dubia*.

Both quantity and frequency of sediment injections were important in causing mortality of *R. arenicola*. Fewer *R. arenicola* survived the greater fluxes (20 cc @ 8 hr) and more concentrated dosage of the 20 cc per day additions than survived the 6.6 cc @ 8 hr treatment or control conditions. *R. arenicola* constructs tubes of fine sand and deposit feeds on the sediment surface. Due to the breakage of the worms during sample processing, a standard width measurement (3rd setiger) was made and, using whole organisms, the regression of length on 3rd setiger width was calculated [length (mm) = 8.4 (width) + 2.4]. Smaller individuals (less than 5.8 mm long and .4 mm wide), abundant in the T1 and B3 experiments (Fig. 2A), were disproportionately fewer in treatments compared to controls than were adults (up to 9.5 mm long and .8 mm wide). This indicates that the greatest level of mortality occurred among smaller individuals.

L. dubia was an extremely abundant species, with mean densities ranging from 416 in B3 to 2600 in T2 per 100 cm². *L. dubia* was significantly less numerous in 7 of 8 treatments compared to controls (Tables 3, 4). Effects of frequency of sedimentation were not evident but those of quantity of deposition were important to *L. dubia*. The tubes of *L. dubia*, often abandoned and rebuilt, are branched with two openings to the surface (L. Richards, unpub. data). Several individuals were seen swimming after sediment was added but they could not escape from the aquaria. *L. dubia* ingests sediment and detritus on the surface, although mature

Table 4. Summary of sediment deposition experiments on fauna of sites T1 and B3. Mean density per 100 cm³ (n = 3) given. Treatments abbreviated as in text. Statistical analyses as Table 1. (—, treatment not performed).

| Treatment | <i>Rhynchospio arenicola</i> | | <i>Leptochelia dubia</i> | | Other tube-builders | | Burrowing & motile forms | |
|----------------|------------------------------|---------|--------------------------|---------|---------------------|------|--------------------------|-------|
| | T1 | B3 | T1 | B3 | T1 | B3 | T1 | B3 |
| Control | 173.0 | 496.3 | 562.3 | 415.7 | 36.3 | 13.3 | 237.7 | 608.4 |
| a) 20cc @ 24hr | 69.3* | — | 521.3* | — | 26.7 | — | 188.2 | — |
| b) 6.6cc @ 8hr | 129.0 | 283.3** | 566.0 | 212.0** | 46.3 | 6.7 | 267.3 | 580.0 |
| c) 20cc @ 8hr | 97.7* | 152.3** | 346.0** | 161.7** | 45.0 | 7.7 | 219.9 | 516.5 |
| a v b (Freq.) | * | — | n.s. | — | n.s. | — | n.s. | — |
| b v c (Quant.) | n.s. | * | ** | n.s. | n.s. | n.s. | n.s. | n.s. |

* P < 0.05, density

+ P < 0.05, size frequency distribution

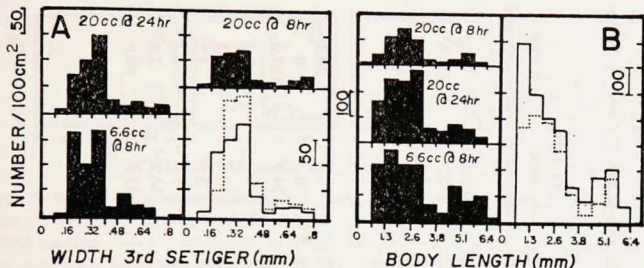


Figure 2. Effects of sediment deposition on size of *Rhynchospio arenicola* (A) and *Leptochelia dubia* (B) in B3 experiments, May 1977. Field controls, ; laboratory controls, ——— ; treatments in cc @ hr (see text) are in black. Scale bar in A = 50 individuals and B = 100 individuals per 100 cm².

males lack mouthparts. Many females were brooding young at sites T2 and B3 during the experimental period and recruitment occurred within those tanks (Fig. 2B). New recruits were defined by a body length of 0-1.6 mm. Mortality was significantly greater among new recruits than among larger individuals having a length up to 6.6 mm (Tables 3, 4, Fig. 2B).

Of the 8 species of burrowers (see also Table 5), only the polychaete *Lumbrineris zonata* had a significantly lower density in any sediment treatment (20 cc @ 24 hr). This result may be spurious, since 20 cc added 3 times as often (every 8 hr) did not elicit a similar decline in density (Table 3).

In summary, the species which were most sensitive to sedimentation in these experiments were dense, shallow-dwelling, tubicolous deposit feeders.

b. Effects of burrowing infauna. A priori hypotheses predicting the effects of bioturbators on community structure were generated from the sediment flux experiments (Tables 3, 4). The mud shrimp *Upogebia* brought sediment to the surface while tunnelling. The lugworm *Abarenicola* also transported sediment to the surface in the form of unconsolidated feces (not bound in mucus). Rates of resuspension 7 cm above the bottom were: (1) controls, 10 cc/tank/day (primarily from the seawater system), and (2) burrower addition, 88 cc/tank/day, an amount which potentially could form a surface layer 18 mm thick over the course of the experiments. However, most sediment deposited on the surface was not resuspended. Photographs of a smaller aquarium (bottom area about 100 cm²) before and 8 d after the addition of 2 *Upogebia* showed the accumulation of sediment above the original T1 surface to be 6-15 mm, with an average of about 10 mm. Hobson (1967) determined that about 3.6 g of sediment passes through the gut of *Abarenicola pacifica* daily at site B4. With 20 worms present in the addition experiment, a

Table 5. Mean densities of infauna per 100 cm² (n = 3 or 4) in laboratory additions of burrowers. Densities significantly different by Mann-Whitney U tests (*), and size distributions significantly different by Chi-square tests (§) are noted.

| Habitat and Year: | | T1 1976 | | T2 1977 | | T1 1977 | | |
|-----------------------------------|-----|-----------------------|-------------------------|---------|----------------------|---------|----------------------|------------------------|
| Duration: | | 6/17-25 | 6/17-25 | 5/18-26 | 5/17-26 | 5/19-29 | 5/19-29 | 5/21-30 ^a |
| Treatment: | | Control | +Burrowers ^a | Control | + <i>Dendroaster</i> | Control | + <i>Dendroaster</i> | + <i>Parastichopus</i> |
| 1. TUBE-BUILDERS | | FT¹ | | | | | | |
| <i>Rhynchospio arenicola</i> | SDF | 94.5 | 57.5*§ | 531.0 | 367.7*§ | 173.0 | 100.3* | 39.7* |
| <i>Leptochelia dubia</i> | SDF | 491.2* ⁴ | 255.2*§ | 2600.0 | 1017.7*§ | 562.3 | 342.7* | 231.0* |
| <i>Axiiothella rubrocincta</i> | DF | 2.0 | 1.2 | 6.7 | 4.3 | 23.0 | 5.6* | 8.0* |
| <i>Onuphis stigmatis</i> | SDF | 21.2 | 13.2* | 20.0 | 12.7* | 13.3 | 10.3 | 15.3 |
| <i>Platynereis bicanaliculata</i> | H | 13.0 | 9.7* | 0 | 0 | 0 | 0 | 0 |
| 2. BURROWING SURFACE FAUNA | | | | | | | | |
| <i>Transennella tantilla</i> | SF | 27.5 | 25.5 | 73.0 | 93.7 | 22.0 | 12.0 | 30.7 |
| <i>Nemertopsis gracilis</i> | P | 3.7 | 2.1 | 2.7 | 7.7 | 0.3 | 0 | 0 |
| <i>Paraphoxus spp.</i> | SF | 18.0 | 22.2 | 148.0 | 90.3 | 132.7 | 94.0 | 147.0 |
| 3. BURROWING INFAUNA | | | | | | | | |
| <i>Lumbrineris zonata</i> | DF | 10.7 | 6.0 | 7.0 | 4.0* | 10.3 | 15.0 | 7.3 |
| Oligochaeta | DF | 17.6 | 17.2 | 1.3 | 1.0 | 7.7 | 3.0 | 3.7 |
| <i>Macoma nasuta</i> | SDF | 0.5 | 1.0 | 10.0 | 6.6 | 4.3 | 5.0 | 6.3 |
| <i>Leptosynapta clarkii</i> | DF | 17.7 | 21.0 | 65.7 | 82.7 | 10.7 | 14.7 | 7.0 |
| Nematoda | — | — | — | 37.0 | 35.0 | 49.3 | 53.3 | 40.0 |

*, § P < 0.05

¹ DF, subsurface deposit feeder; H, herbivore; SDF, surface deposit feeder, SF, suspension feeder; P, Predator

² 10 *Abarenicola* and 4 *Upogebia*, with 2 *Collianassa* removed

³ *Parastichopus* added 5/25/77

⁴ Densities in laboratory control higher than field samples

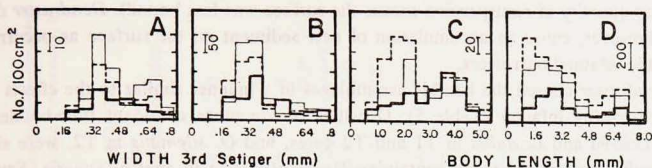


Figure 3. Effects of burrowing infauna (A, C, June 1976) and *Dendraster* (B, D, May 1977) on size of *Rhynchospio arenicola* (A, B) and *Leptochelia dubia* (C, D) in laboratory experiments. Field controls, —; laboratory controls, ----; burrower additions, Scale bars are numbers of individuals per 100 cm²: A, 10; B, 50; C, 20; and D, 200.

sediment layer about 22 mm thick could have formed on the surface in 8 d. Additions of *Upogebia* and *Abarenicola* together give estimates of bioturbation greatly in excess of the amount of sediment added in the deposition experiments (5 or 10 mm accumulating on the surface). I therefore predicted the following: (a) numbers of *L. dubia* and *R. arenicola* should decline in the presence of the burrowers and smaller individuals of both species should be especially affected, and (b) other species affected by the more intense disturbance of the burrowers would have life habits similar to those of *L. dubia* and *R. arenicola*.

As predicted, densities of both *L. dubia* and *R. arenicola* were significantly lower in the burrower additions than in controls and mortality was greatest among small individuals (Table 5, Fig. 3A, C). Two other species, *Onuphis stigmatis* and *Platynereis bicanaliculata*, were also less numerous in the treatment aquaria compared with the control aquaria. Both *O. stigmatis* and *P. bicanaliculata* are tube-builders, but their feeding habits differ from *L. dubia* and *R. arenicola*. *O. stigmatis* feeds from a coarse-sand tube on surface sediment and algae. *P. bicanaliculata* is strictly a herbivore. Woodin (1977) has described how this species gardens its food supply, drift algae, by attaching the algae to its sandy tube. *P. bicanaliculata* is prey for the nemertean *Paranemertes peregrina* (see Roe, 1976). Although alive at site T1 during the June, 1976 experiments, only the jaws of *P. bicanaliculata* could be found there in May, 1977 (Brenchley, 1979). Neither juveniles or adults of *O. stigmatis* or *P. bicanaliculata* were abundant enough to compare size distributions.

Again as predicted, in no case were the densities of burrowing infauna or burrowing surface fauna significantly affected by the addition of the burrowers (Table 5).

c. Effects of burrowing surface forms. The sand-dollar *Dendraster* moved daily in laboratory experiments. Measurements of surface stability demonstrated that after 2 d, *Dendraster* reduced surface stability to levels significantly lower than controls. As an example, a current of approximately 13 cm/sec for 3 min resuspended 5.9 mg/cm² in T1 controls and 12.3 mg/cm² in *Dendraster* additions (note that a

greater quantity of resuspension means the surface was less bound). *Dendraster* did not, however, cause an accumulation of new sediment on the surface as occurred with the infaunal burrowers.

Dendraster altered the benthic assemblages in a manner similar to the effects of the burrowing infauna (Table 5). Densities of the more abundant tube-builders, *R. arenicola* and *L. dubia* in T1 and T2 cores, and *O. stigmatis* in T2, were significantly lower in the tanks containing *Dendraster* than in control aquaria. Small *R. arenicola* and newly recruited *L. dubia* were numerous in the T2 controls and suffered proportionally greater rates of mortality than did adults in the *Dendraster* additions (Fig. 3 B, D).

Axiothella rubrocincta, only abundant in the T1, 1977 experiment, was another tubicolous polychaete that was significantly less abundant when *Dendraster* was present (Table 5). This malidanid ingests sediment at the base of its tube (Weinberg, 1979). Its tube is vertical and rather rigid.

Lumbrineris zonata was the only burrower which was significantly less abundant in the presence of *Dendraster* (Table 5). The low density of *L. zonata* in the T2 control (7 per 100 cm²) and treatment (3), and the variability when at low density at other sites, makes the significance of this result questionable.

In contrast to *Dendraster*, *Parastichopus* ingested and defecated sediment on the surface. Fecal castings remained on the surface during the 4 d period during which the young specimen was present. The presence of this deposit feeder altered the T1 assemblage in a manner (Table 5) similar to *Dendraster*, a suspension feeder. Because juveniles of *R. arenicola* or *L. dubia* were not abundant in the T1 experiments in May 1977, size distributions of neither species were significantly altered by *Parastichopus* or *Dendraster* (Table 5, but see effects of *Dendraster* in T2 cores where juveniles were abundant).

d. Field manipulations. *Dendraster* were added to enclosures placed in replicate at 4 field sites for two reasons: a) to test the generality of results obtained under laboratory conditions, and b) to test the generality of its effects on the structure of assemblages of different species. Three field stations, inhabited by a similar suite of species, were also used in laboratory experiments which were run concurrently. The fourth station, B4, was located in the high intertidal zone (see Fig. 1B) and was inhabited by a different set of species. I predicted that the species most affected by *Dendraster* in the laboratory studies would also be inhibited by *Dendraster* in field situations. Furthermore, I predicted that species inhibited by *Dendraster* at site B4 would have similar life habits to those affected at sites T1, T2, and B3.

Densities of species in control cages without *Dendraster* were compared to unmanipulated sites using Mann-Whitney U tests (Table 6). No differences were significant at $P \leq 0.05$ although densities of some tube-builders were consistently

Table 6. Mean density of infauna per 100 cm² (n = 3 or 4) in field experiments involving *Dendroaster excentricus*. Densities in unmanipulated controls are compared to cage controls, and cage controls are compared to treatments, by Mann-Whitney U tests (*); size frequencies by Chi square tests (§).

| Habitat & Date: | | T2 5/15-23/77 | | | B3 5/15-24/77 | | | B4 5/26-6/4/77 | | |
|-----------------------------------|-----------------|---------------|--------------|----------|---------------|--------------|----------|----------------|--------------|----------|
| Treatment: | | Control | Cage control | Addition | Control | Cage control | Addition | Control | Cage control | Addition |
| 1. TUBE-BUILDERS | | | | | | | | | | |
| | FT ¹ | | | | | | | | | |
| <i>Rhynchospio arenicola</i> | SDF | 629.3 | 733.7 | 287.0*§ | 562.7 | 490.5 | 423.7* | 0 | 0 | 0 |
| <i>Leptochelia dubia</i> | SDF | 1768.7 | 1679.7 | 921.3*§ | 185.4 | 136.0 | 9.0*§ | 0 | 0 | 0 |
| <i>Axiothella rubrocincta</i> | DF | 4.7 | 6.3 | 3.7 | 16.4 | 7.0 | 2.7* | 0 | 0 | 0 |
| <i>Onuphis stigmatis</i> | SDF | 20.7 | 23.0 | 15.7*§ | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pygospio elegans</i> | SDF | 0 | 0 | 0 | 0 | 0 | 0 | 204.3 | 172.9 | 46.7* |
| <i>Pseudopolydora kempfi</i> | SDF | 0 | 0 | 0 | 0 | 0 | 0 | 142.7 | 92.3 | 67.0*§ |
| <i>Corophium</i> sp. | SDF | 0 | 0 | 0 | 0 | 0 | 0 | 550.7 | 606.7 | 463.7* |
| <i>Spio filicornia</i> | SDF | 0 | 0 | 0 | 0 | 0 | 0 | 39.7 | 20.3 | 19.0 |
| 2. BURROWING SURFACE FAUNA | | | | | | | | | | |
| <i>Transennella tantilla</i> | SF | 89.2 | 97.7 | 84.7 | 73.0 | 91.5 | 100.7 | 0 | 0 | 0 |
| <i>Nemertopsis gracilis</i> | P | 12.0 | 13.0 | 8.7 | 28.0 | 37.0 | 20.0 | 2.7 | 2.0 | 2.7 |
| <i>Paraphoxus</i> spp. | SF | 117.2 | 93.7 | 114.3 | 23.0 | 36.5 | 12.0* | 3.7 | 5.3 | 0.3 |
| 3. BURROWING INFAUNA | | | | | | | | | | |
| <i>Lumbrineris zonata</i> | DF | 18.3 | 11.0 | 7.3* | 14.8 | 16.5 | 17.3 | 0 | 0 | 0 |
| Oligochaeta | DF | 14.7 | 4.3 | 6.3 | 523.6 | 405.0 | 426.0 | 197.3 | 251.7 | 211.3 |
| Capitellidae | DF | 0 | 0 | 0 | 0 | 0 | 0 | 73.3 | 45.0 | 42.7 |
| <i>Leptosynapta clarkii</i> | DF | 45.5 | 62.3 | 78.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| Nematoda | | 34.5 | 29.7 | 27.7 | — | — | — | — | — | — |

*, § P < 0.05 (as Table 5).

¹ DF, subsurface deposit feeder; H, herbivore; SDF, surface deposit feeder; SF, suspension feeder; P, predator.

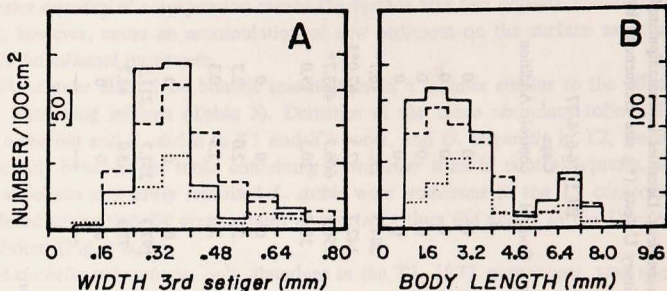


Figure 4. Effects of *Dendraster* on size of *Rhynchospio arenicola* (A) and *Leptochelia dubia* (B) in field experiments at site B3 in May, 1977. Unmanipulated controls, —; cage controls, ---; *Dendraster* additions, Scale bars are 50 in A and 100 in B (individuals per 100 cm²).

lower within cage controls, especially at site B4. Densities of mobile surface fauna tended to be higher within cage controls than outside cages at site B3.

As predicted from laboratory studies, populations of *R. arenicola*, *L. dubia*, *A. rubrocincta*, and *O. stigmatis* were significantly less abundant when *Dendraster* were present than when not (Table 6). While *A. rubrocincta* were too rare to compare size frequency distributions, mortality or emigration of the other 3 named species was significantly more frequent among small individuals (compare Fig. 4 A, B; see also Table 6). Seen swimming in laboratory tanks and known to abandon their tubes, *L. dubia* showed the most dramatic declines in abundance, from 136 to 9 per 100 cm² at site B3 and from 1680 to 921 at site T2.

As predicted, three species of tube-builders, found only at site B4, were significantly less abundant when *Dendraster* were present (Table 6). Two are spionid polychaetes, *Pygospio arenicola* and *Pseudopolydora kempji japonica*, and one amphipod of the genus *Corophium*. Small *P. kempji* were numerous and suffered disproportionately higher rates of mortality than did their adults (see Table 6). Juvenile *Corophium* sp. were also numerous, but mortality or emigration was equally distributed over all size classes of this tube-builder.

With few exceptions, densities of burrowing infauna and surface fauna were not significantly altered by the presence of the sand-dollar in the field studies (Table 6). One exception was the T2 population of *Lumbrineris zonata*, although the equally dense B3 population did not show significant changes. Mortality or emigration rates of *L. zonata* were similar for juveniles and adults. Densities of *Paraphoxus spinosus* and *P. tridentatus* were greatest within cage controls. Their densities in *Dendraster* enclosures were significantly lower than densities of cage controls, but their densities:

did not differ significantly from unmanipulated areas. Thus, the result may be a cage artifact (see Virnstein, 1978). Densities of the predatory nemertean *Nemertopsis gracilis* at site B3 were distributed similar to those of *Paraphoxus* spp., but variability was too great to determine if this pattern was significant.

4. Discussion

a. Mechanisms of interactions. The results demonstrate that densities of tube-builders are reduced in the presence of bioturbating organisms. Results of sediment deposition experiments (Tables 3, 4), similar to those of the biological experiments (Tables 5, 6), implicate the importance of physical events to these interactions.

Densities of the two most numerous tube-builders, *R. arenicola* and *L. dubia*, both surface deposit feeders, declined when sediment was added to aquaria (Tables 3, 4). McLauchlan (1974) has shown a similar result with a tubicolous deposit feeder of fresh-water lakes. *R. arenicola* use fleshy appendages (palps, parapodia, pygidium) to remove sediment from their tubes while *L. dubia* are equipped with jointed appendages and create currents by flexing their abdomen. *L. dubia* could flush small quantities of sediment from their tubes better than *R. arenicola* could since frequency effects (sudden versus more chronic conditions of the same daily flux) were evident for *R. arenicola* but not for *L. dubia*. Sediment in tubes is known to impede the replacement of fouled water with surface water (see Foster-Smith and Shillaker, 1977; Brown and Rosen, 1978). High mortality rates of smaller individuals (Fig. 2) are consistent with the fact that smaller individuals consume oxygen and organic matter dissolved in water faster than do larger ones (e.g., Reish and Stephens, 1969).

Sedentary suspension feeders are similar to tubicolous infauna in these particular ways: both live a rather sedentary existence, keep a permanent connection with the sediment surface, and may starve or suffocate when exposed to high levels of suspended particles. Reduced filtration rates (e.g., Stone and Palmer, 1975; Gerodette and Flechsig, 1979), lower growth rates (e.g., Pratt, 1953; Aller and Dodge, 1974), and high larval mortality rates (e.g., Loosanoff, 1962) are typical responses of sedentary suspension feeders, not represented in this study, to high levels of suspended particles. In contrast, many suspension feeders of intertidal and shallow subtidal habitats are active burrowers, represented in this study by the small clam *T. tanilla* and amphipods *P. spinosus* and *P. tridentatus*, which seek temporary shelter in the sediment and return to the surface or water column to feed during high tide or at night. This vagility can explain the apparent ability of these suspension feeders to escape burial or suffocation (see Tables 3, 5, 6).

Many of the burrowers and tube-builders of this study have similar feeding behaviors or life histories and live in the same shallow layer of sediment (Table 2). For example, the holothurian *Leptosynapta clarkii* lives "up-side-down" in the

sediment like *A. rubrocincta* but it moves to a new feeding site every few days (see Myers, 1977a) and is not restricted by a rigid tube like *A. rubrocincta*. Like several tube-builders, *L. clarkii* and the clam *T. tantilla* were recruiting in May, 1977 (when 8 of the 9 sets of experiments were done). Analyses of their size frequency distributions showed no change under experimental conditions (Brenchley, 1978). Significant treatment effects were detected among many tube-builders whose initial densities were comparable to many burrowers, yet significant effects were rarely seen even for the most abundant burrowers (Tables 5, 6).

In summary, relative mobility, sedentary or tubicolous versus mobile or burrowing, generally seems to characterize those organisms most affected—Group I of Table 2, and least affected—Group II, by the presence of bioturbators and by sediment deposition, a physical property of bioturbation.

b. Community structure. Sediment was redistributed in four observable ways (Table 1), and despite differences in the physical (Fig. 1B) and biological character of the 4 sites and assemblages (see Section 1), these disturbances had a similar effect on community structure (Table 7). A reduction in the numbers of surface deposit feeding, tubicolous species caused the percentages of burrowing forms, subsurface deposit feeders, and suspension feeders to rise in each experiment. This result conflicts with Rhoads and Young's (1970, 1971) hypothesis of "trophic group amensalism," which associates bioturbation with deposit feeders (but see Table 1) and predicts that these forms will selectively remove sedentary suspension feeders but will not inhibit other deposit feeders (thus, amensalism), so that the trophic structure will favor deposit feeders. Rhoads and Young limited their hypothesis to deeper water because seagrasses and tube-builders, common in shallow water, bind the bottom and might render bioturbation ineffectual. The presence of seagrasses (site T1) and dense tube-mats of infauna (sites T1 and T2) were associated with stable surficial sediments, yet bioturbation remained an important structuring agent in this study (Table 7).

A general hypothesis that emphasized relative mobility—sedentary or tubicolous versus mobile—would explain examples of trophic group amensalism known for deeper waters (e.g., tube-builders and mounds of burrowing holothurians—Rhoads and Young, 1970), shallow waters (e.g., sedentary corals and burrowing crustaceans—Aller and Dodge, 1974), and intertidal habitats (e.g., phoronids and burrowing crustaceans—Ronan, 1975), and also Myers' (1977b) apparent exception to that hypothesis which involved organisms of similar mobility (tubicolous deposit feeders and sedentary suspension feeders). This emphasis on mobility would also predict that bioturbation could result in the zonation of deposit feeders (e.g., tubicolous amphipods and burrowing bivalves—Vassallo, 1969), and suspension feeders (e.g., burrowing and sedentary clams—Sanders *et al.*, 1962), and their co-existence when mobilities are similar (see O'Connor, 1972; Thayer *et al.*, 1975;

Myers, 1977b; Brenchley, 1978). However, the application of a model based on relative mobility will be limited by the fact that the spectrum of mobilities is continuous (see Jumars and Fauchald, 1977), and some, albeit few species of tube-builders are mobile or themselves bioturbators (e.g., *Clymenella torquata* and *Pectinaria gouldii*, see Rhoads, 1967, 1974).

The significant levels of mortality among tube-builders measured here in short term (7-10 d) experiments involving contrived situations raise the question as to whether bioturbators have similar effects on community structure in nature. The role of bioturbation can only be inferred from most experimental field studies involving bioturbators due to the predatory activities of the species studied and the artifacts of cages (Virnstein, 1978; Reise, 1977). Studies that have simulated bioturbation by manually disturbing the surface (Orth, 1977; Virnstein, 1977, 1979) or by increasing rates of deposition (McCall, 1977, 1978), or by excluding the bioturbators (Orth, 1977; Virnstein, 1977, 1979; Woodin, 1978; Smith, 1980; Wiltse, 1980), show that excepting prey, shallow-dwelling, surface-deposit feeding, tubicolous species are generally inhibited by bioturbators or the assumed mechanism of bioturbation, as shown also in this study. Smith's (1980) study of *Dendraster* in False Bay shows that this sand-dollar was maintaining tube-builders at low density in its natural habitat near sites T1, T2, and B3 (see Fig. 1B), a result predicted by this concurrent study (Table 6).

Although laboratory studies performed in conjunction with field studies should provide a powerful tool to identify possible mechanisms of interactions and the organisms which are involved, few manipulations of infaunal assemblages have been reported from laboratory settings (see Peterson, 1980). Tube-builders were the species most sensitive to the disturbances associated with the gathering of cores, as they were to other forms of sediment disturbance, yet densities were not significantly altered by that disturbance in this study. In fact, the only significant difference in density involved *L. dubia*, whose density was sometimes greater in the laboratory than in field samples because broods were released and subsequently recruited within the confines of the aquaria. As a result, adult-juvenile interactions (Woodin, 1976) could be documented, a difficult task in the field. In the laboratory, physical events can be separated from other biological activities (e.g., accidental ingestion of infauna) by simulating the mechanism of interaction. However, sediments deposited on the surface by burrowers accumulated in the laboratory, whereas in the field such sediments are redistributed by currents so that the effects of bioturbators may be magnified under laboratory conditions. Field experiments must, therefore, accompany laboratory studies if realism is the objective.

5. Conclusions

The results of this study stress a need to shift emphasis from trophic group to

Table 7. Changes in community composition associated with the presence of bioturbators for 7-10 days in laboratory and field experiments. Total average densities of organisms are listed by mobility group and by trophic group. Changes in percentages of groups sum to 0 within these two categories and reflect proportional changes in community composition.

| Experiment | Mobility groups | | | Feeding groups | | | Other ¹ |
|-------------------------------|-----------------|-------------------|--------------------|--------------------|-----------------------|------------------|--------------------|
| | Tube-builders | Surface burrowers | Infaunal burrowers | Surface deposit f. | Subsurface deposit f. | Suspens. feeders | |
| 1. Laboratory | | | | | | | |
| <i>Infaunal Burrowers, T1</i> | | | | | | | |
| Control | 609.0 | 49.2 | 46.5 | 607.4 | 37.1 | 45.4 | 16.7 |
| Treatment | 334.8* | 50.7 | 45.1 | 326.9* | 53.0 | 47.7 | 11.8 |
| % Change | -8.7 | +4.8 | +3.9 | -10.3 | +5.4 | +4.6 | +0.3 |
| <i>Dendraster, T2</i> | | | | | | | |
| Control | 3159.0 | 223.7 | 118.3 | 3161.0 | 116.3 | 221.0 | 2.7 |
| Treatment | 1402.4* | 191.7 | 132.0 | 1404.7* | 129.3 | 184.0 | 7.7 |
| % Change | -8.9 | +4.7 | +4.2 | -8.9 | +4.2 | +4.4 | +0.3 |
| <i>Dendraster, T1</i> | | | | | | | |
| Control | 783.0 | 154.0 | 87.3 | 752.3 | 118.0 | 154.7 | 0.3 |
| Treatment | 463.2* | 106.0 | 94.0 | 468.0* | 89.2 | 106.0 | 0.0 |
| % Change | -6.7 | +1.0 | +5.7 | -2.8 | +1.9 | +0.9 | 0 |

Parastichopus, T1

| | | | | | | | |
|-----------|--------|-------|------|--------|-------|-------|-----|
| Control | 783.0 | 154.0 | 87.3 | 752.3 | 118.0 | 154.7 | 0.3 |
| Treatment | 301.3* | 177.7 | 70.3 | 292.3* | 79.3 | 177.7 | 0.0 |
| % Change | -21.6 | +17.3 | +4.3 | -20.2 | +2.9 | +17.3 | 0 |

2. Field Experiments—

Dendraster

| | | | | | | | |
|-----------------------|---------|-------|-------|---------|-------|-------|------|
| T2 Control | 2424.0 | 218.4 | 122.9 | 2418.7 | 118.2 | 206.4 | 12.0 |
| Cage Control | 2443.0 | 204.4 | 107.3 | 2436.4 | 113.9 | 191.4 | 13.0 |
| Treatment | 1229.0* | 207.7 | 119.6 | 1224.0* | 124.6 | 199.0 | 8.7 |
| % Change ² | -9.7 | +5.9 | +3.8 | -9.8 | +3.9 | +5.8 | +0.1 |
| B3 Control | 766.1 | 124.0 | 538.4 | 748.1 | 556.4 | 96.0 | 28.0 |
| Cage Control | 634.5 | 165.0 | 421.5 | 626.5 | 438.5 | 128.0 | 37.0 |
| Treatment | 435.3* | 132.7 | 443.3 | 432.7* | 445.9 | 112.7 | 20.0 |
| % Change ² | -9.3 | -0.3 | +9.5 | -8.1 | +6.4 | +0.7 | -1.0 |
| B4 Control | 937.4 | 6.4 | 207.6 | 937.4 | 207.6 | 3.7 | 2.7 |
| Cage Control | 891.3 | 7.3 | 296.7 | 891.3 | 296.7 | 5.3 | 2.0 |
| Treatment | 596.4* | 3.0 | 254.0 | 596.4* | 252.0 | 0.3 | 2.7 |
| % Change ² | -4.7 | -0.3 | +5.2 | -4.7 | +4.9 | -0.3 | +0.1 |

¹ Herbivores and predators² Cage control versus treatment*Significantly different ($P \leq 0.05$) from the appropriate control by Mann-Whitney U tests.

relative mobility (sedentary or tubicolous, mobile or burrowing) in hypotheses relating bioturbation to benthic community structure. This shift, while consistent with examples of trophic group amensalism (Rhoads and Young, 1970, 1971), predicts patterns of coexistence and zonation of feeding groups which are not explained by, or contrary to, a feeding group hypothesis. Both deposit feeding and suspension feeding bioturbators (Table 1) altered community composition (Table 7) by reducing densities of tube-builders, but not other burrowers, an effect which altered the trophic composition in variable ways.

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