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Disturbance, sediment stability, and trophic structure of soft-bottom communities

by P. K. Probert[1]

ABSTRACT

Previous studies of marine soft-bottom communities have shown (1) that natural disturbances (especially biologically-mediated disturbances, which are usually localized and recur reasonably frequently) help maintain spatio-temporal heterogeneity of communities, and (2) that biogenic modification of sediment can affect sediment stability with respect to fluid forces and geotechnical properties and that this is an important factor in community organization, particularly in the trophic structure of the macrofauna. It is argued in this paper that natural disturbances, and the ensuing biogenic alterations to sediment stability, may be important in maintaining trophically-mixed communities where deposit feeders do not have an overriding influence on sedimentary properties. The hypothesis is presented that an initial post-disturbance response by micro- and meiobenthos leads to an increase in sediment stability as a result of mucous-binding of sediment, and that this stage may be of critical significance to potential suspension-feeding colonists if they are competing with deposit feeders for space. It is suggested, partly as a corollary to this hypothesis, that there may be marked differences in the structure and function of meiofaunal communities co-occurring with deposit-feeding and suspension-feeding macrofaunas. Implications for macrofaunal trophic structure of seasonal changes in sediment stability are also examined. Several areas for future research are recommended.

1. Introduction

A correspondence between sediment types and major benthic assemblages has long been recognized (see e.g., review by Pérès, 1982). Moreover, the bottom fauna and flora can themselves substantially alter the properties of a sediment (e.g., Rhoads, 1974; Webb *et al.*, 1976; McCall and Tevesz, 1982). This biogenic influence is generally minimal where, for instance, tidal currents or wave surge have an overriding impact but, where physical processes are less rigorous or are infrequent, biologically-induced modifications to the sediment-water interface assume increasing importance, and the structure of the benthic community becomes defined in part by the dynamic inter-relationships between the sedimentary requirements of one species, the changes to the sediment effected by another, and the hydrodynamics of near-bottom flow.

Benthic organisms, by their various activities, can alter sedimentary properties in a

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number of ways, for example by affecting inter-particle adhesion, grain-size distribution through the formation of fecal pellets, sorting, water content, and bed roughness, and these in turn may alter the stability of the sediment with respect to fluid forces and geotechnical properties. In many shelf and other shallow-water soft-bottom communities, biogenic modifications to the sediment appear to play a critical role in interactions between deposit-feeding and suspension-feeding components of the benthos. An interaction that appears to be of pivotal significance is that of "trophic group amensalism" hypothesized by Rhoads and Young (1970). Intensive near-surface reworking of a mud bottom by infaunal deposit feeders may produce "an uncompacted granular surface consisting of fecal pellets and reworked clasts of semiconsolidated mud." The increased sediment water content (>60% at the surface of highly reworked sediments) and increased roughness of the sediment-water interface lowers the shear velocity for erosion. Rhoads and Young proposed that this change would be stressful to suspension-feeding benthos as it may result in the clogging of filtering and respiratory structures, aid in resuspending and burying newly settled suspension-feeding larvae, or discourage their settlement. Thayer's (1975) study also indicates that a decrease in the bearing capacity of reworked sediment may pose particular problems for suspension feeders because they risk losing contact with their food supply in the overlying water. Consequently, even when food is not limiting to suspension feeders, they may be excluded from muddy shelf sediments as a result of the activities of deposit feeders affecting both fluid/sediment dynamics and the geotechnical properties of muddy sediments.

Gray (1981) critically examined factors controlling benthic community structure and argued that, in reality, end-member communities sharply distinguishable on the basis of their trophic composition are rare, and that mixed communities of deposit feeders and suspension feeders tend to be the general rule. He concluded that although interference competition is undoubtedly important in structuring benthic communities, and may result in the exclusion of suspension feeders from a defined area, "it is more likely that it results in their absence only from small-scale patches and causes local temporal changes in dominance patterns." Similarly, Woodin (1976) argued that dense assemblages of infaunal deposit feeders and suspension-feeding bivalves can occur separately as discrete patches within the other assemblage type. This spatial heterogeneity of benthic populations may account for spatial micro-variability in the critical shear velocity of fine-grained sediment; areas of sea bed only meters apart can thereby have critical shear velocities differing by as much as a factor of 2 (Young and Southard, 1978; see also comments of Rhoads and Boyer, 1982, p. 36). In trophically-mixed communities there may, therefore, be marked small-scale spatial differences in sediment stability with respect to fluid forces.

Such heterogeneity is also likely to have an important temporal component, with localized patterns of succession associated with changes in sediment properties. The dynamic nature of shallow-water soft-bottom communities is a characteristic revealed

in many studies (e.g., Eagle, 1975; Ziegelmeir, 1978) and recognition of this feature led to the development of conceptual models in which such communities are interpreted in terms of spatio-temporal mosaics, each part at a different stage of succession (Johnson, 1972; Grassle and Sanders, 1973), or representing a different state of ecological "neighborhood stability" in terms of changes in dominance patterns of the benthos (Gray, 1977).

A variety of natural disturbances can serve to maintain this structural complexity (e.g., Mills, 1969; Rhoads *et al.*, 1978a; Van Blaricom, 1982). A question that has not, however, been addressed in detail is the effect of natural disturbances on the inter-relationships between sedimentary properties and trophic structure in the community patchwork, though to a large extent this probably reflects the difficulties inherent in conducting appropriate laboratory and field experiments, even with single species. Few studies have been carried out to measure the effect of biological activity on sediment stability (e.g., Eckman *et al.*, 1981; Nowell *et al.*, 1981; Grant *et al.*, 1982), and those researchers who have considered the role of sediment stability in structuring soft-bottom communities have dealt largely with communities that tend toward trophic homogeneity (e.g., Rhoads and Young, 1970; Rhoads and Boyer, 1982).

In this paper I shall consider how disturbances, by affecting benthic community structure and biologically-mediated properties of the sediment, may subsequently influence the trophic dimension of community organization. The paper also examines a related question concerning the implications for trophic structure of seasonal changes in sediment stability. From a consideration of these relationships, some avenues of research are suggested. First, however, a brief discussion of the terms "disturbance" and "sediment stability" is warranted.

a. Disturbance. A disturbance may be defined as an event initiating species populational change from mortality or removal and/or a change in the resource base of the community (Zajac and Whitlatch, 1982). Soft-bottom communities can be affected by a wide variety of disturbances. Typically of large scale, with the area affected often in km^2, are natural disturbances caused by physical factors, such as storms (Eagle, 1975; Carter, 1977; Rees *et al.*, 1977; Glémarec, 1978; Rachor and Gerlach, 1978; McCall, 1978), tidally-induced sand movement (Grant, 1983), internal waves associated with pycnoclines (Carter, 1976), unusually low winter temperatures (Ziegelmeier, 1970), salinity reduction, sometimes with associated hypoxia (Boesch *et al.*, 1976; Stephenson *et al.*, 1977), deposition of fluvial sediment (McKnight, 1969) and associated "mud hopping" (Pilkey *et al.*, 1978).

By contrast, natural disturbances that are biologically caused are typically of small scale, with the affected area usually measured in terms of m^2 or cm^2. Sediment processing by enteropneusts can result in disturbed patches of about 20 cm^2 (Thistle, 1980) to 80 cm^2 (Grant, 1983), and that by a large holothurian 80–700 cm^2 (Rhoads

and Young, 1971). Mounds resulting from burrow excavation by thalassinideans can be of similar size (e.g., Aller and Dodge, 1974) or larger (up to about 0.3 m², Shinn, 1968). Bottom-feeding fish, such as rays, can produce disturbed areas of the order of 500–700 cm² (Gregory *et al.,* 1979) to 0.5 m² (Van Blaricom, 1982; Grant, 1983). Perhaps underestimated in their importance are the local disturbances effected by nearshore populations of several marine mammals while foraging for bottom fauna (Van Blaricom, 1982) (see Oliver *et al.,* 1983, 1984). Of larger magnitude (up to several thousand m²) are disturbances caused by schools of bottom-feeding fish (Fager, 1964; Orth, 1975) and biogenic alteration of sediment grain-size leading to increased susceptibility to erosion (Mills, 1967). Occasionally, biologically-induced disturbances are of large scale, such as the defaunation resulting from red tides (Simon and Dauer, 1977).

Disturbances to soft-bottom communities are also caused by a variety of human activities, such as dredging (Kaplan *et al.,* 1975; Stickney and Perlmutter, 1975; Conner and Simon, 1979), spoil and mining waste disposal (Bourcier, 1969; Leathem *et al.,* 1973; Probert, 1975; Rhoads *et al.,* 1978a), marine mining (De Groot, 1979; Jumars, 1981; Dawson, 1984), organic pollution (Pearson and Rosenberg, 1978), oil pollution (Dauvin, 1982; Elmgren *et al.,* 1983), and bait digging (Jackson and James, 1979; McLusky *et al.,* 1983). A distinction between natural and anthropogenic disturbances may be arbitrary where, for instance, there is physical perturbation of the sea bed.

As Thistle (1981) pointed out, the size of a disturbed patch and the frequency with which patches are produced vary markedly depending on the disturbing agent. Frequency appears to be of particular significance because if a disturbance "recurs frequently enough for there to be reasonable expectation of occurrence within the life cycles of successive generations . . . the selective consequence . . . is therefore likely to be to increase short-term fitness" (Harper, 1977, p. 627). It is the biologically-induced disturbances, resulting, for example, from the activities of bottom-feeding predators, or the burrowing and sediment processing by large infauna, that fall largely in this category. Usually these are also small-scale disturbances in terms of the areal extent of the disturbed patch. Consequently, it is these relatively frequent, localized disturbances that tend to be most important in maintaining spatio-temporal heterogeneity of soft-bottom communities.

b. Sediment stability. Grant *et al.* (1982) have proposed that the net effect of biologically-mediated alterations to the stability of the sediment-water interface be defined by reference to Shields' criterion for the initiation of motion of abiotic sediments; stabilization being defined as an increase of the critical value of shear stress for initiation of motion over Shields' abiotic value, and destabilization as an observed decrease compared to Shields' value. Their results were derived from laboratory flume experiments using moderately well-sorted fine sand (<2% silt-clay) and suggest that

the use of Shields' criterion is appropriate for sediment classified as noncohesive in its abiotic state. A comparable hydrodynamic criterion for defining net biological stabilization or destabilization of muddy sediments is lacking. Cohesion of fine sediments is a complex function of mineral composition, sediment texture, water content, and organic matter content. This means that with abiotic fine sediment (*ca.* <100 μm) there appears to be uncertainty in predicting sediment entrainment as a function of boundary shear stress (Drake, 1976; Nowell *et al.*, 1981). (See Rhoads and Boyer (1982) for an evaluation of the literature on how biological changes in mass sedimentary properties might influence the erodibility of cohesive sediments.)

There is thus a problem, when dealing with a range of sediment types, of quantifying the relative stabilizing or destabilizing effect of a biologically-mediated change in a sedimentary property. In this paper, therefore, the term sediment stability is usually (unavoidably) used in a qualitative sense with respect to biogenic modifications to sedimentary properties that appear potentially significant in influencing sediment stability in terms of fluid forces or geotechnical parameters (e.g., changes in bed roughness, grain size, inter-particle adhesion, sediment packing, shear strength, and water content) (Rhoads and Boyer, 1982). Grant *et al.* (1982) have pointed out the difficulty, resulting from our present limited understanding, of relating "changes in sediment stability [with respect to fluid forces] to any single biological mechanism or process, because several biogenic factors may be operating simultaneously. . . . It is the sum of all biological and physical effects within a given sediment which determines stabilization or destabilization." One can, nevertheless, distinguish major biogenic mechanisms that may influence types of sediment stability. Also, it may often be possible to identify which mechanism is likely to be most important in a particular situation, and in this paper it is argued that following a disturbance, or during a seasonal period of altered sediment stability, the influence of micro- and meiobenthos on sedimentary properties may be important to potential suspension-feeding colonists in trophically-mixed communities.

2. Biological factors affecting sediment stability

a. Microorganisms and algae. Microbial populations of marine sediments are largely associated with particle surfaces and this has important biological implications for the sedimentary environment (Anderson and Meadows, 1978). Webb (1969) drew attention to the significant effects that bacterial films can have on sediment properties, particularly through increasing the adhesion between particles and altering the granulometry (see also Weise and Rheinheimer, 1978). Extracellular and autolytic products of microorganisms living on the grains and within the interstices can also foster sediment stability through the accumulation of mucilaginous materials (Frankel and Mead, 1973). Flume experiments by Rhoads *et al.* (1978b) on the effect of microbial growth and mucous binding on bottom erodibility showed that the growth of

heterotrophic microorganisms on glass microbeads (5–350 μm) increased the critical rolling velocities by 25–60%. Particle-to-particle adhesion increased within a period of 3 to 15 days and then levelled off or declined, possibly as a result of the build-up of interstitial metabolites or grain aggregation, but the decline could be reversed by the addition of a bacterial growth medium.

Frostick and McCave (1979) showed that seasonal accretion of estuarine sediment can be mediated by filamentous and unicellular algae which slow the near-bed flow and bind sediment through the secretion of mucilage. Neumann *et al.* (1970) described subtidal sandy sediments bound by algal mats which, in *in situ* flume experiments, can withstand current velocities 2–5 times higher than those necessary to erode unbound sediment. The sediment grains are bound to each other and to the mat network by mucilage secreted by blue-green algae and diatoms in association with fine filaments of blue-green algae (see also Bathurst, 1967).

Coles (1979) observed that the most abundant microalgae on intertidal flats in the Wash (U.K.) are epipelic diatoms which, as a result of a copious production of mucus, trap and bind fine sediment. She found that sediment accretion on mudflats could be stopped by the removal of the microalgae and, conversely, that mud accretion on the sandflats could be induced by the removal of macroinvertebrate grazers/surface deposit feeders. Regulation of microalgal biomass by deposit feeders has also been reported by Pace *et al.* (1979), Branch and Branch (1980) and Davis and Lee (1983). Holland *et al.* (1974) found that the ability of a particular diatom species to reduce sediment resuspension is related to its ability to secrete a mucilaginous substance. As these authors point out, a mechanism for reducing sediment resuspension, and thereby improving light intensity, would be of obvious selective advantage to such plants. The fact that benthic diatoms can photosynthesize efficiently at extremely low light levels (Round, 1971), that vertical migration is common, at least among intertidal species some of which can move several millimeters vertically (Joint *et al.,* 1982), and that some species are known to be able to survive buried in mud several centimeters beneath the surface (Moul and Mason, 1957) indicates that many benthic diatoms can tolerate disturbances of the sediment, as well as being able to influence sediment stability. This influence may extend at least to mid-shelf depths. For 8 stations in the North Sea (46–84 m depth), Brockmann (1937) recorded a mean density of benthic diatoms of 1.7×10^5 diatoms ml sediment^{-1}. Mare (1942) estimated a minimal density of 5.9×10^4 diatoms cm^{-2} in the top 5 mm of a sandy mud bottom at 45 m in the English Channel; and Bougis (1946) found $5–10 \times 10^4$ diatoms cm^{-2} at 30 m in the top 1 cm of mud in the Bay of Banyuls. On mudflat sites studied by Coles (1979), where epipelic diatoms were found to have a marked binding effect on the sediment, densities were $1-5 \times 10^5$ diatoms cm^{-2} on most occasions.

Risk and Yeo (1980) evaluated the importance of organic binding contributed by bacteria and diatoms on a mudflat. They applied a wide-spectrum antibiotic and an algicide to separate plots on the surface of the mudflat. After one tidal cycle each area

was outlined in negative relief indicating that significant erosion had taken place, but it was not possible to compare the degree of binding effected by each group.

b. Meiofauna. Nematodes are usually the dominant meiofaunal group in marine sediments, particularly if the sediment is muddy. Population densities of nematodes in fine-grained shelf sediments can commonly be of the order of $8\text{-}9 \times 10^5$ indivs m^{-2}, but may reach 4 times this density (Juario, 1975). Cullen (1973) observed that meiofaunal nematodes can rapidly establish "an intricate, closely spaced network of thread-like intergranular burrows" within the surface layer of sediment and he presumed the use of mucous secretions for strengthening these structures. Many meiofaunal nematodes are known to produce copious secretions of mucus which agglutinate sediment and, although these help to maintain burrows, Riemann and Schrage (1978) have hypothesized that their principal function is to entrap small detritus particles, bacteria and macromolecules on which the nematode subsequently browses. Evidence that nematodes can stimulate bacterial production in the sediment (Gerlach, 1978), and increase the microbial activity on detritus (Findlay and Tenore, 1982) suggests that they may be doubly effective in binding sediment.

A mucus-trap mode of feeding is apparently used by the harpacticoid copepod *Diarthrodes nobilis* which discharges copious quantities of mucus through large integumental vents (Hicks and Grahame, 1979). Although this is an algal-dwelling species, similar vents occur in sediment-dwelling species of *Diarthrodes,* and many interstitial harpacticoids use mucous strands to anchor themselves to sand grains (Hicks, pers. comm.). Neumann *et al.* (1970) described tightly packed harpacticoid tubes occurring in the surface of sandy sediments. The tubes consist of sand grains held together by mucus and the authors considered these harpacticoids to be important in sediment binding.

Other meiofaunal taxa also secrete mucoid materials, principally for locomotion, adhesion, or protection, which may assist in binding sediment, e.g., ciliates, turbellarians, nermerteans, gastrotrichs and kinorhynchs (Barnes, 1974).

c. Macrofauna. It has often been reported that tube-dwelling infauna increase sediment stability, and tubicolous polychaetes have been considered particularly effective in this respect (e.g., Fager, 1964; Rhoads and Young, 1971; Probert, 1975; Buhr, 1979). However, recent flume experiments by Eckman *et al.* (1981) suggest that direct, hydrodynamic stabilization of sediments by tubes may be the exception rather than the rule. They tested the influence of varying densities of the tube-building polychaete *Owenia fusiformis* on sediment erodibility and found that the sediment bed was destabilized at all tube densities tested (<7000 m^{-2}). Using the results of Nowell and Church (1979), which indicated that the transition from destabilizing to stabilizing conditions (with the production of a skimming flow) occurs when tube analogs (Lego® blocks) occupy about $1/12$ of the bottom area, they estimated that in the case of

Owenia (average tube diameter 2.7 mm), a density of at least 14,500 m^2 would probably be needed to stabilize the sediment by a modification of the structure of near-bed flow. Experiments using tube densities predicted to induce stabilization have not, however, been carried out. Eckman *et al.* (1981) suggested that the increased sediment stability commonly observed with tube-building infauna is usually the result of the mucous binding of sediments by other organisms in the community, such as bacteria, diatoms and certain invertebrates. Irrigation of the tube may promote microbial growth and result in increased mucous binding of the sediment.

Rowe (1974), working in Buzzards Bay, found that a burrowing cerianthid anemone common in the heavily bioturbated sediment (at a density of several per square meter) can markedly influence sediment shear strength. Using a diver-held vane shear apparatus, he found that at distances greater than 20 cm from the tube of the anemone, shear strength in the surface 5 cm is about 0.98 kPa (10 g cm^{-2}), but that from 20 cm away, to the tube, shear strength increases to about 1.83 kPa (18.7 g cm^{-2}). Rhoads and Boyer (1982) have suggested that this increase may be due to mucus from the oral crown spreading over the sediment and causing particle-to-particle adhesion.

Biogenic reworking can decrease the critical erosion velocity of muds (Young and Southard, 1978) and sands (Grant *et al.*, 1982). The effect of bioturbation on muddy sediments and its implications for macrobenthic trophic structure have already been mentioned. Since the hypothesis of trophic group amensalism was first advanced by Rhoads and Young (1970), it has been invoked to explain the distribution of deposit feeders and suspension feeders in many other muddy bottom locations (e.g., Bloom *et al.*, 1972; Aller and Dodge, 1974; Eagle, 1975; Josefson, 1981). It may also be a factor in clean sandy habitats (Myers, 1977b).

3. Disturbance, sediment stability, and trophic structure

Although bioturbation by deposit-feeding macrofauna is commonly reported to have an inhibitory effect on suspension feeders, it is clear that in some cases small-scale biologically-mediated disturbance provides suspension feeders with an opportunity for localized settlement. Fecal mounds (10-30 cm diameter) produced by the holothurian *Molpadia oolitica* in Cape Cod Bay are colonized by a sabellid polychaete, a caprellid amphipod and a lucinoid bivalve (Rhoads and Young, 1971). These authors presumed that the sabellid tubes helped physically bind the mounds, but the results of Eckman *et al.* (1981) indicate that increased sediment stability is more probably attributable to mucopolysaccharides and glycoproteins of microorganisms and small metazoa. Mucous adhesion between the coils of a fecal mound may also help to increase the stability of the incorporated sediment (Nowell *et al.*, 1981). Similarly, Myers (1977b) observed that the fecal mounds of the holothurian *Leptosynapta tenuis* can be colonized by the tubicolous suspension-feeding polychaete *Prionospio heterobranchia*. The positive relief provided by such mounds (2–3 cm in the case of *Molpadia*) enables

suspension feeders to be raised above an interface where trophic group amensalism operates. One would not expect a small-scale disturbance that results in little or negative change in bottom relief to provide suspension feeders with an opportunity for colonization in an area already dominated by motile subsurface deposit feeders. In the absence of such refuges, and where conditions for suspension-feeder colonization are borderline or better, disturbances may result in settlement opportunities for suspension feeders and act as a mechanism in the maintenance of mixed communities in which trophic structure is an important element in the spatio-temporal mosaic (*sensu* Johnson, 1972). I shall, therefore, examine possible post-disturbance events and their implications for the success of suspension-feeder colonization.

a. Post-disturbance response of microorganisms. If faunal elements that cause sediment instability are temporarily removed or depleted as a result of a disturbance, this may permit the influence of sediment-binding members of the micro- and meiobenthos to be realized.

Bioturbation by deposit feeders results in increased depth of the aerobic habitat in the sediment and thus an increase in the surface area available for colonization by microorganisms (Driscoll, 1975). Also, as a result of the exchange of sediment pore water with the overlying water, continual bioturbation "increases the rate of nutrient mixing within sediment and accelerates the rate of flushing of metabolites and growth inhibitors out of sediment" thereby stimulating bacterial growth rates (Yingst and Rhoads, 1980). A small-scale biogenic disturbance, such as the creation of opened patch by bottom-feeding fish, could initially have much the same effect in stimulating bacterial growth rates. Experimental data appear, however, to be lacking to indicate how long this phase might last in the temporary absence of further disturbance and, once peak abundance had occurred, how bacterial density in the patch would compare to the pre-disturbance density.

Production/biomass (P/B) ratios estimated for sediment bacteria indicate generation times of probably not more than a few days. For the northern Baltic, Ankar (1977) estimated an annual P/B ratio for sediment microorganisms of about 30, although if all bacterial production is within the top centimeter of sediment, a turnover ratio of 80, and hence a generation time of 4–5 days, is obtained. Data compiled by Sorokin (1981, Table II) indicate average daily P/B ratios of 0.21 for bacteria of detrital sediments of shallow estuaries and lagoons, and 0.16 for continental shelf sediments, or annual turnover ratios of the order of 75 and 60 respectively. Such estimates may be significantly less than rates achieved as a result of growth-stimulating conditions that may occur following a small-scale biogenic disturbance.

Few data are available on the response of benthic diatoms to disturbances of soft-bottom communities. Lee and Lee (unpubl., cited by Davis and Lee, 1983) observed that defaunated sediment developed a diatom layer within a few days. From experiments performed on an estuarine intertidal flat of well-sorted fine sand, Davis

and Lee (1983) found that defaunated sediment was rapidly colonized by microalgae; chlorophyll *a* and gross primary production returned to control levels within 10 days. (Infaunal density returned to control levels within 40 days.) The ambient microalgal community was composed primarily of a diverse assemblage of pennate diatoms. In shallow-water systems, transport in the water column would enable benthic microalgae to recolonize disturbed areas rapidly (Baillie and Welsh, 1980).

b. Post-disturbance response of meiofauna. There have been several recent studies that help improve our understanding of the likely responses of the meiofauna to small-scale biogenic disturbances. Soft-bottom meiofauna is normally dominated by nematodes, many species of which can affect sediment adhesion through the secretion of mucus (Riemann and Schrage, 1978). In an experimental study of nematode distribution in a beach, Gerlach (1977a) used 50-ml samples of sand in which the fauna had been killed, and found that after one day nematode densities were 13% of ambient levels in unbaited samples and 34% in samples which had been baited with a piece of fish, and that normal population densities were attained after 7 days and 4 days respectively. Sherman *et al.* (1983) reported that nematodes took more than 48 h to repopulate a 0.7-m^2 area of shallow-water fine sand subject to average current velocities, measured 20 cm above the bottom, of 4.3 cm s^{-1}. Sherman and Coull (1980) dug over a 9-m^2 area of intertidal mud to a depth of 15 cm and raked it smooth, and observed rapid (within 12 h) recolonization by meiofauna (91% nematodes) following this disturbance. Here the mean current velocity 1 m above the bottom of 15.5 cm s^{-1}, produced a boundary shear stress (τ_0) of 0.74 dynes cm^{-2} capable of moving nematodes, equivalent to a shear velocity (u_*) of 0.84 cm s^{-1} ($u_* = (\tau_0/\rho)^{0.5}$, where ρ is fluid density = 1.03 g cm^{-3}). Their results indicate that passive horizontal transport of meiofauna in the overlying water may be an important mode of dispersal in areas with appreciable near-bottom water movement (see also Palmer and Brandt, 1981). Hagerman and Rieger (1981) found that meiofauna from a variety of benthic habitats are regularly resuspended in the subtidal water column and that once resuspended, meiofauna may be carried up to 10 km day^{-1} by residual currents. In shallow-water habitats, the sudden excavation of sediment by wave turbulence may temporarily expose meiofauna living just below the sediment-water interface to increased shear stress capable of suspending meiofauna in the water column (Hagerman and Rieger, 1981). Dispersal of meiofauna may also be aided by biologically-mediated resuspension of sediment, such as through bioturbation by infaunal deposit feeders in lowering the erosion velocity of fine-grained sediment, or through the feeding activities of macroepifauna in resuspending clouds of flocculent material at the sediment-water interface (Bell and Sherman, 1980). Meiofaunal taxa that are most active near the sediment-water interface, such as harpacticoid copepods, tend, however, to be the most susceptible to resuspension and the most rapid recolonizers of disturbed patches of seabed (Bell and Sherman, 1980; Alongi *et al.,* 1983; Chandler and Fleeger, 1983).

Meiofauna may, however, avoid high bed shear stress by moving down from the sediment-water interface (Rhoads *et al.,* 1977; Hagerman and Rieger, 1981; Palmer, 1984). The extent to which they are able to do this will be largely determined by sediment type and the propensity for burrowing of different species. Coull and Bell (1979) point out that in muddy/detrital sediments meiofaunal densities tend to be high and that most of the meiofauna are located in the oxidized topmost layer of sediment (commonly <2 cm in depth), whereas in clean sands not only are densities usually low, but the depth of the oxidized zone (often at least 15 cm) enables much greater vertical penetration of the sediment. In muddy sediments with an abundance of deep-burrowing deposit feeders, oxidized sediment may, however, reach to a depth of more than 10 cm (Rhoads and Boyer, 1982).

These differences in meiofaunal abundance and vertical distribution between sediment types may commonly be accompanied by differences in the structure of the macrofaunal community. Typically, suspension-feeding and deposit-feeding macrofaunal soft-bottom communities are best developed on different sediment types. The proportion of deposit feeders generally increases with decreasing grain size (McNulty *et al.,* 1962; Purdy, 1964; Grange, 1977) whereas, although there is generally a marked increase in the proportion of suspension feeders with an increase in grain size (Craig and Jones, 1966), there may often be a peak in abundance at an intermediate grain size (Sanders, 1958); McNulty *et al.,* 1962; Bloom *et al.,* 1972). Mixed sediments, particularly muddy sands, and also fine sands, commonly support communities in which both suspension feeders and deposit feeders are well represented (see e.g. Jones, 1950; Craig and Jones, 1966). The addition of only a small quantity of silt to a clean sand can markedly decrease sediment permeability and thereby the depth of the oxidized layer (Webb, 1958). Thus, sediments dominated by suspension feeders are often likely also to have a meiofauna of low faunal density that is widely dispersed vertically in the sediment, whereas sediments dominated by deposit feeders or with a trophically-mixed macrofauna are more likely to support a meiofauna of high faunal density confined to a narrow topmost layer of sediment (except where there is an important deep-burrowing deposit-feeding macrofauna). Suspension-feeding communities normally experience higher current velocities than deposit-feeding communities (Wildish, 1977). Nevertheless, for reasons of faunal density and vertical distribution in the sediment, the resuspension of meiofauna may conceivably be as prevalent on muddy bottoms dominated by deposit-feeding macrofauna as on clean sands supporting suspension feeders.

The work of Warwick and Uncles (1980) gives some indication of the potential for meiofaunal resuspension in trophically-mixed macrofaunal communities. They found the distribution of macrofaunal communities in the Bristol Channel (U.K.) to be closely related to the tidally averaged bed shear stress for M_2 tides. The principal soft-bottom communities are *Venus* and *Abra* communities (*sensu* Thorson, 1957) which are associated with areas subject to $\tau_0 < 9$ dynes cm^{-2} ($u_* < 3$ cm s^{-1}). Studies

at representative stations in the *Venus* (*Tellina*) community at 17 m on very fine sand (Warwick *et al.,* 1978) and in the *Abra* (pure) community at 18 m on sandy mud (Warwick and George, 1980) illustrate that both are trophically-mixed communities dominated by a single species of suspension-feeding bivalve (*Pharus legumen* and *Spisula elliptica* respectively). Mean τ_0 values experienced by the *Venus* (*Tellina*) and *Abra* (pure) communities are about 2 dynes cm^{-2} and 3 dynes cm^{-2} respectively ($u_* = 1.4$ cm s^{-1} and 1.7 cm s^{-1}) (estimated from Warwick and Uncles, 1980, Fig. 4b), values which, from the field study of Sherman and Coull (1980), indicate a potential for transport of the associated meiofauna by tidal currents.

In addition to the probable importance of passive dispersal of meiofauna (very few meiofauna species have a pelagic larval stage, Gerlach, 1977b), active migration and habitat selection are undoubtedly important and may cause small-scale spatial patchiness shown by many meiofaunal populations (e.g., Arlt, 1973; Findlay, 1981). The ability of meiofauna to choose a particular microhabitat appears to be influenced largely by the taxonomic composition of the sediment bacteria (e.g. Gray, 1968; Lee *et al.,* 1977). Some harpacticoid copepods can even discriminate between different strains of bacteria offered as food (Rieper, 1982). Given the known sensitivity of meiofauna to microhabitat changes it is likely that a small-scale disturbance will result in a patch that is, or quickly becomes, distinguishable by its microbial community. Processing of sand by the sand dollar *Mellita quinquiesperforata* results in modification of the benthic microbial community (White *et al.,* 1980). Fecal mounds produced by the enteropneust *Ptychodera bahamensis* have a different microbial flora to that of the ambient sediment (Thistle, 1981) and this may be the case with the *Molpadia* mounds studied by Rhoads and Young (1971).

Recent studies provide little evidence that disturbances in themselves are important for maintenance in the community of opportunistic species of meiofauna that can, in the absence of competitors, quickly exploit new habitat patches (Sherman and Coull, 1980; Reidenauer and Thistle, 1981; Hogue, 1982; Sherman *et al.,* 1983; but see Alongi *et al.,* 1983), although, as Thistle (1981) points out, species may respond to a favorable resource generated by a disturbance independent of the relaxation of competition (see e.g. Thistle, 1980; Van Blaricom, 1982). The growth-enhancing conditions for microorganisms that may occur at a newly disturbed patch (Yingst and Rhoads, 1980) are likely to provide an attractive resource for meiofauna.

c. Post-disturbance response of macrofauna. Early studies of macrofaunal recolonization focused on large natural physical disturbances, or the effects of dredging and spoil disposal, and often significant recolonization had occurred by the time the first post-disturbance samples were taken; precise data on the rapidity of recolonization are generally lacking. McCall (1977) placed 0.1-m^2 samples of defaunated mud on the bottom of Long Island Sound at a depth of 14 m and found after 10 days, when the first samples were recovered, that 14 species were present with a total abundance of 4.7×10^5 indivs m^{-2}. Santos and Simon (1980) studied the macrofaunal recolonization of a

large (>3 km^2) soft-bottom area of a Florida bay (water depth of 4–5 m) following summer defaunation attributable to anoxic conditions. They initiated a recolonization experiment immediately after the annual die-off using cups containing azoic sediment. After 7 days, when the first cups were recovered, 15 species were present with a total density of about 8 × 10^4 indivs m^{-2}. Appeciable mortality is generally observed after the initial colonization. In the experimental study of Santos and Simon (1980) total density after 14 days was about 2.5 × 10^4 indivs m^{-2}. In McCall's (1977) study, the next samples were not taken until 86 days after the start of the experiment when total density had fallen to about 3 × 10^4 indivs m^{-2}. McCall (1977) and Santos and Simon (1980) found that more than 90% of individuals were recruited as larvae, but in both cases the containers used were mounted above the bottom which presumably impeded recolonization by adults. However, in the case of large areas of open habitat, initial recolonization by motile adults invading from the edges will be less important than that effected through the water column (Santos and Simon, 1980). Recent results of Bell and Devlin (1983) show that certain adult macrofauna can recolonize small patches (100 cm^2) of defaunated sediment within 7.5 h.

d. Hypothetical model of post-disturbance succession in a trophically mixed community. Rhoads and Boyer (1982) have described an "end-member" successional model of the organism-sediment relations following a physical/chemical disturbance of the sediment that removes or kills most of the macrofauna. The model is based largely on the successional patterns occurring on muds, especially dredge spoils, where bioturbation by infaunal deposit feeders of the equilibrium community may have an overriding influence on community trophic structure (Rhoads *et al.*, 1977; 1978a). The model states that the first macrofaunal colonizers are mostly small, opportunistic, tubicolous species of surface deposit or suspension feeders, which have little bioturbating effects, but that in the absence of further disturbance, these are eventually displaced by infaunal deposit feeders which come to dominate the fauna, eclipsing suspension feeders as a result of trophic group amensalism.

However, where there is the potential for a mixed community to exist, then recolonization does not always lead to deposit-feeder dominance. Where a poly-climax is possible, as appears commonly to be the case with benthic communities (Gray, 1981), succession may result, unpredictably, in one of a series of states, each with a different dominance pattern of the benthos (Gray, 1977). In this case a disturbance may facilitate a switch in the dominant trophic group of a patch. Whether such a change occurs will depend largely on the rapidity of the micro-, meio- and macrobenthic responses to a disturbance. The limited data available indicate that the pattern of succession following a disturbance will be governed to a large extent by the size of the disturbance, the currents, ambient fauna, season, and availability of suitable larvae of macrofauna and motile adults, so that several alternative patterns of patch recovery may be possible.

The probability of recolonization being effected chiefly by adult macrofauna will be

inversely related to the size of the disturbed area. The smaller the area the greater the likelihood that the process of recolonization will be dominated by adult macrofauna invading from the edge of the patch, and the smaller the area the greater also will be the eventual resemblance in community structure between the ambient fauna and that of the previously disturbed area. The responses of macrofaunal larvae, meio- and microbenthos are less dependent on patch area, so that for a given habitat there will be a critical patch size above which the larval macrofauna, meio- and microbenthos may mainly determine eventual community structure. An exception to this may occur in the case of certain large-scale disturbances, such as storm events, which hinder the recovery of the microbenthos (Davis and Lee, 1983), but provide a mechanism for widespread dispersal of post-larval macrofauna (Dobbs and Vozarik, 1983).

It seems reasonable to suppose that the potential influence of the micro- and meiobenthic response on the successional process would not be fully realized if there was an immediate post-disturbance colonization by larvae of macrofauna. Larval recruitment among macrofaunal species tends, however, to be highly variable mainly on account of the usually seasonal spawning and the vulnerability of the larvae (Thorson, 1966). Meiofaunal recolonization is likely to be more predictable since, in addition to a rapid response time, annual P/B ratios for meiofauna (~10) usually average at least 5 times those of macrofauna (see Mann, 1982). Similarly, the response of microbenthos following a disturbance is liable to be rapid (Rhoads *et al.*, 1978b; Davis and Lee, 1983) and may be relatively predictable (Baillie and Welsh, 1980). If, therefore, there are few suitable larvae of macrofauna available for immediate colonization, as may often be the case, initial post-disturbance events will be characterized mainly by a period of increased microbenthic production and rapid repopulation by a nematode-dominated meiofauna (which may further stimulate bacterial production). Activities of a microbenthos-nematode association will tend to increase sediment stability through mucous binding. Colonization at this stage by bioturbating species would severely curtail eventual exploitation of the patch by suspension feeders. This may, therefore, be an especially opportune time for suspension feeders to settle if they are potential competitors for space in the community (Fig. 1), and there would be strong adaptive advantages for larvae of suspension feeders being able to recognize the appropriateness of these conditions for settlement. Many suspension feeders are sedentary species, and for them the selection of a suitable substratum is a more critical event than for mobile species. Among polychaetes, for instance, the ability to select a particular substratum tends to be far better developed in larvae of adults that are sedentary than in those that are errant (Gray, 1971). In the case of tubicolous suspension feeders settlement may not be possible before a certain degree of mucous binding of the sediment has been attained because of the sediment destabilizing effect, with respect to fluid forces, of isolated tubes (Eckman *et al.*, 1981). This effect may be less important to tubicolous deposit feeders since most species of deposit feeders inhabit areas with low current velocities (Wildish, 1977), and
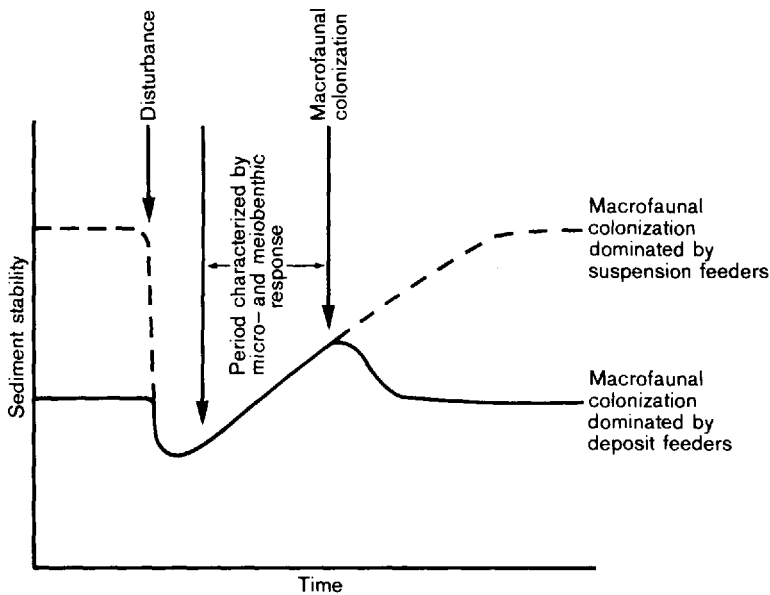
Figure 1. Conceptual scheme of the influence on sediment stability of the timing of micro-, meio-, and macrobenthic responses following a disturbance.

those that feed on the surface have a variety of morphological and behavioral adaptations that enable them to tolerate high levels of suspended solids (Rhoads, 1974).

I suggest, therefore, that sediment stability is likely to increase, with respect to fluid forces and geotechnical properties, during an initial micro- and meiobenthic phase of patch recovery, and that these organisms may provide stimuli that encourage larvae of suspension feeders to settle. The ability of macrofaunal larvae to select a particular substratum is well documented (e.g. Wilson, 1952; Thorson, 1966) and experimental work indicates that microorganisms are largely responsible for the attractiveness of natural sediments (Meadows and Campbell, 1972). In this case bacteria, diatoms and/or their mucous secretions may provide appropriate stimuli. Conceivably, exudates of meiofauna that help bind sediment might also serve as chemical attractants. Disturbance of the sediment may itself provide a geochemical settlement cue for larvae (Cuomo, 1984). Conversely, there is evidence that larvae of several species of sessile epibenthic invertebrates can distinguish and avoid substrata where there is a high probability that post-settlement events will kill them, in this case the recognition of a superior spatial competitor (Grosberg, 1981). Possibly the larvae of some suspension feeders may recognize a settlement of a deposit feeder dense enough to render the sediment uninhabitable to them in the future. Intense adult-larval interactions in conjunction with sediment instability may serve to maintain densities below carrying

capacity (Peterson, 1979) or even supress initial settlement of suspension feeders (Woodin, 1976). Once deposit feeders have colonized a sediment, the physical nature of the sediment-water interface and the degree of mucous binding may provide appropriate physico-chemical stimuli to larvae of suspension feeders as to the suitability of that substratum for settlement. Larvae of macrofauna can delay metamorphosis until a suitable substratum is contacted (Wilson, 1952).

Once a suspension-feeding fauna is established, deposit feeders may have difficulty invading that patch; settling larvae (irrespective of trophic group) risk being filtered from the water (Thorson, 1950; Mileikovsky, 1974) and lateral immigration by adults of motile species may be hindered by pre-emption of space, especially by dense stands of tubicolous species (Brenchley, 1982). Woodin (1976) hypothesized that no infaunal forms should consistently attain their highest densities among densely packed suspension-feeding bivalves. The suspension-feeding component of mixed communities is commonly dominated by one species (Warwick, 1982), which may be explained by Levinton's (1972) hypothesis that there is little scope for trophic diversification among suspension feeders so that one species may exlude others by competition for feeding space (see e.g. Peterson and Andre, 1980). Age-class domination, particularly in the case of tubicolous species which can exclude other larvae and which tend to be annuals, should, however, render the patch short-lived and susceptible to self-destruction (Woodin, 1976).

4. Temporal changes in sediment stability

Seasonal differences in sediment stability may be caused by temperature-related changes in the activity of bioturbators (Yingst and Rhoads, 1978), nutrient flux if coupled to benthic microbial and mucopolysaccharide production (Rhoads and Boyer, 1982), and the build up of bacterial and other metabolites in the sediment over the year (Grant *et al.,* 1982). Predictable, naturally occurring periods of increased sediment stability can be exploited by some suspension feeders (an example of a temporal refuge, *sensu* Woodin, 1978). Yingst and Rhoads (1978), working in Long Island Sound, and Myers (1977a), working in a coastal lagoon in Rhode Island, observed that a depression of bioturbation in winter enabled sediment binding by microorganisms to become effective. In the lagoon studied by Myers (1977b) the virtual cessation of sediment processing (dominated by the holothurian *Leptosynapta tenuis*) in winter coincided with the numerical dominance of the suspension-feeding polychaete *Prionospio heterobranchia* following its reproductive recruitment in the autumn.

Seasonal changes in sediment stability may also result from the migratory behavior or change in foraging activity of bottom-feeding predators, from seasonal growth of microalgae, or from a variety of meteorological conditions such as the formation of seasonal pycnoclines and subsequent development of internal waves capable of eroding bottom sediment (Carter, 1976). In some locations, greater meteorologically-induced disturbance in winter may more than counteract any effects of sediment binding.
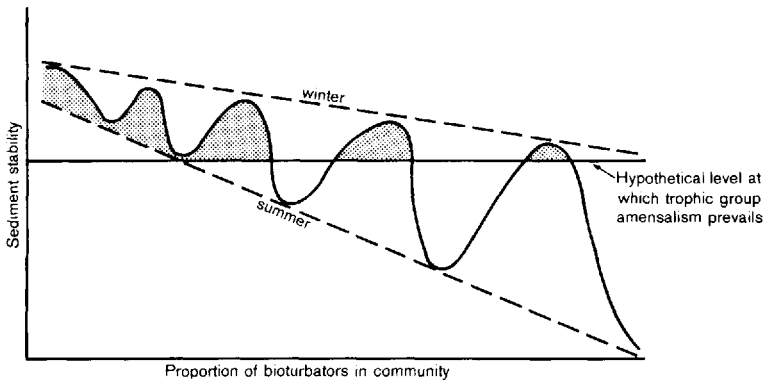
Figure 2. Conceptual scheme of annual changes in sediment stability in relation to the importance of bioturbators in shallow-water soft-bottom communities in temperate waters. Shaded areas represent periods available for suspension-feeder colonization.

Exploitation of a period of increased sediment stability may be a common phenomenon in the case of opportunistic suspension feeders. Rhoads (1974) described how the mortality of deposit-feeder populations of sublittoral muds as a result of an oil spill enabled the mactrid bivalve *Mulinia lateralis* temporarily to exploit the area before the deposit-feeding community became re-established and trophic group amensalism was again operating. If there is a predictable cycle in sediment stability and there are suspension feeders physiologically adapted to take advantage of the opportunity (e.g. if it occurs in winter), there may exist suspension feeders specialized for this niche, in addition to opportunistic species.

Resuspended sediment and detritus represent a food source for some suspension feeders (see e.g. Jørgensen, 1966; Kiørboe *et al.,* 1981; Rhoads *et al.,* 1984), and a lessening of bioturbation in winter may reduce the concentration of biogenically resuspended bottom material to a level where it no longer clogs filtering mechanisms and can be used as a major or complementary source of food. Although the supply of phytoplankton food will be limited in winter, suspension feeders in shallow-water systems may be able to exploit a larger and seasonally stable standing crop of benthic microalgae, a proportion of which is available through resuspension (Baillie and Welsh, 1980).

A decrease in the bearing capacity of the sediment surface may prevent successful larval settlement of suspension feeders (Rhoads and Young, 1970), and for a suspension-feeding species to exploit periods of increased sediment stability, the timing of reproduction would be critical if the species is recruiting into a community dominated by bioturbating species, but assume less importance as the bioturbating element of the fauna declines (Fig. 2). As the potential for bioturbator dominance decreases at a soft-bottom location, then suspension feeders have a greater chance of longer-term spatial separation from deposit feeders rather than a periodic temporal sharing.

5. Recommendations for future research

a. Disturbance, sediment stability, and trophic structure. I have argued in this paper that disturbances, particularly localized biologically-induced disturbances, are likely to be important in maintaining macrofaunal trophic diversity in soft-bottom communities, and that an increase in biogenic sediment stability during initial stages of patch recovery may play a critical role in influencing trophic structure. It is clear that to test this hypothesis, detailed studies would need to be conducted on a variety of aspects of organism-sediment relations. *In situ* studies need to be undertaken in a variety of shallow-water/shelf soft-bottom environments to examine the relative rates of recolonization of micro-, meio-, and macrobenthos, bearing in mind the findings of recent studies which show that significant recolonization may occur within only hours of a disturbance. There is a particular lack of information on the post-disturbance response of sediment bacteria and benthic microalgae. Flume experiments could provide useful information on the influence of benthic organisms on boundary shear stress and erosion velocity (see Rhoads and Boyer, 1982). The effect of micro- and meiobenthic organisms demands especial attention. Experiments need to be performed to determine the response of larvae of macrofauna to patches at different stages of recovery. In particular, do larvae of suspension feeders settle preferentially on patches where micro- and/or meiobenthic organisms have achieved a significant degree of sediment binding? Do extracellular mucopolysaccharides and glycoproteins of microorganisms and meiofauna (e.g., mucus-spinning nematodes) serve as chemical attractants to settling larvae of suspension feeders? (Rhoads and Boyer (1982) point out some of the practical difficulties of assessing the role of mucopolysaccharides in organism-sediment relations.)

b. Meiofauna-macrofauna relations. There is considerable discussion in the literature about different types of macrofaunal groups that may or may not co-occur (e.g. Rhoads and Young, 1970; Woodin, 1976), but so far there has been little consideration of how the meiofauna fit into these models. Considering that the dominant meiofaunal group, the nematodes, may play a significant role in fostering sediment stability, particularly during initial stages of succession following a disturbance, it is worth considering what interrelationships may exist between meiofauna and macrofaunal trophic groups (see Bell, 1980; Bell and Coull, 1980).

Many macrobenthic deposit feeders undoubtedly ingest large numbers of meiofauna, although rapid turnover rates of meiofauna and the ability of some to pass through guts live could still enable them to maintain relatively high population densities (Virnstein, 1980). Meiofauna co-occurring with a predominantly suspension-feeding macrofauna would, by contrast, be subject to only limited mortality by nonselective deposit feeders. One might, therefore, expect a tendency for meiofaunal species with slower turnover rates to co-occur with suspension-feeding macrofauna. There is some evidence for this. An increase in the silt-clay content of fine-grained

sediments is generally accompanied by an increase in the importance of deposit-feeding macrofauna (see e.g., Gray, 1981). For nematodes, it is commonly observed that nonselective deposit feeders normally dominate muddy sediments, whereas epigrowth feeders dominate sands (Coull, 1970; Ward, 1975; Govaere *et al.*, 1980). In general, nonselective deposit-feeding nematodes have faster respiration rates than epigrowth feeders (Warwick and Price, 1979) and thus have higher annual production per unit biomass (Humphreys, 1979).

The mucus-trap hypothesis of Riemann and Schrage (1978) indicates, however, that the question of nematode feeding mechanisms is likely to be more complex than is indicated by the commonly adopted classification of feeding groups of Wieser (1953). From the limited data at present available, nematodes which produce mucus do not appear to be associated with a particular one of Wieser's groups. Of the 14 nematode genera investigated by Riemann and Schrage (1978) which produce mucus (*Spirina* excluded), 4 would be classed as selective deposit feeders (the oncholaimids included here, see Ward, 1975), 6 as nonselective deposit feeders and 4 as epigrowth feeders. Would a mucus-spinning nematode which re-uses its feeding traces be disadvantaged in a sediment that is intensively reworked by macrofauna? If so, one would expect mucus-spinning nematodes to occur more commonly with a macrofauna that has a significant suspension-feeding component. One could conjecture that this situation might even favor the development of a type of mutualism if there is competition for space between suspension and deposit feeders. After a disturbance of the sediment, larvae of suspension feeders would be attracted to settle on areas inhabited by mucus-spinning nematodes, and the nematodes would be able to feed more efficiently in a patch that is not being intensively reworked. Because of their potential sediment destabilizing influence, isolated tube-building suspension feeders may be able to settle only where sediment stability has been increased by nematodes and/or the microbenthos.

c. Ditrophic species. Deposit feeding and suspension feeding are not always clearly distinguishable types of behavior; resuspended bottom material can be an important food source for many suspension feeders (Jørgensen, 1966), and a number of species are capable of both methods of feeding (see e.g., Hughes, 1969; Buhr and Winter, 1977; Fauchald and Jumars, 1979; Salzwedel, 1979; Taghon *et al.*, 1980; Dauer *et al.*, 1981). Taghon *et al.* (1980) suggested that animals able to switch between deposit feeding and suspension feeding typify benthic environments where there is variability in the concentration of suspended particulate matter as a result of varying flow characteristics. Such a variability might reflect primarily a spatial variability in the erosion velocity of fine-grained sediment due to a patchiness of benthic populations (Young and Southard, 1978), and ditrophic species would appear to be well adapted to exploit ecotones between patches occupied predominantly by suspension feeders and deposit feeders. There is evidence that some ditrophic species change their feeding

behavior with season (see Salzwedel, 1979). Temporal variability in particulate flux of bottom water can result, for instance, from a seasonality in the activity of bioturbators (Yingst and Rhoads, 1978), and possibly there are species with feeding adaptations enabling them to contend with cyclical, biologically-mediated, changes in sediment stability. Undoubtedly more infaunal species will be found to possess this type of trophic versatility, but it is unlikely that all such species are gaining the same selective advantage.

d. Paleoecological implications. In this paper I have examined ways by which suspension feeders, in competing for space with deposit feeders, may sometimes circumvent or minimize the problem of trophic group amensalism in modern soft-bottom communities. There may also be paleoecological implications in these strategies. Deposit feeding was probably the last of the basic modes of feeding that evolved among the metazoa (Nicol, 1981). Thayer (1979) suggested that increased bioturbation by deposit feeders has been an important structuring force in the evolution of marine benthic communities. He argued that since the Devonian all benthic groups have suffered a significant reduction among immobile suspension feeders living on the surface of soft substrata, a decline he attributed to a corresponding diversification of deposit feeders able to process large volumes of sediment (e.g. holothurians, irregular echinoids and thalassinidean Crustacea). If large-scale bioturbation has been an evolutionary force in the organization of soft-bottom communities, one would expect there to have been increased pressure on suspension feeders to accommodate, where possible, to the problems of greater sediment instability. I suggest that this pressure may have led to (1) increased spatial separation of suspension feeders from deposit feeders (e.g., greater trophic differentiation in the patch structure of soft-bottom communities, and suspension feeders making more use of spatial refuges, such as fecal mounds and mounds resulting from burrow excavation); (2) suspension feeders making greater use of temporal refuges (e.g., seasonal periods of increased sediment stability); (3) resuspended bottom material becoming more important as a food source for suspension feeders; (4) an increase in the number of benthic species capable of both suspension and deposit feeding given that spatial variability of the erosion velocity of fine-grained sediments attributable to the patchiness of benthic populations may have increased with the diversification of deposit feeders.

It is reasonable to suppose that an increase in bioturbation would have evolutionary implications for the trophic structure of soft-bottom communities, and for the food sources and feeding methods used by associated members of the fauna, but it is clear that the scope for paleoecological investigation is limited. Analysis of fossil assemblages in terms of the spatial relationship of trophic groups is probably the most promising area, bearing in mind though the need for reliable taphonomic information (Johnson, 1960) and the fact that although fine-grained sediments are often the most favorable for the preservation of animals *in situ,* unfortunately the proportion of preservable animals they contain is usually small (Johnson, 1964).

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