LINKING SPECIES & ECOSYSTEMS

edited by

Clive G. Jones
Institute of Ecosystem Studies

John H. Lawton
National Environment Research Council for Population Biology

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BIOTURBATORS AS ECOSYSTEM ENGINEERS: CONTROL OF THE SEDIMENT FABRIC, INTER-INDIVIDUAL INTERACTIONS, AND MATERIAL FLUXES

Jeffrey Levinton

SUMMARY

Deposit feeders are often strong habitat fabric interactors, altering the structural habitat of marine soft sediments. Through their feeding and burrowing activities, deposit feeding populations often change the sediment water content, near-surface sediment stability, grain size, and spatial distribution of grain sizes. As a result of deposit feeders ingesting sediment, the decomposition of particulate organic matter and microbial activity is also accelerated. Deposit feeders can rapidly turn over the sediment, and derive their nutrition from microbial sources, which are assimilated efficiently, and from particulate organic matter, which is far more refractory. Through alterations of the physical characteristics of the sediment, deposit feeders change sediment chemistry, principally by oxygenating pore waters, which in turn changes the environment for microbes. Nearly all aspects of life in muddy sediment are competitions between the activities of microbes, which usually consume oxygen, and the activities of burrowing sediment consumers, which usually bring oxygen to the sediment by mixing of surface sediment with the overlying water or by irrigating burrows. Alterations of the sediment plus direct interference often combine

to cause exclusion of either competing deposit feeding species, or exclusion of functional groups that are ill-equipped to survive in the unstable, watery sediment conditions that are caused by deposit feeding dominance.

At one and the same time, deposit-feeding bioturbators perform the functions of major physical and biological forces in other communities. The vertical fluxes generated are analogous to the major vertical transport of nutrients seen in oceanic water column systems. But the processes seen within guts are analogous to the major contributions that ungulates and other herbivores make in the decomposition and growth of terrestrial plant communities. Deposit feeding bioturbators transport and transform nutrients over the entire physical and perhaps nearly the chemical scale of the soft bottom benthic ecosystem.

INTRODUCTION: SPECIES AND ECOSYSTEMS

Strongly interacting species may affect an ecosystem through two distinct routes. First, species might be *biological interactors* and affect other species by being predators or competitors. In marine ecosystems, predators often exert strong effects on prey species, to the point of devastation. In some cases, predators increase in abundance, change their foraging behavior, and direct the ecosystem into distinct and stable states (e.g., Harrold and Reed, 1985). Both predators and competitors change considerably the relative abundance of species and the nature of food webs.

Alternatively, species may be *habitat fabric interactors*, and alter the physical habitat itself (Lawton and Jones, Ch. 14). Beavers, for example, change the hydrology of streams and radically alter the immediate watershed, nutrient flux, and the structural habitat of aquatic and terrestrial species living in the vicinity. Although beavers cut down trees, of course, their effects on an ecosystem do not involve mainly competitive interactions, or predation on other animal species (see Pollock et al., Ch. 12).

Deposit feeding marine invertebrates burrow in soft sediments and eat some part of the sediment, digesting and assimilating some of the nonliving and living organic matter in the process (see Lopez and Levinton, 1987). Their burrowing and feeding activities alter the fabric of the sediment, which, in turn, changes the environment for the deposit feeders themselves but also for microbial organisms and for other marine benthic species. In the sense of Lawton and Jones (Ch. 14), deposit feeders are therefore *engineers* and affect the habitat fabric of the ecosystem. Deposit feeders, however, interact directly with other species via competition for space and food, and therefore are also biological interactors.

Josiah Wedgewood inspired his nephew, Charles Darwin (1881), to examine carefully the consequences of the activities of earthworms. Darwin's studies over several decades demonstrated that earthworm populations turned over large amounts of earth, which appeared to be beneficial for plants. Worms in densities of hundreds per square meter changed completely the fabric of the soil and introduced large amounts of particulate organic matter by drawing down leaf litter beneath the surface. Marine deposit feeders also consume large amounts of sediment and draw down organic matter beneath the surface, but their activities occur in a sediment whose interstices are filled with water and whose interface is with water, rather than air. It is the purpose of this brief chapter to introduce the reader unfamiliar with deposit feeders to their strong effects on the soft bottom marine ecosystem, both from the point of view of strong biological interactions and habitat fabric interactions. Owing to the brevity of this article, I cannot do justice to the many excellent studies that have led to some of the generalizations made in the sections that follow.

DEPOSIT FEEDERS STRONGLY CONTROL THE PHYSICAL CHARACTERISTICS OF THE SEDIMENT

Deposit feeders (Fig. 3-1) either swallow sedimentary grains whole, or scrape microbial organisms or organic matter from the surfaces. In either case, deposit feeders process large amounts of sediments, often many animal body weights per day (Lopez and Levinton, 1987). The burrowing and feeding activities usually raise the sediment water content, and the formation of copious fecal pellets increases the grain size of the sediment from a fine mud to a fine sand, often oxygenating the sediment in the process (e.g., Rhoads, 1967; Levinton, 1977; Levinton and Lopez, 1977). The establishment of burrows beneath the sediment water interface creates three-dimensional structuring of the sediment ecosystem. The physical stirring of sediment, or *bioturbation*, increases the penetration of oxygen. This usually results in an approximately horizontal interface known as the *redox potential discontinuity* or RPD, which is the border between oxidative reactions above and reducing reactions below (Fig. 3-1). Burrowing bivalves or tube-dwelling polychaetes may extend the RPD as an irregular surface, deep into the sediment. The oxidative and reductive reactions across this interface are facilitated by a variety of bacteria that derive energy from oxidation and reduction of sulfur compounds. Metals involved in sulfur reactions (e.g., Fe, Cd) also exchange across this interface. As a result, bioturbating organisms strongly affect the chemistry of sediment pore waters. Below the RPD, the sediment is anoxic, which allows hydrogen sulfide to persist. By burrowing into the sediment, deposit feeders oxygenate the pore waters and increase the hospitable environment for burrowing organisms that cannot gather dissolved oxygen directly from the sediment surface by means of a siphon or irrigated tube (e.g., Levinton, 1977).

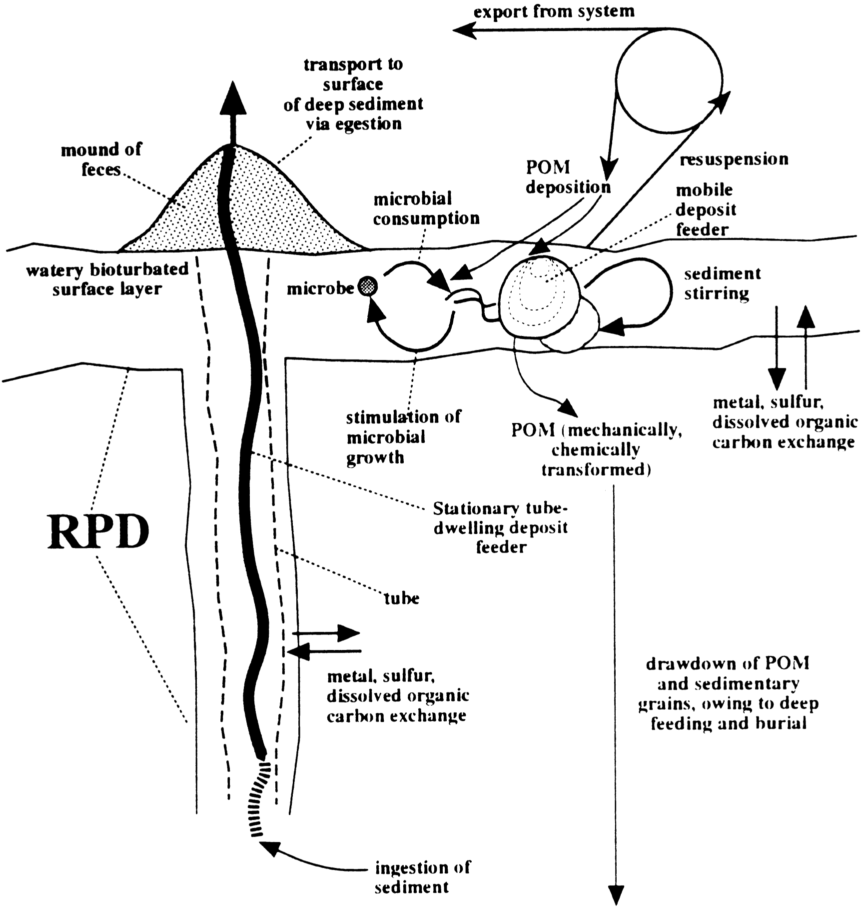

Figure 3-1. General scheme showing cross section of the sediment and interactions generated by marine deposit feeding invertebrates. RPD = redox potential discontinuity, the interface between dominant oxidative processes above and reducing processes below; POM = particulate organic matter.

Other physical changes of the sediment generated by deposit feeders cause profound changes on the benthos. Deposit feeders increase the water content of the sediment and the interaction of near-bottom flow with watery sediment tends to destabilize the interface and increases turbidity in the boundary layer (Rhoads and Young, 1970). Near-bottom flow may also mix particles in the water column, resulting in an intimate coupling between the sea bed and the water column (Fig. 3-2). Suspension feeders have difficulty living in the watery sediment and may be excluded from muddy sediments dominated by deposit feeders (Rhoads and Young, 1970).

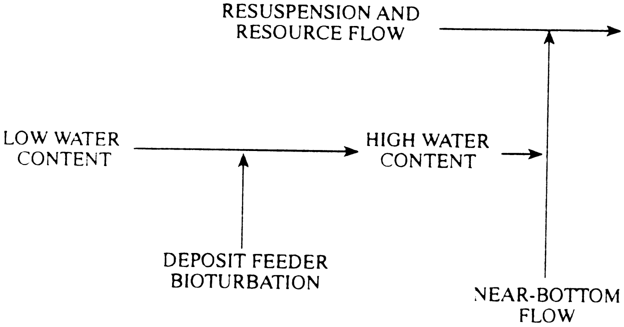

Figure 3-2. The general effect of deposit feeder generated bioturbation on sediment water content and particle resuspension.

Many deep-feeding deposit feeders consume sediment, and transport it through the gut, to be defecated at the surface. On typical intertidal mud flats and the muddy sea floor, mounds of feces and pseudofeces (material that is collected by a feeding organ, but is rejected to the external environment before entering the gut) create a microtopographical surface that alters near-bottom flow (e.g., Eckman et al., 1981), and create microtopographical high points upon which smaller suspension feeding invertebrates can live (Rhoads and Young, 1971). Pits created by surface deposit feeders may slow flow and facilitate the deposition of particulate organic matter. Deep feeders may consume fine particles, transport them to the surface, and thereby create biogenically graded beds (Rhoads and Stanley, 1965). Whether in permanent burrows or free-burrowing, deposit feeders increase the flux of particulate organic matter downwards (Rice and Rhoads, 1989; Fig. 3-1), as well as dissolved pore water oxygen and a host of inorganic ions (Aller, 1982).

MICROBIAL STRIPPING AND FECAL PELLET FORMATION SUGGESTS RENEWABLE RESOURCE MODELS

Microbial organism abundance appears to be related to sediment particle surface area (e.g., attached bacteria) and the area of the sediment–water interface (benthic diatoms, other photosynthetic microorganisms). The stripping of microbial organisms, followed by recovery of microbial populations to an upper limit dictated by space, suggests a model of resource renewal (Fig. 3-3). As the sediment is pelletized, fecal pellets are often not available until the pellets break down to constituent particles, which also suggests a process involving renewable resources. Theoretically there is also a significant inter-

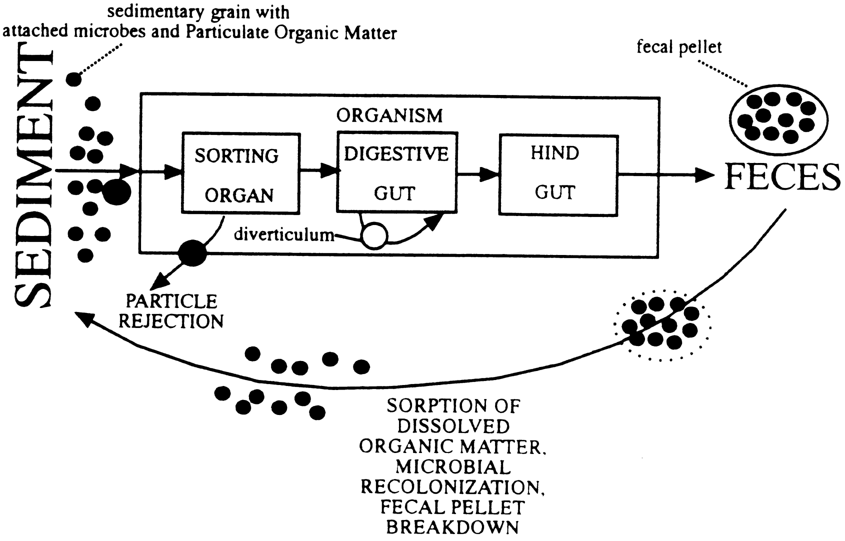

Figure 3-3. The movement of sedimentary grains between the sediment and the feeding and alimentary systems of a deposit feeder.

action effect (Levinton, 1980). If pellets break down relatively slowly, particles "have time" for microbial recolonization. Thus, steady-state microbial abundance will be greater when pellet breakdown is slower, and when microbial recovery is more rapid. Using these models it is possible to predict the population sizes that might be supported, given known rates of microbial growth and fecal pellet breakdown. Pelletization–pellet breakdown models predict densities of the mud snail *Hydrobia* that fall within typical field densities (Levinton and Lopez, 1977)

Studies (e.g., Levinton and Bianchi, 1981) suggest that bacteria recover too rapidly to be grazed down by deposit feeders. Even at high standing stocks, however, bacteria appear to be insufficient to satisfy the carbon needs of deposit feeders (Cammen, 1980). Benthic diatoms are grazed down by natural population densities and appear to be a limiting food resource for some surface deposit feeders, such as the gastropod *Hydrobia*.

Sediment in intertidal and shallow subtidal muds also has considerable amounts of particulate organic matter (POM), which is probably derived mainly from deposition of decomposing sea grasses and seaweeds (see Marsh and Tenore, 1990). POM-derived material is probably the overwhelming majority of the carbon (C) and nitrogen (N) in intertidal soft muddy marine sediments (Levinton and Stewart, 1988). Several studies have demonstrated, however, that assimilation of this material is very poor, relative to living microbial organisms such as diatoms and bacteria (see Lopez and Levinton, 1987). This has led many to suggest that microbial organisms are the main food source for deposit feeders and the POM is a minor source, owing to its refractory nature. This is the basis for the microbial and particle renewable resource models mentioned earlier.

There is a major problem with this trophic hypothesis. As POM is the source of the overwhelming majority of C and N in muddy sediments, a relatively low assimilation efficiency can provide the same yield as a high assimilation efficiency on the relatively rare microbes (Cammen 1980; Levinton, 1980). An exception to this rule would be a species who could specialize on the diatoms living on the surface (species of the gastropod genus *Hydrobia* probably fit this description). This suggests that deposit feeders, particularly subsurface feeders, must rely upon relatively more particulate sources (see Levinton and Stewart, 1988).

POM DEPOSITS ON THE SEDIMENT–WATER INTERFACE AND APPEARS TO BE A MAJOR SOURCE OF FOOD FOR DEPOSIT-FEEDERS

In *Spartina* salt marsh mud flats, the most conspicuous source of POM would be from decaying *Spartina*, but seaweeds are less refractory and might be a major source of labile and digestible organic matter. Seaweeds such as the sea lettuce *Ulva* spp. grow prolifically on mud flats and are deposited on the sediment–water interface. Their movements can be traced by means of photosynthetic pigments, such as lutein (Levinton and McCartney, 1991). In False Bay, San Juan Island Washington, dense invertebrate populations are associated with dense *Ulva* beds and POM deposition (Levinton and McCartney, 1991). Deposition may be seasonal and some evidence suggests that spring detrital falls are nutritionally richer than POM that is deposited in the fall (Marsh and Tenore, 1990). By feeding an oligochaete ^{14}C-formaldehyde labeled POM, we found a progressive decline in absorption from spring to fall. In the spring, the most nutritionally rich organic matter appears to be near the sediment–water interface, presumably because it had recently been deposited on the sediment surface from the water column (Cheng et al., 1993).

"KEYSTONE DEPOSIT FEEDERS" EXERT STRONG CONTROLS ON OTHER SPECIES BY SEDIMENT MODIFICATION AND EXPLOITATIVE COMPETITION

As discussed above, deposit feeders may modify sediment water content, vertical chemical gradients, and food levels. Deposit feeders also take up space and may monopolize the environment, thus excluding other species. The simplest case is that of tube dwellers, which may inhibit the presence of mobile burrowers or other tube dwellers (Woodin, 1974). In subtidal New England muds the bivalve *Yoldia limatula* interferes with burrow establishment of the bivalve *Solemya velum* (Levinton, 1977). Species living at similar levels below the sediment–water interface may compete for space (Levinton, 1977, Peterson and Andre, 1980).

The mud snail *Ilyanassa obsoleta* dominates mud flats of the eastern United States and efficiently grazes the surface microbial layer of diatoms, while disrupting the sediment. It has strong negative effects on other species, often to the point of exclusion. It interferes directly with the smaller mud snail *Hydrobia truncata* and restricts its range in the intertidal (Levinton et al., 1985). *I. obsoleta* disrupts the sediment and causes emigration of tube-dwelling amphipods (DeWitt and Levinton, 1985). Perhaps by sediment disruption, it also inhibits population growth of the otherwise abundance free burrowing oligochaete *Paranais litoralis* (Levinton and Stewart, 1982).

CONCLUSIONS

The vertical and horizontal sediment stirring of bioturbators is the main driving force behind the transport of organic matter and chemical reactions in sediments. These effects are often mediated by microorganisms. Physical stirring also has a strong effect on species that might occupy the same space and bioturbators, often single spécies, regulate the species composition of sediment assemblages, both by modifying sediment chemistry and physical structure and by displacing other species. Marine bioturbators therefore are major controllers of sediment ecosystems.