

Benthic Life Habits

Life Habit Classification

Before going on to read about benthic life habits, it is important that you understand some basic terminology. **Benthos** are those organisms that are associated with the sea bed, or **benthic habitats**. **Epibenthic** organisms (epifaunal, if they are animals) live attached to a hard substratum, or rooted to a shallow depth below the surface, but most of an epibenthic organism projects into the water column. Seaweeds, limpets, crinoids, and corals all fit in this category. By contrast, **infaunal** organisms live below the sediment-water interface. They may be **burrowers**, such as clams and polychaetes, or they may be **borers** such as wood-boring ship worms and isopods. **Semi-infaunal** organisms live partially below the sediment-water interface, but protrude above. These include sea pens, which have a deeply rooted stalk but can protrude to varying degrees above the sediment-water interface. Some mussels live semi-infaunally, with the body partly in the sediment. Many **swimming** animals, such as scallops, sculpins, and shrimps, are essentially benthic. Finally, **interstitial** organisms live and move in the pore waters among sedimentary grains. These include foraminifera and harpacticoid copepods.

Because benthic animals are often collected and separated on sieves, a classification based upon overall size is useful. **Macrobenthos** include organisms whose shortest dimension is greater than or equal to

0.5 mm. **Meiobenthos** are smaller than 0.5 mm but larger than the **microbenthos**, which are less than 0.1 mm in size. **Meiobenthos** and **microbenthos** are **interstitial**.

Feeding Classification

Suspension feeders feed by capturing particles from the water. They include feeders on bacteria (sponges, ectoprocts), phytoplankton (most bivalve mollusks, many polychaetes), and zooplankton (corals, crinoids). **Passive suspension feeders** protrude a feeding organ into a current and collect particles as they are deposited. Crinoids are good examples of such organisms. By contrast, **active suspension feeders** create a feeding current of their own, in order to draw particles toward the mouth parts. Siphonate bivalve mollusks are good examples. **Deposit feeders** ingest sediment and use organic matter and microbial organisms in the sediment as food. They include some bivalve mollusks and gastropods, many polychaetes, some sea cucumbers, and some crustaceans. **Herbivores** eat nonmicroscopic plants, such as seaweeds and sea grasses. They include sea urchins, some benthic fishes, and some polychaetes. **Carnivores** eat other animals and include asteroid starfish, many crabs, many fishes, anemones, and nemertean worms. However, there is no easy way to classify some organisms, such

as the suspension feeders that ingest zooplankton. Finally, scavengers feed on carcasses and remains of other animals and plants. Many deposit feeders also scavenge. A good example of such species are the fiddler crabs, which are normally deposit feeders but can also tear apart dead fish.

Life in Mud and Sand

Mobility in Soft Sediments

Soft sediments are a mixture of inorganic particles, organic particles, and pore water. Benthic organisms are strongly affected by variations in all of these constituents. Particle size is a good measure of current energy; large sedimentary grains are deposited by stronger currents whereas fine-grained sediment indicates quieter water. Because currents carry suspended food to the bottom and also erode sediments, particle size reflects the current regime and helps to define the benthic environment. Burrowing organisms must push aside sedimentary grains, and the combination of grain size and pore-water conditions helps determine whether or not burrowing is possible. The range of adaptations to differing sediments and current regimes involves major differences in morphology, mode of feeding, and response to changes in water temperature, salinity, and pore-water chemistry.

* Sediment grain size is an important determinant of the distribution of benthos and increases with increasing current strength.

The size of soft-sediment particles affects the life styles of benthic organisms and also is a reflection of the hydrodynamic environment. Sediments consisting of only cobbles, for example, will lack the fine particles required of sediment-ingesting benthic animals. By contrast, sediments consisting of only very fine particles may be too unstable for a large and dense animal to maintain its necessary living position within the sediment. Grain size also reflects the current regime of the overlying water column. The silt-clay fraction is the percentage, by weight, of sediments finer than 62 μm in diameter. The percent clay (particles less than 4 μm) may also be useful in describing sediment properties relevant to benthic organisms.

Stronger currents can transport larger particles, so median grain diameter increases in areas of high current velocity (see Box figure 13.1 for a discussion of the measure of grain size). Areas with high currents also experience extensive erosion and transportation

of sediment. An animal in such an environment may be subjected to continual erosion from the substratum and must be capable of rapid reburial in order to re-establish its living position. Sediments from areas with low current strength have very small particle diameters. The abundance of sediment-ingesting animals may increase with the abundance of fine material, as this material contains more organic matter and small, ingestible inorganic particles with attached microorganisms.

* Sediment sorting and grain size angularity also reflect the hydrodynamic regime.

Sorting is an estimate of the spread of abundance of particles among the size classes. A sediment is poorly sorted when most of the sediment is spread over a large range of size classes. In a well-sorted sediment, almost all the weight is confined to a few size classes, with a well-defined peak (Box Figure 13.1 c).

A well-sorted sediment will be deposited in an environment with constant current strength. Sediment may also be well sorted at a given level on a beach, corresponding to a given amount of wave energy. Poorly sorted sediments usually reflect a heterogeneity of sedimentary processes. There may be variable depositional currents, or some historical reason for the sorting, such as the previous deposition of large cobbles by glacial streams, combined with present moderate currents. Some sediments may have more than one distinct size mode in the sediment (Box Figure 13.1c), and the different modes may each indicate a different hydrodynamic regime.

* In very shallow sandy wave-swept bottoms, currents generate ripples and bars, which create strong microhabitat variation for benthic organisms.

It is rare for the sediment surface to be completely flat. In areas of considerable current strength, surface sediment is transported continually and a number of sedimentary structures may be established in equilibrium with this transport. On the largest scale, emergent and submerged bars may develop offshore. On a smaller scale, ripple marks commonly develop where sediment is in motion (Figure 13.1). In areas where currents are unidirectional, ripple marks are asymmetrical in cross section, with the steep slope facing down-current. In strong currents, such ripples may be reestablished to face in opposite directions with every change in tidal direction. By contrast, waves may produce sufficient oscillatory motion to generate symmetrical ripples.

The ripples create a local environment of their own,

Measuring Grain Size of Sediments

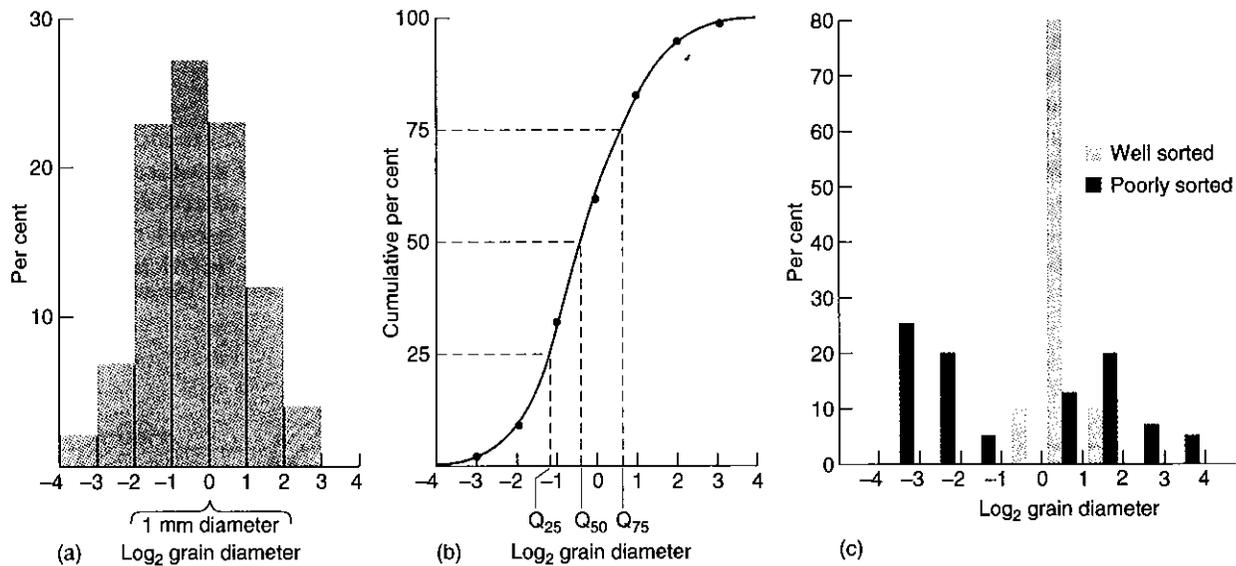
Median grain size is the simplest way to represent the overall particle size characteristics of soft sediments. By washing the sediment through a series of graded sieves, or by measuring the settling velocity of particles (larger particles settle faster in water), one can get the size-class data to construct a histogram of sizes (Box figure 13.1a). We plot grain diameter in logarithmic form (log to the base 2, which means that a value of 1 in box figure 13.1 corresponds to 2 millimeters, a value of zero corresponds to 1 millimeter, and a value of -2 corresponds to a diameter of 0.5 millimeters) in order to accommodate a range of particle sizes of many orders of magnitude within one graph. This diagram can be used to construct a cumulative weight graph, where the percent weight of the successive size classes are accumulated, and cumulative percent weight is plotted as a function of

particle diameter (Box figure 13.1b). The median diameter, M , which corresponds to Q_{50} , is the particle diameter corresponding to 50 cumulative percent. Calculation of the 25 percent and 75 percent classes is also shown.

Sorting is a measure of spread among the grain sizes. This can be quantified by:

$$S = Q_{25}/Q_{75}$$

where Q_{25} is the grain size corresponding to the 25 percent cumulative weight (Box figure 13.1b) and Q_{75} is the same value for 75 percent. As S approaches 1, the sediment is all the same size class and is perfectly sorted. Box figure 13.1c shows an example of a poorly-sorted and a well-sorted sediment.



Box Fig. 13.1 Graphical methods of presenting the particle size distribution of sediments: (a) histogram, showing the weight frequencies of each particle size class as a function of the log of particle diameter (we use the log of particle diameter in order to plot an enormous range of particle sizes on a manageable scale), (b) cumulative frequency distribution curve, showing Q_{25} , Q_{50} (the median particle diameter), and Q_{75} ; (c) example of a poorly sorted (green) and a well-sorted sediment.

which strongly affects sediment stability and movement for those organisms that are much smaller than the size scale of the ripples. For example, fine organic material tends to accumulate in the troughs, and deposit-feeding animals would therefore be attracted to this microenvironment. By contrast, the crests of the ripples are relatively bare of this material, and are also

localized sites of erosion. Because ripple crests migrate continually, benthic invertebrates may have to readjust their living position.

* Soft-sediment burrowers use hydromechanical and simple digging mechanisms to move through the substratum.



Fig. 13.1 Geometry of a sand ripple in a unidirectional current. Note direction of sand ripple movement from upper right to lower left, and the possibility of burial faced by invertebrates in its path.

In order to penetrate the sediment, infaunal organisms must be able to displace sedimentary grains. Sediments may range from completely dry, to plastic, to very watery. Fine-grained sediments of moderate to high water content exhibit the phenomenon of **thixotropy**, wherein a force against the sediment is sufficient to permit further sediment displacement with a smaller force. In effect, the sediment becomes less resistant as you exert a concentrated shear force upon it.

The initial displacement of sedimentary grains requires that a firm structure be pushed into the sediment with a sufficient force. Many burrowing organisms, such as most worms and bivalve mollusks, have a **soft and fluid-filled burrowing structure, which must be erected during the burrowing process. In order to accomplish this, these organisms have a hydrostatic skeleton, which is a flexible tube that can be stiffened by the injection of fluid.** In the case of bivalve mollusks, the otherwise flaccid foot is filled with fluid and becomes a firm digging device. After pushing into the sediment, the distal end of the foot is engorged with fluid, creating an anchor. Contraction then carries the rest of the body along (Figure 13.2). Within the sediment, a part of the body can be dilated to form an anchor, so that another forward part of the body can be extended forward. A series of dilations and extensions allows the animal to move within the sediment. This general principle applies to burrowing in mollusks, polychaetes, sipunculids, burrowing sea cucumbers, and other worm-like animals.

The other major mode of burrowing involves the use of **mechanical displacement, based upon firm structures that act as spades and are moved by muscular action.** A wide variety of crustaceans dig into the substrata by means of specialized digging limbs. For example, the mole crab, *Emerita talpoida*, has spade-like posterior appendages. Inarticulate brachio-

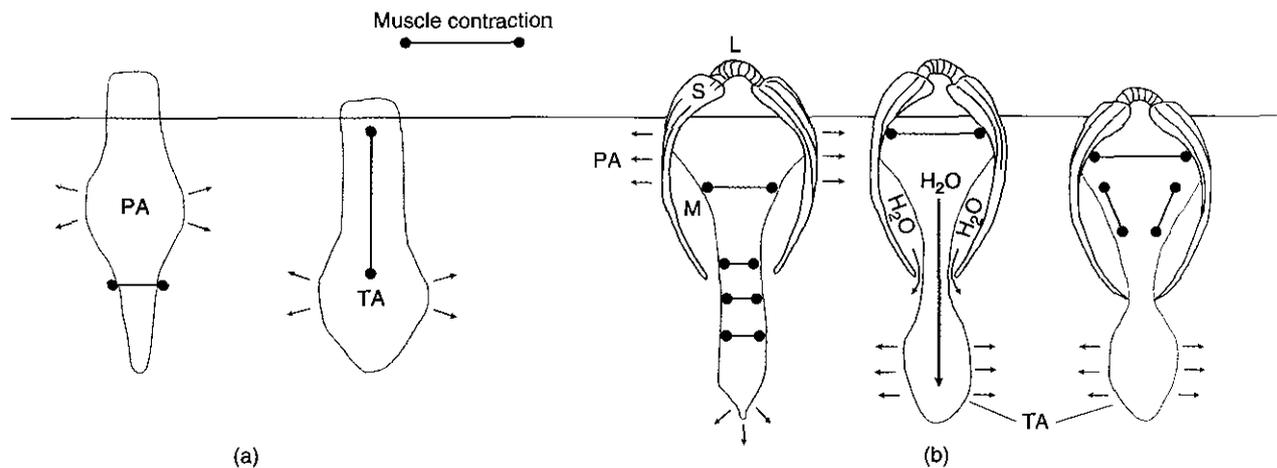


Fig. 13.2 (a) The burrowing of a soft-bodied animal, showing the formation of turgid fluid-filled mass into a penetration anchor, PA, and the dilation of a distal region, forming a terminal anchor, TA. Longitudinal muscles then drag the animal into the sediment. (b) How a clam burrows, using its shell and fluid-filled foot. Left: clam is in sediment and presses shell outward, forming an anchor. At the same time, its fluid-filled foot thrusts into sediment. Middle: The foot fills with fluid at the tip, forming a new anchor. Right: Muscle contraction draws the shell together and drags it downward. (After Trueman, 1975.)



Fig. 13.3 Burrowing inarticulate brachiopods have two symmetrical shells, which are connected by a complex musculature. They burrow in the substratum by scissoring the shells back and forth, which shovels the sediment aside and pushes the animal downward. (Courtesy of Charles W. Thayer.)

ods use a complex musculature to alternately push and rotate the two opposed valves through the sediment. The muscular rocking motion keeps the valves moving and constantly displacing sedimentary grains (Figure 13.3).

* Interstitial animals adapt to water flow and life in small spaces among particles by means of a simplified body plan, a worm-like shape, or by adhering to particles by means of mucus, suckers and hooks.

Interstitial animals¹ move among sedimentary grains but do not displace them in bulk, as do burrowing animals. Because they move through tight spaces, interstitial animals from many different phyla have evolved a worm-like shape and a simplified external body plan (Figure 13.4). For example, interstitial hydroids have reduced numbers of tentacles, relative to their epibenthic relatives, for which capture of suspended prey from the water column is important. Smaller interstitial forms may be attached to sand grains by a variety of hooks and suckers.

The slender body form of some interstitial forms may be related to uptake of dissolved organic matter for food. Nematodes living in the low-oxygen parts of sediments (see the following) tend to be more slender than those living in the aerobic surface sediments. The slender form may be a design to increase surface area in order to take up dissolved organic matter.

1. Interstitial animals are usually meiofauna, although benthos of meiofaunal size may also be epibenthic.

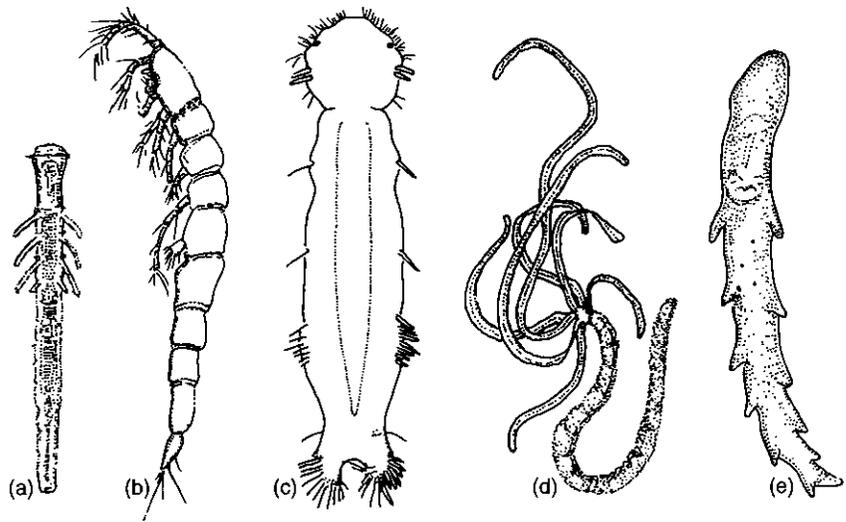


Fig. 13.4 The vermiform shape of meiobenthic animals of diverse phyla: (a) polychaete; (b) harpacticoid copepod; (c) gastrotrich; (d) hydroid; (e) opisthobranch gastropod. (After Swedmark, 1964.)

The Soft-Sediment Microzone

* Sediments consist of an oxygenated layer, overlying an anoxic zone.

If you dig into a protected sandy beach, you will first encounter light-brown sediment, but will soon reach a thin greyish zone, and then a black layer with an odor like that of rotten eggs. **The changes in color and smell reflect a change of chemistry.** The light-brown zone contains pore water with dissolved oxygen, whereas the black smelly zone is devoid of oxygen, and the greyish layer is a transition zone between the two. The smell in the black zone derives from hydrogen sulfide, H_2S , which is generated by sulfate-reducing bacteria. Overall, the oxic-anoxic zonation results from a shifting balance between addition and consumption of dissolved oxygen in the pore waters. **The boundary between the oxygenated zone and the anoxic zone is known as the redox potential discontinuity, or RPD. It represents a sharp boundary between chemically oxidizing and reducing processes (Figure 13.5).**

Near the sediment-water interface, oxygen diffuses into the pore water from the overlying water column, or may be stirred in by current or wave action. As a result, the sediment in exposed beaches may be oxygenated down to depths of nearly a meter. In quiet areas, especially in organic-rich fine-grained sedi-

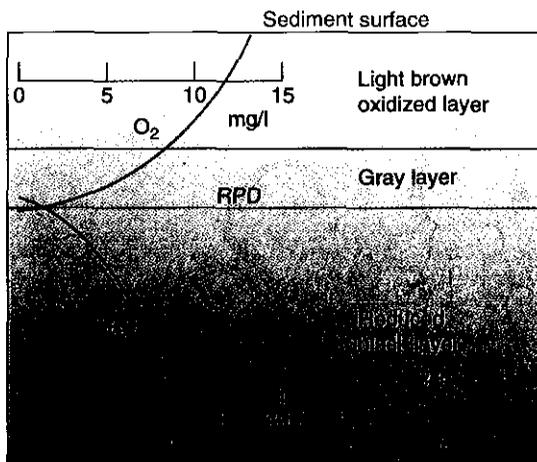


Fig. 13.5 Cross-section of the sediment near the sediment-water interface, showing the redox potential discontinuity (RPD), which is a boundary between oxidative and reducing processes. The diagram shows the concentration of oxygen (above) and hydrogen sulfide (below).

ments, the transition to the anoxic zone can occur only a few millimeters below the sediment surface. **Infaunal organisms may carry in oxygen somewhat deeper by stirring the sediment or by irrigating their burrows.** The combined action of infaunal organisms may bring oxygen down to depths of several centimeters, in muddy sediments that would otherwise have oxygenated depths that would be controlled by diffusion and would never surpass a few millimeters in depth. **Because of vertical burrowers, the RPD may not always be a horizontal surface, but may be vertical in places, parallel with tubes and burrows (Figure 13.10).**

* In sediments in quiet water, there is usually a vertical zonation of species of microorganisms.

As will be discussed later, microorganisms are important as food for soft-substratum benthos. **Microorganisms are consumed as food directly, but they also help decompose particulate organic matter, which is another potential food source. The vertical gradient in oxygen affects the composition of the microorganism community.** Near the surface, aerobic organisms can survive, but only anaerobic organisms can survive below the RPD. Below the RPD, nearly all animals must maintain contact with the sediment above the RPD by means of siphons, irrigated burrows, and tubes. It has been argued that a few metazoans, such as some nematodes, can survive without oxygen, and that some macroinvertebrates can live for extended periods on the proceeds of anaerobic metabolism. The anoxic community, known as the thiobios, was first described by T. Fenchel and R. Riedl. Some researchers, such as Riese and Ax, have argued that this community does not really exist in truly anoxic sediments, but only in sediments of very low oxygen that are adjacent to anoxic microzones. Some protozoans are clearly anaerobic and contain symbiotic anaerobic bacteria.

Microbial organisms may be autotrophic or heterotrophic. Recall that autotrophic organisms produce their own carbohydrates or sugars by means of either photosynthesis or chemoautotrophy. Photosynthesis employs light as an energy source whereas chemoautotrophy employs one of several chemical substrates (e.g., sulfate, hydrogen) to derive energy.

Figure 13.6 illustrates a generalized zonation of microbial communities in soft sediments. **At the surface, aerobic photosynthetic microorganisms, such as diatoms and cyanobacteria, may predominate. These coexist with heterotrophic aerobic bacteria, which use**

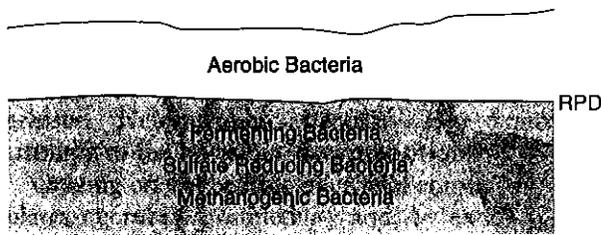


Fig. 13.6 Typical vertical zonation of microbial components of quiet, muddy marine sediments.

oxygen and contribute to the oxygen depletion of the pore waters. Oxygen is the terminal hydrogen acceptor in the decomposition process. In the anaerobic zone, however, heterotrophic microorganisms use a variety of compounds as hydrogen acceptors. Most notable are fermenting bacteria, which use organic compounds and produce end products such as fatty acids and alcohols, and the deeper sulfate-reducing bacteria, which reduce SO_4^{2-} to H_2S . The reduced compounds diffuse upward and are used by chemoautotrophic sulfur bacteria (which oxidize H_2S) at the RPD region. Beneath the sulfate reducers are methanogenic bacteria, which break down organic substrates and produce methane as an end product.

Environmental constraints (e.g., the presence of oxygen) and energetic payoff combine to determine the successive dominance with depth of different heterotrophic bacteria groups (aerobic, fermentative, sulfate-reducing, and methanogenic). In the presence of oxygen, much more energy is obtained from the energy-efficient aerobic breakdown of organic matter by bacteria. Beneath this zone, however, there is little or no oxygen and the energetically less efficient process of fermentation is performed by different bacteria. The processes of sulfate reduction and methanogenesis are still lower in energy efficiency. Ultimately, heterotrophic bacterial activity is limited with depth by the lack of a food source. This can be shown by the steady decrease of substrate use with depth into the sediment.

Feeding in Soft Sediments

* Deposit feeders ingest sediment and derive their nutrition mainly from microalgae and particulate organic matter, and to a smaller extent from the scarcer bacteria.

Deposit feeders are those animals that ingest sedimentary material and derive their nutrition from some

fraction of that material. As is obvious from the previous sections, sediment is a complex mixture of inorganic material, microorganisms, decomposing organic material, and pore water with dissolved constituents. It is therefore more complex to understand the nutrition of these creatures than watching a caterpillar chew on a leaf! Deposit feeders tend to be more abundant in fine-grained sediments, but such sediments contain increased quantities of microorganisms, fine-grained particulate organic matter, and ingestible inorganic particles. Thus, simple correlations will not solve the question of nutrition.

Deposit feeders feed in a variety of ways that are associated with phylogenetic origins of the organisms and the environments within which they live (Figure 13.7). Representatives of many animal groups swallow sediment nonselectively, with the exception of the upper limit that exists as regards to the size of particle that they can ingest. Many polychaetes have tentacles, which gather particles by means of a mucus-laden ciliated tract (Figure 13.7a). Sea cucumbers, such as the large northeast Pacific *Parastichopus*, draw sediment into the mouth by means of a large crown of tentacles. Bivalves in the group Tellinacea use a separate inhalant vacuum-hose siphon to suck up sedimentary grains (Figure 13.7c). In some other groups, the sediment is processed quite noticeably before a residue is ingested by the deposit feeders. Many amphipods tear particulate material apart and ingest quite smaller particles (Figure 13.7e). Fiddler crabs handle sediment extensively and ingest only the fine particulate organic matter; they reject the inorganic sand grains. Although tellinacean bivalves may ingest particles by means of a vacuum cleaner like siphon, particle sorting occurs on palps and even in the digestive tract. Even in the so-called non-selective feeders, specialization is usually common. Feeding rate may increase if the sediment is richer in food.

Feeding structures used for deposit feeding are modified or used for other types of feeding in related groups (for example, the tentacle crown of deposit-feeding sea cucumbers is often used for suspension feeding in other sea cucumber species). When viewed from the perspective of the sediment column, there are a few distinct types of deposit feeders. Surface browsers use tentacles or siphons to collect surface sediment, which is rich in photosynthetic microbes such as diatoms. For example, spionid polychaetes have two tentacles that are pressed to the surface and thus collect both particles and attached photosynthetic forms such as diatoms. At the other end of the spec-

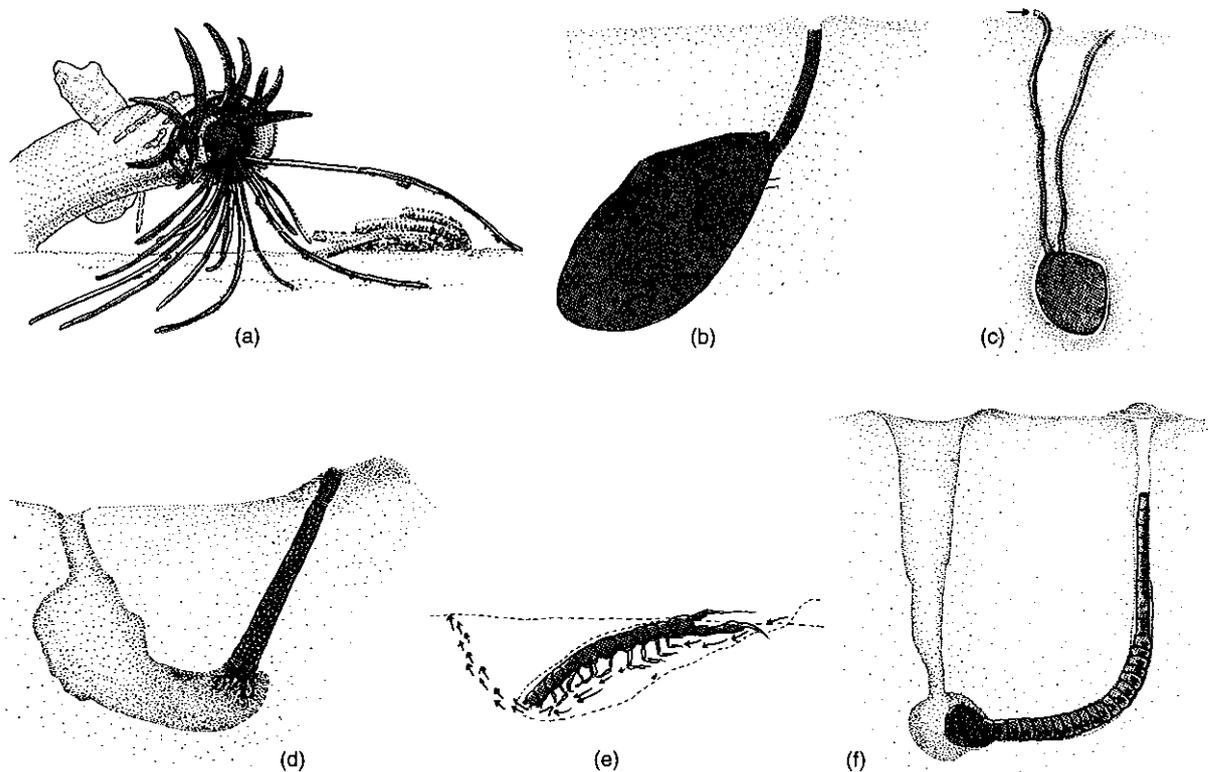


Fig. 13.7 Some deposit-feeding animals: (a) the surface tentacle-feeder *Hobsonia*; (b) the within-sediment tentacle-feeding bivalve *Yoldia limatula*; (c) the surface deposit-feeding siphonate bivalve *Macoma*; (d) the within-sediment feeding polychaete *Pectinaria*; (e) the surface-feeding *Corophium*; (f) the deep-feeding *Arenicola*. (Drawing of *Hobsonia* copied from an original by P.A. Jumars.)

trum, head-down deposit feeders (e.g., many vertical-tube-dwelling polychaete annelids) maintain their long axis vertical, consume particles at depth, and defecate at the surface (Figure 13.10).

A series of experiments gave us some important insights on how deposit feeders deal nutritionally with the complex sediment to which they are exposed. In a classic series of experiments, B.T. Hargrave (1970) fed decaying leaves to a fresh-water amphipod and found that its ability to digest and assimilate the material was very low, in contrast to its high efficiency at digesting bacteria. These results were found to be similar for several marine invertebrate deposit feeders of wide origin (marine amphipods, gastropods, sea cucumbers), showing the results to be of broad application. The **microbial stripping hypothesis** that was developed in the light of this finding states that particulate organic matter is relatively indigestible, and that microbial organisms are therefore the main source of nutrition for deposit feeders. In order to be

nutritionally useful for deposit feeders, therefore, particulate organic matter (POM) must be decomposed and converted by microbes into digestible microbial tissue. Particulate organic matter is indigestible, particularly because deposit feeders usually lack sufficient cellulase enzyme activity to digest the complex carbohydrates in the POM, which is commonly derived from sea grasses that are rich in cellulose.

Particulate organic material is decomposed by three processes, which often act simultaneously. **Fragmentation** involves the breakdown of large particles into smaller ones. This may involve breakup by current action at inherent weak points, but animals, such as amphipods, may tear up material as they feed upon it. This reduces the grain size and increases the surface area available for attack. **Leaching** is the loss of dissolved materials from once-living organisms, and is accelerated by mechanical fragmentation. Finally, **microbial decay** is the active use of POM nutrients by surface-bound microbes. As microbes colonize, they

enrich particulate organic matter with nitrogen (Figure 13.8). In intertidal environments, much decay can be attributed to marine fungi, especially in marsh grasses. Heterotrophic bacteria also contribute strongly to the microbial decomposition.

Grazing on the benthic microbial community stimulates microbial productivity and, by extension, detrital decomposition (Figure 13.9). Oxygen consumption by microbes increases while they are being grazed by consumers. The mechanism behind this stimulation is not well understood. Grazing may reduce the

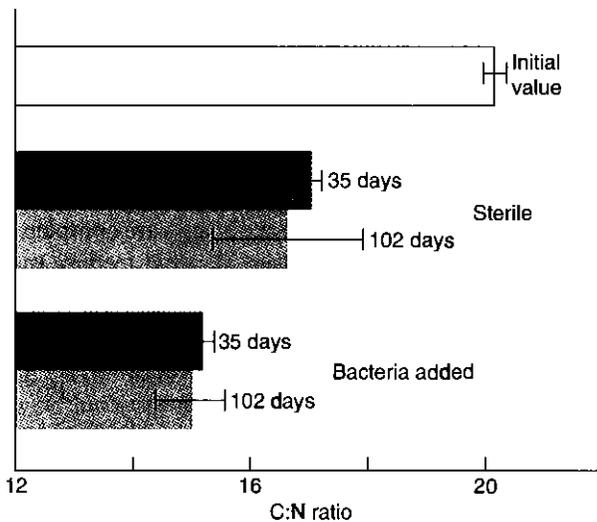
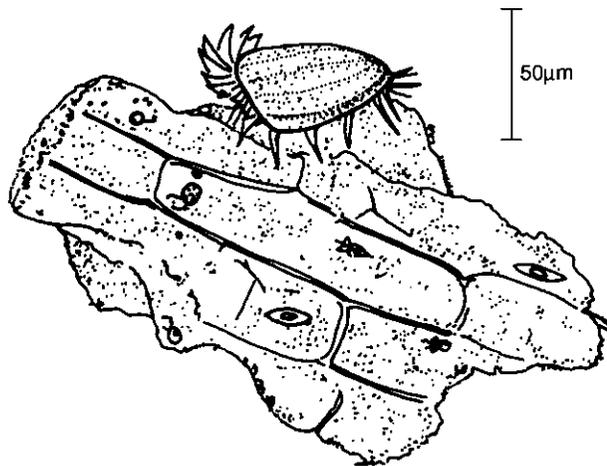


Fig. 13.8 Top: A piece of turtle grass (*Thalassia testudinum*) detritus and its microbiota (redrawn from Fenchel, 1972). Bottom: Change in the carbon-to-nitrogen ratio in particulate organic matter over time, with and without the presence of bacteria (modified from Harrison and Mann, 1975, © Blackwell Scientific Publications, Ltd.).

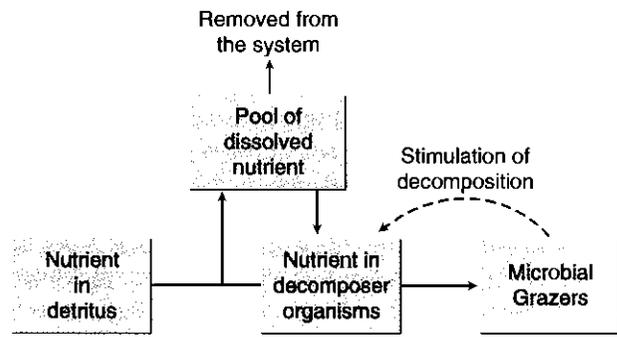


Fig. 13.9 The relationship between deposit-feeding microbial grazers and microbial decomposers, particulate organic matter, and the dissolved nutrients in the pore waters of sediments. Microbial grazers remove microbes, but they also stimulate decomposition by increasing microbial activity and by tearing apart particulate organic particles, which exposes more surface area to mechanical attack. (Modified after Barsdate *et al.*, 1974.)

standing crop of bacteria and select for metabolically active cells with higher cell division rates. Of course, with very high grazing rates, microbial biomass is cropped down faster than it can be renewed, but stimulation is the rule at intermediate levels of grazing.

The microbial stripping hypothesis is imperfect in several respects. First, although the digestion and assimilation of particulate organic matter may be inefficient, POM may be far more abundant than microbes. Sediments in sea grass meadows contain large amounts of decaying sea grass, and deposit feeders cannot help but ingest much of this material. Thus, a poor rate of uptake may be balanced by the sheer abundance of the poor food source. Many other sources of POM exist in marine habitats, particularly the rain of dead phytoplankton in shallow embayments and on the continental shelf. Near shore, seaweeds may provide a significant input of POM. As it turns out, seaweed detritus is far more digestible to deposit feeders than is grass detritus, and seaweed detritus can fuel deposit-feeder population growth. In kelp forests, the rain of decomposing seaweeds supports large populations of benthic suspension feeders.

Because both POM and some microbial organisms are important as food sources, certain habitats are probably dominated by only one type of source. For example, most of the available organic matter in sandy intertidal flats is in the form of living microbial organisms. Here the question of deposit-feeder nutrition is relatively simple. By contrast, mud flats adjacent to salt marshes contain a complex mixture of

POM derived from *Spartina* and seaweeds, combined with bacteria and diatoms and other microbial photosynthesizers. In subtidal shelf bottoms, the sediment is probably dominated by detritus derived from the rain of dead phytoplankton and indigenous bacteria, and even organic material adsorbed onto sedimentary grains.

Some quantitative estimates set some limits on the value of certain food sources. Although heterotrophic bacteria are usually readily digestible, they are too sparse in the sediment to be able to support macrofaunal deposit feeders. This can be shown by comparing the energetic content of bacteria in the sediment with the aerobic requirements of a given deposit-feeding population. A number of studies suggest that bacteria can supply only a small fraction of the energy requirements of a macrofaunal deposit feeder such as a polychaete or a bivalve mollusk. These estimates apply only to bulk calculations of needs for carbon and nitrogen. It is likely that some fractions, such as sediment bacteria, are essential in the supply of important micronutrients such as specific fatty acids, amino acids, and vitamins. Rich diatom mats may be a more adequate food source, but only in intertidal and very shallow subtidal sediments, and surely these cannot be very important in even the relatively shallow waters of bays and estuaries, below the light compensation depth. In estuaries and on the continental shelf, the spring diatom increase is often followed by a sinking of detritus, and this POM may be crucial in fueling the productivity of the deposit-feeding benthos (see Chapter 16).

In contrast to macrofauna, meiofauna probably depend mainly upon a combination of bacteria and fine-grained particulate organic matter. Because of their small size, they cannot feed on particles much larger than 10–30 μm .

In conclusion, it appears that macrofaunal deposit feeders derive their nutrition from most of the conceivable sources within the sediment. Bacteria are probably not a significant component for any but interstitial and very young macrofaunal forms, and POM and benthic microbial algae combine as food for deposit feeders.

* Microbes and particles comprise a complex renewable resource system for deposit feeders.

As we have discussed, many sediments are dominated by POM, but some consist mainly of microbes and particles. In intertidal soft bottom flats, microbes such as benthic diatoms are the main food source for sur-

face feeders. In these cases, microbes may be: (a) free-living among the sedimentary grains, (b) attached to sedimentary grains, or (c) living as a mat on the sediment surface. Because the microbes themselves seem to be limited by some resource, the abundance of microbes at any one time is a balance between the microbial population growth rate and the grazing rate. At high grazing rates, the steady-state abundance of diatoms is kept at a low standing stock.

A balance between production and renewal may also apply to particles that bear attached microbes. Some deposit-feeding invertebrates, such as polychaetes and gastropods, consume fine particles and bundle them into fecal pellets that are often not re-ingested. Deposit feeders may live in a mixture of fecal pellets and fine particles, but ingest only the latter. In some cases, the deposit feeder may try to get rid of the pellets. For example, the Pacific ampharetid polychaete *Amphicteis scaphobranchiata* has a specially modified branchium that flings fecal pellets out of its feeding reach.

When such behavior is not possible the deposit feeder must wait for the pellet to break down into its constituent particles before it can reingest the sediment. In crustaceans, pellets are often surrounded by a distinctive coating, and in mollusks the sediment is bound together by mucus. As the pellets break down, they are probably colonized by microbes, so there is a value to having the particles sequestered for a time. Presumably, the nutritive value of a new fecal pellet is far less than that of one that has had some time to break down and be recolonized simultaneously by microbes. In such a system, there will be an analogous equilibrium abundance of ingestible particles, which is determined by the competing rates of pelletization and pellet breakdown. Some sediments are completely pelletized, and, in these cases, deposit feeders may have reduced access to particles for ingestion. Mud snails of the genus *Hydrobia* slow down feeding and may emigrate from microsites with fully pelletized sediments.

* Many benthic animals do not feed directly on microorganisms, but harbor symbiotic chemoautotrophic bacteria, which derive energy from dissolved ions in sea water.

Although many benthic animals feed actively on sediment, or on suspended organic matter (see section on suspension feeding), a large number of species depend upon symbiotic bacteria, which may live intracellularly or in chambers in various organs, depending on

the group. Many bivalve mollusks, for example, have bacteria living intracellularly in their gills. These bacteria oxidize reduced sulfur compounds. The oxidation processes provide energy, which is used by the bacteria to manufacture ATP, which, in turn, is used in bacterial cellular metabolism. Some species of the infaunal bivalve genus *Solemya* have a very small gut or lack one entirely. These forms rely exclusively on symbiotic sulfur-oxidizing bacteria. The animals are also tolerant to sulfide, which normally is quite toxic, especially to animals that use oxygen in metabolism. Mussels living near hydrocarbon seeps have intracellular bacteria in the gills. These bacteria rely on methane from the seeps for nutrition and energy. The bivalves rely exclusively on the bacteria for nutrition. This life habit is especially prominent in some deep-sea environments that are poor in organic matter, but rich in sources of oxidizable sulfur compounds (see Chapter 16).

Burrowers and Sediment Structure

* Deep feeders cause overturn of the sediment and strongly affect the soft-sediment microzone.

Sediments with abundant burrowing animals may bear no resemblance to sediments that are relatively animal free. Donald C. Rhoads² investigated the properties of burrowed sediments and found their mechanical properties to be quite different. The production of fecal pellets may increase the grain size of the sediment. If a sediment with abundant deposit feeders is wet-sieved, it tends to be dominated by fecal pellets, which are often on the order of 50–150 μm in size. If the same sediment is placed in a blender and sieved, one finds that its constituent particles are more of the order of 50 μm or less. Burrowing, deposit feeding, and production of fecal pellets tends to make the sediment in the top few millimeters very watery, sometimes over 90% water.

* Head-down deposit feeders create biogenically graded beds.

As mentioned above, many deposit feeders feed in a head-down position and they defecate sediment at the surface (Figure 13.10). Head-down deposit feeders tend to ingest particles of sizes that are less than the

2. See Rhoads, 1967, in Further Reading.

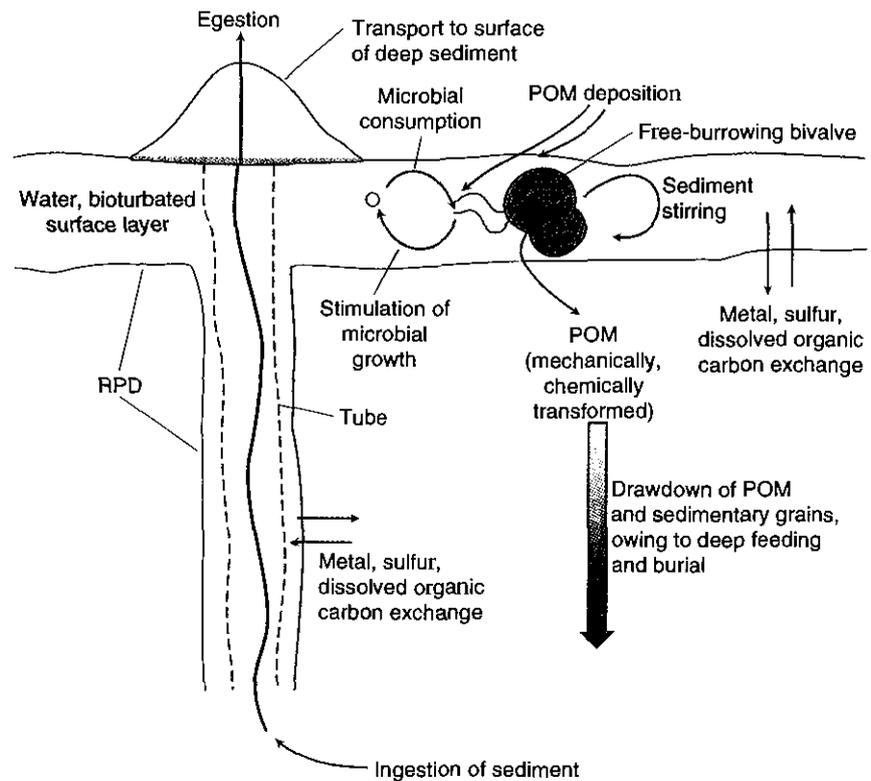


Fig. 13.10 General processes occurring within a sediment dominated by deposit feeders, including various transport processes. In deposit feeding, particles are taken up by a feeding organ, and some of them may be rejected before entering the gut. Particles may be packaged in fecal pellets, which are egested. As the pellets break down, the sedimentary grains are recolonized by microbes, which may be ingested and assimilated as the particles are ingested once again.

average for the sediment. If so, then the animals may sort fine particles to the surface, leaving a lag deposit of coarser material at depth. For example, the bamboo worm *Clymenella torquata* usually does not ingest particles greater than 1 mm. In poorly sorted muddy sediments, dense populations produce a biogenically graded bed, with fines toward the surface (Figure 13.11). Such biogenically graded beds can be easily detected by walkers who suddenly encounter squishy sediment.

* Deposit feeders can optimize their intake of food by adjustments of particle size to be ingested and adjustments of gut passage time.

Natural selection can be expected to optimize food choice and feeding rate to maximize fitness. In the case of deposit feeders, sediments with fine particles tend to be easier to ingest, but fine particles should be preferred in complex sediments. This is related partially to the ease of ingestion of smaller particles, but may also be related to the food value. A unit volume of small particles may have more attached microbial organisms, owing to the greater surface area per unit volume of the particles. This has been shown to be the case for surface-bound bacteria, but some sediments may be characterized by very complex relationships between grain size and organic matter and microbes. If the expected relationship holds, then deposit feeders should select for fine particles, assuming that the cost of rejecting those particles is not too great.

Feeding rate and gut passage time may also be reg-

ulated according to food value. There may be an optimal feeding rate simply because feeding too quickly reduces the time available for digestion, whereas feeding too slowly may waste valuable time that could otherwise be applied to feeding on new material. This idea could be tested by consideration of foods of differing quality. If the cost-benefit approach is appropriate, then deposit feeders should feed more rapidly on richer sediments. This has turned out to be true in several experiments on polychaetes, for which feeding and gut passage are steady.

* Most infaunal suspension feeders in soft sediments generate a current into the burrow or siphon, and strain plankton on a feeding organ.

Many suspension feeders live infaunally and semi-infaunally in soft sediments. For example, the siphonate infaunal bivalve mollusk *Mercenaria mercenaria* creates a current by means of a ciliated gill. Water is drawn into an inhalant siphon, and the cilia strain and sort particles (Figure 13.12). The polychaete *Chaetopterus* lives in a U-shaped burrow, and specialized parapodia drive an inhalant current into the tube. A sheet of mucus stretched between another pair of specialized parapodia captures particles, and this sheet is periodically rolled into a ball and passed through the mouth. Most soft-sediment suspension feeders rely on phytoplankton for food. In coastal waters, large numbers of detrital particles are in the water column, and these are digested poorly. Benthic algae, however, are often resuspended and these may be an important food for benthic suspension feeders.

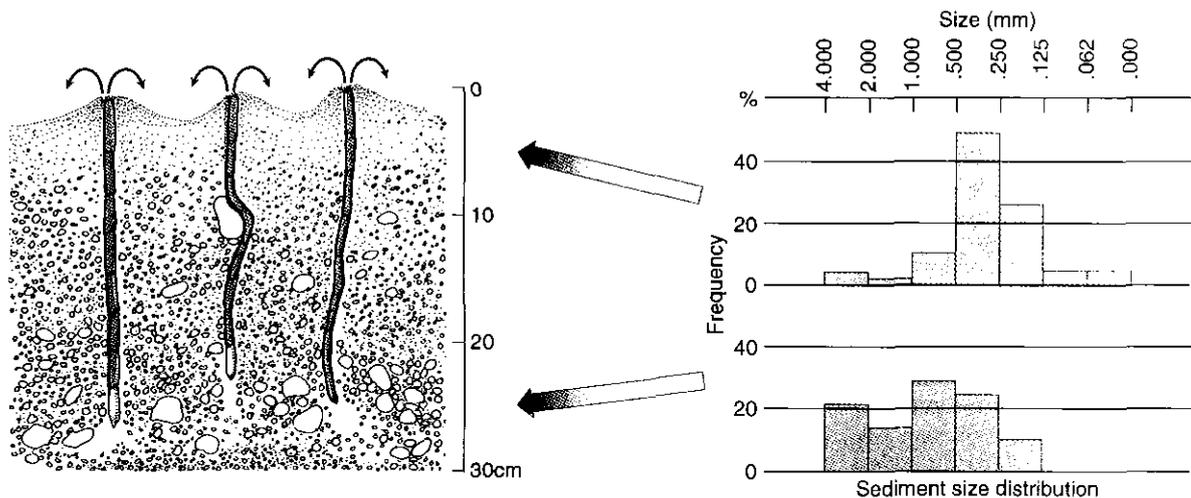


Fig. 13.11 Left: Vertical reworking of intertidal sediments by the tube worm, *Clymenella torquata*. Right: change in the vertical distribution of particle size as a result of vertical reworking of the sediment. (After Rhoads, 1967.)

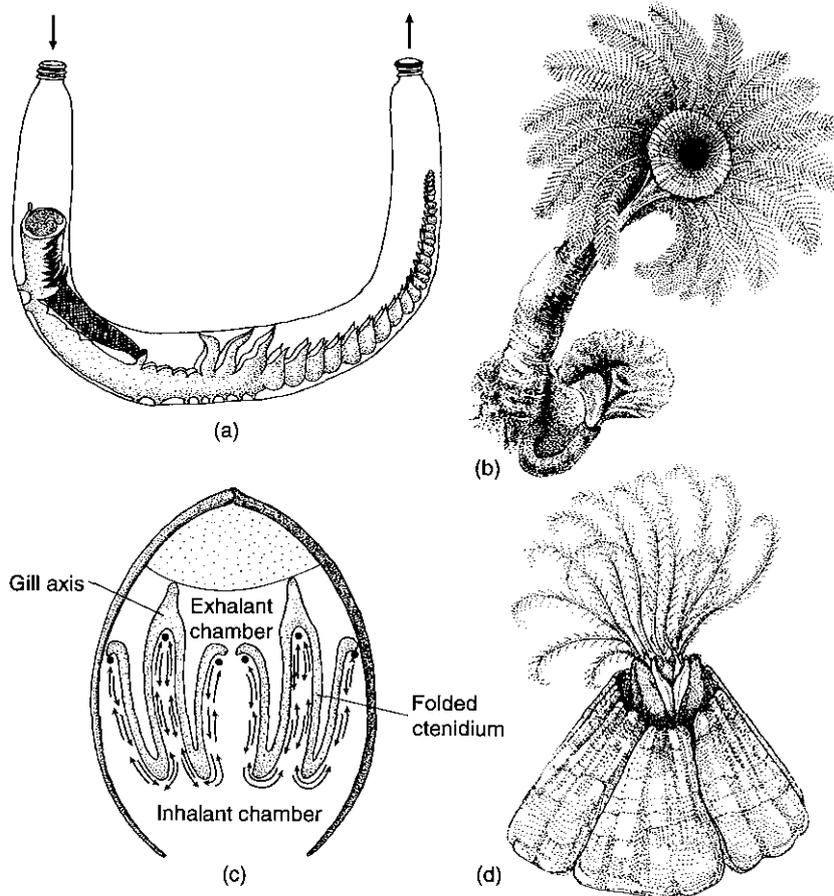


Fig. 13.12 Some suspension-feeding invertebrates: (a) the active suspension-feeding parchment worm *Chaetopterus*; (b) the suspension-feeding polychaete *Serpula*, which uses ciliary currents to draw particles to tentacles; (c) cross section of a bivalve mollusk, an active suspension feeder (arrows denote ciliated tracts transporting particles); (d) the acorn barnacle *Semibalanus balanoides* with cirri protruded like a basket, the concave side pointing into the flow and particles trapped on feeding appendages, which are then withdrawn. If the flow increases beyond a point, the basket is reversed, to maintain stability in the flow.

* Hydrodynamic forces at the sediment-water interface cause sediment transport, which often induces switches of feeding from deposit feeding to suspension feeding.

Deposit feeders are usually found in fine sediments, which are deposited in relatively quiet water. In sand flats, however, deposit feeders may dominate in areas where sediment is transported extensively, owing to tidal and wave action. In a sandy bay, sediment transport may far exceed recycling of the sediment in place by deposit feeders. In other words, in such habitats deposit feeders may look upstream for their next meal. During some periods, the bottom is quiescent, as evidenced by the presence of distinct fecal mounds that continually build up with each tidal cycle. In many cases, however, these mounds are eroded away, indicating that the animals have fresh sediment to deal with from tide to tide or even from wave to wave. In such cases, there is no need for the animal to deal with accumulations of fecal pellets, because they are transported away. During quiescent periods, pellets build

up and feeding may decrease, but the next food supply may be only a wave or a tide away.

If wave action is sufficiently strong, deposit feeders may change their behavior significantly. In moving waters, some of the normally deposit-feeding tellinacean bivalves switch to suspension feeding. This may be a reaction to particle saltation, which would be common during wave action. Spionid polychaetes have tentacles, which in quiet water pick up particles from the sediment surface. If current speed is increased sufficiently to transport particles above the bottom, these worms deploy their tentacles in an erect spiral, which then serves as a suspension-feeding organ. If prominent sedimentary structures, such as sediment ripples, develop, animals may locate themselves in hollows so that they may feed efficiently, perhaps even moving toward fine particles that may accumulate in the hollows.

* Suspension feeders and deposit feeders must be able to avoid clogging from heavy particle loads.

When water moves above a soft sediment, the erosive power of fluids eventually saltates particles into suspension. For suspension feeders, this process dilutes their plankton food source with unwanted inert particles such as sand grains. Higher particle loads usually clog suspension-feeding organs, such as ciliary tracts and siphons. At very high water velocity, sediment moves laterally, and ripples form. As crests and trough alternately pass over a suspension-feeding animal, it becomes difficult for the animal to maintain a stable feeding position. Water eddies often form in the trough of a ripple, which creates a complex flow pattern.

Infaunal animals have a variety of means of dealing with increasing particle flux near the sediment-water interface. Some suspension-feeding siphonate bivalves have a ring of papillae at the siphon opening, which can act as a protective network against influxes of sand grains. The inhalent siphon of some tellinacean bivalves is lined with papillae, which can help in rejecting unwanted sand. Most eulamellibranch bivalves can "sneeze," or suddenly expel water and an overload of sand through the inhalent siphon. In cases of extreme sediment instability, many infaunal animals must continually readjust their burrowing position. Bivalves such as the surf clam *Spisula solidissima* are continually unburied in the surf zone, and must be rapid burrowers. A remarkable series of species that have adapted to a tidal cycle of erosion and burial will be discussed in Chapter 14.

Benthic Life on Hard Surfaces and in Moving Waters

Hard surfaces include rock, clam shells, coral skeletons, or any other surface that does not consist of grains that can be pushed apart. Hard-surface organisms include forms cemented along a flat surface (e.g., acorn barnacles, forms attached by threads or knobby structures (e.g., mussels, seaweeds), and mobile forms (e.g., snails, sea urchins).

Flow and Orientation of Sessile Benthos

* Organisms must adapt to strong laminar flow above the bottom, but experience lower-strength and more-complex flows near the surface.

Sessile benthos may live in widely different current regimes depending upon their living position relative to the sediment-water interface, or rock-water inter-

face. A directional current may be far more irregular near the interface. This has effects on species of different sizes and especially upon species that may experience complex flow as small juveniles but strong directional flow as adults. This can be seen in the sea fan *Gorgonia*. Small colonies have an irregular shape and no preferred orientation, in contrast to larger colonies, whose fan shape is oriented approximately normal to unidirectional currents. It may be that the near-bottom currents are erratic in direction, owing to irregularities of bottom topography and surrounding erect organisms. As the colony grows, it probably protrudes more directly into the main current. The fan-shaped colony probably "grows" into its orientation.

This difference in current direction can be seen among species of feather star crinoids. Feather star species found in crevices generally experience multidirectional currents and have their pinnules arranged in four rows at approximate right angles, which maximizes food capture from several possible directions. By contrast, the erect Caribbean feather star *Nemaster grandis* protrudes strongly into unidirectional currents and has its pinnules arranged in a plane, which maximizes capture under these circumstances. In the brittle star *Ophiothrix fragilis*, tube feet arise from either side of the tentacle and are also arranged in a two-row plane (Figure 13.13). Food particles are captured by the tube feet and are compacted into a mucus-clad bolus that is passed down the arm.

* Sessile epibenthos may experience pressure drag and must have traits to minimize drag by changing orientation.

Sessile benthos feel drag when they protrude from the bottom into a strong current. (Recall that drag is a force parallel to the direction of the current.) In some cases, the shear force on a nonflexible body may be sufficient to tear it from the bottom or snap a weak but erect skeleton. To reduce this problem, sessile organisms must be able to minimize drag by adjustments of behavior, and by having shapes and orientations that minimize drag. There are two distinctly different types of situations. Passive animals are oriented by a strong unidirectional current until some equilibrium orientation is achieved. In many cases, this orientation is no different from that achieved by an inanimate object of the same shape and bulk density. By contrast, active animals may use muscular action, behavior, or other means to orient actively in a flow. The active adjustment minimizes drag, while maintaining access to food.

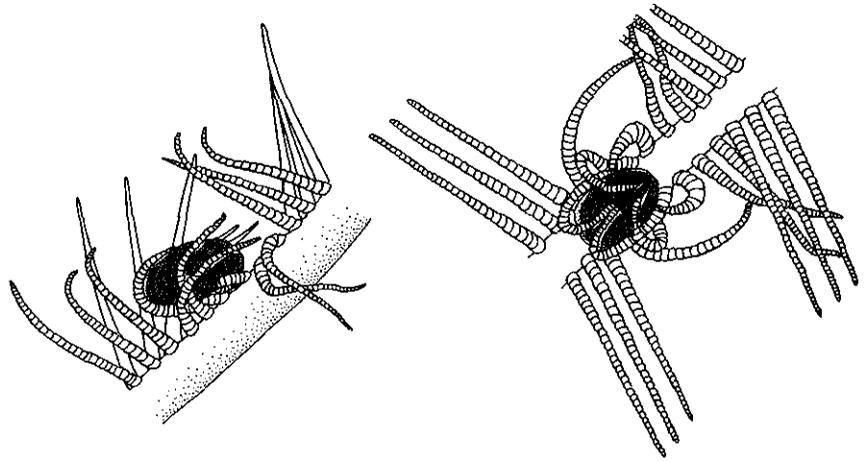


Fig. 13.13 The food-collecting wave of a suspension-feeding brittle star, showing the planar arrangement of the pinnules. (From Warner and Woodley, 1975.)

Under conditions of strong flow it is hard to maintain an erect position. As explained in Chapter 6, pressure drag would be maximal upon a cylinder with its long axis maintained perpendicular to the flow. For example, the Caribbean elk horn coral *Acropora palmata* (Figure 13.14) forms large erect branching colonies, sometimes greater than 2 m across. In the strong currents of exposed reefs, a branch growing perpendicular to the flow can easily snap off. As a result, colonies protruding into strong unidirectional flow tend to have their branches pointing nearly horizontally, in order to minimize the great potential shear. Obviously, this coral is stiff and cannot bend over in a current. Both sessile animals and plants can be flexible and thereby reduce drag. The anemone *Metridium senile* can grow to be quite tall, sometimes exceeding a meter in length. The animal is quite flexible, so in fast currents the body bends over and points downstream. In this posture, the bush-like crown of tentacles can collect food particles in the wake of the flow, although the crown may be withdrawn at very high current velocities. Some seaweeds are equally flexible, and the stipe can bend and point downstream to minimize drag in a strong current. The kelp *Ner-*

eocystis luetkeana has a series of fibrils in the cortical cell walls that have an average angle of 60 degrees to the axis of the stipe. This increases the extensibility of the stipe, which prevents breakage in a strong current.

The eastern Pacific stalked sea squirt *Styela montereyensis* is remarkable for its occurrence in a wide array of environments on the California coast, ranging from wave-swept outer coasts to quiet bays. In quiet water, this species resembles typical solitary sea squirts, and the siphons orient upward. In outer coasts, most animals are attached by relatively slender stalks and sway with the wave surge (Figure 13.15). The incurrent siphon is bent approximately 180 degrees. When the animal is bent over by the current, the water can ram into the siphon, which facilitates flow of water and particles. It is not clear how these two morphologies are determined; they may be genetic variants.

* Mobile benthos may passively orient to the position that minimizes drag.

The rules of drag are not very different for nonsessile benthos. The orientation that minimizes drag is usually preferred. Mobile snails often find themselves in

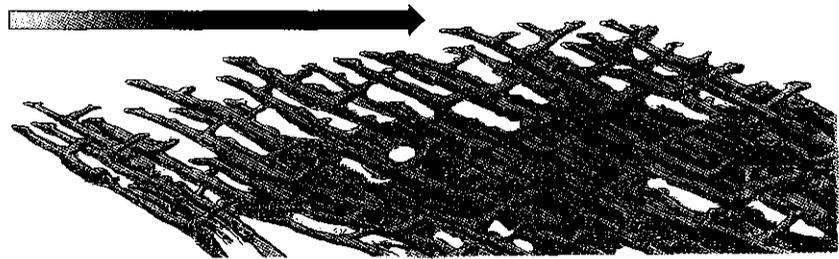


Fig. 13.14 The elk horn coral *Acropora palmata* has a stiff skeleton. In a strong unidirectional or bidirectional flow, the colony grows with the branches sub-parallel to the current; which minimizes drag and the possibility of snapping off of coral branches.

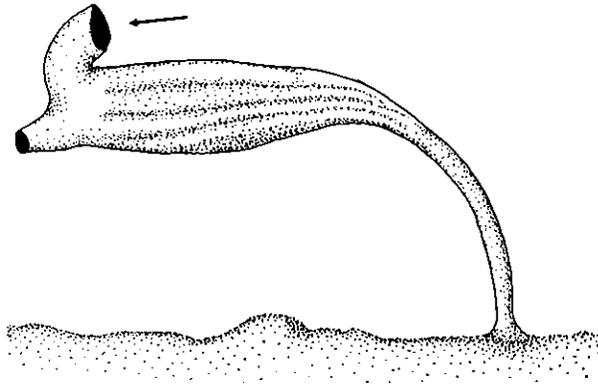


Fig. 13.15 Orientation of the outer-coast form of the sea squirt *Styela montereyensis*. Note that a current causes the individual to bend, but the incurrent siphon is bent, which facilitates intake of water and particles for food. (After Young and Braithwaite, 1980).

strong currents, and an orientation that places the axis of coiling parallel with the current will minimize pressure drag. The mud snail *Ilyanassa obsoleta* often finds itself in tidal creeks with flow exceeding 30 cm sec^{-1} , and orients with the apex pointing upstream. Another possibility is to have a very low profile, to permit streamlines to flow smoothly over the shell. Many intertidal limpets live under conditions of severe wave shock, and have such a low profile.

Animals that are not sessile have the luxury of relatively rapid movement, and can remove themselves from limiting flow conditions. The Caribbean feather star *Nemaster grandis* lives on coral promontories, and seems to prefer high flow conditions. Nevertheless, flow occasionally becomes so extreme that the feather star cannot protrude its arms and tube feet into the mainstream. In the case of strong currents, it actively moves to a protected crevice. Even snails may protrude sufficiently into a stream that they are unable to resist the shear stress. The mud snail *Ilyanassa obsoleta* responds to strong flow by burrowing in the sand; this is especially important during a strong incoming tide, when shear stress is maximized and erosion around the shell is very strong.

Suspension-feeding on Hard Surfaces

* Particle capture may involve simple sieving, but particles may directly impact on tentacles and tube feet, or they may leave the flow by a variety of other mechanisms and impact on the feeding structure.

We intuitively think of particle capture as a sieving process. An animal would therefore capture particles larger than the distance between tentacles (if the animal were a coral), or between tube feet (if it were a brittle star or crinoid). However, velocity drops greatly near any closely spaced structures, and recent studies show that biological sieving is unusual. The Reynolds number in such structures is so low that the water between the fibers is more like a nearly impervious wall than a passage. Instead of considering these structures as simple sieves, we must consider the hydrodynamic features of particles as they approach the suspension-feeding capturing fibers. Figure 13.16 illustrates the possible means of capture by a passive set of fibers:

1. **Sieving.** The particle is trapped between fibers.
2. **Direct Interception.** The particle follows water streamlines and comes within the distance of one particle radius.
3. **Inertial Impaction.** The particle has inertia and crosses streamlines.
4. **Motile Particle Deposition.** The particle moves randomly and hits a fiber.
5. **Gravity Impact.** The particle crosses streamlines because it has inertia and is pulled by the force of gravity to impact on the fiber.

In Chapter 6, we discussed the effect of flow when velocity is low and the structures are small. Under these conditions of low Reynolds number, inertia is not nearly as important as the viscous forces in the water. If sieving does not occur, direct interception is the most likely mechanism of particle capture at low Reynolds number.

* Passive suspension feeders collect food by means of morphological structures that protrude into the flow and capture particles.

Suspension feeders commonly protrude a feeding organ into a mainstream current and suffer the problems mentioned above. In a moderate unidirectional current, the best strategy would be to deploy a network whose plane is perpendicular to the flow. This maximizes the opportunity for food particles to be intercepted. Gorgonians are branch or stem-like colonies of feeding polyps. When small, the branches have no particular orientation, because the current flow is complex near the bottom. However, as the colony gets larger and protrudes into a predictable

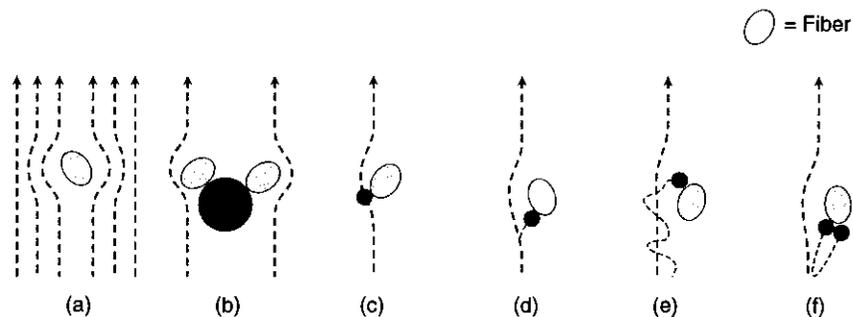


Fig. 13.16 Particles are captured by suspension feeders in a variety of ways, depending upon the hydrodynamic regime, which is characterized partially by the Reynolds number. (a) Streamlines around a fiber; (b) particle is captured between fibers that act like a sieve (this rarely happens in suspension feeders, because there is not enough inertia at the small size scale and low Reynolds number); (c) direct interception, a common means of intercepting phytoplankton particles by cilia of bivalves, and polychaetes; (d) inertial impaction; (e) motile-particle deposition, which occurs because particles are not moving in perfectly smooth streamlines but move erratically and impact on the fiber; (f) gravitational deposition, which occurs when particles are moving rapidly at high Reynolds number or are dense enough to cross streamlines. (Modified from Rubenstein and Koehl, 1977.)

and unidirectional flow, it “pays” for the colony to have a preferred orientation. The branches then often grow into a plane that is perpendicular to the current.

Not all benthic passive suspension feeders adopt a vertical planar form, nor are their feeding structures always oriented upstream. Many suspension feeders are colonial, and are bush-like (e.g., the hydroid coelenterates) or are simply a thin layer over the substratum (e.g., many sponges and corals). Although this may seem inefficient for feeding in a unidirectional current, a multidirectional orientation serves well when the current flow is complex. In many benthic habitats, water motion is oscillatory; the water just sloshes back and forth over the bottom. In other cases, tidal currents cause a reversal of flow. Under such circumstances, a bush-like shape will gather more food and oxygen than will a planar shape with individuals pointing upstream.

It is still not very clear how particles are captured by passive suspension feeders. Overall, viscosity should be very important in particle capture, owing to the small scale of the capturing structures and the relatively low velocity. In animals like corals, crinoids, and suspension-feeding brittle stars, tentacles or tube feet probably capture particles upon impact. However, there may be some cases in which the Reynolds number is sufficiently high that particles may have some inertia and actually fall out of the water, cross

local streamlines, and impact on the feeding organ. In brittle stars, particles much smaller than the distance between the tube feet are captured, indicating that simple sieving is not the main mechanism of capture. Zooplankton landing on the tentacles of large anemones may be a case of suspension feeding by means of gravitational deposition.

* Active suspension feeders have similar constraints as passive suspension feeders, but also generate their own water currents to channel and ingest particles.

In contrast to passive suspension feeders, active suspension feeders create a current to take in planktonic food. In many bivalve mollusks and polychaete annelids, ciliary currents draw particles toward the cilia, which capture particles and transport them down ciliated tracts (Figure 13.12b,c). All of this probably happens at very low Reynolds number, and the cilia must directly reach out and capture particles (see the discussion in Chapter 5 on planktonic larval ciliated feeding for more on this subject). As transport occurs, the tracts reject unsuitable food particles. Many intertidal acorn barnacles use a different active strategy: the thoracic limbs move actively and capture particles that are drawn to and processed by appendages surrounding the mouth. Barnacles can adjust the orientation of the thoracic appendages at different flow ve-

locities. At low velocity, the feeding cirri face into the current and capture particles. If the current passes a threshold velocity, the cirri are suddenly reversed and pointed downstream, in order to minimize drag.

Benthic Carnivores

* Carnivory relies on mechanisms of prey search, location, seizure, and ingestion.

Carnivorous animals hunt and eat other animals (Figure 13.17). Defining *benthic carnivores* is not entirely straightforward, because those that eat zooplankton are as much carnivores as they are suspension feeders. Of necessity, most carnivores are mobile and have a variety of means of prey detection. Many species are capable of detecting soluble substances emanating from the prey. The European sea star *Astropecten irregularis* moves along the sediment surface, but can

detect its prey within the sediment. Many carnivores orient to prey upstream. Specialized bivalve mollusks known as septibranchs detect prey by chemical means. A specialized pumping septum moves suddenly, expels water through the exhalant siphon, and draws water plus prey into the inhalant siphon (Figure 13.17b).

Vision is a common means of prey detection. Bottom-feeding birds, crabs, fishes, and cephalopods such as cuttlefish all detect prey visually. Visual detection is usually accompanied by sophisticated and rapid eye-motor coordination. The oyster catcher *Haematopus ostralegus* can dash onto an open mussel as a wave recedes, plunge its beak into the mussel, and sever its adductor muscles, making it helpless. More rarely the oyster catcher hammers with its bill and crushes the shell. In either case, the oyster catcher assesses the size of the mussel, and tends to take prey that are larger than average size. Lobsters and crabs use both chemical detection and vision in

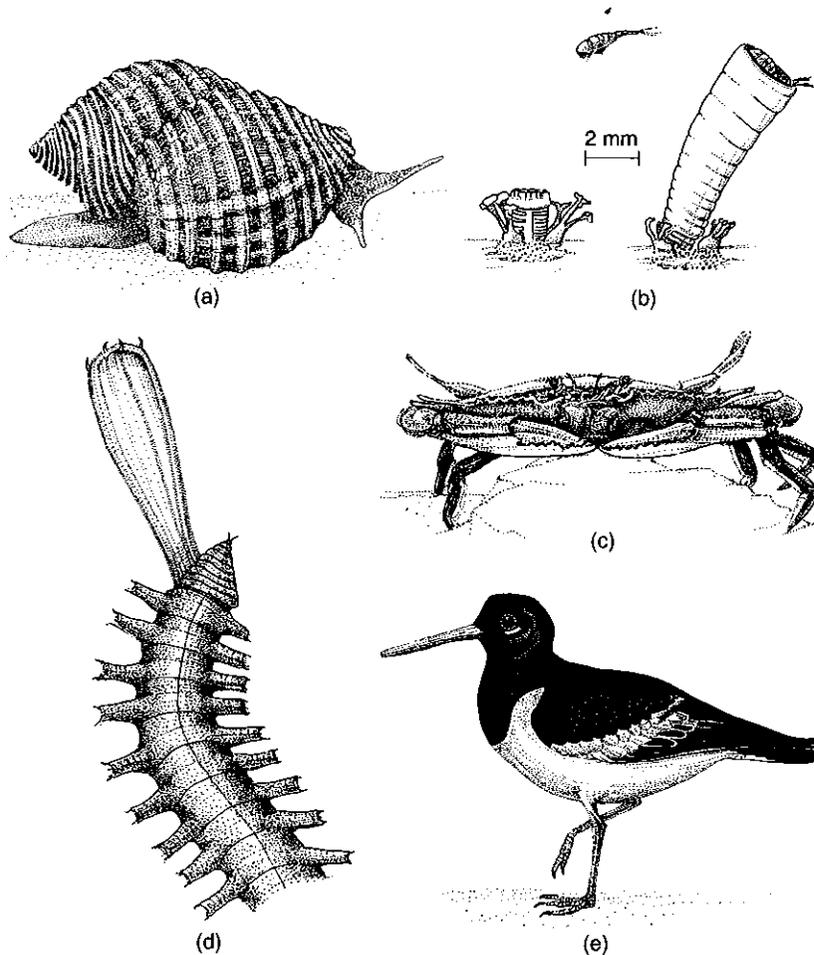


Fig. 13.17 Some marine benthic carnivores. (a) Gastropod *Nucella*, which uses a specialized radula and buccal mass to drill holes in barnacles and bivalve mollusks; (b) bivalve mollusk *Cuspidaria*, which uses a pumping septum to suck up small prey; (c) polychaete *Glycera*, which has a proboscis armed with hooks, used in seizing and tearing prey; (d) decapod crab *Callinectes sapidus*, whose strong claw can crush mollusks; (e) the oyster catcher, *Haematopus ostralegus*, a predator on intertidal bivalve mollusks.

Claws! The Crushing and Tearing Story of Mechanical Advantage

If you have ever handled a blue crab (*Callinectes sapidus*) or a Maine lobster (*Homarus americanus*), chances are your fingers have been pinched. These creatures, like many other crustaceans, have powerful claws capable of extraordinary closing forces. Lobsters and blue crabs feed on mollusks and easily crush even thick shells. How can such great force be exerted?

Like Popeye the Sailor's muscular forearm, most of a lobster's crushing force can be traced to muscles in the claw itself. The claw is a lever system, and muscles attached to one of two sides of the pivot can either open or close the claw (Box figure 13.2a). From the outside, you can see a movable finger, the dactyl, which opposes a fixed finger, which is attached to the main part of the claw. Muscles contract and pull on a slender projection of the dactyl, known as the extensor apodeme. This pulls the lever system around the pivot point, and the dactyl is raised. Relatively little musculature is required to open the claw. Far more muscle is attached to a much broader flexor apodeme, whose pull closes the claw. The flexor apodeme attaches to the dactyl on the other side of the lever, so the dactyl is pulled down. Muscular force is proportional to cross-sectional area; there is much more area for muscle attachment on the flexor apodeme than on the extensor apodeme.

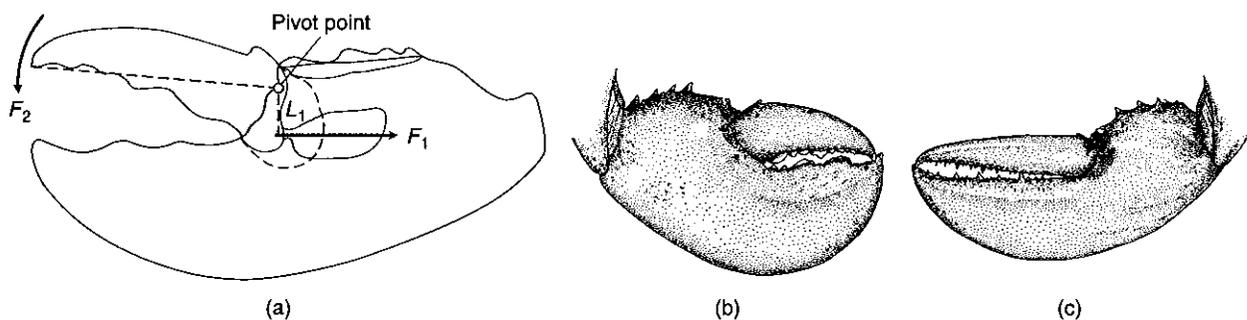
More muscle cross-sectional area can generate more force, but there is another means of changing force, simply by changing the proportions of the lever system. Think of a see-saw in a playground. If the seats are equidistant from the pivot point, then two people of equal weight will exactly balance each other. However, if we move the board so that one side has twice the length of the other, then a person on the long end can exactly balance someone twice her weight on the short end. The weight, after all, is a force, so one can

see that the change of proportions has changed the mechanical properties of the machine. The ratio of lengths of the sides of the see-saw (long to short) is the **mechanical advantage**.

The lobster claw obeys the same principles, though the orientations of this living machine are bent relative to a see-saw. (The pivot and appropriate lengths are shown in Box figure 13.2a.) Force F_1 is exerted over length L_1 , and this generates force F_2 over length L_2 , which is the length of the dactyl. To increase the closing force, one must either increase the ratio of L_1 to L_2 , or increase the area of muscle attachment to the flexor apodeme. Both can be accomplished by increasing the volume of the compartment that encloses the muscles.

All lobsters have two distinct claws. One is a crusher claw, and its proportions are such that the mechanical advantage is greater than the other, which is a slicing claw (Box figure 13.2b,c). Amazingly enough, there is no predictability as to which side each claw type will be on. Various random events cause one claw to develop into the crusher chela and the other into a slicer chela, so a population of lobsters will have approximately equal proportions of right-handed and left-handed crusher claws.

The mechanical advantage of the crusher claw is double that of the cutter claw, but the cutter claw has an advantage, even if it is a bit weaker. The complement of mechanical advantage is speed. To understand this point, remember the see-saw. If you move the tip of the short side of the see-saw a given distance, the longer side will move much more rapidly. Thus, the cutter claw of a lobster can move more rapidly and handle food much more efficiently than the crusher claw can. Thus the lobster uses the cutter claw to manipulate food and the crusher to perform the gruesome final act.



Box Fig. 13.2 Claws of the lobster *Homarus americanus*. (a) Features of the claw, forces and pivot of the claw apparatus; (b) the crusher claw; (c) the cutter claw. (Scale for (b) and (c) is 5 cm.) (After Elner and Campbell, 1981.)

predation, and can rapidly attack and immobilize prey.

The several strategies for attacking and seizing prey are obviously related to the mode of prey detection. Many predators are essentially sessile, and must wait for prey to arrive. Anemones usually remain fixed to a hard surface, and have access only to prey that swims or falls in contact with the tentacles. One large eastern Pacific anemone, the intertidal *Anthopleura xanthogrammica*, lives in low intertidal pools, and depends for food upon mussels that fall from above. This is greatly aided by starfish, which are somewhat sloppy as they pry mussels from the bed and allow some to fall to the anemones below. More-mobile carnivores have a variety of sophisticated search behaviors, aided by vision and olfaction. Some fishes and crustaceans are "sit-and-wait" predators whereas many others cruise continuously until detecting a prey item.

The handling of prey varies with phylogenetic background, because morphologies are so disparate. Seizing prey involves some sort of appendage, such as a crab claw or a starfish arm. Many species of crabs have large crushing claws with denticles that enable handling of prey. Some crabs, such as the stone crab *Menippe mercenaria*, have robust claws and musculature, and can crush thick-shelled mollusk prey. Others, such as the shore crab *Carcinus maenas*, are not terribly strong and have trouble crushing mussels unless they discover a weak spot in the shell. Some crabs repeatedly apply a crushing load to bivalves. Eventually, after several applications of pressure, the shell fatigues and can be crushed. Some tropical crabs can easily peel the shell of a snail, in order to expose the soft parts. Polychaetes such as some species of *Glycera* (Figure 13.7d) have a protrudable proboscis with hook-shaped teeth; other polychaetes have large chitinous jaws that can tear prey apart.

For some carnivores, success involves immobilizing the prey by a sting. Cone snails of the genus *Conus* have a highly movable proboscis and long, barbed radular teeth. The proboscis is protruded very rapidly and one or a few teeth stab the prey, and a poison is injected along a groove. The speed of attack and the virulence of the poison allow some species to immobilize and kill small fishes, which are then swallowed whole. Some nemerteans can seize prey and pierce them with stylets, injecting a poison.

In the gastropods, drilling is a specialized way of penetrating prey that have exoskeletons. This occurs in the prosobranch families Muricidae (*Urosalpinx*,

Murex), Naticidae (*Polinices*), and Thaididae (*Nucella*), and involves alternations of mechanical rasping and chemical secretions from an accessory boring organ.

Benthic Herbivores

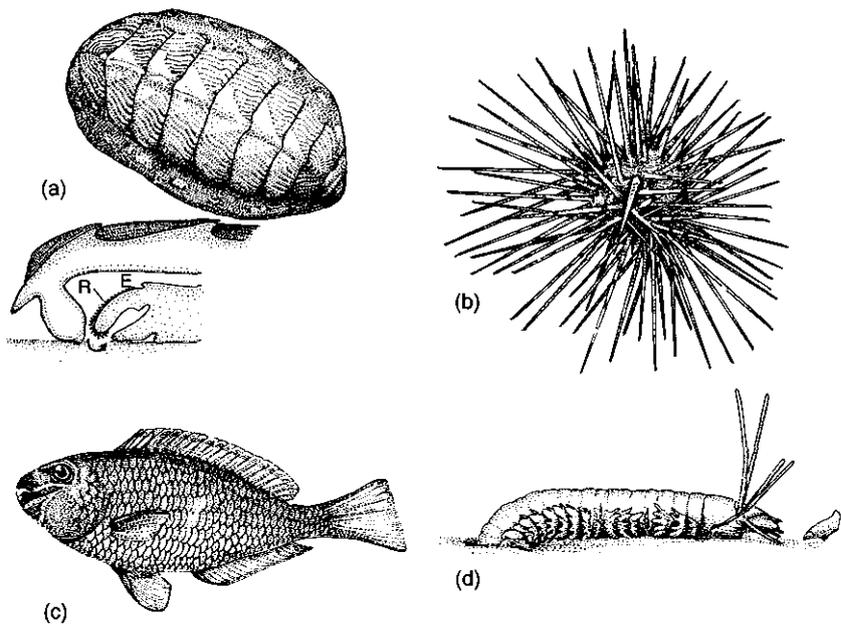
* Benthic herbivores are divided between microphages and macrophages.

The food of benthic herbivores (Figure 13.18) can be divided by size class into two major categories. Benthic microalgae include a variety of groups, such as diatoms, cyanobacteria, and microscopic stages of seaweeds. These organisms may form a thin layer on a rock surface or on the surface of sediment. Consumers have a range of morphological features that allow them to graze efficiently on this layer. Chitons, limpets, and other grazing mollusks employ a radula, a belt of teeth that scrape along the surface. The movement of the subradular membrane over a cartilaginous portion of the buccal mass erects the teeth and scrapes them over the surface. The radula and buccal mass are retracted and food trapped on the teeth is delivered to the buccal cavity. This feature can be used on rocks, and limpet grazing scars are common on rocky shores. However, radular scraping is also employed by gastropods feeding on soft-sediment surfaces. Some polychaetes can graze on sediment microalgae by pressing their tentacles onto the surface and collecting particles and microalgae, which are transported to the mouth by means of a ciliated tract.

A wide variety of herbivorous animals can tear apart and consume macroalgae and marine higher plants. The radular apparatus of many mollusks has been adapted in many cases to tearing apart seaweeds and periwinkles, for example, can rasp and tear apart a large number of seaweeds. Their effectiveness, however, is often restricted to those seaweeds that have rather delicate structures, such as the sea lettuce genera *Ulva* and *Enteromorpha*. Sea urchins possess an Aristotle's lantern, which is a complex of calcareous teeth, ligaments, and muscles. This device can tear apart a variety of seaweeds, and some urchins are even capable of devouring relatively less digestible sea grasses, such as the tropical Caribbean *Thalassia testudinum*.

Many crustaceans are also herbivorous. Many smaller amphipods and isopods feed on relatively soft

Fig. 13.18 Some benthic herbivores: (a) the chiton *Tonicella*, a scraper of microalgae; inset shows anterior sagittal cross section and shows action of radula tooth belt in scraping algae from substratum (*R* = radula; *E* = esophagus); (b) the sea urchin *Arbacia*, which uses a toothed Aristotle's lantern to scrape microalgae or to tear apart seaweeds; (c) a parrot fish, which uses a specialized mouth to scrape algae from coral surfaces; (d) the nereid polychaete *Nereis vexillosa*, which tears apart sea lettuce. (Copied from an original by K. Fauchald.)



seaweeds, or on the microalgae growing on seaweed surfaces. A variety of fishes are also efficient herbivores, particularly on coral reefs. Parrot fishes (Scaridae) have jaw teeth fused into plates, which are capable of cutting material from the surface of coral skeletons. Surgeon fishes (Acanthuridae) also can scrape algae from corals, and the two groups are major causes of erosion on coral reefs. Even smaller invertebrates, such as isopods and polychaetes, have sufficiently strong mouth parts to tear apart algae. The buccal hooks of some species of the sand worm *Nereis* are employed in tearing apart soft green algae.

Although herbivores are usually mobile, many rock-scrapers are capable of homing. A home base may provide a reference location, allowing efficient exploitation of the renewable resource of microalgae living on hard surfaces. The eastern Pacific owl limpet *Lottia gigantea* and the limpet *Patella longicosta* both defend territories.

Although most benthic herbivores search for suitable food, some wait for the food to come to them. Many urchins capture drifting seaweed fragments on their dorsal spines and dorsal tube feet transfer them toward the mouth. Sand-flat polychaetes such as species of *Nereis* and *Lumbrinereis* can drag seaweed fragments down into their burrows. In some cases the downward dragging is incomplete and the seaweed actually can start to grow. Some polychaetes practice farming by attaching fragments of *Ulva* to their tubes and letting them grow.

* Some benthic herbivores can feed on highly indigestible plant material.

Most marine herbivores are restricted to relatively soft seaweeds and microalgae, with a minimum of relatively indigestible complex carbohydrates, such as cellulose. A small number of species, however, have adapted to such difficult food sources. Some invertebrates can bore into wood and digest it or may depend upon the marine microbiota living in the wood. The wood-boring bivalve *Teredo* (ship worm) and *Bankia*

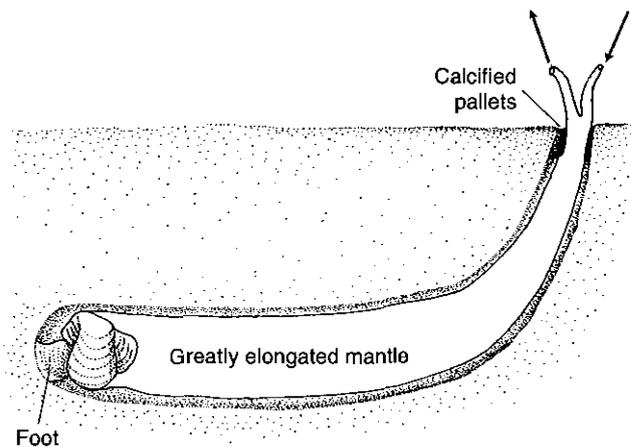


Fig. 13.19 Cross section showing the living position of the wood-boring bivalve mollusk *Teredo*. (After Trueman, 1975, *The Locomotion of Soft-Bodied Animals*, with permission of Edward Arnold (Publisher) Ltd.)

scrape the wood particles and use the digestive enzyme cellulase to attack the cellulose (Figure 13.19). The wood-boring isopod *Limnoria* can also digest cellulose, but it requires wood-boring fungi as a source of nitrogen. Wood-boring bivalves derive their nitrogen from symbiotic nitrogen-fixing bacteria, because nitrogen is not in sufficient quantities in the wood.

Sea grasses, such as eel grass (*Zostera*), salt marsh cord grass (*Spartina*), and Caribbean turtle grass (*Thalassia*), are relatively indigestible to most marine consumers, because of the abundance of cellulose the grasses contain. Some small grazers consumer the microalgal surface layer, but relatively few species can

consume, digest, and assimilate material from the grass itself. As mentioned above, a few species of urchins can deal with turtle grass. Eel grass and cord grass are remarkable for the miniscule amount of grazing they experience from marine herbivores. An interesting exceptional species is the green turtle, *Chelonia mydas*, which can digest cellulose derived from turtle grass. It has a hindgut that bears a functional resemblance to the stomachs of ruminant mammals, such as cows and horses. The postgastric gut region is greatly elongated, and postgastric fermentation is facilitated by the presence of symbiotic bacteria and protozoa, which facilitates digestion.

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Review Questions

1. Distinguish between active and passive suspension feeders.
2. What type of hydrodynamic condition does a well-sorted sediment reflect?
3. What is a burrowing anchor and why is it required in a burrowing organism?
4. What do most interstitial marine animals have in common, in spite of their being from quite different taxonomic groups?
5. What factors help to determine the depth of the redox potential discontinuity?
6. Why do different types of bacteria tend to dominate at different depths below the sediment-water interface of a muddy sediment?
7. What is the microbial stripping hypothesis?
8. Describe the components of decay of particulate organic matter in sediments.
9. How does a bivalve like *Solemya*, which lacks a gut, manage to derive its nutrition?
10. Why and under what conditions do some benthic infaunal species switch between suspension feeding and deposit feeding?
11. How can sessile epibenthos reduce pressure drag?
12. Why are many suspension-feeding structures not simple sieves, whose interfiber distance can be used to predict the diameter of particles that can be captured?
13. What is the advantage to carnivorous crustaceans in having differentiated crusher and tearing claws?
14. Why is it possible for some marine animals to digest cellulose, which is nearly indigestible for most organisms?