



Benthic Life Habits

Introduction

Benthic Size Classification

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 often interstitial, living among sedimentary grains.

Feeding Classification

Deposit feeders ingest sediment and use organic matter and microbial organisms in the sediment as food. **Suspension feeders** feed by capturing particles from the water, usually phytoplankton and smaller zooplankton but possibly bacteria. **Herbivores** eat nonmicroscopic photosynthetic organisms, such as seaweeds. **Carnivores** eat other animals, but there is no easy way to classify some organisms, such as suspension feeders that ingest zooplankton. Finally, **scavengers** feed on 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

Important Features of Soft Sediments

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

Sediment grain size is generally classified as in Table 15.1.

The **silt–clay fraction** is the mass percentage of sediments finer than 62 μm in diameter. The **percent clay** (particles < 4 μm) may also be useful in describing sediment properties relevant to benthic organisms.

The **grain size of sediment** is largely related to the current strength of the overlying water column. Because stronger currents can transport larger particles, median grain diameter increases in areas of high current velocity (see **Going Deeper Box Figure 15.1** for a discussion of the measure of grain size). Areas with strong currents also experience extensive erosion; sediment and fine particles will be transported away. In a weak current regime, fine particles can settle out of the water column and will remain.

- **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, whereas in a well-sorted sediment, almost all the weight is confined to a few size classes, with a well-defined

TABLE 15.1 Size Classification of Sedimentary Particles

CLASS	SIZE RANGE (mm)
Clay	<0.04
Silt	0.04–0.0625
Sand	0.0625–2.0
Gravel	2–64
Cobble	64–256
Boulder	>256



GOING DEEPER 15.1

Measuring Grain Size of Sediments

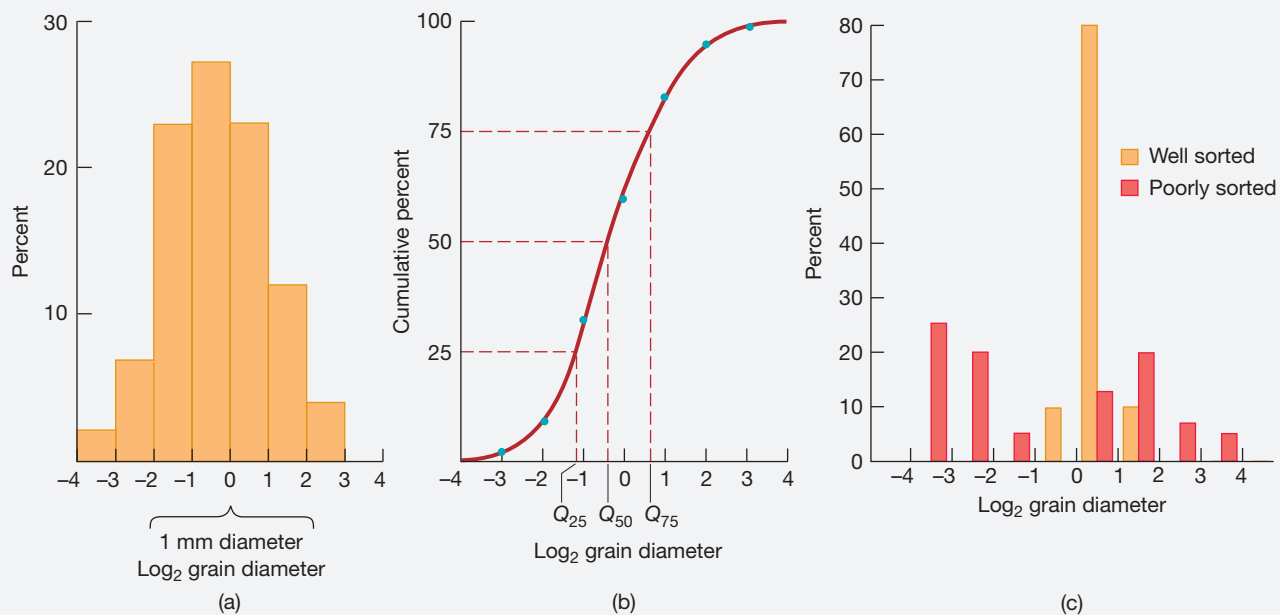
Median grain size is the simplest way to represent particle size characteristics of soft sediments. By washing the sediment through a series of graded sieves, one can get the size class data to construct a histogram of sizes (Box Figure 15.1a). To accommodate a range of particle sizes of many orders of magnitude within one graph, we plot grain diameter in logarithmic form (log to the base 2, which means that a value of 1 in Box Figure 15.1 corresponds to 2 mm, a value of zero corresponds to 1 mm, and a value of -1 corresponds to a diameter of 0.5 mm). The diagram is used to construct a cumulative weight graph, where the percent weights of the successive size classes are accumulated and cumulative percent weight is plotted as a function of particle diameter (Box Figure 15.1b). The median diameter M , which corresponds to Q_{50} , is the

particle diameter corresponding to 50 cumulative percent. Calculation of the 25 and 75 percent classes is also shown.

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

$$S = \frac{Q_{25}}{Q_{75}}$$

where Q_{25} is the grain size corresponding to the 25 percent cumulative weight (Box Figure 15.1b) 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 15.1c shows examples of sediments that have been poorly sorted and well sorted.



BOX FIG. 15.1 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 to be able 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) Examples of a poorly sorted and a well-sorted sediment.

peak (see Going Deeper Box Figure 15.1c). A well-sorted sediment will be deposited in an environment with constant current strength. Poorly sorted sediments usually reflect a heterogeneity of sedimentary processes or origins of the sedimentary grains.

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

In areas of considerable current strength, surface sediment is eroded and transported continually, and a number of sedimentary structures may be established in equilibrium with

this transport. On a large spatial scale of tens of meters and kilometers, emergent and submerged bars may develop off-shore. On a smaller scale of meters and centimeters, sedimentary ripple marks commonly develop where sediment is in motion (Figure 15.1). In areas where currents are unidirectional, ripple marks are asymmetrical in cross section, with the steep slope facing downcurrent. Reversing tidal motion can reverse the form of ripples. By contrast, waves may produce sufficient oscillatory motion to generate symmetrical ripples.

Sedimentary ripples create a local microenvironment of their own, which strongly affects sediment stability and

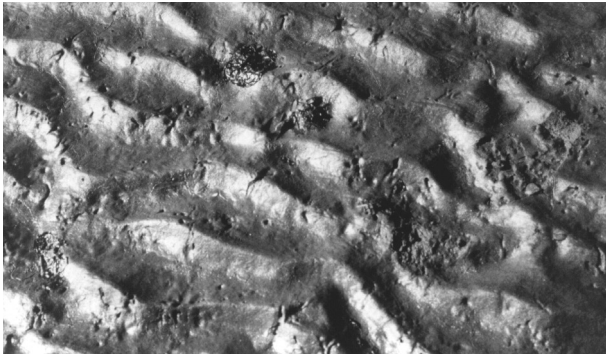


FIG. 15.1 Geometry of a sand ripple in a unidirectional current. Note direction of sand ripple movement from upper right to lower left and the possibility of burial faced by invertebrates in its path. (Photograph by Jeffrey Levinton)

movement for 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, therefore, are attracted to this microenvironment. By contrast, the crests of the ripples are relatively bare of this material and are also localized sites of erosion.

BURROWING

■ Burrowers live in sediment ranging from packed sand to elastic mud to watery mud.

Burrowers live in a wide range of sediments, whether they live in the intertidal or subtidal seabed. On one end of the spectrum, sediments are nearly pure sand particles in the range of 62.5–200 μm . Animals ranging from clams to larger polychaetes to crustaceans burrow into sand. The sand grains are piled onto each other and, because the sand grains are not compressible, the burrowers must exert forces to both compress water from the interstices of the grains and to displace sedimentary grains. Some clams can shoot a jet of water into the sediment just before burrowing, which liquefies the sand and makes it easier to displace.

Muds are a mixture of small mineral grains less than 62 μm , often of clays and organic particles and organic polymer coatings of the mineral grains. The organic polymers cause adhesion among the grains. This adhesion property makes the sediment behave like an elastic material, and a burrowing organ such as a bivalve foot or the proboscis of a worm can propagate cracks in the mud as the proboscis becomes engorged and thrusts into the sediment. As the cracks are generated, the sediment is locally weakened and the burrowing organ can continue to move through the sediment (Dorgan et al., 2005). As the water content of mud increases and the particle size becomes dominated by clay-sized particles, the sediment again changes in character. Sediment at this end of the spectrum is watery. Also, such sediments may consist of fecal pellets, which are aggregated groups of sedimentary grains, which increase the actual sedimentary grain size. As a burrowing

organ is pushed into the sediment, the sediment behaves like a viscous but watery material, simply pushing apart as the organism moves through the sediment. There is a reciprocal action since the burrowing act itself can increase the water content of muddy sediment by stirring in water from above the sediment surface as the animal burrows. As the burrowing organ pushes through, it may require less force to continue moving the burrowing organ. This property is known as **thixotropy**. In effect, the sediment becomes less resistant as you exert a concentrated shear force on it.

■ Soft-sediment burrowers use hydromechanical and simple digging mechanisms to move through soft sediment.

The initial displacement of sedimentary grains requires that a firm structure be pushed into the sediment with a sufficient force. To accomplish this, many burrowing 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 foot is filled with fluid and becomes a digging device. The internal fluid is not compressible, and a set of longitudinal muscles usually operates in opposition to a set of circular muscles. The longitudinal muscles act to shorten the fluid-filled structure (e.g., a worm segment), and the circular muscles act to compress the body and lengthen the structure.

After the fluid-filled and rigid structure (i.e., bivalve foot) has pushed into the sediment, its distal end is engorged with fluid, creating an anchor. In order to propagate cracks into plastic muds, the tips of fluid-filled burrowing structures of many invertebrates are wedge-shaped. After penetration and formation of the anchor by widening of the fluid-filled structure, contraction of longitudinal muscles then pulls the rest of the body along (Figure 15.2). 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 by contraction of circular muscles. 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 wormlike animals. There are some important detailed differences among these burrowing groups, however. Bivalves, for example, must rock the shell back and forth during burrowing, to allow the bivalve shell to work its way into the sediment.

The other major mode of burrowing involves the use of **mechanical displacement**, based on firm digging 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 spadelike posterior appendages. Inarticulate brachiopods 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 15.3).

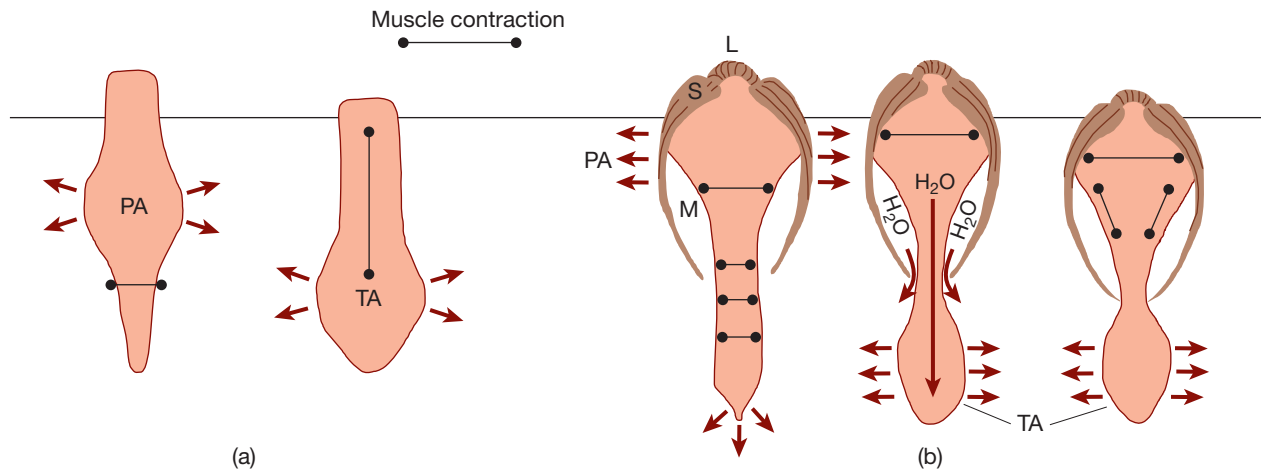


FIG. 15.2 (a) The burrowing of a soft-bodied animal, showing the formation of turgid fluid-filled mass into a penetration anchor (PA) and the dilation of a distal region, forming a terminal anchor (TA). Longitudinal muscles then drag the animal into the sediment. (b) How a clam uses its shell(s) and fluid-filled foot to burrow. 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. 15.3 Burrowing inarticulate brachiopods have two symmetrical shells that 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)

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

Interstitial animals are very small and move among sedimentary grains but do not displace them in bulk, as do

burrowing animals.¹ Because they move through tight spaces, interstitial animals from many different phyla have evolved a wormlike shape and a simplified external body plan (Figure 15.4). Relative to their epibenthic relatives, for example, interstitial hydroids have reduced numbers of tentacles, which are important for capture of suspended prey from the water column. 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.

Soft Sediments and the Role of Burrowers in Sedimentary Structure

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 grayish zone and then a black layer with a rotten-egg-like odor. The changes in color and smell reflect a change of chemistry and microbiological processes. The light brown zone contains pore water with dissolved oxygen, whereas the black smelly zone is devoid of oxygen, and the gray 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 (RPD)**.

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

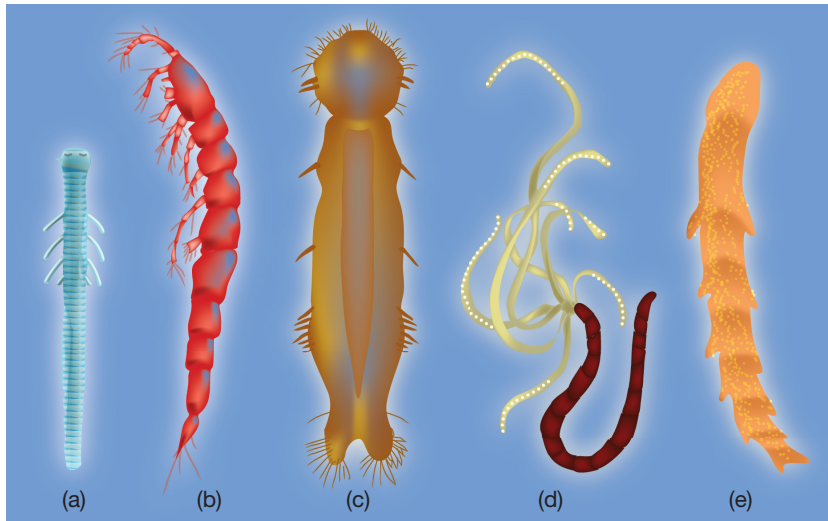


FIG. 15.4 The wormlike shape of interstitial meiobenthic animals of diverse phyla: (a) polychaete, (b) harpacticoid copepod, (c) gastrotrich, (d) hydroid, and (e) opisthobranch gastropod. (After Swedmark, 1964)

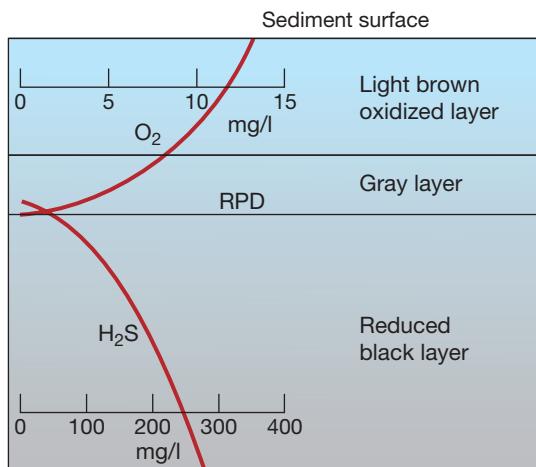


FIG. 15.5 Cross section of the sediment near the sediment–water interface, showing the redox potential discontinuity (RPD), which is a boundary between oxidative and reducing processes. The diagram shows the concentration of oxygen (above) and hydrogen sulfide (below).

It represents a sharp boundary between chemically oxidizing and reducing processes (Figure 15.5).

Near the sediment–water interface, oxygen diffuses or is stirred into the pore water from the overlying water column. In quiet areas, especially in organic-rich, fine-grained sediments, the transition to the anoxic zone can occur only a few millimeters below the sediment surface. Infaunal organisms may transport oxygen somewhat deeper by stirring the sediment or by irrigating their burrows. The combined actions of infaunal organisms may bring oxygen down to depths of several centimeters in muddy sediments that would otherwise have their oxygen content controlled by diffusion and never surpassing a few millimeters 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 (see later, Figure 15.10).

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

Microorganisms are a crucial factor in determining the chemical conditions of the sediment, especially the pore water. Microorganisms help decompose particulate organic matter. The vertical gradient in oxygen, strongly affected by microorganisms, also affects the composition of the sediment microorganism community (see Fenchel et al., 2012). Aerobic bacteria and protists live near the sediment–water interface, but only anaerobic microorganisms can survive below the RPD. In order to obtain oxygen, nearly all animals living below the RPD 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. T. Fenchel and R. Riedl (1970) first described the anoxic community, known as the thioobios. Some researchers, such as Riese and Ax (1979), 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, however, 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. Photoautotrophy employs light as an energy source, whereas chemoautotrophy employs one of several chemical substrates (e.g., sulfate, hydrogen) to derive energy.

Figure 15.6 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 live in pore waters having dissolved oxygen and break down organic matter, and oxygen is the

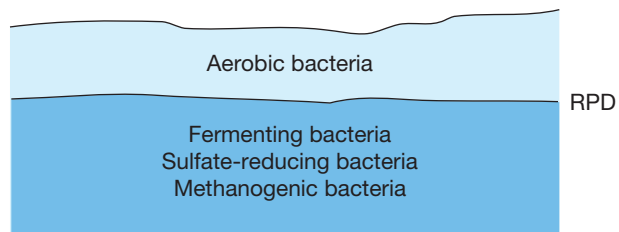


FIG. 15.6 Typical vertical zonation of bacterial components of quiet, muddy marine sediments.

terminal hydrogen acceptor in the decomposition process. In the deeper anoxic pore waters, however, heterotrophic microorganisms use a variety of other compounds as hydrogen acceptors. If the anoxic zone reaches the surface, then one often observes mats of photosynthetic bacteria such as purple sulfur bacteria, which use hydrogen sulfide as a reducing agent, producing elemental sulfur. But if the surface sediment is stirred by burrowers and pore waters contain oxygen, one then sees deeper into the sediment a series of anoxic bacteria beneath the surface aerobic sediment zone (Figure 15.6). Most notable of these 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 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 grow successfully when sulfate is in short supply and 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. Aerobic bacteria therefore are competitively superior in the microzone where pore waters have dissolved oxygen. Oxygen is lacking beneath this zone and different bacteria perform the energetically less efficient process of fermentation. 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 by microbes with increasing depth into the sediment.

Deposit Feeding in Soft Sediments

- **Deposit-feeding macrobenthic animals ingest sediment and derive their nutrition mainly from microalgae and particulate organic matter. Free-living sediment bacteria are digestible but not quantitatively important in the diet of larger macrobenthos.**

Deposit feeders are animals that ingest sedimentary material and derive their nutrition from some fraction of that material. Sediment is a complex mixture of inorganic

material, microorganisms, decomposing organic material, and pore water with dissolved constituents. Understanding the nutrition of these creatures, therefore, is a complex task, not at all like watching a caterpillar chew on a leaf! Deposit feeders tend to be more abundant in fine-grained sediments, because such sediments contain increased quantities of microorganisms, fine-grained particulate organic matter, and small ingestible inorganic particles. From the complex mixture of microorganisms, particulate organic matter, and dissolved organic matter, deposit feeders must obtain essential nutrients including amino acids, polyunsaturated long chain fatty acids, vitamins, and sterols.

Deposit feeders collect particles in a variety of ways that are associated with phylogenetic origins of the organisms and the environments within which they live (Figure 15.7). Representatives of many animal groups **swallow sediment** without particle selectivity, although there is an upper limit on the size of particle they can ingest. Many polychaetes have **tentacles**, which gather particles by means of a mucus-laden ciliated tract (Figure 15.7a). Sea cucumbers, such as the large northeast Pacific *Parastichopus californicus*, 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 15.7c). In some other groups, the sediment is processed quite noticeably before a fraction is ingested by the deposit feeders. Many amphipods tear particulate material apart and ingest considerably smaller particles (Figure 15.7e). Fiddler crabs handle sediment extensively and ingest only the fine particulate organic matter; they reject the inorganic sand grains and drop them on the sand.

Deposit feeders differ in the depth of feeding below the sediment-water interface. **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 benthic diatoms. At the other end of the spectrum, **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.

A series of experiments gave us some important insights on how continental shelf 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 freshwater amphipod and found that its ability to digest and assimilate the material was very low, in contrast to its high efficiency at digesting bacteria. Similar results were found for several marine invertebrate deposit feeders of widely varying origin, including marine amphipods, gastropods, and sea cucumbers. The **microbial stripping hypothesis** states that particulate organic matter is relatively indigestible and that microbial organisms are, therefore, the main source of nutrition for deposit feeders. 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 that derives from plants such as

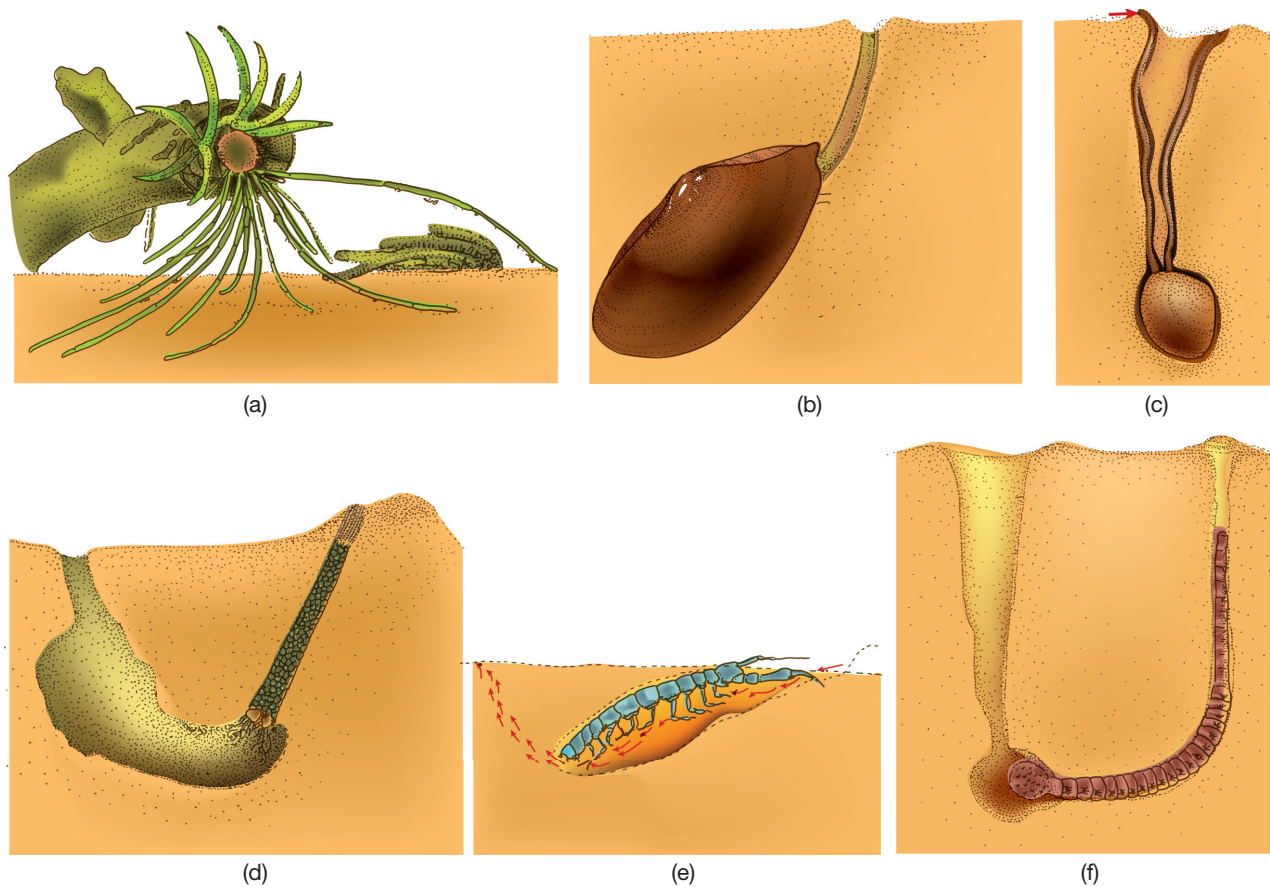


FIG. 15.7 Some deposit-feeding animals: (a) the surface tentacle feeder *Hobsonia*; (b) the within-sediment, tentacle-feeding bivalve *Yoldia limatula*; (c) the surface deposit-feeding siphonate bivalve *Macoma*; (d) the within-sediment-feeding Atlantic polychaete *Pectinaria gouldii*; (e) the surface-feeding *Corophium volutator*; and (f) the deep-feeding *Arenicola marina*. (Drawing of *Hobsonia* copied with permission from an original by P. A. Jumars)

sea grass is often rich in cellulose and indigestible, particularly because deposit feeders usually lack sufficient cellulase enzyme activity to digest the complex carbohydrates in the POM.

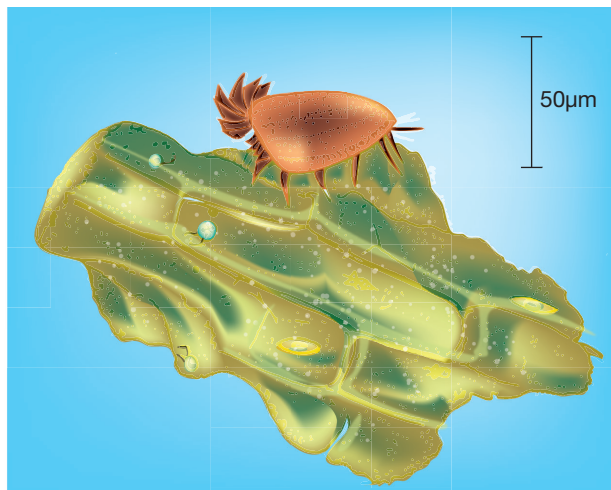
Particulate organic matter is decomposed by three processes, which often act simultaneously. **Fragmentation** involves the breakdown of large particles into smaller ones. This reduces the grain size and increases the surface area available for microbial attack. **Leaching**, the loss of dissolved materials from once-living organisms, is accelerated by mechanical fragmentation. Finally, **microbial decay** is the active use of POM nutrients by surface-bound microbes. As microbes—mainly bacteria—colonize, they enrich carbon-rich particulate organic matter with nitrogen (Figure 15.8). In intertidal environments, much decay can be attributed to marine fungi, especially in marsh grasses.

Grazing by deposit feeders on the benthic microbial community stimulates microbial productivity and, by extension, detrital decomposition (Figure 15.9). Oxygen consumption by microbes increases while consumers are grazing the organisms. The mechanism behind this stimulation is not well understood. Grazing may reduce the standing crop of bacteria and select for metabolically active cells with higher cell division rates. Grazing by some

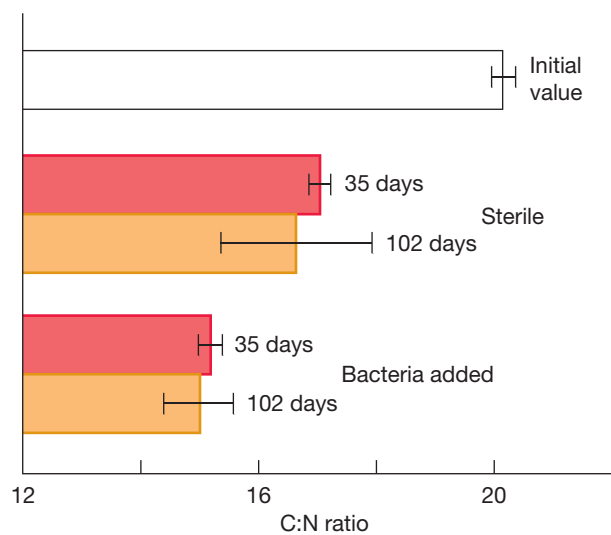
deposit feeders may break up particulate organic matter and make it more accessible to bacteria.

■ **Particulate dead organic matter is also important in the nutrition of many deposit feeders.**

Although microbes may be efficiently digested by deposit feeders, some low-level digestion and assimilation derives from the more refractory POM. Although the digestion and assimilation of particulate organic matter may be inefficient, POM is usually 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 recently dead phytoplankton, known as **phytodetritus**, in shallow embayments and on the continental shelf. Deposition of phytoplankton cells in the spring is a major source of sediment protein and probably sterols and vitamins, because the material is fresh and easy to digest. But as time goes by, the phytodetritus is degraded and becomes more refractory and probably is more difficult for deposit feeders to digest and assimilate (Mayer and Rice, 1992). Near shore, seaweeds may provide



(a)



(b)

FIG. 15.8 (a) A piece of turtle grass (*Thalassia testudinum*) detritus and its microbiota. (Redrawn from Fenchel, 1972) (b) 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.)

a significant input of POM. As it turns out, seaweed detritus is far more digestible to deposit feeders than is sea 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. Sea grass detritus may be rich in carbon, but other nutrients—including essential amino acids, vitamins, sterols, nitrogen, and phosphorus—may be in short supply.

Some quantitative estimates set some limits on the value of certain food sources. A number of studies suggest that the *typical abundance of bacteria in sediment 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 because specific fatty acids, amino acids, and vitamins may be necessary for specialized nutritional needs. Rich diatom mats

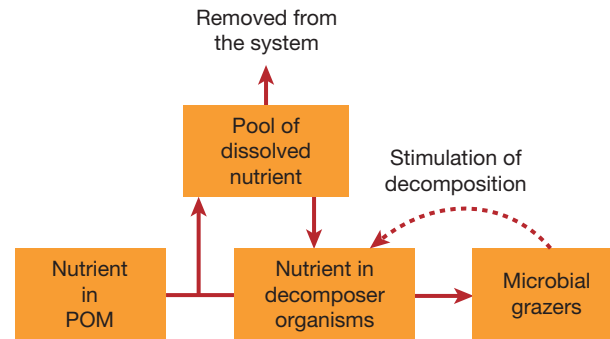


FIG. 15.9 The relationship between deposit-feeding microbial grazers and microbial decomposers, particulate organic matter, and the dissolved nutrients in the pore waters of sediments. Microbial grazers remove microbes, but they also stimulate decomposition by increasing microbial activity and by tearing apart particulate organic particles, which exposes more surface area to mechanical attack. (Modified after Barsdate et al., 1974)

may be a more adequate food source, but only in intertidal and very shallow subtidal sediments, and 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 phytodetritus, and this POM may be crucial in fueling the productivity of the deposit-feeding benthos. Microbial groups that are poorly known in sediments may produce essential fatty acids for deposit feeders. We are very ignorant of important microbial groups that may produce such substances.

In contrast to macrofauna, meiofauna probably depend mainly on 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 but can gain nutrition successfully from the bacterial fraction of the sediment.

■ **Deposit feeders use a cocktail of enzymes and compounds with surfactant properties to digest organic matter from ingested particulate material.**

A simple measure of carbon or nitrogen of sediments does not necessarily tell us how much food is available for deposit feeders. Much of the carbon may be bound up as indigestible complex carbohydrates such as cellulose, and nitrogen may also be bound up as indigestible nitrogenous compounds. Exposure of low-density organic particles from sediments to digestive enzymes shows that the particles are strongly enriched in protein and peptides, which confirms the idea that fine low-density particles are a possible food source for deposit feeders (Mayer et al., 1993).

Many larger deposit feeders employ **surfactants** (compounds with detergent properties that reduce the surface tension between water and hydrophobic organic compounds) in high concentration, which probably enables the stripping of organic material from particle surfaces (Mayer et al., 1997). This activity may allow some deposit feeders to digestively attack relatively refractory organic material in sediments. The surfactants include branched saturated or

unsaturated fatty acids that are linked to amino acid residues (Smoot et al. 2003).

■ **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 surface feeders. In these cases, microbes may be (1) free-living among the sedimentary grains, (2) attached to sedimentary grains, or (3) 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.

Some deposit-feeding invertebrates, such as polychaetes and gastropods, consume fine particles and bundle them into fecal pellets that are often not reingested. Deposit feeders may live in a mixture of fecal pellets and fine particles, ingesting 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 the animal's 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 will 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 as fecal pellets 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 simultaneously break down and be recolonized 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. Mud snails of the genus *Hydrobia* slow down feeding and may emigrate from microsites with fully pelletized sediments.

In some cases, feces may be enriched in organic matter, relative to the surrounding sediment. This occurs when the feeder is very selective and may even involve enrichment by microbial action in the hindgut of the deposit feeder. In such cases some deposit feeders ingest their own feces or the feces of other species and are coprophagous.

■ **Many benthic animals do not feed directly on microorganisms but have symbiotic chemoautotrophic bacteria, which derive energy from dissolved ions in seawater.**

Although many benthic animals feed actively on sediment, or on suspended organic matter (see section on suspension feeding), a large number of species depend on symbiotic bacteria, which may live intracellularly or in chambers in various organs, depending upon 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 18).

Burrowers and Sediment Structure

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

Sediments are strongly altered by burrowing animals. Donald C. Rhoads (1967) 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. A sediment with abundant deposit feeders that is wet-sieved tends to be dominated by fecal pellets, which are often about 50–150 μm in size. If the same sediment is placed in a blender and sieved, one finds that its constituent particles are closer to 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 percent water. Recently, elegant sensors have been developed to measure changes in pressure within sediments. Using pressure sensors, the effect of daily and tide-related changes in burrowing intensity can be related to changes in pore water properties of sediments (Woodin et al. 2016).

■ **Head-down deposit feeders create biogenically graded beds.**

Many deposit feeders feed in a head-down position and defecate sediment at the surface (Figure 15.10). Head-down deposit feeders tend to ingest particles that are smaller than the average size for the sediment. Such animals may select fine particles and transport them 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 small particles concentrated at the surface (Figure 15.11) (Rhoads, 1967). Such biogenically graded beds can be easily detected by walkers who suddenly encounter squishy sediment.

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

Sediment-dwelling invertebrates often live on tidal flats where current energy causes extensive lateral particle transport with each tide and storm. If water turbulence

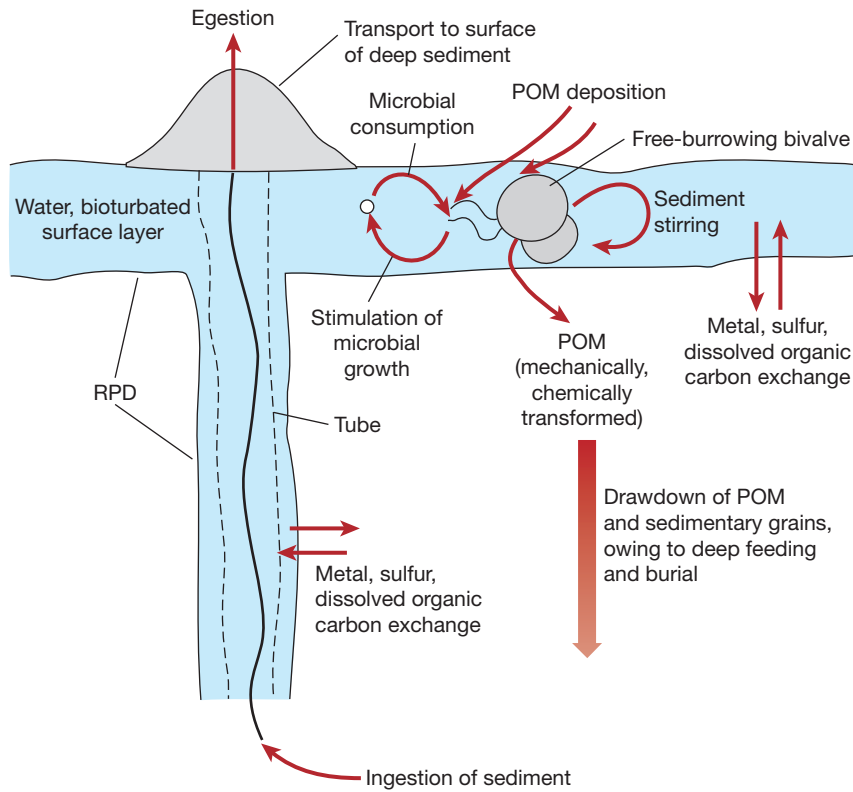


FIG. 15.10 General processes occurring within a sediment dominated by deposit feeders, including various transport processes. In deposit feeding, particles are taken up by a feeding organ, and some of them may be rejected before entering the gut. Particles may be packaged in fecal pellets, which are 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.

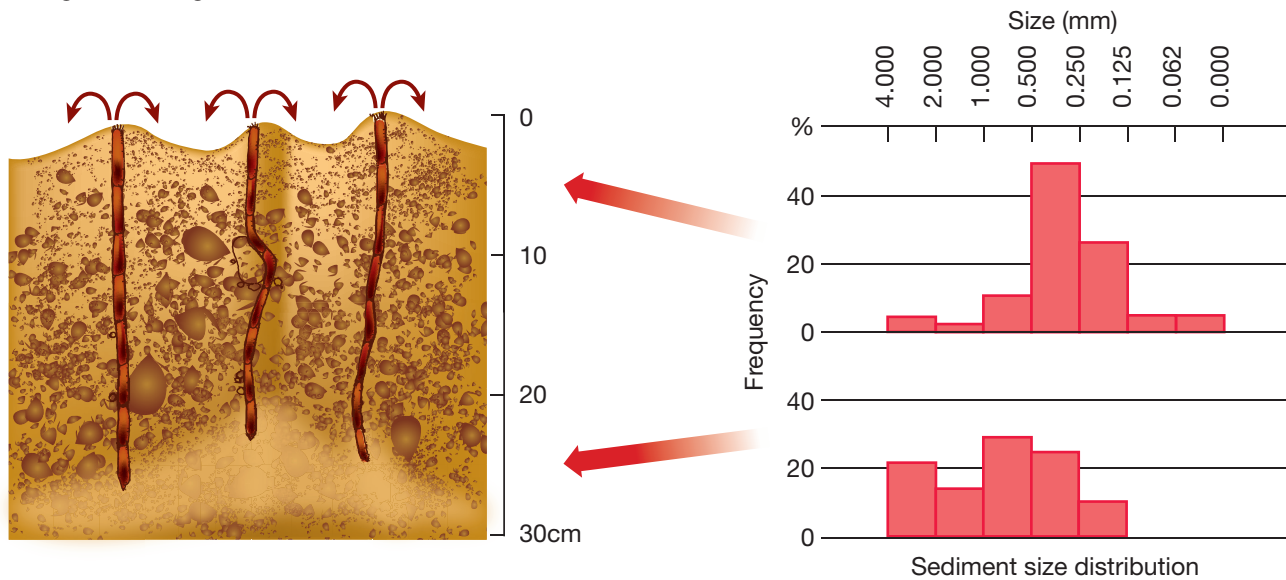


FIG. 15.11 Biogenically graded bed. Left: vertical reworking of intertidal sediments by the tube worm *Clymenella torquata*. Right: change in the vertical distribution of particle size as a result of vertical reworking of the sediment. (After Rhoads, 1967)

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 by keeping the siphon within the burrow. This may be a reaction to particle saltation, which would bring the particles to the feeding organ passively.

Spionid polychaetes have cilia-covered 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.

■ **Deposit feeders can optimize their intake by adjusting food particle size and gut passage time.**

Natural selection can be expected to optimize food choice and feeding rate to maximize fitness. Sediments with fine particles tend to be richer in microbial organisms, owing to the greater surface area per unit volume of the fine particles relative to coarse particles. If the expected surface-area relationship holds, then deposit feeders should select for fine particles.

Feeding rate and gut passage time may also be regulated 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, 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 is steady.

Suspension Feeding

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

Passive suspension feeders such as gorgonian corals and sponges commonly protrude a feeding organ into a mainstream current and collect particles as they encounter the feeding collection device. In a moderate unidirectional current, the best strategy for a colonial suspension feeder would be to deploy a network whose plane is perpendicular to the flow. But 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 bushlike (e.g., the hydroid coelenterates) or simply form a thin layer over the substratum (e.g., many sponges and corals). Although this may seem to be an inefficient way of 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 complex 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.

■ **Active suspension feeders are under some constraints similar to passive suspension feeders, but they also generate their own water currents to channel and ingest particles.**

Active suspension feeders create a feeding current to take in planktonic food. In many polychaete annelids and bivalve mollusks, ciliary currents draw particles toward the cilia, which capture particles and transport them down ciliated tracts (Figure 15.12b, c).

Processes near cilia are at low Reynolds number, and the cilia must directly reach out and capture particles. (See the

discussion in Chapter 7 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 to 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 velocities. 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, to minimize drag and to capture particles passively. Barnacles living in wave-swept environments tend to have shorter and stouter cirri, which strengthen the feeding organs and reduce drag.

Many suspension feeders live infaunally and semi-infaunally in soft sediments. For example, the polychaete *Chaetopterus* lives in a U-shaped burrow (Figure 15.12a), 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 to the mouth. 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 transport particles to a ciliated palp, which can reject poor food particles. Acceptable particles are then ingested and enter the gut (Figure 15.12c). 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.

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

When water moves above the surface of 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 troughs 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 filters out sand grains. The inhalant siphon of some tellinacean bivalves is lined with papillae, which can help in rejecting unwanted sand. Most marine bivalves can “sneeze,” or suddenly expel water and an overload of sand through the inhalant siphon. Even suspension feeders on hard surfaces may suffer clogging when sedimentary loads become high. When sediment is deposited on their colonies, some corals can produce mucus, which transports the clogging material off of the colony.

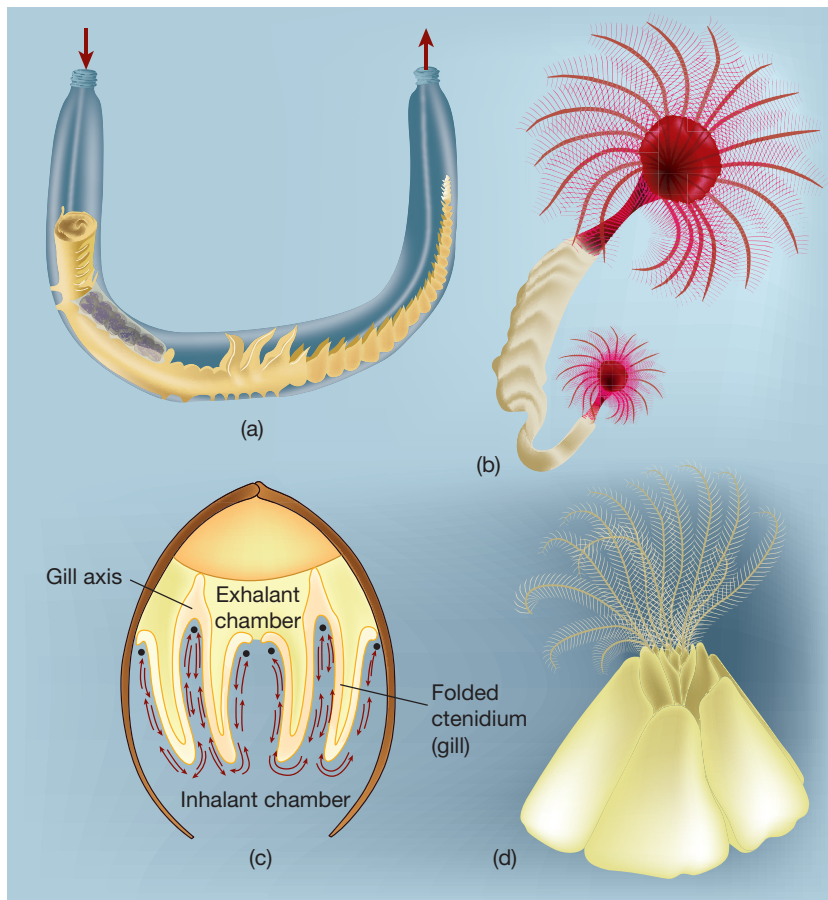


FIG. 15.12 Some suspension-feeding invertebrates. (a) The active suspension-feeding parchment worm *Chaetopterus*. (b) The suspension-feeding polychaete *Serpula*, which uses ciliary currents to draw particles to tentacles. (c) Cross section of a bivalve mollusk, an active suspension feeder (arrows denote 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.

PARTICLE SELECTIVITY BY SUSPENSION FEEDERS

- Many suspension feeders can select for nutritionally valuable particles and reject poor particles before they enter the gut.

Particle selectivity would be strongly adaptive to allow suspension feeders to reject nonnutritive particles such as re-suspended sand grains, even before they enter the gut. Otherwise, the bulk of the gut's volume will be filled with nonfood material.

Ciliary suspension feeders, such as polychaetes with tentacle crowns and bivalves with large gills, collect particles on the ciliated tracts. Can such organs reject particles of low nutritive quality? We know most about suspension-feeding bivalves such as mussels and oysters. These bivalves bring material into the mantle cavity and capture particles, probably mostly by direct interception on cilia in the gills. Then these particles are transferred, via a ciliated groove, to another highly ciliated organ, known as the palp. The palps are very strongly folded and ciliated

and often can reject particles that are poor in nutritive quality or even toxic.

- Selectivity after particle collection can be studied with a surgical endoscope.

Where are the sites of selectivity? Bivalves have long been known to select for nutritionally valuable particles, by simply comparing the organic content of particles that are rejected and released back on the sea bed with the usually higher organic particles that are passed to the mouth and ingested. But the mechanisms of particle selection are particularly difficult to study because it is hard to observe within the mantle cavity of a bivalve. The use of a surgical endoscope (Figure 15.13) helped solve this problem. This instrument is a glass lens, no more than 2 mm wide, that can be inserted within the bivalve's mantle cavity to observe movement of particles with video and even to direct collection of particles using a micropipettor. In the mussel *Mytilus edulus*, particles were captured on the gills and transported

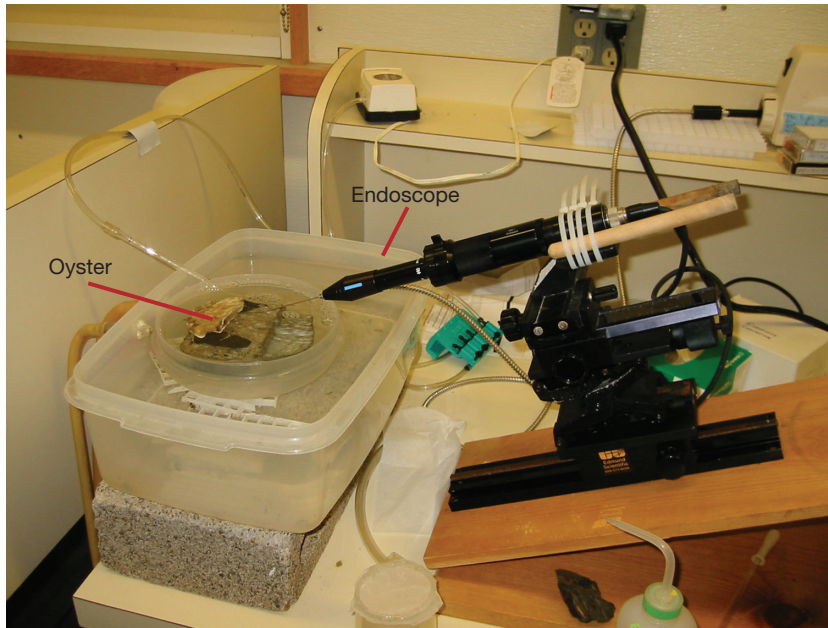


FIG. 15.13 An endoscope inserted into a bivalve. This surgical telescope allows us to observe how internal mantle cavity organs of a bivalve function in processing particles without surgically altering the mantle organs, such as gills and palps. (Photograph by Jeffrey Levinton)

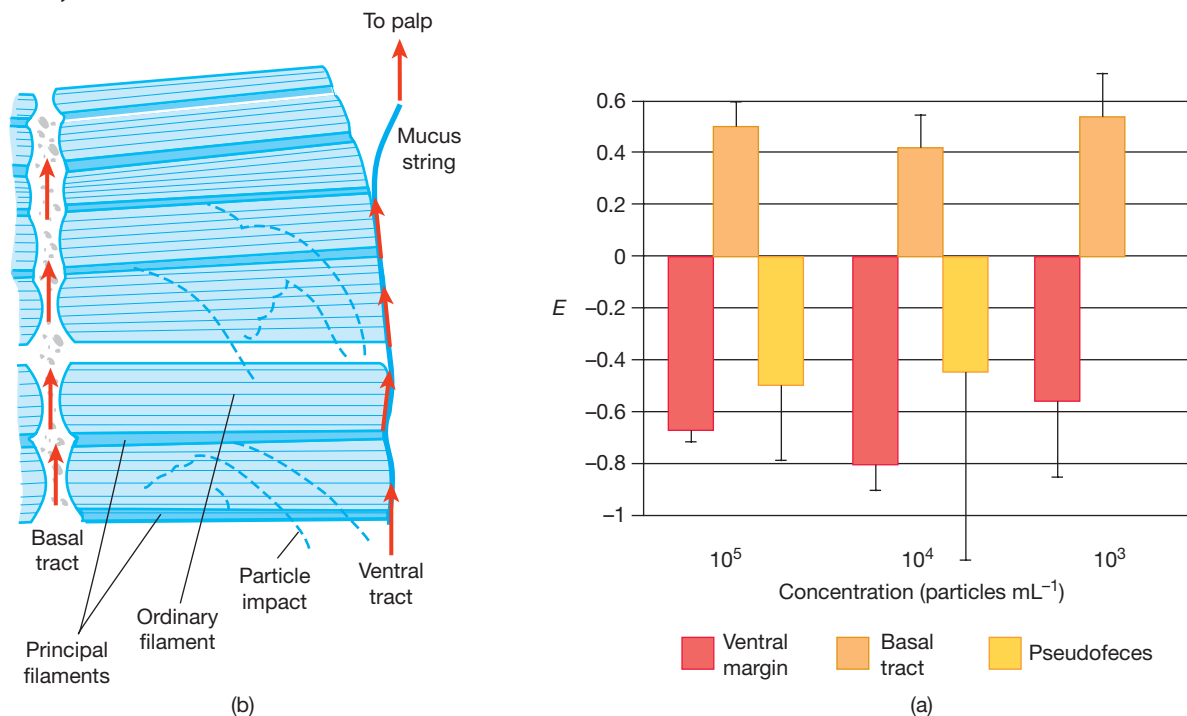


FIG. 15.14 (a) The gill surface of an oyster. Note the different directions in which particles are transported by ciliary tracts. Particles transported to the basal tract are transported to the palp and then to the mouth, where they are ingested. Particles transferred to the ventral tract are eventually rejected by the palps as pseudofeces. (b) Selectivity for algae relative to non-nutritive particles at total particle concentrations of 10^3 – 10^5 particles per milliliter. Positive values indicate selectivity for algae. Note positive values for basal tract, which delivers particles to the mouth. Algal particles are depleted in ventral margin, where particles are rejected as pseudofeces, which also have less algae than was proportionally fed to the bivalve.

to a ciliated tract on the ventral part of the gill. There the particles were enmeshed in mucus and transported to the palps, which were capable of sorting and rejecting poor particles and transporting more nutritive particles to the mouth (Ward et al., 1998a, 1998b).

The structure of oyster gills (Figure 15.14a) is rather different from that of many other bivalves. The gill is folded, and the “valleys” of the folds are lined with cilia that beat dorsally (toward the bivalve hinge). The “hills” also are covered with cilia and can either transfer particles dorsally (refer to

the figure or you will become confused!) or ventrally. Some particles were captured by cilia on the hills and were transported to a ventral tract, enmeshed in mucus, and rejected. But others were trapped by other cilia in the lower folds, transported to a dorsal tract, and eventually transported to the mouth (Figure 15.14a). Thus oyster gills could sort particles on the gill itself, which was not true of mussels.

A creative experiment demonstrated the amazing extent to which selectivity could occur. Sandra Shumway and colleagues (1985) pioneered the use of the **flow cytometer**—a laser-based device that analyzes fluorescence and other characteristics to differentiate particle types. They fed mixtures of algal cultures to see whether species of algae were preferentially ingested, which could be told by comparing available food particles in the water with the material rejected in the pseudofeces. On comparing samples of algal mixtures, it was clear that a variety of bivalves were selectively rejecting certain phytoplankton species and preferentially retaining others for ingestion.

This result was applied to the oysters. Ward et al. (1998a) sampled the particles that had been sorted to the dorsal and ventral tracts. One could sample these two tracts and compare them with the particles in the water, representing the available food. Ward and colleagues fed the oysters *Crassostrea virginica* and *C. gigas* with aged cordgrass (*Spartina alterniflora*) detritus, which they had ground to match an alga (*Rhodomonas*) in particle size. The detritus was very poor in nutrients and essentially indigestible. The results were immediately apparent, especially because *Rhodomonas* is vivid red. The particles in the dorsal tract were clearly red and the ventral tract was tan, the color of the cordgrass detritus. This demonstrated that it was the gill doing the sorting, not the palp, as in most bivalve species. The flow cytometer was able to count particles (Figure 15.15) that were selected for comparison with those that were rejected. In other bivalve species, the gill just captures particles, which are transported in ciliary tracts to the palp, where selection occurs. In all cases, bivalves can distinguish

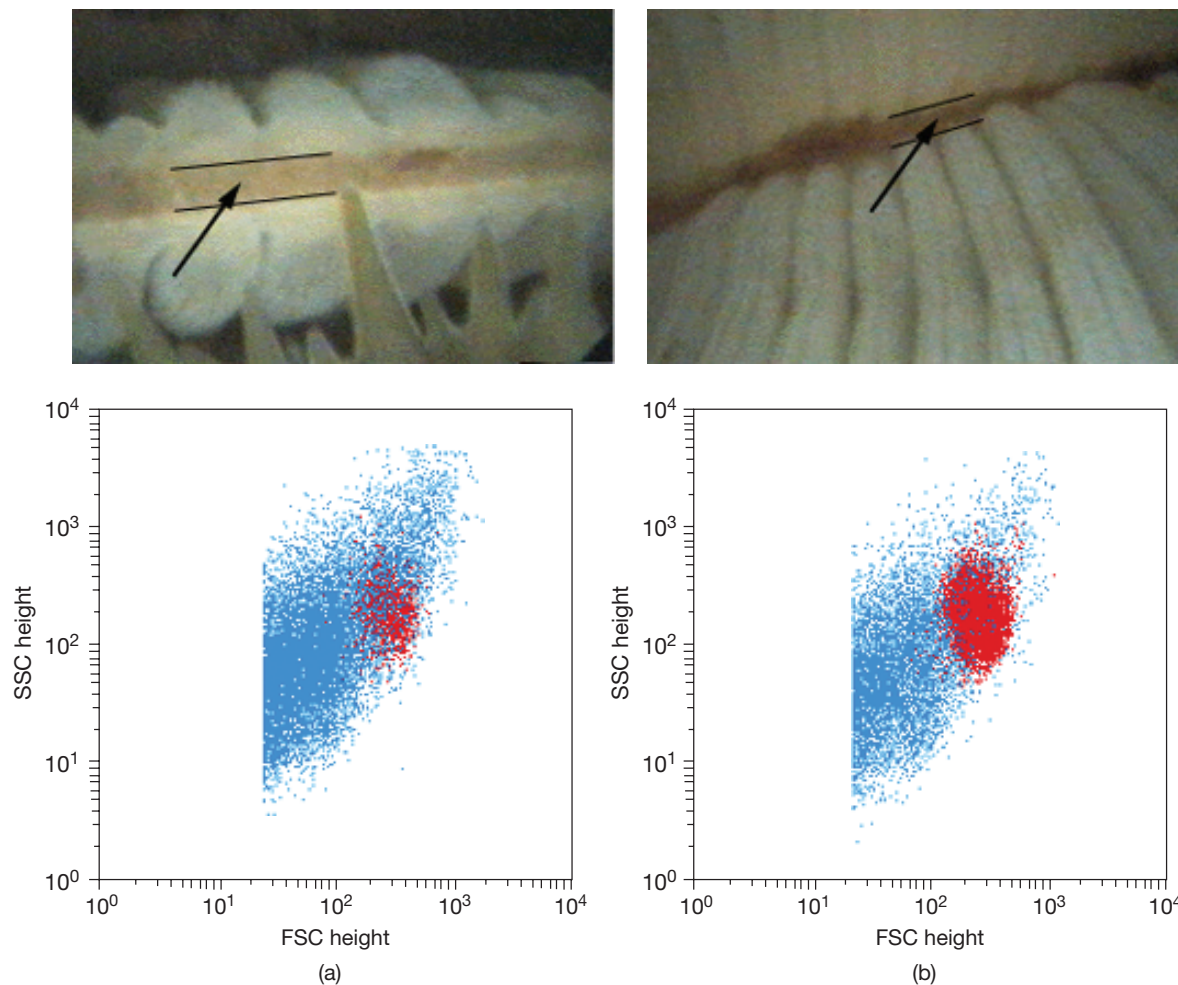


FIG. 15.15 Plot showing distinction between two particle types, the red alga *Rhodomonas lens* (red areas of graphs) and cellulose-rich particles derived from the decomposition of the cordgrass *Spartina alterniflora* (blue areas of graphs): FSC, forward light scatter (estimate of particle size); SSC, side scatter (estimate of index of refraction). (a) Particles sampled from a ciliated tract (arrow in photo) that collects rejected particles; note the enrichment of cordgrass detritus. (b) Particles sampled from another ciliated tract (arrow in photo) that collects particles that will be passed to the palp and then ingested. Note the increased abundance (big red dot) of *Rhodomonas lens* and relatively smaller amount of cordgrass detritus.

nutritive particles and eventually reject poor particles *before* they enter the mouth. This is a tremendous advantage to the bivalve, since the gut does not have to waste time and energy on poor food particles, which are abundant in the environment.

- **Suspension feeders may live in current regimes that deliver particles in uniform currents, but sometimes flow and particle supply direction may be very complex.**

Suspension feeders such as barnacles and sea squirts may live in widely different current regimes depending on their living position relative to the sediment–water or rock–water interface. A directional current may become far more irregular near the seabed. This has effects on species of different sizes and especially on species that may experience complex flow as small juveniles but strong directional flow after the juveniles grow to be larger adults. Small colonies of the tropical sea fan *Gorgonia* have an irregular shape and no preferred orientation, in contrast to larger colonies, whose fan shape is oriented approximately perpendicular to unidirectional currents. Near-bottom currents are erratic in direction, owing to irregularities of bottom topography and surrounding erect organisms. As the colony grows, it changes its orientation and grows into a fan shape that faces perpendicular to the mainstream current. This will maximize food particle interception.

This difference of adaptation to unidirectional and variable 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 plane (Figure 15.16). Food particles are captured by the tube feet and are compacted into a mucus-clad bolus that is passed down the arm.

Benthic Carnivores

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

Carnivorous animals hunt and eat other animals (Figure 15.17). Defining benthic carnivores is not entirely straightforward because those that eat zooplankton are as much suspension feeders as they are carnivores. 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 upstream prey. 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 15.17b).

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 oystercatcher *Haematopus ostralegus* can dash onto an open mussel as a wave recedes and plunge its beak into the mussel, severing the prey’s adductor muscles, thus making it helpless. More rarely, the oystercatcher hammers with its bill and crushes the shell. In either case, the bird assesses the size of the mussel and tends to take prey that are larger than average. Lobsters and crabs use both chemical detection and vision in predation, and can rapidly attack and immobilize prey.

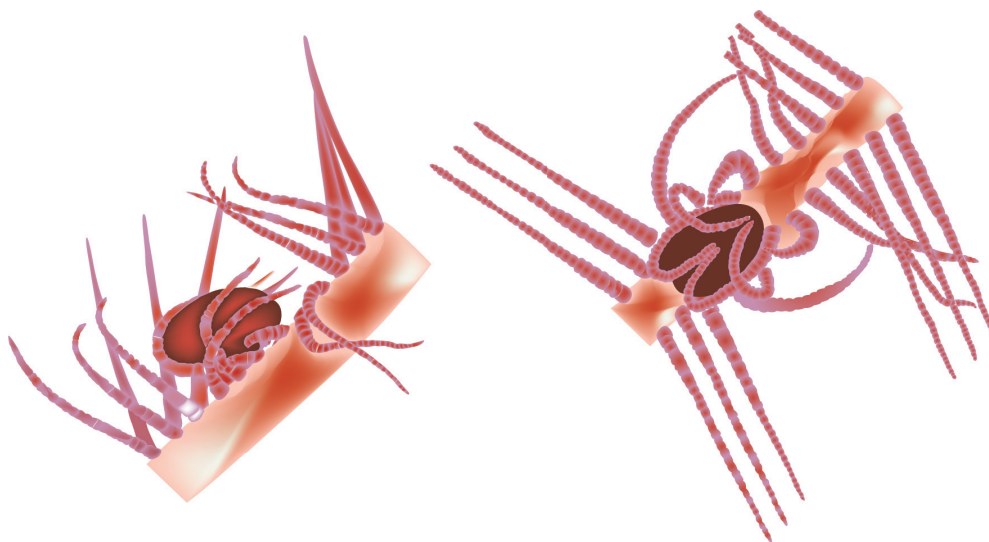


FIG. 15.16 The food-collecting wave of a suspension-feeding brittle star, showing the planar arrangement of the pinnules. (From Warner and Woodley, 1975)



FIG. 15.17 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) Crab *Callinectes sapidus*, whose strong claw can crush mollusks. (d) Polychaete *Glycera*, which has a proboscis armed with hooks, used in seizing and tearing prey. (e) The oystercatcher *Haematopus ostralegus*, a predator on intertidal bivalve mollusks.

Odor detection is crucial in the behavior of many predators. Many prey organisms release signals such as excretory products into the water column, and predators use stereotyped movements to seek increased concentrations of the prey odors. In Chapter 6, we discussed the odor-seeking behavior of the blue crab *Callinectes sapidus*, which allows it to locate odors emanating from the exhalant siphon of buried clams. A **threshold concentration** of a signal molecule is required for detection. The relationship of this threshold to actual behavior is poorly understood in marine systems (Weissburg et al., 2004). On the other side of the relationship, prey also use odor signals to detect the presence of predators. Crabs are major predators of sessile benthos, and many are capable of cracking shells of mollusks. In the intertidal zone, snails and mussels can detect the odor of conspecifics being dismembered by crabs or even the odor of predatory crabs. As a quick response, they may move away. The mud snail *Tritia obsoleta* rapidly burrows into the sediment when it detects the odor of conspecifics that have been crushed by crabs. If predation persists in the area, some snails may devote resources to thickening their

shells. This can be demonstrated by placing crabs in cages near to molluscan prey (Trussell and Smith, 2000).

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.

The handling of prey varies with phylogenetic background because morphologies and neurodetection mechanisms are so disparate. Seizing prey involves some sort of appendage, such as a crab claw or a starfish arm. Many crab species 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 to expose the soft parts. Many crabs and lobsters have a crushing claw, but the other claw is specialized for cutting tissue. Crushing claws have a high mechanical advantage and greater muscle mass (Figure 15.18). Spider crabs use pincers to rip apart seaweeds, sea stars, and other macroinvertebrate prey. Polychaetes, such as some species of *Glycera* (Figure 15.17d), have a protrusible proboscis with hook-shaped teeth; other polychaetes have large chitinous jaws that can tear prey apart.

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 Thaiidae (*Nucella*) and involves alternations of mechanical rasping and chemical secretions from an accessory boring organ. Some octopods drill holes in their molluscan prey and may inject a paralyzing venom through the hole.

Cone snails of the genus *Conus* consist of several hundred species living mostly in the tropics and subtropics. Venom, consisting of a cocktail of toxins, is produced by epithelial cells in a venom duct and injected into the proboscis by a squeeze of a specialized bulb. A highly modified radular tooth punctures the prey and delivers the venom (Figure 15.19). The shape of the proboscis varies with the method of capture and the type of prey. In some fish-hunting species, the snail has a part of the proboscis modified into a

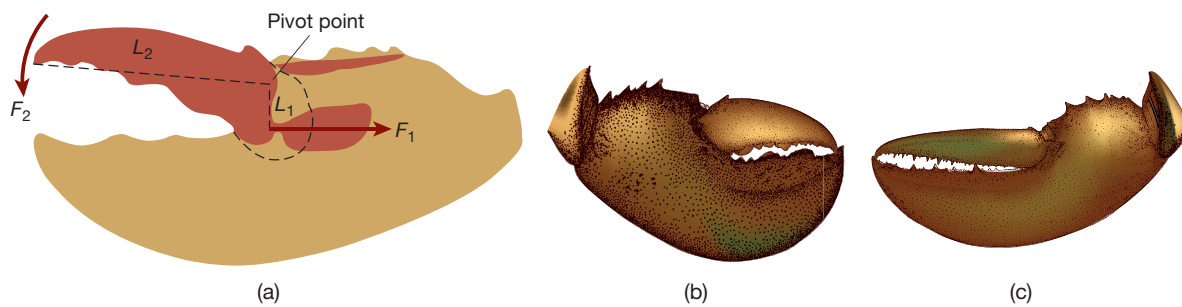


FIG. 15.18 Claws of the lobster *Homarus americanus*. (a) Features of the claw: forces and pivot of the claw apparatus. (b) The crusher claw. (c) The cutter claw. (After Elner and Campbell, 1981)

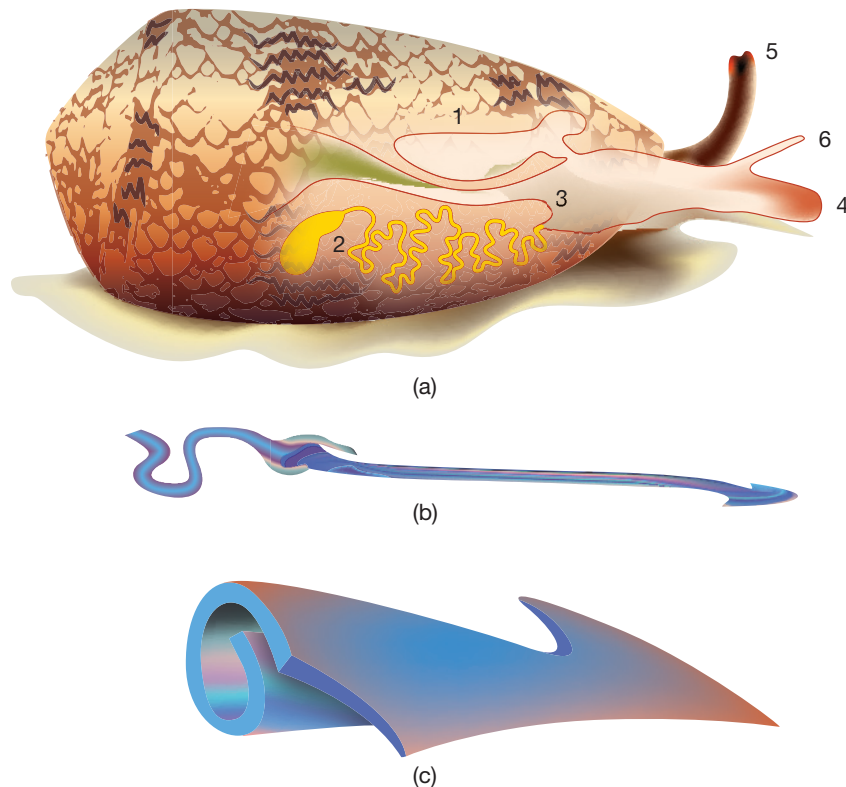


FIG. 15.19 (a) The stinging apparatus of a cone snail: (1) harpoon sac; (2) venom gland; (3) pharynx; (4) proboscis; (5) siphon; (6) eyestalk. (b) Harpoon-shaped specialized radular tooth. (c) Close-up of tip. (Courtesy of Dietrich Mebs)

lure, which attracts fish. The attraction is fatal because the disposable tooth harpoons the fish, paralyzes it, and reels in the prey, which is swallowed whole.

The toxin is usually a mixture of as many as 50 highly specific peptides, which are short chains of amino acids that usually attack a group of cellular ion channels, such as sodium channels. The peptides appear in the venom duct as precursors that are cleaved by enzymes in order to obtain final toxicity as they are injected into the prey. The combination of different venoms overwhelms the prey and immobilizes it almost immediately after the harpoon-like tooth is injected.

Benthic Herbivores

■ Benthic herbivores are divided between microphages and macrophages.

The food of benthic herbivores (Figure 15.20) 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. **Microphages** 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. 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 **macrophages** can tear apart and consume macroalgae and marine higher plants. Periwinkles, for example, use the radula to rasp and tear apart delicate seaweeds such as species of the sea lettuce *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*. Sea grasses are usually thought to be relatively indigestible, but a number of urchins and fishes regularly consume them.

Many crustaceans are also herbivorous. Many smaller amphipods and isopods feed on relatively soft seaweeds or on the microalgae growing on seaweed surfaces. A variety of fishes are also efficient herbivores. The jaw teeth of parrot fishes (Scaridae), which are fused into plates, are capable of cutting material from the surface of coral skeletons. Surgeon fishes (Acanthuridae) also can scrape

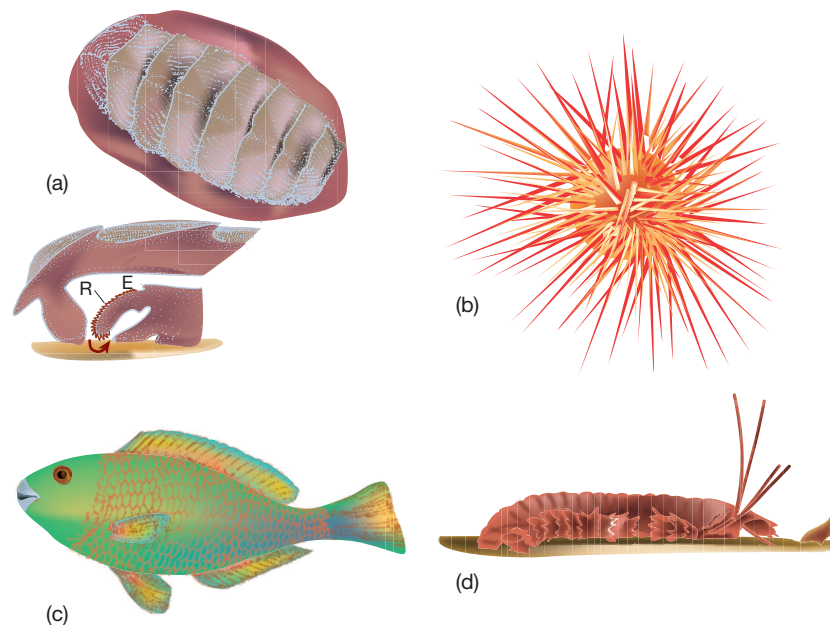


FIG. 15.20 Some benthic herbivores. (a) The chiton *Tonicella*, a scraper of microalgae; inset shows anterior sagittal cross section, indicating the action of the radular tooth belt in scraping algae from the substratum (R, radula; E, esophagus). (b) The sea urchin *Arbacia*, which uses a toothed Aristotle's lantern to scrape microalgae or to tear apart seaweeds. (c) A parrot fish, which uses specialized fused teeth to scrape algae from coral surfaces. (d) The nereid polychaete *Nereis vexillosa*, which tears apart sea lettuce with buccal hooks. (Copied from an original by K. Fauchald)

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 sandworm *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 a home spot, which often appears as a scar on the rock.

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 *Lumbrineris* can drag seaweed fragments down into their burrows. In some cases, the downward dragging is incomplete, and 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 on the marine microbiota living in the wood. The wood-boring bivalves *Teredo* (shipworm) and *Bankia* scrape the wood particles, and symbiotic bacteria synthesize the digestive enzyme cellulase to attack the cellulose (Figure 15.21). 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, since nitrogen is not present in sufficient quantities in the wood.

Sea grasses, such as eelgrass (*Zostera*), salt marsh cordgrass (*Spartina*), and Caribbean turtle grass (*Thalassia testudinum*), are relatively indigestible to most marine consumers because of the abundance of cellulose the grasses contain. Some small grazers consume the microalgal surface layer, but relatively few species can consume, digest, and assimilate material from the grass itself. As mentioned earlier, a few species of urchins can deal with turtle grass. Eelgrass and cordgrass are remarkable for the minuscule 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 (Fenchel et al., 1979). 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 digestion-aiding symbiotic bacteria and protozoa. In the Caribbean, green turtles often feed within a restricted area, and cropping of leaves encourages new growth with lower concentrations of complex structural carbohydrates and higher nutritional content (Moran and Bjorndal, 2007). In effect, the turtles are prudently altering the sea grasses. Green turtles have also been found to be feeding either on sea grasses or seaweeds, and this may relate to the difficulty of switching microfloras in the hindgut to specialize on efficiently digesting both food types in rapid succession. It may be that the low grazing pressure on eelgrass and cordgrass is misleading. Valentine and Heck (1999) have argued that many tropical sea grasses are consumed by urchins and fishes to a far greater degree than has been appreciated.

■ **Benthic plants have evolved both mechanical and chemical defenses to deter herbivory.**

The sessile habit of benthic plants makes them very susceptible to herbivores, but many groups have evolved mechanical and chemical defenses to deter feeding. Many marsh grasses are difficult to tear apart when alive. The common cordgrass *Spartina* secretes silica particles, which can exceed 1 percent by mass and make grass blades difficult to chew. Many seaweeds, such as red calcareous algae, are calcified. It is common for these seaweeds to survive in areas of intense herbivory and to dominate hard substrata in both the tropics and high latitudes. In addition, many marine plants have evolved chemical defenses. The cordgrass *Spartina alterniflora* synthesizes cinammic acid esters of glucose, which are stored in vacuoles and deter herbivores. Lignins also deter predation by inhibiting digestion of herbivores. In the tropics, many seaweed species on coral reefs combine calcification and toxic compounds to deter herbivory. Calcified seaweeds always have such chemical defenses, suggesting that calcification is also an adaptation to deter herbivores, such as fishes and urchins (Paul and Hay, 1986).

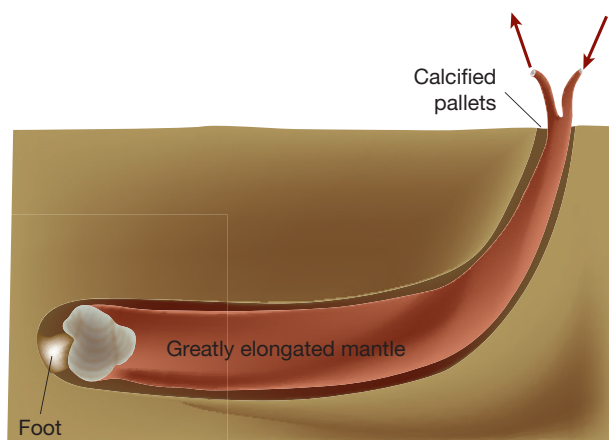


FIG. 15.21 Cross section showing the living position of the wood-boring bivalve mollusk *Teredo*. (After Trueman, 1975, *The Locomotion of Soft-Bodied Animals*, with permission of Edward Arnold [Publisher] Ltd.)

■ CHAPTER SUMMARY

- Epibenthic organisms live attached to the surface and usually protrude into the flow. Infaunal benthos live below the sediment–water interface. Demersal animals are mobile but associated with the seabed. Interstitial animals are elongate and live among sedimentary grains.
- Benthic feeders include deposit feeders, suspension feeders, herbivores, carnivores, and scavengers.
- Soft sediments are a mixture of inorganic particles, organic particles, and pore water. Grain size determines the distribution of benthos and increases with increasing current strength. In very shallow, sandy, wave-swept bottoms, currents generate ripples, bars, and other sedimentary structures.
- Sediments range from packed sand to elastic mud to more watery mud. Organic molecules may make sediment sticky and prone to cracking as burrowers move through. Because they move through tight spaces, interstitial animals from many different phyla have evolved a wormlike shape and a simplified external body plan.
- Sediments consist of an oxygenated layer overlying an anoxic zone. In quiet water there is usually a vertical zonation of microorganisms. In the oxygenated surface layer, aerobic microorganisms most efficiently break down organic matter and coexist with aerobic photosynthetic microorganisms. In the anaerobic zone beneath, microorganisms may use substrates as hydrogen acceptors. Sulfate-reducing bacteria produce H_2S .
- Deposit feeders ingest sediment and derive their nutrition from microalgae, particulate organic matter, and to a smaller extent from bacteria. Particulate matter decomposes by fragmentation, leaching, and microbial decay. Burrowing and feeding by benthic animals stimulates microbial activity. Particulate dead organic matter is also important in the nutrition of many deposit feeders.
- Deposit feeders use a cocktail of enzymes and compounds with surfactant properties to digest organic matter. Many benthic animals do not feed directly on microorganisms but rather harbor symbiotic chemoautotrophic bacteria, which derive energy from dissolved ions in seawater.
- Deep feeders cause overturn of the sediment and strongly affect the soft-sediment microzone. Head-down deposit feeders create biogenically graded beds, with finer particles often transported toward the surface and deposited as feces. Deposit feeders can optimize their intake of food by adjusting the particle size to be ingested and its gut passage time.
- Active suspension feeders create a current, usually with cilia, to draw particles toward a feeding structure. Passive suspension feeders protrude the body into the current and capture particles directly by impact without the aid of an active current.
- Suspension feeders may be capable of extensive particle selectivity, which allows the feeder to avoid ingesting too many particles of low nutritive content, which may be abundant in the water column.
- Organisms must adapt to strong laminar flow above the bottom, but near the surface they experience more complex flows. Epibenthos must have traits to minimize pressure drag by changing orientation.
- Benthic carnivores rely on prey search, location, seizure, and ingestion. Odor detection allows predators to cover large ranges, even if their traveling velocity is relatively low.
- Benthic herbivores are divided between microphages and macrophages. Some benthic herbivores can feed on highly indigestible plant material. Benthic microalgae, seaweeds, and sea grasses have evolved both mechanical and chemical defenses to deter herbivory.

■ REVIEW QUESTIONS

1. How do active and passive suspension feeders differ?
2. What type of hydrodynamic condition do well-sorted sediments 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 being from quite different taxonomic groups?
5. What factors help to determine the depth of the redox potential discontinuity?
6. Why do bacteria of different types tend to dominate in muddy sediment at different depths below the sediment–water interface?
7. What is the microbial stripping hypothesis?
8. What are the components of decay of particulate organic matter in sediments?
9. How does a bivalve such as *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 of 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?

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