8 Benthic Organisms and Environmental Reconstruction

8.1 On the Large Diversity of Benthic Organisms

8.1.1 A Quick Look at the Diversity of Mollusks

When discussing diversity, marine geologists commonly emphasize foraminifers. However, mollusks also are highly diverse, and many or most of them are marine organisms. Quite commonly they serve as guide fossils, especially in Mesozoic sedimentary rocks. Ammonites (cephalopods) are prominent in this (Fig. 8.1).

Producing highly diverse assemblages evidently takes long time spans. This requirement of time has been invoked by some geologists to deal with gradients of diversity of modern organisms from the poles to the tropics, which invariably shows the higher diversity in the (geologically much older) tropics. Fossil mollusks are plentiful even back in the early Paleozoic, hundreds of millions of years ago. Among the best known fossil forms are the "ammonites," extinct coiled cephalopods somewhat similar to the modern cephalopod Nautilus (Fig. 13.3) and serving as guide fossils in Mesozoic shelf rocks. While they were presumably largely pelagic, judging from distributions, we must assume that some of them were benthic, from arguments centered on morphology as well as on diversity patterns.

8.1.2 On the Contrast Between Benthos and Plankton Diversity

Snail shells are abundant on the deep seafloor in places, notably in pteropod ooze, an accumulation of pelagic shells, not benthic ones. There are much fewer species in pteropod shells than in benthic snails in general, the discrepancy being greater than a factor of 100 (i.e., hardly subtle). Since the shells of pteropods are easily dissolved in deep cold waters and in sediments rich in carbonic acid, the occurrence of pteropod shells tends to be restricted to the more shallow regions on the deep seafloor away from continents (as noted by John Murray of the *Challenger* Expedition). The fact that the pelagic shells

Fig. 8.1 The great diversity of marine mollusks, even without ammonites. Considerable diversity is evident at all taxonomic levels, including shelled forms that can guide geologists in biostratigraphy. Graph on *right* from the drawings by the German biologist Ernst Haeckel (1834–1919). *Left*: Large squid, Baja California. [Photo W.H. B]

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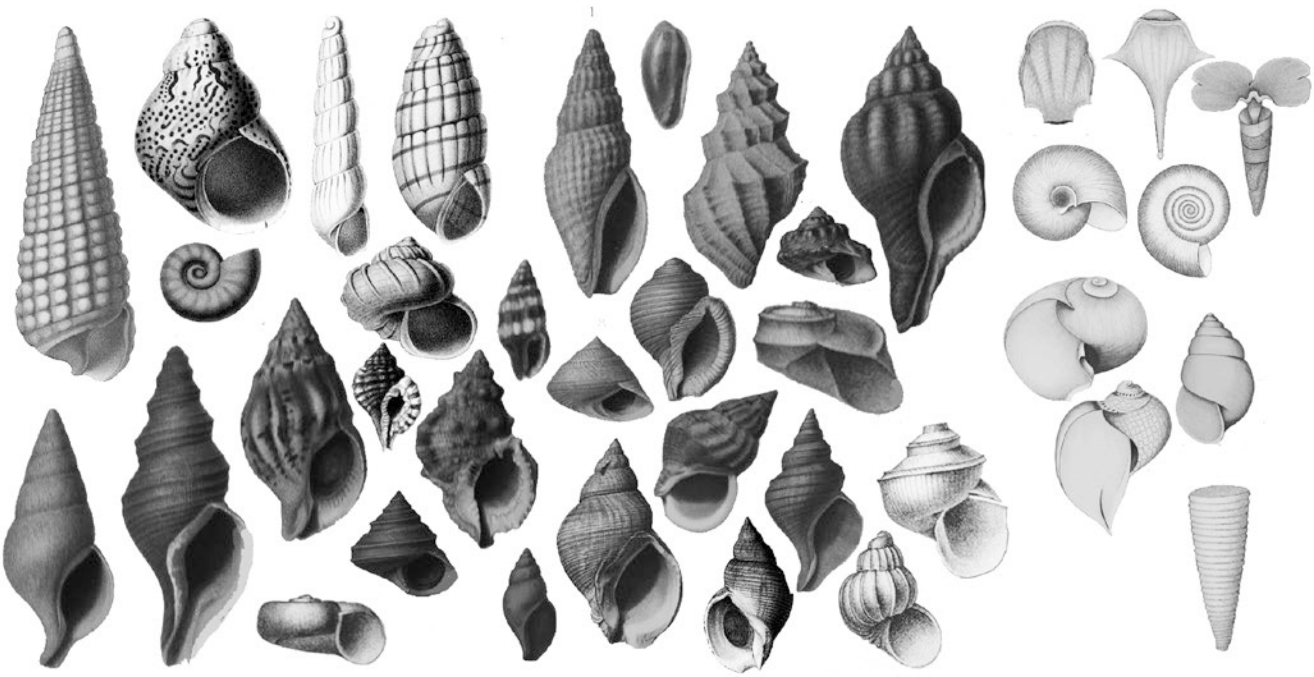

Fig. 8.2 High benthos diversity compared with plankton diversity. Marine gastropods from the North Atlantic. *Left* (dark): benthic forms (i.e., species living on the seafloor). *Right*: a selection of the light-colored and right (light gray): small plankton forms (i.e., gastropods living in the water and commonly called pteropods) [All drawings from expedition reports of Prince Albert I of Monaco, 1848–1922]

are made of aragonite, there is a likelihood that aragonite precipitation is widespread in mollusks (ammonites also had aragonitic shells). To some degree, fossil distributions reflect preservation, of course (Fig. 8.2).

As far as the latitudinal diversity change, it is well studied on the shelf of the US East Coast, where it is in striking evidence. Gastropods (snails) seem to show a greater change across latitudes than do bivalves (clams, mussels, cockles, and close relatives; also referred to as lamellibranchs or pelecypods). Many of the clams live *within* the sediment, in contrast to snails. Seasonal variability and inclement weather conditions appear to be important factors that help determine diversity patterns, presumably in addition to overall temperature patterns. In any case, the patterns observed presumably largely reflect evolutionary development, that is, history and adaptation. There are reasons why tropical species are more abundant than Arctic ones, and one reason may well be with the geologically short time that cold regions have been prominent on the northern hemisphere. The cold deep water may have to do with the fact that many benthic deep-sea organisms have close relatives on high-latitude shelves.

There is yet another consideration. Arctic environments are very demanding as regards benthic life. Paucity of species is a characteristic. One lagoon in Alaska, southeast of Point Barrow, was observed to be covered with ice for much of the year. On freezing, saltwater yields the salt that is excluded from the ice, thus producing brine. The brine is diluted again upon melting of the ice in summer, when also normal marine seawater enters the lagoon. The enormous variations in temperature and salinity attending these processes may be quite inimical to a proliferation of highly diverse shell-producing organisms.

As far as explaining the overall diversity difference between drifting organisms and their benthic relatives, we also might assume that the living space of the open ocean has fewer nooks and crannies than the seafloor. The many types of habitat on the seafloor presumably call for being filled by different species. In all benthic organisms, there are many different types of habitat to occupy for benthos, from shelf to abyss and from above the surface of the seafloor to various (shallow) depths below the seafloor. Such differences in habitat (and sediment types!) commonly are reflected in differences in taxonomy. Also in the case of benthic foraminifers, there are different ways to make shells (“agglutinating” forms use existing particles on the seafloor; calcareous forms precipitate calcium carbonate). In contrast, the various parts of the open sea are well connected, so that there is less opportunity than on the seafloor for evolution linked to specific localities.

8.2 The Seafloor as Habitat and the Task of Reconstruction

8.2.1 Depth and Food Supply

To a large degree, it seems, differences in biodiversity reflect differences in the diversity of available habitats and life styles. Perhaps the most drastic differences in benthic habitats are those arising between the shelf and the seafloor below the shelf edge. On the upper part of the shelf, there is sunlight as

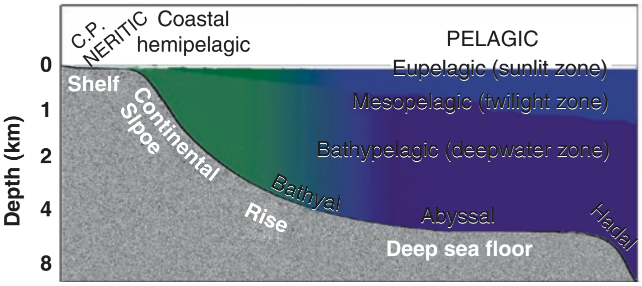

Fig. 8.3 Common environmental terms for the ocean and for seafloor studies. C.P., coastal plain. The beach forms at the upper shelf edge [Based on various texts in oceanography and geology, starting with an article by the late Californian marine biologist Joel Hedgpeth]. Not to scale

an energy source (in a layer less than about 30 m thick). In addition, nutrients are plentiful in places because of coastal upwelling and of other estuarine-type circulation. Stimulated by sunlight and nutrients, benthic primary production by marine algae can be very vigorous indeed. Sunlight limitation would imply that only 2% or 3% of the seafloor are involved in shelf benthic production. However, benthic production here can be 100 times greater than the regular background production of phytoplankton in the open sea. Kelp production in an upwelling setting, for example, has been estimated at 10,000 gC/m^{2}year (grams of carbon per square meter per year). Much benthic production is linked to shallow waters. It takes place in salt marshes and in kelp forests, but also in calcareous reefs, within the minute symbiotic algae of shallow-water coral. Some ecologists point out that higher food supply seems to come with lowered diversity.

Assuming that habitat is crucial for taxonomy, we need to focus on the environment to understand distributions of organisms. How are we to classify marine habitat in simple fashion? As is well-appreciated (see previous Chapter) productivity and the supply of organic matter to the seafloor decrease away from the shore and therefore quite generally with depth. Additional controls, especially on the shelf, are provided by temperature and seasonality in temperature. If the seasonality is between warm and not quite so warm, it is much less effective as a habitat factor than is variation that includes the formation of ice. Light is important; shallow waters have it; deep waters do not. Depth, in itself, may not be all that important, although it does imply great differences in water pressure. Nevertheless, simplicity of classification of environments (based on depth) commonly wins among the possibilities (Fig. 8.3). Food supply, while crucially important, is complicated and difficult to measure.

8.2.2 Salinity and Temperature Reconstruction

Life in the sea also depends on other factors besides sunlight and nutrients, that is, the chief controls on productivity. A large number of organisms can tolerate *salinity fluctuations* only if salinity stays between about 30 and 40 permil. Such species are referred to as *stenohaline* (*narrow salt tolerance*). Examples are among radiolarians, reef corals, cephalopods, brachiopods, and echinoderms. In general, the remains of such organisms indicate marine conditions for the sediments that contain them. However, a few representatives of the groups mentioned may have relatively wide tolerances toward salinity. Also, it is well to remember that remains embedded in sediments do not necessarily agree with the environment of deposition: they may be redeposited.

With increasing salinity, for example, in lagoons of arid regions, fewer and fewer species are able to survive, until only a few organisms remain – an *impoverished* fauna and flora. Some ostracods (bivalved crustaceans of millimeter size) can tolerate salinities of more than 10%. As such hardy forms have few competitors (or predators) in places requiring special adaptations, impoverished faunas can be very rich in individuals. Quite generally, of course, species-poor but individual-rich faunas indicate *restricted environments*. The word “restricted” in this case does not apply to space but to unusual environmental conditions that are stressful to most organisms, excluding them from thriving here.

In the open ocean, where salinities are well within the tolerance limits of all marine organisms, temperature change with depth may play a decisive role in controlling distributions. Temperature also presumably controls much of the observed latitudinal zonation (Chap. 9). In polar regions, the temperature in the water can fall to noticeably below 0 °C (when ice can form). In marginal seas in the subtropics, it can rise to well over 30 °C, as it does in the Red Sea and in the Persian Gulf. Outside the tropics, temperature can vary strongly with the seasons in the upper 100–200 m of the water column. Below this depth, however, the temperature stays rather low throughout the year. Most of the ocean is very cold: in the abyssal deep sea, the temperature stays below 4 °C, reliably so since the Neogene, with cold poles. The cold temperature in itself may not affect diversity. Instead, food supply may be the crucial factor, again. It is very low at the abyssal seafloor. Yet, there is an astounding variety of small benthic organisms. Concerning diversity, local disturbances may be important in providing different opportunities for making a living.

Can we reconstruct temperature distributions from the study of the remains of organisms?

In shallow seas and on the shelves, the oxygen isotopic composition of coral (Fig. 8.4) and also of mollusk shells, among other remains of carbonate-secreting organisms, provide records of changing temperatures within oxygen isotopes of shells.

Relevant studies by the Caltech geochemist Samuel Epstein (1919–2001) and associates introduced the methodology to marine geology. Some fossils definitely give a biased record – biased against unfavorable periods within their life histories. Clearly, whenever there is no or slow growth, there is no record or record compression. Abundance

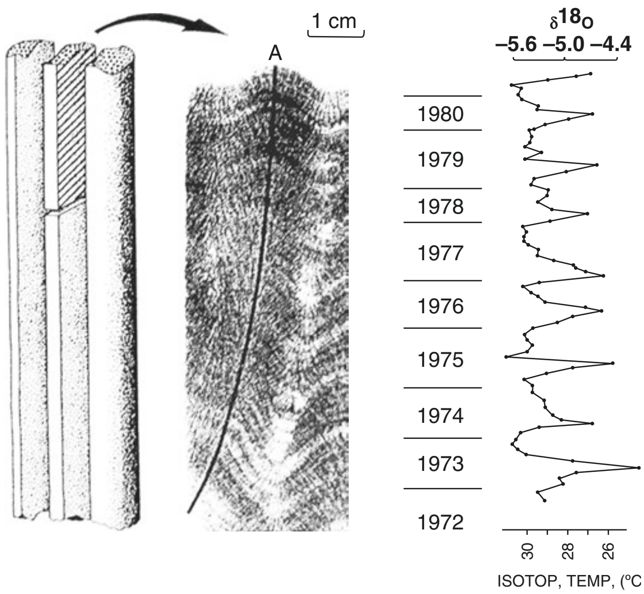

Fig. 8.4 Temperature reconstruction from isotopic variation in *Porites lobata*. In the example shown, sampling was along the profile marked *A*. A second profile (not shown here) was used to check on the width of *error bars*. Temperature varies by several degrees Celsius (colder T is to the right.). Details require additional information, e.g., on precipitation. Note the biased seasonality of the signal: Growth is largely in summer [X-ray photo and graph of oxygen isotopes courtesy of J. Pätzold, Kiel, and Bremen].

distributions of organismic remains on the seafloor change with temperature, and considerable effort has been spent on defining the appropriate statistical relationships that allow a conversion from changes in the distribution of foraminifers and other eukaryotic microbes to changes in temperature patterns, notably by John Imbrie (Brown Univ.) and his associates. For shelf seas and for enclosed basins, the reconstructions are rather more difficult than for the open ocean. At the margins, environmental factors other than temperature play an important role. Thus, a change in the faunal assemblage may reflect stress (or release of stress) in salinity, muddiness of the water, weather condition, or some other influence. One difficulty that exists for both deep and shallow environments, as far as temperature reconstruction, is the selective preservation of faunal and floral assemblages within the sediment. To separate the effects of early diagenesis from those useful for estimating the temperature of growth can be a formidable task, for any and all methods of reconstruction and throughout the geological record.

8.2.3 Oxygen Reconstruction

The content of *dissolved oxygen* in the water is an environmental factor of great importance, especially for cases in which concentrations are close to low levels of 1 ml of oxygen gas per liter of water or less. (“Normal” today is 4–7 ml/l, with the colder water holding more oxygen.) When conditions are “*anoxic*” (no oxygen) or “*dysoxic*” (extremely low oxygen), higher organisms (including shell-bearing protists) may stay away, eventually leaving only anaerobic bacteria and archaea to populate the sediment. When only microbes are present, *varved sediments* can form, as there is then no disturbance by burrowing organisms. Much can be learned from such sediments regarding climate change on the scale of decades to millennia provided the record is continuous (Chap. 15).

The shells of certain benthic foraminifers (i.e., relatively large eukaryotic microbes) have been used to reconstruct the variation in the level of oxygenation in basins off California by the USC (Los Angeles) paleontologist R. Douglas. A pioneering effort with a somewhat similar goal of documenting the changing abundance of benthic foraminifers with water depth was the mapping of portions of an oxygen minimum layer in the Mediterranean by the US micropaleontologist F.L. Parker, in the 1950s, using samples from the Swedish *Albatross* Expedition (Fig. 8.5).

In our time of the ice ages, with oxygen tending to be abundantly present in the marine environment, we have to go to certain special areas to study anaerobic conditions and the sediment they generate – for example, certain fjords in

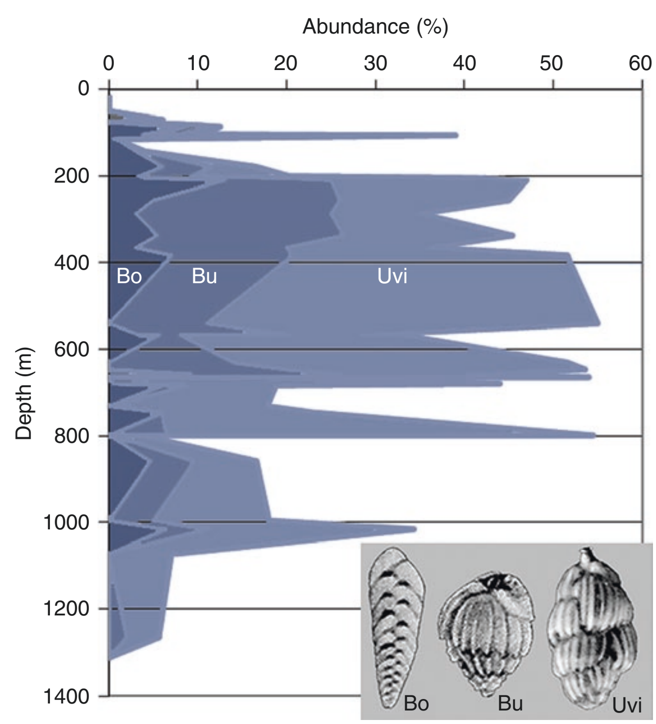

Fig. 8.5 Oxygen minimum zone seen in benthic foraminifers (genera *Bolivina*, *Bulimina*, and *Uvigerina*) in the eastern Mediterranean. Data: Study by F.L. Parker, based on Albatross samples featuring quantitative tables for fossil species (a pioneering feat itself). The three species also respond to high production [Drawings of foraminifers: H.B. Brady, Challenger Expedition]

Norway and Alaska, the Black Sea basin, and the Santa Barbara Basin off southern California north of Los Angeles. In the distant geologic past, when the poles were not icy cold and did not yet deliver oxygen-rich water to the deep ocean, conditions of oxygen deficiency apparently were much more common (Chap. 13).

Basically, oxygen deficiency arises where demand for oxygen is strong and supply is weak. For example, in the Black Sea, the saltwater filling the basin (through the Bosporus, from the Mediterranean) is covered with a layer of freshwater brought in by the Danube, the Dnieper, and other rivers, thus generating an estuarine situation typified by high production (i.e., there is plenty of organic matter). The light freshwater forms a lid on the heavy deep water, thus greatly reducing the oxygen supply by cutting down the exchange of gases with the atmosphere. As a result of the combination of high production and reduced supply of oxygen, the deepest waters of the Black Sea are entirely anaerobic.

The reconstruction of the level of oxygenation is in all cases a highly challenging task for the geologist, involving the interpretation of clues from lamination, from the presence and nature of burrowing, from mineralogy (such as habit and abundance of sulfides), and from the types of organic matter preserved. In addition, the abundance and composition of benthic foraminifer assemblages hold useful clues to both low (or high) oxygen values and correspondingly high (or low) productivity.

8.3 Living on the Seafloor

8.3.1 General Features

The greatest part of the seafloor is teeming with benthic organisms. There is benthos that stays put, called *sessile*. All sponges, corals, brachiopods, and bryozoans are sessile. And there is benthos that moves about, termed *vagile*. Vagile organisms can move rapidly, like a startled crab, or slowly, like the sluggish sea urchins, starfish, most bivalves, snails, and most worms. Both groups, sessile and vagile, have members living *on* the floor or attached to other exposed organisms (such as mussels or snails or kelp): the *epifauna*. Or they live within rocks or sediment: the *infauna*. Representatives of the epifauna are several times more abundant than those of the infauna, for reasons not known (but perhaps similar to those governing the tropical-high latitude contrast).

Benthic animals, ultimately, live on foodstuff falling down through the water or coming in from upslope along the seafloor. Both living plankton and dead *detritus* drift in the water: the *seston*. The detritus consists of organic and inorganic particles. One consequence of the dependence of the benthos on food from the sunlit zone is a pronounced decrease in benthic biomass with depth: the farther away from the productive coastal zone, the smaller the amount of nutritious rain reaching the benthic environment. Although so very little reaches the abyss (order of 1% of production or less, as suggested in Fig. 7.7), hundreds of species – tiny crustaceans and worms – and hundreds of types of benthic foraminifers make their living from the scraps coming down. They must be extremely energy-efficient to survive on such starvation diets. Exceptions to the meager nourishment are provided by falls of large dead organisms. The carcasses are quickly found by highly mobile forms or settled by large organisms growing from larvae presumably looking for this type of opportunity.

The *sessile benthos* waits for the water to bring suspended material from which to extract nourishment. The *suspension feeders* (sponges, corals, brachiopods, crinoids, bryozoans, and others) filter the water, either passively, using the natural flow of the surrounding water, or actively, moving water past their straining apparatus. *Commensals* may seek a free meal in addition to shelter provided by a *host*. For foraminifers living in sponges, it is convenient that the host provides both protection and food. Sessile benthos is especially common in food-rich agitated environments where the water is not too muddy.

The *vagile benthos* on a rocky substrate – starfish, sea urchins, gastropods, and ostracods – commonly feed on epibenthic organisms, for example, by scraping minute algae off the rocks or by preying on sessile animals. The mobile epifauna protects itself from storms and predators by hiding in nooks and crannies, by growing thick shells, and also in cases by firmly clinging to the rock, as do the chitons and patellas using their strong sucker foot. On soft bottom (in less agitated environments), most vagile benthic animals ingest sediment, especially surface detritus that contains a good portion of organic particles (*deposit feeders*). Others hunt for prey. Many use the soft bottom to make holes for hiding, as do fiddler crabs in intertidal mudflats in Southern California (Fig. 8.6) and the ubiquitous "lugworm" in the "wadden" (next section).

8.3.2 The Wadden

The most intensively studied wetlands for large organisms living within soft sediment is the intertidal flat called the "wadden" at the rim of the eastern North Sea. A great abundance of burrowing clams and a long polychaete worm ("lugworm") is notable in these muddy and sandy deposits (Fig. 8.7). The substrate commonly is strongly influenced by the activity of benthic organisms, making bioturbation and other aspects of biological sedimentation an integral aspect of the environment.

Organisms living within the sediment are effective in hiding from potential predators. However, hiding can interfere

Fig. 8.6 Fiddler crabs next to burrows in an intertidal mudflat in Southern California. *Left*: male. *Right*: female. Hole diameter: 0.5–1 in. [Photos W.H. B]

with getting oxygen or food. Many of the infaunal organisms have means to access the sediment surface, where there is nutrition, without exposing most of the body (such as a siphon in burrowing clams). In contrast, organisms living on top of the sediment and on rocks commonly have a different problem, that is, how to fend off or avoid predators aware of their presence. The differences between infaunal and epifaunal habit are rather evident to an observer examining hard parts. But In some cases, differences are strictly behavioral, which means they tend to be cryptic for geologists, although some of the behavior of organisms in and on soft sediment can be fossilized as tracks and burrows, of course.

8.3.3 Carbonate Production Rate

One aspect of ecology that is of central interest to geologists is the *production rate* of hard parts of organisms, that is, mainly of carbonates (Figs. 8.8, 8.9, and 8.10). Availability of light is a crucial factor in carbonate production, making shallow water a favorite place for this type of production. Off Miami, the macrobenthos (large organisms) has been found to produce annually about 1000 g of carbonate per square meter in the tidal zone and between 1 and 400 g per m^2 in the deeper water offshore. In shallow areas of the Persian Gulf, a single species of foraminifer (the light-processing symbiont-bearing *Heterostegina depressa*) delivered annually 150 g of carbonate per m^2.

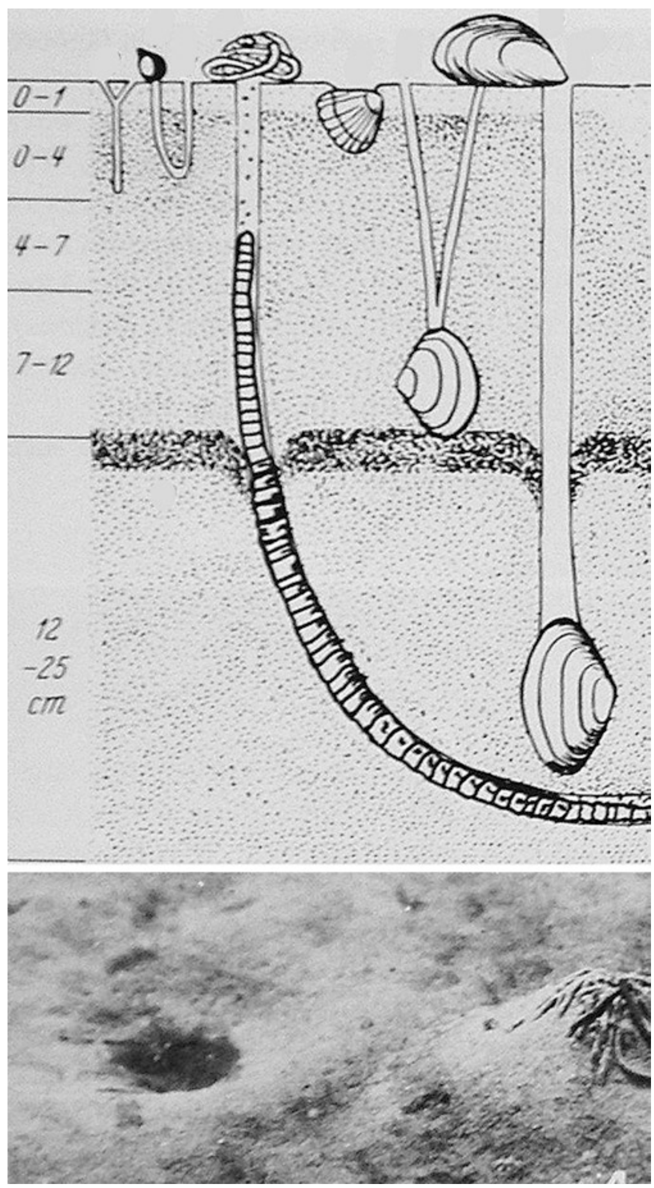

Fig. 8.7 Sediment reworking by infaunal benthic organisms in sandy tidal flats of temperate regions. One of the most abundant and active large wadden animals is the lugworm [From H.M. Thamdrup, 1964, in R. Brinkmann (ed.) Lehrbuch der allgemeinen Geologie. F. Enke, Stuttgart, modified. See Schweizerbart website for "Enke." Photo below graph: E. S]

Calcareous algae are very common contributors to the sediment made by benthic organisms. As primary producers, they need sunlight, that is, they occur in shallow waters – actually right into the surf zone in favorable habitats. Being quite accessible, they have been studied extensively for their rate of growth (Fig. 8.8), with important implications for the rates of sediment production as well. Rates of production are significant, as is the contribution of the algae to carbonate platforms and soft calcareous sediments, especially in subtropical regions.

The production of carbonate in almost all stony corals is entirely dependent on the activity of symbiotic algae ("*zooxanthellae*") living within the coral tissue. The coral species in question grow in shallow warm water, wherever temperatures do not drop below about 20 °C, that is, in tropical and subtropical waters. The organisms are colonial. Many of them make the familiar bush-like calcareous structures, and they need a rocky substrate to anchor to. The symbiosis between coral animals and their dinoflagellates allows these benthic organisms to flourish in rather nutrient-poor waters, that is, in the deserts of the sea. Nutrients are captured and recycled by the animals, and carbon is fixed by the algae. (In recent years, environmental conditions of coral growth are widely reported to have deteriorated. Much "bleaching" has been observed, a process preceding coral death. Commonly heating and acidification are cited as stressors, as well as disease of weakened corals.)

While there is tremendous biodiversity associated with reefs, the coral genus *Acropora* is clearly among past and present dominant forms within the Caribbean. Bush-like corals also dominate elsewhere (e.g., in the Great Barrier Reef in the Pacific, Fig. 8.9) and in many other places rich in reef coral. *Acropora* is a fast-growing form. Presumably the coral was selected for keeping up during the rises of sea level whenever much of the polar ice masses on the northern hemisphere melted on termination of a glacial period. Growth rates of modern individual coral can easily exceed 1 cm per year, suggesting that fast coral growth can be linked to necessity, at least on the millennial scale. Early determinations were based on coral growing on sunken ships. (This is not the same rate as that of the buildup of a reef, of course.) According to the marine paleontologist and reef scientist Jeremy Jackson (S.I.O. and Smithsonian), the coral genus *Acropora* has suffered significant reduction in abundance in the Caribbean in past decades, compared with earlier distribution, presumably largely from human impact, including fishing (pers. comm., 2000).

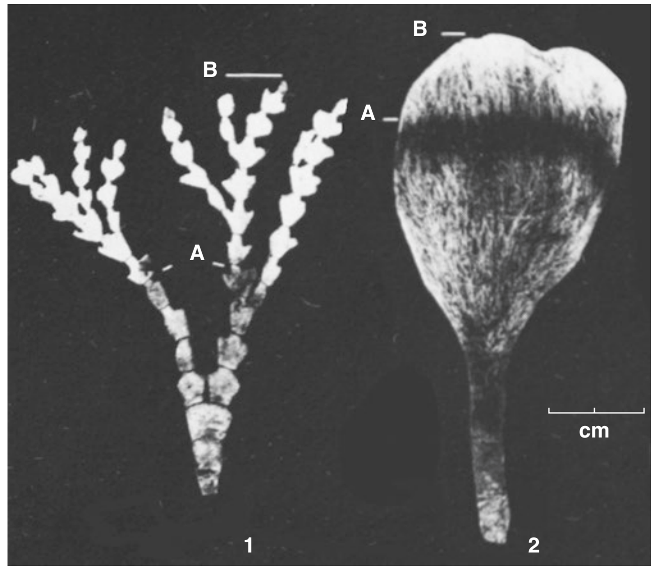

Fig. 8.8 Production of algal carbonate. The rate of production was measured in the field by staining live specimens and noting growth till collection. (*A*) Termination of staining procedure and (*B*) collection. (**1**) *Halimeda* and (**2**) *Penicillus*. Both types of algae have numerous species. The ones shown are common in Bermuda [Photos and experiments by G. Wefer, 1980. Nature 285: 323; Photos courtesy of G. Wefer]

In the geologic record, the evidence that benthic foraminifers with photosynthesizing symbionts were ubiquitous in once widespread shelf seas is very strong. Grain-shaped Fusulinids 200 million years old apparently belong into the group, as do coin- and lens-shaped relatively large benthic foraminifers from the shelf of the Tethys sea, from the Mesozoic to the early Cenozoic. Thus, large foraminifers were still dominating certain shelf environments in the early Tertiary. For example, Eocene nummulites (up to dime size and even larger) are famous for having made limestone used in building the great pyramids in Egypt. The species *N. gizehensis* bears a name that reflects the association. Quite generally, symbiosis is thought to be a major driver of evolution in foraminifers, both benthic and planktonic. In any case, the association between photosynthesizing algae and shallow-water eukaryotic foraminifers (and other shell-making fossils) results in an enormous output of carbonate minerals (Fig. 8.10).

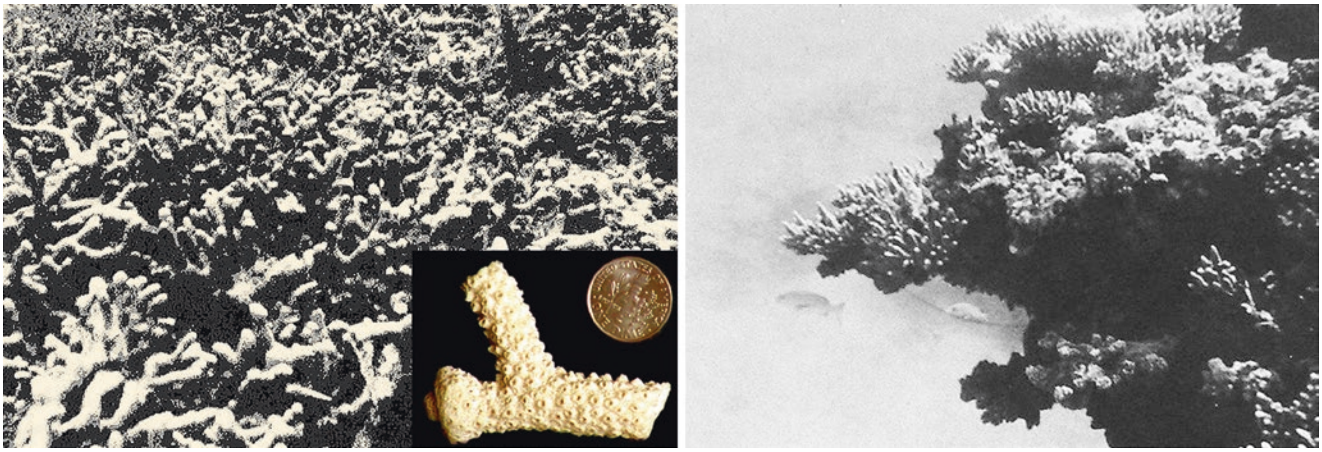

Fig. 8.9 Bushy coral growth. *Left*: *Acropora* meadow, Florida. Penny-sized coin for scale of fragment (Photos W.H.B.). *Right*: Lizard Island, Great Barrier Reef (Photo E. S)

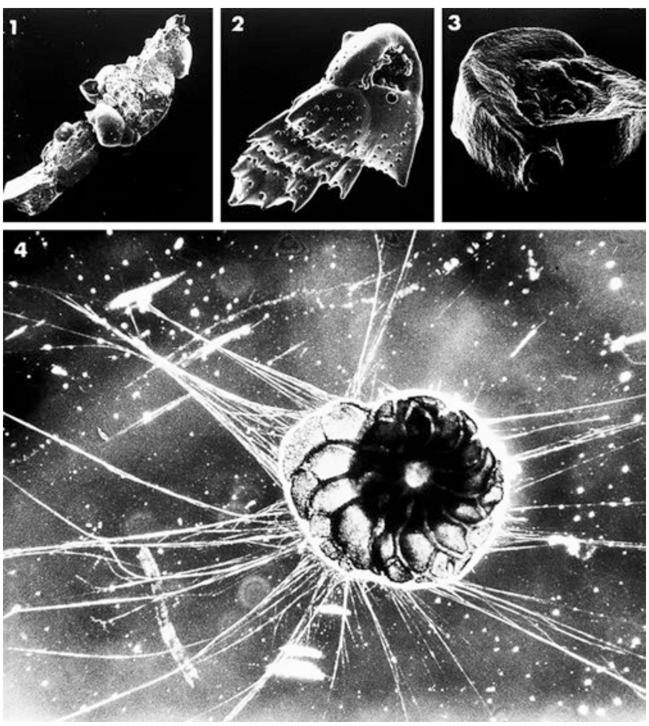

Fig. 8.10 Benthic foraminifers without and with photosynthesizing symbionts. (**1**) Arenaceous form (*Reophax* sp.) agglutinating available particles from the sea floor; (**2**, **3**) calcareous forms (*Trimosina* sp., ×150; *Spiroloculina* sp., ×50). The species of *Trimosina* shown lives below about 25 m in the Indian Ocean. *Spiroloculina* prefers shallow water and coarse substrate. (**4**) *Heterostegina depressa* (diameter of test: 0.84 mm) is a symbiotic form living in sunlit waters. The "pseudopods" radiating from the test are used in locomotion and as anchor. In other forms pseudopods can serve for catching prey. [SEM photos of benthic foraminifers courtesy C. Samtleben and I. Seibold, Kiel. Microphoto courtesy R. Röttger, Kiel]

8.3.4 Life on Bedrock

A great number of different materials can be called "rock": ancient sandstones and limestones of wave-cut platforms or along submarine canyons, basaltic scarps and manganese pavements, submerged dead coral and cemented beach sand (*beach rock*), and boulders dropped from icebergs or in moraines on the shelf. For animals normally attached to natural rock, sunken ships, and other man-made objects can serve as a substitute for attachment. All such substrates can be densely covered by benthic organisms, in some cases (if resting on deep-sea sediment or on mud) forming epibenthic "oases" on an otherwise empty-looking seafloor. The most abundant type of rocky substrate presumably is provided by basaltic outcrops on the deep seafloor, but the most visible colonies are in rocky shores of the intertidal zone and on rocks of other highly productive regions (Fig. 7.2). The abyssal basaltic outcrops are commonly rather barren (except in local spots of hydrothermal exhalation).

In shallow sunlit areas, rocky bottoms are commonly covered by algae. The algae can be *diatoms* (many of these move about on the rocks) or, in the case of macro-algae, up to several meters long soft ribbons waving in the currents and providing hideouts for fishes. Rocky areas may be good fishing grounds (even though they can be hard on a fisherman's net). Encrusting algae tend to cover rock outcrops permanently. Depending on water temperature and depth, familiar epifaunal associations are corals, tubeworms, oysters, barnacles, bryozoans, and encrusting foraminifers. Sponge thickets grow in certain nutrient-rich places that have plenty of dissolved silicate, especially around Antarctica.

The infauna on rocks consists of organisms that bore actively into the substrate (relatively soft rocks being preferred.). The remarkable ability to do so has been acquired by many types of organisms, including sponges, worms, and mollusks. Some sea urchins with unpleasantly (for human swimmers) long and brittle spines live in custom-made cavities. Some algae and some microbes also live within rock; some process sunlight within transparent rocks in shallow water. At first glance, a heavily burrowed rock may look quite solid, the entrances to burrows being small. However, in reality, the rock may look like Swiss cheese inside and thus, in the tidal zone, be very vulnerable to attack by storm surf. Shallow-water limestone is especially susceptible. In certain warm-water lagoons of the Pacific coast, some 30% of the calcareous sediment is delivered by boring sponges.

In shallow rocky areas, organisms commonly are removed periodically by wave action. Their remains collect in depressions at the base of the rock outcrops. Much of the calcareous *reef talus* deposits are of this origin. They are coarsely layered thick sequences surrounding a reef structure and are familiar from ancient reefs exposed on land (e.g., the Permian El Capitan Reef in Texas and New Mexico, Jurassic Malm reefs in central Europe, Cretaceous Albian reefs in Arizona). In the oilfields of the Middle East, highly porous reef talus typically serves as a reservoir rock for petroleum.

8.3.5 Life on a Soft Substrate

We have earlier referred to organisms living in and on mud. The benthic communities on muddy or sandy seafloor are commonly not much in evidence. Organisms living on soft sediment tend to hide by burrowing. Another factor to consider in assessing abundances is the stability of the substrate. Where the seafloor is moderately stable, sea grass can take hold and further stabilize it. Epibenthic diatoms, foraminifers, and bryozoans grow on such grass. Vagile benthos with or without burrows to return to can be quite abundant on sandy and muddy bottom; crabs and snails are common sights in the intertidal zone. A large variety of nonmarine invaders seek food here during low tide, mainly birds feeding on resident organisms. Conversely, during high tide, the invasion is from the sea. It brings plenty of shallow-water fishes digging up worms and mollusks.

The abundance of predators along with the sporadic shifting of the sand, which can suddenly expose the infauna, fosters evolution of the ability to burrow very rapidly. Some clams demonstrate this adaptation very obviously, as is well known to clam diggers. Burrowing clams have a long strong foot that is extended into the mud or sand below and then inflated by water pressure anchoring it, with the rest of the body following by muscle contraction. A smooth shell, usually quite sturdy, characterizes such clams.

Burrowing clams regularly are suspension feeders with an inhaling and an exhaling siphon. After death of a bivalve, the shells – hydraulically quite different from the surrounding sand – are sorted out and concentrated into layers of *coquina*. Presumably reflecting certain favorable conditions for clam growth, such coquina deposits are common in the geologic record and can be used as marker beds locally (i.e., assuming they represent a time horizon), when mapping.

There are some types of challenges that differ for sandy and muddy substrate even though both are soft. In consequence the faunal assemblages of muddy habitats can be quite different from those of sandy environments. As a result of the presence of fine material, the muddy substrate is somewhat firmer than the sandy one because of the high cohesion between clay particles. Thus, the mud is more difficult to burrow into than the sand, but burrows once made have a better chance of persisting. In addition, the high content of organic matter in clayey sediment makes it worthwhile for many organisms to pass the mud through their guts and extract the digestible fraction. For this reason, *deposit feeders* are commonly found on and in this type of substrate. Many of the larger burrows, though, are made by crabs and other mudflat denizens hiding away from sunlight and its predators.

Of course, *suspension feeders* would thrive on the organic matter in clayey sediment also, just as do deposit feeders. However, their filtering apparatuses tend to become clogged with the abundant clay, which is useless to them. Deposit feeders, incidentally, make it difficult for sessile benthos to find a stable foothold by constantly reworking the mud. Thus, once there is much deposit, feeding it tends to exclude sessile organisms, including many plants.

Commonly, on muddy seafloor in shelf waters, brittle stars (ophiurids) are abundant (Fig. 8.11). These are suspension feeders that are anchored within the sediment, with only their arms exposed, for catching food. Their abundance may grow with an increase in food supply (i.e., *eutrophication*). The Danish ecologist Gunnar Thorson (1906–1971) has studied shallow-water communities in northern latitudes. He suggested that such associations are similar for various upper shelf regions, albeit made up of different species (*parallel communities*). In many of them, brittle stars are important members.

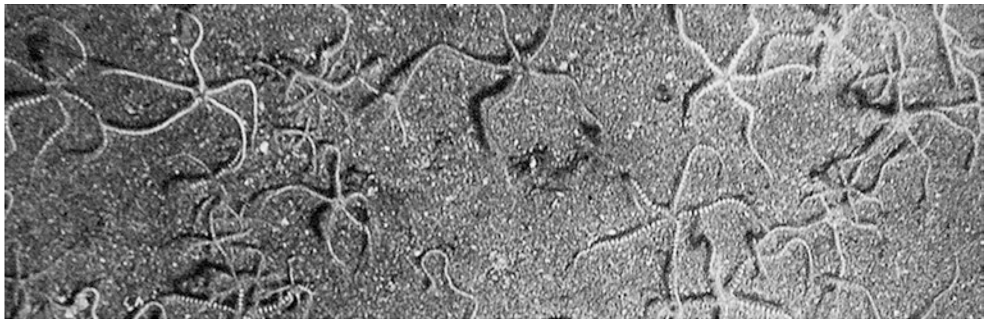

Fig. 8.11 Brittle star community on the uppermost continental slope off Senegal [Photo E. S]

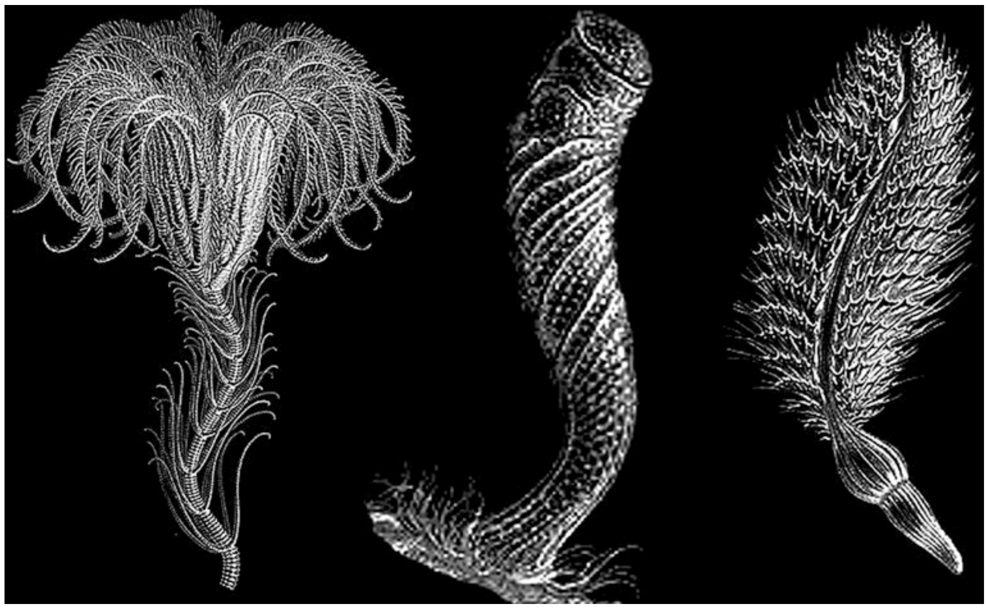

Fig. 8.12 Sessile benthos on the deep seafloor: crinoid, sponge, and sea pen (soft coral) [After E. Haeckel]

On the muddy upper slope off Senegal (NW Africa), abundant brittle stars were seen on the very top of the seafloor, presumably filtering the water. The abundance there of these animals suggests "restricted" conditions unfavorable for diversity (lack of oxygen?) rather than a "regular" Thorson community.

Muddy bottom, it turns out, largely consists of fecal material, many times recycled. This is also true for the deep seafloor, although here the cycling takes thousands of years rather than months as in tidal mudflats. The low level of benthic activity on the deep seafloor and the relatively greater importance of the infauna is illustrated by the fact that on more than 100,000 photographs from 2000 different deep-sea stations, only about 100 visible animals were counted. As B. Heezen and C. Hollister pointed out in their book on the deep seafloor, what is seen in deep-sea photographs largely belongs to the echinoderms (e.g., as is true for holothurians). Some of the animals seen are sessile suspension feeders found on the continental slope: crinoids, sponges, and sea pens (Fig. 8.12). There is, however, plenty of indirect evidence for the activity of vagile burrowing infaunal animals in barren-looking "Red Clay" (Fig. 8.13).

8.4 Trails and Burrows

8.4.1 Trace Fossils

An entire branch of geology – *ichnology* – has grown from the study of the tracks, trails, burrows, and other sedimentary disturbances made by organisms. Such disturbances include *bioturbation*, that is, the mixing that disturbs the orderly recording of events in all sorts of sediment, from which we hope to extract detailed sequences reflecting history. Effects of bioturbation are always annoying but especially so in marine deposits with a high potential for resolution on a century scale. On the deep seafloor, even just

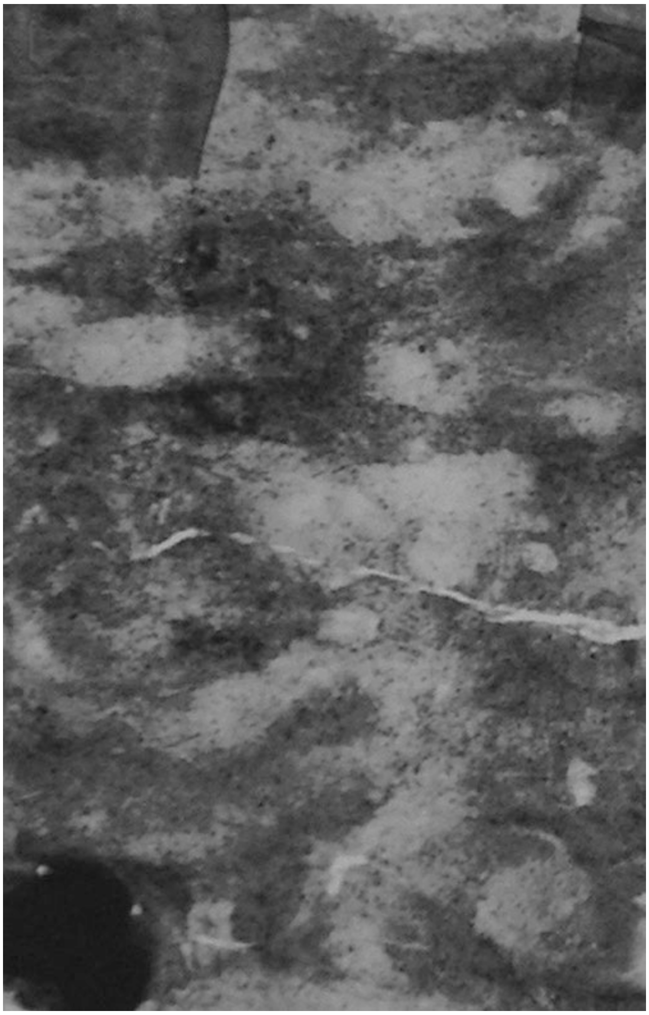

Fig. 8.13 X-ray radiograph of a slab of deep-sea sediments. The core was taken about 1000 km SE of Hawaii in a water depth of roughly 5 km. The image is a positive. It shows abundant burrowing within the deep-sea clay ("Red Clay") during the millennia represented by the sediment [Photo courtesy of F.C. Kögler, Kiel]

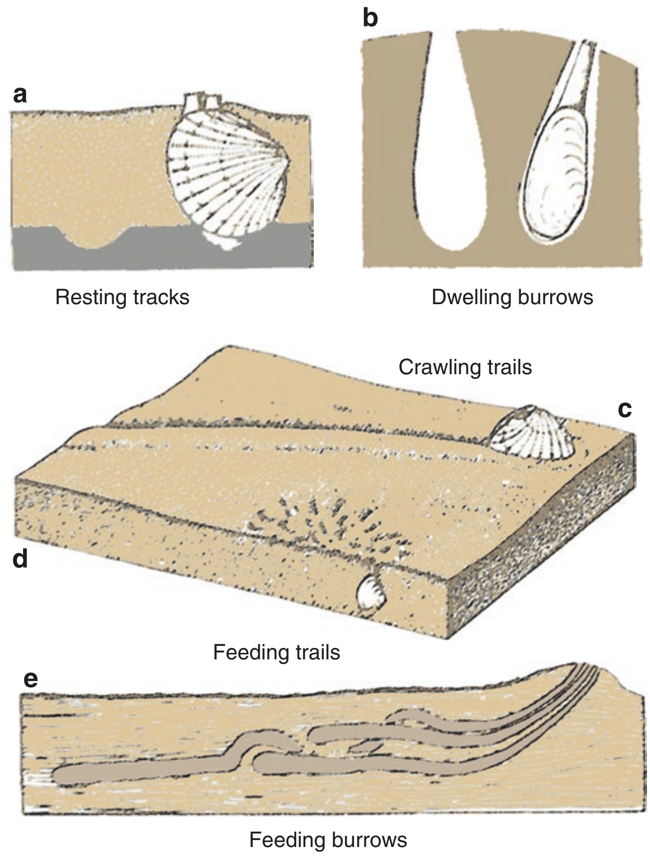

Fig. 8.14 Various types of "lebensspuren." (**a-d**) Bivalves; (**e**) burrowing worms [A. Seilacher 1953. Neues Jahrbuch Geol. Palaeont. Abh. 96:421 and 98: 87. See Schweizerbart website. Minor modification; color here added]

attaining a millennial resolution may require the *stacking* (averaging) of several records to reduce idiosyncratic errors from bioturbation by large animals that move sediment.

There is a great variety of traces that eventually become trace fossils: trails, feeding tracks, fecal strings and mounds, burrows stuffed with fecal matter, burrows used for housing (and later filled by washed-in sediment), and other legacies of animal activities (Fig. 8.14). Various kinds of worms, snails, bivalves, crabs, holothurians, sea urchins, and starfish make such tracks and burrows, and it can be very difficult indeed to assign the likely maker to a given *ichnofossil*. Crabs and shrimp make the longest and deepest burrows. In certain cores from off Northwest Africa, vertical burrows more than 3 m long were found! Such "*lebensspuren*" have been and are being studied intensely by marine geologists in Wilhelmshaven on the North Sea, in Kiel (Schleswig-Holstein, next to Denmark) and in Tübingen (Baden-Württemberg, next to Switzerland). Thus, the German word *Lebensspuren*, which is "life traces" in English, has been adopted as a technical term in geology.

8.4.2 Lebensspuren

Tracks and burrows preserve environmental information. Unlike shells, lebensspuren cannot be transported by currents but stay in the sediment where they were made. Thus, they definitively indicate in situ conditions, whether it be food supply, oxygen availability, sediment stability, or water motion.

Just like shells (which are inanimate particles after death of the maker), tracks and burrows can transmit information pertaining to physical geology rather than to ecologic reconstruction. In the deep sea, for example, vertical burrows do

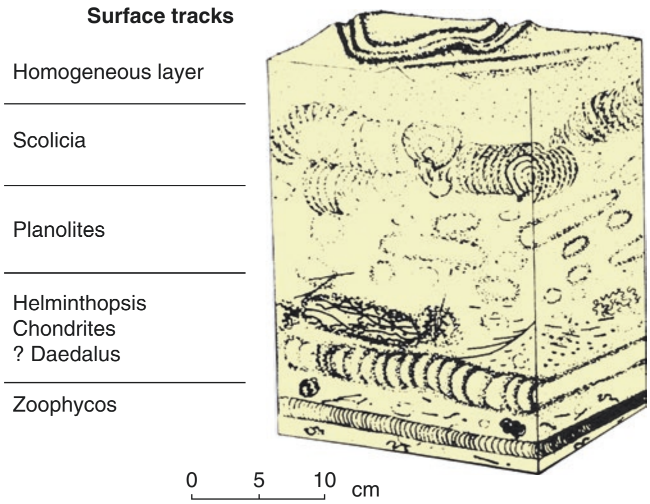

Fig. 8.15 Biogenic sedimentary structures in deep water off NW Africa (at about 2000 m). Tiered arrangements of active burrowers reach about 30 cm into the sediment. Bioturbation homogenizes the uppermost 3 cm of the sediment, destroying surface tracks and smoothing the record. Various burrowers make traces within the sediment. These tend to persist but likewise affect the reliability of the historical record negatively [A. Wetzel, 1979, Ph.D. Thesis, Geol. Inst. Kiel; slightly modified; color here added]

not last if the sediment has a tendency to shear horizontally by moving downslope. The effect is seen in deep areas, where dissolution of carbonate makes the sediment soft. Sediment presumably creeps downhill whenever shaken by earthquakes, a common occurrence in areas with volcanic activity. The motion destroys vertical burrows. Such downhill gliding may also be important on many continental slopes in areas of a muddy seafloor substrate, notably in volcanic areas or sedimentary slopes with high gas pressures.

Lebensspuren show different degrees of preservation, of course. A delicate trail made by a starfish or a mussel has but little chance of entering the record. On the other hand, a 30-cm-deep *Arenicola* or *Mya* burrow or especially a 2-m-deep crab burrow has an excellent chance, since much sediment would have to be moved to obliterate it once the burrow is made. In general, surface tracks can only be preserved by catastrophic deposition such as by flood or turbidity current. In the case of continuous accumulation, when sediment builds up gradually and there is a mixed layer from bioturbation, surface tracks are destroyed, and only burrows penetrating the mixed layer are preserved in the record (Fig. 8.15).

8.5 Partial Preservation and Bioturbation

8.5.1 Gaps in the Record

Only a selected portion of the biological community can be fossilized. Of Thorson's parallel communities of shallow water environments, for example, we can expect to find some of the shells and some of the burrows he identified but not all of them. Nothing readily recognizable will be left of most worms or shrimp. Nothing much remains of the fish and other predators that come during high tide to feed on intertidal organisms, and nothing virtually of the predaceous birds that take advantage of low tide to capture food. Nevertheless, predation from flatfish, rays, and birds presumably exerts considerable control on the composition of the nearshore communities. For example, muddy sand and deeper waters are commonly settled by the *Syndosmya* community. The name-giving clam is a favored food item of certain flatfish – something that certainly would be hard to tell from the fossil record, putting a crimp in reconstructing the evolution of both the clams and the flatfish.

8.5.2 Bioturbation and Radiocarbon

Bioturbation prevents the preservation of thin layers, whether thin turbidite layers or layers produced by contour currents (contourites) or some other layer. The result is a loss of resolution in the sediment record. In times past, however, when the ocean was much less well oxygenated, burrowing organisms may have been much less abundant, so that the process of homogenization would have been less widespread than today. In ancient shelf seas, we quite commonly see finely layered sediment in the geologic record on land. Perhaps only since the planet acquired ice caps has there been plenty of oxygen supplied to waters in contact with the seafloor. In summary, possibly bioturbation was possibly much less vigorous before there was ice.

In finely layered sediments, each layer has a message somewhat different from adjacent ones. Scientific questions are usefully centered on the length of time for which an average is made. Clues are derived from the *dating* of the sediment. Appropriate detailed studies have been made for deep-sea box cores with some promise for (geologically) detailed paleoclimatic reconstruction (Fig. 8.16).

For calcareous sediments younger than 30,000 years, radiocarbon-age dating can deliver excellent results. The *radiocarbon* (^{14}C) enters the sedimentary record within the calcium carbonate of calcareous shells. A certain proportion of the carbon dioxide in the air contains the radioisotope, which is produced from ^{14}N, by bombardment with cosmic particles. The carbon-14 produced decays back to nitrogen, half of it being gone in 6000 years. This is called the "half-life." The short half-life (6000 years being geologically "short") implies a severe limit on dating: after 42,000 years, only a tiny fraction of the original radiocarbon is left ($1/2^7$ or 1/128). At such low concentrations of radiocarbon (<1% of the original ^{14}C in a sample), contamination problems become huge on a planet (ours) with lots of carbon. Other problems also arise, and they affect the entire radiocarbon record. For example, an assumption has to be made about the

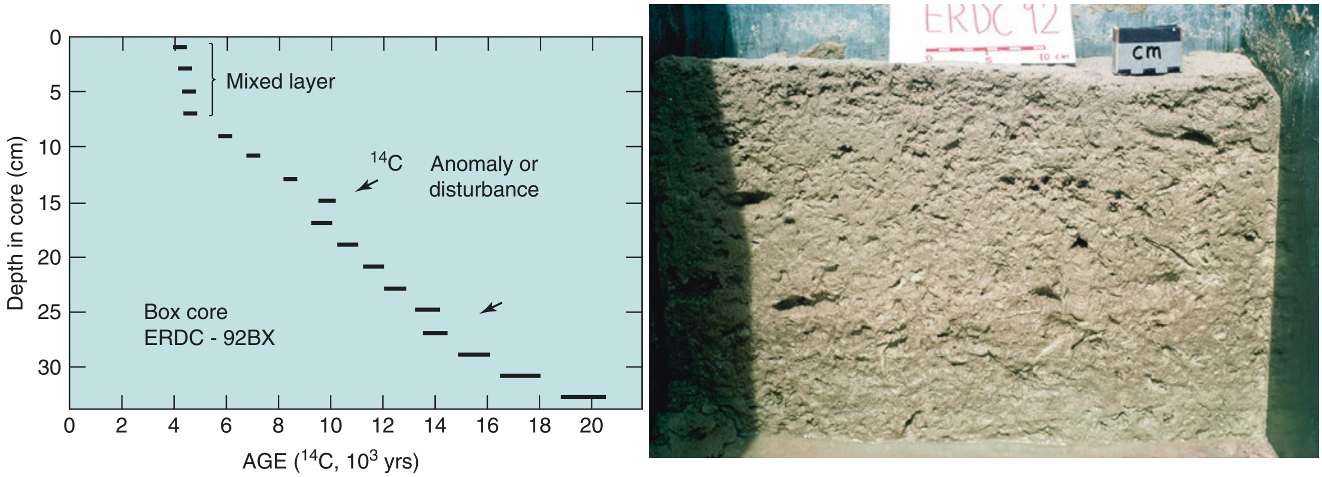

Fig. 8.16 Radiocarbon stratigraphy of box core ERDC-92 from Ontong Java Plateau in the western equatorial Pacific [Graph and data in T. H. Peng et al., 1979. Quat. Res. 11:141]. *Right*: ERDC 92 shortly after recovery and washing of face [Photo W.H.B. and J.S. Killingley]

original concentration of the radiocarbon where a shell was made. The assumption introduces guesswork to otherwise perfectly quantitative methods.

The radiocarbon stratigraphy of the deep-sea box core shows the signal of a mixed layer for the uppermost several centimeters, suggesting that assuming a homogenizing layer of 2 cm is quite conservative (Fig. 8.16).

In the example shown, there seem to be two major disturbances in the radiocarbon record after the last glacial maximum, in the millennia during the transition from glacial to postglacial conditions. The nature of the disturbances suggests sudden deposition of upslope material. The timing of the deeper disturbance is close to the age of a proposed impact of a bolide from outer space on the surface of the Earth. If it hit close to a continental margin, such a bolide would probably have set off tsunamis (either directly or via earthquakes and landslides), which disturbed sediments on top of submarine mountains such as the one where the core was taken. However, the sediment is heavily burrowed here, so the disturbance may owe to bioturbation rather than impact. Alternatively, it may be the result of redeposition of shallower ooze, for example, following a quake on the plateau. What is most puzzling is that the events seem to mark a change in long-term sedimentation rate. This is unexplained.

8.5.3 Mixing and "Stacking" of Deep-Sea Cores

On cutting a vertical face of a deep-sea box core, one realizes that the record is severely disturbed, on a scale of centimeters. Given a sedimentation rate between 1 and 2 cm per 1000 years, a resolution of better than a 1000 years would seem impossible to obtain directly from any one record. Possibly, resolution can be improved by *stacking* several records, thus diminishing the weight of aberrant values introduced by bioturbation. However, a limit for resolution of about 1000 years will persist. "Stacking" averages the input data. Averaging degrades resolution, although it can improve overall results by reducing extremes that may be spurious.

8.6 The Deep Biosphere and Methane

The exciting discovery of hot vent microbes feeding hot vent tube worms (Fig. 1.9) may have somewhat eclipsed the equally interesting and significant discovery, by deep-ocean drilling, of abundant microbial life forms in the sediments of the deep sea, especially in those accumulating on continental slope and rise. Even at great depths within the sediment (hundreds of meters), there are signs of biological activity, albeit decreasing markedly with depth in the sediment (Fig. 1.11). At great depth within sediments, the effects from a rise in temperature become noticeable as one approaches deeper layers of the crust. It has been suggested that this rise in temperature (typically between 20 and 30 °C for each additional kilometer) may be ultimately the limiting factor for the distribution of life at depth within sediments. Interestingly, archaea make up a substantial portion of microbes at great depths, more than one half of the mass in places. Presumably, their relative abundance is linked to the extreme conditions prevalent in this environment (high temperature, low food supply). In addition, it is assumed, archaea are responsible for the production of methane from organic matter within sediments. If so, this would mean that much or all of the "natural gas" below the seafloor is really an indicator of microbial activity there, rather than indicating supply from the crust or mantle.

A host of questions, largely unanswered as yet, arise in the context of prokaryotic microbes living deep within marine sediments. How long do these microbes live? What do they live on? How did they get to where they are? What are their closest relatives on the surface, and how do they differ from them genetically? Answers will come from microbial investigations, including studies from biogeochemistry focused on the carbon cycle.

Suggestions for Further Reading

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