

Soft-Sediment Communities

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Marine sediments constitute one of the largest habitat types on Earth, covering roughly 80% of the ocean bottom (Lenihan and Micheli 2001; Nybakken and Bertness 2005). As a result, to truly understand the processes that shape communities on our planet, it is critical to understand the underpinnings of this habitat. In fact, much effort has been focused on studying this habitat (especially in nearshore areas), and the results have been well summarized over the past several decades. For a thorough description of this habitat, including detailed depictions of the processes that occur in it, we direct the reader to the works by Olafsson and colleagues (1994), Gray (2002), and especially Lenihan and Micheli (2001). Rather than repeating these excellent descriptions, this chapter provides a brief summary of general patterns of distribution and abundance in soft-sediment environments and an illustrated list of the main structuring processes and mechanisms that have emerged from the large literature on these habitats (**Box 10.1**). The distillation of these generalizations and principles provides a basis for the focus of this chapter on four areas of distinctive and pronounced recent advances in soft-sediment ecology.

General Patterns

Four taxonomic groups dominate the macrofauna of soft-sediment communities: polychaetes, crustaceans, echinoderms, and molluscs (Thorson 1955; Nybakken and Bertness 2005). Sublethal predation on these taxa is frequent, especially on clam siphons, polychaete segments, and brittle star arms (Lindsay 2010). In addition to the direct reduction in feeding efficiency and decreased time spent foraging that accompanies sublethal predation, this damage can also increase the likelihood of subsequent lethal predation (Meyer and Byers 2005).

Most soft-sediment communities are below the photic zone and are thus dependent on subsidies from other autotrophic communities. But in shallow water and on intertidal shores, the flora is dominated by angiosperms (e.g., salt marsh grasses, mangroves, and seagrasses) and microalgae growing directly on the sediment surface, whereas macroalgae are a relatively minor component due to the often turbid water and the difficulty of attaching in a fluid sedimentary environment. Both chemosynthetic and photosynthetic bacteria in the sediment contribute substantially to primary production (Valiela 1984). In addition to their role in primary production, the microphytobenthos (photosynthetic algae and bacteria) structure the physical environment by mediating oxygen and nutrient flux and stabilizing the sediment (Yallop et al. 1994; MacIntyre et al. 1996).

BOX 10.1 Mechanistic and Process-Based Organizing Principles of Marine Soft-Sediment Communities

These principles, which are intended as useful rules of thumb, include classic paradigms as well as principles that have emerged more recently. There are, of course, exceptions to these generalizations, but the cited literature provides a useful entry into these debates.

1. Animal–sediment interactions

Deposit feeders and suspension feeders can negatively affect each other through their effects on sedimentary properties (Rhoads and Young 1970; Woodin 1976). Through their movement and activities, deposit feeders resuspend sediment, clogging suspension feeders' filtering apparatuses and burying larvae.

Aerobic organisms reside in the top few centimeters of sediment unless they have a connection to the surface via a siphon or a burrow, which is often ventilated (**Figure A**). Deeper organisms deal with low oxygen levels and high levels of sulfides and other toxic chemicals (Fenchel and Riedl 1970).

2. Recruitment

Aboveground structure, such as aquatic vegetation, can enhance the recruitment of benthic fauna by increasing passive deposition of larvae (**Figure B**; Eckman 1983).

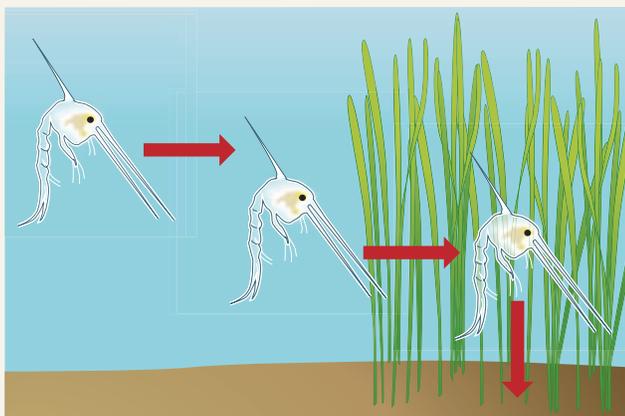


Figure B Aquatic vegetation baffles water flow and can enhance the recruitment of benthic fauna.

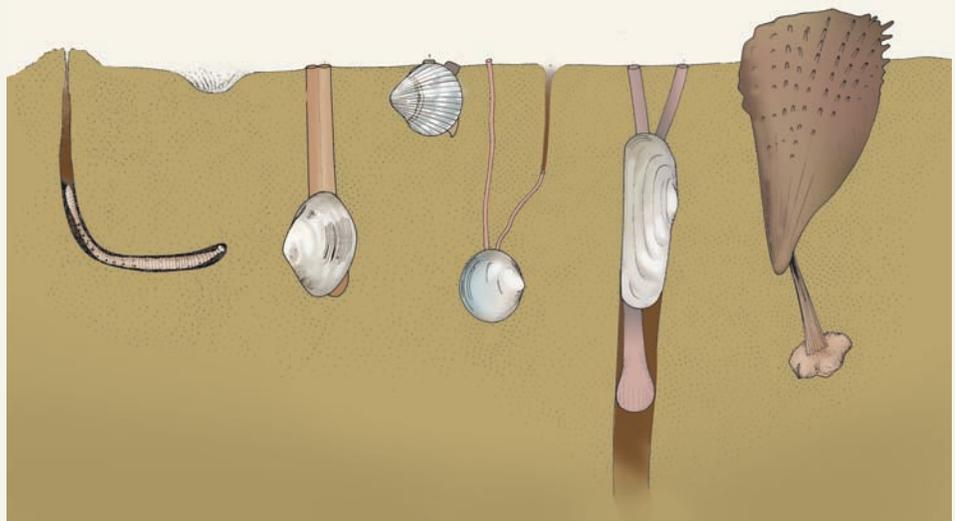


Figure A The majority of macrofaunal soft-sediment infaunal organisms are aerobic and must therefore live near the oxygenated water at the sediment surface. Deeper living is possible if the organism possesses a siphon or maintains a ventilated burrow that keeps contact with oxygenated water.

3. Biotic interactions

Predation can be intense, but spatially and temporally variable, and thus is one of the main processes maintaining high variation in the distribution of organisms (**Figure C**; Peterson 1979; Olafsson et al. 1994; Thrush 1999). Predators often have more influence in areas lacking structure because structure provides refuges for prey or interferes with predator foraging efficiency (**Figure D**).



Figure C Dense aggregations of migratory predators, like the shorebirds pictured here, can exert large pulses of predatory pressure on soft-sediment infauna. (From Peterson 1991. Photo © Yva Momatiuk and John Eastcott/Minden Pictures/Corbis.)

BOX 10.1 (continued)

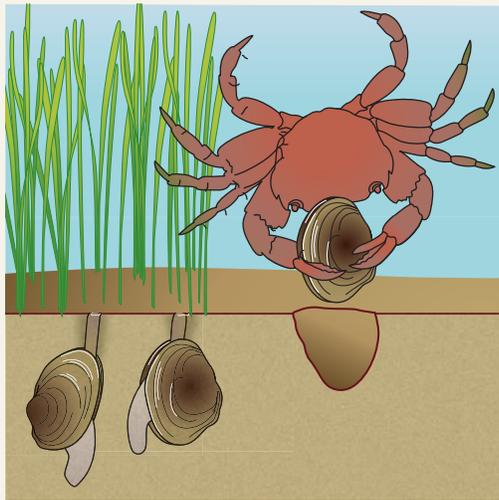
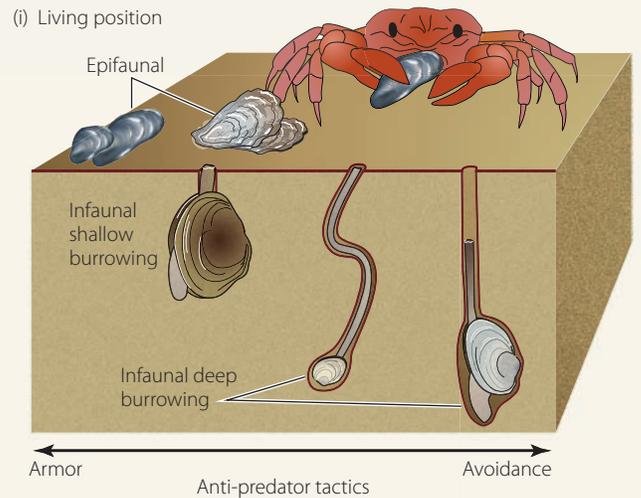


Figure D Structure often protects prey because they benefit from the resulting refuge and reduced predator foraging efficiency.

In high-predator areas, soft sediment bivalves often follow an armor–avoidance continuum. Armored species use morphological refuges, like thicker shells, which often result in Type II predator functional responses (Figure E iii). Avoidance species reduce predator encounter rates through burial, which often results in Type III predator functional responses. For example, in the Chesapeake Bay, the blue crab (*Callinectes sapidus*) is a predator of the mussel *Mytilus edulis*, the oyster *Crassostrea virginica*, and the clams *Mercenaria mercenaria*, *Macoma balthica*, and *Mya arenaria*. To defend against predation, *Mytilus* and *Crassostrea*, both epifaunal species, have high armor. Conversely, the clams (especially the deeper ones) have lower armor, but all are infaunal species that burrow into the sediment to avoid predators (Figure E; Seitz et al. 2001).

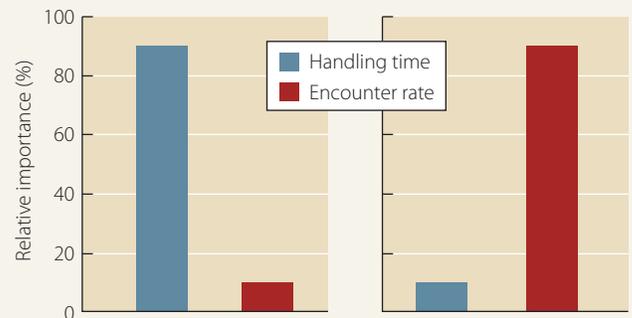
Figure E (i) Living position as a defense against predation, as shown here in the armor versus avoidance continuum. (ii) Components of predation (handling time and encounter rate) and their relative importance for prey emphasizing armoring and avoidance. Handling time is relatively more important in prey employing armor, whereas factors affecting encounter rate (e.g., habitat structure, low densities) are more important for prey using avoidance. (iii) The predator functional response changes from inversely density dependent (Type II) in prey utilizing armor to density dependent (Type III) in prey using avoidance or burrowing. (iv) Proportional mortality of prey ranging from inversely density dependent to density dependent. Analysis of the components of predation predicts that predators foraging on bivalves living on or near the sediment surface will exhibit a Type II functional response, but those foraging on deep-burrowing prey with a low encounter rate will exhibit a Type III functional response. (After Seitz et al. 2001.)



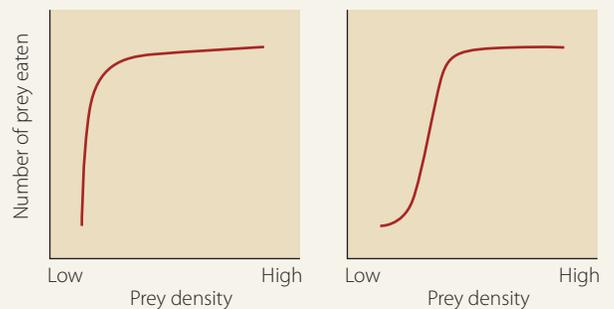
Armored prey, Type II functional response

Prey using avoidance, Type III functional response

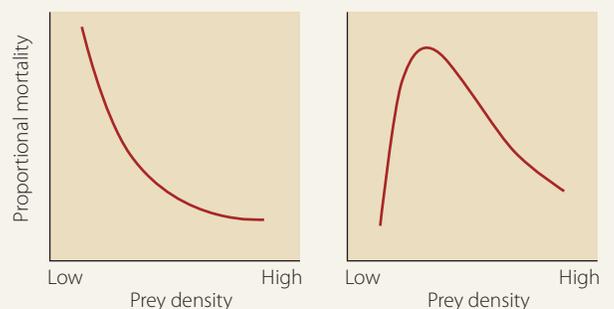
(ii) Components of predation



(iii) Functional response



(iv) Proportional mortality



BOX 10.1 (continued)

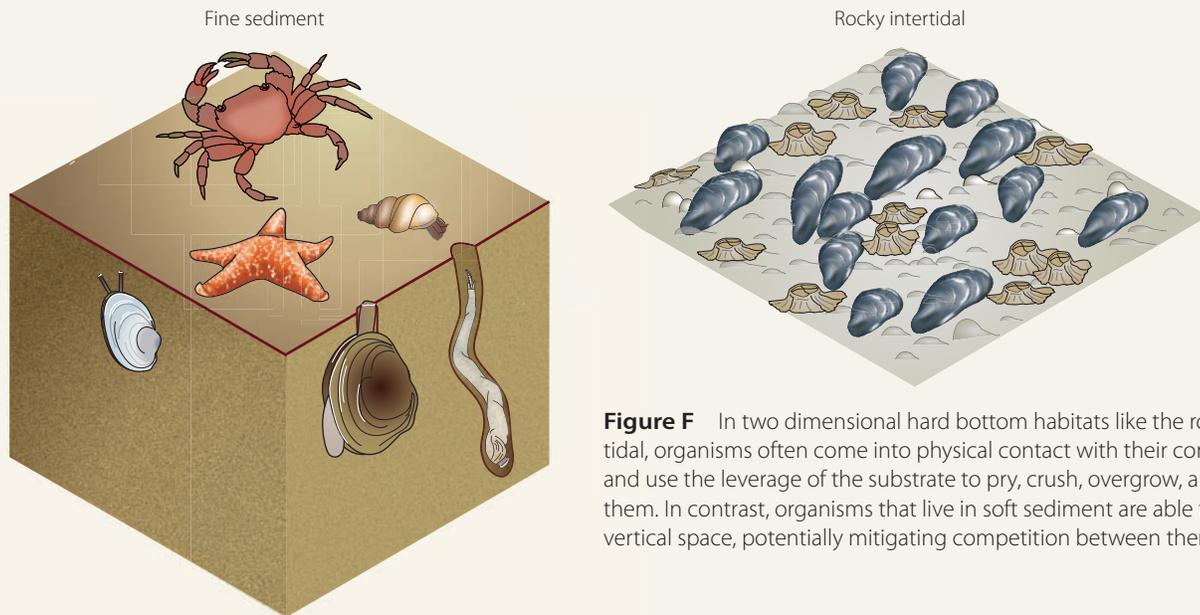


Figure F In two dimensional hard bottom habitats like the rocky intertidal, organisms often come into physical contact with their competitors and use the leverage of the substrate to pry, crush, overgrow, and bulldoze them. In contrast, organisms that live in soft sediment are able to partition vertical space, potentially mitigating competition between them.

Competition for space among infauna is mitigated by three-dimensional living space that allows organisms to partition vertical space (**Figure F**; Peterson 1977, 1991). Infaunal densities are usually not high enough for space to be limiting (but see Levin 1981, Brenchley 1982).

In contrast to hard substrate, where many organisms are sessile, post-settlement dispersal is common in soft sediments. Continued mobility can ameliorate competition through emigration and speed recovery of disturbed patches (Whitlatch et al. 1998).

In contrast to hard substrate, exploitative competition is more common than interference competition in soft sediments, since there is no physical leverage to crush or bulldoze competitors. Thus competition does not typically result in death, but rather in migration and reduced feeding and growth (Peterson 1979; Levinton 1985; Olafsson 1989; Barnes 1999; Lenihan and Micheli 2001).

Suspension feeders experience less exploitative competition than deposit feeders, since their pelagic food resources can be replenished by currents, decoupling local populations from food availability (Levinton 1972; Peterson 1979; Olafsson 1986; Byers 2005). However, oligotrophic conditions can elicit competition even among suspension feeders (Peterson 1982a; Peterson and Black 1987, 1993).

4. Ecosystem engineers and habitat modifiers

Habitat modification by aboveground foundation species (e.g., oysters, seagrasses, marsh plants, and corals) markedly affects soft sediments because there is otherwise little topographic relief or abiotic structure above ground (Bruno and Bertness 2001; Gutierrez et al. 2003; Hastings et al. 2007;

see Chapter 3; see p. 236, *Habitat Complexity and Soft Sediment Communities*, and see p. 234, *Invasive Species in Soft Sediment*).

Ecosystem engineering is also important to infauna. Burrowing and tube building (and the water pumping and irrigation that often accompany them) create aerobic habitat by oxygenating deeper sediments and providing refuges (**Figure G**; Gray 1974; Woodin 1978; Aller and Yingst 1985; Rosenberg et al. 2001; Reise 2002).

Benthic microalgae have emerged as important ecosystem modifiers, acting to stabilize sediments (Underwood and Paterson 1993) and promote other ecosystem engineers such as salt marsh plants (Piehler et al. 1998; see p. 242, *The Microphytobenthos*).

5. Disturbance

The legacy of disturbance effects correlates with sediment grain size. Due to ionic charges on mud sediments that make them cohesive, and due to low water velocities over muddy areas, physical recovery rates are much slower than in coarser, sandier sediments (Norkko et al. 2002, Dernie et al. 2003).

Biotic disturbances are common, especially from foraging or nesting predators that create pits, such as rays, walrus, gray whales, and horseshoe crabs (see Figure 10.5). Their digging activity incidentally kills infauna and creates physical effects such as topographic alteration and increased turbidity (Oliver et al. 1984; Fukuyama and Oliver 1985; Thrush et al. 1991; Lee 2010).

Waves influence shallow-water zonation through direct effects (McCall 1977, Hall 1994) and indirectly by affecting grain size (Oliver et al. 1980, Dyer 1986).

BOX 10.1 (continued)

Similar opportunistic groups of macrobenthic organisms (i.e., motile crustaceans and polychaete worms) are the first to recolonize chemically and physically disturbed areas across much of the globe, oxygenating sediments and facilitating succession (Lenihan and Oliver 1995).

Eutrophication increases oxygen demand, and associated hypoxia/anoxia kills many sessile and low-mobility species, causes mass emigration of mobile species, and alters sediment biogeochemistry (Tenore 1972; Diaz and Rosenberg 1995; Diaz 2001; Lenihan et al. 2001; Levin et al. 2009; see p. 240, *Anoxia and Eutrophication in Soft-Sediment Communities*).

Soft-sediment areas have a higher number of non-native species than do other marine habitats (Ruiz et al. 2000; Wasson et al. 2005; Byers 2009a). The impacts of invaders are also expected to be higher in these habitats (Byers 2009a; see p. 234, *Invasive Species in Soft Sediment*).

6. Study approaches

Experimental artifacts are often exacerbated in soft-sediment systems because devices used for manipulation, such as predator exclusion cages, add structure to an otherwise structureless area, changing hydrodynamics, flux, and especially sedimentation (Dayton and Oliver 1980; Hulberg and Oliver 1980; Olafsson et al. 1994).

Direct observation of species interactions is difficult because they often occur beneath the sediment surface. Even tracking abundance over time requires destructive sampling in most cases, complicating the detection of experimental treatment effects (Ambrose 1984; Lindsay et al. 1996).

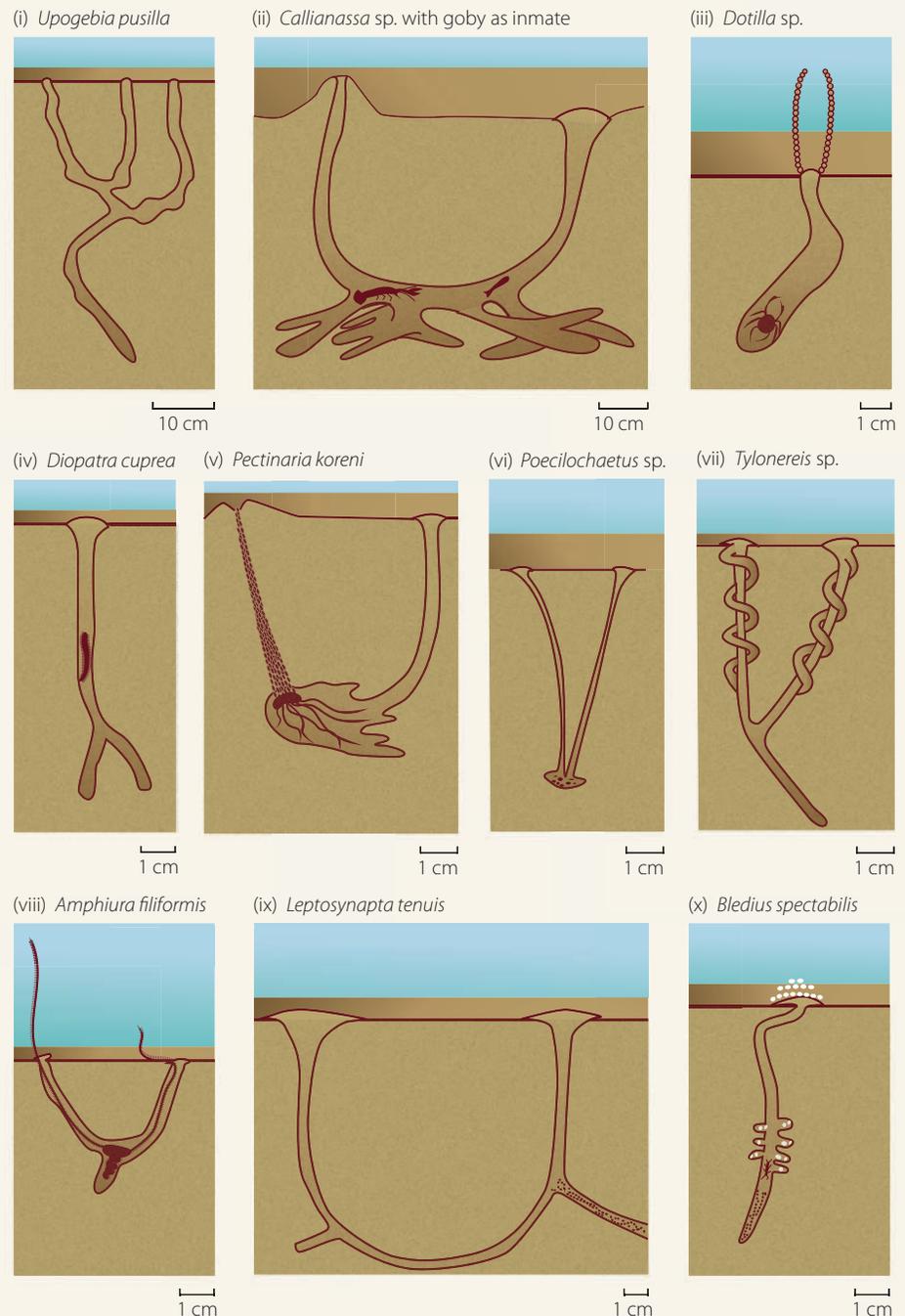


Figure G Burrowing organisms are important ecosystem engineers in soft-sediment habitats because they help water and oxygen reach deeper sediments. The amounts and depths of oxygen and solutes delivered below the surface can vary greatly depending on the species. (i, ii) Burrows of thalassinidean shrimps. The wider areas in (i) are turning chambers. (iii) Burrow of an ocipodid crab. The chimney, made of sand pellets, traps air when the tide comes in. (iv–vii) Burrows of polychaetes. (vi) A spionid burrow with fecal chamber at the basement. (vii) Secondary ducts spiraling around vertical shafts. (viii) Burrow of an ophiuroid from which the animal waves its appendages in the water above to suspension feed on plankton. (ix) Burrow of an apodous holothurian, showing a previous feeding pit and an old shaft filled with fecal castings. (x) Burrow of a staphylinid beetle, showing lateral egg chambers and fecal pellets at the basement. (After Reise 2002.)

Soft sediment is a habitat in which macrofauna are often differentiated by functional rather than taxonomic group (e.g., burrowing deposit feeders, suspension feeders, tube builders). Functional groups have been usefully employed to explain how different organisms facilitate or hinder others in the environment (Woodin 1976), for insight into ecosystem function and resilience (Blackford 1997; Bolam et al. 2002), and for applied purposes such as characterizing responses of communities to fishing impacts (Frid et al. 1999).

Sediment composition is largely controlled by hydrodynamic forces over the substrate. Coarse, sandy substrates with low organic content predominate in high-energy environments, while silty–muddy sediments with higher organic content accumulate in low-energy environments (Snelgrove and Butman 1994). These physical differences have direct consequences for the biological community. Wave-swept, well-flushed areas with large sediment grain sizes are dominated by long-lived suspension feeders, whereas lower-flow areas typically have muddier sediments, have more deposition of organic materials, and are dominated by deposit feeders (**Figure 10.1**; Sanders 1958; Ricciardi and Bourget 1999; Lenihan and Micheli 2001). As a general rule, as grain size becomes finer (the proportion of silt and mud increases), the oxic sediment layer becomes shallower, because finer grains pack together more tightly, leaving less interstitial space for water and air passage. Finer sediments also accumulate in flatter areas with stiller water, further reducing drainage (Nybakken and Bertness 2005). In addition to sediment composition and hydrodynamics, the attributes of soft-sediment habitats are governed by organic inputs and disturbances.

The biota do not just passively respond to these sediment characteristics, however—they actively influence all of these processes by modifying the chemical and physi-

cal environment within the sediments (Barry and Dayton 1991; Snelgrove and Butman 1994). These modifications include organismal effects on hydrodynamics and sediment conditions, such as organic content, topology, grain size, water content, porosity, and chemical composition (e.g., Myers 1977; Bender and Davis 1984; Steward et al. 1996). Thus soft-sediment systems are environments with large roles for ecosystem-engineering species (Woodin 1978; Levinton 1994; see Chapter 3).

Soft-sediment communities depend on the nature, amount, and predictability of organic carbon inputs and their use by benthic organisms. Both allochthonous and in situ carbon are controlled by water column productivity, water depth, water clarity, and transport mechanisms (Barry and Dayton 1991; Dauwe et al. 1998). Allochthonous inputs of carbon are often particularly important, especially in deeper water (Levin et al. 2001). The average depth of the ocean is 3800 m, well below the photic zone, so dependence on allochthonous carbon dominates most soft-sediment habitats. In contrast, the benthos of estuaries are some of the most productive habitats on Earth because they are shallow and have large influxes of nutrients from land to drive high levels of in situ productivity by microphytobenthos and salt marsh angiosperms (Kennedy 1980; see Chapters 11 and 12). Both scenarios highlight the primacy of benthic–pelagic coupling, which links water column processes with the benthos (Dayton and Oliver 1977; Graf 1992).

As with most fields of ecology, the earliest quantitative studies in marine soft sediments were correlative. Researchers correlated community composition with grain size and organic carbon content (Petersen 1918, 1924; Ford 1923; Thorson 1957; Sanders 1958). One of the earliest reviews of soft-sediment habitats focused on larval biology (Thorson 1950). With the explosion of experimental ecol-

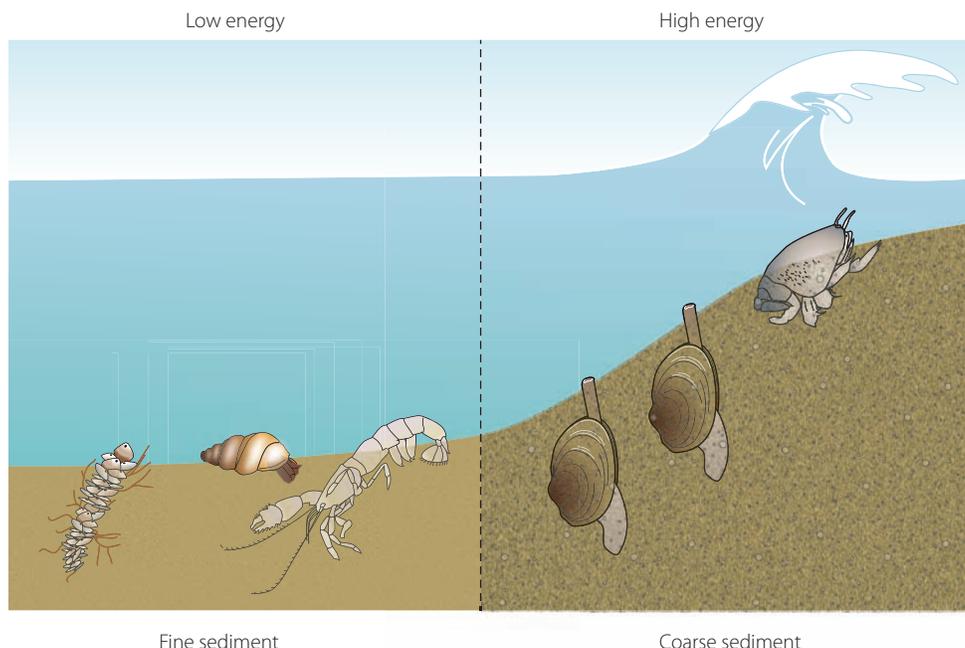


Figure 10.1 Wave-swept, well-flushed areas tend to have large sediment grain sizes and are dominated by long-lived suspension feeders. Low-flow areas typically have muddier sediment, have more deposition of organic matter, and are dominated by deposit feeders.

ogy and technological advances such as scuba gear in the 1960s and 1970s, soft-sediment habitats received increasing attention, especially the processes and mechanisms that shape the communities. Detailed reviews on many specific aspects of soft-sediment communities followed (e.g., Gray 1974; Rhoads 1974; Rhoads et al. 1978; Nowell and Jumars 1984; Reise 1985; Butman 1989; Kneib 1991; Peterson 1991; Hall 1994). Such a large literature has amassed over the last 50 years that it is possible to assess consistent generalities and themes that emerge as mechanistic, process-oriented organizing principles for soft-sediment systems (see Box 10.1). While some are more contentious than others, all are useful at least as an entry point for interesting debates about the structure and dynamics of soft-sediment communities, including why, when, and where exceptions occur.

Many of these organizing principles have helped us to understand how soft-sediment communities are affected by human disturbances and when we can expect this system to be most vulnerable. For example, chemical contamination is associated more with nearshore soft-sediment habitats than with other habitats. This association stems from both the convenience to humans of dumping in nearshore quiescent areas and the fact that soft-sediment areas are typically the outlets for watersheds in which large volumes of anthropogenic pollutants are deposited (Fox et al. 1999; Sanger et al. 1999; Holland et al. 2004). Chemical contamination effects can be persistent due to the bonding of chemicals with charged mud particles and organic content (Bryan and Langston 1992). Meanwhile, human activities, such as bottom-disturbing fishing practices as well as dredging and filling, can create high rates of benthic disturbance over large areas of 100–1000 km² (Friedlander et al. 1999; see Chapter 20). Eutrophication and introduced species are also large, increasing problems in soft-sediment habitats (see pp. 234 and 240).

Although ecologists increasingly define themselves by the processes they address rather than the habitats in which they work, it is still the case that increased understanding of certain processes comes disproportionately from studying certain habitat types. This can be due to historical legacy or because the unique physical and biological aspects of a particular system make it well suited to the study of particular processes. Since Lenihan and Micheli (2001) reviewed marine soft-sediment ecology for *Marine Community Ecology*, our understanding in four areas has increased dramatically. While not exclusive to soft-sediment habitats, these four topics seem distinctive of, more pronounced in, or best studied in soft sediments. In some cases, insights from soft-sediment systems can be compared with findings from other systems to illustrate contrasts in influential ecological processes. There is also overlap among these areas, which collectively build toward a more cohesive understanding of soft-sediment communities. Thus our four focal topics are fundamental areas of research that are continuing to contribute to our understanding of the organizing principles outlined in Box 10.1.

1. Soft-sediment habitats are heavily invaded relative to other marine habitats. There are multiple explanations for this difference, including the high amount of soft-substrate habitat relative to other habitat types, differential inputs of propagules, and the ecological processes characteristic of soft sediments, which may make them less resistant to invasion. That is, the high rates of invasion success in soft-sediment habitats could be determined by factors coincidentally associated with these habitats or by properties of the recipient community itself. We argue for some of both, and we suggest that the preponderance of invasive species may be tied in part to features of the processes that structure soft substrates, such as reduced competition and different effects of predators on diversity.
2. Soft sediments are less structurally complex above ground than other benthic marine habitats and can serve as important controls in studies of habitat complexity and heterogeneity. Since soft sediment is the baseline habitat within which many other structured habitats, such as seagrass beds, mangroves, and bivalve reefs, are embedded, it is an important end of a continuum of many such studies. In other words, to parse the exact influence of a structurally important species, studies often compare biological and physical attributes of areas with the structural species present with those of soft-sediment areas where it is absent.
3. Eutrophication and associated anoxia in soft sediments is a growing issue in estuarine and coastal ecosystems globally. Although low-oxygen events affect all bottom habitats, their effects on soft-sediment habitats are multifaceted because they are not only acute but chronic, and they often have more far-reaching effects due to alterations of sediment biogeochemistry.
4. Microphytobenthos, or benthic microalgae and cyanobacteria, have been recognized as a key component of estuarine ecosystems because of their roles in stabilizing sediments, producing a basal energy source that is readily accessible in estuarine food webs, and processing nutrients.

While these four topics have emerged over the past two decades as separate research themes, they have often overlapped. For instance, invasive species can create habitat complexity, which magnifies their influence on soft-sediment systems. Similarly, microphytobenthos can promote habitat complexity by enhancing the growth of macrophytes. Meanwhile, anoxic events that induce mortality of structure-forming organisms can reduce habitat complexity, but have less of an impact on benthic microalgae. Furthermore, anoxic events not only disturb native communities, but can also facilitate invasions. Although these four topics cannot fully capture the rich contributions that have occurred in soft-sediment ecology over the past two decades, we have focused on them because of their important interactions and collective influence on

our understanding of soft-sediment systems and marine community ecology more generally.

Invasive Species in Soft Sediment

Soft-sediment estuaries and associated marshes are the most invaded marine habitats

Perhaps the best-documented example of the possible extent of invasive species in soft sediments and their effects is San Francisco Bay, where more than 240 non-native species reside and 90–95% of the biomass is exotic in many areas of the bay (Cohen and Carlton 1998; Lee et al. 2003). Compared with open coasts, a much higher number and proportion of exotic species are found in embayments, marshes, and estuaries (e.g., Ruiz et al. 1997, 2000; Reise et al. 2002; Nehring 2002). In Elkhorn Slough, an estuary in California, Wasson and colleagues (2005) documented 526 invertebrate species, of which 443 were natives, 58 exotics, and 25 cryptogens (species whose geographic origin is uncertain). Rocky intertidal habitat immediately outside of the slough on the open coast contained 588 species, of which only 8 were exotic and 13 cryptogenic. The number and proportion of exotics was significantly higher in the estuary (11%) than on the adjacent coast (1%). Furthermore, the exotic species in the estuary (including the mud snail *Batillaria attramentaria*, the orange sponge *Hymeniacion* sp., and the reef-building tubeworm *Ficopomatus enigmaticus*) were not only more diverse, but also more abundant, than on the open coast. Similarly, of the more than 240 non-native species in San Francisco Bay, fewer than 10 are found on the adjacent outer coast (Ruiz et al. 1997).

Perhaps even more puzzling is the observation that species that typically reside on hard substrates on the open coast in their native habitats often remain in embayments and marshes in their introduced range (Griffiths 2000; Robinson et al. 2005; Wasson et al. 2005). For example, the snail *Littorina saxatilis*, which lives almost exclusively on coastal rocky intertidal substrate in northeastern North America and Europe, where it is native, has not left the confines of San Francisco Bay, where it has been established for more than a decade (Cohen and Carlton 1998).

This pattern of more non-native species in bays, marshes, and estuaries may be due in part to a sampling bias. These habitats are located near shore in close proximity to humans, who as a result have examined them more intensely than other marine habitats (e.g., Ruiz et al. 1997, 2000; Cohen and Carlton 1998; Hewitt et al. 1999). In addition, compared with open marine systems, enclosed bays and estuaries have discrete boundaries and a high proportion of benthic, tractable species. However, these two explanations cannot fully explain the stark difference in invasion rates that has been quantified. Three general factors probably contribute to a real pattern of higher numbers of introduced species in soft-sediment habitats. First, bays and estuaries receive vast quantities of exotic propagules from ballast water. In U.S. ports alone, tens of billions of

liters of ballast water from ports of origin around the globe are discharged yearly, and each liter contains up to 10 zooplankton organisms (Verling et al. 2005). Second, bays are retention zones where larvae often are not advected away. Byers and Pringle (2006) showed that the advection typical of open coastlines limits retention, and thus population establishment, and consequently may be largely responsible for the dearth of invasive species in coastal habitats. The correspondence of larval retention and fine sediments is in many ways self-evident, since the processes that reduce resuspension and export of sediment apply to larvae as well. Third, estuarine habitats best match the habitats from which most non-native propagules are exported. Two of the largest vectors for non-native marine species are ballast water and aquaculture, particularly shellfish imports, which most often originate from estuaries and bays (Ruiz et al. 2000). The similarity of source and recipient habitats, especially in the case of intentionally introduced oysters and their associated organisms (Ruesink et al. 2005), results in a high rate of successful establishment.

With all three of these factors, the association of high numbers of invasions with soft sediments is somewhat incidental. That is, the invasions of these areas are occurring not necessarily because they are soft sediments per se, but because they dominate nearshore and inshore environments and are areas where humans are most active and propagules are most easily retained. As a case in point, when humans place hard substrates such as docks and boats inside nearshore soft-sediment embayments, non-indigenous fouling species can be common on those substrates (Stachowicz et al. 2002; Wasson et al. 2005; Tyrell and Byers 2007). However, even though the association between soft-sediment substrates and inoculation pressure of non-native species may be largely incidental, the effects of non-native species are expected to be enhanced in soft sediment because of the high human disturbance associated with soft sediment as well as the properties of the soft-sediment environment itself.

Exotic species may have greater impacts in soft-sediment habitats

Naturally, with more non-native species, soft-sediment areas should experience higher cumulative impact of invasions. But perhaps more importantly, if the impact of non-native species is random with respect to invasion probability, having more non-native species also increases the odds of having some non-natives with a high per capita impact. That is, having more non-natives essentially creates a sampling effect, in which more non-natives simply means that non-natives with greater impacts have a higher probability of being among those established. However, even after standardizing for the number of introduced species, soft sediments may still be expected to experience larger impacts from non-native species for at least three reasons.

First, nearshore soft sediments are often heavily disturbed by anthropogenic activities. Pollutants, eutrophica-

tion, and bottom-water hypoxia, destructive fishing practices, habitat filling, and dredge and fill activities are a few of the many, often severe, abiotic alterations humans have imposed on soft sediments (e.g., Kennish 1992, 2001; Diaz 2001; Valiela et al. 2004; Bertness et al. 2009; Crain et al. 2009). Estimates of global losses of salt marsh to human impacts range from 50% to 80% (Kennish 2001; Lotze et al. 2006; Airoidi and Beck 2007). The novel and sustained environmental changes that anthropogenic disturbances impose may directly eliminate a resident species. Alternatively, the species may be able to persist, albeit in an environment whose parameters are now far removed from those that defined its evolutionary history and to which it was adapted (Byers 2002). This selection regime modification may cause a native species to suddenly find its environment to be just as novel in key ways as it is to a non-native species (Byers 2002). Selection regime modification can therefore reduce a native species' relative performance and eliminate any prior advantage that local adaptation might have given it ("home field advantage"), thereby accentuating the competitive impacts of exotics on natives. Thus disturbances increase invader establishment and impacts not only by creating new microhabitats, introducing propagules, and decreasing populations of native species that can resist invasion, but also by potentially weakening the per capita ability of the native biota to resist invasion. Because nearshore soft sediments are usually heavily altered by humans, they are a prime environment for selection regime modification and thus for large resultant impacts through competition with exotic species (Byers 2000, 2002). To be clear, this influence stems from the high disturbance rate of soft sediment and not from the inherent properties of soft sediment per se.

Second, as discussed on p. 234, a retentive environment has reduced advection that can contribute to increased establishment of non-native species. Such retentive environments are typical of sheltered, protected areas, which are places where sedimentary processes tend to dominate. Thus low advection contributes to the retention of both larvae and suspended (fine) sediments. The retention of more propagules of species, including non-native species, in such embayments probably enhances the population-level competitive effects of the invasive species (Byers and Pringle 2006; Byers 2009b). This notion may initially seem counterintuitive because some types of competition (e.g., competition for space among larger infauna) on a per capita level are generally thought to be lower in soft sediment (Peterson 1977). However, in sheltered, semi-enclosed areas (where soft sediment often predominates), larger-scale processes may enhance population-level competitive effects. Specifically, within embayments, populations tend to be closed, and effects of exotic species on natives may therefore be intensified. Because closed populations have

tight coupling between adults and successive generations, local density-dependent effects of exotic species may result in lower population growth rates for resident native populations. Separation between disparate embayments along coasts helps ensure isolation and provides little chance that a declining native population will receive a rescue effect from an immigration pulse.

Third, invasive ecosystem engineers that create novel structure have a larger scope for exerting system-wide effects in soft-sediment environments. Ecosystem engineers that create, modify, or destroy structure often disproportionately affect the communities they invade (Byers et al. 2006; Hastings et al. 2007). These species alter the entire playing field on which ecological interactions occur by changing habitat structure, refuge availability, and even abiotic processes such as hydrography and sedimentation (Wright and Jones 2006; Crain and Bertness 2006). Invasive ecosystem engineers often introduce aboveground substrates that provide novel habitat, and thus often increase the habitat heterogeneity and species diversity, including that of other non-native species (Heiman et al. 2008; Gribben et al. 2009a). In soft sediment, the physical structure imposed by invasive ecosystem engineers typically contrasts with the low topographic relief and uniform habitat characteristic of the pre-invaded state. Thus their invasion can provide novel habitat that greatly increases variation in habitat complexity and, consequently, the abundance and diversity of epifauna and infauna in the system.

Examples of influential non-native habitat engineers in soft-sediment areas include oysters, the tubeworm *Ficopomatus enigmaticus* (Figure 10.2; Schwindt et al. 2004;



Figure 10.2 *Ficopomatus enigmaticus* reefs in Argentina. *Ficopomatus enigmaticus* is a reef-building serpulid polychaete that has been introduced to many estuaries worldwide, including estuaries of California and coastal lagoons of Argentina. Reefs can grow up to 4 m in diameter and 0.5 m high, altering the bed load sediment transport and water flow, increasing habitat structure, modifying the abundance of species that use it for shelter, and changing distribution patterns of benthic species. (Courtesy of Martin M. Bruschetti and C. Bazterrica.)

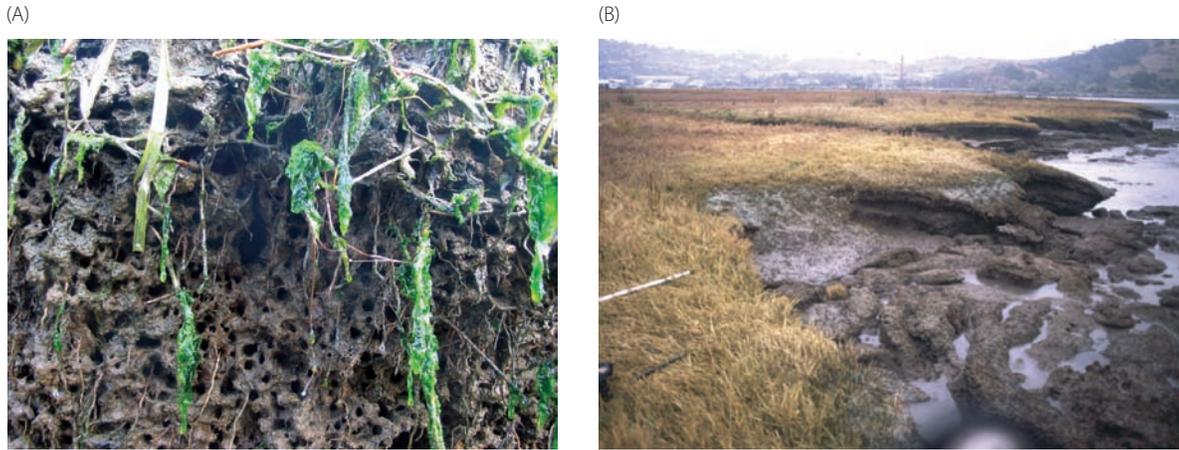


Figure 10.3 The Australasian burrowing isopod *Sphaeroma quoyanum* has been introduced to salt marshes of San Diego and San Francisco Bays in California, and Coos Bay, Oregon. It forms dense, branching burrow networks that cut into the edges of marsh banks, reducing sediment stability and causing erosional loss in excess of 1 m of marsh edge per year, accelerating the conversion of marsh into mudflat. (A) Extensive burrowing by *Sphaeroma quoyanum* in vertical marsh banks, Coos Bay. (B) Such burrowing loosens sediment, undercuts banks, and releases chunks of marsh surface, reducing marsh habitat as it has done here in Corte Madera Marsh, San Francisco Bay. (A courtesy of Tim Davidson; B courtesy of Theresa Talley and Springer.)

Schwindt and Iribarne 2000), the marsh grass *Spartina alterniflora*, the mussel *Musculista senhousia*, the burrowing isopod *Sphaeroma quoyanum* (Figure 10.3; Talley et al. 2001), and the green seaweed *Caulerpa taxifolia* (Figure 10.4; Devillele and Verlaque 1995; York et al. 2006; Wright and Gribben 2008; Byers et al. 2010; Gribben et al. 2009b;



Figure 10.4 The subtropical green alga *Caulerpa taxifolia* in Lake Conjola, New South Wales, Australia. This species is highly effective in converting soft-sediment areas into vegetated habitat. Organisms in invaded estuaries accustomed to soft-sediment environments now find themselves dealing with novel structure, reduced flow, and increased sediment and boundary layer hypoxia. (Courtesy of Paul Gribben.)

McKinnon et al. 2009; Wright et al. 2010). These species engineer habitat in their native ranges as well; however, in a novel soft-sediment environment where their effects on physical structure and habitat arise de novo, or where there are few checks on their abundance and thus on the scale or rate at which habitat is altered, they can strongly affect native biota that do not share a common evolutionary history with them (Crooks 2002; Neira et al. 2005; Gribben et al. 2009b).

Habitat Complexity and Soft-Sediment Communities

Abiotic and biogenic structure in soft sediments

Marine soft sediments historically have provided a pointed counterexample to rocky intertidal habitats because organisms can live in three spatial dimensions (i.e., within the sediment) and are often mobile as larvae and as adults (see Box 10.1, Figure F). Furthermore, while the rocky intertidal zone contains both abiotic (i.e., rock ledges and boulders) and biotic structural features (e.g., algae, mussels, and bryozoans), soft-sediment systems are generally thought of as featureless habitats with little aboveground complexity. In fact, soft-sediment habitats contain microhabitats formed by both abiotic and biotic processes. In high-energy systems dominated by coarser sediments, physical forcing can lead to the formation of sand ripples and waves (Harris and Stokesbury 2010; Harris et al. 2012). While coarser sediment habitats are occupied by polychaetes and other organisms that rework the sediments, physical processes can lead to rapid bed load turnover and sediment transport, thereby dominating microhabitat formation (Harris and Stokesbury 2010; Harris et al. 2012).

Biogenic structures can be formed in high-energy soft-sediment systems, however, such as the bryozoan reefs in areas of high tidal flow and high wave energy off southern New Zealand (Cranfield et al. 2003). When topography-altering species such as these have positive effects on other epifauna by creating refuges, they are often characterized as foundation species (Dayton 1972; Bruno and Bertness 2001). For example, *Corymorpha pendula*, a hy-

drozoan found anchored in coarse sand, provides cover that is positively correlated with the density of shrimp ($r^2 = 0.852$; Auster et al. 1996). Even when these species are more sparsely distributed, their biogenic structure can positively influence biodiversity at multiple spatial scales (Hewitt et al. 2002, 2005). Furthermore, biogenic processes such as these often contribute to, and are facilitated by, abiotic processes, forming important interaction networks with positive feedbacks (Thrush et al. 2008a, 2012).

In lower-energy systems dominated by fine sediments, the creation of habitat structure stems largely from biotic processes that modify sediment dynamics. Many soft-sediment species create structure by modifying the surface topography and stabilizing sediments, including ecosystem engineers that create emergent biogenic microhabitats (e.g., individual ascidians, hydrozoans, and bivalves) and larger habitat patches (e.g., oyster reefs, marshes, and seagrass beds). There are also species that create structure by building tubes and creating burrows (i.e., allogenic engineers) such as polychaetes, fishes, and crustaceans (see Box 10.1, Figure G). Tilefish (*Lopholatilus chamaeleonticeps*) seek refuge by creating conical burrows in clay sediments along the continental shelf, and these burrows are also used by crabs, lobsters, rockfishes, and conger eels (Able et al. 1982; Grimes et al. 1986). In general, several taxa, such as demersal fishes, squids, and crustaceans, seek refuge and forage within the temporary structures that allogenic engineers create (Able et al. 1982; Grimes et al. 1986; Shepard et al. 1987; Auster et al. 1991, 1994, 1995, 1996; Lindholm et al. 2004; Hallenbeck et al. 2012).

While many species stabilize sediments and create habitat, there are also those that rework and displace sediments by creating depressions and burrows. These animals include marine mammals, rays and other fishes, and arthropods such as horseshoe crabs (Figure 10.5). When these animals are actively foraging, they can alter infaunal communities both directly by consuming prey and indirectly by exposing prey to other potential predators (Nakaoka et al. 2002; Lee 2010, 2012). Nakaoka and colleagues (2002) found that epifaunal and infaunal densities were two- to threefold higher in seagrass beds than in the mud pits or trails created by dugongs. In areas heavily disturbed by anthropogenic activities such as fishing, loss of habitat complexity can stem directly from disturbance to the seafloor bottom or indirectly from overharvesting of the engineering species that stabilize sediments, bioengineer emergent structure, or create

burrows and depressions (Auster et al. 1996; Currie and Parry 1996).

Soft sediments as a model for understanding structural complexity effects

Studies of foundation species and ecosystem engineers are helping us to form a new understanding of the structure of soft-sediment communities. Appreciation for facilitation and positive interactions among species is on the rise in general (see Chapter 3; Bruno and Bertness 2001). But particularly in soft sediments, ecosystem engineers and foundation species seem to play a pronounced role. As articulated on p. 235, their effects are enhanced because they occur against a backdrop of very little aboveground habitat and topography. In other habitats with some existing aboveground physical structure, a habitat-forming species is not as novel, and thus would not contribute as much proportionately to habitat heterogeneity. For example, seagrass beds, *Spartina* marsh grasses, and oyster reefs in estuaries of the southeastern United States are the linchpins of large amounts of biodiversity (Wells 1961; Peterson 1979; Bertness and Leonard 1997; Lenihan et al. 2001; Grabowski et al. 2005). They stabilize sediments and create habitat complexity and are thus foundation species in that system (Figure 10.6). Similarly, in tropical soft-sediment areas, corals, mangroves, and seagrasses provide aboveground habitat in an otherwise soft-sediment-dominated area (Figure 10.7). These examples suggest that ecosystem engineers are dominant structuring agents in soft sediments. Furthermore, while other habitats, such as rocky shores and subtidal hard-bottom substrates, can also contain important biogenic structure such as algal, sponge, and coral species, these habitats are different from soft sediments because physical structure and topographic relief already exist even without biological additions and engineering.



Figure 10.5 Pits created by horseshoe crab foraging in Great Bay, New Hampshire. (Courtesy of Jean Lee.)

Figure 10.6 The marsh grass *Spartina alterniflora* and oysters (*Crassostrea virginica*) in Ace Basin, South Carolina. In estuaries of the southeastern United States, these two ecosystem engineers are key facilitators of huge amounts of sediment stability, habitat complexity, and biodiversity. (Courtesy of James Byers.)



Because soft sediments offer little complexity relative to other marine habitats, they can serve as comparative systems for investigating the effects of habitat complexity on species abundances, distributions, and interactions. Moreover, since soft sediment is the baseline habitat within which many other structured habitats are embedded, it is an important end of a continuum of many such studies. Structured habitats in estuaries and shallow embayments, such as seagrass beds and oyster reefs, typically have much higher densities and species diversities than unstructured sediments (Wells 1961; O’Gower and Wacasey 1967; Thayer et al. 1975; Orth 1977; Peterson 1982b, Grabowski et al. 2005; Commito et al. 2008). Thus mud habitats have been used to quantify the degree to which these structured habitats augment invertebrate populations. Furthermore, these comparisons of soft-sediment and structured habitats serve as an important baseline for natural resource agencies and ministries conducting and scaling damage assessments when structured habitats are destroyed and restoration is being considered for mitigation (Peterson and Lipcius 2003; Peterson et al. 2003).

Soft sediments and more complex habitats have been used to examine why the complex habitats have higher infaunal and epifaunal densities and biomass. It has been hypothesized that the increased densities and biomass are due to the emergent structure that these habitats create, which baffles wave energy and traps invertebrate larvae (see Box 10.1, Figure B; Eckman 1983; Summerson and Peterson 1984). An alternative,

not mutually exclusive, hypothesis is that the physical structure provided by emergent and belowground organisms inhibits predators and thus provides refuge to prey and intermediate predator species that would probably be consumed in unvegetated sediments (see Box 10.1, Figure D; Heck and Wetstone 1977; Orth 1977; Peterson 1979; Summerson and Peterson 1984).

More recent work on the effects of habitat complexity on predator–prey interactions and predator behavior has contributed to our understanding of how marine communities are structured. For example, at high predator densities, habitat complexity can reduce intra- and interspecific interference interactions among predators and potentially increase predation rates on prey (Finke and Denno 2002; Grabowski and Powers 2004; Siddon and Witman 2004; Griffen and Byers 2006). Hughes and Grabowski (2006) found that whelks reduced their consumption of mussels, a less preferred prey, when another predator (the stone crab) was present, and that this effect was greater in soft sediments

Figure 10.7 In tropical soft-sediment areas such as Punta Pozuelo, Puerto Rico, pictured here, the roots of mangrove trees provide a unique aboveground hard substrate in an otherwise soft-sediment-dominated area. (Courtesy of Virginia Schutte.)



than on oyster reefs. They hypothesized that the absence of complexity in soft sediments increased interference interactions between whelks and stone crabs, and consequently increased resource partitioning between them.

Complex habitats embedded within soft-sediment areas create a habitat mosaic or landscape. Orrock and colleagues (2013) reviewed the effects of refuge availability in aquatic studies and found that while it increases prey survival, there are often fitness costs, such as reduced growth, when prey are restricted to refuges. In other words, species that seek refuge in structured habitats are probably forgoing foraging opportunities in prey-rich adjacent habitats, especially if food resources are depleted within the refuge. More generally, the spatial configuration of such habitat mosaics, coupled with the size and shape of patches, mediates landscape-level processes that affect animal behavior, connectivity, and metapopulation dynamics. The blue crab (*Callinectes sapidus*), a generalist predator in temperate estuaries, can exert strong top-down pressure on bivalves and other infaunal invertebrate prey (Micheli 1997), but occupies the shelter of seagrass beds during the day and forages in adjacent soft sediments at night (Summerson and Peterson 1984). Thus the proximity of patches of mud to seagrass beds and other structured habitats influences the degree to which blue crabs, and other mobile species that require refuge, exert top-down forcing in soft sediments.

The spatial structure of habitat patches and their associated prey can also influence intraspecific interactions among predators. Interference interactions among blue crabs have been shown to be more intense, and to more negatively affect foraging rates, when prey patches were closer to one another (Clark et al. 1999). The degree of connectivity among prey patches may also influence the access of intermediate predators to prey-rich patches when top predators are prevalent. For instance, Micheli and Peterson (1999) found that intermediate blue crabs predators will forage on intertidal oyster reefs that are connected to salt marshes by seagrass corridors, but not on those surrounded by soft sediment and thus isolated from vegetated habitats. Meanwhile, Grabowski and colleagues (2005) found that juvenile fishes, another important intermediate predator in this system, use oyster reefs on mudflats isolated from vegetated habitats, suggesting that these fishes are more mobile than blue crabs and not as limited spatially. They also found that oyster reefs on mudflats had much higher densities of oysters and other invertebrates, such as non-oyster bivalves, polychaetes, and crustaceans, than did reefs along the marsh edge. These studies collectively suggest that soft-sediment patches are important components of estuarine landscapes that directly or indirectly influence population and community processes such as predation, dispersal, and animal behavior.

Losses of habitat complexity to anthropogenic impacts

Habitat complexity is typically lost when microhabitat features such as worm tubes, burrows, depressions, and

ripples in the sediments and structure created by emergent epifauna are destroyed by human activities. One of the greatest threats to the organisms that live in soft sediments and depend on these microhabitat features is fishing gear that degrades benthic habitat, such as trawls, tongs, clam rakes, and dredges. This gear gouges the bottom and resuspends sediments, affecting bottom-water turbidity; changes surficial sediment processes such as the depth of the redox layer and the oxygenation of sediments; destabilizes the features created by ecosystem engineers, such as burrows, tubes, mats, and depressions on mud bottoms (Auster et al. 1996; Currie and Parry 1996; Watling and Norse 1998), and those created by physical processes, such as sand ripples and waves on coarser sediments (Bridger 1972); and removes or damages emergent epiflora (Peterson et al. 1983; Fonseca et al. 1984; Peterson et al. 1987; Guillen et al. 1994) and epifauna, such as ascidians, hydrozoans, and polychaetes (Van Dolah et al. 1987; Thrush et al. 1995; Auster et al. 1996; Collie et al. 1997, 2000, 2005; Engel and Kvitek 1998; Freese et al. 1999; Kaiser et al. 1999; Smith et al. 2000; Kenchington et al. 2006). Other anthropogenic effects that reduce soft-sediment complexity include terrestrial sediment runoff, dredge and fill activities, and the growing threat of offshore mining (Thrush et al. 2004).

Collectively, these effects result in the degradation and loss of microhabitat structure in a habitat already at the low end of the complexity spectrum. Recovery rates of microhabitat features are thought to be much quicker in coarse-grained than in fine-grained habitats (but see Thrush and Dayton 2010). In coarse sediments, physically generated structures such as sand ripples can re-form rapidly, and these substrates typically experience a much greater frequency of natural disturbance, so their associated species may be better adapted to disturbance (Stokesbury and Harris 2006). Even these habitats, however, can require longer recovery periods for certain taxa, such as larger, slower-growing bivalve species that also provide important secondary substrate for encrusting species. On the other hand, disturbances to muddy habitat are generally much longer lived (Lenihan and Oliver 1995; Dernie et al. 2003), especially when foundation species and ecosystem engineers and their associated structures are destroyed, so that they must recolonize and rebuild (Thrush et al. 1996). Ultimately, the spatial extent and temporal dynamics of disturbances influence species and habitat recovery dynamics in coastal marine ecosystems (Thrush et al. 1996, 2008b). Specifically, as the spatial extent and frequency of disturbance increase and outstrip the ability of these habitats to recover, the result is a highly fragmented landscape with impaired ecosystem functioning, reduced connectivity, and the loss of ecosystem services (Micheli and Peterson 1999; Thrush et al. 2008b, Grabowski et al. 2012; Thrush et al. 2013).

Protection from disturbance is a management option, though one seldom considered for soft-sediment habitats

without vegetated habitat or bivalve reefs. Marine protected areas are typically designed to protect hard-bottomed habitats; however, in some cases, soft sediments are also protected. In such cases, reserves have been found to preserve microhabitat features and resident biota (Auster et al. 1996; Collie et al. 2005). For instance, Auster and colleagues (1996) found fewer biogenic depressions and holothurians in sand–shell habitat outside than inside the Swan Island Conservation Area in the Gulf of Maine after it had been closed to fishing for ten years.

At the other end of the disturbance spectrum are activities that are increasing the amount of soft-sediment habitat. For instance, in the coastal and estuarine zone, dredge and fill activities as well as destructive fishing techniques have severely altered highly productive, structured habitats such as coral reefs, seagrass beds, oyster reefs, salt marshes, and mangroves. Estimates of the amounts of these coastal habitats that have been lost range from 20% to 85% (Lotze et al. 2006; Airoidi and Beck 2007; Wilkinson 2008; Waycott et al. 2009; Beck et al. 2011; Grabowski et al. 2012; zu Ermgassen et al. 2012). Severe habitat degradation often results in the conversion of these highly structured habitats to far less complex soft-sediment habitats, making soft-sediment a rapidly expanding habitat over the past century or two. This conversion to a more homogeneous, less structured landscape probably alters species interaction strengths and trophic transfer rates. For instance, in areas where structured habitats provide critical movement corridors, the loss of these structured habitats probably results in greater fragmentation of prey-rich habitats, so that mobile intermediate predators may no longer be capable of accessing prey-rich patches when their predators are prevalent (Micheli and Peterson 1999). Furthermore, many of these structured habitats provide important ecosystem services, such as supporting biodiversity hot spots, sequestering carbon, removing anthropogenic nitrogen, and providing nursery and foraging habitat for recreationally and commercially important fishes and invertebrates.

Anoxia and Eutrophication in Soft-Sediment Communities

Eutrophication and bottom-water hypoxia

Biological–physical coupling is strong in depositional soft-sediment systems. For instance, estuarine and coastal systems are vulnerable to bottom-water anoxia events when the water column stratifies and biological oxygen demand exceeds available dissolved oxygen levels (Tenore 1972; Officer et al. 1984; Stanley and Nixon 1992; Lenihan and Peterson 1998). Nutrient loading, which is common in coastal estuaries due to terrestrial fertilizer use, discharge of human and animal wastes, loss of riparian buffers and wetlands, and increased atmospheric nitrogen deposition (Paerl 1985; Cooper and Brush 1991; Nixon 1995), has resulted in estuarine eutrophication and intensified

bottom-water hypoxia (Diaz and Rosenberg 1995; Paerl et al. 1998; Lenihan and Peterson 1998; Diaz and Rosenberg 2008). Furthermore, the multiple stressors typically facing urban estuaries, such as increased sediment runoff, overfishing of filter-feeding bivalves, and toxin loading, which reduce populations of the bioturbators that process excess nutrients, exacerbate the frequency and intensity of hypoxic events. Low dissolved oxygen levels in bottom water are now a defining feature of, and major threat to, many estuaries and embayments (Diaz and Rosenberg 2008), and hundreds of estuaries globally now experience occasional to persistent hypoxic events which often lead to mass mortalities (Diaz 2001; Diaz et al. 2010). Given the projection of continued human population growth in coastal regions worldwide, which will probably increase nutrient loading in these ecosystems, coupled with global warming as a consequence of anthropogenic-induced climate change, the frequency, intensity, and spatial extent of bottom-water hypoxic events are all likely to increase.

Although bottom-water hypoxic events certainly affect all bottom habitats, soft-sediment habitats are unique in that these events not only affect epifaunal animals, but also influence sediment biogeochemistry and infaunal organisms (Levin et al. 2009; Middelburg and Levin 2009). Meanwhile, habitats providing vertical relief, such as oyster reefs that extend above the hypoxic zone, are not as vulnerable to the lethal effects of bottom-water hypoxia (Lenihan and Peterson 1998). Reefs can be influenced indirectly during hypoxic events by refugee fish and mobile invertebrates that relocate to and forage in areas with normoxic conditions (Lenihan et al. 2001). Still, normoxic reefs, which are often in shallow water, are affected only indirectly by immigrating “refugee” predators and are not subjected to the mass mortality that is common in deeper soft-sediment environments that experience bottom-water hypoxia.

Nitrogen (N), one of the primary nutrients that mediate bottom-water hypoxia, can be removed from estuaries through biological uptake, denitrification, or permanent burial in sediments (Savage et al. 2004). In temperate estuaries, long-term storage of N within organisms is thought to be relatively low (Boynton et al. 1995; Nixon et al. 1996; Savage and Elmgren 2004), and will probably only decrease in altered food webs with reduced secondary biomass. Denitrification is the bacterial conversion of nitrates (NO_3^-) in estuarine watersheds to gases (N_2 and N_2O) that can enter the atmosphere. Piehler and Smyth (2011) examined denitrification in a range of temperate estuarine intertidal and shallow subtidal habitats and found that denitrification rates were lower in soft sediments than in salt marshes, seagrass beds, and oyster reefs. Seitzinger (1988) estimated that benthic denitrification is responsible for removing 20–50% of total N inputs in estuaries; the percentage varies as a function of water residence time and N loading rate (Nixon et al. 1996). Meanwhile, sediment burial can account for the fate of up

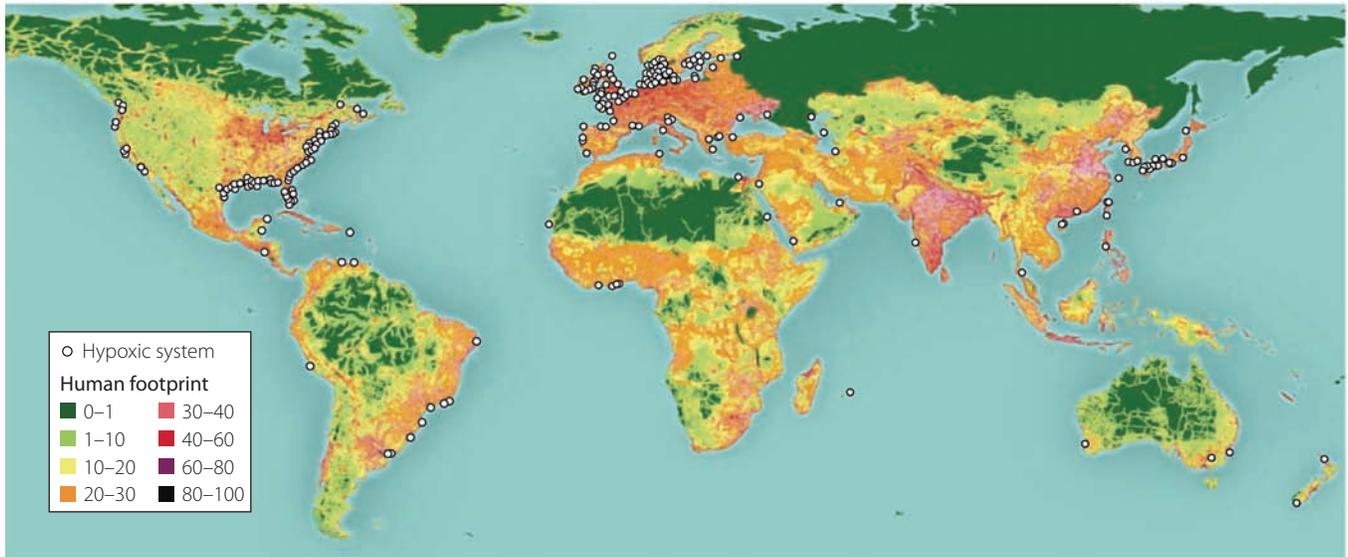


Figure 10.8 Several hundred coastal systems globally have experienced bottom-water hypoxia and associated mass mortalities. In the Northern Hemisphere, the prevalence of hypoxia correlates positively with the human footprint (the normalized human influence is expressed here as a percentage). Meanwhile, hypoxia in the Southern Hemisphere is only beginning to be reported. (From Diaz and Rosenberg 2008.)

to 50–75% of N that enters estuaries, especially in aquatic ecosystems with lower flow and longer residence times, which favor higher deposition of diatoms (Boynton et al. 1995; Holmes et al. 2000; Savage et al. 2004). However, high rates of N burial in the sediment can result in excessive organic matter, increasing microbial productivity in these sediments (Diaz and Rosenberg 2008) and thus potentially fueling bottom-water hypoxia even after the eutrophication “spigot” has been turned off (Conley et al. 2007). Furthermore, as nutrients accumulate in the sediments, the severity, spatial extent, and frequency of hypoxic events continue to increase until microbes begin to generate toxic H_2S (Diaz and Rosenberg 2008). These effects are compounded by the loss of filter-feeding bivalves, which normally reduce eutrophication by enhancing water quality and thus promoting benthic microalgae as well as by increasing denitrification in surrounding sediments (Newell et al. 2002; Piehler and Smyth 2011). Thus their loss reduces the ability of soft-sediment systems to withstand future nutrient loading.

Immediate and longer-term impacts of hypoxic events on community structure and biogeochemistry

Bottom-water hypoxia can dramatically alter resident and transient communities in soft-sediment and other habitats through direct and indirect pathways. In embayments and seas experiencing occasional to periodic hypoxic events, mass mortality events are now common globally (Figure 10.8; Tenore 1972; Seliger et al. 1985; Llanso 1993; Diaz 2001; Diaz and Rosenberg 2008). Even estuaries that experience only periodic hypoxic events have often sustained benthic mass mortality (Diaz 2001). Most of these affected ecosystems appear to be locked in an early successional stage, relying on annual recruitment to continually restart the benthic community after anoxia occurs. A likely consequence of hypoxia is the favoring of “*r*-selected” species

capable of producing high numbers of gametes and larvae to rapidly resettle areas after mass mortality events occur. As the persistence, frequency, and magnitude of hypoxic events increases, recolonization rates for many species significantly decline once source populations can no longer recover from these events.

Furthermore, as an estuary or embayment transitions from normoxic to periodic hypoxic to persistent hypoxic/anoxic conditions, the transfer of energy from the benthos increasingly shifts from supporting mobile predators to supporting microbes (Figure 10.9; Diaz and Rosenberg 2008; Middelburg and Levin 2009). This process seems to be occurring in parts of the Black Sea where bottom-water hypoxia is severe and persistent (Diaz 2001; Diaz and Rosenberg 2008). Since the dominant species that inhabit soft sediments (i.e., polychaetes, crustaceans, echinoderms, and molluscs) include important prey for predators that forage in estuaries, such as fish, birds, and marine mammals, mass mortality of these invertebrates indirectly affects the transfer of energy to higher trophic levels. Thus hypoxic events directly and indirectly affect recreationally and commercially harvested mollusc, crustacean, and fish species common to these systems.

While mass mortality of the benthos is typically the immediate response to bottom-water hypoxia, soft-sediment communities are also vulnerable to longer-term impacts from hypoxia when sediment chemistry is altered. Typically, when bottom-water hypoxia occurs, anaerobic respiration occurs in bacterial communities within the sediment,

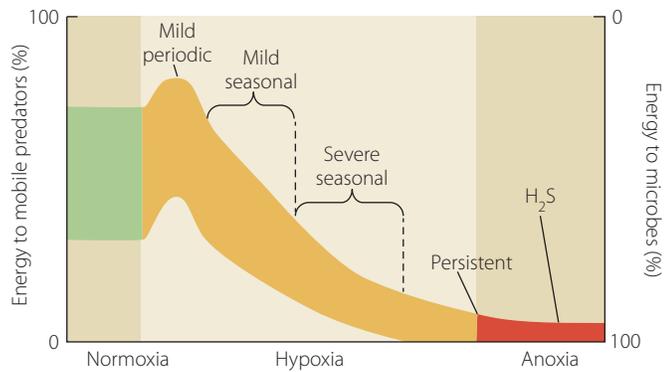


Figure 10.9 Schematic diagram conceptualizing the relationship between the frequency of hypoxia/anoxia and the change in energy flow within ecosystems. Under normoxic conditions (green zone), 25% to 75% of macrobenthic carbon is transferred from the benthos to higher-level predators. Mild hypoxia can increase energy transfer to predators, but this phenomenon is ephemeral if and when it occurs. As hypoxia increases (yellow zone), energy transfer to mobile predators decreases rapidly and is replaced by increased microbial production. Under persistent anoxia (red zone), no benthic energy is transferred to higher trophic levels. Instead, energy transfer occurs solely through microbial pathways, and hydrogen sulfide is produced, which reinforces and accentuates these perturbations to the system. (After Diaz and Rosenberg 2008.)

resulting in the production of hydrogen sulfides by sulfate reduction. Hydrogen sulfides act as respiratory poisons for most infaunal and epifaunal organisms, and accumulation of sulfides in sediments can result in sediment toxicity to resident biota (Wang and Chapman 1999). Sulfide production is common a few millimeters to centimeters beneath the sediment surface during normoxic conditions. Bottom-water hypoxia, however, results in sulfide production at the sediment surface and into the water column once oxygen is depleted (Luther et al. 1991), thereby increasing the toxicity of surficial sediments. Sulfide production has been linked to the mortality of some estuarine bivalve species that would otherwise be capable of surviving several days to a couple of weeks of hypoxic conditions (Theede 1973).

Sulfides exist in two forms in water: hydrogen sulfide (H_2S) and sulfide ion (HS^- ; Wang and Chapman 1999). H_2S has been shown to be more capable than HS^- of diffusing across animal cell membranes, causing toxicity to common estuarine and marine species such as the shrimp *Crangon crangon* (Visman 1996) and the echiuran worm *Urechis caupo* (Julian and Arp 1992). The balance of these two sulfide forms, and hence the toxicity of sulfide, is pH dependent. At a pH of 8.0, approximately 91% of sulfide is in the less toxic form HS^- . At a pH of 6.0, however, approximately 91% of sulfide is in the more toxic form H_2S (Martell 1997). Although these two pH scenarios represent a major regime change, these results suggest that ocean acidification may increase the production of H_2S and consequently the toxicity of future hypoxic events. Organisms that inhabit sedi-

ments that are typically rich in sulfides exhibit some degree of tolerance (Wang and Chapman 1999). Adult bivalves and polychaetes are thought to be among the most sulfide-resistant invertebrates that inhabit estuarine and marine sediments (Theede 1973; Caldwell 1975). However, H_2S production can limit reestablishment in affected soft sediments by groups of benthic organisms such as crustaceans that are less sulfide-resistant. These effects also indirectly influence higher trophic levels that feed on the organisms that are lost from affected sediments in estuaries.

Even if hypoxic events themselves are acute in nature, another potential consequence is that mass mortality events greatly reduce benthic biomass, at least temporarily, and can remove potential competitors that might limit the successful establishment of invasive species (see p. 234, *Invasive Species in Soft Sediment*). This competitive release may explain in part why estuarine and coastal systems affected by high levels of bottom-water hypoxia are also often highly invaded. Thus changes to sediment biogeochemistry and community structure as a consequence of bottom-water hypoxic events can result in impacts that persist long after an actual anoxic event.

The Microphytobenthos

A fourth area in which great research progress has been made over the past two decades is the investigation of the role of the microphytobenthos in soft-sediment communities and ecosystem functioning. The microphytobenthos are the benthic unicellular eukaryotic algae and cyanobacteria that grow in the upper millimeters of intertidal and shallow subtidal coastal and estuarine sediments. These benthic microalgae play important roles as ecosystem modifiers, primary producers, and nutrient processors. For instance, Underwood and Paterson (1993) demonstrated in the Severn estuary in southwestern Britain that microphytobenthos biomass was positively correlated with sediment shear strength and critical shear strength, suggesting that these algal mats play an important role in stabilizing soft sediments.

Although phytoplankton have received far more attention from marine ecologists (see Chapters 15 and 16), the biomass of the microphytobenthos often exceeds that of the phytoplankton in overlying waters (MacIntyre et al. 1996). Furthermore, MacIntyre and colleagues (1996) concluded that benthic microalgae, when resuspended, can increase microalgal biomass in the water column. In general, benthic algae are also thought to play a large role in fueling estuarine food webs because of their high accessibility to consumers such as amphipods, copepods, snails, and annelids. Although salt marsh plant production can be much higher than that of benthic microalgae, very little salt marsh plant material is consumed live (Montague and Wiegert 1990), and much of this production is lost to respiration of the microbial community (Kneib 2003). Currin and colleagues (1995) demonstrated that both detrital *Spartina* and ben-

thic microalgae are important food sources for consumers in marsh systems along the east coast of the United States. Thus, based on their high productivity and accessibility, benthic microalgae are important primary producers that contribute to the trophic dynamics of coastal and estuarine soft-sediment systems (MacIntyre et al. 1996).

Benthic microalgae can also enhance habitat restoration by promoting the recovery of salt marshes. In particular, by fixing N and increasing inorganic N availability, benthic microalgae and associated bacteria probably stimulate salt marsh plant growth (particularly of *Spartina*) and provide food for marsh infauna (Piehler et al. 1998). Piehler and colleagues (1998) also demonstrated that the microphytobenthos may influence the success of salt marsh restoration efforts by providing inorganic N. Collectively, studies over the past two decades have demonstrated that the often overlooked microphytobenthos are an important driver of food web dynamics, sediment stability, and ecosystem functioning. Furthermore, in spite of their tiny stature, the microphytobenthos can indirectly promote greater habitat heterogeneity in coastal estuarine ecosystems.

Benthic microalgae (at least as a functional group) appear to be fairly robust to different types of stressors. For instance, Alsterberg and colleagues (2011) exposed benthic microalgal and heterotrophic (i.e., bacteria and meiofauna) communities to experimental warming and found that these communities remained highly autotrophic even though community respiration and remineralization rates increased because of the high photosynthetic activity of the benthic microalgae. Benthic microalgae also appear to be fairly robust to the joint effects of warming and eutrophication. For instance, Alsterberg and colleagues (2012) demonstrated that even though benthic microalgae responded to both of these stressors, they assimilated nitrogen at rates equal in magnitude to those of nitrogen min-

eralization. Engelsen and colleagues (2010) manipulated bottom-water anoxia in mesocosms with benthic microalgae and demonstrated that anoxia did not substantially affect their biomass, even in the presence of shading by macroalgae and grazing pressure. Piehler and colleagues (2003) examined the effects of diesel fuel on microphytobenthic communities and found effects on primary productivity only at high concentrations analogous to a major spill event, with no long-term effects on benthic microalgal biomass. In general, although it is generally unknown how stressors affect changes in the species composition of the microphytobenthos, these studies suggest that benthic microalgae as a functional group are robust to the range of stressors facing many estuaries globally.

CONCLUSION

Soft sediment covers more than 80% of the ocean bottom, making marine soft sediments one of the most extensive habitats on Earth. We have briefly distilled some major principles that address how these soft-sediment communities are structured (see Box 10.1), and we have discussed four major areas in which studies of soft-sediment systems over the past two decades have furthered our understanding of their population, community, and ecosystem dynamics, including their responses to rising anthropogenic impacts. These four areas—non-native species; contrasts of habitat complexity, including that which arises through ecosystem engineers; anoxia; and the microphytobenthos—are receiving increased attention in soft-sediment communities, and by studying these areas, researchers have contributed to the organizing principles (see Box 10.1) that have emerged from this system. In all four cases, exploration of these factors has led to a more mechanistic understanding of ecological processes (Table 10.1).

Quantifying processes in soft sediments, such as invasion rate, the influence of structure, the effects of hypoxia, and the role of benthic microalgae in modifying ecosystem processes and mediating food web dynamics, can enable contrasts with other marine systems that provide insight into the relative importances of these processes in various environments. One of the most dominant themes to emerge is how strongly physical factors influence the biology of soft-sediment systems. This finding is surely not a conclusion exclusive to soft sediments, nor is it a particularly new theme, but the strong role of physical forcing in spite of (or perhaps because of) the superficial simplicity of the system emphasizes this point most dramatically. A second dominant theme is the importance of foundation species and ecosystem engineering in shaping the habitat and envi-

TABLE 10.1 Emergent principles and refinements in our understanding of soft-sediment processes over the past decade

Invasive species	Invasive species are common in soft sediments because they dominate nearshore habitats where species are commonly introduced. Their impacts are high because of the high disturbance and low advection characteristic of soft-sediment environments.
Habitat complexity	Ecosystem engineers have especially profound effects in soft sediments as habitat providers, sediment stabilizers or destabilizers, and creators of habitat diversity.
Anoxia	Soft sediments are particularly susceptible to anoxia because they occur in anoxia-prone physical environments and are vulnerable to longer-term effects of hypoxia due to its alteration of sediment chemistry.
Microphytobenthos	Benthic microalgae are important and resilient ecosystem modifiers and are also important in estuarine food webs because of their high accessibility to consumers.

ronmental properties that in turn affect community structure and food web dynamics in soft-sediment systems. A third theme focuses on the relative susceptibility and vulnerability of soft-sediment systems to perturbation. In particular, soft-sediment systems face severe impacts from invasions, losses of structure-forming species, eutrophication, and anoxia; however, both high-energy soft-sediment communities and benthic microalgae have emerged as relatively resistant or resilient to some perturbations. Furthermore, because coastal soft-sediment communities have been subjected to high levels of disturbance and are highly tractable, they provide an important system in which to study the effects of multiple stressors on community structure and ecosystem function. Although fewer and fewer ecologists define themselves as soft-sediment ecologists, rich contributions continue to emerge from this system.

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