7.04 Physical Ecosystem Engineers and the Functioning of Estuaries and Coasts

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Abstract

A great diversity of organisms modify the physical structure of estuarine and coastal environments. These physical ecosystem engineers – particularly, dune and marsh plants, mangroves, seagrasses, kelps, reef-forming corals and bivalves, burrowing crustaceans, and infauna – often have substantive functional impacts over large areas and across distinct geographic regions. Here, we use a general framework for physical ecosystem engineering to illustrate how these organisms can exert control on sedimentary processes, coastal protection, and habitat availability to other organisms. We then discuss the management implications of coastal and estuarine engineering, concluding with a brief prospectus on research and management challenges.

7.04.1 Introduction

Estuarine and coastal ecosystems carry out many important functions such as storm protection, erosion and deposition control, habitat creation for species, and biogeochemical processing (Kennedy, 1984; Costanza et al., 1993; Levin et al., 2001; Barbier et al., 2008; 2011; Koch et al., 2009; *see* Chapter **12.06**). These ecosystems are often physically variable, sometimes to the extreme (e.g., exposed to high or low salinity, temperature, oxygen, or moisture), are subject to continuous or periodic external forcing (e.g., tides, storms, and river discharges), and are markedly impacted by human activities, impacts that will continue in the future via human-induced climate change (Officer, 1976; Kennedy, 1984; Perillo, 1995; Hobbie, 2000; Valiela, 2006). Given the highly physical nature of the environment, organisms that affect the physical structure of these ecosystems (i.e., physical ecosystem engineers; Jones et al., 1994, 1997) can often have significant influences on functions and services (e.g., Barbier et al., 2008; 2011; *see* Chapter **12.06**).

A diversity of organisms physically engineer estuarine and coastal ecosystems, affecting benthic and pelagic (aquatic), nearshore (terrestrial), and interface (intertidal) environments composed of sediments, soils, and rock (**Table 1**). They

Table 1 Diversity of physical ecosystem engineering mechanisms relevant to (a) coastal protection, erosion, and sedimentation and (b) habitat creation to other organisms

(a) Storm attenuation, erosion, and deposition processes

Structural change	*Abiotic change*	*Engineering organisms*
Production of emergent, sessile structures occurring in isolation in the benthic environment.	Local water flow disruption and formation of erosion features (scour pits) around structures.	Macrophytes, tube-building polychaetes, bivalves.
Production of emergent, sessile structures that are massive *per se* or form large aggregations in the benthic environment.	Large-scale water and wind flow disruption and/or attenuation with concomitant, local increases in sedimentation; altered intensity and distribution of erosional and depositional processes at the landscape level, with concomitant alteration of whole-system sediment budgets.	Macrophytes (dune grass, cordgrass, seagrass, and mangroves), algae, reef-forming organisms (oysters, mussels, corals, and polychaetes), other sessile epibenthos.
Extensive creation and maintenance of emergent physical structure proximate to coasts (etiher autogenic or allogenic).	Attenuation of storm surge and wind impacts, decreased shoreline erosion, and protection of inland ecosystems.	Dune-accreting and dune-fixing grasses, mangroves, coral reefs, salt marsh plants, seagrasses.
Creation of more or less persistent basally depressed roughness elements (burrows, pits, depressions) via sediment excavation.	The hydrodynamically quiescent environment of burrows, pits, and depressions favors particle deposition enhancing spatially averaged sedimentation.	Burrowing benthos (crabs, shrimp, polychaetes, and echiurans), epibenthic deposit feeders (crabs and holoturians), epibenthic predators that consume infaunal prey (crabs, and fish).
High proportion of three-dimensional empty space within intertidal sediments due to the presence of macrofaunal burrows.	Increased erosion due to increased area exposed to water flow; in the case of steep intertidal areas, increased probability for gravitational slope failure and cliff collapse.	Crabs, isopods, shrimp, and other intertidal burrowers.
Sediment mixing, breakdown of sediment aggregates, and creation of more or less ephemeral galleries via deposit feeding and organismal movement into sediments.	Decreased sediment aggregation, stability and shear strength, increased sediment erodibility.	Polychaetes, bivalves, gastropods.
Creation of water fluxes from the water column to anoxic sediments and vice versa via active burrow irrigation.	Increased sediment transport via particle ejection and resuspension.	Thallassinidean shrimp, polychaetes, echiurans.
Production of particle aggregates (such as feces and pseudofeces) that differ in size and density from baseline sediments.	Changes in sediment shear strength and overall erodibility (either increased or decreased).	Polychaetes, bivalves, gastropods.
Binding of sediment particles via mucous secretions.	Increased sediment shear strength and overall resistance to erosion.	Polychaetes, amphipods, diatoms.
Subsurface production of persistent materials (macrophyte roots, shells, and tubes) and their accumulation in the sediment matrix.	Progressive compression of sediments resulting in increasing aggregation, hardness, shear strength, and overall resistance to erosion; in some cases (e.g., root growth and accumulation of senesced roots in salt marsh sediments) compression contributes to surface accretion and decreased flooding depths.	Dune plants, marsh plants, seagrass, bivalves, tube-building polychaetes.
Creation of holes in rock, shell, or coral via boring	Increased potential for rock, shell, or coral fragmentation, release of sediment particles.	Bivalves, anemones, sipunculids.

(*Continued*)

Table 1 (*Continued*)

(b) Habitat creation to other organisms

Structural change	*Abiotic change*[a]	*Biotic change*	*Engineering organisms*
Production of emergent, sessile structures that are massive *per se* or form large aggregations in the benthic environment.	Increased three-dimensional complexity of the bottom, increased availability of interstices with limited predator access and exposure to environmental extremes (currents, temperature), increased zonation.	Increased abundance of interstitial and refugee species; creation of critical habitat for the recruitment and juvenile survival for many species that use other habitats when adults (i.e., nursery role).	Macrophytes (dune grass, cordgrass, seagrass, and mangroves), algae, reef-forming organisms (oysters, mussels, corals, and polychaetes), and other sessile epibenthos (e.g., cirripedians).
Autogenic creation of epibenthic surfaces.	Increased abundance and diversity of colonizable surface, increased zonation.	Availability of habitat for epibionts.	Macrophytes (dune grass, cordgrass, seagrass, and mangroves), algae (e.g., kelps), corals, bivalves, tube-building polychaetes, other sessile epibenthos, some mobile epibenthos (gastropods and crabs).
Epibenthic accumulation of hard structures with cavities.	Availability of cavities with limited predator access and ameliorated exposure to environmental extremes (currents, temperature).	Increased abundance of refugee species. Major population constraint for certain species (e.g., hermit crabs).	Gastropods, bivalves, tube-building polychaetes.
Creation of more or less persistent basally depressed bottom roughness elements (burrows, pits, and depressions) via sediment excavation or rock boring.	Increased three-dimensional basal complexity, increased availability of cavities with limited predator access, and decreased exposure to environmental extremes (currents, temperature, dessication).	Increased abundance of refugee species (including burrow comensals).	Burrowing benthos (crabs, shrimp, polychaetes, and echiurans), rock-boring organisms (bivalves, anemones, and sipunculids), epibenthic deposit feeders (crabs and holoturians), epibenthic predators that consume infaunal prey (crabs and fishes).
Subsurface production of persistent materials (macrophyte roots, shells, and tubes) and its accumulation in the sediment matrix.	Progressive compression of sediments resulting in increasing aggregation and hardness.	Decreased density of large burrowers when structures occupy a high proportion of the sediment volume; decreased epibenhic predation on infauna.	Marsh plants, seagrass, bivalves, tube-building polychaetes.
Sediment mixing, breakdown of sediment aggregates, and creation of more or less ephemeral galleries via deposit feeding and organismal movement into sediments.	Decreased sediment aggregation, stability and shear strength, increased sediment transport an resuspension.	Decreased abundance of filter feeders, sessile epifauna and little-mobile, surface dwelling infauna.	Polychaetes, bivalves, gastropods.
Release of feces and pseudofeces in the benthic environment by aggregations of suspension feeders.	Increased inputs of particulate organic matter from the water column to the benthic environment.	Increased food supply to deposit-feeders. In rocky bottoms, this contributes to sediment accumulation and habitat creation for infaunal organisms.	Bivalves, corals.
Binding of sediment particles via mucous secretions.	Increased sediment stability and shear strength, decreased sediment transport and resuspension.	Increased abundance of filter feeders, sessile epifauna, and relatively immobile surface-dwelling infauna.	Polychaetes, amphipods, diatoms.

[a] These biotic effects will occur only if the regional species pool contains species that are sensitive to the abiotic change.
The list is illustrative, not exhaustive.

encompass all kinds of life forms (from microbes to plants to animals, including humans), physically modify environments in a variety of ways (e.g., burrowing, reef building, sediment binding, and rock boring), and have impacts on other species, ecological processes, and overall ecosystem functioning that range from the trivial to the substantial.

In this chapter, we focus on the impacts of physical ecosystem engineers on three key functional attributes of estuaries and coasts – sedimentary processes (erosion/sedimentation), coastal protection, and the creation and modification of habitat for other organisms. We first briefly present a general framework for physical ecosystem engineering, using it to illustrate how organisms can exert control on these three functional attributes. We also use the framework to organize a more detailed examination of these influences by major groups of estuarine and coastal physical ecosystem engineers – dune plants, marsh plants, mangroves, seagrasses, kelps and other macroalgae, reef-forming corals and bivalves, and burrowing crustaceans and infauna. We then briefly examine how human activities have and will likely continue to affect estuarine and coastal ecosystem engineering species, and then explore the management implications. To do this, we apply the framework to human physical engineering of estuaries and coasts, asking: (1) How do human engineering influences compare to those of Nature's engineers; (2) How can lessons from Nature's engineers be used to improve human environmental engineering of these ecosystems where required; (3) How can animal and plant engineering be used to enhance ecologically based management of estuaries and coastal zones. We conclude with a brief prospectus on research and management challenges that emerge from the juxtaposition of the framework, the more detailed examination of the major groups of estuarine and coastal physical ecosystem engineers, and the analysis of their management.

7.04.2 Making Sense of the Diversity: A Framework for Physical Ecosystem Engineering of Estuaries and Coasts

7.04.2.1 Framework

Seagrass meadows trap sediments. Coral reefs attenuate wave action and increase the three-dimensional structure of the seafloor. *Thallassinidean* shrimp alter sediment topography and increase solute exchange via burrow digging and irrigation. Seagrasses, reef-forming corals, and thalassinidean shrimp – together with a myriad of other organisms – share the common characteristic of changing physical structure within the environment. These structural changes influence abiotic conditions that can feed back to the original ecosystem engineer and other organisms (**Figure 1**). Such organisms are known as physical ecosystem engineers (i.e., organisms that directly or indirectly modulate the availability of resources (other than themselves) to other organisms by causing physical state changes in biotic or abiotic materials; *sensu* Jones et al., 1994, 1997).

The concept of physical ecosystem engineering addresses the combined influence of two coupled interactions – process and consequence (**Figure 1**; for definitions and detailed explanation, see Jones and Gutiérrez, 2007). 'Process' considers how organisms change the abiotic environment and encompasses any physical influence of organisms on the abiotic environment via structural change, irrespective of whether or not the abiotic changes have any biotic effects (Jones and Gutiérrez, 2007; Gutiérrez and Jones, 2008). Engineers can cause structural change by their own physical structures (autogenic engineering) and/or by altering the physical structure of living and nonliving materials (allogenic engineering; Jones et al., 1994, 1997). Structural change will lead to abiotic change because structures interact with kinetic energy and materials within the abiotic milieu (see **Table 1** for examples). The above can be used to distinguish physical ecosystem engineering from purely abiotic forces causing structural change, and abiotic changes caused by the universal processes of organismal uptake and release of materials and energy.

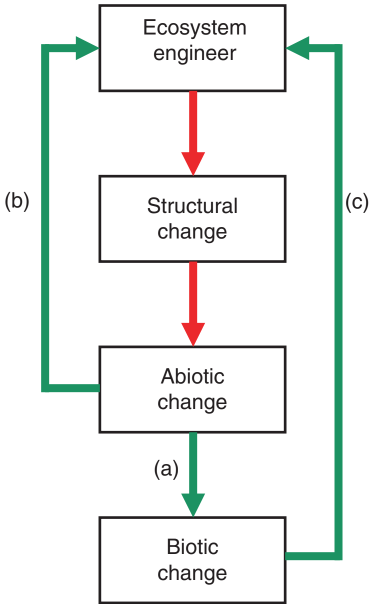

Figure 1 Pathways of ecosystem engineering process (red arrows) and biotic consequence (green arrows). Biotic consequences comprise effects of abiotic change on other organisms (a), and feedback effects to the engineer mediated either by the abiotic change (b) or by its biotic impact on other species (c).

The term 'consequence' addresses the biotic effects of the engineering process on organisms – other species and the engineer itself. This is a function of the degree of abiotic change caused by the engineering process and the degree of abiotic limitation, constraint, or enablement experienced by associated species, including the engineer. The combination of process and consequence thereby distinguishes the engineering effects from other influences of the engineer (e.g., resource uptake that occurs between predators, competitors, or facilitators), although these may well affect the engineer and its engineering activities. Biotic influences of engineers can encompass organisms, populations, communities, ecosystems, and landscapes, and can be integrated by thinking of physical ecosystem engineering as the creation, modification, and maintenance of habitats (see **Table 1**(**b**) for examples).

Consideration of physical ecosystem engineering as a process and a consequence reveals four general components (engineer, structure, abiotic, and biotic) linked by three cause/effect relationships (**Figure 1**; Jones et al., 2010):

1. engineer causes structural change;
2. structural change causes abiotic change; and
3. abiotic change causes biotic change.

The first two relationships are processes, while the third is a consequence.

7.04.2.2 Framework Application

7.04.2.2.1 Engineer causes structural change

Macroalgae, grasses, epibenthic bivalves, tube-building polychaetes, reef-forming corals, and mobile invertebrates that create habitat are all autogenic engineers. Allogenic engineers include a diversity of organisms whose activities change bottom sediment structure (e.g., burrowing invertebrates, bioturbators, epibenthic and demersal predators that excavate infaunal prey, macrophytes that create pores in sediments via root growth, and diatoms that bind sediments via mucous secretions), physically alter rock structure (e.g., borers) and biotic structures (e.g., grazers, coral borers, and wood borers), and alter sediment suspension in the water column (e.g., filter feeders that change the structure of a water/sediment column). The degree of structural change caused will be a function of their *per capita* engineering activity and density (Jones et al., 1994), although not necessarily the simple product of both (e.g., engineering may be size or stage dependent; cooperation or interference among engineers may also occur; Jones et al., 2010).

Engineered structures are diverse in size (ranging from small invertebrate fecal pellets to coral reef lagoons to kilometers of dune hills tens of meters high) and composition (calcium carbonate, sediment, mucus, detritus, sand, etc.) with diverse physical properties directly relevant to abiotic change (see Section 7.04.2.2.2). Like all physical structures, engineered structures deteriorate and disappear unless maintained. Their persistence – and hence persistence of their abiotic effects – is a function of the intrinsic durability of the structural materials and the intensity of structurally destructive forces (Jones et al., 1997) and ranges from the ephemeral (e.g., sand pellets made by fiddler crabs during burrow maintenance that are completely destroyed by each tide; Botto and Iribarne, 2000) to the highly persistent (e.g., 1000- to 4000-year-old bivalve shells affecting current bottom structure; Gutiérrez and Iribarne, 1999).

7.04.2.2.2 Structural change causes abiotic change

Although many abiotic variables may be simultaneously changed by engineering, they can be constrained by focusing on a particular abiotic process or biotic consequence of interest. Thus, erosion, sedimentation, and coastal protection invoke erosion or accretion rates, sediment transport rates, changes in seabed elevation, shoreline displacement, damage to terrestrial coastal areas, and the like. Abiotic variables relevant to habitat creation and modification for other organisms are, of course, more diverse and include not only changes in accretion/erosion, but also changes in light availability, temperature, moisture, oxygen availability, water flow exposure, attachment substrates, enemy- or stress-free space, etc. Such complexity may require recourse to a structural proxy in order to predict, for example, community changes (e.g., descriptors of surface roughness as a predictor of fish diversity in coral reefs; McCormick, 1994). However, the diversity of relevant abiotic variables can be somewhat constrained if we focus on habitat creation and modification for a specific organism or group of organisms. For example, the establishment of submersed aquatic vegetation (SAV) depends on light availability, sediment grain size and organic matter content, sulfide concentrations, and the physical impact of waves and currents (Koch, 2001). Engineering impacts on SAV establishment can, in principle, be predicted by considering the magnitude and direction of engineering impact on any or all of these abiotic variables.

Abiotic change can be construed as a structure *per se* (e.g., creation of living space for epibionts by mussel shells). Commonly, however, it is the result of work done on kinetic energy by structure (e.g., water flow attenuation by seagrass canopies), or vice versa (e.g., erosion of bioturbated sediments), often accompanied by changes in the distribution of material fluids and solids (e.g., sedimentation and seabed topography), but not necessarily so (e.g., heat dissipation by an engineered structure, such as the modulation of radiative heat transfer to sediments by marsh plant canopies; Bortolus et al., 2002). The kinetic energy underlying changes in material distribution in estuaries and coasts will usually be water movement and wind (as in the case of coastal dune ecosystems) and the relevant materials will often be sedimentary, although other materials, including those engineered by humans (e.g., rock, concrete, wood, and metals), can be relevant to coastal protection. Materials relevant to habitat creation and modification, including the habitat for the engineer, are more diverse, comprising consumable energy and materials (e.g., carbon, nutrients, and water), nonconsumable resources (e.g., living space and enemy-free space), constraining or enabling abiotic factors (e.g., sediment grain size, salinity, and oxygen), and abiotic cues used by organisms (e.g., waterborne chemicals). Heat and radiant energy also interact with engineered structure causing abiotic change relevant to the process of habitat creation and amelioration to other organisms (e.g., changes in temperature or light incidence).

The physical properties of engineered structures are central to understanding abiotic change (Jones et al., 2010). Flow attenuation by aquatic macrophytes increases with shoot stiffness (Bouma et al., 2005); particle trapping by burrows varies with burrow entrance shape (Botto and Iribarne, 2000); enemy-free space for coral reef fish varies with reef architecture (Beukers and Jones, 1998); and so forth. Nevertheless, the overall abiotic impact of an engineered structure will also depend on the baseline abiotic state (i.e., not engineered). For example, although seagrass beds attenuate flows and enhance sedimentation under moderate flow regimes, they do not do so under wave-exposed, extreme flow conditions (Fonseca and Bell, 1998; Koch and Gust, 1999). Similarly, although mussels have little influence on the availability of hard substrates on rocky shores, they have a very large effect in soft-sediment systems (Gutiérrez et al., 2003). In general then, the impact of engineered structure on abiotic variables will also depend on the presence of other, nonengineered structures with similar, relevant physical properties (e.g., rock and mussel shells as noted above or suspended sediments vs. plankton and light penetration into the water column). Structural effects on physical transport of materials (e.g., sediments, consumable abiotic resources, chemical cues, and abiotic materials affecting conditions such as pH, oxygen, or salinity) will also depend on the physical properties of the materials and the strength of physical forces capable of transporting them (e.g., erosion resistance via macrophyte root binding in fine sands vs. cohesive muds or flow attenuation by seagrasses in moderate vs. extreme flows, as noted above). When abiotic effects arise from the interaction of structure with kinetic energy other than energized fluids (e.g., heat and light), the overall impact of structure will likewise depend on the baseline energy levels (e.g., impact of burrows on heat transfer to sediments in warm vs. cool waters or diurnal sediment shading by mangroves).

7.04.2.2.3 Abiotic change causes biotic change

The direction and magnitude of biotic change can be predicted by combining the difference between engineered and unmodified abiotic states with an underlying abiotic dose/biotic response relationship that describes the degree to which species are limited, constrained, or otherwise influenced by abiotic variables across a range of values (Jones et al., 2010). Such relationships can be applied to the engineer as well as other species. For example, light availability affects the establishment of SAV (Koch, 2001), whereas filter feeding by zebra mussels decreases water turbidity enhancing light availability; hence, SAV establishment might be expected to increase due to zebra mussel impacts on light availability (e.g., Strayer et al., 1999). Similarly, tube-building polychaetes generally require stable sediments for establishment, whereas bioturbators generally destabilize sediments. Consequently, tube-building polychaetes should find it more difficult to establish when bioturbators are abundant (Brenchley, 1981).

Engineering can also affect the engineer, as a consequence of the abiotic and/or biotic changes they cause (**Figure 1**). For example, mussel recruitment depends on the availability of hard substrate. Initial establishment of mussels in areas dominated by soft substrates increases the availability of hard substrate (i.e., abiotic change) with a positive feedback effect on subsequent mussel recruitment (Bayne, 1964). Mussel shells, however, often serve as a substrate for epibionts (e.g., barnacles, tubeworms, sponges, hydrozoans, and algae). Epibiont establishment on mussel shells (i.e., biotic change due to mussel engineering) can also have feedback effects on the mussels, such as a decrease in predation risk (Laudien and Wahl, 1999), or an increase in the probability of mussel dislodgement by waves and currents (Witman and Suchanek, 1984).

7.04.3 Major Ecosystem Engineers: Exemplification of the Framework

A few groups of organisms are known to have a major influence on erosion, sedimentation, coastal protection, and habitat creation via physical ecosystem engineering. They are reviewed here in some detail, organized around, and illustrating the general framework.

7.04.3.1 Dune Plants

Dune plants are common but traditionally understudied coastal ecosystem engineers that have the capacity to dramatically modify their physical environment. By capturing blowing sand, dune plants stabilize and shape what otherwise would be a highly unstable, shifting sand environment. Some dune plants can create foredunes, large ridges of sand parallel to the shoreline; in some cases, they can be tens of meters tall. These plant-produced physical barriers of sand, held in place by vegetation, have the potential to mitigate large storms and tsunamis and have important ecological and economic consequences for coastal dune communities worldwide.

How do dune plants accrete and stabilize sand and thus influence the geomorphology of dunes? Plants cause the deposition of sand via two simple mechanisms. As sand is blown by wind across the dune landscape, it either drops to the surface when (1) wind energy is dissipated by a boundary layer formed around the vegetation and/or (2) sand actually hits the surface of the plants (Pethick, 1984). The effect of vegetation on the reduction of wind speed and sand deposition can be very large (e.g., Olson, 1958a; Lancaster and Baas, 1998; Kuriyama et al., 2005). For example, Olson (1958a) found a 30-fold decrease in sand transport over vegetated compared to unvegetated foredunes. How does this decrease in sand transport result in the formation of foredunes? Pethick (1984) described a process that begins with the nucleation of sand around plant seedlings or fragments of rhizomes (**Figure 2**(**a**)). As the plants grow in stature, more sand is deposited in these embryo dunes, which stimulates further plant growth and sand deposition, creating a positive feedback between plant spread and sand deposition (**Figure 2**(**b**); see Maun (2004) for a review). If a plant cannot maintain an emergent structure either due to lack of growth and/or due to too much sand deposition, these sand mounds will eventually either stop growing or even erode. Over time, given net positive growth of these small dunes, they will eventually coalesce and form foredune ridges typically 5–20 m in height (**Figure 2**(**c**)). Similar processes of embryo dune formation can be initiated by the accumulation of seagrass wrack on sandy beaches (Hemminga and Nieuwenhuize, 1990; see Section 7.04.3.4).

A number of interrelated factors can influence foredune shape, which include dune plant species morphology and density, sand supply, and wind speed (Hesp, 1989). For example, studies of dune plant morphology show that tall, dense canopies such as those found with beach grasses (e.g., *Ammophila*, *Elymus*, and *Uniola*), shrubs (e.g., *Myrica* and *Prunus*), and trees (e.g., *Salix* and *Populus*) all rapidly attenuate wind energy and thus increase the amount of sand trapped around the base of the vegetation (e.g., Cowles, 1899; Olson, 1958b; Buckley, 1987; Hesp, 1989). Shorter, more compact plant morphologies such as those found in mounded or creeping species (e.g., *Cakile*, *Ambrosia*, and *Lupinus*) allow more wind to flow over their surface, causing lower sand deposition. Experimental and modeling studies show that if plant species identity is held constant but plant density or height is increased, sand deposition and dune height consistently increase (e.g., Buckley, 1987; Hesp, 1989; van Dijk et al., 1999; Kuriyama et al., 2005). These studies also show that the threshold for significant sand accretion is low; Kuriyama et al. (2005) found that cover as low as 28% can reduce sand transport by 95%.

Despite the role of vegetation, sand supply is a critical mitigating factor of foredune morphology. In a simple conceptual model, Psuty (1986) proposed that positive sand deposition from the ocean onto the beach produces shorter and wider foredunes compared with little, no or negative sand

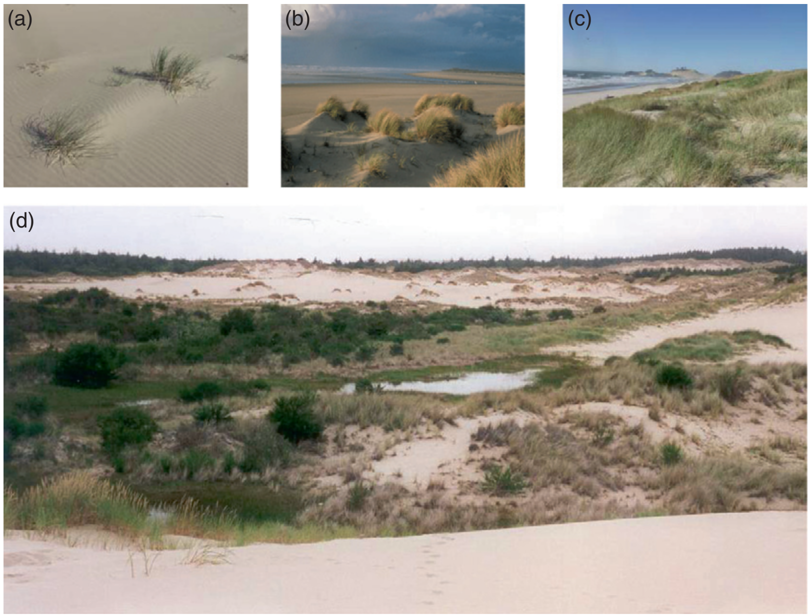

Figure 2 Stages of foredune development including (a) an embryo dune, (b) dune hummocks, (c) mature foredune, and (d) dune slack behind mature foredune. Photo credits: Sally Hacker.

deposition, which produces taller and narrower foredunes. Recently, Hacker et al. (in press) found that sand supply is a critical mediating factor in the engineering effects of invasive dune grass species on the Oregon Coast, USA. Although two invasive congeners (*Ammophila arenaria* and *A. breviligulata*) have similar morphology, their sand-accreting capacities differ significantly depending on the oceanic delivery of sand, a highly variable factor along the coast. Thus, it is clear that the sand budget of beaches strongly interacts with plant structure to shape dune geomorphology (Miyanishi and Johnson, 2007).

The effect of dune plants on foredune development has important implications for coastal protection. Foredunes serve to attenuate large waves produced by storms or tsunamis (e.g., Leatherman, 1979), and thus their economic value to human populations is potentially quite large (Barbier et al., 2008; 2011; *see* Chapter **12.06**). Studies predicting the coastal protection services of foredunes are increasing (e.g., Ruggiero et al., 2001; Stockdon et al., 2007) but there is far less known about how dune plants (particularly at the species level) influence foredune height and ultimately coastal protection (but see Barbier et al., 2008; Hacker et al., in press). This information will be important as coastal dunes are increasingly impacted by human development, and as climate change causes sea-level rise and heightened storm intensity (Ruggiero et al. 2010). It is under these conditions that dune plants as ecosystem engineers have great potential to provide critical ecosystem services at large spatial scales.

Not surprisingly, the formation of foredunes by dune plants can have strong local and landscape-level consequences for dune communities. Although dune plants can themselves have both positive and negative interactions with other plant species (Martínez and García-Franco (2004), for review) and animals (Baeyens and Martínez (2004), for review), it is through the sand accretion by these ecosystem engineers, and their subsequent dune stabilization, that the greatest overall effect on dune community structure occurs. In the simplest terms, the physical structures of foredunes act as barriers to waves, winds, and blowing sand to the backdune, thus creating a physical template for plant zonation that includes a landward decrease in disturbance and stress (Doing (1985), for review). Depending on the height and width of the foredune, this reduction in disturbance can be considerable, allowing less physiologically tolerant species to inhabit the backdune where sand burial, salt spray, and wind shear are lower, but nutrient and water availability is higher (e.g., Maun and Perumal, 1999; Wilson and Sykes, 1999; Lortie and Cushman, 2007). Experimental work on dune zonation, although limited, suggests that sand burial may be a critical factor controlling plant diversity and zonation (Maun and Perumal, 1999; Wilson and Sykes, 1999; Franks and Peterson, 2003).

At a landscape scale, foredunes can facilitate the formation of large dune slacks or deflation plain communities that start at the leeward base of the dune and extend landward (**Figure 2**(**d**)). Here, sand deposition is so minimal due to the effects of the foredune that the water table is shallow and often exposed, creating extensive wetlands that harbor a high diversity of plants and animals (Grootjans et al., 2004). Depending on the water depth and source, dune slack communities can be highly heterogeneous, consisting of ponds, marshes, swamps, and/or wet forests. As dune slacks undergo succession, they become terrestrialized as vegetation dominates and soil formation proceeds rapidly. In addition, many species living in dune slacks are flood and/or drought tolerant due to seasonal, yearly, or decadal fluctuations in hydrology.

The landscape-level change that dune plants can create is exemplified by the introduction of two nonnative grasses (*A. arenaria* and *A. breviligulata*) to the dunes on the west coast of North America at the turn of the century (Wiedemann and Pickart, 2004; Hacker et al., in press). Widely planted to stabilize a highly dynamic, shifting sand environment, *Ammophila* has created foredunes 5–15 m in height across roughly 45% of the coast. Large, highly vegetated deflation plain communities, sometimes kilometers wide, continue to reduce sand movement and vegetate large areas of the dune ecosystem. Although overall species diversity may have increased due to the invasion of this ecosystem engineer, there are a number of federally listed endangered species adversely affected by *Ammophila* and small-scale restoration efforts are underway.

7.04.3.2 Tidal Marsh Plants

Mid-elevation coastal zones around the world are dominated by vascular plants that have specific adaptations for dealing with high salinity and tidally driven cycles of inundation. Mangroves dominate this zone in the tropics (see Section 7.04.3.3), but herbaceous plants form extensive salt marshes in temperate regions (**Figure 3**). These salt marshes regulate the flow of energy and material between land and sea (Adam, 1993). Many important ecosystem services stem from this regulation, prompting increasing efforts to conserve and restore functioning salt marshes (Bromberg-Gedan et al., 2009). These efforts are complicated by the fact that the ecosystem services provided by salt marshes emerge from a diversity of interacting mechanisms that operate over varying spatial and temporal scales (Koch et al., 2009; *see* Chapter **12.06**). The ecosystem engineering framework provides a useful way of organizing this complexity.

How do tidal marsh plants affect sedimentary processes? The drag created as water moves through the dense plant canopies reduces flow velocity and wave energy, which, in turn, increases sediment deposition and reduces erosion (Leonard and Luther, 1995; Nepf et al., 1997; Christiansen et al., 2000). Plant roots also potentially contribute to this process by binding sediment (**Figure 3**; Coops et al., 1996). However, there is evidence that this effect is mostly an indirect consequence of the deposition of fine, cohesive sediments rather than a direct consequence of root binding (Faegin et al., 2009). At local scales, the strength of this engineering effect increases with the density of the vegetation within the water column (Shi and Hughes, 2002; Leonard and Croft, 2006). Consequently, marsh species that differ in plant architecture and growth form vary in the manner and degree to which they alter the hydrologic environment (Leonard and Luther, 1995; Neumeier and Amos, 2006). Species also differ in the biomechanics of how their parts interact with water; species with stiff stems can reduce wave energy up to 3 times more than species with flexible stems (Bouma et al., 2005).

Figure 3 Hybrid *Spartina* (*S. alterniflora* × *S. foliosa*) invading San Francisco Bay, CA. The immense above- and belowground *Spartina* biomass drives a number of physical changes that convert open tide flat into dense salt marsh. In this case, growth of the *Spartina* root mass and increased sediment accretion have raised marsh elevation about 0.5 m above the surrounding tide flat. Photo credit: John Lambrinos.

At larger spatial scales, the attenuation of hydrodynamic energy declines exponentially with distance from the marsh-water edge (Möller et al., 2001). Additionally, factors that influence vegetation biomass and canopy architecture, such as seasonality, productivity, and species composition, create considerable spatial and temporal heterogeneity in the magnitude of wave and flow attenuation. These factors contribute to strong nonlinearities in the relationship between vegetation, energy attenuation, and the value of the associated coastal protection service (Koch et al., 2009).

A positive feedback between plant productivity and accretion has maintained salt marshes in dynamic equilibrium with the mean sea level for the past 4000 years (Redfield, 1972; Morris et al., 2002). This equilibrium is sensitive to salt marsh productivity, relative rates of sea-level rise, and sediment supply (Morris et al., 2002). The engineering feedbacks and the relative stability of the ecosystem states they generate are also acutely scale dependent. Sedimentation within small colonizing patches of *Spartina alterniflora* facilitates stem growth causing more sedimentation. At the same time, the resulting raised mound promotes lateral erosion, creating gullies that inhibit lateral expansion of the patch (van Wesenbeeck et al., 2008b; Bouma et al., 2009a). These feedbacks contribute to abrupt transitions (thresholds in both space and time) between vegetated and nonvegetated patches across the intertidal zone (van de Koppel et al., 2005b; van Wesenbeeck et al., 2008a). Heterogeneity is greatest during the early colonization stages of a marsh, but declines over time. Vegetated patches likely synergistically alter landscape patterns of flow and sedimentation in ways that promote further recruitment and eventually the development of a more uniform and stable vegetated marsh state (van Wesenbeeck et al., 2008a).

Just as they do in wholly terrestrial environments, plants play a key role in regulating salt marsh diversity patterns by creating and modifying habitat (Crooks, 2002; Levin and Talley, 2002). The intertidal zone is typified by strong gradients in abiotic stress that generally correlate with elevation: the relationship is generally negative for more terrestrial organisms and positive for more aquatic organisms. The effect of ecosystem engineering on diversity is hypothesized to be greatest at the extremes of these stress gradients (Crain and Bertness, 2006; Bouma et al., 2009b). However, the way in which marsh plants influence diversity involves a complex suite of interacting mechanisms operating over a range of temporal and spatial scales that defy such a broad generalization. The regulation of diversity patterns by members of the genus *Spartina* illustrates this complexity. *Spartina* species have an inordinate influence on diversity patterns across much of the world's salt marshes. Two broad categories of engineering effects contribute to this. First, plants create habitat by modifying a complex suite of abiotic factors and processes. Second, plant structures themselves serve as habitat for sessile epibionts or preempt space for benthic-dwelling organisms (Grosholz et al., 2009). In their native range, *Spartina* create habitat for a range of other species by ameliorating many of the stresses associated with inundation, salinity, and wave action (Bertness and Hacker, 1994; Bertness and Leonard, 1997). In contrast, *Spartina* species invading Pacific mudflat habitats cause a dramatic decrease in the diversity and abundance of the benthic macrofuana community, and a broad shift from a trophic structure dependent on primary production to one dependent on detritus (Levin et al., 2006; Neira et al., 2006). Vertebrate species such as shorebirds and estuarine fish are also negatively affected by this shift (Grosholz et al., 2009). A range of engineering-mediated processes contribute to these changes, including preemption of belowground habitat by *Spartina* roots; reductions in light, temperature, and salinity; increases in organic matter accumulation; changes in sediment chemistry; reductions in the supply of propagules and seston food to filter-feeding bivalves; the creation of refuges for predators; and the creation of substrate for sessile epibionts (Grosholz et al., 2009). However, in some invaded habitats, *Spartina* either have little effect on diversity or actually increase the diversity of some groups (Neira et al., 2005; Hacker and Dethier, 2006).

The variability in how *Spartina* engineering influences diversity patterns develops through several distinct pathways. The strength of the engineering effect can depend on ambient abiotic conditions. For example, invasive *Spartina* modifies habitat to the greatest extent and has its strongest impact on diversity at unvegetated, high-energy sites (Grosholz et al., 2009). Similarly, engineering strengths depend on plant biomass and architecture, which can vary with environmental conditions such as stress levels or nutrient availability. For instance, shortened, nitrogen-deficient stands of *S. foliosa* in restoration sites provide poor habitat for clapper rails (Boyer and Zedler, 1998). Other ecosystem engineers can modify environmental conditions that in turn influence plant biomass or architecture. For instance, *S. densiflora* roots are associated with nitrogen-fixing arbuscular mycorrhizal fungi, but only in the presence of burrowing crabs that oxygenate sediments; removal of the mycorrhizae greatly reduces *S. densiflora* biomass (Daleo et al., 2007). Other biotic interactions can influence both the quality and nature of engineered habitat even if the magnitude of the engineering remains the same. In Argentinean salt marshes, colonizing *S. densiflora* find refuge from herbivorous crabs within the canopy of the succulent *Sarcocornia perennis*. However, the strength of this facilitation is greatest in the fall and winter when crab herbivory is most intense (Alberti et al., 2008). In the same vein, Grosholz et al. (2009) hypothesized that the reason *Spartina* have a predominantly positive effect on diversity in their native range, but a predominately negative effect in their invasive range, is partly related to greater predation pressure in Atlantic systems. Finally, genotypic differences in *Spartina* structure independent of environmental conditions also influence the magnitude of engineering modifications and the associated community effects (Seliskar et al., 2002; Proffitt et al., 2005; Brusati and Grosholz, 2006).

The engineered habitat created by marsh plants can affect diversity patterns at some distance from the plant itself or long after the plant has died. The senescent biomass of marsh plants is often moved considerable distances by waves and tides and deposited as wrack. In addition to subsidizing primary production, wrack serves as physical habitat for a number of invertebrate species (Rossi and Underwood, 2002). Wrack can also influence plant diversity patterns by serving as a refuge for vertebrate herbivores (Crain and Bertness, 2005) and by burying plants and influencing the timing and distribution of bare patches within a marsh (Bertness and Ellison, 1987). After a plant dies, the raised accumulation of sediment and dead roots it leaves behind can persist and continue to influence diversity. Sites where invasive *Spartina* have been eradicated are often colonized by other plant species more typical of mid-elevation salt marsh rather than the preinvasion low elevation mudflat (Lambrinos, 2007). The persistence of this habitat legacy depends on the environmental context of a site not only through its present influence on degradation processes, but also through its previous influence on the magnitude of the engineering process that created the habitat in the first place (Hacker and Dethier, 2009).

7.04.3.3 Mangroves

Mangroves are a group of trees and shrubs, almost exclusively tropical or subtropical. They typically occupy muddy and anoxic sediments in the intertidal zone of estuaries, or fringing the shoreline, and are adapted to waterlogged and anoxic soil, and to saline conditions. Underground roots are aerated by aerial roots or by respiratory pneumatophores that protrude from the substrate (**Figure 4**). High salinity is dealt with by a combination of exclusion by the roots, tissue tolerance, and elimination by secretion through leaf salt glands. Other vascular plants are unable to survive the anoxic and saline conditions and macroalgae require a firm substrate for attachment. Mangroves are, therefore, the dominant macrophytes, and the principal primary producers in tropical and subtropical muddy intertidal systems.

Mangroves are important ecosystem engineers. A few studies have evaluated the net effects of removal or establishment of mangroves (McKee and Faulkner, 2000; Alongi and de Carvalho, 2008; Granek and Ruttenberg, 2008). In these cases, their engineering effects are often difficult to separate from complex and often reciprocal interactions between the different elements of mangrove ecosystems. Nevertheless, a variety of engineering mechanisms can be inferred from these or other studies where physical variables, process rates, and

Figure 4 Mangroves (*Avicennia marina*) in Sinai, Egypt, showing dense pneumatophore growth. Photo credit: Peter Hogarth.

organismal distributions are evaluated in relation to the mangrove-created environment.

Mangroves promote sedimentation, enhance accretion, and retard coastal erosion. The dynamics of sedimentation are complex (Furukawa et al., 1997). A typical estuarine mangrove habitat consists of an extensive forest on a very shallow gradient intersected with narrow tidal creeks, which connect with the open sea. As the tide rises, water flows rapidly through the creeks, and then spreads laterally across the forest floor. Because this area is greater than that of the creeks, current velocity falls sharply. In one mangrove area in northern Australia, creek current velocity was typically >1 $\mathrm{m\,s^{-1}}$, falling to 0.1 $\mathrm{m\,s^{-1}}$ within the forest (Wolanski et al., 1992). Current velocity is also greatly reduced by the density of tree trunks, aerial roots, and pneumatophores. This effect is greater during ebb tide. Small-scale turbulence around the aerial roots and pneumatophores keeps particles in suspension while the tide is advancing. At slack water, the particles sink, and the retreating current is too slow to resuspend and remove them. Sedimentation rates correlate with pneumatophore density (Young and Harvey, 1996). About 80% of suspended sediment brought in from coastal waters may be trapped in mangroves (Furukawa et al., 1997). Clearance of sediment from coastal waters means that mangroves, as ecosystem engineers, may affect conditions in distant habitats such as coral reefs.

Mangrove roots avoid deeper, more anoxic, sediments by growing horizontally, close to the mud surface. The roots of adjacent trees intermingle, creating a dense mesh that holds the sediment together. This protects against erosion, while the aboveground aerial roots, trunks, and branches are effective in absorbing wave and wind energy. Mangroves afford significant protection against cyclones and tsunamis (Danielsen et al., 2005; Hogarth, 2007; Alongi, 2008; Das and Vincent, 2009).

Mangroves introduce significant environmental heterogeneity, growing in soft, muddy, and generally uniform substrates. Trunks, aerial roots, and pneumatophores introduce a hard intertidal substrate that may be comparable in area to the surrounding soft sediment, and may even exceed it (**Figure 4**). Large numbers of sessile marine organisms settle on this hard substrate, including algae, barnacles, bivalve mollusks, sponges, corals, and ascidians, thus supporting, in turn, grazing and predatory animals such as gastropod mollusks and crabs (Hogarth, 2007). The dense growth of aerial roots and pneumatophores above the surface, and of the tangle of roots below, creates a complex and heterogeneous intertidal environment that protects a variety of small mobile organisms from predation or stress. This includes intertidal invertebrates that use such protective habitat to avoid desiccation during low tide as well as invertebrates and small fish that use it to avoid predation when the submerged forest is invaded by fish (Hogarth, 2007).

High soil moisture due to canopy shading and litter accumulation also fosters the survival of low-tide foragers such as the amphibious sesarmid and ocypodid crabs, gastropods, and mudskippers (Hogarth, 2007). Burrowing crustacea – such as most sesarmid and ocypodid crabs – are themselves significant ecosystem engineers, affecting topography, hydrology, and nutrient cycling; greatly expanding the area of mud surface in which much of the microbial activity occurs; and increasing substrate heterogeneity (Hogarth, 2007; Kristensen, 2008; see Section 7.04.3.8). Nevertheless, limited incident light due to shading results in minimal algal and microbial photosynthesis (Alongi and de Carvalho, 2008; Granek and Ruttenberg, 2008).

Trunks, branches, and the forest canopy provide a habitat similar to that of a terrestrial forest, occupied by typical terrestrial animals, including insects, reptiles, birds, and mammals, as well as by epiphytes. Mangrove biota therefore comprises plants and animals of both marine and terrestrial origins, few of which are unique to mangroves. The overlap of tidally fluctuating marine habitats with terrestrial ones, as well as spatial heterogeneity, largely explains the paradoxical feature of mangrove forests: a relatively low tree species diversity (a handful of dominant species, often growing in monospecific patches or zones) supports a relatively high animal biodiversity.

Many of the ways in which mangroves engineer their environment have implications for the mangroves themselves. Mangrove pneumatophores promote sedimentation, but sediment accumulation may stifle them, requiring compensatory growth (Young and Harvey, 1996). Shading of the soil surface limits growth of mangrove seedlings (Putz and Chan, 1986). Secondary feedbacks also occur via the organisms whose presence is enabled by the mangroves. Epiphyte growth on pneumatophores impedes gas exchange, whereas settlement of algae on seedlings restricts photosynthesis, and increases hydraulic drag, leading to seedling removal by wave action (Clarke and Myerscough, 1993). Even more indirectly, organisms whose presence is made possible by mangrove ecosystem engineering are themselves ecosystem engineers with indirect feedback effects on the mangroves. Burrowing organisms, particularly sesarmid crabs, increase subsurface water flow and oxygenate the soil, benefiting the mangroves (Smith et al., 1991). On the other hand, sesarmid crabs also devour large numbers of mangrove seeds, leaves, and seedlings (Lee, 1998). The ecosystem engineering activities of mangroves thus involve a number of feedbacks, both positive and negative.

7.04.3.4 Seagrasses

Seagrass meadows are important ecosystems, very much comparable in appearance to grasslands in terrestrial ecosystems (**Figure 5**). They occupy about 177 000 $\mathrm{km^2}$ along the coasts of all continents, except those in Antarctica, and extend from the intertidal zone down to depths in excess of 40 m (Duarte, 1991; Hemminga and Duarte, 2000). Seagrass meadows develop from about 60 clonal, rhizomatous angiosperm species restricted to living in the sea and may be monospecific or multispecific (e.g., up to 12 seagrass species in SE Asian meadows; Duarte et al., 2000; Hemminga and Duarte, 2000). These meadows rival tropical forests and efficient crops as the most productive ecosystems on Earth (Duarte and Chiscano, 1999), and are a source of important ecosystem services to humans, such as support for biodiversity, carbon sequestration, and sediment stabilization and coastal protection (Duarte, 2000; Hemminga and Duarte, 2000; *see* Chapter **12.06**).

The lush canopies developed by seagrass meadows affect water flow (**Figure 5**). The presence of seagrass canopies within the boundary layer alters the roughness of the bottom (Nepf and Vivoni, 2000; Granata et al., 2001) as well as the vertical flow profile over the canopy, especially when canopy height represents more than 10% of the height of the water column (Nepf and Vivoni, 2000). Depending on seagrass species and

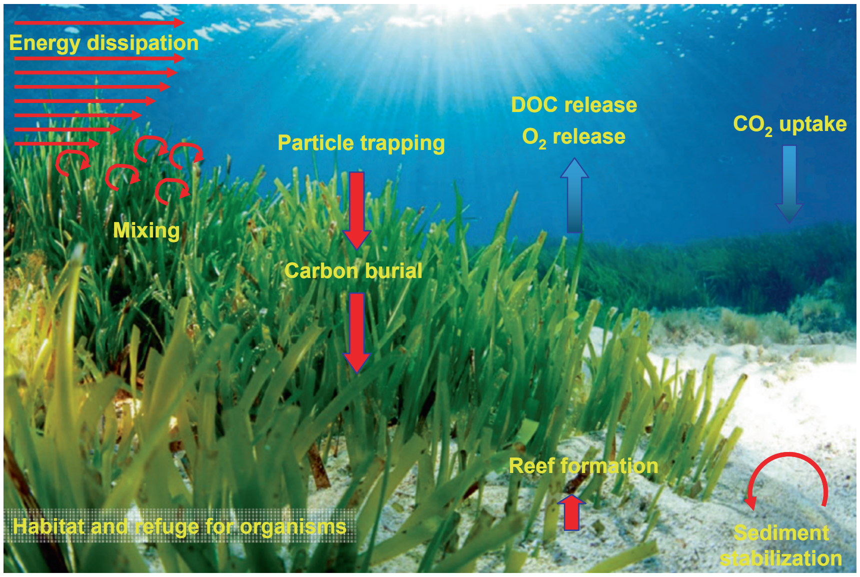

Figure 5 Seagrass (*Posidonia oceanica*) meadow in Formentera Island (Spain). Main ecosystem engineering roles of seagrass meadows are indicated with red arrows. Other important ecosystem impacts of seagrass are indicated with blue arrows. Photo credit: Manu Sanfélix.

shoot density, flow reduction resulting from current deflection by the canopy ranges from 2-fold to more than 10-fold compared to water flow outside the seagrass bed (Ackerman, 1986; Gambi et al., 1990; Hendriks et al., 2008). Seagrass canopies also have a dampening effect on waves. Although wave attenuation is maximal when the meadow occupies a large portion of the water column (i.e., more than 50%; Fonseca and Cahalan, 1992), reduction in wave energy and orbital velocity occurs even when beds are located at 5–15 m depth and the plants occupy a small portion of the water column (Verduin and Backhaus, 2000; Granata et al., 2001).

The dampening of waves and currents by seagrass canopies leads to increased sediment deposition (Gacia et al., 1999; Gacia and Duarte, 2001; Hendriks et al., 2008) and decreased resuspension (Lopez and Garcia, 1998). However, seagrass can also directly intercept suspended sediment particles with their canopies. The collision of suspended particles with seagrass leaves causes momentum loss and increased path length (Hendriks et al., 2008), resulting in increased deposition. In addition, exopolymeric substances secreted by epiphytes can bind sediment particles to seagrass leaves (Agawin and Duarte, 2002). Field estimates indicate that the potential for particle contact with leaf surface sometimes approaches 100% in *Zostera marina* canopies (Ackerman, 2002). Epiphytic layers on seagrass leaves may also contribute to the trapping of particles in seagrass beds by increasing both the roughness of the canopy and the boundary layer on the leaf surface (Koch et al., 2006).

The capacity of seagrasses to trap and retain sediment particles via either of the above mechanisms can decrease water turbidity (thus having a positive feedback effect on seagrass photosynthesis and growth; see van der Heide et al., 2007) while elevating the seafloor to some degree. However, sediment accumulation can be seasonal, with net sediment accretion during summer when seagrasses reach their maximum density, and net sediment resuspension in winter when plants disappear or their density decreases (Van Keulen and Borowitzka, 2003). Sediment accumulation rates of 2 mm yr^{-1} were observed within perennial subtidal seagrass meadows in the Mediterranean Sea (Gacia and Duarte, 2001; Gacia et al., 2002), indicating net annual sediment accretion. A net accretion rate of 0.5 mm yr^{-1} was also observed in Western Australia (Walker and Woelkerling, 1988). Nevertheless, complete winter removal of the sediment accreted during the growing season (5–7 mm), plus some additional erosion, was observed in intertidal meadows of the Dutch Wadden Sea (Bos et al., 2007). Although seagrasses are generally considered to stabilize sediments and trap particles (**Figure 5**), fine sediment resuspension can be dominant in wave-exposed, high-flow environments where seagrasses do not effectively attenuate water flow (Fonseca and Bell, 1998; Koch and Gust, 1999).

Seagrass can also affect the seafloor topography through the accretion of rhizomes and roots in the sediments, thus exerting additional engineering influences on flow and sedimentation patterns. Reef-building seagrasses – especially the endemic Mediterranean species *Posidonia oceanica* – provide a striking example of this process. *P. oceanica* is a long-lived species, with individual shoots and clones that live for decades and centuries, respectively (Duarte et al., 1994; Mateo et al., 1997), and the thick (1 cm) ligneous rhizomes are preserved in the sediments over millennia. Although leaf-bearing seagrass rhizomes grow vertically at rates of only a few millimeters per year (Marbá and Duarte, 1997), they form a rhizome network called 'matte' (Mateo et al., 1997) that, over the years, elevates above the seafloor forming reef-like structures. These seagrass reefs lead to a coastal topography comparable to that of tropical bays, where a reef located 1–2 m below the water surface occurs a few hundred meters offshore, confining a shallow lagoon between the reef and the beach. *P. oceanica* reefs play a role comparable to coral reefs in the dissipation of wave energy and the protection of the shoreline. Reef-forming seagrasses include other species characterized by ligneous, persistent rhizomes, such as the tropical species *Thalassodendron ciliatum* that forms reefs in coastal areas of the Indian Ocean (Duarte et al., 1996).

As is the case of salt marsh plants (see Section 7.04.3.2), seagrass can also modify environments via the export of litter and its accumulation in adjacent ecosystems. Seagrass litter often accumulates in beaches. *P. oceanica* litter creates up to 3-m-tall deposits called 'banquettes' (Mateo et al., 2003) that protect the shoreline from erosion (Coupland et al., 2007). Seagrass litter can also act as seed material for dune formation by creating roughness and promoting sand accumulation (Hemminga and Nieuwenhuize, 1990).

The role of seagrass meadows in maintaining high biodiversity is supported by their capacity to expand and diversify the habitat available for other organisms. Dense seagrass canopies (**Figure 5**) multiply the surface area available for colonization by benthic, bottom-dwelling organisms by up to 12-fold compared to the bare sediments (Duarte and Chiscano, 1999). Seagrass leaves – which typically create 2–12 m^2 of additional surface per square meter of sediments (Duarte and Chiscano, 1999) – as well as the emerging portions of seagrass rhizomes are colonized by a variety of organisms, ranging from bacteria to filter-feeding hydrozoans and sponges (Duarte, 2000; Hemminga and Duarte, 2000). Seagrass meadows and patches also serve as refuge to a range of epibenthic organisms that hide from predators in the seagrass canopy, and infaunal species that suffer decreased risk of epibenthic predation within the dense matrix of seagrass roots and rhizomes (Hemminga and Duarte, 2000; Heck and Orth, 2006). The physical interaction between seagrass canopies and flows can also facilitate organismal recruitment within seagrass beds. For example, the back-and-forth motion of seagrass leaves enhances vertical mixing of the water column (Koch and Gust, 1999; Ghisalberti and Nepf, 2002) and the delivery of planktonic larvae and spores to the seabed (Grizzle et al., 1996). A similar mechanism could also contribute to increased delivery of suspended particulate food to the seabed observed in seagrass meadows together with a concomitant increase in the growth of benthic organisms (Judge et al., 1993; Irlandi, 1996).

The above-mentioned physical influences of seagrass structure (leaves, roots, and rhizomes) on biotic variables (predation risk, food availability, and larval retention; Orth et al., 1984; Judge et al., 1993; Irlandi, 1994, 1996) can lead to increased organismal abundance and/or species richness in seagrass meadows relative to adjacent unvegetated habitats (Heck, 1977; Heck and Thoman, 1984; Edgar et al., 1994; Jenkins et al., 1997). Indeed, seagrass habitats are often considered as 'biodiversity hot spots' and 'nursery habitats' because of their respective roles in sustaining higher species richness than nearby unvegetated habitats, and because of enhanced growth and survival of juveniles of commercially important species (Heck and Thoman, 1984; Beck et al., 2001). Seagrasses can also contribute to other types of habitat diversity. Seagrass wrack deposited in sandy beaches can locally enhance moisture and provide living space to a variety of organisms (Coupland et al., 2007). As noted earlier, accretion of recalcitrant root and rhizome material by certain species of seagrass can lead to the formation of seagrass reefs. The reef habitat, by itself, is heterogeneous in height due to local variations in accretion rates and the time span since accretion began (Kendrick et al., 2005), resulting in within-reef variation in abiotic factors relevant to other organisms (e.g., light incidence and wave exposure). Like coral reefs (see Section 7.04.3.6), seagrass reefs consist out of a patchwork of distinct environments with reef, fore reef, back reef and lagoonal habitats, each characterized by distinctive communities (Borg et al., 2006; Somaschini et al., 2008).

7.04.3.5 Kelp and Other Macrophytic Seaweeds

Aggregations of marine macroalgae occur in coastal ecosystems around the world. Seaweeds vary dramatically in size and structure, from turf algae no more than a few centimeters high to canopy-forming kelps, such as *Macrocystis pyrifera* (**Figure 6**) and *Nereocystis luetkeana*. Of the many taxa of macroalgae, kelps tend to be most recognized for the important ecosystem engineering role they play in coastal environments (reviewed by Dayton (1985)). Aggregations are often referred to as kelp forests and can extend up to hundreds of meters. Kelps are generally attached to hard substrates by a root-like holdfast, which is connected to the blades via one or more stipes. Through their physical presence, kelps create habitats very distinct from adjacent waters. The degree to which kelps

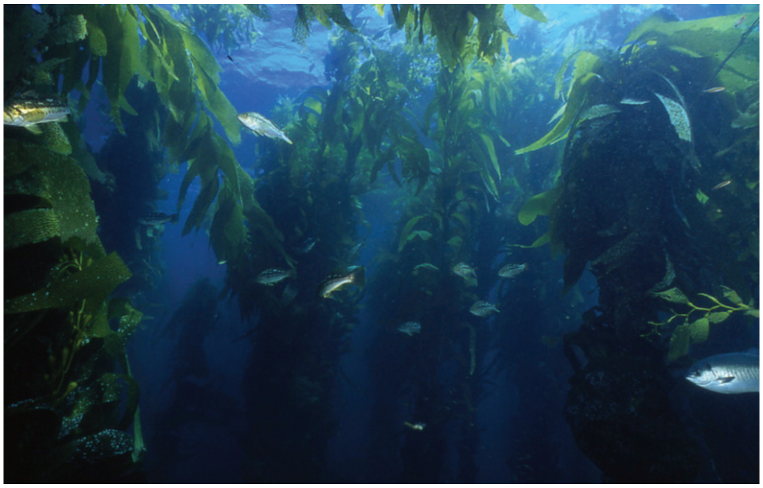

Figure 6 Kelp forests (*Macrocystis pyrifera*) off the coast of Santa Barbara, California, USA, provide habitat for the kelp bass (*Paralabrax clathratus*). Photo credit: Santa Barbara Coastal Long-Term Ecological Research project.

modify their surrounding physical environment depends on species morphology (e.g., stipe length, number, and blade area) and the areal extent and density of individuals within aggregations. Kelp forest extent and density can vary dramatically in response to intra- and interannual disturbance, and the potential for rapid recolonization and high productivity (Kennelly, 1989; Graham et al., 1997; Edwards and Estes, 2006).

Unlike other coastal ecosystem engineers, there is scant evidence that kelps modify storm surge or influence large-scale patterns of erosion and sedimentation. However, aggregations of kelp can have significant dampening effects on ocean currents (Jackson, 1997; Gaylord et al., 2007). For example, alongshore currents on the edge of a large giant kelp forest in southern California were an order of magnitude greater ($2.1 \pm 9.9\,\mathrm{cm\,s^{-1}}$) than those in the interior ($0.2 \pm 2.0\,\mathrm{cm\,s^{-1}}$; Jackson, 1997). Water flow can also be attenuated by smaller forests of *M. pyrifera* (Gaylord et al., 2007) and understory kelps (Eckman et al., 1989), such that the extent and density of the forest determine the degree of attenuation (Gaylord et al., 2007). Local rates of sedimentation may be influenced by the interaction between water motion and the structure of kelps. For example, off the coast of Washington, USA, particulate deposition was higher beneath canopies of the understory kelps *Agarum fimbriatum*, *A. cribrosum*, and *Laminaria groenlandica* because of longer particle residence times and a higher probability of particulate redeposition from direct material trapping (Eckman et al., 1989). In contrast, sedimentation was lower beneath *Ecklonia radiata* canopies, off the coast of Australia, because the sweeping motion of the blades cleared the sediment from the benthos (Connell, 2003). Whether kelp forest structure influences longer-term and larger spatial scale processes of erosion and sedimentation remains unclear (Elwany and Flick, 1996).

Like terrestrial forests, surface and subsurface kelp canopies diminish light (Pearse and Hines, 1979; Reed and Foster, 1984). Light reduction depends on the structure of the kelp forest (e.g., kelp stipes and canopy blades; Stewart et al., 2008) and can have important consequences for understory species. Abundances of understory primary producers tend to be lower in shady environments created by canopy kelps (Reed and Foster, 1984; Clark et al., 2004). In contrast, canopy shade may positively affect sessile invertebrates by providing refuge from competition with algae for space (Eckman and Duggins, 1991; Arkema et al., 2009), and by facilitating settlement of invertebrate larvae that exhibit negative phototaxis (e.g., Linares et al., 2008). Because understory algae and sessile invertebrates have different light requirements, giant kelp allows for temporal and spatial coexistence of these competitors by creating alternative niches for them to occupy (Arkema et al., 2009).

The dampening effects of kelp forests on currents may also influence species diversity in coastal ecosystems. Suspension feeders that exhibit species-specific feeding responses to water flow (Eckman and Duggins, 1991; Wildish and Kristmanson, 1997) may dominate high-flow environments along the edge, or outside, whereas those with low-flow requirements may be more common in the interior. Variation in currents may also influence larval distribution in and around forests (Bernstein and Jung, 1979) and suspended food for kelp forest fishes (Bray, 1981).

Many of the ways in which kelp forests engineer their environment also have implications for the kelps themselves. Low light levels beneath canopies can inhibit kelp recruitment and growth (reviewed by Dayton (1985) and Jackson (1987)). For example, density-dependent shading may contribute to the negative relationships that have been observed between growth and standing stock of *M. pyrifera* (Gerard, 1976; Reed et al., 2008). Dampened currents may also decrease mass transfer of key nutrients to individuals in the center of forests. However, neither small nor large aggregations of giant kelp in southern California seem to affect concentrations of nitrates (Jackson, 1977; Fram et al., 2008). Individuals along the edge of forests, where light is readily available, have been shown to accumulate more nitrogen and carbon than interior individuals (Fram et al., 2008; Stewart et al., 2008); however, these differences appear to be due to negative effects of the kelp canopy on the amount of light reaching the bottom.

The production of large kelps creates three-dimensional complexity in coastal environments, providing habitat for numerous species of plants and animals. Fish and invertebrates take refuge within kelp holdfasts and among stipes and canopy blades. Often, the population size of kelp forest animals depends upon the density and structural complexity of the kelp (Holbrook et al., 1990). For example, Carr (1994) found that the recruitment of kelp bass, *Paralabrax clathratus* (**Figure 6**), was positively and asymptotically related to the structural complexity of giant kelp (e.g., blade biomass and stipe density). The wide, flat blades of many kelps also increase the surface area and diversity of colonizable substrate for epiphytic animals and plants. For example, giant kelp off the west coast of the US and New Zealand provide habitat for various species of bryozoans and hydroids (Bernstein and Jung, 1979). Kelps provide substrate for epiphytes, but large aggregations may alter the physical environment such that surrounding conditions become inhospitable to the animals and plants recruiting to their surfaces (Arkema, 2008).

7.04.3.6 Coral Reefs

Reef-building (hermatypic) scleractinian corals (hereafter referred to as corals or coral reefs) generate complex habitats in extremely oligotrophic tropical and subtropical shallow waters (Odum and Odum, 1955; Kinsey, 1983; Hatcher, 1990) as well as deeper, colder waters with higher nutrient concentrations (Freiwald et al., 2004; Roberts and Hirshfield, 2004; Roberts et al., 2006). Although, less than 10 reef-building coral species are known from cold waters, in contrast to several hundred species in warm waters, there is a similar variety of associated habitats with positive effects on biodiversity (Freiwald et al., 2004; Henry and Roberts, 2007). This suggests similar habitat engineering features between both reef types. Knowledge of the engineering roles of corals with respect to erosion/sedimentation and biogeochemical processing is still limited (in particular for cold water reefs), but it is becoming increasingly evident that they can fulfill several important functions as both autogenic and allogenic engineers.

Corals, as well as many other reef-associated organisms such as mollusks and echinoderms, build calcareous endo- or exoskeletons. Through fragmentation and erosion, as well as consumers (e.g., parrot fish), these hard structures transform into biogenic calcareous sands that often cover a major fraction of the adjacent seafloor (Hochberg et al., 2003), thereby allogenically engineering bottom sediment structure. These calcareous sands have larger grain sizes (usually in the sand to gravel grain size; i.e., >500 μm) and are much more permeable (typically in the range of 10^{-9}–10^{-11} m^2) relative to many other kinds of sediments with different mineralogy (e.g., silicate sands) and smaller grain size (permeability usually $\leq 10^{-11}$ m^2). Large volumes of water can continuously flow through these permeable calcareous reef sands (e.g., 5 billion liters, equating to 16% lagoon water volume is filtered through the lagoon sands each day at the Heron Island platform reef system in the Australian Great Barrier Reef; Wild et al., 2004b). Suspended particles are transported into the sands and trapped by the permeable sand filter (Rusch and Huettel, 2000; Rusch et al., 2000). Biogenic calcareous sands also accommodate high abundances of microbes, because of their large specific surface for microbial colonization (Wild et al., 2006). These microbes degrade both dissolved organic material in the inflowing water as well as the organic particles trapped by the sands, thus leading to fast recycling and concomitant release of regenerated nutrients (Wild et al., 2004b, 2005).

It is worth noting that extensive biogenic sand beds do not usually occur in association with cold water reefs, because their location along steep slopes of continental shelves and seamounts results in gravitational sand transport (Roberts et al., 2006).

Corals can also allogenically affect sedimentation by means of their mucous secretions (**Figure 7**). Mucus detached from corals traps suspended inorganic and organic particles in the water column, forming aggregates that sink rapidly to bottom sands (Wild et al., 2004a). Mucus is secreted by corals in quantities that can make it the dominant form of suspended organic matter within and around coral reefs (Johannes, 1967; Marshall, 1968). Consequently, particle trapping by mucus may well significantly contribute to sedimentation in coral reef ecosystems.

Coral reefs also have autogenic geomorphological impacts. They are usually situated parallel to the coastline and grow to the water surface, thus acting as an obstacle for waves, protecting terrestrial coastal ecosystems and human populations from storm impacts (Moberg and Folke, 1999). Typically, coral reef morphology interacts with waves generating zones with low- (back reef, lagoons) and high-energy (fore reef) dissipation and concomitantly steep environmental gradients in the quantity and quality of deposited and suspended sediments (Stoddart, 2008).

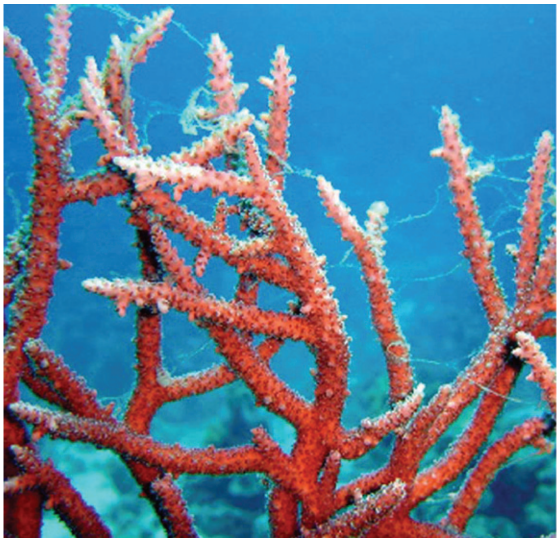

Figure 7 Branching coral of the genus *Acropora*, Northern Red Sea. Note mucus strings between branches. Photo credit: Christian Wild.

Corals are archetypical autogenic ecosystem engineers largely because of the great number of other organisms that find habitat in the complex, three-dimensional structures generated by their hard aragonite skeletons (Jones et al., 1994). These structures persist long after the corals die, and different coral growth forms (e.g., branching, massive, foliose, and disklike) lead to the formation of reefs of varying three-dimensional complexity. The communities associated with coral structures are usually distinct from that of the surrounding sandy habitats. The massive and complex structures provide diverse microhabitats that other organisms use in response to higher food availability or decreased impact of predators and currents (Connell, 1978). Coral skeletons also provide stable surfaces for the settlement of an extraordinary diversity of sessile organisms (Huston, 1985). Because of their key role in habitat creation, coral reefs are regarded as major biodiversity hot spots in the tropical coastal oceans (Roberts et al., 2002). Cold water reefs play a similar role in deeper, temperate waters, as well as sustaining not only communities that differ from those of the surrounding environments (Schöttner et al., 2009) but also biodiversity levels similar to those found in tropical coral reefs (Freiwald et al., 2004; Henry and Roberts, 2007). At a landscape scale, wave energy dissipation by coral reefs occurring parallel to the shoreline leads to the formation of distinctive back reef and lagoon environments, which also support communities that differ in composition from those of the reef and fore reef habitats. Although these broadscale environmental changes may have negative feedback effects on corals (e.g., decreased coral recruitment and survival in reef lagoons; e.g., Brown, 1997b), they nevertheless contribute to the overall effect of corals engineering on biodiversity.

7.04.3.7 Reef-Forming Bivalves

Reef-building bivalves create spatially and topographically complex habitats that foster unique assemblages of organisms (**Figure 8**). This relationship was first recognized in the nineteenth century by Karl Möbius, who described oyster reefs in the German Wadden Sea. Today, 150 years later, ecologists are affirming the central roles that these kinds of physical ecosystem engineers play in structuring marine benthic communities in many coastal and estuarine ecosystems (Bertness and Leonard, 1997; Gutiérrez et al., 2003; Commito et al., 2005, 2008; Coen et al., 2007; Gutiérrez and Jones, 2006, 2008; Bouma et al., 2009b; Buschbaum et al., 2009). The best-known examples of reef-building bivalves are intertidal and shallow subtidal mussels and oysters. These suspension feeders create persistent, extensive, dense populations that are attached to each other and the substrate by byssal threads (mussels: e.g., *Mytilus edulis, Musculista senhousia, Perumytilus purpuratus*, and *Limaria hians*) or calcification (oysters: e.g., *Crassostrea virginica, Crassostrea gigas*, and *Ostrea edulis*). Non-reef-building bivalves can also have significant physical ecosystem engineering effects

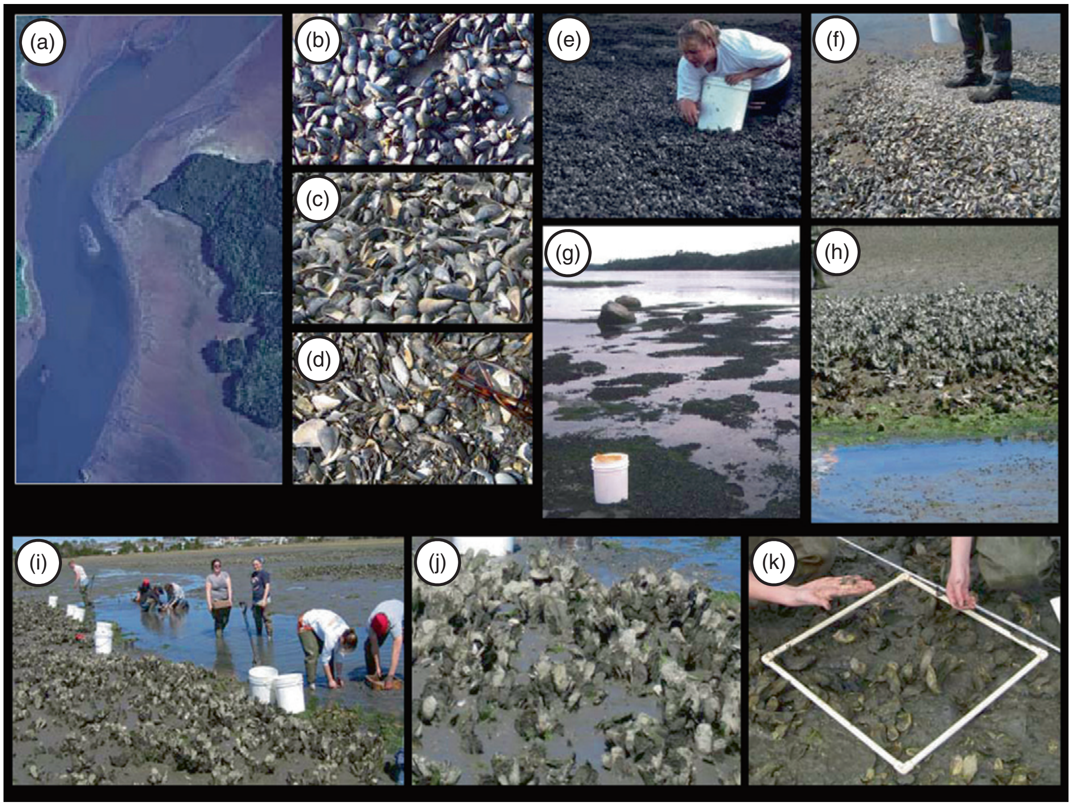

Figure 8 Reef-building bivalves. (a–g) Mussels (*Mytilus edulis*) in Maine, USA, mudflats; (h–k) oysters (*Crassostrea virginica*) in North Carolina, USA, sand flats. (a) Mussel bed extending 2500 m along low tide line on east side of Pleasant River estuary channel. Note patchy, dissected bed structure at this spatial scale. (b) Live mussels. (c) Disarticulated mussel valves. (d) Mussel shell fragments. (e) Extremely soft, deep mud in bed with high proportion of live mussels. (f) Firm surface of bed with high proportion of disarticulated mussel valves and shell fragments. (g) Mussel bed patches raised above ambient soft bottom at low tide. (h) Section of 3-m-wide oyster reef extending tens of meters along interface between salt marsh (*Spartina alterniflora*) at top of image and sand flat with ephemeral green algae at bottom of image. (i) Extensive oyster reef divided by tidal creek. (j) High vertical relief created by live oysters. (k) Moderate vertical relief created by disarticulated oyster valves. Photo credits: (a) Sewall Company by permission of Maine Department of Marine Resources and (b–k) John A. Commito.

in marine, estuarine, and freshwater ecosystems (Bertness and Leonard, 1997; Hewitt et al., 2002; Gutiérrez et al., 2003; Strayer, 2009).

Bivalves create reefs at a wide range of spatial scales, often with hierarchical spatial structure from individuals to small clumps to large patches to extensive beds and reefs that cover thousands of square meters and extend kilometers in length (**Figure 8**; Smith et al., 2003; Crawford et al., 2006). Mussel beds and oyster reefs can show a high degree of temporal variation in persistence at small spatial scales, but over large spatial scales bivalves and shell material can persist for hundreds and even thousands of years in the same general location (Gutiérrez and Iribarne, 1999; Commito and Dankers, 2001; Hertweck and Liebezeit, 2002; Smith et al., 2003; Stone et al., 2005).

Reef-building bivalves produce shells that add hard substrate to soft, unstable, and often relatively flat bottoms in sedimentary systems. In both rocky and soft-bottom habitats, they can create a topographically rugose surface with fractal complexity (Commito and Rusignuolo, 2000). The patchy nature of reef and bed structure contributes to a spatially heterogeneous variety of autogenic and allogenic effects, both positive and negative, on the environment, other species, and the reef builders themselves, across scales from individual shells to large spatial aggregations.

Mussels and oysters are roughness elements that alter the flow environment (Meadows et al., 1998; Commito et al., 2005; Kochmann et al., 2008). Individual mussels and the edges of small mussel patches reduce the critical erosion velocity around them, resulting in local sediment scouring. Winnowing and advection of fine particles occur in this erosion trough and further downstream. Large patches have greater impacts on the flow boundary layer, resulting in erosional wave patterns and increased detritus accumulation, especially outside the patch boundary on the down-slope side. Threshold effects may occur when a patch is large enough to produce skimming flow. Sediment capture rates are higher within beds than over adjacent bare sediment (Commito et al., 2005). Thus, mussels can have impacts on both erosion and deposition, with the net result depending on bed structure and hydrodynamics. Oysters have similar effects (Coen et al., 2007), and mixed assemblages of mussels and oysters show interesting interactive influences (Kochmann et al., 2008). Reef-building bivalves not only alter water flow, but also are themselves affected by flow. Live bivalves and shell material can be retained within beds and reefs or exported over large areas by waves, water currents, and ice scour (Commito and Dankers, 2001).

Some mussel beds and oyster reefs are autogenic structures consisting primarily of live animals and empty articulated, disarticulated, and broken shells (Smith et al., 2003; Stone et al., 2005). Where wave action and tidal currents are moderate, increased deposition over beds and reefs causes sediment to build up to form banks higher than the ambient substrate (Meadows et al., 1998). In these banks, fine sediment constitutes most of the structure, analogous to the woody plant material placed by beavers to create allogenic dam structures. Although the local production of bivalve feces and pseudofeces is not an example of physical ecosystem engineering *per se*, the alteration of flow by the physical structure of the bed or reef helps retain these waste products, so their presence is in part due to physical ecosystem engineering. Autogenic and allogenic banks create vertical relief. Intertidally, the upper portions of banks have reduced immersion time. Banks also act like dams to hold pools of water and increase immersion time above the shoreward bank margin. Their massive structure can attenuate storm surge, direct water flow, and stabilize the shoreline (Stone et al., 2005; Coen et al., 2007; Koch et al., 2009; Palumbi et al., 2009).

Within the array of habitats and physicochemical parameters resulting from reef and bed complexity, benthic and demersal animals, macrophytes, and microorganisms vary greatly. Organisms respond to individual shell traits and shell spatial arrangements, including the provision of attachment substrate; refuges from predation, competition, thermal stress, desiccation, and hypoxia; transport of materials and solutes; and delivery of larvae and postlarval juveniles and adults, including recruitment of mussels and oysters themselves (Gutiérrez et al., 2003; Commito et al., 2005, 2008; Coen et al., 2007). Other physical ecosystem engineers such as kelps, seagrasses, and marsh grasses (e.g., Altieri et al., 2007) also interact with these bivalves.

Epifauna in hard- and soft-bottom habitats respond favorably to the provision of rugose, hard substrate by mussels and oysters. Rocky shore systems generally show enhanced species richness within bivalve assemblages (Thiel and Ullrich, 2002; Tsuchiya, 2002). This pattern generally does not occur in soft-bottom systems, primarily because some infauna have lower abundances and diversity within beds and reefs (Commito et al., 2005, 2008; Buschbaum et al., 2009; Ysebaert et al., 2009), while oligochaetes, nemerteans, and opportunistic species may be enhanced, especially species with no free-swimming larvae but a tolerance for low-oxygen, sulfide-rich environments. Epifauna and infauna abundance and diversity are strongly linked to spatial variation in live mussels and their shell material (Commito et al., 2008), demonstrating that reef-building bivalves are an important autogenic determinant of benthic community structure. However, universal species assembly rules cannot be applied because the effects on macrofauna are quite variable, depending on bivalve species, geographic location, and local environmental conditions (Thiel and Ullrich, 2002; Commito et al., 2005, 2008; Coen et al., 2007; Buschbaum et al., 2009; Kochmann et al., 2008; Ysebaert et al., 2009).

Oyster reefs extend above the ambient bottom, resulting in strong vertical gradients in hypoxia and predation (Lenihan et al., 2001). The effects of mussel bed height are not as well understood, but it is likely that similar vertical gradients exist. Trophic cascades have been well studied in oyster reefs, where topographic complexity regulates the effects of multiple predators and their prey, including feedbacks on oysters themselves (Grabowski et al., 2008). Within mussel beds, foraging efficiency of epibenthic predators is influenced by bed topographic complexity (Commito and Rusignuolo, 2000; Commito and Dankers, 2001), and altered abundances of predatory infauna may play a role in regulating densities of prey species via trophic cascades (Commito and Ambrose, 1985).

7.04.3.8 Burrowing Crustaceans

Burrowing crustaceans are ubiquitous components of coastal sedimentary environments, where they frequently occur at high densities (**Figure 9**; Suchanek, 1983; Ziebis et al., 1996; Iribarne et al., 1997; Botto and Iribarne, 2000). They create semi-permanent burrows, ranging from small, shallow structures to complex systems greatly extended laterally and to sediment depths >1 m (Swinbanks and Murray, 1981).

Figure 9 Modification of sediment topography by burrowing crustaceans. (a) Sediment mounds created by ghost shrimp *Callianassa filholi* bioturbation resulting in an uneven microtopography at the sediment surface, Papanui Inlet, southeastern New Zealand. (Inset) Male *C. filholi* (total length: ~7 cm). (b) Burrows and excavated sediment mounds generated by the grapsid crab *Neohelice* (*Chasmaghnathus*) *granulata* in a tidal flat-salt marsh transition, Mar Chiquita coastal lagoon, Argentina. (Inset) Male *N. granulata* (carapace width: ~3 cm). Photo credits: (a) Katrin Berkenbusch and (b) Pablo Ribeiro.

Interactions with the sediment result in considerable bioturbation, which is intensified in species that also process sediment for food (Iribarne et al., 1997; Berkenbusch and Rowden, 1999). The burrows and bioturbation activities have a profound impact on physical and biogeochemical properties and processes, with knock-on effects for associated biota. As a consequence, the functional importance of burrowing crustaceans has been recognized in many coastal soft-sediment environments (Suchanek, 1983; Berkenbusch and Rowden, 2007; Escapa et al., 2007).

Physical habitat modifications by burrowing crustaceans occur in all sedimentary habitats, including sand flats, salt marshes, mangroves, and coastal lagoons. The creation of burrows extends the sediment–water interface to considerable depth – depending on the species and ecosystem involved, the primary surface area can be enlarged by over 400% (Fanjul et al., 2007). In addition to the structural change, active burrow irrigation accelerates the exchange of burrow/interstitial water with overlying water with concomitant oxygenation of the sediment column (Ziebis et al., 1996).

The most visible physical impact of burrowing crustaceans is a highly uneven microtopography at the sediment–water interface (**Figure 9**). Continuous excavation of sediment leads to negative reliefs of depressions and pits, interspersed with unconsolidated mounds of expelled material. The roughness created by these biogenic features influences shear strength and boundary layer velocities at the sediment–water interface, hence pore-water advection and the potential for sediment erosion and deposition (Ziebis et al., 1996; Rowden et al., 1998). Depressed areas such as pits enhance the deposition of sediment particles, with burrow openings functioning as passive traps for sediment and organic matter (Botto and Iribarne, 2000). At the same time, mounds of expelled sediment are often susceptible to erosion and contribute substantial amounts of sediment particles to bedload transport and resuspension when burrowing species have prodigious sediment turnover rates (Suchanek, 1983; Rowden, et al., 1998).

Burrowing and feeding activities also affect seabed stability by altering substrate particle size distribution, penetrability, and water content (Bertness, 1985; Botto and Iribarne, 2000). Although the spatial extent of such habitat modification is closely linked to burrow dimensions, changes at the sediment–water interface are particularly critical as they determine the cohesiveness and erodibility of surficial sediments (Botto and Iribarne, 2000). In areas that are prone to erosion, for example, tidal creeks in salt marshes, this biologically mediated increase in erosion has far-reaching consequences, as it promotes the landward growth of tidal creeks and thereby overall erosion of the coastal environment (Escapa et al., 2007).

The ecological significance of burrowing crustaceans is closely linked to their physical habitat modifications, which create spatial and/or structural heterogeneity, affecting the distribution and abundance of associated biota (including plants) and determining community patterns. Their burrows provide physical structure in otherwise unstable environments, extend the sediment–water interface, and oxygenate deeper sediments, extending the available living space and enabling associated organisms to persist at sediment depth (Bromley, 1996). Because burrows buffer environmental extremes such as oxygen deficiency and temperature change (Powers and Cole, 1976) they provide refuge and ameliorate predation and competition pressure. Species directly benefiting from the provision of habitat are burrow commensals, encompassing crustaceans, bivalves, polychaetes, and fish. The favorable microenvironment created within burrows also increases the abundance and diversity of infaunal species, including meiofauna (MacGinitie, 1934; DePatra and Levin, 1989).

At the same time, physical changes to sediment properties, that is, grain size and stability, can have both positive and negative effects on benthic organisms that are reflected in overall assemblage composition (Dittmann, 1996; Berkenbusch and Rowden, 2007). Bioturbation substantially increases habitat suitability for species dependent on uncompacted sediment (Tamaki et al., 1992). Via elevation of sediment oxygen and nutrient concentrations, burrowing stimulates salt marsh plant growth – including enhancement of mycorrhizal mutualism (Montague, 1980; Daleo et al., 2007).

In contrast, high levels of sediment disturbance and resuspension can be detrimental for susceptible species such as meio-, macrofauna, and plants. Displacement/burial and/or interference with feeding activities caused by substantial amounts of suspended particles decreases the growth and survival of associated species (e.g., suspension-feeding bivalves), leading to drastic declines in their abundance (Murphy, 1985; Dumbauld et al., 2001). Plants are negatively affected when high turbidity impedes photosynthesis and burrowing erodes suitable habitat (Suchanek, 1983; Escapa et al., 2007). As roots and rhizomes (e.g., of seagrass) can interfere with burrowing and feeding activities (Brenchley, 1982), this detrimental impact on plants also signifies a positive feedback effect for the bioturbating crustacean.

7.04.3.9 Infauna

Infauna are invertebrates living within the matrix of aquatic sediments and include polychaetes, oligochaetes, bivalves, nemerteans, echiurans, sipunculids, as well as small crustaceans such as burrowing amphipods and isopods. Infaunal organisms are responsible for the reworking of sediments via crawling and burrowing, feeding and irrigation; they also create burrow structures in soft sediments. Despite their small size relative to other coastal and estuarine engineers, their abundance and activity levels dramatically impact the seascape. They add suspended materials to bottom sediments and vice versa, change sediment particle composition and/or spatial distribution, alter bottom topography and near-bed hydrodynamics, facilitating drainage, and change overall sediment chemistry (Reise, 2002).

Five functional categories of infaunal bioturbators are currently distinguished: (1) biodiffusors, organisms whose activities on the surface result in random diffuse movement of sediments; (2) upward conveyors and (3) downward conveyors, organisms oriented vertically relative to the sediment–water interface that move materials upward or downward via ingestion and egestion, respectively; (4) regenerators, digging species that relocate sediments and create open burrows that remain part of the sediment matrix when abandoned; and (5) gallery-biodiffusors, organisms that dig extensive galleries of tubes or burrows that are linked and irrigated by body movement (Gardner et al., 1987; Francois et al., 1997, 2002; Gerino et al., 2003). However, infauna can cause structural change by mechanisms other than sediment burrowing, redistribution, and irrigation, such as the production of tubes and shells or the binding of sediment particles via mucous secretions.

Infauna can either destabilize or stabilize sediments, making them more or less prone to erosion. Destabilization is generally a consequence of sediment reworking, resulting in a decrease in the critical erosion velocity of the seabed (e.g., due to changes in sediment grain size and microtopography), or in the direct displacement and resuspension of particles by the infauna (Rhoads and Young, 1970; Jumars and Nowell, 1984; Luckenbach, 1986). For example, lugworms, *Arenicola marina*, deposit fecal casts at the sediment surface that are primarily made of fine particles. Given their lower erosion threshold, the fine sediment particles that form casts are rapidly washed away by waves and currents, resulting in significant losses of fine sediments from the intertidal habitat (Volkenborn et al., 2007). In contrast, sediment stabilization generally involves the binding of sediment particles by mucous substances secreted by the infauna (e.g., Miller et al., 1996; Palomo and Iribarne, 2000). For example, feeding and burrowing by the deposit-feeding polychaete, *Laeonereis acuta*, results in extensive production and accumulation of pellets (**Figure 10**). These pellets differ from the casts made by *A. marina* in that they consist of large sediment particles agglutinated by important quantities of mucus. The combination of mucus binding and increased particle size at the sediment surface results in an overall increase in the erosion threshold of the seabed causing net sediment stabilization (Palomo and Iribarne, 2000).

Infauna can have impacts on coastal protection via their own engineering activities as well as via their engineering and nonengineering effects on other coastal engineers. It is currently argued that salt marsh erosion in Southeast England is primarily a consequence of recent increases in the abundance of the polychaete, *Hediste* (*Nereis*) *diversicolor*, rather than a consequence of physical oceanographic factors alone (e.g., sea-level rise and increased wave and tidal action; Hughes and Paramor, 2004). Burrowing and bioturbation by *H. diversicolor* in tidal creeks increase creek erosion, leading to a positive feedback where export of sediment from the creeks causes increased floodable volume and current speeds, and hence further creek bank erosion (Paramor and Hughes, 2004). In addition, *H. diversicolor* prevents the establishment of pioneer marsh vegetation (*Salicornia* sp.) in the seaward edge of the marsh as a consequence of grazing, as well as incidental seed burial and seedling disturbance due to sediment reworking (Hughes and Paramor, 2004; Paramor and Hughes, 2004). By doing so, *H. diversicolor* seemingly contributes to reductions in overall marsh area, thus reducing the ability of these marshes to protect coastal areas from storm flooding (Hughes and Paramor, 2004; see Section 7.04.3.2).

Infaunal ecosystem engineers affect three-dimensional structure and thus the diversity of microhabitats in marine soft sediments (**Figure 10**). In the absence of infauna, soft sediment environments show well-defined sediment layers and a smooth and homogeneous surface (Kogure and Wada, 2005). However, when infaunal organisms recruit into soft sediment habitats, they seek refuge by entering into the sediments and – in many cases – by producing shells, tubes, or burrows (Marinelli and Woodin, 2002). Burrows are often lined with mucus and fine-grained sediment particles; tubes have solid polysaccharide linings (Reise, 2002); and shells are relatively more persistent structures made of calcium carbonate (Gutiérrez et al., 2003). All these structures generate a remarkably more diverse environment within the sediment matrix relative to the originally smooth soft sediment. Their effects on abiotic factors such as pore water circulation and solute distribution have concomitant influence on microorganisms, meiofauna, and other infauna (Aller, 1988).

Surface structures, such as feeding pits, fecal casts, mounds of excavated sediments, the protruding portion of tubes, or the internal burrow space, further dramatically alter sediment topography with impacts on near-bed hydrodynamics and other organisms (Reise, 2002). For example, tubes and funnels made by lugworms, *A. marina*, are avoided by most infauna, though some mobile invertebrates such as fast-swimming copepods and their plathyhelminth predators aggregate in the funnels (Reise, 1981). The amphipod *Bathyporeia sarsi* also aggregate near the lugworm fecal casts as a consequence of advective particle intrusion (Lackschewitz and Reise, 1998). The surface-protruding tubes made by *A. marina* provide attachment for ephemeral algal tufts (*Berkeleya* colonies and *Enteromorpha* thalli; Volkenborn et al., 2009). Inside lugworm galleries, commensals are common, such as the scaleworm *Harmothoe sarsi* (Wetzel et al., 1995). Increased oxygenation (and concomitant changes in biogeochemistry) near burrow

Figure 10 Fecal pellets of the polychaete *Laeonereis acuta* in a tidal flat at Mar Chiquita coastal lagoon, Argentina. Photo credit: Gabriela Palomo.

walls also alter conditions for other infauna living in the surrounding sediments (Bouma et al., 2009b).

In general, sediment reworking by infauna can have both positive and negative effects on subsurface deposit feeders and other burrowing worms (including recruits and juveniles of the same species; e.g., Olivier et al., 1996; Reise, 2002) but negatively affects sessile, tube-building species that require more stable surfaces to recruit and develop (e.g., Woodin, 1976; Volkenborn and Reise, 2006). As illustrated by studies on *N. diversicolor* (Hughes and Paramor, 2004; Paramor and Hughes, 2004, see example above) and *A. marina* (van Wesenbeeck et al., 2007; Reise et al., 2009), sediment mixing by infauna may cause the burial of marsh plant seeds and seedlings leading to plant exclusion from lugworm-dominated areas. As these infaunal species cannot invade plant-dominated areas due to root preemption of belowground space (Paramor and Hughes, 2004; Meysman et al., 2006), lugworms and marsh plants mutually exclude each other. This leads to a patchy intertidal landscape where the alternation of destabilized and stabilized sediments is expected to have a diversifying effect on the marine benthos (van Wesenbeeck et al., 2007; Bouma et al., 2009b; Reise et al., 2009).

7.04.4 Major Ecosystem Engineers in Estuaries and Coasts: Human Impacts and Management

Human development and other activities have major impacts on all the major groups of coastal and estuarine engineers. There are well-documented global declines and progressive losses of important functions fulfilled by engineers, hence a deterioration in ecosystem services provided to humanity (i.e., erosion control, sedimentation regulation, coastal protection, habitat provisioning, and diversity conservation; e.g., van Dijk and Grootjans, 1993; Farnsworth and Ellison, 1997; Steneck et al., 2002; Pandolfi et al., 2003; Orth et al., 2006; Barbier et al., 2008; 2011; Bromberg-Gedan et al., 2009; *see* Chapter **12.06**). The impacts have major economic ramifications and real risks to human lives (e.g., loss of salt marsh storm surge protection and hurricane impacts; Day et al., 2007), while simultaneously causing cultural impoverishment (e.g., biodiversity loss; Coleman and Williams, 2002). The pathways of human impact on these engineers are multiple. They include direct exploitation of engineers at unsustainable levels (e.g., oysters, mussels, and infaunal bivalves; Rothschild et al., 1994; Peterson, 2002); destruction of engineered structure due to fishing activities (e.g., bottom trawling effect on seagrasses, bivalves, and beds of burrowing organisms; dynamite fishing on coral reefs (Engel and Kvitek, 1998; Riegl, 2001)); waste production (e.g., effects of pollution and euthrophication-induced anoxia on organisms; Long, 2000; Diaz and Rosenberg, 2008); habitat transformation for urbanization and other human uses (e.g., dune loss or fixation, salt marsh reclamation and filling, and mangrove forest conversion into shrimp farms; Páez-Osuna, 2001; Wiedemann and Pickart, 2004; Barbier et al., 2008; Bromberg-Gedan et al., 2009); and, finally, current and future impacts related to global climate change (e.g., storm force amplification, sea-level rise and salt marsh submergence and loss, ocean warming and coral bleaching, ocean acidification, and mollusk shell and coral reef production; Brown, 1997a; Allan and Komar, 2006; Bromberg-Gedan et al., 2009; Wei et al., 2009). While addressing these problems will often require action beyond the estuary or the coast, more local management action is nevertheless critical. Given the focus of this chapter on physical ecosystem engineering, it is worth reflecting on humans as engineers; the similarities to and differences from other engineering species; and how humans may utilize such species, or the lessons learned from studying them, to restore function and services to estuaries and coasts.

7.04.4.1 Human Estuarine and Coastal Engineering

Physical engineering of estuaries and coasts by humans is often intentional – designed to build, or in some cases remove, structure. Much of human physical engineering is motivated by the fact that in recent times, marshes and coastal areas are valuable real estate. Kennish (2001) calculates that more than 50% of original tidal salt marsh in the US has been hydrographically transformed through physical alteration of filling, diking, and dredging. Major motivations include dredging to maintain inlets and coastal rivers, seabed mining and oil/gas exploration, stabilizing shifting sediments, attenuating storm energy, and replenishing beach sand.

Shoreline protection is a good case in point. Although the engineering is intentional, its consequences include some that are unforeseen and undesirable. Humans seek to armor shorelines to attenuate storm and wave surge and anchor naturally migrating sediments. Sea walls, riprap, jetties, and groins are often built for these purposes. They often accomplish the task, at least in the short term. However, there are almost always longer-term consequences that usually stem from the attenuation of the abiotic impact at nearby unprotected sites. For example, groins in surf zones often retain sand, but starve downstream beaches of sand. Sea walls can block wave energy, protecting areas behind from erosion, but often accelerate erosion on beaches below (Hall and Pilkey, 1991).

There are many other examples of human physical engineering with unintended consequences. Removal of mangroves to build shrimp farms or otherwise develop a coastline, in turn, removes a critical ecosystem engineer. Loss of mangrove habitat decreases storm attenuation and habitat/species diversity (Barbier et al., 2008; Das and Vincent, 2009; Krauss et al., 2009). Building canals not only increases ship connectivity but also creates a conduit for propagule transfer of exotic species (Mathieson and Pederson, 2008). More than half of the 573 nonnative species in the Mediterranean Sea were introduced via the Suez Canal alone (Galil, 2009). Likewise, by deepening ports and building berms to protect harbors, we increase water retention, and thus exotic propagule retention, and their subsequent success and establishment (Byers and Pringle, 2006). Fishing often employs techniques – dynamite fishing on coral reefs, bottom trawling, and oyster reef dredging – that destroy critical habitat structure for species (Engel and Kvitek, 1998; Riegl, 2001).

7.04.4.2 How does Human Engineering Compare to Nature's Engineers?

The answer to this question may depend on the type of human engineering carried out. As in many of the above-mentioned examples, humans often impose very foreign kinds of engineering (i.e., no natural analog); in other cases, the engineering is more equivalent to that done by Nature's engineers. Because Nature's engineers are often part of the evolutionary history of species in the system, human engineering that best matches natural engineering should, in principle, have less impact on resident species, and hence the functioning of the system. In the discussion that follows, human engineering is grouped into two broad categories: (1) humans attempting to use or imitate Nature's engineers and (2) humans attempting to engineer something Nature is not already doing.

7.04.4.2.1 Humans using or imitating Nature's engineers

Restoring an engineered ecosystem. The most direct and effective approach to replicating Nature's engineers is to put them back into the ecosystem (Byers et al., 2006; Halpern et al., 2007). Such a restoration ecology approach allows the engineer to cause the desired abiotic state change. Some of the most innovative and successful coastal engineering today involves growing ecosystem engineers in desired, appropriate locations. For example, in the Living Shorelines program, oyster reefs are seeded and developed along erosion prone tidal channels (Bilkovic and Roggero, 2008). Another example is the recognition that mangroves and salt marshes attenuate storm energy. The urgent call for replanting and protecting mangroves in many areas of the South Pacific following the 2004 tsunami was a clear recognition of their vital importance in storm protection (Das and Vincent, 2009; Teo et al., 2009). Similarly, after Hurricane Katrina in 2005 many scientists called for extensive salt marsh vegetation restoration throughout the US Gulf Coast to restore hydrological function and sediment stabilization (Day et al., 2007).

Using an ecosystem engineer in a novel place or setting. A close equivalent to restoring an ecosystem engineer is placing it in a novel area to engineer an important function. An excellent example is creation of cattail marshes (*Typha latifolia*) to filter water, sewage, and runoff in order to enhance water quality. Such marshes have proved far more cost effective than water treatment plants for small-scale projects (Gessner et al., 2005). Sea oats and other coastal vegetation are effectively used to stabilize dunes and barrier islands (Levin et al., 2006). Mendelssohn et al. (1991) demonstrated that sand fencing in conjunction with vegetation planting is the most successful way to build protective dunes. The method combines a human engineering method to start the sand trapping process with completion of the process by using a natural engineer that holds the engineered structure in place.

A major caveat to placing nature's engineers in novel settings is that unintended consequences often accrue when using nonnative engineers. Good examples of this are the introductions of nonnative *Ammophila* and *Spartina* on the Pacific coast of North America discussed previously (see Sections 7.04.3.1 and 7.04.3.2). Another example is nonnative mangroves (*Rhizophora mangle*) that were introduced to Hawaii for the purpose of stabilizing coastal mud flats. Prior to the early 1900s, there were no mangroves in the Hawaiian Archipelago. This species is now well established in Hawaii and is found on nearly all of the major islands. Although mangroves are highly regarded for the many ecosystem services they can provide, in Hawaii, their positive effects are few; they include some ecological services attributed to mangroves elsewhere, such as sediment retention and organic matter export. On the other hand, known negative impacts include reduced habitat quality for endangered waterbirds such as the Hawaiian stilt (*Himantopus mexicanus knudseni*); mangrove colonization of habitats that displace native species (e.g., in brackish water pools); overgrowth of Hawaiian archaeological sites; and drainage and aesthetic problems (Allen, 1998).

We need to recognize the potential for antagonisms and negative feedbacks among impacts caused by invasive species and human engineering, including the inadvertent engineering discussed above. Human engineering can increase establishment and impacts of non-native species by skewing environmental conditions away from the optimum to which native species are adapted. Therefore, human engineering may often set the stage for more frequent, successful, and impactful biological invasions. The novel, often-sustained environmental changes that human engineering imposes may be sufficient to move a species out of the adaptive parameter space defined by its evolutionary history – a process called selection regime modification (SRM; Byers, 2002). A native species may therefore suddenly find itself in an environment that in many ways is just as novel to it as it is to a nonindigenous species (Byers, 2002). SRM can therefore accentuate competitive impacts of exotics on natives by eliminating a native species' prior resident effect or home court advantage; that is, human engineering can increase invader establishment and impact not only by creating new microhabitats and decreasing populations of native species that can resist invasion, but also by potentially weakening the *per capita* capacity of the native biota to resist invaders.

Imitating an ecosystem engineer. The structures and functions of ecosystem engineers can sometimes be imitated without organisms. Armoring shorelines with riprap, dikes, etc., mimics the functions, though not always the form, of many storm-attenuating engineers such as mangrove, dune, and salt marsh plants. Artificial reefs are perhaps the most obvious example. A diversity of materials have been used (with mixed success) from molded plastic to derelict cars, boats, and used tires (Clavijo and Donaldson, 1994; Bolding et al., 2004). Although fish are clearly abundant on these structures, there is still much scientific debate as to whether higher fish abundance on these reefs represents increased regional production or just local aggregation (Powers et al., 2003).

7.04.4.2.2 Humans engineering something Nature does not

By imposing foreign, no-analog engineering, humans will typically be fighting the ecosystem. Aquatic habitats such as estuaries and coasts are such physically influenced environments that doing something novel usually requires constant maintenance and upkeep. Furthermore, if human intervention contravenes natural processes, the system can end up storing massive potential energy that can get suddenly unleashed with disastrous effect. For example, levees prevent normal, regular flooding and distribution of alluvial sediments onto the flood plain (over-bank storage; Day et al., 1995). With natural sediment accrual eliminated, banks can become sediment starved, lower in elevation, and with no natural riverbank levee (Kesel, 2003). This accentuates damage from flooding when levees break. Jetties that starve downstream beaches of sediment often accelerate erosion; in Florida, jetties are estimated to cause 85% of beach erosion (Finkl, 1996). Dredged channels allow easier navigation, but require continuous dredging to counteract inevitable infill. The increase in the tidal prism caused by dredging then increases the frequency and duration of submergence of fringing salt marsh. The marshes are then subjected to wave action for longer time periods, increasing erosion risk (Cox et al., 2003). In yet other cases it has been shown that dredging for beach nourishment or construction materials perturbs natural littoral processes, and can change wave transformation patterns that ironically causes a new loss of sand from the littoral system (Demir et al., 2004).

7.04.4.3 Ecosystem Engineers and Ecosystem-Based Management

There is increasing recognition that the most efficient and effective way to manage natural systems is often through ecosystem-based management (EBM; Leslie and McLeod, 2007; Altman et al., 2011). Given the dominant influences of some engineers in coastal ecosystems, protecting and restoring them may be the most parsimonious and effective means of guaranteeing proper ecosystem functions and services (Byers et al., 2006; Halpern et al., 2007; Barbier et al., 2008; Koch et al., 2009; Granek et al., 2010; *see* Chapter **12.06**).

Identifying engineered habitats that are essential for protection/preservation is critical. For most of the US Atlantic and Gulf coastal estuaries, two species – the marsh cordgrass *Spartina alterniflora*, and the Eastern oyster *C. virginica* – hold dominant sway on functioning, stability, and diversity of the system. These species control sedimentation rates, erosion/deposition, buffer upland runoff, and provide biogenic habitat. Oyster reefs also stabilize sediment, filter water, and provide refuges for commercially valuable species (Grabowski and Peterson, 2007). Protecting or sustainably managing these species is, in and of itself, EBM because by their very nature the two species control many ecosystem goods and services. Their strong influence on multiple properties and flows within ecosystems exemplifies that major coastal ecosystem engineers might form a good starting point for EBM programs (Koch et al., 2009). If the ecosystem services produced by these species were removed, they would be at least very costly for humans to replace, and often impossible to achieve (Barbier et al., 2008; *see* Chapter **12.06**).

There are encouraging signs that managers are starting to recognize the potential contributions of ecosystem engineers to EBM (Koch et al., 2009; Granek et al., 2010). For example, oyster reefs create protective structure that is an essential habitat for many other ecologically and commercially important species. Grabowski and Peterson (2007) showed that oyster reef structure is economically more valuable than the oysters themselves. The State of North Carolina has therefore now changed their approach to oyster restoration, not only by targeting restoration in key habitat areas, but also by greatly limiting oyster harvesting techniques (such as tonguing) that damage reef structure (Grabowski and Peterson, 2007).

7.04.4.4 Lessons from Nature's Engineers: Improving Human Environmental Engineering

Based on the above we suggest a two-tiered approach to human engineering:

1. *Using, protecting, and restoring engineers:* This means that we should use existing ecosystem engineers, prevent damage to engineered habitat, intervene/preempt impacts on engineers, and, if necessary, restore engineers (e.g., Byers et al., 2006; Halpern et al., 2007).
2. *Human engineering as a last resort.* In essence, we should use human engineering as a last engineering option, and, if implemented, be vigilant.

7.04.4.4.1 Using, protecting, and restoring engineers

Often we only recognize the important engineering work that was being done by species once they are missing, diminished in density, or impaired in their engineering activity. Certain areas such as coastal deltas and marshlands of New Orleans/Southern Louisiana may have been irreversibly changed given the scale of habitat loss and transformation. The loss of mangrove, beach dunes, and coral in Indonesia intensified tsunami impacts (Lui et al., 2005; Das and Vincent, 2009). Loss of wetlands in the US Gulf coast intensified Katrina damage (Tornqvist et al., 2008). Although these recent disasters were accentuated by human elimination of important ecosystem engineers, one encouraging aspect is that we are now getting better at identifying them in advance. We should therefore preempt problems stemming from the loss of ecosystem engineers wherever possible, recognizing their potential role in EBM and ecosystem services.

We must recognize that Nature often engineers better – natural selection is a powerful force and evolutionary context is too important to ignore. Putting back an engineer, if lost, may be the best way to restore abiotic conditions because it can allow the ecosystem to recover on its own more readily (Byers et al., 2006; Halpern et al., 2007). Clearly, restoration efforts should be prioritized based on habitat engineers (e.g., oysters and reef-building polychaetes) because of their often far-reaching and lasting legacy effects, and their ability to transform abiotic properties and thus alter ecosystem services (Byers et al., 2006; *see* Chapter **12.06**). In many cases, engineering of the environment is most readily done by Nature's engineers. For example, mangroves and oysters are cheaper, easier, and often better at buffering storms and preventing erosion than human dikes and levees (Lewis, 2005; Piazza et al., 2005; Das and Vincent, 2009; Krauss et al., 2009); they are self-renewing and they run on solar energy not fossil fuel.

We must use caution in taking ecosystem engineers out of their native range. Subtle performance differences in introduced ranges have led to unintended consequences, as we have seen for dunes and salt marshes. For example, *Ammophila* and *Spartina* grasses engineer critical biogenic habitat on the US east coast where they are native, but have caused substantial, adverse system changes on the US west coast where they where introduced (Wiedemann and Pickart, 2004; Lambrinos, 2007; Hacker et al., in press).

7.04.4.4.2 Human engineering as a last resort

Humans often try to replicate some ecosystem services, for example, stabilize sediment with dikes, because they want larger-scale protection of greater magnitude and higher certainty than what Nature's engineers provide. However, if the desired engineering to be imposed is outside or above the magnitude of what is naturally done in the system, managers will have to be vigilant for system changes, buildup of energy, and potential unintended collateral consequences of engineering. Such changes will be altering the environmental conditions and selective forces outside of the realm typically experienced by the resident species. Thus, human engineering is likely best when designed for resilience, not rigidity – that is, when engineered structures that properly mesh with the context of their environment have natural pressure-release valves and when the resulting abiotic changes are within the evolutionary experience of resident organisms.

In many cases, using a native or even an exotic ecosystem engineer may be impossible if the species no longer exists or if the abiotic conditions are not suited for its establishment. In such cases, human engineering is often the only sensible approach. The good news is that humans are increasingly learning to refine their engineering approaches, in no small part from mimicking as closely as possible the actions of beneficial Nature's engineers (Rosemond and Anderson, 2003). Increased ecological training for engineers working in areas of ecosystem restoration will help enhance such approaches.

7.04.5 Prospectus

The general framework for physical ecosystem engineering helps reveal commonalities among the major groups of coastal and estuarine ecosystem engineers. For instance, all the above-mentioned engineers, and the structures they create, constitute dense and extensive aggregations and sometimes massive, discrete structures (e.g., coral, bivalve, and seagrass reefs). Such remarkable changes in the physical structure of the ecosystem largely affect the characteristics of living space and the incidence of the different forms of kinetic energy, leading to changes in sedimentary process and the habitat available to other organisms. However, as pointed out in Jones et al. (1994) "the devil is in the details"– particular attributes of species and local environmental conditions often make a real difference. For example, although the physical structure of seagrass meadows limits predator access and provide refugia to a variety of organisms (Hemminga and Duarte, 2000; Heck and Orth, 2006; see Section 7.04.3.4), there are some particular aspects that cannot be predicted from generalities of the framework, such as the effect of seagrass patchiness on the survival of blue crabs (Hovel and Fonseca, 2005). In ecology. one cannot get away from this (Dunham and Beaupre, 1998; Lawton, 1999). This tension between general and specific is both a research and a management challenge. How far can the framework, underlying relationships, principles, and derived models take us before we must have recourse to local understanding? Can adequate prediction be achieved with general models – and we must recognize here that much of our current understanding is descriptive and explanatory – or will we always need a locally specified model? Physical ecosystem engineers play central roles in coastal and estuarine structure and function. There is a pressing need to address substantive deterioration. There are substantial uncertainties surrounding future threats such as climate change. The more powerful our general understanding, the more useful it can be in informing policy and guiding shifts in management strategies, even if management practice will always require local knowledge.

While there is a richness of general and specific current understanding revealed in this chapter, there are also clear knowledge lacunae of scientific and management relevance. First, coasts and estuaries play very significant roles in biogeochemical processing (Kennedy, 1984; Bianchi, 2007), and humans have significantly, adversely affected this capacity in a variety of ways (e.g., eutrophication and hypoxia due to anthropogenic organic matter loads (Diaz and Rosenberg, 2008) and acidification due to increased atmospheric CO_2 altering the natural carbonic acid cycle in the ocean (Wei et al., 2009)). Physical ecosystem engineering is known to markedly affect such processing, largely because abiotic conditions changed by engineers (e.g., sediment porosity/permeability, sedimentation and organic matter deposition, water flow, and solute advection) are major controls on biogeochemical processes. There is a conceptual framework for these effects (Gutiérrez and Jones, 2006) that is compatible with the framework we presented here. Some, albeit scant, reference was made to engineer control on biogeochemistry (e.g., organic matter trapping and increased biogeochemical process rates in permeable coral sands, increased oxygen availability, and nutrient concentrations in deep sediments due to crustacean burrowing; see Sections 7.04.3.6 and 7.04.3.8, respectively). In general, the presence of any of the major coastal and estuarine engineers discussed above is accompanied by high variation in biogeochemical processing relative to the unmodified baseline state (e.g., decreases in pH and calcium carbonate and increases in nutrients associated to dune plants (Willis, 1989); increased nitrogen and carbon accumulation in kelp individuals located at the edge of forests relative to those at the forest interior (Stewart et al., 2008); and increased oxygen, organic carbon, and bacterial activity in seagrass sediments relative to adjacent, bare sediments (Hemminga and Duarte, 2000)). Nevertheless, while the biogeochemical differences between habitats with and without engineers may be attributable to engineering mechanisms in some cases (e.g., changes in sediment surface area available for microbial biomass and reactive exchange due to sediment sorting by marsh canopies (Pinay et al., 2000) and accelerated advective porewater flow and increased transport of oxygen deep into the sediments due to the uneven topography created by crustacean burrows (Ziebis et al., 1996)), in other cases it may not (e.g., increased sedimentary carbon due to inputs in the form of linings secreted by burrowing invertebrates (Papaspyrou et al., 2005); changes in sediment redox potential due to oxygen leaked from plant roots (Thibodeau and Nickerson, 1986; Hacker and Bertness, 1995; Pedersen et al., 1998)); or is unknown. The paucity of information reflects a research challenge of direct management relevance. We need to better understand how biogeochemical processing is affected by ecosystem engineers (humans included), and how management can maintain, restore, and enhance these functions.

Second, we need a much greater understanding of spatial and temporal dynamics and the role of engineer feedbacks in these coastal and estuarine ecosystems, especially if we seek to effectively manage in an uncertain future. While there is an obvious connection between, for example, sand interception by plants and dune system formation, or coral growth and coral reef formation, explicitly relating fine-scale phenomena to the larger-scale patterns and their consequences is not facile, particularly if there are feedbacks across scales. Yet understanding these relationships is central to maintaining or reestablishing engineers and their functions.

Third, it is clear that physical ecosystem engineering in these coastal and estuarine systems invokes relationships to other general ecological concepts that warrant further intellectual development; most notably, self-organization (van de Koppel et al., 2005a, 2005b; Crawford et al., 2006; Fonseca et al., 2007), resilience (Snover and Commito, 1998; Nyström et al., 2000; van de Koppel et al., 2005a; Crawford et al., 2006; Alongi, 2008), and evolutionary history. Many coastal and estuarine ecosystems can be thought of as at least partially self-organized by engineers (e.g., salt marshes, van de Koppel et al. (2005b); mussel beds, van de Koppel et al. (2005a); and seagrass meadows, Fonseca et al. (2007)) and as systems capable of persistence or reestablishment (resilience) in the face of external forcing (e.g., coral reefs, Nyström et al. (2000); mussel beds, van de Koppel et al. (2005a); and mangrove forests, Alongi (2008)). Their capacity to do so and their many positive effects via habitat creation are, in part, the result of evolutionary processes (e.g., gregarious settlement in reef-forming corals and bivalves; Wood, 1998). Knowing the engineer attributes that are most influential in self-organization and resilience, along with the factors affecting these attributes, including external forcing, helps identify critical features that should be the focus of management. For example, macrophyte stiffness is a critical feature determining sediment deposition and the self-organization of salt marsh ecosystems (Bouma et al., 2005). Similarly, knowledge of the evolutionary history of the engineer and associated biota may be of real value. For example, the duration of association – in combination with knowledge of the abiotic requirements and sensitivities of species – can inform expectations in the face of environmental change. The degree of functional similarity between an introduced and native engineer (either deliberately or accidentally substituted) can likewise inform expectations for similarities and differences in effects.

Finally, the recognition that humans are powerful coastal and estuarine ecosystem engineers (Jones et al., 1994), despite our often adverse effects, should provoke deep reflection on how we should change the conduct of our activities. Our growing understanding of the central roles of Nature's physical ecosystem engineers in these ecosystems, as illustrated in this chapter, must be used to formulate powerful arguments for changes in human engineering strategies and practices, and a new set of ecologically based engineering principles upon which this can be based.

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