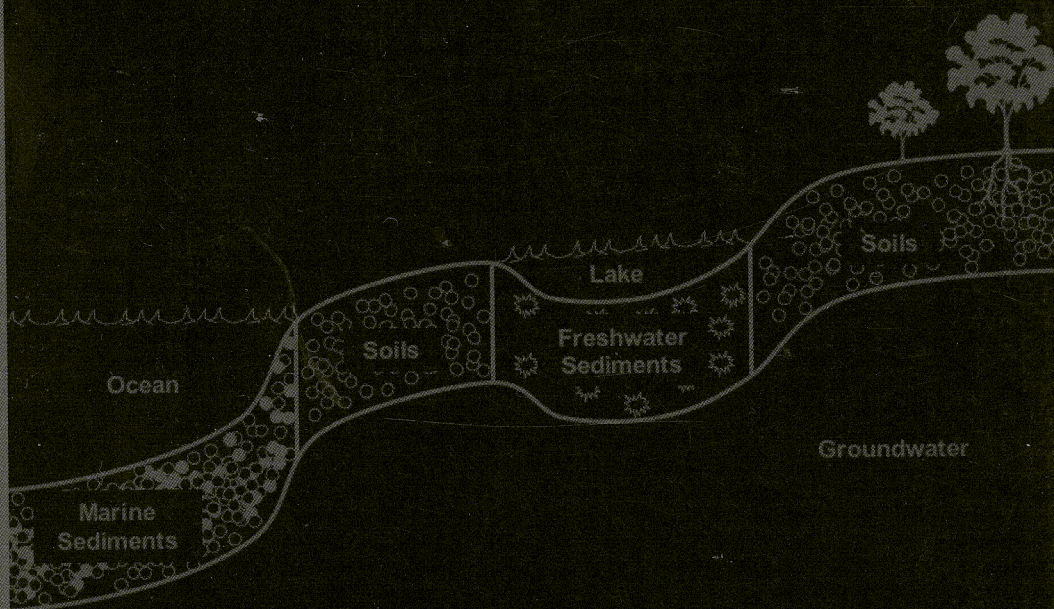


SUSTAINING BIODIVERSITY AND ECOSYSTEM SERVICES IN SOILS AND SEDIMENTS



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Marine Sedimentary Biota as Providers of Ecosystem Goods and Services

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Marine sediments cover more of the Earth's surface than all other ecosystems combined (Snelgrove 1999), yet direct human experience is limited largely to the narrow zone at the interface between land and sea. Although 62 percent of the Earth's surface is covered by water greater than 1,000 m deep, only approximately 2 km² (Paterson 1993) has been quantitatively sampled for macrofauna (invertebrates greater than 300 microns but not identifiable in photographs) and only 5 m² (Lamshead 1993) has been sampled for meiofauna (invertebrates greater than 300 microns but retained on a 44-micron sieve). With most of the ocean sedimentary biota out of sight, we tend to ignore their role in regulating rates and processes that maintain the integrity of marine systems (Snelgrove et al. 1997), instead focusing on biologically generated products or consequences that are of direct economic benefit. The publicity associated with the Kyoto Protocol (United Nations 1992), particularly with respect to atmospheric carbon dioxide increases and carbon sequestration, has helped to broaden public concern about the role of the sea in climate regulation, but even here, the primary focus has been on the water column above the seafloor and its processes (Martin et al. 1994; Hanson et al. 2000). Public outcry in the United States and elsewhere has driven major changes in environmental policy over the last 20 years, resulting in significant improvement in environmental standards for air, land, and drinking water, and improved protection for species that are considered endangered. Unfortunately, oceans have not received similar levels of protection. Seaward deposition of waste materials generated in the terrestrial domain continues generally without regard for effects on sediments and marine benthos. Most marine sedimentary organisms are undescribed (Grassle & Maciolek 1992) and have no degree of protection.

Table 4.1. Goods and services provided by sedimentary systems.

The role of sedimentary invertebrates has been inferred from published studies; ratings are based on estimated global importance. Public concern is based on qualitative observations of how frequently the good or service is discussed in the popular press.

	<i>Role of Sedimentary Biota</i>	<i>Public Concern</i>
<i>Provisioning</i>		
Animal food	moderate	high
Plant food	low	low
Medicine & models for human research	moderate	low
Fuels & energy	high	low
	(on geological time scales)	
Clean water	high	moderate
Fiber	low	low
<i>Regulating Services</i>		
Remineralization	high	low
Waste treatment	high	low
Biological control	moderate	low
Gas and climate regulation	moderate	moderate
Disturbance regulation	moderate	low
Erosion and sedimentation control	high	low
<i>Habitat Maintenance Services</i>		
Landscape linkage & structure/ habitat/refugia	high	moderate
<i>Aesthetic Services</i>		
Recreation, tourism, and education	high	high

Although oceans are responsible for approximately 60 percent of the estimated total value of global ecosystem services (Costanza 1999), efforts to value the specific roles of sedimentary biota are effectively nonexistent.

In this chapter we identify ecosystem processes that are strongly influenced or regulated by marine sedimentary systems, and consider how marine sedimentary organisms contribute to economically important extractable *ecosystem goods/products* (e.g., fish) and influence *ecosystem services* (e.g., water purification and shoreline stabilization, see Chapter 1, Figure 1.1) within the marine environment. We include a summary of important ecosystem goods and services provided by marine sedimentary biota (Table 4.1), the roles that living organisms play in delivering those goods and services, the biotic and abiotic factors that regulate provisioning of services, and specifically how biodiversity

contributes to regulation and provisioning of ecosystem goods and services. The marine systems considered here are grouped into estuarine, continental shelf, and deep-sea sediments. *Estuaries* encompass sedimentary habitat at the land-sea interface where freshwater input measurably dilutes seawater, *continental shelf sediments* refer to the submerged, gently sloping seafloor between continents and the upper edge of the continental slope (~130 m deep), and *deep-sea sediments* include the comparatively steep (~4°) continental slope that extends from the edge of the continental shelf to the less steep continental rise (~4,000 m) that grades into the abyssal plains (4,000–6,000 m). Abyssal plains are primarily sediment-covered, flat rolling plains that cover approximately 40 percent of the Earth's surface; in some areas they contain submerged mountains known as *seamounts* that can extend thousands of meters above the seafloor to relatively shallow depths. Threats and sustainability of goods and services in these habitats are addressed in Chapter 7.

Estuarine and Continental Shelf Sediments

Approximately 39 percent of the global human population, or approximately 2.2 billion people, lived within 100 km of the coast in 1995, most within estuarine watersheds (Burke et al. 2001). In countries such as the United States, coastal populations have increased faster than the overall population (Beach 2002). Historically, human populations have depended on estuaries for food (e.g., fish and shellfish), transportation, trade (e.g., waterways, sheltered ports), and recreation. Ancient civilizations in the Fertile Crescent (area around the rivers Tigris, Euphrates, Nile, and on the western slopes of the Mediterranean coast) are now recognized to have had a culture and society that were based on utilization of wetlands and estuaries (Pournelle 2003). This dependence on estuaries has arisen because these sedimentary environments harbor abundant fishes and shellfishes, are habitats for many invertebrates that are also integral parts of estuarine and oceanic food webs, and are essential for the long-term sustainability of coastal ecosystems.

Wherever they occur, vascular plants contribute to virtually every ecosystem service associated with estuaries. Although restricted to intertidal (e.g., marshes and mangroves) and shallow subtidal (seagrass beds) portions of temperate and tropical estuaries, the contribution of these plant communities to estuarine production can be greater than suggested by their modest areal extent (Heymans & Baird 1995). Above-ground plant structures (e.g., stems and leaves of marsh plants or prop roots of mangroves) trap and retain sediments, and provide substrata, refugia, and food for estuarine biota (Thayer et al. 1987; Covi & Kneib 1995). Plant roots help to stabilize sediments and promote the structural integrity of tidal channels, and mediate biological activity in the sediments by transporting oxygen to the root zone and detoxifying sediments (Lee et al. 1999). Benthic plants and animals also maintain environmental

quality by binding and removing particulates and contaminants from the water column and sediments and are an integral part of the aesthetic vistas of coastal landscapes that enrich the human spirit.

Although estuarine sediments contain few species relative to most other sedimentary habitats, they nonetheless represent hotspots for ecosystem processes that can extend well beyond the estuarine sediments. Of the ecosystem goods and services associated with shelf and nearshore ocean areas, people are most aware of provisioning of food (e.g., fish and shellfish), which has huge commercial and cultural importance in coastal societies worldwide. Even aquaculture businesses often rely on wild (natural) fisheries (e.g., for fishmeal) or natural supply of food (e.g., phytoplankton) for aquaculture species and, in some cases, for provision of brood and juvenile stocks. Marine plants are used as food, particularly in Asia, and seaweed extracts such as alginates and other phycocolloids are used in many industrial and food applications (e.g., manufacture of films, rubber, linoleum, cosmetics, paints, cheeses, lotions). The living components of estuarine systems provide not only the primary and secondary production that supports commercial, recreational, and subsistence fishing and other extractable resources, but also much of the structure that stabilizes sediments to provide flood and erosion control, and maintains the integrity of wetlands and coastal waterways (Levin et al. 2001a; Tables 4.2a–4.2b).

Sedimentary fauna are a critical part of the diet for many estuarine and shelf species that feed near or on the bottom, such as cod and flatfish (Feder & Pearson 1988; Carlson et al. 1997). Some pelagic fish feed directly on benthic invertebrates at the seafloor-water interface during various phases in their life cycles. Many benthic fauna spend the early parts of their life cycle in the plankton and, in some cases, are extremely abundant and potentially important for pelagic food chains (Lindley et al. 1995). Structure-rich sedimentary habitats, particularly marshes, mangrove swamps, and seagrass beds, create refuges for juveniles of commercially exploited pelagic fish and invertebrates (Laurel et al. 2003).

Nutrient cycling and sediment oxygenation (redox) processes are interlinked to lesser known, but key, services of detoxification and disposal of waste by shelf and estuarine sediment biota. These processes are regulated directly by microbial organisms and indirectly by larger, bioturbating organisms (Henriksen et al. 1983; Pelegri & Blackburn 1995). Detoxification and immobilization of contaminants may represent a service or a disservice, depending on the circumstances. Detoxification is performed primarily by microbes (Geiselsbrecht et al. 1996) and may be facilitated by bioturbation, which strongly influences oxygenation and physical movement of contaminants. Bioturbating organisms such as polychaete worms relocate sediment particles and water as they feed, and amalgamate fine particles into fecal pellets (Levinton 1995). Microbes process organic wastes and organic compounds into less hazardous breakdown products (Boyd & Carlucci 1996; Lee & Page 1997), which can be recirculated back into the water column through bioturbation. Microbial processing of toxic waste such as organometallic

compounds can produce harmful breakdown products that can be biomagnified through the food web (Srinivasan & Mahajan 1989). Bioturbation activity by large invertebrates can also accelerate pollutant burial by feeding and removing material at the sediment surface and defecating deeper in the sediment, but feeding at depth by other species that defecate at the surface can also remobilize buried contaminants (Gallagher & Keay 1998).

Sediment-dwelling organisms contribute to sediment formation through their skeletal remains (e.g., the shells and calcareous structures of mollusks, foraminifera, and lithothamnia [algae]). More importantly, particularly in nearshore, shallow-subtidal habitats, sedimentary organisms directly affect sediment stability and erodability (Levinton 1995; Paterson & Black 1999). Sediment particles are bound together by extracellular polymeric substances (mucus) within diatom and microbial films (Grant & Gust 1987), and within meiofaunal and macrofaunal secretions. Macrofaunal fecal and pseudofecal production also binds sediments (Rhoads 1963). Although biological adhesion (Grant et al. 1982) and biological structures above the sediment (such as seagrass, Fonseca & Fisher 1986), can stabilize sediment, biologically generated bottom roughness (Wright et al. 1997) and increased water content of sediments as a result of bioturbation (Rhoads & Young 1970) can also increase erodability.

Shelf and estuarine sediments are habitats for many fishes and invertebrates, and are valued for recreation, sport and subsistence fishing. Sandy beaches, for example, are of particular importance as recreational areas (Weslawski et al. 2000). Sediments provide educational value because of their role in the ecosystem and can have spiritual importance for humans as a source of food, ornaments, and even currency (shells).

Estuaries are the most accessible marine sedimentary habitats for humans, and they are also the most productive. The value of ecological services from estuaries can be substantial, an observation that can be attributed to the service of nutrient cycling defined as the storage, internal cycling, processing, and acquisition of nutrients (Costanza et al. 1997; Ewel et al. 2001). In open estuaries, much of the nutrient cycling occurs in the water column, but the benthic component in shallow subtidal and intertidal systems is also important. As with estuaries, depending on the local communities' values and willingness to pay (Daily et al. 2000; Dasgupta et al. 2000), the value of ecosystem services for intertidal wetlands could be substantial. Intertidal wetlands provide critical services such as waste treatment, environmental buffering/flood control, recreation, and food production. Many service categories (e.g., nutrient cycling) must be considered based on their value at local levels; thus, total economic value of these systems may be underestimated at regional and global levels. It is also important to recognize that many methods have been applied in placing monetary values on estuarine habitats, including the substantial cost of restoration to recover lost functionality (Kruczynski 1999). There is insufficient evidence available to know whether estuaries can be restored to all previous functions, although partial restoration of some functions has been achieved in some cases (see Snelgrove et al. Chapter 7).

Table 4.2a. The provisioning of goods and services for estuaries.

We have used a qualitative ranking scale from -3 to +3 to compare the relative importance of a given good or service ("Rank") within estuaries. Negative scores denote situations where sedimentary fauna can negatively influence a good or process (e.g., remobilizing pollutants into the environment). We have also estimated the relative importance of species, functional, and habitat diversity in the delivery of a given good or service ("Diversity Importance") using a relative scale from 0 to 3. These rankings are qualitative and largely based on inference rather than diversity studies *per se*. Where information was insufficient to allow assignment of a rank value, a question mark was entered in the table and a value of zero was used in sums.

	Rank	Biotic Contributors	Abiotic Regulators	External Interaction	Diversity Importance		
					Species	Functional	Habitat
<i>Provisioning Services</i>							
Plants as food	-1 to 1	grazers, pathogens	oxygen, circulation, substrate, nutrients		1	1	1.5
Animals as food	-3 to 3	fish, invertebrates, all zoo- and phyto-benthos, pathogens	oxygen, circulation, substrate	food, life history, detritus	3	3	3
Other biological products	-3 to 3	bait worms	sediment type		1	1	2
Biochemical/medicine/models for human research	2	microbes, natural products, invertebrate models	temperature, chemical availability, sediment type		3	3	3
Fuels/energy	1	microbes, peat, mangroves	temperature, time		1	1	1
Fiber	1	sponges, sea grasses, mangroves	water flow, sediment type		1	1	2
C sequestration	1	microbes, peat	sediment type, redox		1	2	2
Nonliving materials (geological effects)	2	bioturbators, microbes, infauna, maerl, shellgravels	hydrodynamic processes, sediment type		1	1	2
Clean seawater	3	seagrasses, saltmarsh plants, biofiltration, bioturbators	hydrodynamic processes, redox, sediment type		2	3	3
<i>Regulation Services</i>							
Sediment formation: biodeposition	-1 to 3	microbes, lithothamnia, biogenic sediments, vegetation, filter feeders, infauna	hydrodynamic processes, freshwater & land runoff, sediment type	sinking of particulates	1	2	3
Nutrient cycling	3	microbes, bioturbators, macrofauna, fishes, phyto-benthos	hydrodynamic processes, temperature	resuspension	3	3	3
Biological control: disease, invasive species resistance	?	?	oxygen, eutrophication, sedimentation, salinity		3	3	3
Detoxification, waste disposal	-3 to 3	microbes, zoo- & phyto-benthos, bio-filters & bioturbators	circulation, resuspension, sedimentation		3	3	3
Climate regulation (C sequestration)	1	bioturbators, microbes, infauna, mobile fauna	hydrodynamic processes, upwelling, resuspension, sedimentation	terrestrial & pelagic input	1	1	3
Food web support processes	3	entire benthos	hydrodynamic processes, upwelling, resuspension, sedimentation, oxygen	terrestrial & pelagic input	3	3	3
Atmosphere composition	2	microbes, kelps, wetlands	oxygen, substrate, turbulent mixing, wind	?	1	1	2
Flood and erosion control	3	vascular plants, biostabilizers			1	2	2
Redox processes	3	bioturbators, microbes	oxygen	carbon flux	3	2	2

(continued)

Table 4.2a. (continued)

	Rank	Biotic Contributors	Abiotic Regulators	External Interaction	Diversity Importance		
					Species	Functional	Habitat
<i>Habitat Maintenance Services</i>							
Landscape linkages & structure/ habitat/refugia	3	vegetation, biogenic reefs, migrating fauna	oxygen, temperature, depth, substrate	carbon flux, larval stages	2	3	3
<i>Aesthetic Services</i>							
Spiritual/cultural	3				3	1	3
Aesthetic	3				3	1	3
Recreation	3				2	1	3
Scientific understanding	3	ecological paradigms & education			3	3	3

Table 4.2b. The provisioning of goods and services for shelf sediment ecosystems.

See Table 4.2a for explanation of ranking scheme.

	Rank	Biotic Contributors	Abiotic Regulators	External Interaction	Diversity Importance		
					Species	Functional	Habitat
<i>Provisioning Services</i>							
Plants as food	0						
Animals as food	3	fish, invertebrates, all benthos	oxygen, circulation, substrate	food, life history	3	3	3
Other biological products	0						
Biochemical/medicines/ models for human research	2	microbes, natural products, enzymes	temperature, chemical availability		2	2	2
Fuels/energy	3	microbes	temperature, time		1	1	0
Fiber	1	Sponges			1	1	2
C sequestration	1	bioturbators, microbes, infauna	CO ₂ , temperature, advection	carbon pump	1	2	1
Nonliving materials (geological effects)	0						
Clean seawater	1				1	1	1
<i>Regulation Services</i>							
Sediment formation: biodeposition	2	microbes, lithothamnia, biogenic sediments	currents, freshwater and land runoff	sinking of particulates	2	2	2
Nutrient cycling	3	microbes, bioturbators, macrofauna, fishes	circulation, temperature, tides	resuspension	2	3	2
Biological control: disease, invasive species resistance	?				?	?	?

(continued)

Table 4.2b. (continued)

	Rank	Biotic Contributors	Abiotic Regulators	External Interaction	Diversity Importance		
					Species	Functional	Habitat
Detoxification, waste disposal	-3 to 3	microbes, benthos	circulation, resuspension, sedimentation		3	3	3
Climate regulation (C sequestration)	1	bioturbators, microbes, infauna, mobile fauna	hydrodynamic processes, upwelling, resuspension, sedimentation	terrestrial & pelagic input	2	2	2
Food web support processes	3	entire benthos	hydrodynamic pro- cesses, upwelling, resuspension, sedi- mentation, oxygen	terrestrial & pelagic input	3	3	3
Atmosphere composition	1	microbes	oxygen, substrate, turbulent mixing		1	1	1
Flood and erosion control	1				1	2	2
Redox processes	3	bioturbators, microbes	oxygen	carbon flux	3	3	3
<i>Habitat Maintenance Services</i>							
Landscape linkage & structure/ habitat/refugia	2	deep sea corals, methane seeps	oxygen, temperature, depth, substrate	carbon flux, larval stages	2	2	2
<i>Aesthetic Services</i>							
Spiritual/cultural	2				2	1	0
Aesthetic	2				2	1	3
Recreation	2				2	1	3
Scientific understanding	1	new life forms, microbes, symbioses	depth, sulfide, methane		2	2	2

Deep-Sea Sediments

Deep-sea sediment ecosystems are often ignored when considering the services provided by the ocean. Although human activities continue to expand to greater depths with improved technology, much of the current exploitation (Table 4.2c) is concentrated in the upper 1,000 m. These upper slope sedimentary habitats are repositories for organic carbon moving off the shelf (Walsh et al. 1981) and support expanding commercial and sport fisheries.

Continental slope sediments have higher carbon input and higher abundances of fishes and invertebrates than deeper areas. These are sites of relatively new fisheries for bony fishes such as orange roughy, pelagic armorhead, sablefish, flatfish, and rattails (which occur deeper as well) (Merrett & Haedrich 1997), and for invertebrates such as snow crabs, tanner crabs, golden crabs, northern shrimp, and red crabs (Elner 1982; Otto 1982). Many fisheries have focused on seamounts as well as the continental margin. On seamounts, black and pink corals are harvested for jewelry (Grigg 1993). All of the deepwater fishery taxa are slow-growing, long-lived forms that cannot sustain fishing pressure; most of their populations have declined or will in the near future, and the provisioning of fish secondary production is therefore short-lived and marginal at best (see Snelgrove et al., Chapter 7). Other deep-sea species, such as blue hake, spintail ray, and spiny eel, have experienced major declines in the past few decades from take as bycatch (i.e., individuals that are removed incidentally as a result of a fishery that is non-selectively targeting some other species) (Baker & Haedrich 2003).

To the extent that biodiversity is considered a valuable resource (e.g., for future uses, scientific interest) in itself, the deep sea functions to maintain and promote high species diversity (Rex 1983; Gage & Tyler 1991). The continental slopes are regions of high diversity, possibly because of the highly heterogeneous environments in space and time. Specific habitats within the deep sea, such as coral (*Lophelia*) reefs (Fossaa et al. 2002), seamounts (Koslow et al. 2001), and some reducing environments (hydrothermal vents, whale falls, and methane seeps) (Van Dover 2000) are recognized as valuable refugia that are important in the maintenance of diversity. More than 99 percent of the deep-sea floor has yet to be sampled (Snelgrove & Smith 2002), so there is considerable potential for future discovery and uses. One emerging area is the exploitation of microbial forms for specific industrial properties, among them their ability to degrade lipids at low temperatures and to break down hydrogen sulfide, and for enzymes to function at high temperatures (Prieur 1997).

Ecological processes that are regulated by deep-sea marine sediment biota include (1) the capture and deposition of organic matter onto the seabed, (2) the transfer of organic matter to higher consumers, (3) the burial of organic matter, and (4) the oxygenation of sediments through bioturbation. In deep-sea sediments, foraminiferans related sarcodines, macrofauna, and nematodes are key bioturbators and regulators of organic cycling. Active suspension and plankton feeders such as sponges, tunicates,

Table 4.2c. The provisioning of goods and services for deep-sea sediment ecosystems.

See Table 4.2a for explanation of ranking scheme.

	Rank	Biotic Contributors	Abiotic Regulators	External Interaction	Diversity Importance		
					Species	Functional	Habitat
<i>Provisioning Services</i>							
Plants as food	0						
Animals as food	1 to 2	fish, invertebrates, all benthos	oxygen, circulation, substrate	food, life history	3	2	2
Other biological products	0						
Biochemical/medicines/models for human research	1	microbes, natural products, enzymes	temperature, chemical availability		3	3	3
Fuels/energy	3	microbes	temperature, time		1	1	0
Fiber	1	sponges			1	0	0
C sequestration	1	bioturbators, microbes, infauna	CO ₂ , temperature, advection	carbon pump	2	3	3
Nonliving materials (geological effects)	0						
Clean seawater	0						
<i>Regulating Services</i>							
Sediment formation: biodeposition	1	microbes, lithothamnia, biogenic sediments	currents, freshwater and land runoff	sinking of particulates	1	1	0
Nutrient cycling	1	microbes, bioturbators, macrofauna, fishes	circulation, temperature, tides	resuspension	3	3	2
Biological control: disease, invasive species resistance	?				0	0	0
Detoxification, waste disposal	2	microbes, benthos	circulation, resuspension, sedimentation		2	2	1
Climate regulation (C sequestration)	3	bioturbators, microbes, infauna, mobile fauna	hydrodynamic processes, upwelling, resuspension, sedimentation	terrestrial & pelagic input	2	3	3
Food web support processes	1	entire benthos	hydrodynamic processes, upwelling, resuspension, sedimentation, oxygen	terrestrial & pelagic input	3	3	3
Atmosphere composition	1	microbes	oxygen, substrate, turbulent mixing		1	2	2
Flood and erosion control	0						
Redox processes	3	bioturbators, microbes	oxygen	carbon flux	2	3	2

(continued)

Table 4.2c. (continued)

	Rank	Biotic Contributors	Abiotic Regulators	External Interaction	Diversity Importance		
					Species	Functional	Habitat
<i>Habitat Maintenance Services</i>							
Landscape linkage & structure/habitat/refugia	1	deep sea corals, methane seeps	oxygen, temperature, depth, substrate	carbon flux, larval stages	2	2	2
<i>Aesthetic Services</i>							
Spiritual/cultural	1				0	0	0
Aesthetic	1				3	1	2
Recreation	1				0	0	0
Scientific understanding	3	new life forms, microbes, symbioses	depth, sulfide, methane		3	3	3

anemones, and bryozoans capture, ingest, and deposit organic matter or small plankton onto the sea floor in quiescent regions. Passive suspension feeders such as corals, crinoids, selected polychaetes, ophiuroids, and brisingid starfish do the same in higher energy settings. Epibenthic holothurians consume massive deposits of phytodetritus that carpet deep-sea sediments following phytoplankton blooms (Billet 1991), while other surface-deposit feeders are often the first to ingest and transform incoming organic matter into tissue. Nearly all metazoans participate in deep-sea food chains, although diets of most species are unknown (Fauchald & Jumars 1979; Sokolova 2000).

Areas at a depth of greater than 1,000 meters are thought to have reduced biological activity and therefore to be relatively stable compared with shallower ecosystems, and thus they have been a repository for many different kinds of wastes over the last half century (see Snelgrove et al., Chapter 7). However, recent studies show that labile organic matter reaching the deep sea is processed rapidly by benthic macrofauna such as sipunculans and malmanid polychaetes (Graf 1989; Levin et al. 1997), despite low overall faunal biomass (Rowe 1983).

Microbes account for a significant proportion of sediment community oxygen consumption (e.g., 80 percent, Heip et al. 2001), contributing to nutrient cycling through transformation, degradation, and sequestration of organic matter. They control redox conditions within sediments, provide food for protozoan and metazoan consumers (via heterotrophy and symbioses), and their role in nutrient cycling relates strongly to sediment oxygenation (Fenchel & Finlay 1995). Microbes form unusual natural products, enzymes, and detoxification functions (Bunge et al. 2003) that may be exploited commercially. Living microbes have been discovered much deeper in the Earth's crust than any other life form (Parkes et al. 1994).

Key benefits from sediment-based nutrient cycling and carbon burial may include removal of carbon over extended periods of centuries or longer (Heip et al. 2001). The deep sea is currently being considered for more rapid removal of CO₂ in liquid form through direct injection (Ozaki 1997; and see Snelgrove et al., Chapter 7).

Factors Affecting Biodiversity

Numerous abiotic environmental factors influence species diversity (Levin et al. 2001b) and potentially affect processes, goods, and services provided by marine sediments. Salinity, soil texture, organic content, nutrients, waves, currents, and oxygen are abiotic factors that control species composition, densities, and diversity. All of these factors are affected by natural and human-altered regional control of sediment supply, nutrient input, water depth, exposure to disturbance, and hydrologic environment (Diaz & Rosenberg 1995; Parsons et al. 1999; Gray 2002).

Sediment resuspension and motility in shelf and coastal regions is dictated by hydrodynamic processes such as currents, tides, and wave action (Boudreau 1997). This disturbance affects recycling services, the maintenance of sediment oxygenation (e.g.,

Ziebis et al. 1996), and potentially the detoxification of pollutants (Bunge et al. 2003) and rates of biogeochemical cycles (Turner & Millward 2002). It also significantly affects species composition (Ysebaert & Herman 2002).

Hydrodynamic processes primarily determine sediment granulometry and therefore substrate type. This is important to food production, as substrate or habitat availability affects survival of food species of fish and invertebrates (Snelgrove & Butman 1994). Oxygen availability and temperature influence the survival of organisms, reproduction, and function (Garlo 1982), and hence the provision of goods and services by shelf biota. Oxygen availability is particularly important in maintaining sediment redox chemistry (Rhoads et al. 1978; Fenchel & Finlay 1995).

The perception of the deep sea as a species-depauperate and homogeneous habitat has been debunked in the last few decades by evidence of strong regional and temporal variation in the abundance and diversity of deep-sea sediment biota (Levin et al. 2001a; Snelgrove & Smith 2002). The density and biomass of deep-sea infauna are most strongly influenced by organic matter availability (Rowe 1983). Input of organic carbon to the seabed mirrors (but is only a fraction of) surface primary production; it is also influenced strongly by circulation and local flow conditions. Where particulate organic input is high, infaunal species are abundant, animals live deeper in the sediments, and bioturbation rates are greater (Schaff et al. 1992). The continental margins and the north Atlantic are areas of particularly high organic matter input. Topographic features such as seamounts, ridges, canyons, and gullies have accelerated flows where particulate flux is elevated. Because the benthos provides critical trophic support for larger fish and invertebrates, production of harvested species is greatest in these areas, as are rates of carbon processing, burial, and sequestration.

In some estuarine and shelf areas, excess production from surface waters can lead to hypoxia in bottom waters (see discussion of nutrient loading in Chapter 7). An intriguing parallel occurs in some deep-sea areas when high production from surface waters sinks to bottom areas with sluggish circulation, leading to the formation of mid-water oxygen minimum zones (OMZs) at depths of 100 to 1,000 meters. Within OMZs, there is reduced productivity, less remineralization of carbon, and lowered functional and species diversity of the sediment biota. These effects occur over huge areas ($>10^6$ km²) of the sea floor (Levin 2003). Temporal changes in the boundaries of OMZs exert tremendous control on seabed productivity and diversity over ecological time (e.g., with El Niño events; Arntz et al. 1988) and over geological time (Rogers 2000).

The structure and function of deep-sea sediment biota is also influenced by benthic storms (Hollister & McCave 1984) and turbidity flows or mass wasting (Masson et al. 1996). Microbial function and activity are greatly influenced by availability of oxygen, organic matter, and reduced compounds such as methane and sulfide. Amazing discoveries of microbial syntrophy (symbioses involving microbes of different metabolic func-

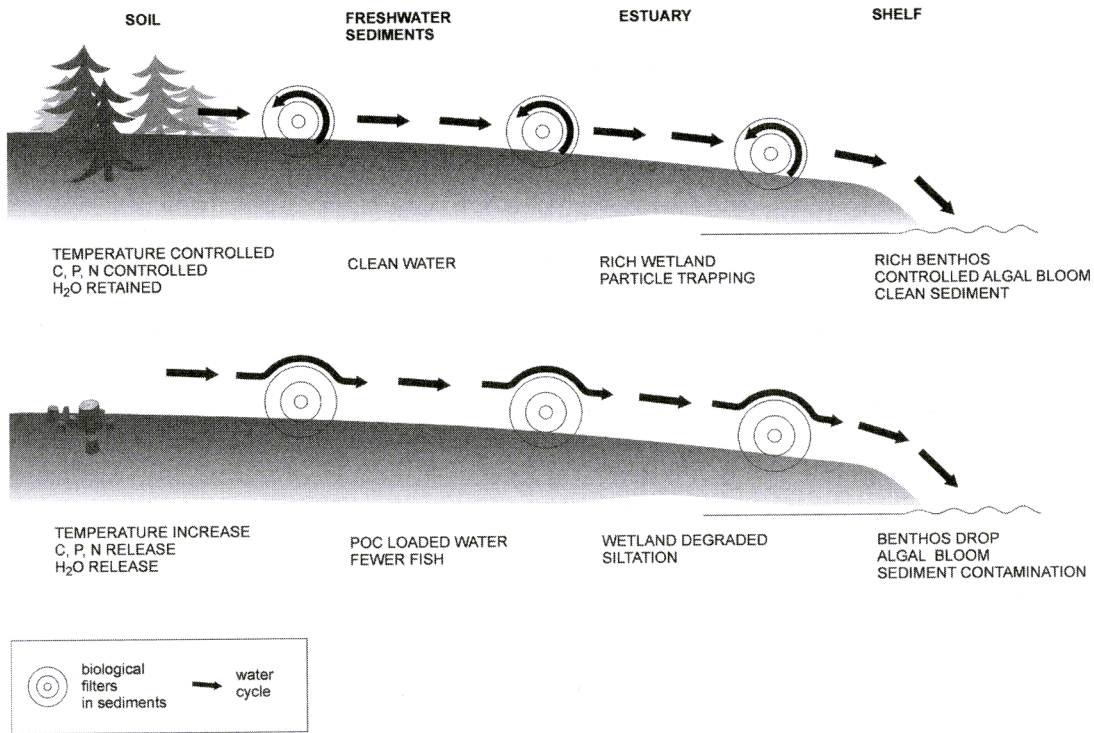


Figure 4.1. Schematic depiction of interrelated nature of soil, freshwater, and coastal marine sedimentary ecosystems. The top diagram depicts a functioning ecosystem prior to deforestation. The lower diagram illustrates the cascade of changes that may occur from disturbance to soils. Deep-sea ecosystems are not shown because their linkages with terrestrial and freshwater domains are indirect and expressed only at long temporal and large spatial scales. Arrows indicate flow of materials (water, nutrients, organic matter), and circles indicate biological filters. POC is particulate organic carbon, C is carbon, P is phosphorus, and N is nitrogen.

tions), multiple bacterial symbioses within invertebrates, and sediment ecosystems reliant on methane for carbon have come from highly reduced sediments in the deep sea.

Linkages to Marine Sedimentary Systems

Marine sedimentary goods and services are linked to adjacent ecosystems, including the water column above, the coastal zone, and even freshwater systems (Figure 4.1; see also Chapter 1, Figure 1.1). Because they are open transitional systems between land and sea, estuaries and their associated biotic components have direct hydrological links to coastal seas and upland watersheds. Tides provide the principal natural vector for marine-derived inputs to estuaries and freshwater flows from surface or groundwater sources that convey materials, nutrients, and organisms from upland drainage basins.

Sedimentary inputs to estuaries may be from either marine or upland sources, whereas biological linkages occur through movement of organisms in and out of estuaries (Levin et al. 2001a). The food provision and food web supporting services of estuarine and shelf sediments are closely linked with the overlying pelagic realm and particularly their food webs (Steele 1974). Many benthic invertebrates and fishes spend the first part of their life cycle within the plankton, providing linkages with pelagic species through predator-prey interactions (Bullard et al. 1999). Among deep-sea taxa, this is true of many commercially harvested taxa such as snow crab, golden crab, armorhead, sablefish, and grenadiers (Zheng & Kruse 2000). The terrestrial linkage of supplying estuaries and coasts with input of detritus and nutrients are also important to trophic support processes and food provision from estuarine through slope sediments.

Marine Sediment Diversity and Ecosystem Function

The role of species diversity in regulating ecosystem processes and services in sedimentary systems has received considerably less attention than its role in terrestrial systems (Estes & Peterson 2000). Although there are many examples of living organisms that play critical roles in providing services and functions, there is little evidence that biodiversity *per se* is critical for the delivery of services and functions. In many instances, it is likely that the availability of specific functional groups is most important in providing a given service or function (Tables 4.2a–4.2c). The benthic biota of estuaries are the least diverse of the marine sediment realms, but specific groups perform valuable functions: they create habitat, trap and retain sediments (e.g., rooted vegetation), maintain water quality (e.g., filter-feeding bivalves), contribute to aeration of subsurface sediments (e.g., bioturbators/burrowing crabs), and shunt production from the microbial decomposers to higher trophic levels (e.g., grazing snails and amphipods). There is some evidence that diversity decreases variability in rates of nutrient recycling and there are complementary effects of diversity on function, but there is no consistent relationship between species richness and function (Emmerson et al. 2001; see also Biles et al. 2003). However, few experiments to test these questions have been conducted in marine systems. Experiments with hard substrate communities have suggested that species diversity enhances resistance to invasive species (Stachowicz et al. 1999), but similar experiments are lacking for estuarine sediments. Nonetheless, estuaries have a public visibility that seems to confer a high value to the limited species diversity for aesthetic, recreational, and scientific reasons.

The role of species diversity on the continental slope is not well documented in provision of trophic support, nutrient cycling, and waste disposal/detoxification, but it is clear that multiple species are involved. In cases where multiple species are eliminated by hypoxic events, for example, the loss of key sedimentary functions has resulted (Rabalais et al. 1996), but it could be argued that loss of functional groups, rather than species, is more important (Elmgren & Hill 1997). In estuarine and shelf ecosystems,

the diversity of structure-forming species often contributes to habitat diversity, which subsequently increases the diversity of species that utilize that habitat and therefore may enhance key services such as food production (Auster et al. 1996).

The high diversity of infaunal species in the deep sea raises many questions about rates and redundancy that are largely unanswered (Snelgrove & Smith 2002). The relative importance of species diversity for the efficiency of the deep-sea functions discussed above has not been tested experimentally. In general, measures of macrofaunal density, biomass, or diversity have been poor predictors of functions such as bioturbation, whereas particulate organic carbon (POC) flux and densities of selected megafauna can be good predictors (Smith 1992; Smith & Rabouille 2002).

One formidable challenge is to determine whether diversity at the level of habitats, functional groups, species, genes, or gene expression (functional genomics) is most critical for sustaining ecological processes and services. Recent research has considered the role of landscape configuration (Archambault & Bourget 1999) and the effect of anthropogenic modifications and structures on estuarine biodiversity (Chapman & Bulleri 2003). These foci have potential applications for restoring and conserving biodiversity in the face of growing pressures for increased coastal development; they also have potential consequences for processes and services.

Theory based on the terrestrial literature suggests that if each species performs a function slightly differently, then sediments with high diversity are likely to achieve the most effective function (i.e., sampling effect) (Loreau et al. 2001; Zedler et al. 2001). Inter-specific facilitative interactions are particularly likely to enhance functions in areas with low oxygen, high sulfides, food scarcity, physical disturbance, or other stressors (Levin et al. 2001b). Structures on the sea floor such as polychaete feeding mounds, tracks in sediments from surface burrowers, and discarded shell material provide heterogeneity, which facilitates adults and juveniles of many deep-sea species, providing food, substrate, and refugia (Levin et al. 1997; Snelgrove & Smith 2002).

Research Needs and Recommendations

The vast majority of marine sedimentary organisms are undescribed and unknown (e.g., 10 million macrofaunal species are estimated in Grassle & Maciolek 1992), with the diversity of the smaller organisms much less well understood than that of larger organisms. There is a fundamental need to document the taxonomic composition of sedimentary biota through biodiversity surveys of representative marine habitats. Although the large area of marine sedimentary habitat precludes a comprehensive biodiversity survey, it is reasonable to survey representative areas in order to generate diversity estimates for different habitat types and biogeographic maps for relatively common species. This information is critical to manage and conserve the functional properties of marine ecosystems for the long term, particularly in areas that are vulnerable to human activities (see Snelgrove et al., Chapter 7; Wall et al. 2001). A significant obstacle to the study

of biodiversity is the “taxonomic impediment”—a worldwide shortage of taxonomists (Hoagland 1995; Environment Australia 1998).

The role of marine sediment biodiversity in the regulation of ecosystem processes and services is poorly understood, particularly for groups such as the fungi, protists, and meiofauna. Even for macrofauna and megafauna, the role of biodiversity has been examined in only a few studies. Levels of functional redundancy within and across groups and their relative importance must be characterized to offer predictive capabilities concerning controls on, and threats to, ecosystem processes. Given the many abiotic variables that influence biodiversity patterns and the linkages between different sedimentary ecosystems, studies of ecosystem processes and services must consider marine sediments and their biodiversity when establishing and implementing marine conservation strategies. Finally, efforts to value sedimentary biota are effectively nonexistent. Lack of direct experience alone limits our capacity to value marine sedimentary services. Aside from coral reefs, sandy beaches, and wetlands, most sedimentary habitats generate little public concern and hence often rate low in conservation priority. This situation can be altered as both scientists and the public improve their understanding of the critical roles and services provided by marine sediments in the biosphere.

Literature Cited

- Archambault, P., and E. Bourget. 1999. Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. *Journal of Experimental Marine Biology and Ecology* 238:161–184.
- Arntz, W.E., E. Valdivia, and J. Zeballos. 1988. Impact of El Niño 1982–83 on the commercially exploited invertebrates (mariscos) of the Peruvian shore. *Meeresforschung* 32:3–22.
- Auster, P.J., R.J. Malatesta, R.W. Langton, L. Watling, P.C. Valentine, C.L.S. Donaldson, E.W. Langton, A.N. Shepard, and I.G. Babb. 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (northwest Atlantic): Implications for conservation of fish populations. *Reviews in Fisheries Science* 4:185–202.
- Baker, K., and R.L. Haedrich. 2003. Could some deep-sea fishes be species-at-risk? International Deep-Sea Biology Conference, Aug. 2003, Coos Bay, Oregon. (Abstract)
- Beach, D. 2002. *Coastal Sprawl: The Effects of Urban Design on Aquatic Ecosystems in the United States*. Arlington, Virginia, Pew Oceans Commission. http://www.pewoceans.org/oceanfacts/2002/04/12/fact_25649.asp.
- Biles, C.L., M. Solan, I. Isaksson, D.M. Paterson, C. Emes, and D.G. Raffaelli. 2003. Flow modifies the effect of biodiversity on ecosystem functioning: An *in situ* study of estuarine sediments. *Journal of Experimental Marine Biology and Ecology* 285–286:165–177.
- Billett, D.S.M. 1991. Deep-sea holothurians. *Oceanography and Marine Biology: An Annual Review* 29:259–317.
- Boudreau, B.P. 1997. A one-dimensional model for bed-boundary layer particle exchange. *Journal of Marine Systems* 11:279–303.
- Boyd, T.J., and A.F. Carlucci. 1996. Rapid microbial degradation of phenolic materials in California (USA) coastal environments. *Aquatic Microbial Ecology* 11:171–179.

- Bullard, S.G., N.L. Lindquist, and M.E. Hay. 1999. Susceptibility of invertebrate larvae to predators: How common are post-capture larval defenses? *Marine Ecology Progress Series* 191:153–161.
- Bunge, M., L. Adrian, A. Kraus, M. Opel, W.G. Lorenz, J.R. Andreesen, H. Goerisch, and U. Lechner. 2003. Reductive dehalogenation of chlorinated dioxins by an anaerobic bacterium. *Nature* 421:357–360.
- Burke, L., Y. Kura, K. Kassem, C. Revenga, M. Spalding, and D. McAllister. 2001. *Pilot Analysis of Global Ecosystems: Coastal Ecosystems*. Washington, DC, World Resources Institute.
- Carlson, J., T. Randall, and M. Mroczka. 1997. Feeding habits of winter flounder (*Pleuronectes americanus*) in a habitat exposed to anthropogenic disturbance. *Journal of Northwest Atlantic Fishery Science* 21:65–73.
- Chapman, M.G., and F. Bulleri. 2003. Intertidal seawalls: New features of landscape in intertidal environments. *Landscape and Urban Planning* 62:159–172.
- Costanza, R. 1999. The ecological, economic and social importance of the oceans. *Ecological Economics* 31:199–213.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–260.
- Covi, M.P., and R.T. Kneib. 1995. Intertidal distribution, population dynamics and production of the amphipod *Uholorchestia spartinophila* in a Georgia, USA, salt marsh. *Marine Biology* 121:447–455.
- Daily, G.C., T. Söderqvist, S. Aniyar, K. Arrow, P. Dasgupta, P.R. Ehrlich, C. Folke, A. Jansson, B.-O. Jansson, N. Kautsky, S. Levin, J. Lubchenco, K.-G. Mäler, D. Simpson, D. Starrett, D. Tilman, and B. Walker. 2000. The value of nature and the nature of value. *Science* 289:395–396.
- Dasgupta, P., S. Levin, and J. Lubchenco. 2000. Economic pathways to ecological sustainability. *BioScience* 50:340–345.
- Diaz, R.J., and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: An Annual Review* 33:245–303.
- Elmgren, R., and C. Hill. 1997. Ecosystem function at low biodiversity: The Baltic example. In: *Marine Biodiversity: Patterns and Processes*, edited by R.F.G. Ormond, J.D. Gage, and M.V. Angel, pp. 319–335. Cambridge, UK, Cambridge University Press.
- Elnor, R.W. 1982. Overview of the snow crab *Chionoecetes opilio* fishery in Atlantic Canada. *Proceedings of the International Symposium on the Genus Chionoecetes*, May 3–6, 1982, pp. 3–19. Lowell Wakefield Symposia Series, Alaska Sea Grant Report. Alaska Sea Grant Program.
- Emmerson, M.C., M. Solan, C. Emes, D.M. Paterson, and D. Raffaelli. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* 411:73–77.
- Environment Australia. 1998. *The Darwin Declaration*. Australian Biological Resources Study. Canberra, Environment Australia.
- Estes, J.A., and C.H. Peterson. 2000. Marine ecological research in seashore and seafloor systems: Accomplishments and future directions. *Marine Ecology Progress Series* 195:281–289.
- Ewel K.C., C. Cressa, R.T. Kneib, P.S. Lake, L.A. Levin, M.A. Palmer, P. Snelgrove, and D.H. Wall. 2001. Managing critical transition zones. *Ecosystems* 4:452–460.

- Fauchald, K., and P.A. Jumars. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology* 17:193–284.
- Feder, H.M., and T.H. Pearson. 1988. The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. V. Biology of the dominant soft-bottom epifauna and their interaction with the infauna. *Journal of Experimental Marine Biology and Ecology* 116:99–134.
- Fenchel, T., and B.J. Finlay. 1995. *Ecology and Evolution in Anoxic Worlds*. Oxford Series in Ecology and Evolution. Oxford, UK, Oxford University Press.
- Fonseca, M.S., and J.S. Fisher. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series* 29:15–22.
- Fossaa, J., P. Mortensen, and D. Furevik. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: Distribution and fishery impacts. *Hydrobiologia* 471:1–12.
- Gage, J.D., and P.A. Tyler. 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge, UK, Cambridge University Press.
- Gallagher, E.D., and K.E. Keay. 1998. Organism-sediment-contaminant interactions in Boston Harbor. In: *Contaminated Sediments in Boston Harbor*, edited by K.D. Stolzenbach and E.E. Adams, pp. 89–132. Cambridge, Massachusetts, MIT Sea Grant College Program.
- Garlo, E.V. 1982. Increase in a surf clam population after hypoxic water conditions off Little Egg Inlet, New Jersey. *Journal of Shellfish Research* 2:59–64.
- Geiselsbrecht, A.D., R.P. Herwig, J.W. Deming, and J.T. Staley. 1996. Enumeration and polyphyletic analysis of polycyclic aromatic hydrocarbon-degrading marine bacteria from Puget Sound sediments. *Applied Environmental Microbiology* 62:3344–3349.
- Graf, G. 1989. Pelagic-benthic coupling in a deep sea benthic community. *Nature* 341:437–439.
- Grant, J., and G. Gust. 1987. Prediction of coastal sediment stability from photopigment content of mats of purple sulphur bacteria. *Nature* 330:244–246.
- Grant, W.D., L.F. Boyer, and L.P. Sanford. 1982. The effects of bioturbation on the initiation of motion of intertidal sands. *Journal of Marine Research* 40:659–677.
- Grassle, J.F., and N.J. Maciolek. 1992. Deep-sea species richness: Regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139:313–341.
- Gray, J.S. 2002. Species richness of marine soft sediments. *Marine Ecology Progress Series* 244:285–297.
- Grigg, R.W. 1993. Precious coral fisheries of Hawaii and the U.S. Pacific islands. *Marine Fisheries Review* 55:50–60.
- Hanson, R.B., H.W. Ducklow, and G.G. Field, editors. 2000. *International Geosphere-Biosphere Programme Book Series*, No. 5. Cambridge, UK, Cambridge University Press.
- Heip, C.H.R., G. Duineveld, E. Flach, G. Graf, W. Helder, P.M.J. Herman, M. Lavaleye, J.J. Middelburg, O. Pfannkuche, K. Soetaert, T. Soltwedel, H. de Stigter, L. Thomsen, J. Vanaverbeke, and P. de Wilde. 2001. The role of the benthic biota in sedimentary metabolism and sediment-water exchange processes in the Goban Spur area (NE Atlantic). *Deep-Sea Research Part II* 48:3223–3243.
- Henriksen, K., M.B. Rasmussen, and A. Jensen. 1983. Effect of bioturbation on microbial nitrogen transformations in the sediment and fluxes of ammonium and nitrate for the overlying water. *Ecological Bulletin* 35:193–205.

- Heymans, J.J., and D. Baird. 1995. Energy flow in the Kromme Estuarine ecosystem, St. Francis Bay, South Africa. *Estuarine, Coastal and Shelf Science* 41:39–59.
- Hoagland, K.E. 1995. *The Taxonomic Impediment and the Convention on Biodiversity*. <http://www.science.uts.edu.au/sasb/TaxImp.html>.
- Hollister, C.D., and I.N. McCave. 1984. Sedimentation under deep-sea storms. *Nature* 309:220–225.
- Koslow, J.A., K. Gowlett-Holmes, J.K. Lowry, T. O'Hara, G.C.B. Poore, and A. Williams. 2001. Seamount benthic macrofauna off southern Tasmania: Community structure and impact of trawling. *Marine Ecology Progress Series* 213:111–125.
- Kruczynski, W. 1999. The importance of coastal wetlands: Why do we need to protect them? *ASB Bulletin* 46:246–272.
- Lambhead, P.J.D. 1993. Recent developments in marine benthic biodiversity research. *Oceanis* 19:5–24.
- Laurel, B.J., R.S. Gregory, and J.A. Brown. 2003. Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. *Marine Ecology Progress Series* 251:245–254.
- Lee, R.F., and D.S. Page. 1997. Petroleum hydrocarbons and their effects in subtidal regions after major oil spills. *Marine Pollution Bulletin* 34:928–940.
- Lee, R.W., D.W. Kraus, and J.E. Doeller. 1999. Oxidation of sulfide by *Spartina alterniflora* roots. *Limnology and Oceanography* 44:1155–1159.
- Levin, L.A. 2003. Oxygen minimum zone benthos: Adaptation and community response to hypoxia. *Oceanography and Marine Biology: An Annual Review* 41:1–45.
- Levin, L.A., N. Blair, D.J. DeMaster, G. Plaia, W. Fornes, C. Martin, and C. Thomas. 1997. Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. *Journal of Marine Research* 55:595–611.
- Levin, L.A., D.F. Boesch, A. Covich, C. Dahm, C. Erseus, K.C. Ewel, R.T. Kneib, A. Moldenke, M.A. Palmer, P. Snelgrove, D. Strayer, and J.M. Weslawski. 2001a. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4:430–451.
- Levin, L.A., R.J. Etter, M.A. Rex, A.J. Gooday, C.R. Smith, J. Pineda, C.T. Stuart, R.R. Hessler, and D. Pawson. 2001b. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics* 132:51–93.
- Levinton, J.S. 1995. Bioturbators as ecosystem engineers: Population dynamics and material fluxes. In: *Linking Species and Ecosystems*, edited by C.G. Jones and J.H. Lawton, pp. 29–36. New York, Chapman and Hall.
- Lindley, J.A., J.C. Gamble, and H.G. Hunt. 1995. A change in the zooplankton of the central North Sea (55 degrees to 58 degrees N): A possible consequence of changes in the benthos. *Marine Ecology Progress Series* 119:299–303.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D.A. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804–808.
- Martin, J.H., K.H. Coale, K.S. Johnson, S.E. Fitzwater, R.M. Gordon, S.J. Tanner, C.N. Hunter, V.A. Elrod, J.L. Nowicki, T.L. Coley, R.T. Barber, S. Lindley, A.J. Watson, K. Vanscoy, C.S. Law, M.I. Liddicoat, R. Ling, T. Stanton, J. Stockel, C. Collins, A. Anderson, R. Bidigare, M. Ondrusek, M. Latasa, F.J. Millero, K. Lee, W. Yao, J.Z. Zhang, G. Friederich, C. Sakamoto, F. Chavez, K. Buck, Z. Kolber, R. Greene, P.

- Falkowski, S.W. Chisholm, F. Hoge, R. Swift, J. Yungel, S. Turner, P. Nightingale, A. Hatton, P. Liss, and N.W. Tindale. 1994. Testing the iron hypothesis in ecosystems of the equatorial Pacific Ocean. *Nature* 371:123–129.
- Masson, D.G., N.H. Kenyon, and P.P.E. Weaver. 1996. Slides, debris flows and turbidity currents. In: *Oceanography: An Illustrated Guide*, edited by C.P. Summerhayes and S.A. Thorpe, pp. 136–151. London, Manson.
- Merrett, N.R., and R.L. Haedrich. 1997. *Deep-Sea Demersal Fish and Fisheries*. London, Chapman and Hall.
- Otto, R.S. 1982. An overview of the eastern Bering Sea tanner crab fisheries. *Proceedings of the International Symposium on the Genus Chionoecetes*, May 3–6, 1982. Lowell Wakefield Symposia Series, 1982, pp. 83–115, Alaska Sea Grant Report. Alaska Sea Grant Program.
- Ozaki, M. 1997. CO₂ injection and dispersion in mid-ocean depth by moving shop. *Waste Management* 17:369–373.
- Parkes, R.J., B.A. Cragg, S.J. Bale, J.M. Getliff, K. Goodman, P.A. Rochelle, J.C. Fry, A.J. Weightman, and S.M. Harvey. 1994. Deep bacterial biosphere in Pacific Ocean sediments. *Nature* 37:410–413.
- Parsons, M.L., Q. Dortch, R.E. Turner, and N.N. Rabalais. 1999. Salinity history of coastal marshes reconstructed from diatom remains. *Estuaries* 22:1078–1089.
- Paterson, D.M., and K.S. Black. 1999. Water flow, sediment dynamics and benthic biology. *Advances in Ecological Research* 29:155–193.
- Paterson, G.L.J. 1993. Patterns of polychaete assemblage structure from bathymetric transects in the Rockall Trough, NE Atlantic Ocean. Ph.D. thesis. University of Wales. 252 pp.
- Pelegri, S.P., and T.H. Blackburn. 1995. Effect of bioturbation by *Nereis* sp., *Mya arenaria* and *Cerastoderma* sp. on nitrification and denitrification in estuarine sediments. *Ophelia* 42:289–299.
- Pournelle, J.R. 2003. The littoral foundations of the Uruk state: Using satellite photography toward a new understanding of the 5th/4th millennium BCE landscapes in the Warka Survey Area, Iraq. In: *Chalcolithic and Early Bronze Age Hydrostrategies*, edited by D. Gheorghiu, pp. 5–23. BAR International Series 1123. Oxford, UK, Archaeopress.
- Prieur, D. 1997. Microbiology of deep-sea hydrothermal vents. *Trends in Biotechnology* 15:242–244.
- Rabalais, N.N., W.J. Wiseman, Jr., R.E. Turner, D. Justic, B.K. Sen Gupta, and Q. Dortch. 1996. Nutrient changes in the Mississippi River and system responses on the adjacent continental shelf. *Estuaries* 19:386–407.
- Rex, M.A. 1983. Geographic patterns of diversity in deep-sea benthos. In: *The Sea*, edited by G.T. Rowe, Vol. 8. pp. 453–472. New York, Wiley Interscience.
- Rhoads, D.C. 1963. Rates of sediment reworking by *Yoldia limatula* in Buzzard's Bay, Massachusetts, and Long Island Sound. *Journal of Sedimentary Petrology* 33:723–727.
- Rhoads, D.C., P.L. McCall, and J.Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. *American Scientist* 66:577–586.
- Rhoads, D.C., and D.K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* 28:150–178.
- Rogers, A.D. 2000. The role of the oceanic oxygen minima in generating biodiversity in the deep sea. *Deep-Sea Research Part II* 47:119–148.

- Rowe, G.T. 1983. Biomass and production of the deep-sea macrobenthos. In: *The Sea*, edited by G.T. Rowe, Vol. 8 pp. 97–121. New York, Wiley Interscience.
- Schaff, T., L. Levin, N. Blair, D. DeMaster, R. Pope, and S. Boehme. 1992. Spatial heterogeneity of benthos on the Carolina continental slope: Large (100 km)-scale variation. *Marine Ecology Progress Series* 88:143–160.
- Smith, C.R. 1992. Factors controlling bioturbation in deep-sea sediments and their relation to models of carbon diagenesis. In: *Deep Sea Food Chains and the Global Carbon Cycle*, NATO Asi Science Series C: Mathematics and Physical Science, Vol. 360, pp. 375–393. Dordrecht, The Netherlands, Kluwer Academic Publishers.
- Smith, C.R., and C. Rabouille. 2002. What controls the mixed layer depth in deep-sea sediments? The importance of POC Flux. *Limnology and Oceanography* 47:418–426.
- Snelgrove, P.V.R. 1999. Getting to the bottom of marine biodiversity: Sedimentary habitats. *BioScience* 49:129–138.
- Snelgrove, P.V.R., T.H. Blackburn, P. Hutchings, D. Alongi, J.F. Grassle, H. Hummel, G. King, I. Koike, P.J.D. Lamshead, N.B. Ramsing, and V. Solis-Weiss. 1997. The importance of marine biodiversity in ecosystem processes. *Ambio* 26:578–583.
- Snelgrove, P.V.R., and C.A. Butman. 1994. Animal-sediment relationships revisited: Cause versus effect. *Oceanography and Marine Biology: An Annual Review* 32:111–177.
- Snelgrove, P.V.R., and C.R. Smith. 2002. A riot of species in an environmental calm: The paradox of the species-rich deep-sea. *Oceanography and Marine Biology: An Annual Review* 40:311–342.
- Sokolova, M.N. 2000. *Feeding and Trophic Structure of the Deep-Sea Macrobenthos*. Enfield, New Hampshire, Science Publisher Inc.
- Srinivasan, M., and B.A. Mahajan. 1989. Mercury pollution in an estuarine region and its effect on a coastal population. *International Journal of Environmental Studies A & B* 35:63–69.
- Stachowicz, J.J., R.B. Whitlatch, and R.W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579.
- Steele, J.H. 1974. *The Structure of Marine Ecosystems*. Oxford, UK, Blackwell Scientific.
- Thayer, G.W., D.R. Colby, and W.F. Hettler, Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in South Florida. *Marine Ecology Progress Series* 35:25–38.
- Turner, A., and G.E. Millward. 2002. Suspended particles: Their role in estuarine biogeochemical cycles. *Estuarine, Coastal and Shelf Science* 55:857–883.
- United Nations. 1992. *United Nations Framework Convention on Global Climate Change*. New York, United Nations.
- Van Dover, C.L. 2000. *The Ecology of Hydrothermal Vents*. Princeton, New Jersey, Princeton University Press.
- Wall, D.H., P.V.R. Snelgrove, and A.P. Covich. 2001. Conservation priorities for soil and sediment invertebrates. In: *Conservation Biology*, edited by M.E. Soulé and G.H. Orians, pp. 99–123. Washington, DC, Island Press.
- Walsh, J.W., G.T. Rowe, C.P. McRoy, and R. Iverson. 1981. Biological export of shelf carbon is a sink of the global CO₂ cycle. *Nature* 291:196–201.
- Weslawski, J.M., B. Urban-Malinga, L. Kotwicki, K.W. Opalinski, M. Szymelfenig, and M. Dutkowski. 2000. Sandy coastlines: Are there conflicts between recreation and natural values? *Oceanological Studies* 29:5–18.
- Wright, L.D., L.C. Schaffner, and J.P.Y. Maa. 1997. Biological mediation of bottom

- boundary layer processes and sediment suspension in the lower Chesapeake Bay. *Marine Geology* 141:27–50.
- Ysebaert, T., and P.M.J. Herman. 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft sediment environment. *Marine Ecology Progress Series* 244:105–124.
- Zedler, J.B., J.C. Callaway, and G. Sullivan. 2001. Declining biodiversity: Why species matter and how their functions might be restored in Californian tidal marshes. *BioScience* 51:1005–1017.
- Zheng, J., and K.H. Kruse. 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. *ICES Journal of Marine Science* 57:438–451.
- Ziebis, W., M. Huettel, and S. Forster. 1996. Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. *Marine Ecology Progress Series* 140:227–237.