MARINE CONSERVATION

Science, Policy, and Management

G. Carleton Ray
Jerry McCormick-Ray

Illustrations by Robert L. Smith, Jr.

free companion website

WILEY Blackwell

CHAPTER 4

MARINE SYSTEMS: THE BASE FOR CONSERVATION

> We feel clearly that we are only now beginning to acquire reliable material for welding together the sum total of all that is known into a whole; but on the other hand, it has become next to impossible for a single mind to fully command only a small specialized portion of it.
>
> E. Schrödinger (1944)

4.1 A SYSTEMS APPROACH

This chapter presents an overview of the marine environment as a system of global significance. It highlights major attributes in which biological diversity plays a critical role important to ecosystem structure and function in a constantly changing environment. The global ocean covers more than 70% of the Earth and holds 97% of Earth's water, with complex linkages to land, air, astronomical forces, and to chemical, biological, and hydrologic cycles. Uncertainty is pervasive, especially about ecological stability resulting from energy and fisheries exploitation of already-disturbed ocean systems, exacerbated further by the vast variability of the ocean system itself. In the wake of climate change and with poor understanding of the potential hazards such disruptions might bring, a systems perspective is essential to guide conservation efforts.

4.2 DYNAMIC PLANETARY FORCES

The global ocean is a vast, continuously moving body of water driven by planetary forces connected to the Moon and Sun. Planet Earth is habitable due to a hospitable climate and a capacity to capture and recycle water, energy, and nutrient chemicals, globally balanced in levels of organization modified over geologic time. Thermodynamics, gravity, motion, and chemistry in the many hierarchical dimensions of time and space drive its behavior. As the ocean plays a major role in this whole-Earth system, modern technologies—satellites, submersibles, and monitoring systems—are revealing its mysteries.

4.2.1 The global ocean and climate

The global ocean absorbs >97% of solar radiation, which powers the global circulation pattern (Bigg *et al.*, 2003). Its thermal capacity is a thousand times greater than the atmosphere, making the ocean a major heat reservoir for the planet (Riebesell *et al.*, 2009). Its interactions with continents and the deep sea result in the redistribution of large quantities of heat, water, gases, particles, and momentum. The ocean expands in volume when heated and contracts when cooled, causing sea levels to rise and fall on scales related to global climate change. And through complex processes and feedbacks in recycling of energy and vital elements (e.g., carbon, nitrogen, others), the protean ocean maintains a delicate balance with climate at all scales of interactions.

The nature of the ocean and its role in climate regulation relates to its major component, water (H_2O). Water is a polar chemical compound composed of two hydrogen atoms and one oxygen atom, with a molecular size of less than a nanometer and instantaneous reactions in less than nanoseconds. The water molecule has unique properties that give the ocean attributes of thermal capacity, surface tension, viscosity, elasticity, and solvency. Under specific conditions, water is transformed into gas or ice, and can hold gas molecules (carbon dioxide, CO_2; oxygen, O_2; methane, CH_3; etc.) in solution to be exchanged with the atmosphere. Due to its vibrating hydrogen bonds, water absorbs heat and can release large amounts of heat without changing much in temperature. The massive extent of ocean water thus plays important roles in the global water cycle and climate, with carbon dioxide connecting climate to ocean acidity, ocean warming, and climate change.

4.2.2 Solar radiation and energy transfers

Solar radiation received by the oceans is influenced by Earth's tilt and its axis of rotation. This interaction creates uneven distributions of energy and seasonal, latitudinal, and thermodynamic differences in the global land-ocean-atmosphere system. The only places that receive perpendicular radiation from the Sun at some time of the year are between the Tropics of Cancer and Capricorn, located 23°30′ latitude north and south of the equator, respectively. These low latitudes gain more solar radiation than is lost, unlike high latitudes that lose more energy than they gain. The transfer of excess heat from low to high latitudes maintains the energy balance between the atmosphere and the oceans, producing seasonal surpluses of heat at lower latitudes and deficits of heat at

Marine Conservation: Science, Policy, and Management, First Edition. G. Carleton Ray and Jerry McCormick-Ray.

higher latitudes. Any alteration of this energy-transfer system may affect climate. This differential heat absorption and re-radiation from the ocean, in combination with landmass configuration, Earth's rotation, and gravitational forces, highlights the ocean's importance in the global, cybernetic system.

The Sun's electromagnetic energy is also a driving force for physical and bio-energetic processes. The Sun emits a radiation spectrum of ultraviolet (30–400 nm), visible "light" (400–700 nm), and infrared (700–3000 nm) that the ocean differentially absorbs according to its water depth and transparency. Fifty percent of solar radiation is absorbed within the top half-meter of ocean surface (Soloviev and Lukas, 2006). Light penetrates only a few tens to hundreds of meters depth (the "photic zone", 300 m maximum) where the photic zone receives only 1% or less of the surface value, limiting photosynthesis, animal vision, and photoperiodic responses of plants and animals (Fig. 4.1). In this thin surface layer where 90% of sea life occurs, plants capture radiant energy, utilize carbon dioxide, release oxygen, and package elements (carbon, nitrogen, phosphorus, sulfur, etc.) into complex living matter.

4.2.3 Earth's rotation, gravity, and fluid motions

Circulation patterns of the world's oceans are products of complex interactions driven by Earth's rotation, winds, and the configuration of ocean basins. Due to Earth's rotation on its axis, surface fluids (i.e., air, water) shift from a straight line of flow to a direction that is approximately perpendicular to the original direction of flow, a phenomenon known as the Coriolis effect. This force has a strength that is proportional to the speed of Earth's rotation, which differs with latitude, tending to deflect moving currents and objects (e.g., plankton, fish) to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. For example, a particle at 60° north latitude moving northward and not attached to the Earth initially moves eastward at about 1500 km h^{-1}, but at 30° latitude moves only 800 km h^{-1}. Coriolis force is an important factor in forming cyclonic weather systems and in affecting long-distance migration paths of species such as marine mammals, sea turtles, and sea birds. Within five degrees of the equator, the Coriolis force is weak and hurricanes do not form.

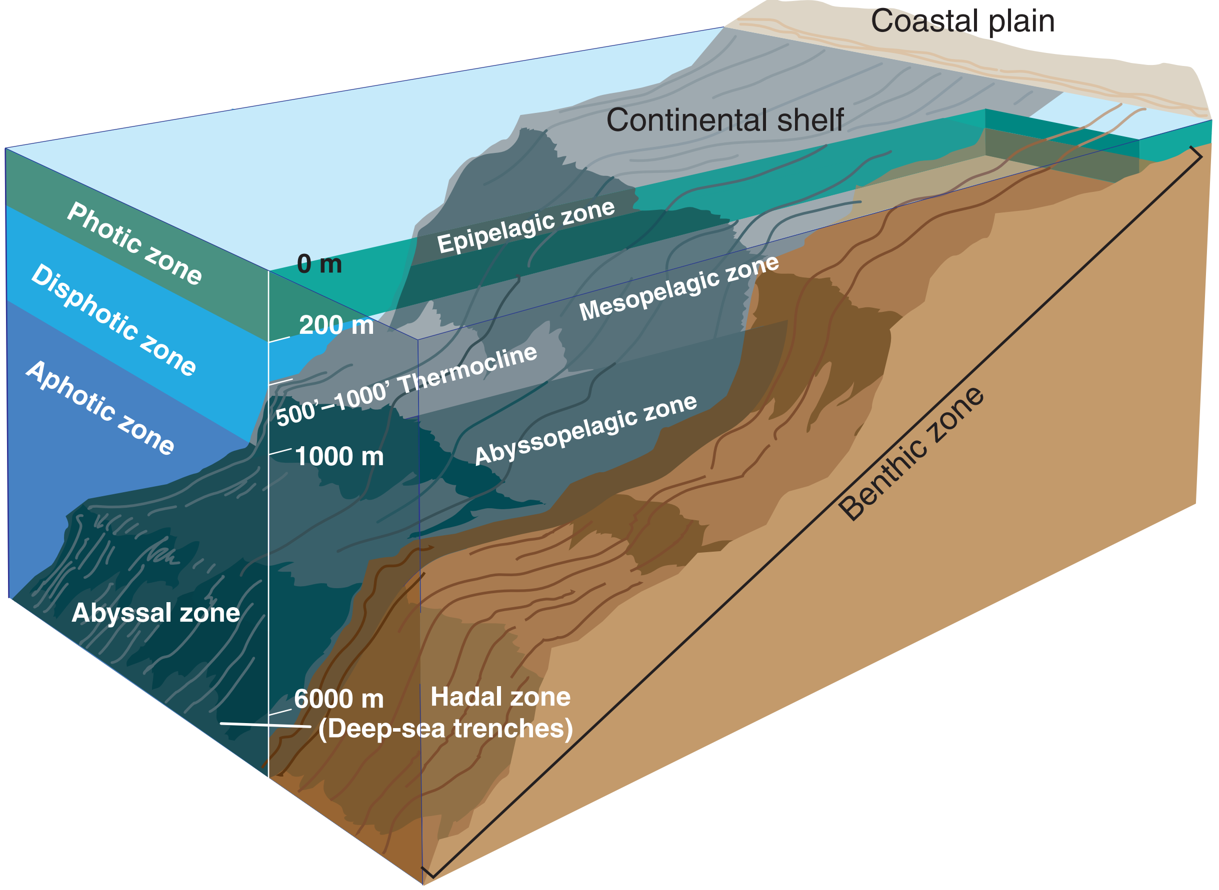

Fig. 4.1 Ocean Zones: Euphotic zone supports a high diversity of epipelagic organisms and 90% of marine life. Disphotic, twilight zone supports mesopelagic species. Aphotic zone lacks sunlight, where relatively few species live in low abundance. Below the photic zone, the bathyal, abyssal, and hadal are deep-sea regions. Benthic zones (brown) grade from shelf at the shore to continental slope and rise (together the "margin") and then to the deep-sea bed. See text for explanation.

Earth's rotation also powers ocean movements, further affected by wind and tidal forces, with horizontal and vertical circulation patterns modified by variations in water density, gravity, wind friction, and continental boundaries.

Another phenomenon known as the Ekman spiral acts to change current direction with depth. When wind sets surface water into a direction of motion, this direction down to a depth of about 100 m is deflected (theoretically) 45° to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. Hence, deeper layers are progressively deflected to the right (or left) of the overlying layer's movement. When movements of all ocean layers are combined, net deflection is approximately 90°. At large scales, an Ekman circulation pattern is observed as ocean gyres that cover large oceanic basins (e.g., Pacific Gyre) with a center of lighter, less dense water becoming elevated to form a "hill," where gravity forces water to flow outward and downward, a phenomenon known as geostrophic flow. Ocean gyres are associated with large surface currents, the ocean "rivers" that affect regional climates around the world and serve as transport for many marine organisms. Major oceanic current systems that are in balance with Earth's rotational and gravitational forces are significant ocean features, and play significant roles in regional climate.

In all ocean basins (Table 4.1) on both sides of the equator, strong western and eastern boundary currents flow for thousands of kilometers. In general, western boundary currents flow from the equator to deliver warm water toward the poles, and eastern boundary currents flow from high latitudes toward the equator and deliver cold water to the tropics. And as warm air from the tropics moves toward the poles at faster rates than the Earth spins (the Coriolis effect), winds are created that affect ocean currents. Most importantly, westerly winds (40–50° latitudes) blow from west to east to force equatorial water eastward. Trade winds (20° latitudes), on the other hand, blow east to west. The North and South Equatorial Currents in lower latitudes flow west and the Equatorial Counter Current flows east. In El Niño years, equatorial currents in the Pacific Ocean intensify. Such ocean current systems not only affect climate, but also can be important transport systems for migratory marine mammals, sea turtles, oceanic fishes, and larvae of many species.

In the Atlantic Ocean, the best-known western boundary current is the Gulf Stream. This warm surface current transports warm water from the Gulf of Mexico and tropical Atlantic to the northern, colder Atlantic Ocean towards Europe. The northward transport of heat by the Gulf Stream moderates Europe's northern climate. At speeds of 97 km day^{-1}, this powerful current moves 100 times as much water as all the rivers on Earth (USGS, online). The Gulf Stream is modified by continental boundaries and follows the edge of the coastal-ocean boundary. It helps form the clockwise-flowing mid-Atlantic ocean gyre. The Gulf Stream provides a transport mechanism and habitat for many forms of life, its initial course being set by the North American continental slope, where warm- and cold-core rings spin off. In the Pacific, the Kuroshio Current, the world's second largest current, flows across the Pacific at speeds up to 121 km day^{-1}, and is approximately 1000 m deep. It forms south of Japan as the western boundary current of the North Pacific Gyre.

Table 4.1 Major oceans of the world and their significance.

Ocean	Areal extent 10^6 mile^2 (km^2)	Significance
Pacific Ocean	64 (165)	Global weather phenomena El Niño/La Niña; fisheries (60% of 1996 world's total fish catch); ocean-atmosphere interactions, climate control, global carbon fluxes; covers 1/3 earth surface; highest mountain on Earth (Mauna Kea, 33,476 ft/10,203 m) and deepest trench (Mariana Trench, 36,198 ft/11,033 m deep)
Atlantic Ocean	30 (77)*	Covers 20% Earth surface; receives ~4x more riverine inflow from land than either Pacific or Indian Oceans; initiates thermocline circulation (conveyor belt) in transport of heat and salt on a planetary scale; world's most heavily trafficked sea routes. Supports major fishing, dredging of aragonite sands (Bahamas), crude oil/natural gas production (Caribbean Sea, Gulf of Mexico, North Sea)
Indian Ocean	26 (68)*	Third largest ocean. The most expressed monsoon system; contains major sea routes (oil and petroleum products); oil and gas fields (40% world's offshore oil production), fish, shrimp, sand, gravel aggregates, placer deposits, polymetallic nodules
Southern Ocean	8 (20)*	Fourth largest ocean, surrounds Antarctica; freezes in winter; potential large/giant oil and gas fields; manganese nodules, possibly placer deposits, sand & gravel, freshwater storage in icebergs; supports major fisheries; marine mammals
Arctic Ocean	5 (14)	Contains widest continental shelf; winter ice cover (thinning); ecosystem slow to change and recover from disruptions or damage; receives large watershed inputs; contains sand and gravel aggregates, placer deposits, polymetallic nodules, oil and gas fields. Supports major fisheries, marine mammals (seals, walruses, whales)

*The International Hydrographic Organization in Spring (2000) delimited a fifth world ocean by removing the Southern Ocean from the Atlantic Ocean (from Longhurst, 1998b).

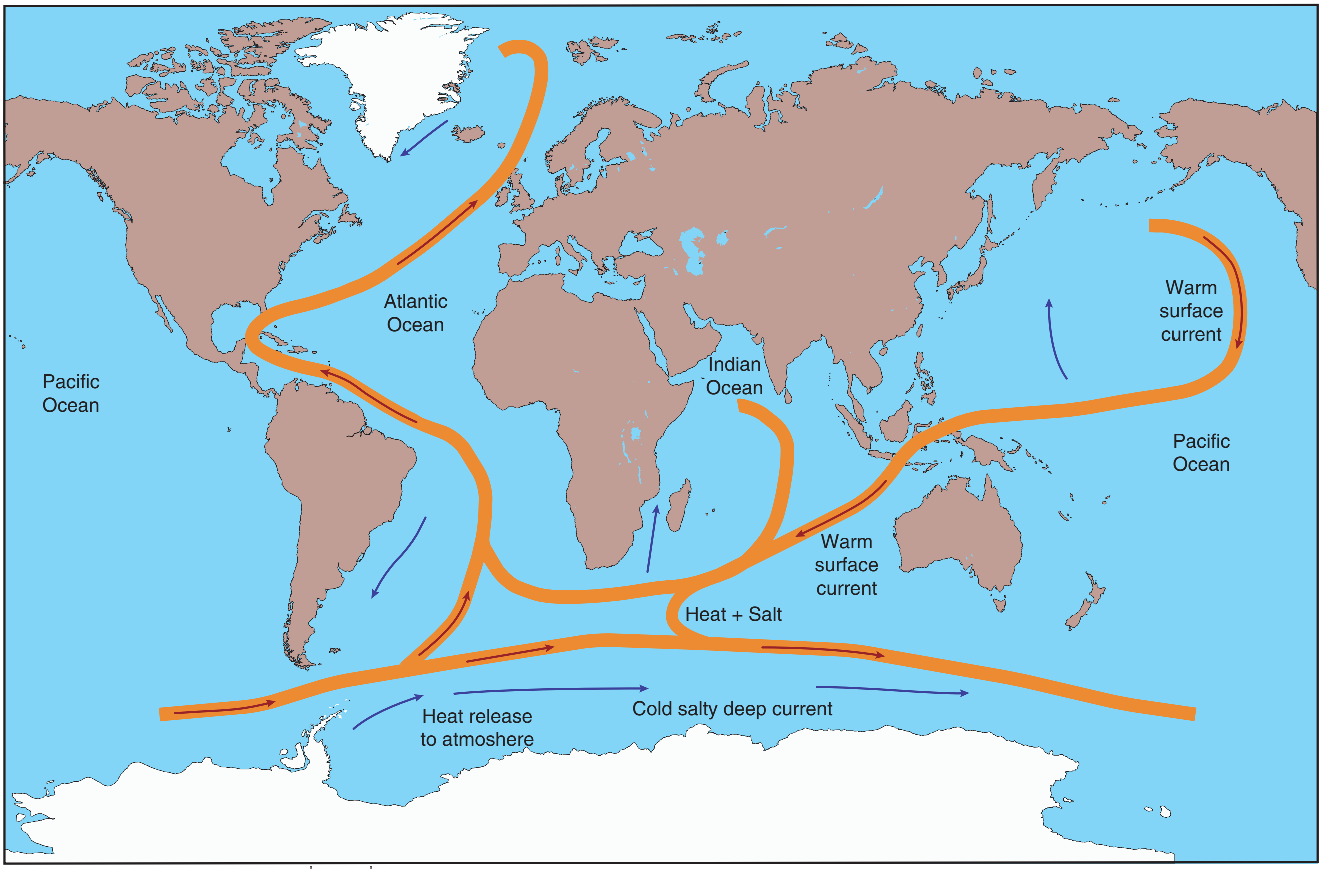

Fig. 4.2 Ocean conveyor belt: a simplified, conceptual model of the redistributionof global water masses. High-salinity North Atlantic water cools and sinks into cold, deep, high-salinity North Atlantic Deep Water current moving south into the Southern, Indian, and Pacific oceans, where upwelling moves into shallow and warm waters, then in a return current to the North Atlantic. Part of this global ocean circulation includes the buoyancy-driven thermohaline circulation, which transports heat from the tropics to the northern North Atlantic and causes a northward heat flux through the Atlantic. Based on data from Broecker (1991); IPCC (2001); Richardson (2008).

On a planetary scale, ocean surface circulation connects with the deep thermohaline (deep mass) circulation in a global pattern of water movement, captured in the scientific concept as the "global oceanic conveyor belt" (Broecker, 1991, 1997; Fig. 4.2). This circulation transports heat, energy, and solutes through processes that can be thought to begin in the North Atlantic with the North Atlantic Current and formation of North Atlantic Deep Water (NADW), initiated through evaporation and sinking of cold, salty surface water. This deep water flows southward to form the Antarctic Circumpolar Current, then northward along the ocean bottom into the Pacific and Indian Oceans, gradually warming and mixing with the overlying surface water. If North Atlantic surface-water salinity somehow drops too low to allow for the formation of deep-ocean water masses, the system can weaken or shut down entirely, as apparently happened during the Little Ice Age (about 1400 to 1850 AD). Broecker (2006) and colleagues suggest that the ocean's overturning was responsible for the rapid climate fluctuations experienced during Earth's last glacial period. Because of the ocean's crucial role in the Earth's climate system and its massive uptake, transport, and storage of heat and carbon dioxide (CO_2), scientists are intensively debating the conveyor-belt concept (Lozier, 2010, 2012), particularly in the context of climate change.

4.2.4 Major geologic movements

The Earth is made up of moving layers. The Earth's upper mantle and crust (the lithosphere) were built from its hot molten core. The hard lithosphere is broken into dynamic, continental, tectonic plates that move and cause earthquakes, volcanic activity, and continental drift. Over hundreds of millions of years, the Earth's land surface has been rearranged in patterns very different than today, as plates have drifted apart or together in a series of supercontinents during the ancient Archean Eon, forming Rodinia, and subsequently Pangaea surrounded by Panthalassa (ocean) about 400 million years ago. The Pangean plates began to separate about 135 million years ago into two landmasses: Laurasia to the north and Gondwanaland to the south, intercepted by the Tethys Ocean. As the plates continued to drift apart, the continents and oceans took their present positions (Blakey, 2008).

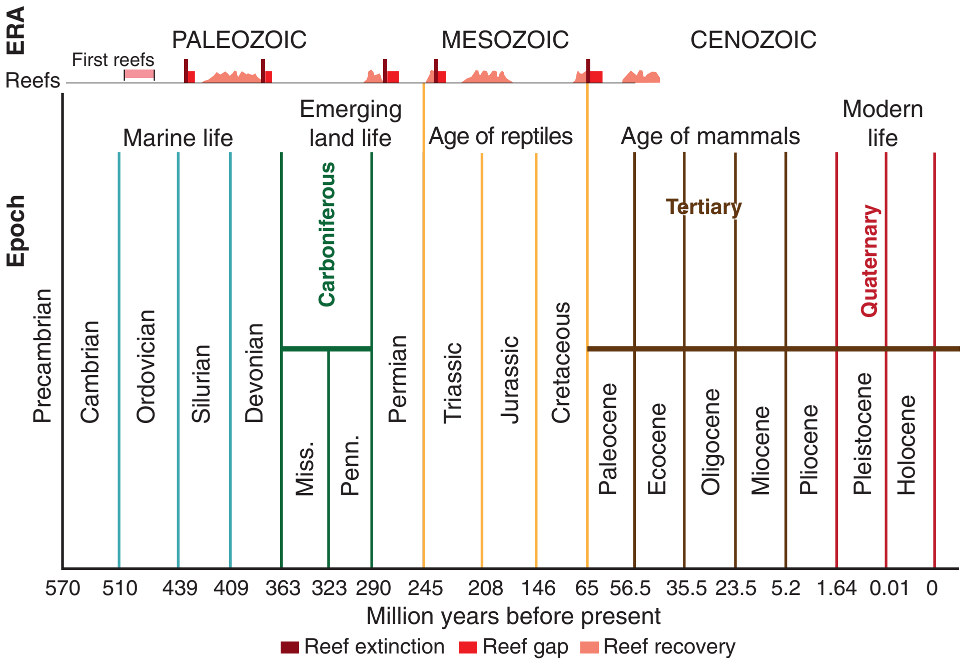

Fig. 4.3 Earth and its life have changed dramatically during 570 million years of geologic time, evolving through major eras (Paleozoic to Cenozoic) and epochs (Precambrian to the Holocene), with coral reef extinctions and recoveries into the present, diverse modern age. Reefs were first observed in the Ordovician and underwent five major extinction events (vertical dark purple bars) that left the Earth without living coral reefs for at least four million years (reef gaps = red, smaller rectangles), and recovery into different, prolific reef growth (pink pattern). Modern reefs are not shown. Based on data from USGS (2010) and Veron, JE (2008).

This geological history provides the basis for tracking Earth's time and evolution. Time scales called geological eras, periods, and epochs (Fig. 4.3) highlight changes in life forms up to the modern era. Within the 300 million-year Paleozoic Era and formation of Pangaea, life moved onto land, and most invertebrate and vertebrate groups and vascular plants evolved. This period of no less than two ice ages and diversifying marine life ended with the Permian/Triassic extinction 250 million years ago, the greatest mass extinction event in geologic history. In total, five mass extinctions have occurred during Earth's history, followed by new and diversified marine and terrestrial life. The Mesozoic Era is marked by the formation of the present land and ocean configuration—the Age of Reptiles—when reptiles flourished and birds and small mammals evolved only to suffer a second great extinction event at the end of the Cretaceous Period. Biotic evolution then resulted in the Age of Mammals, which continues today. Five extinction events affected coral reefs as much as any other ecosystem, with recovery requiring at least four million years during "reef gaps" before living reefs returned (Veron, 2008).

4.3 MAJOR OCEAN STRUCTURES AND CONDITIONS

A conceptual view of the dynamic ocean system is facilitated by identification of its major structural features. Boundaries in the water column that affect species distributions include pressure, light, temperature, oxygen, pH, and salinity, each of which change with depth, season, and circumstances. Combinations of these factors and a shared common history create water masses, i.e., identifiable bodies of water with physical properties distinct from the surrounding water, most reliably determined by temperature and salinity. Water-column features and ocean patterns are influenced by continental landmasses that contribute lithospheric and continental shelf boundary conditions.

4.3.1 Physical structuring

Water masses, currents, eddies, gyres, and upwelling areas form prominent coherent features of the water column, with peripheries marked by steep transition zones known as fronts. Frontal systems (tidal, shelf-edge, oceanic) are separated by physical discontinuities of current speed, temperature, salinity, and density, with sharp boundaries and abrupt ecological changes (Longhurst, 1998a). Vertical structure is created by sharp changes in temperature (thermoclines), oxygen, and salinity/density (pycnoclines) that can stratify the water column into different biological zones. Thus, when water movement is slowed at a boundary, as between water masses, sea bottom, land and air, and encountering hard objects, a steep transition over relatively short distances creates a spatial zone of discontinuity, which can demarcate distinct but sometimes "leaky" seascapes and biogeographic patterns (Ch. 5).

Physical forces that drive circulation patterns and create eddies and fronts at mesoscales (1–500 km) form large-scale coherent oceanographic, chemical, and biological patterns, and also form patches down to millimeters in size. Physical forces that create eddies and fronts may play a role in the generation of phytoplankton and zooplankton patchiness at all scales (Martin, 2003). Physical oceanographic processes such as turbulent advection, upwelling, convergence, and vertical mixing can drive various biological responses such as growth, grazing, and behavior, and strongly regulate and are correlated with planktonic spatial patterns. At frontal zones, marine productivity and biomass increase to sometimes exceptionally

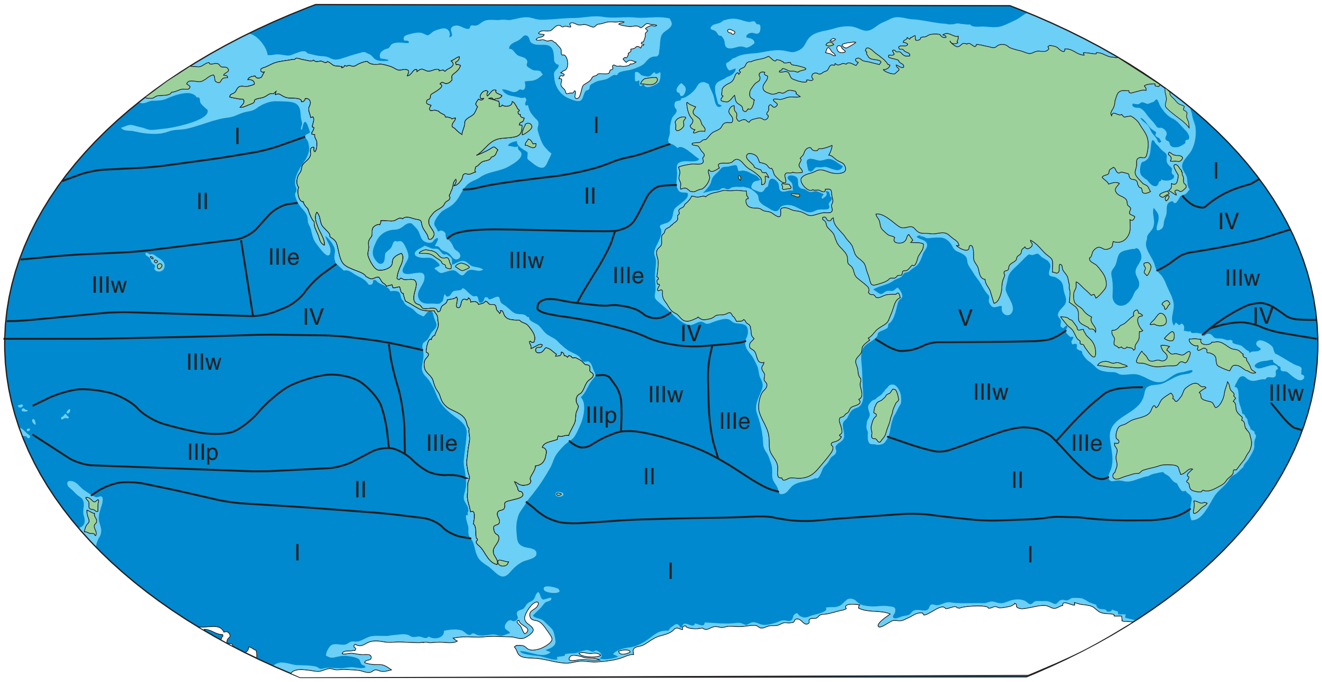

Fig. 4.4 Continental shelf (light blue) extends offshore around the land. Physio-oceanographic features distinguishocean provinces, classified as: (I) variable eastward; (II) weak and variable; (III) trade wind; (IV) strong westward and equatorward; and (V) monsoons with seasonal reversals. Category III is further subdivided into: (IIIe) strong equatorward; (IIIw) westward; and (IIIp) strong poleward. Based on data from Hayden *et al.* (1984); Holligan and Reiners (1992).

high levels that attract top predators, where organisms aggregate on a variety of spatial scales, depending on their size, evolutionary inheritance, life history, and physiological capacity (Bost *et al.*, 2009). In areas of surface-water discontinuities where strong and dynamic interfaces separate eddies and fronts, many large predators (tuna, birds, turtles, and cetaceans) come to feed (Kai *et al.*, 2009). Furthermore, eddies and their attendant fronts entrap fish eggs and larvae to form important pelagic habitats for fisheries production (Govoni *et al.*, 2010).

The relatively shallow continental shelf that surrounds nearly all landmasses is an extension of the continental geologic crust that creates a benthic boundary condition between land and sea (Fig. 4.4). This shelf begins at the littoral zone and extends to outer edge depths of approximately 200 m, over which "neritic water" is distinguished from ocean pelagic deep water off the shelf (Huthnance, 1995), although both are commonly referred to as "pelagic." Similarly, marine sediment that covers most of the shelf is distinct in composition from that under the open ocean beyond the shelf. Depth, motion, and seafloor stability establish conditions that influence the water column's heterogeneous structure.

At the edge of the continental shelf, identified as the continental/ocean margin (slope and rise; Fig. 4.1), the deepening seafloor abruptly descends from 200 to approximately 4000 m. Here, the ocean-shelf exchange and stratification are interrupted by water masses of different characteristics (notably temperature and salinity), and special internal ocean processes are created (Huthnance, 1995). The relatively narrow continental margin that covers only about 11% of the global seabed contains sharp environmental gradients and tectonic activity (Buhl-Mortensen *et al.*, 2010; Levin *et al.*, 2010). Over the abruptly deepening continental slope, ocean processes interact with complicated topography marked by submarine canyons that exceed any canyon on land. The depth changes from approximately 2000 to 5000 m then becomes gradual, distinguishing the margin from the deep-sea floor at the continental rise (Menot *et al.*, 2010). The continental margin, a most heterogeneous environment characterized by multiple water masses, distinct hydrographic characteristics, and stratified water, separates the neritic and ocean systems.

The dynamic continental margins are highly productive, and can be unstable (Helly and Levin, 2004). Some receive massive river inflows with exceptional inputs of floodwater, macrophytic detritus, suspended organic matter, and debris of terrestrial origin, and are marked by coastal longshore transport systems. Some margins are naturally hypoxic and low in biodiversity. In other margins, upwelling brings nutrients to the surface that stimulates productivity and brings large marine predators such as elephant seals (Ch. 12) and sperm whales (*Physeter macrocephalus*) into these major feeding areas. Tectonic activity can jolt, and subduction can squeeze, triggering downward-flowing turbidity flows that carve into the substrate and force reduced fluids out of the system that would otherwise fuel chemosynthetic (seep) ecosystems. These events can be episodic, and violent cascades can lead to erosion and material deposition, which impose variable temporal and spatial constraints on living fauna. In some margins at mid-bathyal depths, naturally hypoxic waters can smother the seabed.

The open ocean, with an average depth of approximately 4000 m, is distinguished by its deep bathyal, abyssal, and hadal zones (Fig. 4.1). The approximately 4°C bathyal zone in 1000 to 3000 m depths falls below the photic zone, and overlaps with the upper abyssal zone in 2000 to 6000 m depths. Abyssal water, which originates at the air-sea interface of polar regions, spreads over the 300 million km^2 abyssal plain 1 km below the surface, an area that represents 83% of ocean and 60% of Earth's surface. This is the world's largest habitat and last remaining wilderness, a cold, lightless, high-pressure environment rich in rare species (Grassle and Maciolek, 1992; Van Dover, 2000), but of low abundance, a high level of endemism, and patchy biotic distributions (Vinogradova, 1997). Mobile epibenthic megafauna at 4100 m depth can exhibit inter-annual changes in abundance from one to three orders of magnitude that reveal time scales relevant to the biota that live there (Ruhl, 2007). In the abyssal benthos, long dead carbonates of protozoan origin forms massive areas of benthic mud and siliceous ooze (Van Dover, 2000). Bodies of dead whales form islands of production (Ch. 5). The deepest ocean zone is the hadal, in water depths greater than 6000 m, water temperatures of 1.0–2.5°C, and dominated by ocean trenches ventilated by deep currents. The deepest trench is the Marianas Trench at almost 11,030 m (11 km). The hadal environment is under tremendous hydrostatic pressure, and species are often restricted to local areas; 95% occur only in a single trench or groups of adjacent trenches (Vinogradova, 1997).

Submarine mountain ranges of high relief occur in the mid-ocean. They result from planetary-scale processes of ocean crust formation at spreading centers where ocean plates diverge and where new oceanic crust is formed. When plates separate, global heat is lost, and ridges with fissures or cracks along their crests are formed. In these mid-ocean ridge systems, active volcanism accounts for a significant number of Earth's total volcanism (www.mbari.org). Hydrothermal vent systems are a conspicuous feature of Earth's oceanic crust. Spatial and temporal scales of venting are influenced by the rate of new crust formation and the amount of tectonic activity. Unique endemic faunal vent assemblages were first discovered in 1977 (Van Dover, 2000). Numerous others have since been found that host assemblages of giant clams and mussels, tubeworms, eyeless shrimp, and bacteria that all depend on sulfur as the primary energy source, rather than oxygen gained through photosynthesis. As vent biota are intimately linked to the geologic and chemical environment, they depend on obtaining reduced inorganic chemicals from chemosynthesis, a process known since 1887 to occur in surface marine sediments described by the Russian scientist, Sergei Winogradski, as the "black layer" (Kiel and Tyler, 2010).

Seamounts are prominent, widespread underwater topographic features ("mountains") that rise from the sea bottom, but do not break the surface. On abyssal plains and continental slopes, seamounts can be interspersed with topographic features that may extend >1000 m vertically upward from the seafloor (McClain *et al.*, 2009). Estimates of their numbers vary, but up to 200,000 may exist (Clark *et al.*, 2010). Seamounts host rich communities of fish (Williams *et al.*, 2010) and algae (Littler *et al.*, 2010). Isolating mechanisms on some seamounts create highly endemic faunas (Richer de Forges *et al.*, 2000); some lack endemic species yet contribute structures different from the seafloor and potentially provide larvae to recolonize suboptimal, non-seamount habitats (McClain *et al.*, 2009).

Emergent features in any depth of water are islands or island chains classified as continental, marginal, or oceanic. Islands exhibit continental features proportional to their size, the largest being microcosms of continents. Continental and marginal islands are often formed by sedimentary processes and have structural links to continents. Others such as Fiji and the Azores are oceanic islands surrounded by deep oceanic water, with many formed by volcanism, e.g., the Hawaii chain. Due to their isolation, oceanic islands often exhibit unique biological conditions with dynamic barriers and steep gradients to the surrounding ocean. Although islands cover only about 3% of the world's surface, they support a disproportional amount of biodiversity, especially endemics. Biota on oceanic islands may be as different as are the islands themselves, hosting 12 m sunflowers, 250 kg tortoises, marine iguanas, and many others that occur nowhere else. Islands known as atolls, as Charles Darwin correctly hypothesized, are submerged ocean mountains crowned with a ring of actively growing coral reefs; most occur in the Indian and Pacific oceans; only a few are Caribbean, notably in the western Caribbean and The Bahamas. The Saba Bank Atoll in the Caribbean Netherlands is one of the three largest among 400–500 atolls that exist worldwide.

Many islands totally lack capacity for surface or ground water storage, and the biota are adapted to episodic rain events and desert conditions surrounded by a salty sea. Estuarine conditions and anadromous/catadromous species are often lacking. Islands are vulnerable habitats, exhibiting the world's highest extinction rates. About half of the 724 recorded animal extinctions in the last 400 years were island species (CBD Secretariat, 2010, online).

4.3.2 Chemical structuring

Chemical reactions involving temperature, dissolved sodium, chloride, carbon dioxide, carbonate, crystalline calcium carbonate, etc., give the ocean its saltiness, with a salinity of approximately 36 (°/oo) and a mildly basic pH of approximately 7.8–8.2. Water temperature and salinity greatly affect water density, and interact with light to characterize ocean systems.

Living structures depend on three elements that make up 99% of organic molecules: carbon, hydrogen, and oxygen. Nitrogen forms a crucial organic molecule in the blueprint of a cell—its nucleic acid. The development of an oxygenated atmosphere in ancient times advanced life beyond single-celled organisms, which with improving oxygen concentrations is broadly linked to ecological diversification and biological complexity (Knoll *et al.*, 2006). When oxygen was lacking more than two billion years ago, an important constituent of Earth's early atmosphere was hydrogen gas, likely released by microbes (chemoautotrophs; Falkowski, 2012). When oxygen-producing cyanobacteria, a major primary producer in primordial seas, arose to be the source of oxygen for the planet, this most significant event changed the history of life and the evolution of life itself (Canfield, 2005). As oxygen levels in the atmosphere rose, shallow oceans became mildly oxygenated, but deep oceans remained anoxic (Holland, 2006). When atmospheric oxygen reached modern levels during the early Phanerozoic Eon (544 ma to present), visible life emerged and diversified. Shallow oceans became oxygenated and deep-ocean oxygen fluctuated considerably on geologically short time scales (Holland, 2006). This allowed a high diversity and abundance of marine life to evolve, until approximately 250 million years ago at the end of the Permian as much as 82% of all genera and perhaps 80–95% of all marine species went extinct. On land, vertebrates, plants, and insects also underwent mass extinctions presumably due to climatic effects, including acid rain, global warming, and volcanic eruptions that involve chemical change (Erwin *et al*., 2002). Knoll *et al*. (1996) proposed that the deep anoxic ocean overturned and high concentrations of carbon dioxide came to the surface. Carbon dioxide in excess is soluble in seawater and increases acidity, which may have affected calcifying taxa, replacing them with highly productive non-calcifying taxa.

Today, oxygen and nitrogen are the most abundant gases dissolved in seawater. These with carbon, phosphorous, and others, play key roles in forming biological structures and complex life forms through ecological transformation. Oxygen minimum zones are a permanent, natural feature of the ocean, with over one million km^2 of permanently hypoxic shelf and bathyal sea floor in existence today, over half (59%) of which occurs in the northern Indian Ocean with dissolved oxygen levels of $<0.5\,\mathrm{ml\,l^{-1}}$ (Helly and Levin, 2004). Due to warming oceans, nutrient enrichment, high atmospheric concentrations of carbon dioxide, and enormous changes in ocean chemistry are occurring, inducing ocean acidification and causing rapid declines in mid-water oxygen concentrations (Brewer and Peltzer, 2009). Coastal "dead zones," i.e., areas deficient in oxygen (hypoxic) or depleted of oxygen (anoxic; Box 2.5) restrict development of complex life forms.

4.4 PLANETARY CYCLES

The Earth's planetary system appears to be unique in the universe; a system maintained by the cycling of matter, water, and living resources (Kleidon *et al*., 2010).

4.4.1 Water cycle

Water is a naturally circulating resource that is constantly recharged (Oki and Kanae, 2006). Global movement of water on, in, and above the Earth (the water cycle) is driven by convection and atmospheric motion that solar radiation and evaporative processes create. Water connects atmospheric, terrestrial, and ocean processes in a cycle that has continued for millions of years, as water changes from liquid to vapor or ice and back again. Ocean currents and evaporation move water into clouds that fall back to Earth as rain, fog, hail, snow, or sleet. Water moves through forests, plants, and soils, draining from land in surface runoff or stored in lakes, aquifers, reservoirs, and groundwater (Fig. 4.5). Freshwater from land sources eventually moves to the ocean. Globally, the high variability and availability of water make it a vulnerable natural resource, even more critical under scenarios of climate change.

The global water system is central to Earth dynamics. It integrates and regulates biogeochemical and biogeophysical processes that maintain terrestrial and aquatic ecosystem integrity (Crossland *et al*., 2005). It controls terrestrial ecosystem dynamics through interactions with biota and climate, ecosystem feedbacks, and watershed connectivities, all of which modulate hydrologic processes and rates of flow (D'Odorico *et al*., 2010). Climate controls globally variable moisture, precipitation, temperature, water storage, and water availability. Thick snow falls at certain times and places in colder climates, compacting into ice to form glaciers and ice sheets that when melted provide water sources. In warmer regions or periods of drought, water availability affects terrestrial and coastal ecosystems, especially estuaries (Ch. 6).

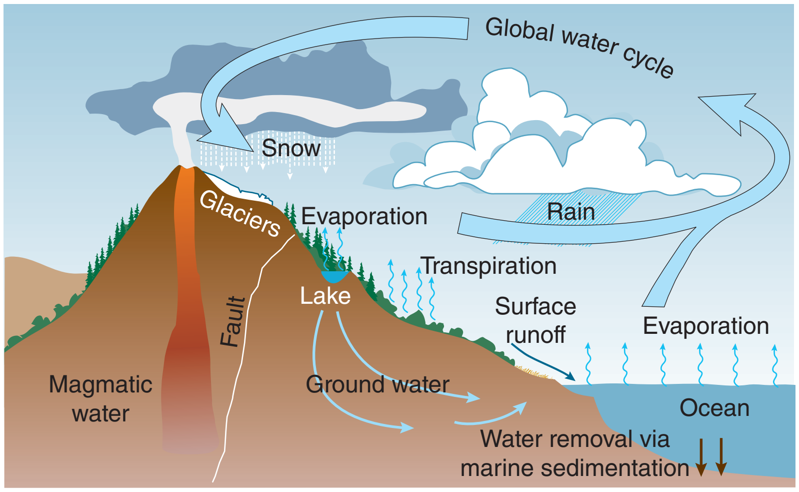

Fig. 4.5 The global water cycle is driven by the sun as water is recycled through land, ocean, air, forests, plants, and soils. The sun heats water, water evaporates, falls as snow and rain, is stored in glaciers, lakes, aquifers, reservoirs, groundwater and the ocean, and drains from land as surface stream flow and groundwater seepage back to the sea.

4.4.2 Biogeochemical cycle

At Earth's surface, matter and energy are exchanged and reused through extremely complex biogeochemical cycles (Fig. 4.6a; Hedges, 1992). Interacting processes operate on timescales of microseconds to eons, in domains as small as a living cell to domains encompassing the entire atmosphere-ocean system. In marine systems, nutrient chemicals (nitrogen, phosphorus) can become limiting unless captured and recycled by organisms and returned to the system through upwelling, bioturbation, river flow, etc. Elemental carbon, in close association with nitrogen and phosphorus, moves through living matter, where biochemistry and global biogeochemical cycling are linked in characteristic stoichiometric ratios: e.g., C:N:P Redfield ratio (Redfield, 1958), a measurement tool indicating that ocean water is in chemical equilibrium. As essential constituents of living systems, organisms regulate the rates of recycling of these elements and where and which chemical form accumulates. Thus, living organisms play key roles in biogeochemical reactions and global recycling pathways, facilitated by atmospheric motion and transformations of elemental chemicals (Schlesinger, 1997).

Carbon cycling is of particular importance (Fig. 4.6b). The global ocean is the largest reservoir of organic (biogenic) carbon on Earth's surface (Hedges, 1992), where colloids in surface waters form a globally significant fraction of dissolved organic carbon (Kepkay, 2000). Marine organisms mediate carbon flow in a series of processes referred to as the "biotic pump," consuming and cycling dissolved and particulate organic matter. Marine photosynthetic activity captures more than half of the global carbon (Falkowski *et al*., 2000; Nellemann *et al*., 2009), with biotic growth and respiration; microzooplankton grazing also plays important roles (Calbet and Landry, 2004). Among other small organisms, ubiquitous unicellular cyanobacteria produce organic carbon, heterotrophic bacteria metabolize carbon, and viruses are important in recycling (Wilhelm and Suttle, 1999). Carbon dioxide gas (CO_2) released to surface waters through respiration and decay is balanced, in part, by the calcification and growth of organisms.

Large amounts of calcium carbonate fall out of surface waters from sinking dead marine plant and animal exoskeletons (e.g., microscopic protozoans, foraminiferans, coccolithophores). This sinking of biogenic particles drives respiration in the water column and helps maintain a strong vertical ocean gradient of inorganic carbon. Under various circumstances, a reverse biological pump moves carbon back into the water column, such as when deep-sea fishes spawn on the bottom and their eggs rise up to the thermocline to hatch, and larvae become consumers in surface waters. If carbon is not released or transported out of deeper waters (e.g., bioturbation, Ch. 5), it becomes trapped on and in the ocean floor.

The marine nitrogen cycle is perhaps the most complex of all. Nitrogen is a major component of the atmosphere, and its role in primary production is critical, being fixed by biota and bacteria into useable nitrate (NO_3) and ammonium ion forms (NH_4), or released as inert nitrogen gas (N_2) to the atmosphere through denitrification. Nitrogen circulates through biota, the atmosphere, and back through biota, thereby exerting a significant influence on cycles of many other elements, in particular carbon and phosphorus. Phosphorus also plays a major role in coastal systems and global oceanic primary production, being a vital macronutrient in living systems. Most chemical forms of nitrogen in the ocean are bioavailable, but dissolved nitrogen gas (N_2), the most abundant form of nitrogen, is generally not. Nitrification and denitrification are critical processes linked to the global carbon cycle and climate (Canfield *et al*., 2010; Gruber and Galloway, 2008).

The sulfur cycle is of special interest because the ocean is Earth's main sulfur sink (Liss *et al*., 1994). Sulfate is the second most abundant anion in seawater, with oxygen playing a key role in the oxidative part of the sedimentary sulfur cycle. In ocean surface waters, decomposition of phytoplankton releases a volatile gas, dimethyl sulfide (DMS), that is significant in cloud formation and climate, and contributes to atmospheric sulfur dioxide (SO_2). DMS is also linked to coral spawning, fish abundance, and to squid aggregations over coral reefs (DeBose and Nevitt, 2008).

Humans have affected virtually every major biogeochemical cycle (Falkowski *et al*., 2000), and the way that nutrients cycle and place constraints on the rates of biological production and land/sea ecosystem structures. Understanding the complex interactions and relationships among nutrient cycles and other biogeochemical and climatological processes requires a systems approach (Falkowski *et al*., 2000). Atmospheric carbon dioxide (CO_2) exchanges rapidly with the oceans and results from both biotic and human activities. The ocean stores an estimated 93% of all of Earth's CO_2 (Nellemann *et al*., 2009) as well as a third of anthropogenic CO_2 from fossil fuel and deforestation emissions (Siegenthaler and Sarmiento, 1993). The marine carbon cycle controls CO_2 partitioning between oceans and atmosphere, with ocean productivity playing an important part. Coastal sediments under high carbon loading and high oxygen demand may become anaerobic and sulfate reducing (Middelburg and Levin, 2009). The carbon cycle is influenced by the rate of atmospheric change of CO_2 and depends on biogeochemical and climatological processes, and human interactions, which with other long-lived greenhouse gases (e.g., methane, CH^4; nitrous oxide, N_2O), trap heat to cause global warming.

4.5 MAJOR PLANETARY INTERFACES

The interfaces between land and sea, benthos and water column, and air and sea are dynamic boundaries characterized by steep, transitional gradients and inter-exchanges. These interfaces result in directional fluxes of nutrients, energy, and materials important to species and ecological processes in adjacent systems. The pulses of energy and materials across these interfaces drive land and seascape formation, further modified by tectonics, climate, biota, and sea-level change.

4.5.1 Land-sea interface

Rivers and ocean tides mingle at shallow-water interfaces. There, terrestrial and oceanic forces overlap spatially, and

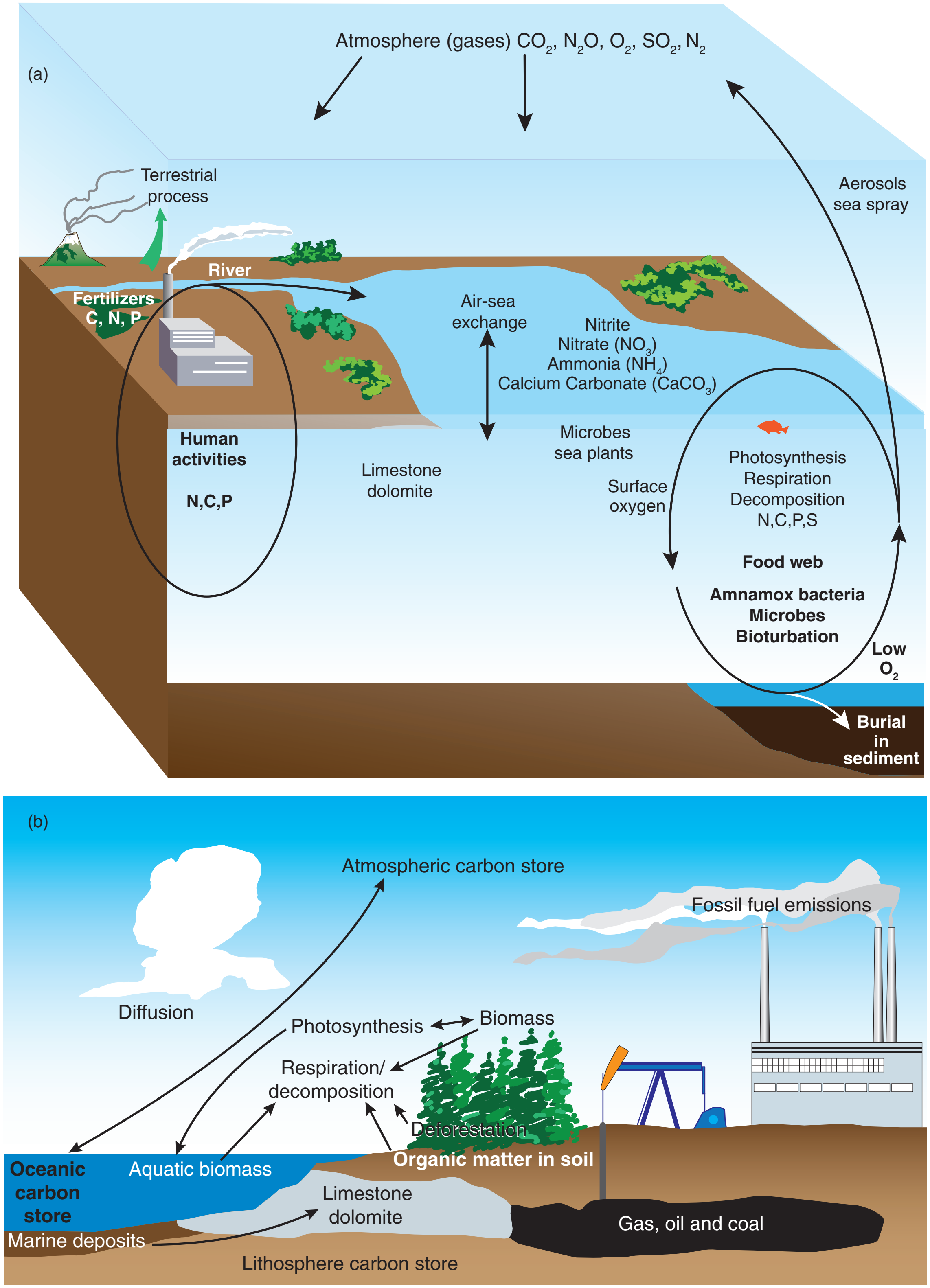

Fig. 4.6 Biogeochemical cycles are extremely complex. (a) Nitrogen (N_2O, N_2, NO_3, NH_4), carbon (CO_2, $CaCO_3$), phosphorus (P), and sulfur (S) move through various compartments on land, in air, in the water, to become transformed through biological, geological, and physical processes. Dimethyl sulfide (DMS) is produced by bacteria in phytoplankton and released to the atmosphere. Phosphorus accumulates in both organic and inorganic sediments, with no biological process generating an important gas flux to the atmosphere in the phosphorus cycle, as sea-salt aerosols can. (b) Carbon is stored in elemental rocks of carbonate minerals (limestone, shale), in thick coal beds, petroleum reservoirs, and in the atmosphere as carbon dioxide. In seawater, carbon exists in several forms (dissolved organic and inorganic, and particulate organic forms of living and dead matter), and large amounts of carbon dioxide can be absorbed from the atmosphere. Carbon in its dissolved inorganic form in seawater is a major, active reservoir. Carbon dioxide gas exchange with the atmosphere occurs through a gradient affected by winds and other environmental factors.

alternations of salt and freshwater, desiccation and drowning, intense heat and cold, and unique adaptations for survival are required to withstand variable tidal and wind energies that can move, crush, and smother. Tides powered by Earth, Moon, and Sun move energy and ocean water toward coastlines, further modified by changing weather, winds, seafloor topography, local water depths, and coastline configuration. Coalescing rivers and underground flows deliver freshwater and terrestrial materials through watersheds, where rooted vegetation controls surface runoff, stabilizes substrates, and cleans and transpires water in modified energy gradients to the ocean (Crossland *et al.*, 2005). On land, hydraulic gradients result in groundwater seepage near shore that may contribute to flows further out on the shelf through confined aquifers delivering chemicals and nutrients into coastal sediments (Burnett *et al.*, 2003). New materials far from original sources, driven by terrestrial and marine forces, create a nearshore, shallow-water, benthic system exposed to varying motion and constant change.

At this interface, the intermingling of different chemicals influences coastal water quality. Watersheds deliver freshwater (rain, rivers) with rich supplies of positively charged calcium, carbonate, and bicarbonate ions that interact with seawater delivery of abundant, negatively charged, dissolved chloride and sodium ions to affect coastal water density, electrolytes, and nutrients. When freshwater meets seawater, colloids are formed and deposited on the benthos, especially in estuaries, to play important roles in biogeochemical cycling of trace elements (Guo and Santschi, 1997). And the degree of fresh or saline water affects distributions and biogeography of coastal species (Ch. 6), while loading of carbon and nutrient chemicals affect the structure and dynamics of the coastal environment.

4.5.2 Benthic-pelagic interface

The seabed is the most extensive habitat on the planet, excepting the ocean itself. It provides habitat for living structures that are among the most prominent and most productive ecosystems (seagrass beds, biogenic reefs, algal flats, clam beds, etc.). The largest faunal assemblage in areal coverage of any biome on Earth resides on and in the marine benthos (Snelgrove, 1998), where life histories of many benthic organisms involve hatching, cysting, and larval releases to the water column. Between the benthos and the overlying water body, the seabed involves a two-way exchange, or flux, of matter that contribute nutrients, particulate matter, and microorganisms to the pelagic system (i.e., plankton), with profound influences on the dynamics of populations and communities (Raffaelli *et al.*, 2003). The soft mud/sandy bottom and harder gravel/rocky bottoms play important roles in biogeochemical cycling, hydrodynamic modulation, and pelagic/benthic coupling and exchanges. On or above this interface or within the mixed sediment layer, detritus, debris, and fecal pellets are consumed, degraded, exported, or trapped. Macroorganisms are key drivers of biogeochemical fluxes between water and sediment by aerating the benthos through burrows, bioturbation (Ch. 5), and active and passive bio-irrigation. Microorganisms degrade plant products into small organic remnants and release denitrifying gases (N_2O). Under low light energy and an external organic carbon source, microorganisms (chemoautotrophs) reproduce and release hydrogen gas (Falkowski, 2012). Hence, a flux of matter and chemicals crosses this interface through processes that involve complex exchanges governed by hydrology, biological production, and organic and dissolved material fluxes through processes of decomposition and regeneration.

4.5.3 Air-sea interface

At the marine-atmosphere interface, globally significant exchanges of heat, momentum, and water vapor take place (Sikora and Ufermann, 2005). The ocean's heat capacity within its top 2–3 m is the same as the atmosphere above it (Soloviev and Lukas, 2006). The atmospheric layer is a variably thick medium through which exchanges with land and ocean result in large quantities of heat and momentum, energy, gases, particles, and materials (Box 4.1). At this interface, wind energy is converted into surface waves (Wang and Huang, 2004), kinetic energy is dissipated (Terray *et al.*,

Box 4.1 Dust-to-dust: wind-blown material

Michael Garstang
[Retired, Department of Environmental Sciences, University of Virginia], Charlottesville, Virginia, USA

Amber J. Soja
NASA National Institute of Aerospace, Hampton, Virginia, USA

Upwards of a billion tons of terrigenous material is lifted into the atmosphere and distributed around the globe every year (Fig. B4.1.1). Most of this material originates over the global deserts. Almost half of the above amount leaves the west coast of North Africa, originating over the Sahara and Sahel. Vast quantities of dust pour off the Gobi Desert into the Pacific Ocean. Saharan dust has been found over the Near East, in the Alps, in Finland, and in Scotland and pervasively in the Caribbean, the Amazon Basin, the coastal southern United States, and Mexico.

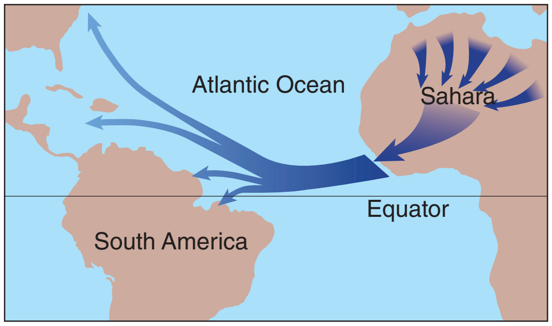

Fig. B4.1.1 Aerial transport of dust from continent to continent and ocean. Courtesy of M. Garstang.

Sources of the airborne particles or aerosols are numerous. A large fraction is soil dust, but organic matter from dry vegetation, products from biomass burning, and input from human activity, including cooking fires, agriculture, and industry, all contribute to the total airborne load. Particle sizes range from 1–200 mm for smoke from intense fires, to submicron sizes, which include pollen and spores. Silicon is often the dominant element, with abundant iron originating from the iron-rich red lateritic (oxisol) soils of the subtropical deserts. As many as 22 elements have been found in African dust captured in the middle of the Amazon rainforest. Phosphates, potassium, and nitrogen are present in amounts which when deposited reach kilograms per hectare per year.

The large particles and the greater part of the mass of aerosols are deposited in the coastal waters of the source region, and constitute a significant input of nutrients to these waters. Primary productivity in the coastal waters is dependent upon a suite of abundant (e.g., iron, carbon, nitrogen, and phosphorus) and trace nutrients (e.g., silicon, copper, and zinc), all present in the airborne load. Iron limits productivity in some oceanic regions and is abundant in the airborne soil dust. Evidence from the Pleistocene period suggests that increases of export production, which may have contributed to lower CO_2 concentration in the glacial atmosphere, were accompanied by a greater supply of iron from wind-blown aerosols. While upwelling is conventionally believed to provide the nutrients required for phytoplankton production, aeolian events may play a far greater role than has been previously recognized.

Patterns of phytoplankton blooms detected from the Coastal Zone Color Scanner carried on the Nimbus 7 satellite show expansion and contraction of blooms off the west coast of Africa which are spatially and temporally synchronous with dust outbreaks. As dust is transported by the atmosphere away from source regions, the total airborne load and deposition rates decrease. Both, however, remain significant. Annual transport through a hypothetical wall erected from the ocean surface to 4 km altitude and extending from 10 to 25° N latitude along 60° W longitude is estimated at 25–37 MT per year. This dust load enters the Caribbean Sea and continues onward across the Florida Peninsula and into the Gulf of Mexico. Similar transports extend northwestwards over the Sargasso Sea and southwestwards into the Amazon Basin. Estimates based upon calculations made over land in the nearly closed system of the Okavango Delta in northern Botswana show that dust from the atmosphere can on an annual basis contribute between 6 and 60% of the nutrient load. Previous studies had assumed all of the nutrients in this delta to be waterborne. Similar conditions may exist over coastal waters remote from the major sources of airborne material. Waters such as the Sargasso Sea, known to be largely oligotrophic, may receive significant nutrient supplies from atmospheric deposition. The same transport and deposition processes that deliver airborne nutrients to coastal waters can import trace elements from industry and agriculture (e.g., pesticides, fungicides, other organics). Such deposition has been suggested as a possible cause of coral die-off in the Caribbean. Advances in remote sensing from satellites now allow daily monitoring of dust over the oceans as well as detailed descriptions of long-range transport.

Sources: Garstang *et al*. (1998); Kaufman *et al*. (2005); Liu *et al*. (2008); Mahowald *et al*. (2005); Prospero (1999); Swap *et al*. (1992)

1996), and turbulent flux and breaking waves contribute 85% of the atmospheric water vapor and accentuate releases of important gases. Chemical processes involving marine aerosols may significantly impact tropospheric oxidation processes, sulfur cycling, radiation balance, climate, and ocean surface fertilization (Keene *et al*., 1998). Wave dynamics, gas transfer, nutrient and pollutant mixing, and plankton photosynthetic efficiency are major factors in air-sea exchanges.

A host of important gases that influence climate are exchanged, absorbed, and emitted at this interface. The ocean is both a sink and source for trace gases, and surface waters are supersaturated with gases, especially sulfur gases, e.g., hydrogen sulfide and dimethyl sulfide (DMS; Section 4.4.2). Any volatile organic compounds such as iodine and nitrates can react with chloride atoms released from sea-salt aerosols (Keene and Jacob, 1996; McFiggans *et al*., 2002). Iodine in high concentrations in the troposphere contributes to ozone destruction (Carpenter, 2003), and air-sea fluxes in the coastal ocean may be higher than in the open ocean (Carpenter *et al*., 2009). Atmospheric aerosols in significant amounts are important in regulating the composition of atmospheric greenhouse gases that contribute to ocean warming and acidification when mixed into the ocean interior.

4.6 THE DYNAMIC COASTAL REALM

The land/sea, benthic/pelagic, and air/surface interact most intensely in the broad domain of the coastal realm (Frontispiece). This region encompasses the approximately 200 m land elevation to the approximately 200 m marine depth (Pernetta and Milliman, 1995; Crossland *et al*., 2005; Ducklow and McCallister, 2004; Longhurst, 1998a) in accord with geologic rises and falls of sea level. Ketchum (1972) defined this region as a "coastal zone," i.e., a "band of variable width" that functionally "is the broad interface between land and sea where production, consumption, and exchange processes occur at high rates of intensity." This region exhibits features and functions very different from land or ocean alone, qualifying it as a third major subdivision of Earth—a "realm," used here to signify the highest biogeographic category (Fig. 4.7; Pielou, 1979), ranking it equally with land and open-ocean realms. This geochemically and biologically active region plays a dominant role in biogeochemical cycles (Gattuso *et al*., 1998), production, biodiversity, and services disproportionate to its global size (Table 4.2), with a resiliency that persists through seasonal and annual cycles, perturbations, and alterations of sea-level change. Human activities and conservation efforts need to account for the coastal realm's unique set of conditions.

4.6.1 Sculpting coastal land and seascapes

Interacting forces on different time and space scales sculpt the coastal realm into hierarchical patterns. Geologic and climatic events shape and move, adding much complexity to a strongly inhomogeneous and dynamic system. Understanding large-scale coastal behavior requires understanding short-term events and long-term processes (Schwarzer *et al*., 2003), where

Table 4.2 Coastal realm attributes of global significance. Based on data from Holligan and Reiners (1992); Pernetta and Milliman (1995); Gattuso *et al*. (1998); Beck *et al*. (2003); Borges and Gypens 2010.

Significance	Attribute
Spatial coverage	18–20% of Earth surface; 8% of ocean surface; <0.5% of ocean volume
Biogeochemistry process	~50% of global denitrification; 80% of global organic matter burial; 90% of global sedimentary mineralization; 75–90% of global sink of suspended river load, associated elements, and pollutants; ~20% of surface pelagic oceanic calcium carbonate stock; >50% of present-day global carbonate deposition
Production	New primary production rates significantly higher than open oceans; ~1/4 global primary production supply; ~14% of global ocean production; ~90% of world fish catch; Major nursery for fish and shellfish production
Human services	40% of the world population; 2/3 of world's major (>1.6 million people) cities; Concentrated global trade; Major oil and mineral reserves; Major sport fisheries supported; Major military centers for national defense

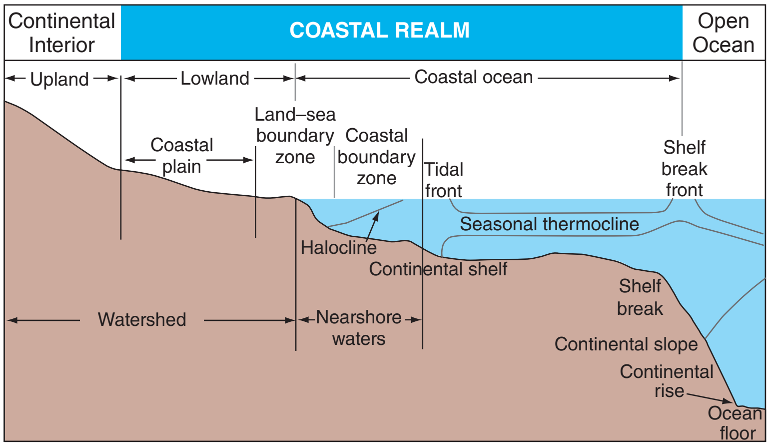

Fig. 4.7 Diagrammatic representation of coastal realm structure. Major boundaries occur in close proximity (land-sea, air-sea, benthos-water column) and strongly influence biotic distributions. Based on data from Holligan and Reiners (1992); Pernetta and Milliman (1995).

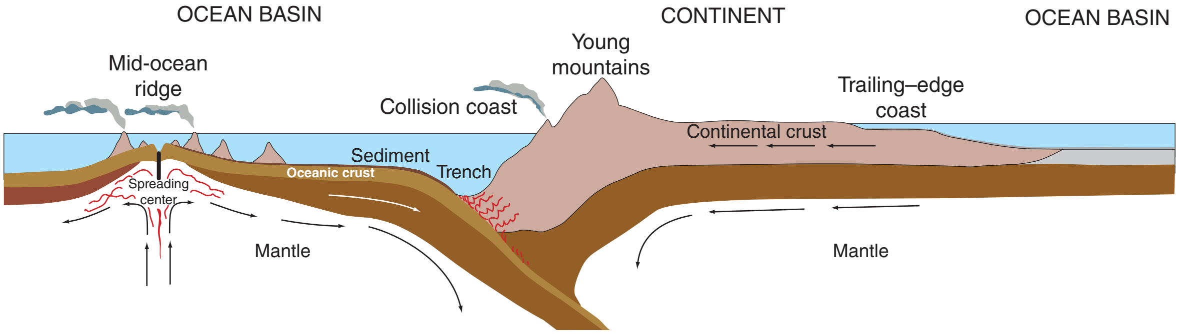

Fig. 4.8 Coasts and tectonic plates. A cross-section across South America and extending into the Atlantic illustrates a trailing-edge east coast. A spreading center at the eastern Pacific Rise through the Peru-Chile trench creates conditions for a collision coast. From Inman DL, Nordstrom CE (1971) Tectonic and morphologic classification of coasts. *Journal of Geology* **79**, 1–21 © 1971 The University of Chicago. With permission from University Chicago Press.

Fig. 4.9 Mountains and sea interact to create clouds and coastal weather phenomena resulting from land/water contrasts. Thermally driven effects result from contrasts in heating, modulated by contrasts in surface friction between land and water, and interactions between larger-scale meteorological systems (hurricanes, typhoons) that pass over water and coastlines. These produce distinct smaller-scale systems, and orographic effects driven by steep coastal terrain induces strong winds and longshore flows. This photograph from Betty's Bay, South Africa, shows cloud formation due to the orographic effect of onshore winds rising against the mountain. Photograph © Ray & McCormick-Ray.

antecedent conditions over geologic time have established large-scale coastal conditions, further modified by short-term oceanographic, climatic, and watershed events.

Plate tectonics create a great variety of coastal types important to biodiversity and conservation. Collision coasts, characterized by active volcanic and earthquake zones, occur where continental plates collide and one of the plates is subducted. The terrestrial relief is relatively straight, with mountain ranges and a steep narrow continental shelf (Fig. 4.8). On trailing-edge coasts, plates spread apart and the continental shelf is generally wide, giving rise to barrier islands and large regionally variable estuaries and lagoons. Neo-trailing-edge coasts are recently formed coasts that exhibit rifting (Red Sea, Sea of Cortez). Afro-trailing-edge coasts occur on both coasts of southern Africa (Atlantic and Indian Ocean), and Amero-trailing-edge coasts occur on North and South America east coasts. Coasts of marginal seas have typically curved coastlines with back-arc basins (seas within island arcs; e.g., Aleutians and Kurile Islands). Such coasts are frequently modified by large rivers and deltas, provide more protection from the open ocean than other coasts, and are most biologically diverse.

Coastal conditions create climates important to coastal diversity. Elevated coastal surfaces and uneven landscapes complicate meteorological transformations, generating winds that create sea-surface waves, atmospherically induced coastal-ocean currents, upwelling, fog, haze, stratus clouds, and orographic effects (Fig. 4.9). Changes in heat flux can introduce instabilities, cloud cover, and unique coastal phenomena (land and sea breezes, thunderstorms, atmospheric and oceanic fronts). The convergence of marine air over coastlines can also result in strong convection, heavy precipitation, and runoff that together increase erosion and pollution loads and disperse sediments. Coastal meteorology is thus unique due to exchanges between the atmosphere and heterogeneous coastal surfaces, complicated further by interactions with the

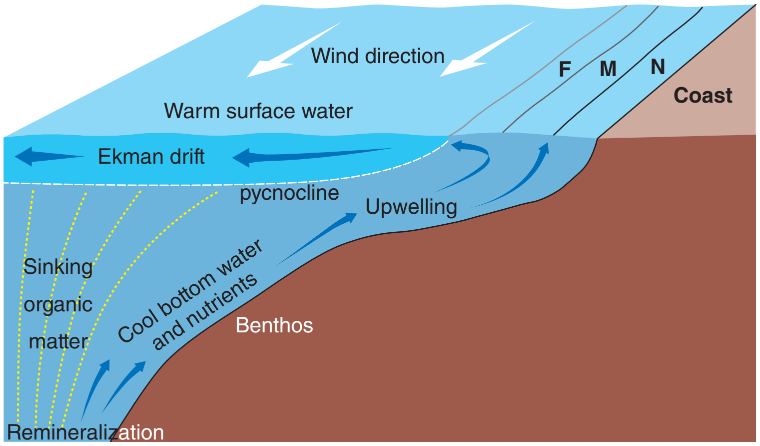

Fig. 4.10 Coastal upwelling. An oceanographic process usually driven by longshore winds that push warmer, nutrient-poor open surface waterawayfrom the coast, drawing nutrient-rich water to sunlit surface waters, enhancing photosynthesis. Water mass types: [N] nearshore waters of high primary productivity dominated by small cell-size phytoplankton and few zooplankton organisms and fishes; [M] mid-zone waters with abundant large phytoplankton, large zooplankton, very abundant small filter-feeding planktivorous fishes, and numerous sea birds; [F] frontal zone waters contain few plankton and planktivorous fishes, but plentiful carnivores (fishes, sea birds, marine mammals). Based on data from Bakun (1996); Gross and Gross (1996); Mann and Lazier (1991).

oceans (NRC, 1992). And coastal climate at global scales dramatically affects CO_2 exchange, photosynthesis, and biological productivity, played out at smaller scales through rapid and significant atmospheric events such as storms, wind events, and interactions caused by pressure gradients and topography.

Winds also interact with geomorphological and ocean processes to shape coastal landforms, sea-ice fields, coastal waters, and intertidal areas. Maximum wind speeds come from hurricane activity in areas where sea-surface temperatures usually exceed 26°C and with intense pressure gradients, causing massive flooding and high waves that wash over extensive land/sea areas (Trenberth, 2005). Storms and tectonic events deliver long-wavelength ocean surges (tsunamis) that cause severe beach, cliff, and dune erosion, much flooding, and human mortality. Winds also interact with ocean Coriolis force and Ekman transport (Section 4.2.3) to upwell nutrient-rich bottom water into sunlit surface water above thermal stratification (Fig. 4.10), stimulating high phytoplankton productivity, intense biological activity, and high fisheries production that often occurs close to shore (Mann and Lazier, 1991) and mostly on the west coasts of continents, e.g., U.S., Peru, and southwest Africa.

Sea-level changes sculpt the coasts, being intimately associated with global climate cycles of cooling, warming, and geologic adjustments on regional scales. Warming the ocean expands its volume and increases storm activity, storm surges, and strong waves that move sediment and erode coasts. Ocean thermal expansion raises sea levels, which involves a combination of global sea-level change (eustasy) and gravitational equilibrium of Earth's crust (isostasy). Through isostasy, Earth's crust maintains equilibrium relative to a fixed point where shelf subsidence is compensated by an uplift of coastal land, typically on rugged coastlines with narrow shelves. These vertical and horizontal displacements facilitate new coastal geometries and topographies. For example, ice sheets can influence isostatic changes; the weight of Antarctic ice sheets has depressed the entire continent hundreds of meters, and in the present interglacial period, sea level has varied across the coastal plain from a maximum upper height at 50–100 m land elevation to a lower limit of approximately 100–200 m at the outer edge of the continental shelf (Fig. 4.11).

New technological advancements in satellite altimetry and geodetic leveling have increased the accuracy of global sea-level measurements (Nicholls and Cazenave, 2010), providing new evidence of higher 20th century levels than in the 19th century. However, the rise and fall of sea level due to isostasy and eustasy varies with location and may not always be apparent. If the land surface subsides as ocean volume increases, the rate of submergence will be greater than induced by changes in ocean volume alone. Furthermore, sediment flux to coasts from increased human activities affects coastal-ocean, floodplain, and delta-plain functions (Syvitski et *al*., 2005; Syvitski and Kettner, 2012). Massive withdrawal of water, gas, and oil can cause land to subside, and massive amounts of sediment from sediment-laden rivers deliver added weight onto the continental shelf (Milliman and Haq, 1996).

4.6.2 Land-ocean interactions

Watersheds sculpt the coastal realm into many permutations of land and seascape patterns. Watersheds can be simple, compound, or complex, depending on whether their drainage system originates near shore, or upland and across a coastal plain, in either case to empty into coastal waters through five land/sea drainage compartments (Fig. 4.12). Watersheds interact with coastal receiving-basins in a freshwater gradient and delivery of sediment. Seaward, in water depths generally less than 20 m (the subtidal shoreface entrainment volume) and with much mixing, surface water interacts with waves and tidal mixing to entrain a volume of oscillating water with sediment. Seaward in shelf depths of 20–50 m, water temperatures are generally homogeneous with depth in winter but may be stratified (often nearly two-layered) in summer (Mooers, 1976). At mid-shelf depths of 50–150 m, the water column is generally vertically stratified, with frequent exposures to coastal jets and surface fronts. At the outer shelf-break in 150–250 m depths, surface and bottom fronts are common, and shelf and oceanic waters interact most intensively. Farther

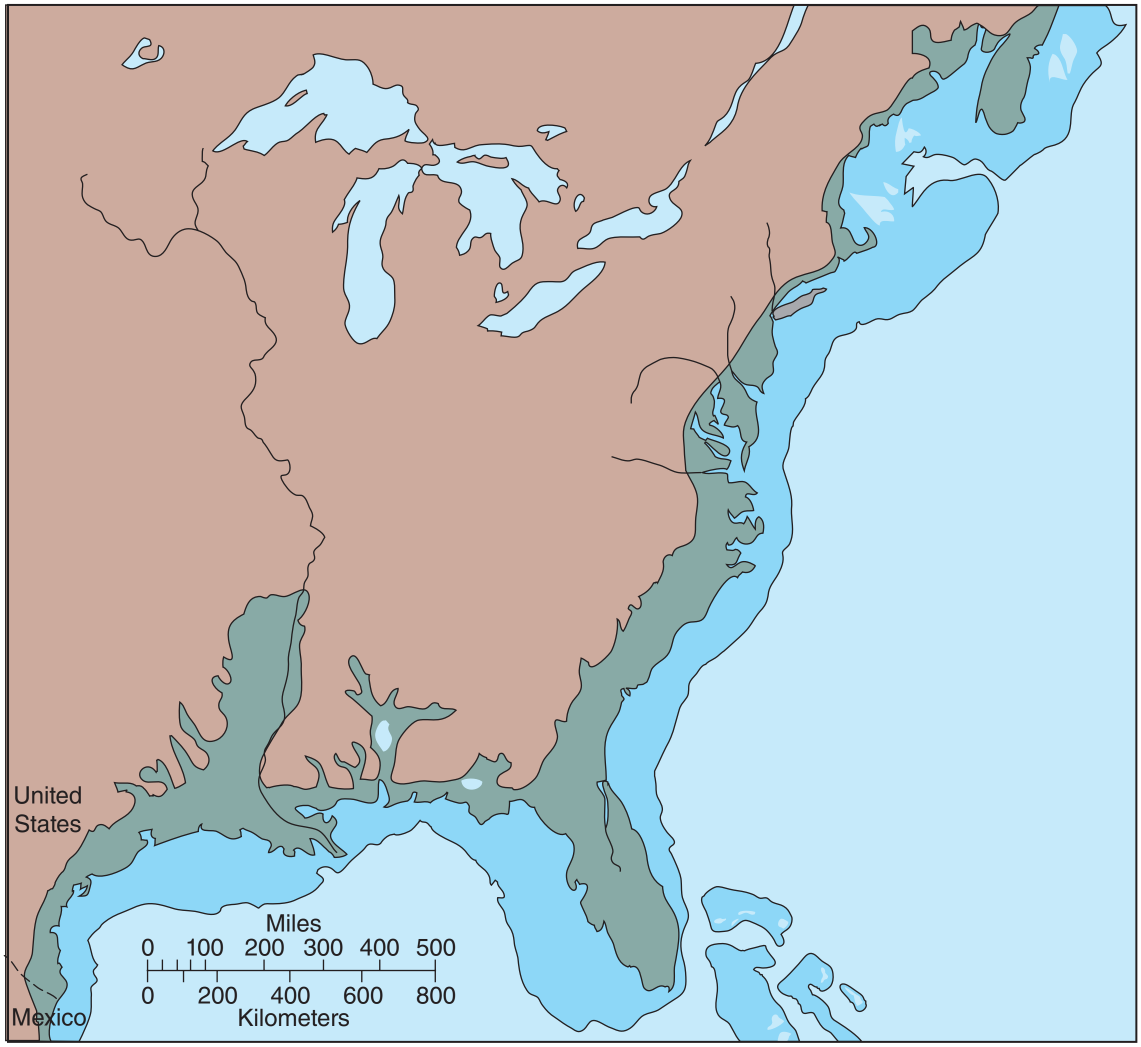

Fig. 4.11 Sea-level rise and fall helps define the area of the coastal realm. Brown color represents historic maximum sea-level rise as uplands today; dark green defines present-day coastal plains; aqua blue represents the extent of land during minimum sea level that occurred during the latest Pleistocene ice age. Based on data from Emery (1969).

offshore over the continental slope, oceanic water masses and boundary currents usually dominate.

4.6.3 Geomorphologic patterns

Shorelines derived from river-driven forces may protrude into coastal waters as deltas (Fig. 4.13) and headlands, or recede into protected embayments exposed to freshwater-tidal interactions as in estuaries or bays. Others forces create steep, rugged, high-energy shores and rocky outcrops exposed to intense sea, sun, and air, or into low, flat, lower-energy beaches. All are exposed in varying degrees to hydrological and meteorological forces that pulse and flux across their boundaries.

Offshore, deltas and headlands strongly influence coastal circulation, hydrodynamics, and sedimentation patterns. Deltas provide habitat for shellfish, birds, and juvenile fish, and also support extensive agriculture, fisheries, and, occasionally, rich deposits of coal, oil, and natural gas. The Mississippi River Delta, for example, receives large amounts of sediment, nutrients, and debris every year from its extensive, complex watershed that covers 31 states and more than 3.2 million km^2 of the United States. This drainage, highly modified by human activities, moves terrestrial products and sediment into shallow estuarine areas, forming a delta that protrudes into shallow Gulf of Mexico waters. Intensive channeling and diking of the watershed and hurricane activity have changed this delivery system, contributing to delta erosion and extensive loss of habitat for juvenile fishes, crabs, oysters, and waterbirds.

Embayed coasts broadly include estuaries, bays, and lagoons and support extraordinary production and ecological complexity. Estuaries are geologically ephemeral and depend on

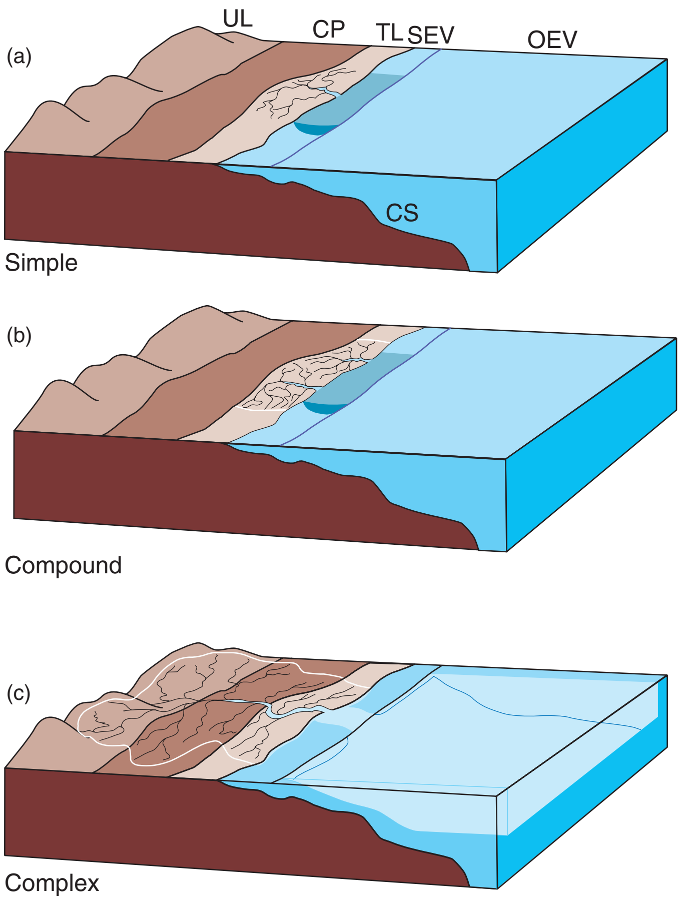

Fig. 4.12 Watershed types defined broadly by comparison of their reach across five divisions: [UL] uplands; [CP] coastal plain; [TL] tidelands; [SEV] shoreface entrainment volume; [OEV] offshore entrainment volume; [CS] indicates continental shelf. (a) Simple systems: terrestrial-marine exchanges through only one watershed unit; e.g., tidelands [TL] that drain into the shoreface entrainment volume [SEV]. (b) Compound systems reach across more than one watershed, e.g., multiple streams or estuaries drain into a common shoreface volume within a longshore reach of coast. (c) Complex systems involve two or more units; e.g., a large drainage that includes all three terrestrial subdivisions [UL, CP, TL] has sufficient flow to bypass the shoreface volume to empty directly into the offshore entrainment volume [OEV]. Many other permutations of this five-part scheme are possible. From Ray GC, Hayden BP (1992) Coastal zone ecotones. In *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows* (ed. di Castri F, Hansen AJ). Springer-Verlag, New York, pp. 403–420. With kind permission from Springer Science+Business Media B.V.

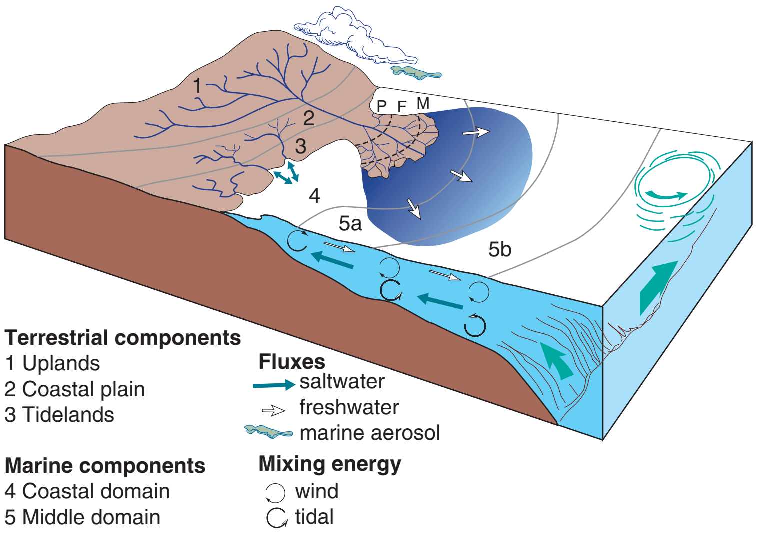

Fig. 4.13 Coastal watershed subdivisions (1–3; Fig. 4.12) interact with the offshore entrainment volume (5a,b). Drainage from subdivision 1 forms a delta that is influenced by circulation patterns of tides and winds, and consists of a delta plain [P], delta front [F], marine prodelta [M], with a freshwater plume that extends offshore, indicated by the dark-blue shaded area. Ray and McCormick-Ray (1989). Coastal and marine biosphere reserves. In: *Proceedings of the Symposium on Biosphere Reserves*. The 4th World Wilderness (eds Gregg, Jr, WP, Krugman SL, Wood Jr. JD) U.S. Dept Interior, Atlanta, Georgia, pp. 68–78.

freshwater input, being semi-enclosed water bodies that were built by the latest major episodes of sea-level fall and rise (Ch. 6). They have free connections to the open ocean in which varying amounts of seawater are diluted by freshwater. Rivers deliver dissolved inorganic chemicals of positively charged freshwater ions, especially cations of calcium, magnesium, sodium, ammonium, and hydrogen, that interact with ocean electrolytes of sodium, potassium, and chloride salts. This interaction forms distinct transitional regions between fresh and saline water that vary with location and season. In summer, warm, buoyant freshwater flows seaward over incoming, relatively cold seawater, between which is an internal

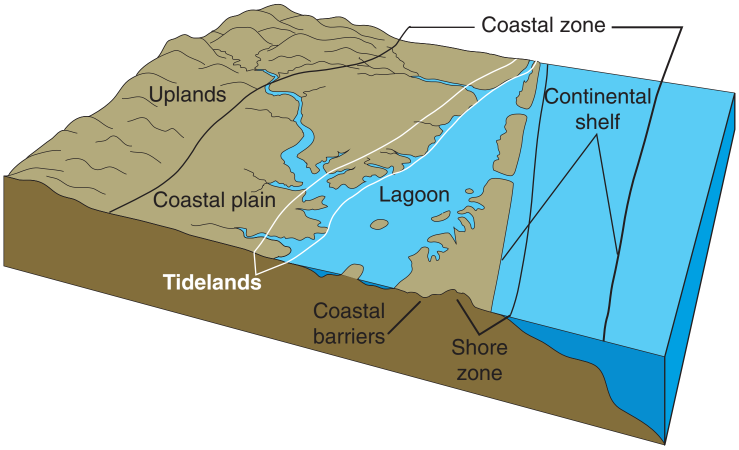

Fig. 4.14 Lagoons interface with land and sea and are protected by a coastal barrier (land, coral reef), with variable influences from watershed drainages. From Figure 1: "Coastal barriers within the broader context of the coastal zone," G. Carleton Ray and William P. Gregg Jr., "Establishing Biosphere Reserves for Coastal Barrier Ecosystems," in *BioScience*, vol. 41, no. 5, May 1991. © 1991 by the American Institute of Biological Sciences. Published by the University of California Press.

boundary. Interactions with ocean tides create estuarine gradients, from fresh and mildly brackish to fully saline zones. Salt content (salinity based on ppt, parts per thousand, or PSU, Practical Salinity Unit) is a useful indicator for subdividing estuarine zones: limnetic (freshwater 0.5 ppt; oligohaline 0.5–5.0 ppt; mesohaline 5–18 ppt; polyhaline 18–30 ppt; euhaline >30 ppt). Salinity demarcates living conditions based on osmotic regulation that determines distributions of higher taxa (Telesh and Khlebovich, 2010), separating biota into spatially different types of communities that are among the most productive on Earth.

Other embayed coasts have less freshwater influence. Bays and gulfs can be large enough to be considered marginal seas: Bengal Bay (Indian Ocean) and Biscay Bay (eastern Atlantic) are similar in scale to the gulfs of California (eastern Pacific) and Guinea (eastern Atlantic). Sounds combine bay and estuary features: e.g., Long Island Sound (western Atlantic). And lagoons (Fig. 4.14) are important and widely distributed coastal features, often associated with estuaries, but usually have lesser freshwater inputs, smaller tides, and react differently to hydrological and meteorological forces. Also commonly associated with estuaries and lagoons are coastal marshes that maintain and improve water quality by trapping sediment and reducing silt delivered by rivers, otherwise destined to fill channels and settle on shellfish and seagrass beds, coral reefs, and tidal flats. At the low end of a wind-and-wave energy spectrum, are tidal mud and sand flats; they occur on coasts with low-energy tides and unconsolidated shores, especially along shallow, estuarine-channel banks where sediment sorting, tidal movements, and benthic chemistry create horizontal and vertical zonation patterns. Clam beds flourish on these biologically rich habitats, which also host mixtures of algae and vascular plants in or anchored to shallow sand and mud bottoms, and on which small organisms may grow abundantly on fronds and leaves. Some tidal flats serve as sources of dissolved salts and nutrients and as local heat reservoirs.

Open coasts are dominated by waves of intense energy, generated mostly by tides and winds, but also by earthquakes, fallen objects, mudslides, and other disturbances. Oscillating waves encountering the bottom become asymmetrical and break into a surf zone of high turbulence and powerful longshore currents. Tremendous force is applied to shore and sediment interfaces by waves 12 m-high, which may reach velocities of approximately 16 $\mathrm{ms^{-1}}$ and accelerations reaching 1000 $\mathrm{ms^{-2}}$, or about 100 times the acceleration of gravity. A wave 3 m-high at its crest line can transmit 100 kW of energy per meter, moving sediments in water depths up to about 20 m depth (Inman and Brush, 1973). Coastal and topographic structures such as coral and oyster reefs are important structures that modify wave energy and behavior.

Open coasts are among the most dynamic of coastal environments, often being formed of unconsolidated sediment. High-energy beaches represent a net balance between wave energy and sediment supply, a balance that can be changed by storms, hurricanes, tsunamis, earthquakes, and human activities. Waves deliver sand that becomes deposited behind beaches into sand dunes, which provide habitat for unique biological communities adapted to cope with poor soils, drought, heat, and desiccation. Dunes, stabilized by grasses and other vegetation, buffer shores against erosive waves and wind and help regulate the water table. Dunes provide shelter for many species, with adjacent beaches filtering large volumes of seawater, recycling nutrients, and supporting coastal fisheries. A single beach can contain several hundred invertebrate species, each uniquely adapted to this highly dynamic, three-dimensional environment. Beaches attract a diversity of reproducing organisms, including nesting sea birds, sea turtles, and fishes (Schlacher *et al.*, 2007; Defeo *et al.*, 2009; Dugan and Hubbard, 2010). Some oystercatchers (*Haematopus* spp.) and the endangered North American piping plover (*Charadrius melodus*) nest only on exposed beaches.

Rocky coasts are rugged, high-energy environments, being exposed to the full energy of currents, waves, and wind, but support many sessile invertebrates and macroalgae able to withstand those forces. The sea palm (an alga, *Postelsia palmaeformis*) attaches to rocky cliffs and reefs and thrives under strong wave action in the temperate eastern Pacific. Intertidal rocks contain unique fauna exposed to breaking waves, high-velocity water, and salt spray projectiles. In temperate latitudes, rocky shores display distinct biotic zonation patterns: an upper zone of littorinid snails and lichens, a middle zone of barnacles and mussels, a lower zone of algae, and a subtidal zone where kelp forests (i.e., a diversity of macroalgae and flourishing kelp gardens) can dominate. The high physical disturbances in subtidal zones decrease with depth. Research on zonation, competition, and predation on rocky coasts is a scientific pillar of community ecology.

Islands provide habitat for a diversity of unique species. Continental islands (Section 4.3.1) share a relatively low proportion of terrestrial biodiversity, but often support endemic species. Island size is presumed to be an important factor in species diversity; some data suggest that as island area increases so do numbers of species. The "island biogeography" hypothesis has been developed for terrestrial species, but is not well understood for coastal-marine environments. Rather, habitat variety surrounding islands, as well as species invasions initiated by humans, may have greater influence on species richness, being independent of island size.

Sea ice is a prominent feature of both Arctic and Antarctic polar regions. Many portions are seasonally ephemeral, more so as global climates warm (Ch. 7). Sea-ice area increases from summer to winter by about 35% in the Arctic and 85% in the Southern Ocean. Lower seasonal Arctic variability in sea-ice cover is due to its being surrounded by land, unlike the Southern Ocean that surrounds the Antarctic continent, and thus is lower latitude. Sea ice forms an important habitat in both regions; diatoms accumulate on its underside where fish, crustaceans, and other species find refuge. Sea ice also forms substrate for abundant marine birds and mammals (penguins, seals, walruses) to rest and breed (Ch. 7). Although sea ice hosts much biota, it can be inimical to benthic and shore life when currents and wind move it shoreward to scour the benthos deep into subtidal areas, inhibiting algae growth and sessile organisms. Abutment of sea ice on shores, however, is advantageous to some forms of life such as Arctic foxes (*Alopex lagopus*) that venture onto sea ice, but do not swim. When sea ice is relatively contiguous with shores, it expands foraging opportunities far onto sea ice for both foxes and polar bears (*Ursus maritimus*). Polar bears hunt for seals on sea ice and may swim and walk hundreds of miles on ice in pursuit of prey; the foxes follow, seeking scraps of polar bear kills.

Superimposed on coastal realm seascape structures are familiar biogenic structures: marshlands, seagrass and macroalgal beds, and shellfish and coral-reef habitats, among others. These sessile, shallow-water benthic living seascapes generally depend on currents to deliver food and nutrients and to disperse wastes and reproductive products. Through a sum of interactions over time, geologic and biogenic structures influence their hydrological surroundings by mobilizing or depositing soft sediment, increasing spatial heterogeneity, providing and amplifying options for colonization, and increasing biodiversity. Although biogenic seascapes occupy only a small fraction of the total area of marine and estuarine systems, their importance is out of scale with their size. For example, autotrophic seascapes (wetlands, marshes, mangroves, algal flats, seagrass beds), which form between low and high water levels, modify alternating periods of tidal action. Those near shore depend on hydrologic and sedimentary dynamics, where minimal wave action consolidates soft sediment clays and silts and accumulates fine to very fine sand (Perillo *et al.*, 2009). Corals, mollusks, coralline algae, sapporellid and vermetid worms, and other "biological engineers" (Ch. 5) often cement to one another to form extensive reef systems (e.g., oysters, Ch. 6). These living seascapes directly or indirectly control nutrients and the availability of sediment, modulate current flows, and modify, maintain, or create habitat for other species. Biogenic seascapes thus add dimensional complexity as they concentrate intensive biotic activity into high production for internal use and for export.

4.7 THE COASTAL REALM: AN ECOSYSTEM OF GLOBAL IMPORTANCE

Ecosystem ecologists concerned with land and seascape transformations focus on large-scale biophysical processes, accumulation of matter, and energy flow. A focus on interactions among linked processes at multiple scales draws attention to the coastal realm as a high-level, complex ecosystem of global significance, a system filled with surprises, where species are most often hidden from easy view.

Dynamic forces in the coastal realm operate on many scales to dissipate energy, create structures, and sustain ecosystems. Physical environments establish the context in which organisms capture and transform kinetic and radiant energies into ecological efficiencies. Biotic capacity draws on inherited blueprints acquired over evolutionary time that give rise to high production, persistence, and resiliency. Seascape structures that persist under conditions of intense dynamic forces exhibit high ecological biomass, productivity, and diversity, thereby providing entry points into marine ecosystems and spatial units for conservation. Biophysical seascapes and their scale-related interconnections (processes, nutrient networks, natural history, and metapopulation linkages) establish a spatial context for measuring biomass, chemical fluxes, and qualities of resiliency, stability, persistence, and change. While temporal variability may modify seascape patterns, many characteristic biotic communities maintain their identities. But will coastal functions persist at characteristic levels if biota or seascape patterns change, or will costly human interventions be required?

4.7.1 Attributes of the coastal realm

Coastal realm attributes make apparent that this realm is best understood as a system. Through linked environments, species, and processes, this realm supports distinctive biota, persistent biophysical structures, exceptionally high primary productivity, and exceptional secondary animal biomass production. It is also the major source of the world's commercially valued shellfish and fisheries, and a carbonate factory for biologically diverse reefs and tropical beaches. Its massive capacity to maintain water quality and high production is maintained through a series of energy gradients from headwaters to the ocean. Through periodic and aperiodic pulses and fluxes, biological opportunities are enhanced, energy needs are subsidized, reproductive success is facilitated, and coastal functions are restored under conditions of change. Two other major ecological attributes stand out.

4.7.1.1 Dimensional complexity

Coastal realm environments require a diversity of biological and ecological mechanisms to efficiently capture energy, transform nutrients, and adjust to change. A fundamental, self-evident property of all living things is geometric (exponential) growth that operates under a specific set of limited resources; i.e., all populations of living organisms grow geometrically when unaffected by their environments (Berryman, 2003). Coastal realm structures add ecological dimensions that increase opportunities for growth, population expansion, and survival. Frontal systems, eddies, and benthic topography are seascape structures that are quasi-stationary, seasonally persistent, or prominent year-around features on which migratory species and major fisheries depend (Belkin *et al.*, 2009). Living coral (Ch. 8) and oyster reefs (Ch. 6) create hard bottom structures that buffer energies while providing dependable shelter and habitat for a diversity of species to grow, feed, and reproduce. Such “hot spots” of high biological activity add dimensional complexity and expand opportunities for feeding and shelter, resulting in high production in an otherwise less-productive environment. Reefs also protect lagoons for seagrass beds to flourish and to support high biomass of fishes and invertebrates, as well as endangered dugongs, manatees, and green turtles. Reefs, marshes, and seagrass beds are linked at larger scales through feeding networks and reproductive pathways (Ch. 8). Nevertheless, reef diversity and complexity carry high maintenance costs, such that little energy remains available for export, making these environments particularly vulnerable to disturbance, e.g., fishing (Fig. 4.15).

In temperate regions, macroalgal communities such as kelp beds are extremely productive. The largest and among the most productive alga is the giant kelp (*Macrocystis pyrifera*), which can reach more than 60 m in length and grows along cool-temperate rocky coasts. Water motion plays a key role in top-down, consumer-driven food webs (Gerard, 1984; Halpern *et al.*, 2006). Kelp support very large standing stocks of associated species (Heck *et al.*, 1995), including marine mammals, fishes, crabs, sea urchins, mollusks, other algae, and epibiota that collectively make them among the most diverse and productive ecosystems of the world (Mann, 1973; Steneck *et al.*, 2002; Gattuso *et al.*, 1998).

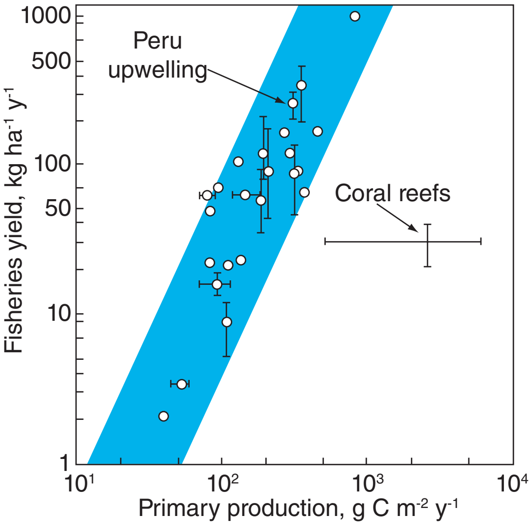

Fig. 4.15 Comparison of fisheries yield and gross primary production for Peru upwelling vs.coral reefs. Coral reefs are high primary producers but energy production does not support high fisheries yield. Their low net productivity makes them especially vulnerable to fishing. From Birkeland C, ed. (1997). *Life and death of coral reefs*. Chapman and Hall, New York. © Chapman and Hall 1997. With kind permission from Springer Science+Business Media B.V.

Coastal marshes and tropical mangroves add other dimensions. These seascapes filter, recycle, and modulate coastal energies, being interconnected by hydrology and species at particular stages of their life cycles (Ch. 5). Collectively and individually, these structures support juveniles of commercial fishes and sustain large populations of migratory waterfowl. Their products (abiotic materials, larvae, etc.) are hydrodynamically delivered to offshore habitats, a scale-dependent vector that links topographic heterogeneity to community structure (Guichard and Bourget, 1998).

4.7.1.2 Spatial heterogeneity

Spatial heterogeneity among coastal types, as between high-energy and low-energy coastal systems, creates major differences in biotic composition and in processing and exchanging materials. Scales of coastal heterogeneity and hydrologic interactions, driven by short-term fluctuations and events (e.g., storms, precipitation), produce many interacting variables that influence biological richness and ecological performance. Spatially varied coastal realm structures have nested within them smaller-scale seascape patches of high to low production, depending on their different species assemblages. Through life-history options to disperse, colonize, feed, and reproduce, many organisms move between land and sea, benthic and pelagic environments, and rarely stay within any one habitat throughout their lives. Short-term, spatially variable abundance, diversity, and function add robust dimensions to ecological processes that may be lost when only long-term averages across coastal types are measured.

4.7.2 Ecosystem properties

The coastal realm, when studied as a whole system, displays a distinctive character not apparent from its individual components alone. When observed as an interconnected whole, autotrophic production and habitat heterogeneity yield greater relevance to fisheries, algal blooms, metapopulations, and transient or migrating species moving among compartments. Ecosystem attributes result from properties of the ecosystem—energy, biochemistry, and evolution—harnessed, transformed, and modified through networks of interactions that connect organisms with the environment as a functional whole.

4.7.2.1 Energy

Organisms capture physical energy from their environment, package it, transform it, and cycle it. Transformation of one kind of energy into another involves thermodynamic laws, natural history, and food webs (Ch. 5). How energy is captured, stored, transformed, and used is a property of the ecosystem.

Thermodynamic laws reveal energy in a closed system. The first thermodynamic law generally states that energy may be transformed, but is never created or destroyed (conservation of energy). Heat and work are two forms of energy, and when work is performed, a significant portion of energy is lost as heat. The second law involves direction, which is more relevant for ecosystems. It generally states that for isolated systems that do not exchange energy or mass with their surroundings, transformation always involves some irreversible loss of energy or degradation; i.e., energy moves irreversibly toward increasing disorder, i.e., entropy (Prigogine, 1980).

Central to all species' life histories and survival is energy acquisition, storage, and transfer. Living cells capture and process energy in very organized compartments that contribute to an organism's growth, metabolism, and reproduction. Primary producers (plants, phytoplankton) capture solar energy, generally expressed as grams of carbon fixed per meter squared per year (gm^{-2} yr^{-1}). Gross production is the total amount of organic matter produced in an area over a given time, and net production is the amount of organic matter produced in excess of an organism's physiological needs (growth, maintenance, reproduction, etc.) and that is available to the ecosystem. Biomass is the total weight of living material in a specified area. This capture and transfer of bounded, useful energy (called *exergy*; Kay, 2000) provides high-quality fuel for the ecosystem that is transferred through food webs (Jørgensen and Fath, 2006). Organisms and ecosystems have evolved essential thermodynamic attributes to maintain a high state of order with low entropy (Jørgensen, 2002).

Organisms capture and move energy through irreversible processes, with substantial loss to the ecosystem. Energy for life comes from cellular process involving the oxidation of carbon-hydrogen bonds (Falkowski, 2012). Energy conversion and transfer involves expending energy in biological metabolism, movement, growth, and reproduction, with energy loss through respiration and generation of heat, and in transfers between biological compartments and food webs. More precisely, photosynthetic capture of solar energy has a thermodynamic efficiency of approximately 3–5% that becomes available for maintenance of plant physiological processes. Transfers from plant to predator are about 10 to 20% efficient, with considerable variability among herbivores, carnivores, cold-blooded (ectothermic) invertebrates, fishes, and some warm-blooded (endothermic) fishes, birds, and mammals. Yet high productivity and availability of resources has yielded high biomass, observed as large populations of marine mammals, flocks of seabirds, and abundant fishery resources. Sustaining this large biomass depends on high turnover rates of high-quality primary producers and small consumers at the base of the food web, as well as high turnover rates of energy among top consumers.

Marine food chains tend to be longer than terrestrial ones, hence more complex. For example, a top land predator such as a wolf exhibits three trophic levels (vegetation to herbivore to wolf), but tuna involve four or five trophic levels (phytoplankton to zooplankton to small fish and/or larger fish to tuna). Thus, less total annual production is apportioned to top marine predators than to terrestrial predators, which is partially compensated by higher turnover rates for marine primary producers (phytoplankton) than for land plants. Phytoplankton may have low biomass at any one time, which when compounded over seasonal periods results in high production. Furthermore, energy demands of most large terrestrial predators, mostly endothermic birds and mammals, are greater than for most top marine predators, which are mostly ectothermic invertebrates and fishes. The exceptions are marine birds and mammals, all of which have high energy demands; these energy demands are compensated by a number of morphological and behavioral adaptations, for example, adopting short food chains—sea cows (Sirenia) are herbivores and baleen whales eat zooplankton. Killer whales (*Orcinus orca*) are an exception; their position at the very top of marine food webs forces them to be few in number and relatively low in biomass.

The coastal realm represents <0.5% of ocean volume (Chen and Borges, 2009), yet its overall net primary productivity is generally greater than for either the open ocean or land (Valiela, 1984). Coastal ecosystems host autotrophic producers that process and release a large production of detritus (Duarte and Cebrián, 1996). These primary producers have high turnover rates, processing high inputs from watersheds, airsheds, and coastal upwelling, thereby performing a major role in the carbon cycle (Duarte *et al.*, 2005). They play critical roles through rate-setting processes, with turnover rates that can be measured in hours as in the case of bacteria and up to a day for some phytoplankton, in comparison with one to two times a year or even decades for most terrestrial plants. Most large marine plants such as kelps grow new leaves at exceptionally high rates as measured annually, in contrast to terrestrial woody plants that devote much of their biomass to hard tissue as support against gravity, meaning that production is low relative to biomass. Tidal marshes, mangroves, and seagrasses not only transform sunlight through photosynthesis into primary production, but also modulate tidal and hydrologic energies in varying degrees, providing protective habitat for breeding, feeding, and resting for fish and wildlife. While the open ocean yields more than 60% of total marine production due to its overwhelming area and volume (Longhurst *et al.*, 1995; Table 4.3), it lacks the high biomass concentration and turnover rates of primary producers that together fuel coastal-realm food webs.

4.7.2.2 Biogeochemicals

The coastal realm is the most geochemically and biologically active area of the biosphere (Gattuso *et al.*, 1998), receiving massive inputs of terrestrial organic matter, nutrients, sediment, and detritus that organisms process and the system exchanges with the open ocean (Chen and Borges, 2009). Chemicals are properties of ecosystems, notably carbon, nutrient chemicals (nitrogen, phosphorus), sulfur, and iron most critical to biological systems. These elements are captured and redistributed through bioactive compartments, being cycled through processes that enable microbes, plants, and animals to create physical structures and regulate nutrient fluxes

Table 4.3 Estimated total net primary production (NPP) in billion tons of carbon per year for estimated area of global ocean and different coastal sectors, and percentage. Based on data from Duarte and Cebrián (1996); Jennings *et al*. (2001).

MARINE PRIMARY PRODUCERS	Total NPP (10^9t C y^{-1})	Area Covered (10^6km^2)	Area (% of total)	NPP (% of total)
Ocean: Phytoplankton	43.00	332.00	88.46	81.10
Coastal: Phytoplankton	4.50	27.00	7.19	8.49
Macroalgae	2.55	6.80	1.81	4.81
Mangroves	1.10	1.10	0.29	2.07
Coral reef algae	0.60	0.60	0.16	1.13
Seagrasses	0.49	0.60	0.16	0.92
Marsh plants	0.44	0.40	0.1	0.83
Microphytobenthos	0.34	6.80	1.81	0.64
Total	**53.00**			

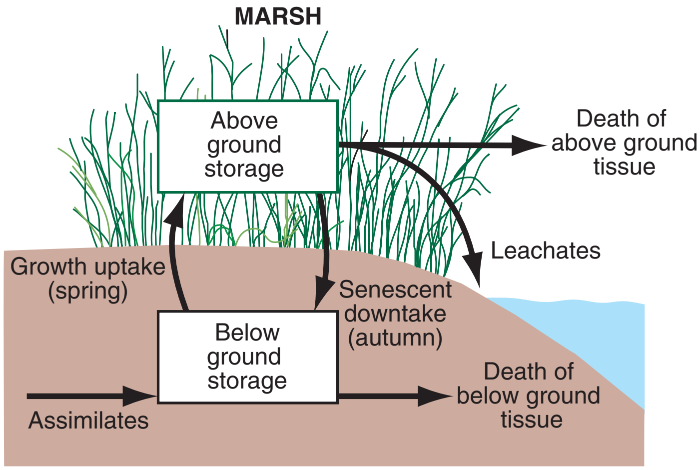

Fig. 4.16 Saltmarsh-grass systems filter pollutants, buffer wave action, support fisheries, contribute detritus, and more. *Spartina alterniflora* re-oxygenates anaerobic marsh soils by enhancing bacterial and nitrogen-producing activity. In winter, storage is in roots; in summer growing season, most storage is above ground. When young and growing vigorously, saltgrass is a net carbon importer, but with maturation becomes a major exporter, providing an energy subsidy to surrounding systems.

(Berhe *et al*., 2005). Biologically important processes in wetlands, estuaries, seas, coastal waters, and sediments are linked to increased greenhouse gas concentrations of methane (CH^4) and nitrous oxide (N_2O) in the atmosphere (Bigg *et al*., 2003). The net uptake of CO_2 in the coastal realm represents about 20% of the world's ocean uptake of anthropogenic CO_2 (Thomas *et al*., 2004. Although much uncertainty remains about the transformation, transport, and cycling of carbon and nitrogen (Thomas *et al*., 2004; Cai, 2011), the interchange of biogeochemicals through biotic reservoirs focuses attention on coastal species and ecosystems.

The coastal realm supports abundant marine species that translocate chemicals across regions. Migratory species transport significant amounts between land and sea, as for example, migratory fish, mammals, and birds that move between coastal-ocean and estuarine environments and deposit substantial amounts of ocean nutrients to coastal systems annually. Anadromous fish on return from the sea (e.g., shad, salmons) spawn in freshwaters and, through their waste products or dead bodies, enhance stream productivity important to their developing young (Ch. 6). Birds and marine mammals transfer organic matter from sea to land, an especially significant function in high-latitude systems; e.g., bears eat spawning salmon and deposit waste products in forests. Individual species in coastal habitats rework, import, and export considerable amounts of materials at local scales (Fig. 4.16), and their aggregate in mass at landscape scales contributes to ecosystem performance. Organisms construct hard carbonate reefs by capturing abundant supplies of calcium carbonate through a process constrained by eutrophication, anoxia, and watershed activities that affect carbonate chemistry (Feely *et al*., 2004; Borges and Gypens, 2010). Seagrass beds represent only 0.1 to 0.2% of the global ocean, but contribute above- and below-ground biomass at high rates of production that makes this plant community among the most productive on Earth (Duarte, 2002; Duarte and Chiscano, 1999), thus contributing significantly to nutrient cycling and food-web structure (Orth *et al*., 2006). Degradation plays a key role; as autotrophic production is processed, leaves and roots are degraded, and nutrients in the form of detritus are buried or made available for transport to deep, offshore waters (Suchanek *et al*., 1985).

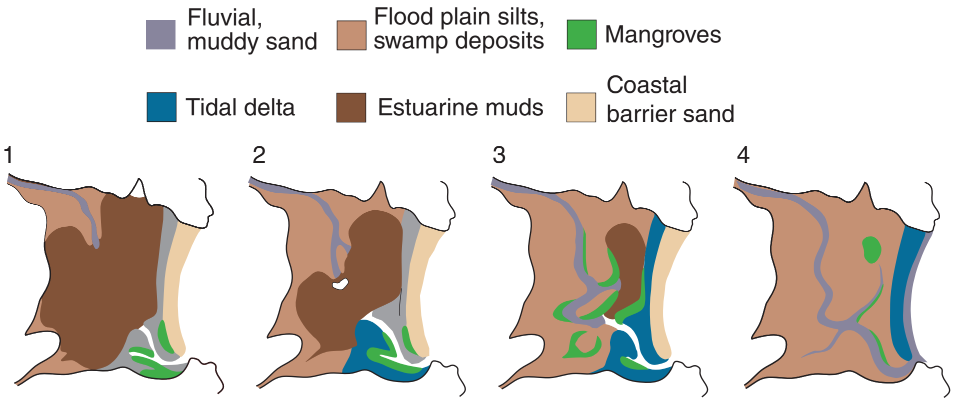

Fig. 4.17 Evolutionary change for two Australian estuaries: (a) drowned river valley; (b) barrier estuary. As a river continues to flow in and a barrier closes off the tidal exchange, water covers estuarine muds and fluvial muddy sand. The deeper-water portions underlain by estuarine muds become smaller as water drains into channels, and mangrove re-locate. This process can be altered or reversed by storm events. From Roy (1984). New South Wales estuaries: their origin and evolution. In *Coastal Geomorphology in Australia* (ed. Thom BG). Academic Press, Sydney, pp. 99–121.

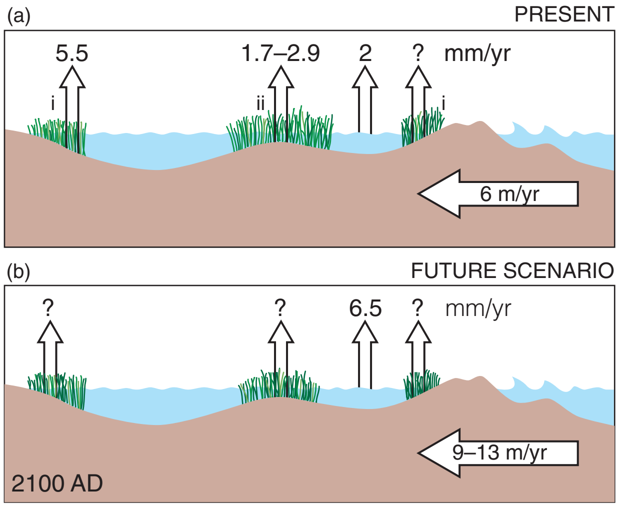

Fig. 4.18 Sea-level rise presently measured (a) and predicted (b) at the Virginia Coast Reserve Long-Term Ecological Research Site indicates differences in rates of change at three locations of this barrier island/lagoon. Horizontal arrows indicate landward erosion rate of the barrier island. Upward arrows indicate rates in change of marsh elevation and sea level. (a) Under present sea-level rise, mid-lagoon marshes will likely disappear (ii) while mainland fringing marshes will persist, because sea-level rise of 4 mm yr^{-1} is more than 1.7–2.9 for mid-lagoon marshes, but less than 5.5 for mainland fringing marshes (i). (b) Under future scenario (2100 AD), marsh elevation must increase for marshes to keep pace and persist at sea-level rise rates of 6.5 mm yr^{-1} (IPCC, 2007). Courtesy of Karen McGathery and Patricia Wiberg.

A major concern for biogeochemical processes is the exponential spread of dead zones in coastal oceans (Diaz and Rosenberg, 2008; Box 2.5). The rapid spread of ocean deoxygenation since the 1960s has major consequences (Middelburg and Levin, 2009); with rising temperatures, ocean acidification will result in substantial changes affecting marine ecosystems and biogeochemical cycles (Gruber, 2011).

4.7.2.3 Evolution

An important property of ecosystems is evolution, i.e., change over time. Biota respond and adapt to dynamic coastal ecosystems through inheritance and behavior to better obtain nutrients, materials, and energy, and to survive over generations of time. The outcome of these actions and interactions over large and small scales can enhance a particular ecosystem's growth, expansion, maturity, or under less optimum conditions, move the ecosystem into senescence and decay.

Large-scale coastal, geomorphologic evolution involves a number of factors in which antecedent conditions set the stage for a sequence of change (Stephenson and Branderb, 2003). Macroscale forces of sea-level rise, glaciation, tectonics, storms, winds, and climatic events, interacting with changing chemistry of the atmosphere, impose historical constraints and conditions for future change. Shorelines cross continental shelves in sequences of sea-level advance and retreat. Sediment is mobilized and redeposited through feedbacks among topography, biology, and fluid dynamics to initiate new landforms. Lagoons and marshes transgress across the landscape, where large portions of estuaries sequentially become mud flats through interactions and feedbacks among physical and biotic processes (Fig. 4.17). Living structures keep pace by adapting, moving, adjusting, and systematically evolving through self-generation and self-organization into steady-state patterns (Koppel *et al.*, 2008), operating within larger and smaller, external and internal pulsing mechanisms (Odum *et al.*, 1995), thereby to balance against forces of disequilibrium. To enhance survival options, organisms may adapt to tidal pulses, for example by utilizing the energy of oscillating water flow for transport, feeding, and larval dispersion. If life-history strategies fail to keep pace with change, species perish. If change is too sharp, it can be catastrophic, as exhibited in geologic history with five episodes of mass extinction (Fig. 4.3; Knoll *et al.*, 1996; Veron, 2008).

How organisms move, colonize, and stabilize coastal ecosystems is difficult to predict because of diverse evolutionary responses to environmental changes among taxa. For example, under different forecasted sea-level-rise scenarios that affect lagoon and marsh development, marsh growth rates can differ significantly (Fig. 4.18). Organisms acquire energy and nutrients as they organize over time into spatial patterns that evolve into quasi-equilibrium states. Of considerable influence is biological capacity for high gross turnover rates, expansion in numbers (individuals, species), and increase in living matter (biomass). But as all natural systems are constrained by energy, mass, momentum, and other properties, interference with system structure may force the ecosystem to move toward maximum disorder, with a potential to change into a disorganized steady state (Kleidon *et al*., 2010). While prediction is difficult for a host of species, many marine species that disperse as juveniles will be affected by increased stormy weather as predicted by climate change; some that undertake long-distance migration near the ocean surface (e.g., sea turtles, whales, etc.) may reach unfavorable locations (Monzón-Argüello *et al*., 2012). Opportunistic plant species with capacities for widespread seed dispersal and high levels of energy utilization and fecundity may colonize new areas, only to compete with native biota responding to changing conditions. And the loss of certain "key" species (Ch. 5) can result in consequences difficult to predict.

4.8 THE ECOSYSTEM CONCEPT

The ecosystem has long been recognized as a fundamental unit of nature. It is a special kind of system in steady-state quasi-equilibrium, recognized by its structure and identified by emergent organization and measurable quantities of production, complexity, and resiliency (Box 4.2). Composed of species, chemicals, materials, and energy exchanges that interact with the surrounding environment, ecosystems are driven by processes that create both "order from order" and "order from disorder" (Schrödinger, 1944; Kay, 2000). The appearance of high-level order from low-level chaos is explained by theoretical non-equilibrium thermodynamics (Prigogine, 1980; Kay 2000). As "open" and locally produced steady-state systems, ecosystems are far from equilibrium and act within a larger system of increasing disorder under conditions of the second law of thermodynamics. This law establishes the universal rule that spontaneous change is always accompanied by degradation into a more dispersed and chaotic state (Jørgensen, 2002).

Henry Louis Le Châtelier's (1850–1936) basic principle about a system in equilibrium is that when a stress or disturbance is brought to bear, the system tends to counteract the disturbance to achieve a new equilibrium state. The interaction of two systems not in mutual equilibrium tends to drive them to a final common equilibrium. In biological systems, "homeostasis" is the tendency of the system to maintain internal stability when a disturbance is applied, which is supported by growing evidence of the stabilizing effect that species play in maintaining steady state (Ernest and Brown, 2001). Homeostasis in ecosystems depends upon feedbacks among components and properties that serve to achieve a dynamic equilibrium between order and disorder, growth and dissipation. That is, the ecosystem is presumed to exist in a reasonably stable yet dynamic state or condition, maintained through coupled interactions arising from antecedent conditions, captures of energy, and counter forces against disequilibrium dictated by the second law of thermodynamics.

Systems theory in ecology arose notably during the 1950s and 1960s with the hope that ecology might turn into an exact science that potentially could predict and be guided by a set of uniform theoretical foundations (Voigt, 2011). Ecosystem theory is concerned primarily with organismal communities, their abiotic environment and interactions with one another. With organisms in mind, ecosystem science has been approached in at least three different ways: the organism as the focus of the ecosystem; the ecosystem as a set of processes involving the roles of organisms in the transfer and alteration of matter and energy; and the ecosystem as a geographic area of sufficiently similar topography, climate, and biota (Blew, 1996).

Ecosystems process continuous fluxes of energy and materials across their boundaries (Fig. 4.19). Ecosystems are regulated by physical exchanges and species' transformations of materials and energy delivered in pulsed dispersals and migrations. Within ecosystems, biological communities display timed oscillations in cycles of predator and prey abundance and form aggregations to feed or reproduce. Functional attributes of ecosystems under dynamic, presumably multistable conditions may undergo a variety of trajectories in both time and space, as observed by Orians (1975): (i) constancy, lacking change in some system parameter (e.g., species number); (ii) inertia, resisting external perturbations; (iii) elasticity, the rate at which the system returns to its former state following a perturbation; (iv) amplitude, the area over which the system is stable; (v) cyclic stability, the system cycles about some central point or zone; and (vi) trajectory stability, the system moves toward some final endpoint or zone despite differences in starting points, or the system converges to a particular state from a variety of starting positions. If biological and physical systems are in harmony, ecosystem performance can be amplified; if not, it can degrade. System adjustment involves delays, lags in recovery, and resiliency, where thermodynamics, complexity, positive and negative feedbacks, and thresholds are important variables (DeAngelis *et al*., 1986). In some cases, feedbacks from natural histories of species enhance conditions for their own survival: e.g., self-stereotaxis of oysters and anadromous fishes that deliver nutrients to natal streams (Ch. 6).

Feedback dynamics is key to maintaining ecological function. System feedback is a process whereby when change occurs in one quantity, a second quantity in turn changes the first. Positive feedbacks increase and amplify change in the first quantity; negative feedbacks reduce it, resulting in attenuation, time delays, oscillatory instability, etc. When critical thresholds are passed, homeostatic mechanisms no longer operate and amplification can drive ecosystems towards new regimes or equilibrium states, in shifts that may be smooth, abrupt, or discontinuous (Fig. 4.20; Lees *et al*., 2006); however, ecosystem response is not a fixed property (Scheffer and Carpenter, 2003). Kay (1991) queried whether change occurs along the original developmental pathway or a new one; i.e., if the system organizes or disorganizes to return to an original state, or whether the ecosystem flips into some new, catastrophic state unacceptable to humans.

Combinations of hierarchy, structure, energy, and self-organization can result in an emergent condition (Nielsen and Müller, 2000; Jørgensen, 2002), that is, a higher level of organization markedly different from lower levels (Allen and

Box 4.2 What is an ecosystem?

A “system” is composed of parts with inter-dependent connections and feedbacks that form a complex whole and maintains an internal steady state, or homeostasis, despite a changing external environment. A system can be thought of as a construct of the human mind to explain a phenomenon, and its delineation can be somewhat arbitrary.

Weinberg (1975, 2001) conceived three types of systems (Fig. B4.2.1). System 1 is a *small-number system*, characterized by “organized simplicity,” as for example in mechanical systems (automobiles) whose parts follow basic physical laws, e.g., Newton’s laws. Such laws explain interactions and predict outcomes by means of mathematical equations. System 3 at the other extreme is a *large-number system*, characterized by “unorganized complexity” of a large number of identical components that are random in behavior and yield to overall statistical averaging, for example, random motions of molecules of a perfect gas, on the order of 10^{23} molecules. The individual motions of the molecules are virtually unknowable, as they collide and rebound unpredictably. Their overall motions, however, at a given temperature follow the predictive power of gas laws.

Ecosystems do not fit either of these categories. Rather, they are System 2 *medium-number systems* characterized by structural and functional interactions among an intermediate number of components. Weinberg’s term for these is “organized complexity.” The components express a wide spectrum of process rates and spatial characteristics. Ecosystems are not easily amenable to either mechanical or statistical solutions. Some degree of abstraction is required to study ecosystems, but they are not merely abstractions. Rather, they are best understood as organized units of nature. A key to understanding them is to make their space- and rate-dependent organization and linkages explicit. That is, ecosystems cannot be understood on any single spatio-temporal scale, and no single type of observation can be extrapolated to define the nature of the underlying processes.

Ecosystems are in constant change, whereby they may be said to lose identity, exhibit trajectories, or exist in a state of dynamic equilibrium. The systems that exist at any one time have been selected from all systems of the past, being the best “survivors.” System survival thus refers to the length of time a system exists and its evolutionary history. Thus, an ecosystem’s identity becomes synonymous with its resiliency and viability.

Sources: O’Neill *et al*. (1986); Weinberg (1975, 2001)

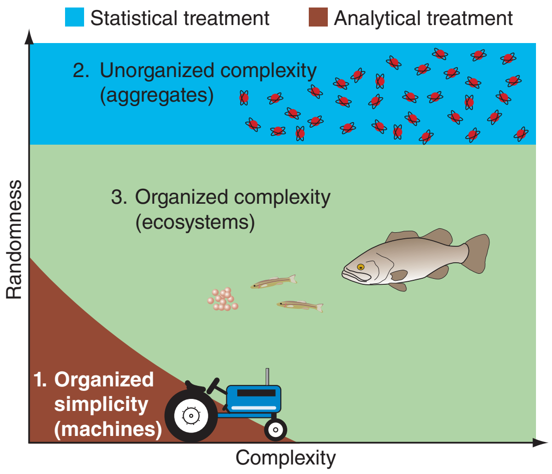

Fig. B4.2.1 Three types of systems differ in degree of complexity and organization. (1) Organized simplicity, e.g. machines: small-number systems contain so few components that analytical treatment applies. (2) Unorganized complexity, e.g., gas molecules large-number systems contain so many identical, randomly interacting components that their statistical properties appear to be deterministic, and statistical treatment can be applied. (3) Organized complexity, e.g. ecosystems: medium-number systems that contain an intermediate number of components that interact non-randomly, and therefore cannot be analyzed by traditional methods and often appear to be stochastic, a situation that is encapsulated into the “law of medium numbers,” e.g., Murphy’s law, *Anything that can happen will happen*. Based on data from Weinberg (1975, 2001).

Starr, 1982). When major and multiple pressures pass an ecosystem's critical point, the system may switch to an alternate stable state—a process called a "regime shift." Some shifts may be driven by external forcing (climate change, alien invasions, cultural eutrophication, overfishing, etc.) or internal perturbations, or be triggered by a disproportionately small time-lagged force in a process referred to as "hysteresis." When a critical threshold is passed, substantially stronger driving forces may be required for recovery to an initial steady state. At critical thresholds, the forward reaction may reverse to a lower critical threshold (Scheffer *et al.*, 2009), through failures in ecosystem structure, or surprise, or heightened complexity that makes the system vulnerable to "collapse" (DeAngelis *et al.*, 1986). For a world experiencing dramatic anthropogenic changes in environmental conditions and severe perturbations, changes to alternative stable states may have serious, unexpected consequences (Schröder *et al.*, 2005).

The different ways that ecosystems respond to change, and survive, indicates that they can be viewed as "complex adaptive systems" (Brown, 1995; Levin, 1998). Species and biotic communities tend to persist with a resiliency that is rarely predictable and an outcome that is rarely if ever stable. Environmental conditions constrain or enhance a system's natural capacity to expand, but through localized interactions and selection, biotic processes emerge into higher levels of organization that maintain ecological stability. In a hierarchy of interactions, constraints imposed on biotic capacity come from lower and higher levels; i.e., lower- and higher-level components interact to add new levels of organization and increasing levels of complexity that are vulnerable to change, and even collapse (Fig. 4.21). Positive feedbacks reinforce change in the direction of the deviation, with the potential to destabilize the system (Milsum, 1968; DeAngelis *et al.*, 1986); negative feedbacks do the opposite.

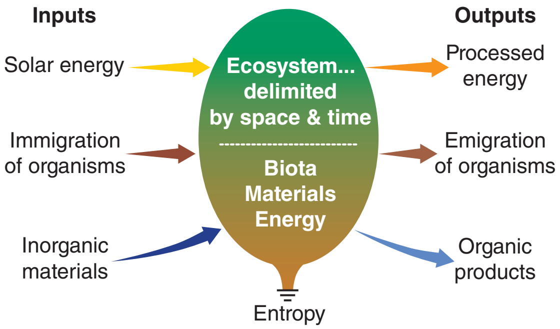

Fig. 4.19 A conceptual delineation of a spatially explicit ecosystem in time and space. The ecosystem is open to inputs, thermodynamically at non-equilibrium, and subject to degradation as a result of increased entropy. Output quality depends on ecosystem efficiency. Boundaries may be natural (watershed contours, coastal-ocean fronts, interface of water-benthos) or arbitrary (whatever spatial feature is of special interest, e.g., species range, trophic, etc.). Based on data from Odum (1989).

In a normal, quasi-stable equilibrium state under optimum conditions, ecosystems move over time toward ever-greater complexity. Complex marine ecosystems may maintain stability through alternative steady states, consistent stable states, or dynamic regimes (Knowlton, 1992; Scheffer and Carpenter, 2003; Folke *et al.*, 2004; Petraitis and Dudgeon, 2004; Schröder *et al.*, 2005; Daskalov *et al.*, 2007). How long an ecosystem may endure in a quasi-equilibrium state is a measure of its *persistence*, and how fast it returns to that state is a measure of its *resiliency*. If a deviation occurs in one direction, negative feedbacks force the system in the opposite direction to maintain system *identity*. To maintain functional resiliency, some ecosystems may switch easily between alternative states (Holling, 1973; Walker and Myers, 2004; Ives and Carpenter, 2007; Walker and Salt, 2012). Complex dynamic systems (ecosystems, financial markets, climate), however, can reach tipping points and abruptly shift from one equilibrium state to another.

4.9 ECOSYSTEM BASE FOR CONSERVATION

Although the "ecosystem" concept is fundamental to conservation and management, its concept needs clarification (Jax, 2005, 2007), especially for highly variable and dynamic coastal and marine environments. That is, as the observer delineates an ecosystem of interest, he/she imposes a perceptual bias, a filter through which the system is viewed (Levin, 1992).

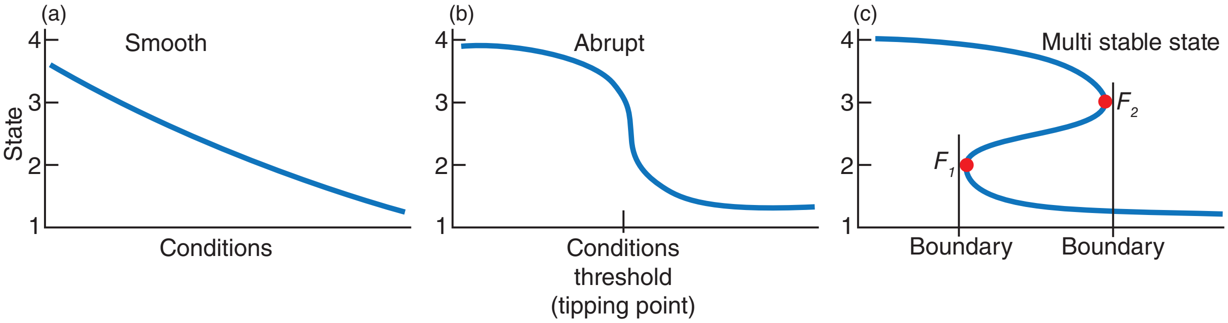

Fig. 4.20 Ecosystem responses to change in external conditions. (a) Smooth transition; (b) profound transition, when conditions approach a critical level; (c) switch to alternate stable state (F_1, F_2) over a range of conditions (hysteresis). Response is not a fixed property of a system, although some systems tend to respond in a more non-linear way than others. From Scheffer M, Carpenter SR (2003) Review: catastrophic regime shifts in ecosystems: linking theory to observation. *TRENDS in Ecology and Evolution* **18**, 648–656.

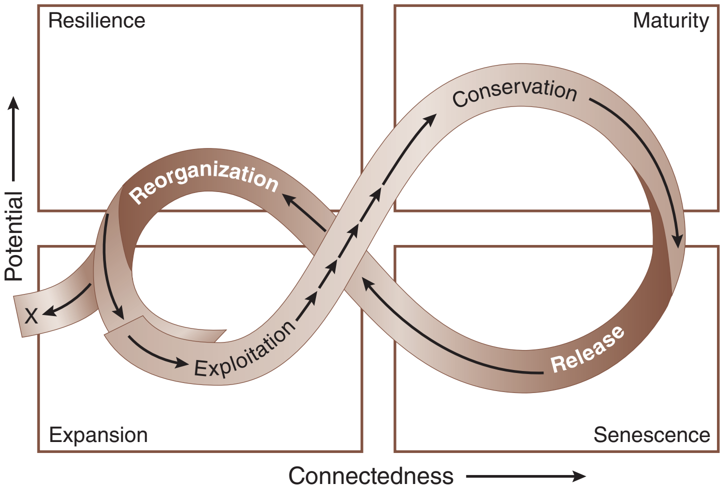

Fig. 4.21 Panarchy concept of an ecosystem (Holling and Gunderson, 2002). Ecosystems are complex adaptive systems that cycle through four functional stages: expansion, maturity, senescence, and resilience. The ecosystem loses and gains potential, i.e., inherent in accumulated resources, biomass (exergy) where nutrients can leak away (x). The ecosystem moves from low to high connectedness as aggregated elements gain advantages among controlling variables. Initially, a growing and expanding ecosystem rapidly changes towards maturity, with conservation of aggregated elements that control or mediate influences of external variability. The ecosystem loses potential and connectedness. Low connectedness is associated with loosely connected, diffuse elements dominated by outward relations and affected by outside variables with accumulating assets (exploitation). Arrows indicate flow speed in the cycle: short, closely spaced arrows indicate slow changes. From Holling CS (2001) Understanding the complexity of economic, ecological, and social systems. *Ecosystems* **4**, 390–405. With kind permission from Springer Science+Business Media B.V.

Functional ecosystems are spatial components of the marine and coastal environment, interacting holistically and viewed at different hierarchical scales. The open-ocean and coastal realms as ecosystems become apparent through recognition of their supporting processes and inter-relationships that provide services for humans and other organisms, through the roles organisms play within them and their subsystems, and through processes that sustain smaller ecological units. Scientific questions thus relate to: how open-ocean and coastal realm systems and their subsystems function hierarchically as ecological units, how functional attributes are sustained, how specific parts contribute to persistence and stability of attributes, and at what scale individual components fulfill particular kinds of functions—ecological production, biomass, biodiversity, resiliency, and services important to people, i.e., food, clean water, oxygen, etc. In particular, recognizing the coastal realm as a complex adaptive ecosystem exposed to most of the issues described in Chapter 1, and that plays significant roles in global and local processes, establishes the context and urgency for ecosystem-based approaches at appropriate scales to meet marine conservation needs.

REFERENCES

Allen TFH, Starr TB (1982) *Hierarchy: Perspectives for ecological complexity*. University of Chicago Press, Chicago.

Bakun A (1996) *Patterns in the ocean: ocean processes and marine population dynamics*. California Sea Grant College System, National Oceanographic and Atmospheric Administration, La Jolla.

Beck MW, Heck Jr. KL, Able KW, Childers DL, Eggleston DB, *et al.* (2003) The role of nearshore ecosystems as fish and shellfish nurseries. *Issues in Ecology* **11**, 1–12.

Belkin IM, Cornillon PC, Sherman K (2009) Fronts in large marine ecosystems. *Progress in Oceanography* **81**, 223–236.

Berhe AA, Carpenter E, Codispoti L, Izac A-M, Lemoalle J, Luizao F, *et al.* (2005) Nutrient cycling. In *Ecosystems and Human Well-Being*, Chapter 12, **vol. I**, Current State and Trends. Millennium Ecosystem Assessment, Island Press, Washington, D.C., 331–353.

Berryman AA (2003) On principles, laws and theory in population ecology. *Oikos* **103**, 695–701.

Belkin M, Cornillona PC, Sherman K (2009) Fronts in large marine ecosystems. *Progress In Oceanography* **81**, 223–236.

Bigg GR, Jickells TD, Liss PS, Osborn TJ (2003) Review: the role of the oceans in climate. *International Journal of Climatology* **23**, 1127–1159.

Birkeland C, ed. (1997) *Life and death of coral reefs*. Chapman and Hall, New York.

Blakey RC (2008) Gondwana paleogrography from assembly to breakup—a 500 m.y. odyssey. In *Resolving the late Paleozoic ice age in time and space* (eds Fielding CR, Frank TD, Isbell JL). Geological Society of America, Special Paper 441, 1–28.

Blew RD (1996) On the definition of ecosystem. *Bulletin of the Ecological Society of America* **77**, 171–173.

Borges AV, Gypens N (2010) Carbonate chemistry in the coastal zone responds more strongly to eutrophication than to ocean acidification. *Limnology and Oceanography* **55**, 346–353.

Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, *et al.* (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems* **78**, 363–376.

Brewer PG, Peltzer PT (2009) Limits to marine life. *Science* **324**, 347–348.

Broecker WS (1991) The giant ocean conveyor. *Oceanography* **4**, 79–89.

Broecker WS (1997) Thermohaline circulation, the Achilles heel of our climate system: will man-made CO_2 upset the current balance? *Science* **278**, 1582–1588.

Broecker WS (2006) Abrupt climate change revisited. *Global and Planetary Change* **54**, 211–215.

Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago, Illinois.

Buhl-Mortensen L, Vanreuse A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, *et al.* (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology* **31**, 21–50.

Burnett WC, Bokuniewicz H, Huettel M, Moore WS, Taniguchi M (2003) Groundwater and pore water inputs to the coastal zone. *Biogeochemistry* **66**, 3–33.

Cai W-J (2011) Estuarine and coastal ocean carbon paradox: CO_2 sinks or sites of terrestrial carbon incineration? *Annual Review of Marine Science* **3**,123–145.

Calbet A, Landry MR (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography* **49**, 51–57.

Canfield DE (2005) The early history of atmospheric oxygen: homage to Robert M. Garrels. *Annual Review of Earth and Planetary Sciences* **33**, 1–36.

Canfield DE, Alexander N, Glazer AN, Falkowski PG (2010) The evolution and future of earth's nitrogen cycle. *Science* **330**, 192–196.

Carpenter LJ (2003) Iodine in the marine boundary layer. *Chemical Reviews* **103**, 4953–4962.

Carpenter LJ, Jones CE, Dunk RM, Hornsby KE, Woeltjen J (2009) Air-sea fluxes of biogenic bromine from the tropical and north Atlantic Ocean. *Atmospheric Chemistry and Physics Discussions* **9**, 1805–1816.

CBD (online) Island biodiversity—what's the problem. Convention on Biological Diversity Secretariat, www.cbd.int.

Chen CTA, Borges AV (2009) Reconciling opposing views on carbon cycling in the coastal ocean: continental shelves as sinks and near-shore ecosystems as sources of atmospheric CO_2. *Deep-Sea Research II* **56**, 578–590.

Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI, *et al*. (2010) The ecology of seamounts: structure, function, and human impacts. *Annual Review of Marine Science* **2**, 253–278.

Crossland CJ, Kremer HH, Lindeboom HJ, Crossland JIM, LeTissier MDA (2005) *Coastal fluxes in the Anthropocene*. Springer, Berlin, 231pp.

Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 10518–10523. www.pnas.org

DeAngelis DL, Post WM, Travis CT (1986) Positive feedback in natural systems. *Biomathematics* **15**. Springer-Verlag, Berlin, 290pp.

DeBose JL and Nevitt GA (2008) Dimethylsulfoniopropionate is linked to coral spawning, fish abundance and squid aggregations over a coral reef. *Proceedings of the 11th International Coral Reef Symposium*. Ft. Lauderdale, Florida, 7–11 July, 275–279.

Defeo O, McLachlan A, Schoeman DS, Schlacher TA, Dugan J, Jones A, *et al*. (2009) Threats to sandy beach ecosystems: a review. *Estuarine, Coastal and Shelf Science* **81**, 1–12.

Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* **321**, 926–929.

D'Odorico P, Laio F, Porporato A, Ridolfi L, Rinaldo A, Rodriguez-Iturbe I (2010) Ecohydrology of terrestrial ecosystems. *BioScience* **60**, 898–907.

Duarte CM (2002) The future of seagrass meadows. *Environmental Conservation* **29**, 192–206.

Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. *Limnology and Oceanography* **41**, 1758–1766.

Duarte CM, Chiscano CL (1999) Seagrass biomass and production: a reassessment. *Aquatic Botany* **65**, 159–174.

Duarte CM, Middelburg JJ, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* **2**, 1–8.

Ducklow H, McCallister SL (2004) The biogeochemistry of carbon dioxide in the coastal ocean. In *The Sea* (eds Robinson AR, McCarthy, Rothschild BJ). The President and Fellows of Harvard College.

Dugan JE, Hubbard DM (2010) Loss of coastal strand habitat in southern California: the role of beach grooming. *Estuaries and Coasts* **33**, 67–77.

Emery KO (1969) The continental shelves. *Scientific American* **221**, 107–122.

Ernest SKM, Brown JM (2001) Homeostasis and compensation: the role of species and resources in ecosystem stability. *Ecology* **82**, 2118–2132.

Erwin DJ, Bowring SA, Yugan J (2002) End-Permian mass extinctions: a review. In *Catastrophic Events and Mass Extinctions: Impacts and Beyond* (eds Koeberl C, MacLeod KG). Geological Society of America Special Paper 356, Boulder, Colorado, 363–383.

Falkowski PG (2012) The global carbon cycle: biological processes. In *Fundamentals of Geobiology*, First Edition (eds Knoll AH, Canfield DE, Konhauser KO). Blackwell Publishing Ltd, Oxford, UK, 5–19.

Falkowski PG, Scholes J, Boyle E, Canadell J, Canfield D, Elser J, *et al*. (2000) The global carbon cycle: a test of our knowledge of earth as a system. *Science* **290**, 291–296.

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* **305**, 362–366.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology and Systematics* **35**, 557–581.

Garstang M, Ellery WN, McCarthy TS, Scholes MC, Scholes RJ, Swap RJ, Tyson PD (1998) The contribution of aerosol- and water-borne nutrients to the functioning of the Okavango Delta ecosystem, Botswana. *South African Journal of Science* **94**, 223–229.

Gattuso J-P, Frankignoulle M, Wollast R (1998) Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecology and Systematics* **29**, 405–434.

Gerard VA (1984) The light environment in a giant kelp forest: influence of *Macrocystis pyrifera* on spatial and temporal variability. *Marine Biology* **84**, 189–195.

Govoni JJ, Hare JA, Davenport ED, Chen MH, Marancik KE (2010) Mesoscale, cyclonic eddies as larval fish habitat along the southeast United States shelf: a Lagrangian description of the zooplankton community. *ICES Journal of Marine Science* **67**, 403–411.

Grassle JF, Maciolek NJ (1992) Deep-Sea species richness: regional and local diversity estimates from quantitative bottom samples. *The American Naturalist* **139**, 313–341.

Gross MG, Gross E (1996) *Oceanography: A View of Earth*. Prentice Hall, Upper Saddle River, New Jersey, USA.

Gruber N (2011) Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philosophical Transactions of the Royal Society A* **369**, 1980–1996.

Gruber N, Galloway JN (2008) An earth-system perspective of the global nitrogen cycle. *Nature* **451**, 293–296.

Guichard F, Bourget E (1998) Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. *Marine Ecology Progress Series* **171**, 59–70.

Guo L, Santschi PH (1997) Composition and cycling of colloids in marine environments. *Review of Geophysics* **35**, 17–40.

Halpern BS, Cottenie K, Broitman BR (2006) Strong top-down control in southern California kelp forest ecosystems. *Science* **312**, 1230–1232.

Hayden BP, Ray GC, Dolan R (1984) Classification of coastal and marine environments. *Environmental Conservation* **11**, 199–207.

Heck KL, Able AW, Roman CT, Fahay MP (1995) Composition, abundance, biomass, and production of macrofauna in a New England estuary: comparisons among eelgrass meadows and other nursery habitats. *Estuaries* **18**, 379–389.

Hedges JI (1992) Global biogeochemical cycles: progress and problems. *Marine Chemistry* **39**, 67–93.

Helly JJ, Levin LA (2004) Global distribution of naturally occurring marine hypoxia on continental margins. *Deep-Sea Research I* **51**, 1159–1168.

Holland HD (2006) The oxygenation of the atmosphere and oceans. *Philosophical Transactions of the Royal Society B* **361**, 903–915.

Holligan PM, Reiners WA (1992) Predicting the responses of the coastal zone to global change. *Advances in Ecological Research* **22**, 211–255.

Holling CS (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* **4**, 1–23.

Holling CS (2001) Understanding the complexity of economic, ecological, and social systems. *Ecosystems* **4**, 390–405.

Holling CS, Gunderson LH (2002) Resilience and adaptive cycles. In *Panarchy* (eds Gunderson LH, Holling CS). Island Press, Washington, D.C., Chapter 22, 25–26.

Huthnance JM (1995) Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge. *Progress in Oceanography* **35**, 353–431.

Inman DL, Brush BM (1973) The coastal challenge. *Science* **181**, 20–32.

Inman DL, Nordstrom CE (1971) Tectonic and morphologic classification of coasts. *Journal of Geology* **79**, 1–21.

IPCC (2001) *Climate Change: The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (eds Houghton JT, Ding Y, Griggs DJ, Noguer M, Linden PJ, Dai X, *et al*.). Cambridge University Press, Cambridge, UK and NY, USA, 881pp.

IPCC (2007) *Climate Change 2007: Synthesis Report*. An Assessment of the Intergovernmental Panel on Climate Change. Adopted section by section at IPCC Plenary XXVII, Valencia, Spain, 12–17, November 2007.

Ives AR, Carpenter ST (2007) Stability and diversity of ecosystems. *Science* **317**, 58–62.

Jax K (2005) Function and "functioning" in ecology: what does it mean? *Oikos* **111**, 641–648.

Jax K (2007) Can we define ecosystems? On the confusion between definition and description of ecological concepts. *Acta Biotheoretica* **55**, 341–355.

Jennings S, Kaiser MJ, Reynolds JD (2001) *Marine fisheries ecology*. Blackwell Science Ltd, Oxford, UK, 417pp.

Jørgensen SE (2002) *Integration of ecosystem theories: a pattern*, Third Edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Jørgensen SE, Fath BD (2006) Examination of ecological networks. *Ecological Modelling* **196**, 283–288.

Kai ET, Rossi V, Sudre J, Weimerskirch H, Lopez C, Hernandez-Garcia E, *et al.* (2009) Top marine predators track Lagrangian coherent structures. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 8245–8250.

Kaufman YJ, Koren I, Remer LA, Tanré D, Ginoux P, Fan S (2005) Dust transport and deposition observed from the Terra-Moderate Resolution Imaging Spectroradiometer (MODIS) spacecraft over the Atlantic Ocean. *Journal of Geophysical Research* **110**, D10S12.

Kay JJ (1991) A nonequilibrium thermodynamic framework for discussing ecosystem integrity. *Environmental Management* **4**, 483–495.

Kay JJ (2000) Ecosystems as self-organizing holarchic open systems: narratives and the second law of thermodynamics. In *Handbook of Ecosystem Theories and Management* (eds Jørgensen SE, Müller F). Lewis Publication, CRC Press, 135–160.

Keene WC, Jacob DJ (1996) New directions reactive chlorine: a potential sink for dimethylsulfide and hydrocarbons in the marine boundary layer. *Atmospheric Environment* **30**, i–iii.

Keene WC, Sander R, Pszenny AAP, Vogt R, Crutzen PJ, Galloway JN (1998) Aerosol pH in the marine boundary layer: a review and model evaluation. *Journal of Aerosol Science* **29**, 339–356.

Kepkay PE (2000) *Colloids and the ocean carbon cycle. The Handbook of Environmental Chemistry*, Chapter 2 (ed. Wangersky P), **vol. 5**, Part D Marine Chemistry. Springer-Verlag, Berlin, Heidelberg.

Ketchum BH, ed. (1972) *The Water's Edge: Critical Problems of the Coastal Zone*. The Massachusetts Institute of Technology Press, Cambridge, Massachusetts.

Kiel S, Tyler PA (2010) Chemosynthetically-driven ecosystems in the deep sea. In *The Vent and Seep Biota. Topics in Geobiology* (ed. Kiel S). **33**, 1–14.

Kleidon A, Malhi Y, Cox PM (2010). Maximum entropy production in environmental and ecological systems. *Philosophical Transactions of the Royal Society B* **365**, 1297–1302.

Knoll AH, Bambach RK, Canfield DE, Grotzinger JP (1996) Comparative earth history and late Permian mass extinction. *Science* **273**, 252–225.

Knoll AH, Javaux EJ, Hewitt D, Cohen P (2006) Eukaryotic organisms in Proterozoic oceans. *Philosophical Transactions of The Royal Society* **361**, 1023–1038.

Knowlton N (1992) Thresholds and multiple stable states in coral-reef community dynamics. *American Zoologist* **32**, 674–682.

Koppel J van de, Gascoigne JC, Theraulaz G, Rietkerk M, Mooij WM, Herman PMJ (2008) Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. *Science* **32**, 739–742.

Lees K, Pitois S, Scott C, Frid C, Mackinson S (2006) Characterizing regime shifts in the marine environment. *Fish and Fisheries* **7**, 104–127.

Levin LA, Sibuet M, Gooday AJ, Smith CR, Vanreusel A (2010) The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction. *Marine Ecology* **31**, 1–5.

Levin SA (1998) Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* **1**, 431–436.

Levin SA (1992) The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology* **73**, 1943–1967.

Liss PS, Malin G, Turner SM, Holligan PM (1994) Dimethyl sulphide and *Phaeocystis*: a review. *Journal of Marine Systems* **5**, 41–53.

Littler MM, Littler DS, Brooks BL (2010) Marine macroalgal diversity assessment of Saba Bank, Netherlands Antilles. *PLoS ONE* **5**, e10677.

Liu Z, Omar A, Hair J, Kittaka C, Hu Y, Powell K, C Trepte, *et al*. (2008) CALIPSO lidar observations of the optical properties of Saharan dust: a case study of long-range transport. *Journal of Geophysical Research* **113**, D07207.

Longhurst A (1998a) *Ecological geography of the sea*. Academic Press, San Diego, 398pp.

Longhurst A (1998b) Oceans and seas. In *World of Earth Science* (eds Lerner KL, Lerner BW). Gale Cengage, 2003. eNotes.com. 2006. 29 Mar, 2010.

Longhurst A, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research* **17**, 1245–1271.

Lozier MS (2010) Review: deconstructing the conveyor belt. *Science* **328**, 1507–1511.

Lozier MS (2012) Overturning in the North Atlantic. *Annual Review of Marine Science* **4**, 291–315.

Mahowald NM, Baker AR, Bergametti G, Brooks N, Duce RA, TD Jickells, *et al.* (2005) Atmospheric global dust cycle and iron inputs to the ocean. *Global Biogeochemical Cycles* **19**, GB4025, 15pp.

Mann KH (1973) Seaweeds: their productivity and strategy for growth. *Science* **182**, 975–981.

Mann KH, Lazier JRN (1991) *Dynamics of marine ecosystems*. Blackwell Scientific Publications, Boston, 466pp.

Martin AP (2003) Phytoplankton patchiness: the role of lateral stirring and mixing. *Progress in Oceanography* **57**, 125–174.

McClain CR, Lundsten L, Ream M, Barry J, DeVogelaere A (2009) Endemicity, biogeography, composition, and community structure on a northeast Pacific seamount. *PLoS ONE* **4**, e4141.

McFiggans G, Cox RA, Mössinger JC, Allan BJ, Plane JMC (2002) Active chlorine release from marine aerosols: roles for reactive iodine and nitrogen species. *Journal of Geophysical Research* **107** (D15), 4271.

Menot L, Sibuet M, Carney RS, Levin LA, *et al.* (2010) New perceptions of continental margin biodiversity. Chapter 5, In *Life in the World's Oceans* (ed. McIntyre AD). Wiley-Blackwell, Oxford UK, 79–101.

Middelburg JJ, Levin LA (2009) Coastal hypoxia and sediment biogeochemistry. *Biogeosciences Discuss* **6**, 3655–3706. www.biogeosciencesdiscuss.net/6/3655/2009/

Milliman JD, Haq BU, eds (1996) *Sea-level Rise and Coastal Subsidence: Causes, Consequences, and Strategies*. Kluwer Academic Publishers, The Netherlands.

Milsum JH (1968) Mathematical introduction to general system dynamics. In *Positive Feedback* (ed. Milsum JH). Pergamon Press, New York, 23–65.

Monzón-Argüello C, Dell'Amico F, Marco A, López-Jurado LF, *et al*. (2012) Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. *INTERFACE Journal of the Royal Society*, online before print February 8, 2012.

Mooers CNK (1976) Overview of the physical dynamics of the continental margin. *Hydrological Sciences Bulletin* **21**, 467–471.

Nicholls RJ, Cazenave A (2010) Sea-level rise and its impact on coastal zones. *Science* **328**, 1517–1520.

Nielsen SN, Müller F (2000) Emergent properties of ecosystems. In *Handbook of Ecosystem Theories and Management* (eds Jørgensen SE, Müller F). Lewis Publications, CRC Press, 195–216.

NRC (1992) *Coastal Meteorology: a Review of the State of the Science*. Panel on Coastal Meteorology, National Research Council. National Academy Press, Washington, D.C.

Nellemann C, Corcoran E, Duarte C, Valdes L, DeYoung C, Fonseca L, Grimsditch G, eds (2009). Blue Carbon. A rapid response assessment. United National Environment Programme, GRID-Arendal. www.grida.no

Odum EP (1989) *Ecology and Our Endangered Life-Support Systems*. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Odum WE, Odum EP, Odum HT (1995) Nature's pulsing paradigm. *Estuaries* **18**, 547–555.

Oki T, Kanae S (2006) Review: global hydrological cycles and world water resources. *Science* **313**, 1068–1072.

O'Neill RV, DeAngelis DL, Waide JB, Allen TFH (1986) *A Hierarchical Concept of Ecosystems*. Monographs in Population Biology 23. Princeton University Press, Princeton, New Jersey.

Orians GH (1975) Diversity, stability and maturity in natural ecosystems. In *Unifying Concepts in Ecology* (eds van Dobben WH, Lowe-McConnell RH). W. Junk BV Publishers, The Hague, 139–150.

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck Jr. KL, Hughes AR, *et al*. (2006) A global crisis for seagrass ecosystems. *BioScience* **56**, 987–996.

Perillo GME, Wolanski E, Cahoon DR, Brinson MM, eds (2009) *Coastal Wetlands: an Integrated Ecosystem Approach*. Elsevier, Amsterdam, The Netherlands.

Pernetta JC, Milliman JD (1995) *Land-ocean Interactions in the Coastal Zone—Implementation Plan*. IGBP Global Change Report. International Geosphere—Biosphere Programme, Stockholm, No. 33.

Petraitis PS, Dudgeon SR (2004) Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology* **300**, 343–371.

Pielou EC (1979) *Biogeography*. John Wiley and Sons, New York.

Prigogine I (1980) *From being to becoming*. W. H. Freeman and Company, New York, 272pp.

Prospero PM (1999) Long-term measurements of the transport of African mineral dust to the southeastern United States: implications for regional air quality. *Journal Geophysical Research* **104**, 15917–15927.

Raffaelli D, Bell E, Weithoff G, Matsumotoc A, Cruz-Mottad JJ, P Kershawe, *et al*. (2003) The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic–pelagic coupling. *Journal of Experimental Marine Biology and Ecology* **285–286**, 191–203.

Ray GC, Gregg Jr. WP (1991) Establishing biosphere reserves for coastal barrier ecosystems. *BioScience* **41**, 301–309.

Ray GC, Hayden BP (1992) Coastal zone ecotones. In *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows* (ed. di Castri F, Hansen AJ). Springer-Verlag, New York, 403–420.

Ray GC, McCormick-Ray MG (1989) Coastal and marine biosphere reserves. In *Proceedings of the Symposium on Biosphere Reserves*. The 4th World Wilderness (eds Gregg, Jr. WP, Krugman SL, Wood Jr. JD). U.S. Dept. Interior, Atlanta, Georgia, 68–78.

Redfield AC (1958) The biological control of chemical factors in the environment. *American Scientist* **46**, 205–221.

Richardson PL (2008) On the history of meridional overturning circulation schematic diagrams. *Progress in Oceanography* **76**, 466–486.

Richer de Forges BR, Koslow JA, Poore GCB (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* **405**, 944–947.

Riebesell U, Körtzinger A, Oschlies A (2009) Sensitivities of marine carbon fluxes to ocean change. *Proceedings of the National Academy of Sciences USA* **10**, 20602–20609.

Roy PS (1984) New South Wales estuaries: their origin and evolution. In *Coastal Geomorphology in Australia* (ed. Thom BG). Academic Press, Sydney, 99–121.

Ruhl HA (2007) Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. *Ecology* **88**, 1250–1262.

Scheffer M, Carpenter SR (2003) Review: catastrophic regime shifts in ecosystems: linking theory to observation. *TRENDS in Ecology and Evolution* **18**, 648–656.

Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, *et al*. (2009) Early-warning signals for critical transitions. *Nature* **461**, 53–59.

Schlacher TA, Dugan J, Schoeman DS, Lastra M, Jones A, Scapini F, *et al*. (2007) Sandy beaches at the brink. *Diversity and Distributions* **13**, 556–560.

Schlesinger WH (1997) *Biogeochemistry: an Analysis of Global Change*. Academic Press, 588pp.

Schröder A, Persson L, De Roos AM (2005) Direct experimental evidence for alternative stable states: a review. *Oikos* **110**, 3–9.

Schrödinger E (1944) *What is life?* Cambridge University Press, Cambridge, UK.

Schwarzer K, Diesing M, Larson M, Niedermeyer R-O, Schumacher W, Furmanczyk K (2003) Coastline evolution at different time scales—examples from the Pomeranian Bight, southern Baltic Sea. *Marine Geology* **194**, 79–101.

Siegenthaler U, Sarmiento JL (1993) Atmospheric carbon dioxide and the oceans. *Nature* **265**, 119–125.

Sikora TD, Ufermann S (2005) Marine atmosphere boundary layer cellular convection and longitudinal roll vortices. In *Synthetic Aperture Radar Marine User's Manual* (eds Jackson JR, Apel JR). Office of Research and Applications, NOAA, Washington, D.C., Chapter 14, 321–330.

Snelgrove PVR (1998) The biodiversity of macrofaunal organisms in marine sediments. *Bioscience and Conservation* **7**, 1123–1132.

Soloviev A, Lukas R (2006) *The Near-Surface Layer of the Ocean*. Springer, The Netherlands, 574pp.

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29**, 436–459.

Stephenson WJ, Branderb RW (2003) Coastal geomorphology into the twenty-first century. *Progress in Physical Geography* **27**, 607–623.

Suchanek T, Williams SL, Ogden JC, Hubbard, DK, Gill IP (1985) Utilization of shallow-water seagrass detritus by Caribbean deep-sea macrofauns: *del* $_{13}C$ evidence. *Deep Sea Research* **32**, 201–214.

Swap R, Garstang M, Greco S, Talbot R, Kallberg P (1992) Saharan dust in the Amazon Basin. *Tellus* **44B**, 133–149.

Syvitski JPM, Kettner A (2012) Sediment flux and the Anthropocene. *Philosophical Transactions of the Royal Society A* **369**, 957–975.

Syvitski JPM, Vörösmarty CJ, Kettner AJ, Green P (2005) Impact of Humans on the Flux of Terrestrial Sediment to the Global Coastal Ocean. *Science* **308**, 376.

Telesh IV, Khlebovich VV (2010) Principal processes within the estuarine salinity gradient: a review. *Marine Pollution Bulletin* **61**, 149–155.

Terray EA, Donelan MA, Agraval YC, Drennan WM, Kahma KK, Williams III AJ, *et al*. (1996) Estimates of kinetic energy dissipation under breaking waves. *Journal of Physical Oceanography* **26**, 792–807.

Thomas H, Bozec Y, Elkalay K, de Baar HJW (2004) Enhanced open ocean storage of CO_2 from shelf sea pumping. *Science* **304**, 1005–1008.

Trenberth K (2005) Uncertainty in hurricanes and global warming. *Science* **308**, 1753–1754.

USGS (1970) *The national atlas of the United States of America*. U.S. Dept. Interior Geological Survey, Washington, D.C.

USGS (2010) *Divisions of geologic time—major chronostratigraphic and geochronologic units*. Fact Sheet 2010–3059, 2pp.

Van Dover CL (2000) *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton University Press. Princeton, New Jersey.

Veron JE (2008) Mass extinctions and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs* **27**, 459–472.

Valiela L (1984) *Marine Ecological Processes*. Springer-Verlag, New York, 546pp.

Vinogradova NG (1997) Zoogeography of the abyssal and hadal zones. *Advances in Marine Biology* **32**, 325–387.

Voigt A (2011) The rise of system theory in ecology. In *Ecology Revisited* (eds Schwarz A, Jax K). Springer, Dordrecht, Part 5, Chapter 15, 183–194.

Vinogradova NG (1997) Zoogeography of the abyssal and hadal zones. *Advances in Marine Biology* **32**, 32–387.

Walker B, Myers JA (2004) Synthesis: thresholds in ecological and social–ecological systems: a developing database. *Ecology and Society* **9**, 3. Online. www.ecologyandsociety.org/vol9/iss2/art3

Walker B, Salt D (2012) *Resilience Practice*. Island Press, Washington DC.

Wang W, Huang RX (2004) Wind energy input to the surface waves. *Journal of Physical Oceanography* **34**, 1276–1280.

Weinberg GM (1975, 2001) *An Introduction to General Systems Thinking*. John Wiley & Sons, New York. Reprinted, *Silver Anniversary*, Dorset House Publication Company, NY.

Wilhelm SW, Suttle CA (1999) Viruses and nutrient cycles in the sea. *BioScience* **49**, 781–788.

Williams JT, Carpenter KE, Van Tassell JL, Hoetjes P, Toller W, *et al*. (2010) Biodiversity assessment of the fishes of Saba Bank Atoll, Netherlands Antilles. *PLoS ONE* **5**: e10676.