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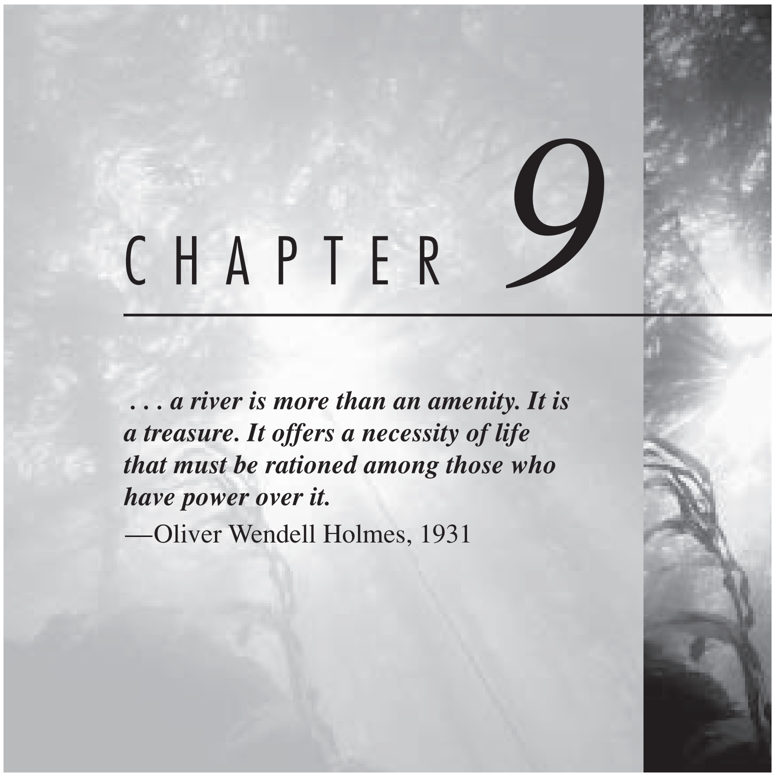

CHAPTER 9

. . . a river is more than an amenity. It is a treasure. It offers a necessity of life that must be rationed among those who have power over it.
—Oliver Wendell Holmes, 1931

The Conservation of Aquatic Ecosystems

In this chapter, you will learn about:

1. the ecological properties of aquatic habitats.
2. types of freshwater and marine ecosystems.
3. conservation problems, goals, and management strategies associated with freshwater and marine ecosystems.

The majority of literature in conservation biology, as in the rest of biology, focuses on terrestrial environments and the creatures that inhabit them. Yet 71% of the globe is covered by oceans, not land. Freshwater and marine environments may hold the majority of all earth's species, but because they are foreign and threatening to humans, and more difficult to investigate, they are not as well studied as terrestrial sites. The resources of aquatic habitats are vast and essential, but even those we use most frequently are mysterious to us. We often receive them, or exploit them, without truly understanding their value or the processes that sustain them.

Aquatic creatures are important in the diets of most people throughout the world, yet we have no real idea of the sizes of the populations that support most fisheries, especially in the oceans. Our lakes, rivers, and seas are repositories for all types and quantities of human and industrial refuse, yet we do not know the capacity of these systems to hold such waste, or its effects on ecosystem functions. The majority of our commercial fisheries are fully exploited, overexploited, or in decline, yet we go on taking. The oceans of the world have long been one of the principal regulators of its climate, yet, as human activity alters the climate, we are only beginning to appreciate how such changes will affect ocean systems. Subsurface ocean topography and structure determine the abundance of many creatures on which humans depend for food, yet humans alter ocean topography and structure in harvesting food and other resources. Such alterations leave us with less food to harvest and fewer resources to use. Because aquatic habitats are so different from terrestrial ones, the problems associated with their conservation also are vastly different. Their uniqueness deserves special attention.

HETEROGENEITY IN AQUATIC ENVIRONMENTS

Terrestrial habitats are defined and described primarily by their dominant vegetation and landform or topographic characteristics. In aquatic habitats, there may be little or no vegetation structure, and physical structures may play only a minor role in habitat characteristics. Unlike air in a terrestrial environment, which is rarely considered in a study of "habitat," water in an aquatic environment *is* the habitat. That is, the physical and chemical properties of water often must be considered as the dominant habitat features. Differences in light, temperature, oxygen, and nutrients make aquatic habitats highly heterogeneous, resulting in heterogeneity in the abundance and distribution of aquatic populations.

Heterogeneity in water, as in all environments, may be spatial or temporal. In an aquatic environment, spatial heterogeneity is created less by underwater topography and the structure of physical objects than by depth. Changes in levels of light, temperature, oxygen, pressure, and nutrient availability, among other variables, create different conditions and associated niches at different depths, with corresponding changes in the communities of organisms. The greater the range of depths,

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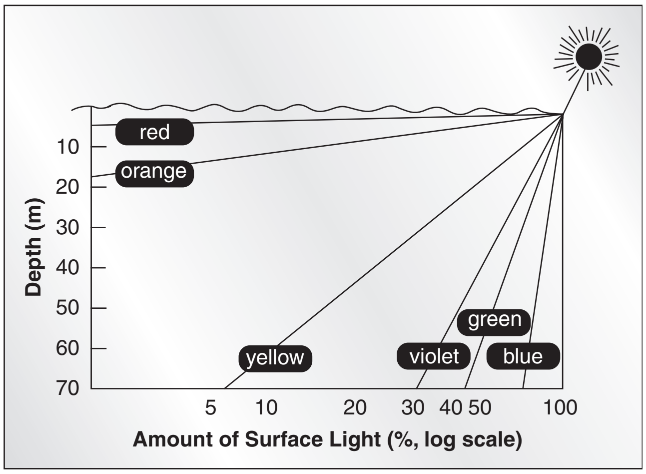

Figure 9.1
The absorption of different wavelengths of light by pure water as a function of depth. Red light is absorbed in the first few meters, whereas blue light can penetrate to depths greater than 70 m. An increase in the turbidity of the water, typical of real aquatic systems, causes light at each wavelength to be absorbed at lesser depths.

Adapted from Brönmark and Hansson (1998).

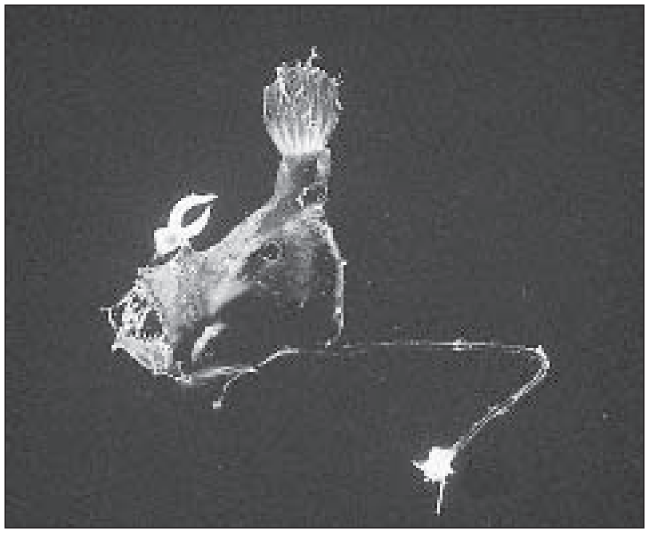

Figure 9.2
The deep sea angler fish (*Melanocetus johnsoni*), a photoluminescent marine creature of extreme depths, uses a luminescent "lure" at the end of the long stalk on its head to attract prey.

the greater the diversity of conditions, and the greater the diversity of organisms.

Light, for example, travels through air with comparatively little change, but is radically altered when transmitted through water. Depth of light penetration depends on wavelength, and different wavelengths ("colors") are selectively removed with increasing depth (fig. 9.1). Most of the red light entering water is absorbed in the first few meters, depending on temperature, density, turbulence, turbidity, and the presence of organisms. Blue light, in contrast, can penetrate to more than 70 m (Brönmark and Hansson 1998). Below 100 m, there is little or no light. In marine environments, many creatures that live constantly at these depths are bioluminescent or have "lights" on various body parts to serve them in navigation, reproduction, and predation (fig. 9.2).

Marine Habitats

Heterogeneity may be created in oceans by global forces of atmospheric heating, cooling, and air movement. Zonal winds, driven by the uneven heating of the earth's surface, produce circulation patterns that divide oceans into distinct hydrographic regions differing markedly in horizontal and vertical motion, nutrient fluxes, and seasonality (Barry and Dayton 1991). These patterns are determined by the earth's rotational forces and lead to the formation of prevailing currents at global and regional scales (fig. 9.3).

Energy from mesoscale features, tidal and regional wind forcing, and interactions of wave movement with bottom topography or continental margins generate upwellings, fronts, eddy currents, continental shelf waves, filaments, internal waves, and other phenomena that affect the productivity and distribution of aquatic organisms. Whereas surface waves move material over the sea surface, internal waves are generated by tidal and wind stress forces. If the water column is stratified, internal waves will travel horizontally along the layer of ocean water that exhibits the most rapid change in density. The orbital motion of water associated with these internal waves causes the formation of zones of convergence and divergence at the ocean's surface, altering the distribution of populations of zooplankton and phytoplankton (Barry and Dayton 1991).

Undersea topography is also important in creating heterogeneity. Water moving along the ocean's surface is deflected as it encounters continental shelves and continents, forming cells of water called **gyres**, which define the provinces of animals in a marine community. Below the surface, the interaction of currents with undersea pinnacles and seamounts generates intensified currents and attracts filter-feeding organisms at higher densities than at similar depths over flatter subsurface terrain. Plankton communities also increase in density and diversity near these same features.

In marine habitats, the actions of living organisms are among the most important determinants of habitat characteristics and availability. For example, in benthic communities, tube-building species make major modifications in ocean floor habitats that may enhance or restrict the abundance and diversity of other species. Tube builders bind sediment in place and thus stabilize the seafloor. They also change concentrations of key nutrients and so create unique communities associated with their activities (fig. 9.4) (Barry and Dayton 1991). Kelp also make major modifications in habitat, growing to huge sizes (up to 700 feet for a single individual) and occurring at high densities in kelp beds and even kelp "forests." A large kelp bed creates a drag on coastal currents, causing the currents to sweep around the bed. Internal waves,

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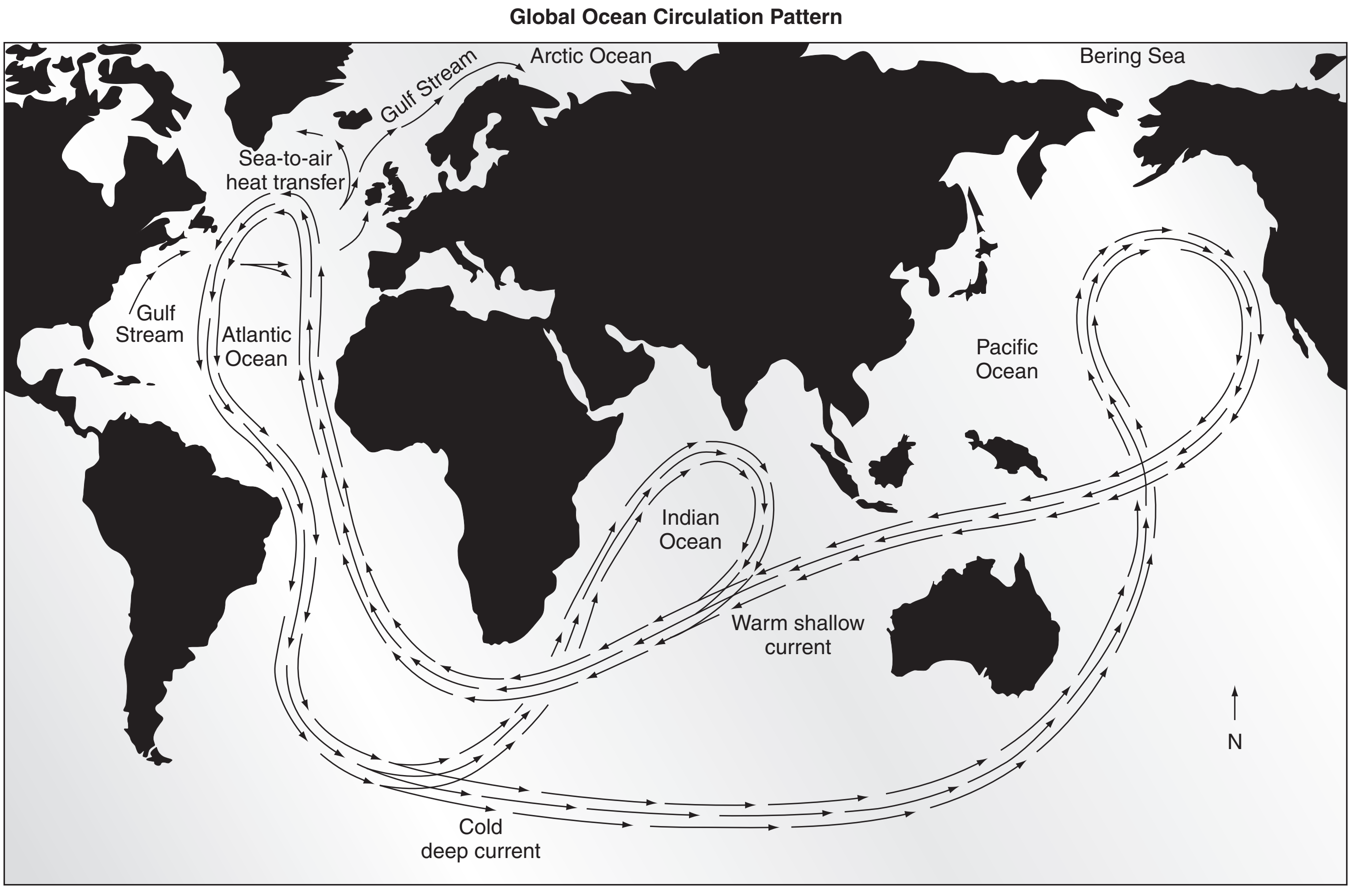

Figure 9.3
Global circulation patterns of marine currents established by prevailing winds and the earth's rotation.
After Broecker (1991).

Figure 9.4
A community of tubeworms (phylum Polychaeta) living in sediment on the floor of the Atlantic Ocean. Tubeworms and other sediment-dwelling species may, through differential use of sediment and sediment nutrients, create microhabitats with unique nutrients and communities of organisms.

transporting pelagic larvae and nekton (free-swimming animals) shoreward, are slowed and disrupted by kelp beds, causing them to lose energy and deposit organisms at disproportionately high numbers at the leading edge of a bed. As a result, fish congregate around the edges of kelp beds where prey organisms accumulate.

Lotic Systems

In streams (technically, *lotic* [flowing water] environments), characteristics of the watershed's climate, topography, vegetative cover, soil, land-use patterns, and bedrock are the primary determinants of habitat characteristics. Streams and rivers have been described as "nothing else than functional parts of higher units: of landscapes . . . of geosynergies . . . or biogeocoenoses . . . , on whose existence they depend" (Sioli 1975:276). Climate, specifically temperature and precipitation, determines the amount of moisture input to the watershed and its rate of evapotranspiration. Topography determines the rate and erosive force of surface runoff entering the stream channel. Vegetative cover determines the rate of erosion of soil in the watershed, and thus the rate at which sediment enters the stream. Soil type also affects the rate of

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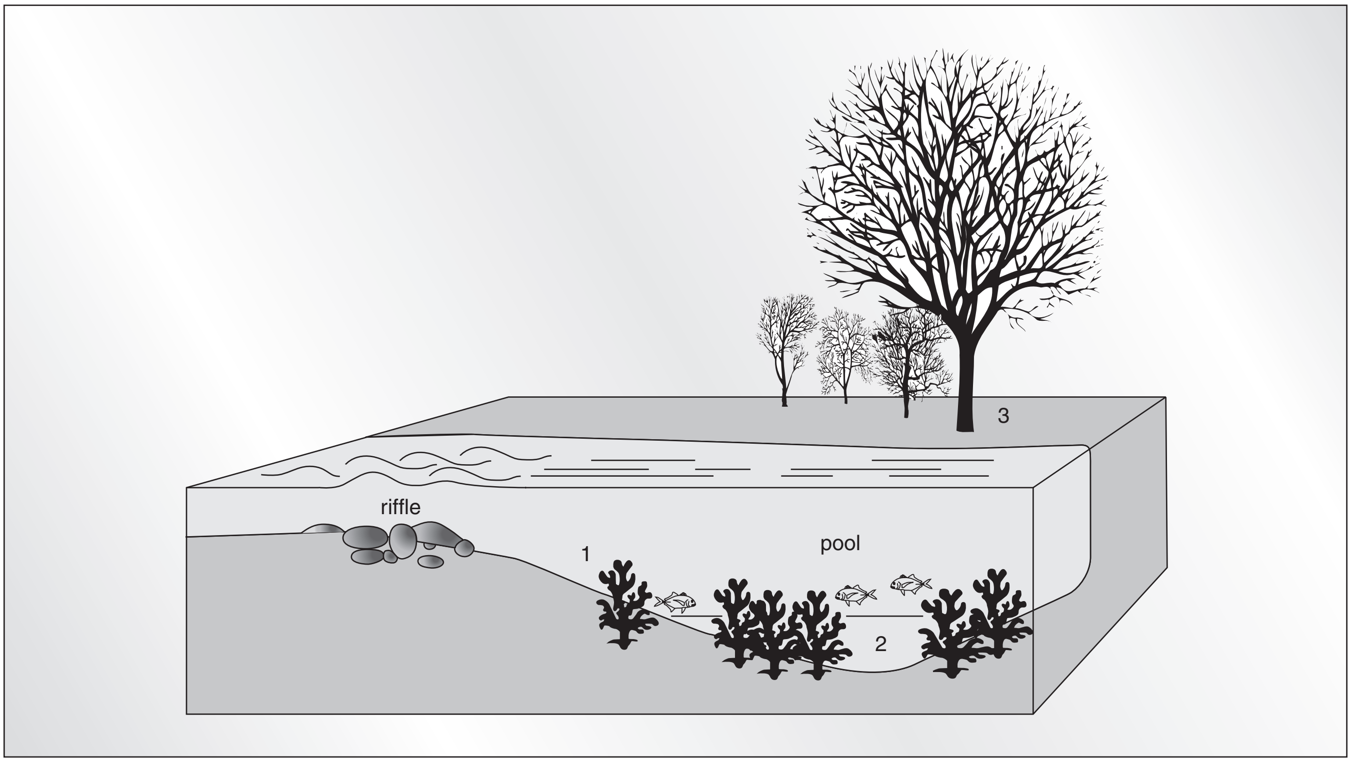

Figure 9.5
Principal categories of material input into a stream. Within the stream flow, the majority of the organic matter is typically dissolved. Organic matter enters the stream ecosystem from autochthonous (stream-derived) and allochthonous (derived from the terrestrial system) sources and may exit via respiration of aquatic organisms. Autochthonous material (1 and 2) may be from sources such as algae and aquatic plants, or from organisms living in stream sediments. Allochthonous substances (3) originate from sources such as throughfall and litter fall.

erosion and the chemical characteristics, turbidity, and bottom features of the stream. Land-use patterns influence rates of erosion and types of material entering the stream through surface runoff and other sources. Characteristics of a stream's watershed also determine input of coarse particulate matter, fine particulate matter, and dissolved organic matter (fig. 9.5).

Within a stream, two dominant habitat features are **riffles** and **pools** (fig. 9.5). These are particularly prominent where water flows at rates of 50 cm/sec or more (fast-water streams). Riffles are sites of primary production in streams where *periphyton,* a community of organisms composed of diatoms, blue-green and green algae, and various aquatic mosses, dominate. Periphyton is ephemeral in nature, constantly being transported through the stream channel by flowing water. Thus, the quantity and composition of the periphyton community within the riffles changes temporally and seasonally, especially in streams in temperate latitudes.

Above and below riffles are pools, catchbasins in which stream topopgraphy permits the velocity of water to decrease. For a given volume of water, pools will form if the stream gradient decreases, the volume of the stream channel increases, or both. Velocity is a measure of energy, so, as the velocity of water decreases, so does its ability to do work. In pools, the ability of the current to carry its load declines, and heavier material is deposited, so pools are sites of biomass accumulation and decomposition. Larger consumers, such as fish, may congregate in pools at the edge of the upstream riffle because this is often the location where food items appear in highest quantity.

Substrate type is another important determinant of heterogeneity in lotic habitats. Sand and silt substrates generally are the poorest habitat for stream organisms because they offer few attachment sites for periphyton or larger organisms. Bedrock substrate is more solid, but exposes an organism directly to the full force of the stream's flow; few organisms can afford the constant expenditure of energy against a swift current. Gravel, rubble, and boulder bottoms generally characterize the most productive stream habitats because they (1) provide large surface areas and many points of attachment for periphyton, (2) provide cover and refuge for organisms of varying sizes, and (3) divert the force of the stream's current from organisms positioned behind pieces of gravel, rubble, and boulders, thus allowing them to conserve energy.

Lentic Systems

Heterogeneity in lake habitats (**lentic** environments) is little affected by internal currents (flow rates in lakes may be extremely slow) and more by the effect of prevailing surface winds. The two most common effects of wind activity on circulation in lakes

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are seen in **Langmuir rotations** or **cells** and **seiches.** Langmuir rotations are established by prevailing winds and extend vertically throughout the water column, and are most often observed as "foamlines" at the downwelling boundary of the cell. The circulation of water in such cells is an important mechanism for transporting matter and energy vertically in the lake's water column, affecting the quality of aquatic habitat from the surface to the bottom. Perhaps even more important are external and internal *seiches.* Defined as oscillations of a body of water around points or nodes, seiches are recurring, rocking water movement patterns within a lake basin generated by prevailing winds (external seiches) or by differences in density of water in different layers (internal seiches). In external seiches, prevailing winds "push" water to the far side of the lake, causing a buildup of water volume on the lake's leeward side. When the wind recedes, the displaced water flows back to its original position, initiating a rocking motion of the water in the lake's basin.

Temporal and spatial heterogeneity in aquatic environments are most strongly determined by seasonal variation in temperature, but other factors also change seasonally. Water density changes with temperature, and in temperate lakes, density differences create the most dramatic examples of temporal heterogeneity in aquatic environments. Mobile aquatic creatures respond to changes in temperature and density in the same ways that terrestrial organisms respond to changes in vegetative cover in a landscape. Organisms optimize foraging, reproduction, and growth rates by moving to different strata on seasonal and daily schedules. For example, juvenile sculpins (a bottom dwelling fish, family Cottidae) feed in benthic environments during the day, but move to the warmer waters of the epilimnion during the night where they digest their food more quickly and experience increased growth rates (Neverman and Wurtsbaugh 1994).

Wetlands

Wetlands have been defined as *lands transitional between terrestrial and aquatic systems where the water table is at or near the surface or the land is covered by shallow water* (Cowardin et al. 1979). Wetlands make disproportionately large contributions to global biodiversity and primary productivity. Wetlands often harbor high numbers of endangered species, game species, and other economically important species. But because many wetland areas are transitory or ephemeral in nature, both their definition and their dynamics make it difficult to estimate the exact extent of wetlands in the world today. Not surprisingly then, estimates of global wetland area vary from 5.3 million km^2 (Matthews and Fung 1987) to 8.6 million km^2 (Maltby and Turner 1983).

As habitats and ecosystems, wetlands provide services and products far in excess of the approximately 6% of the earth's surface that they cover (Matthews and Fung 1987; Gosselink and Maltby 1990). Like an economic entity whose value is made up of assets, services, and attributes, wetlands have corresponding values in their structural components, environmental functions, and system organization (Barbier 1995).

Included among the structural components of wetlands are species that form the basis of many sport and commercial fishing industries, hunting, and agriculture (e.g., various forms of domestic and wild rice), as well as wildlife products (especially fur and meat), wood, and water (Barbier 1995). In fact, most game and fur-bearing animals in temperate regions, and many species of game fish spend at least part of their life cycle or at least one season of the year in wetlands, even if they are not "wetland species." A disproportionate number of threatened and endangered species also are wetland dependent.

Wetland functions are varied and essential. For example, because wetlands have the capacity to absorb large inputs of water from surface runoff or upstream sources and yet release relatively little of these inputs downstream in the short term, intact wetland systems protect downstream landscapes, natural systems, and human communities from storm and flood damage. Also because wetlands contain dense, highly productive plant communities, they can absorb large quantities of waste and nutrient runoff. Wetlands also provide opportunities for many types of recreation and water transport. Other wetland services are provided by "constructed wetlands," which are the products of human engineering for specific purposes. Constructed wetlands are created on sites where wetlands did not previously exist or where the original wetlands were destroyed or degraded (Mitsch, Mitsch, and Turner 1994). The most common type of constructed wetland is designed for wastewater treatment (Brix 1994; Kadlec 1994), but wetlands also are constructed for wildlife habitat, for research, and as compensation for loss of natural wetlands under "no net loss of wetlands" statutes in various states and countries.

Wetland organizational characteristics support high levels of primary productivity and biomass. Because water is shallow throughout the wetland environment, all parts of the system can be photosynthetically active, unlike deepwater environments where light cannot penetrate below certain depths. Because water levels vary spatially and temporally (seasonally) within a wetland, the wetland experiences strong moisture and other environmental gradients that support a variety of plant species, including plants of diverse life and growth forms. Such plant diversity creates physical heterogeneity and complexity greater than most terrestrial environments, and often supports a more diverse biotic community.

CONSERVATION CHALLENGES OF FRESHWATER HABITATS

Freshwater habitat quality is degraded worldwide by a small constellation of common factors and processes. The most important threats to freshwater streams and lakes are physical habitat alteration, chemical alteration or pollution of the water, introduction of exotic species (Abell et al. 2000), and, in streams and rivers, alteration of flow regimes, especially as a result of dams (Benke 1990). In the United States, from 1972 to 1982, four times more lake acreage was degraded than was improved in quality (Karr 1991). The only large U.S. stream (more than 1,000 km in length) that has not been severely altered in its flow regimes for hydropower and navigation is the Yellowstone River of Wyoming and Montana (Benke 1990). Along with alteration of flow rates and habitat, pollutants and exotic species have rendered many

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$$CaCO_3 + H_2CO_3 \rightleftharpoons CaCO_3 + CO_2 + H_2O \rightleftharpoons Ca(HCO_3)_2 \rightleftharpoons Ca^{2+} + 2HCO_3^-$$

Figure 9.6

Normal buffering reactions that take place in fresh water. Note that a source of carbonate ions, such as calcium carbonate ($CaCO_3$) must be present for hydrogen ions (H^+, from acid sources such as H_2CO_3) to be removed from solution and stabilize the system's pH. Basic carbonate rocks found within the stream or from surrounding terrestrial rocks and soils provide a source of calcium carbonate for the reaction. If carbon dioxide or bicarbonate (HCO_3^-) is removed, calcium carbonate will precipitate and hard water will form.

rivers unfit for most human uses. A recent survey of the majority of U.S. rivers, covering some 643,000 miles of waterways, found that only 56% could support multiple uses such as drinking water, fish and wildlife habitat, recreation, and agriculture. In the 44% of rivers that could not support multiple use, the most important problems were chemical alternation or pollution of the water, specifically sedimentation, nutrient overloading (also known as eutrophication [Farrell 1998]), and acidification. Fifty-six percent of U.S. streams suffer reduced fishery potential because of chemical contamination (Karr 1991).

Eutrophication

The process of **eutrophication** occurs when nutrients, particularly phosphorus, are released into rivers from upstream or surrounding agricultural areas (in the form of fertilizer runoff) or from towns and cities (in the form of human waste) (Brönmark and Hansson 1998). Higher levels of phosphorus trigger a chain of events that begins with a massive increase in the growth of primary producers (usually limited by a scarcity of phosphorus in fresh waters). Periphytic (attached) algae and submersed macrophytes increase in biomass at the beginning of the process, but then decline as phytoplankton and cyanobacteria (blue-green algae) increase in abundance and reduce the amount of light that filters through the water. Dead organisms accumulate as sediment and the bacteria that remove minerals from decaying organic matter extract large amounts of oxygen from the water. Fish kills of some species may follow as oxygen is depleted, but cyprinid fishes (family Cyprinidae, carps and minnows) typically increase in abundance because they can survive in poorly oxygenated waters and are efficient predators of zooplankton, whose numbers increase in the initial stages of eutrophication. As a result of the cyprinid predation, grazing zooplankton decrease. Levels of phytoplankton, the prey of zooplankton, then increase, further increasing the turbidity of the water (Brönmark and Hansson 1998). As eutrophication progresses, the biological community is radically altered, and the lake declines in value as a source of drinking water, recreation, and food.

Acidification

Acidification is a process through which the pH of surface fresh waters, especially lakes, declines (becomes more acidic) because of inputs of acidic precipitation in the form of rain, snow, or fog. Emissions of hydrogen sulfide (H_2S), most commonly associated with the burning of coal to generate electricity, and nitrous oxide (NO), an exhaust waste from cars, can combine with atmospheric water vapor to form weak concentrations of sulfuric acid and nitric acid that fall as precipitation into water bodies or their surrounding drainage areas.

Acidic inputs generally do not affect pH in areas where soil and rock substrates contain significant amounts of calcium carbonate ($CaCO_3$) or other carbonate compounds. These compounds react with water to form carbonate and bicarbonate ions that can buffer a system against acidic inputs (fig. 9.6). In areas without such buffering capacities, however, such as those with granitic substrates or granitic-derived soils, the same inputs of acid precipitation can have disastrous effects on aquatic communities.

The sequence of events begins with a lowering of pH in the aquatic system due to acidic inputs, especially during periods of heavy rain or during spring snowmelt. The most common and immediate effect of lower pH is a lowering or cessation of reproductive effort in many species of fish, amphibians, and aquatic invertebrates, and some species may suffer direct mortality. An indirect, but often more devastating effect of the lower pH is a change in the chemical reactions occurring in the aquatic system, especially those involving metallic ions such as aluminum, lead, or cadmium. Such metals usually remain in solution at higher pH (7 or above), but begin to precipitate out of solution at lower pH levels. Aluminum is deadly to fish because it binds to their gills and impedes respiration (Brönmark and Hansson 1998). When fish populations are reduced in acidified lakes, many invertebrates are released from predation pressure and invertebrate populations may then grow (especially predatory invertebrates) (Brönmark and Hansson 1998). In addition, once aluminum begins to precipitate out of solution, it binds with phosphorus, producing aluminum phosphate. Such a reaction takes phosphorous out of the system and makes it unavailable as a nutrient for organisms.

Habitat Alteration by Nonindigenous Species

Although the problem of nonindigenous species is now a worldwide concern affecting all types of environments (chapter 7), aquatic habitats are especially sensitive to alterations by foreign invaders. Aquatic environments are particularly vulnerable to invasion if a disturbance occurred recently, if predators are absent, or if effective competitors of the invader are absent (Ashton and Mitchell 1989).

Aquatic plants follow a predictable pattern of invasion characterized by four distinct stages: introduction, dispersal, adaptation, and colonization of new habitat (fig. 9.7). Available evidence suggests that, although many aquatic plants can

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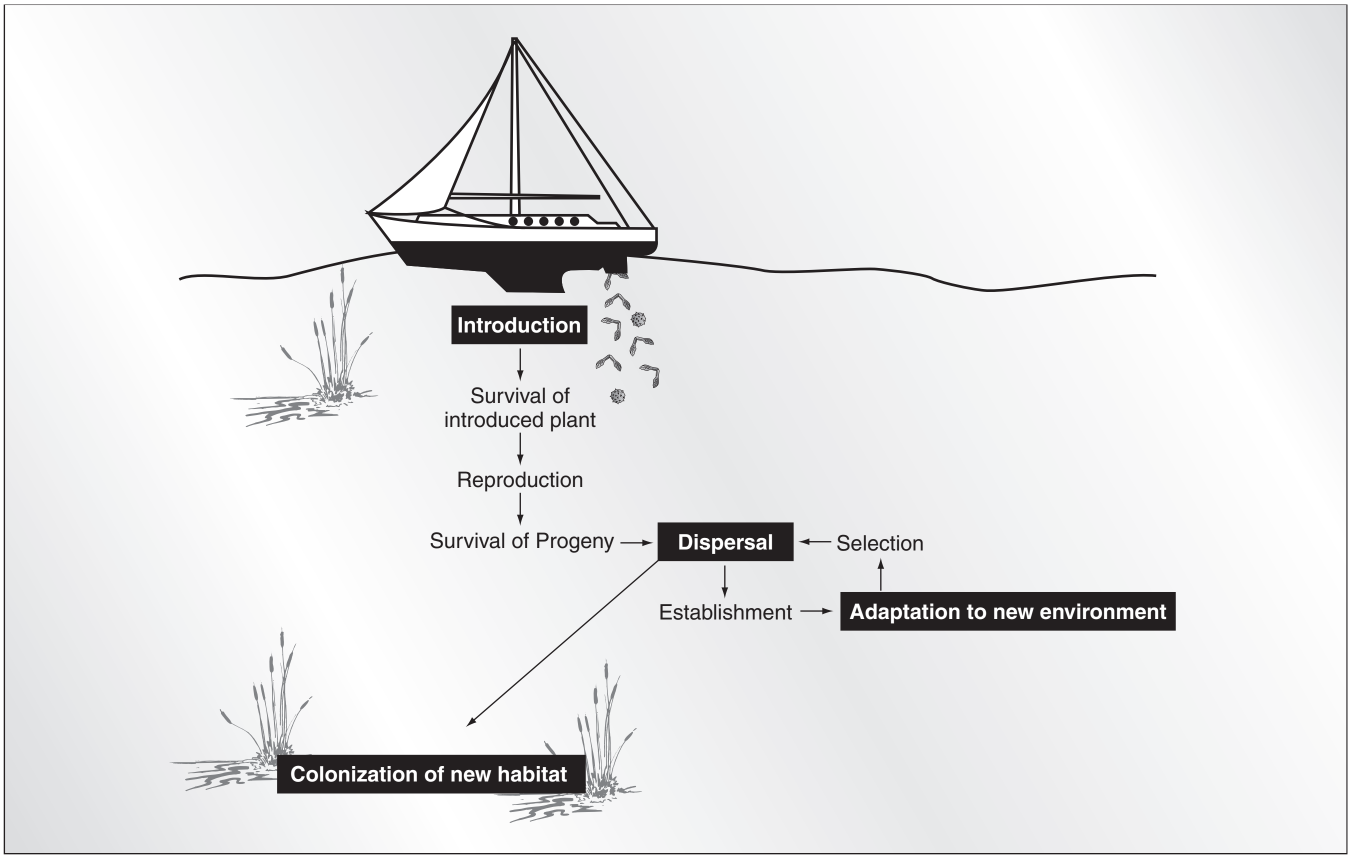

Figure 9.7
Processes and stages associated with the invasion and establishment of an aquatic plant species.

survive unfavorable conditions for extended periods of time, and are readily transported by biological agents such as birds, fish, and insects, almost all invasions of plants that have caused significant habitat alteration and other problems have been human mediated. Assessing the complete history of invasions by aquatic plants, Ashton and Mitchell (1989:117) commented, "we have seen that few aquatic plants are dispersed between unconnected water bodies by natural mechanisms. Indeed, more initial introductions of aquatic plants to new continents have been deliberate in that the introduced species was perceived to have some special attraction and/or intended use for humans. . . . In every case, man has been implicated in their deliberate or accidental introduction to continents outside their native range."

The list of such invaders, including Eurasian water milfoil (*Myriophyllum spicatum*), purple loosestrife (*Lythrum salicaria*), and water hyacinth (*Eichornia crassipes*), and their natural and introduced histories, are beyond the scope of this chapter. But invasive aquatic plants tend to have certain traits in common. First, vegetative reproduction is their common, if not exclusive method of propagation. Second, human activity and transport are their main means of dispersion. Third, all are species capable of extremely rapid reproductive rates. The majority of successful invaders also have free-floating life forms (Ashton and Mitchell 1989). Aquatic invaders, such as purple loosestrife, may rapidly invade shallow water habitats, especially wetlands, forming dense stands that choke out native species. Water hyacinth, in contrast, is an emergent species that can form dense mats in deeper water, but with the same result. Eurasian water milfoil is a perennial aquatic herb with a slender, elongate floating stem. Often reproducing vegetatively, Eurasian water milfoil can disperse long distances by floating, and may cling to boats or other manufactured structures, facilitating its distribution.

We typically think of animals as being dependent upon plants and their physical environment. But in fact, some aquatic animals may radically alter the physical environment itself or even the properties of the surrounding ecosystem. For example, the zebra mussel (*Dreissena polymorpha*) is a classic invasive species with high reproductive rates, wide environmental tolerances, and large dispersal distances. A native of the Black and Caspian Seas in Eurasia, the mussel spread throughout Europe in the nineteenth century. It had reached Lake St. Clair (shared by the U.S. state of Michigan and the Canadian province of Ontario) by 1986, probably arriving via discharges of ballast water from European ships using the Great Lakes via the St. Lawrence Seaway. Downstream dispersal was rapid. By 1991, the zebra mussel was present in New York's Hudson River and in the St. Lawrence River in Quebec. Upstream dispersal, facilitated by commercial shipping, also occurred. The species reached the Mississippi River by 1992 via the Chicago Sanitary and Ship Canal. From there, the zebra mussel has spread through the Mississippi to Louisiana and has begun to move upstream into the Mississippi's major tributaries (Johnson and Carlton 1996).

The zebra mussel exemplifies the third quality of successful invaders, that of ecological match. Unlike any native species of bivalve in North America, the zebra mussel possesses a tuft of filaments (*byssal threads*) that allows it to attach to any stable surface, including other living creatures. This trait gives the mussel not only access to niches that native clams cannot exploit, but a rapid means of dispersal as well. The zebra mussel produces large numbers of plankton-feeding larvae (*veligers*) that are easily, rapidly, and widely dispersed by prevailing currents.

The zebra mussel is a relatively long-lived species that can actively pump the water it filters while feeding, thus making it better suited than short-lived, passive filter feeders, like insect larvae, to exploit calmer waters associated with lakes and slow-moving rivers. Efficient and voracious filter feeders on phytoplankton, zebra mussels at high densities can exceed the combined filtering activities of all zooplankton (Johnson and Carlton 1996). At densities now found in western Lake Erie, zebra mussels may remove up to 25% of the system's primary production in phytoplankton *daily*! Taken together, these traits make the zebra mussel a unique harvester of planktonic primary productivity. Although such feeding may increase water clarity, it also removes nutrients, energy, and biomass from the pelagic portion of the lake community and shunts it to the benthic zone in the form of increased mussel biomass and feces (Brönmark and Hansson 1998). This shift of matter and energy can radically change community composition and species diversity. The zebra mussel's physiological traits suggest that it is capable of colonizing the fresh waters of most of the United States and southern Canada. The effects of the zebra mussel on native species are of particular concern because 70% of the 297 species of freshwater mussels native to North America are listed as extinct, endangered, threatened, or of special concern (Johnson and Butler 1999). At extremely high densities, the zebra mussel not only displaces similar species from a habitat or substrate, but will even use the bodies of other living creatures *as substrates*. Mollusks and slow-moving crustaceans, such as crayfish (*Orconectes* spp.), are particularly vulnerable, and some individuals die after becoming completely encrusted with zebra mussels (Abell et al. 2000). Economic losses from structural damage and clogging of underwater structures, such as pipes, are estimated in the millions of dollars. Initial infestations may reduce water turbidity because of the enormous amount of water collectively filtered by the population, but the zebra mussel's combination of high reproductive rate and short life span can eventually lead to the accumulation of large numbers of dead mussels that foul the water (Hayes 1998).

Larger nonindigenous species also can radically alter aquatic habitat. The carp (*Cyprinus carpio*), a bottom-feeding fish native to Europe, was brought to the United States in the 1830s and was the subject of massive, intentional introductions to freshwater rivers and streams by the 1890s. Such

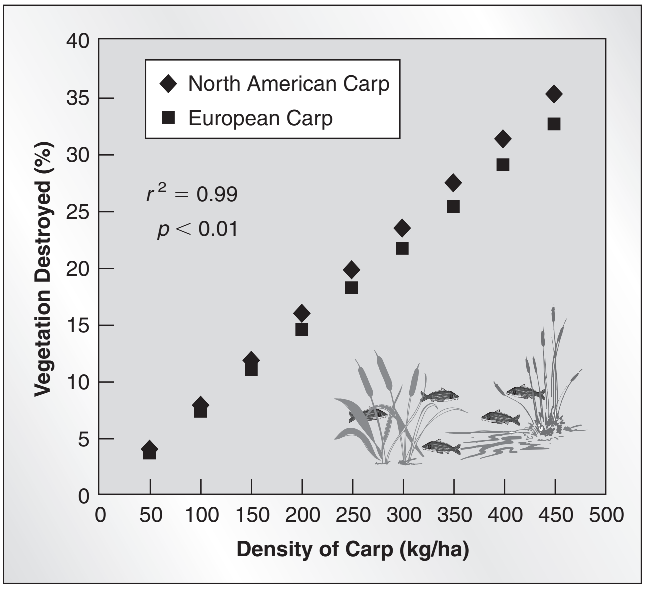

Figure 9.8
The effect of carp (*Cyprinus carpio*) on aquatic vegetation in experimental enclosures.The durations of the North American and European experiments were 92 and 71 days, respectively. Vegetation loss increased linearly with increasing carp biomass.

Original data from studies by Robel (1961) in Utah (U.S.A.) and Crivelli (1983) in France.

introductions were celebrated with high hopes for the carp as an outstanding game fish. Bands played. Politicians made speeches. The outcome, however, was less pleasant than the day's happy events. Tolerant of turbid, poorly oxygenated, even chemically polluted waters, carp proliferated as prophesied, but not to many anglers' delight. Among their other undesirable habits, carp routinely destroy emergent wetland vegetation through their rooting action in the sediment. In controlled experiments in which carp were confined in enclosures, they destroyed up to one-third of all submergent aquatic vegetation. The variation in the proportion of vegetation destroyed can be almost completely explained by variation in the biomass of carp in the exclosure (fig. 9.8). More remarkably, the pattern of plant destruction was almost identical in experiments performed on two different continents, North America and Europe (Robel 1961; Crivelli 1983).

Some nonindigenous species do not change the habitat itself, but may cause profound changes in the use of habitat by other species. The Nile perch (*Lates niloticus*), a large and voracious predatory fish, was introduced into Lake Victoria in east Africa in 1954 as a food source for human populations to supplement dwindling supplies of native fish. Its populations remained low for nearly two decades, but exploded in the 1980s, to the detriment of many endemic species. Lake Victoria's rich biodiversity of haplochromine (*Haplochromis* spp.) cichlids, species found nowhere else in the world, experienced

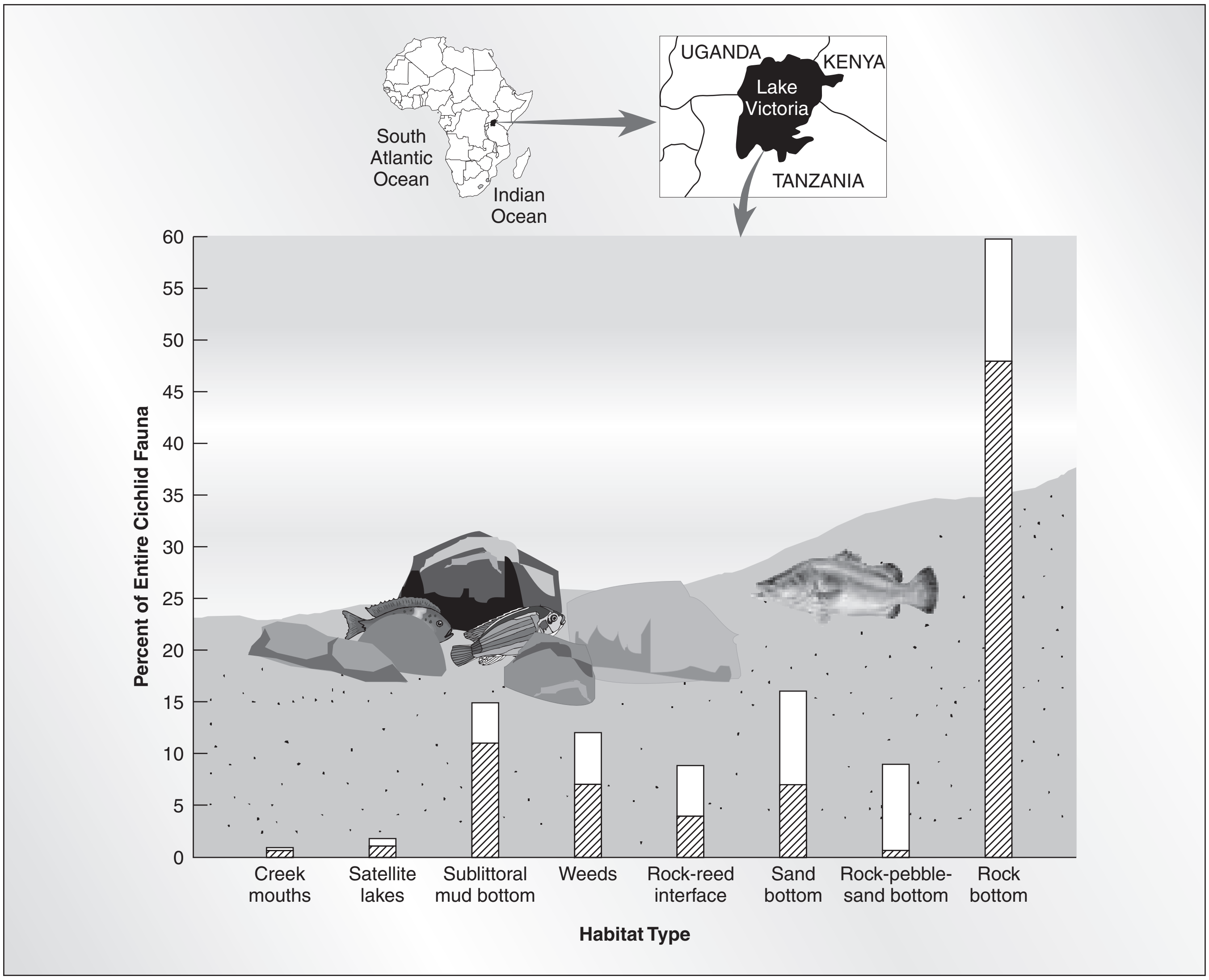

Figure 9.9
Proportions of extant haplochromine (cichlid) fauna in eight microhabitats in southern Lake Victoria, Africa. Striped portions of bars indicate proportion of species that are restricted to the given habitat. Total bar length indicates proportion of species that use the given habitat as one of their major habitats. The Nile perch (pictured, right), introduced in 1954, exterminated many species of cichlids, and patterns of extinction were habitat specific. Habitat shifts have subsequently occurred in many cichlid species, apparently as a means of avoiding predation.

a massive episode of extinction during the Nile perch's population explosion, what some conservation biologists have called "the largest mass extinction of contemporary vertebrates" in recent history (Seehausen et al. 1997). Two hundred endemic species of cichlids disappeared (Seehausen et al. 1997). Many of these species, as well as many other species that survived, were not randomly distributed in Lake Victoria, but were concentrated in particular habitats (fig. 9.9). The extinctions also were not randomly distributed, but rather habitat specific. Most extinctions occurred in offshore and sublittoral zones. Many species that survived the introduction of the Nile perch have made major shifts in habitat use. For example, in the pre-Nile perch era, *Haplochromis tanaos* and *H. plagiodon* were restricted to littoral sand bottom habitats on the east side of Lake Victoria's Mwanza Gulf (Witte el al. 1992). In the 1990s, after the Nile perch had reached large population levels, these species were found in littoral and sublittoral mud bottom habitats on the west side of Mwanza Gulf (Seehausen et al. 1997). Such habitat shifts are consistent with a general pattern of habitat selection documented in terrestrial and aquatic species—namely, that in the presence of a predator, individuals shift from optimal foraging habitat to optimal cover habitat, or to any habitat where the predator is not present (Rosenzweig 1991). The population survives, but growth and reproduction are often reduced. Managers must consider that if nonindigenous predators enter a system, habitat management and conservation strategies may have to be fundamentally altered to preserve biodiversity.

MANAGEMENT OF FRESHWATER HABITATS FOR CONSERVATION

Managing Chemical and Physical Inputs to Aquatic Systems

Preserving and restoring the conservation value of aquatic systems can be accomplished only by active management. In North America, the leading threats to freshwater fauna are increased sediment loads and nutrient inputs from agriculture, interference from exotic species, altered hydrologic regimes associated with dams, and acidification. In particular, problems such as sedimentation, eutrophication, and acidification are *input-oriented* problems, and their best solution lies in input regulation.

Managing Sedimentation and Eutrophication

The sources of sedimentation and eutrophication are soil and fertilizer inputs, respectively, from surrounding lands, especially agricultural lands, and urban waste. Both are usually non-point pollution problems, aggravated through high levels of erosion associated with modern agricultural methods. Thus, the best management to address both problems would be sociopolitical in nature, occurring through laws and policies that (1) reduce the use of fertilizers, particularly on highly erodable lands and on lands near watercourses; (2) require removal of fertilizers, especially phosphorus, nitrate, and nitrite from urban sources, before allowing urban discharge to proceed downstream; and (3) reduce erosion on agricultural lands through increased vegetative cover bordering streams and through cultivation methods less destructive of soil structure. However, managers of specific aquatic systems, such as individual lakes and streams, lack power and jurisdiction to implement such sweeping changes over entire regions and drainage basins. The systems they are responsible to conserve may be degraded by inputs from detrimental land-use practices around them that they cannot directly control. In such cases, managers must use site-specific approaches within their jurisdiction. They must stop such inputs from entering the system even as they reach it, or they must remove or neutralize such inputs after they have entered.

The most immediate and direct ways to stop such inputs into an aquatic system, such as a lake or wetland, are (1) to install filters and other devices at the proximate source of input, such as the inflow stream, that remove the sediment and fertilizer when they arrive and (2) to surround shorelines and banks with vegetation that can remove high levels of phosphorus and nitrate/nitrite from runoff. The installation of filters and other devices can be expensive and the planting and management of appropriate vegetation both costly and labor intensive, but, when properly employed, both techniques can work.

Such practices may dramatically lower the amount of sediment and fertilizer entering an aquatic habitat, but reductions of fertilizer input will not necessarily restore the damage done by previous nutrient loading. What does one do with the phosphorus and other nutrients that have already entered and remain in the system? Remedies for this problem are dredging, chemical manipulation, and biomanipulation.

Dredging is the most direct approach. In this method, sediment from a eutrophied lake, pond, or wetland is physically scraped off the bottom using large, earth-moving machines. Sediment may then be placed in an artificially constructed basin where the phosphorus is removed by physical or chemical means. Thus purified, the sediment may then be returned to the original system. Although admirably direct, dredging is expensive, labor intensive, and disruptive to existing populations and communities, especially the benthos. Dredging may require temporarily draining the system, and the method is seldom suitable or effective in large, deep lakes. During the dredging operation itself, the aquatic habitat may not be suitable for other uses by humans.

Some chemical methods can convert phosphorus into chemical states that prevent it from entering or interacting in the system. One of the most well known is the so-called Riplox method ((Brönmark and Hansson 1998). In this method, the sediment surface is first oxidized, causing the phosphorus that is present to precipitate in metal complexes. Then calcium nitrate ($Ca(NO_3)_2$) and iron chloride ($FeCl_3$) are added to the sediment, increasing the levels of oxygen and iron concentrations present. The pH of the system, which would tend to decline at this point, is stabilized through the addition of calcium hydroxide ($Ca(OH)_2$). At a suitable pH, denitrifying bacteria in the sediment will transfer the nitrate in the added calcium nitrate to nitrogen gas (N_2), releasing it to the atmosphere. If these reactions proceed as planned, a chemical "lid" is placed over the surface of the sediment that prevents the release of phosphorus from the sediment into the water.

The third method, biomanipulation, attacks the eutrophication problem by manipulating populations of living creatures in the system. First, the densities of zooplanktivorous fish (generally the cyprinids) are reduced, either by adding piscivorous (fish-eating) species or by removing the cyprinids directly by trawling with gill nets or by poisoning. Theoretically, if the number of zooplanktivorous fish are reduced, zooplankton populations will grow and the grazing rate on algae and phytoplankton will increase. As a result, algal blooms will decrease and water clarity will improve. Biomanipulation has worked best where at least 80% of the zooplanktivorous fish are removed, and its success appears not to be due to the reasons originally believed. Rather, removal of the fish seems to lead to an increase in the levels of submerged macrophytic plants and periphytic algae at the sediment surface (recall the destructive effect of carp on aquatic vegetation). These plants in turn absorb large amounts of nutrients that are then no longer available for phytoplankton. Further, the plants oxidize the surface of the sediment, reducing the absorption of phosphorus into the water. Removal of fish reduces bottom disturbance by benthic-feeding fish, excretion of nutrients by fish, and phosphorus released into the water from the dead and decomposing fish.

Interestingly, lake systems can, with respect to phosphorus, exist in **alternative stable states**, in which, at similar nutrient levels, they may be dominated by submerged macrophytes in clear water or by high densities of phytoplankton and associated turbid water. The transition from one state to the other is not gradual but rapid. The theory can be illustrated visually by the "marble in a cup" model developed by Sheffer (1990)

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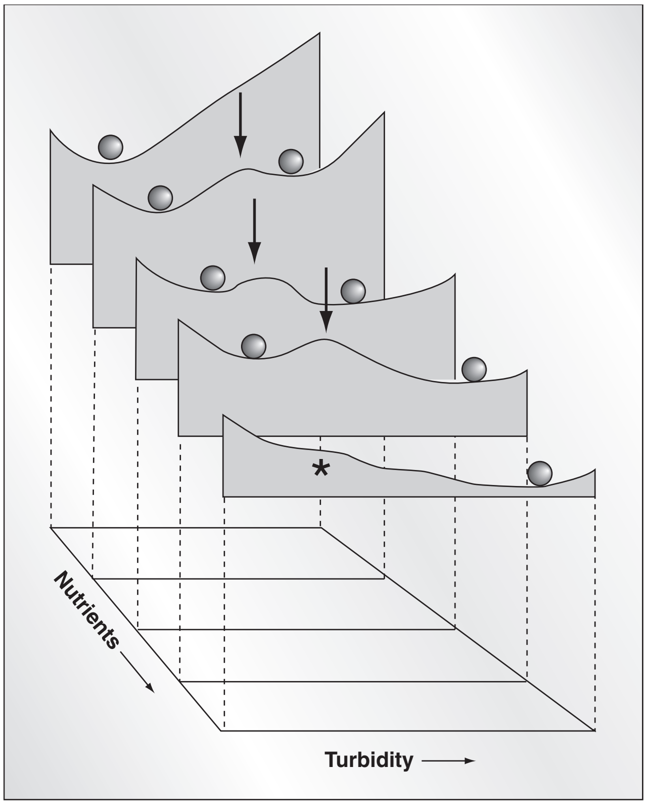

Figure 9.10
The "marble in a cup" model of alternative stable states of lakes relative to different levels of phosphorus inputs. Position of the marble(s) indicates the position(s) of one or more potentially stable states of the system. Stability of the system is achieved through a combination of biomanipulation and control of phosphorus inputs, but not one or the other exclusively. Typically, turbidity increases as nutrient levels increase. With small increases in nutrient levels, turbidity may not change unless a disturbance (represented by arrows) occurs. However, at a certain point (*) nutrient levels are too high for the water to remain in a clear state.

Adapted from Sheffer (1990).

(fig. 9.10) Under high levels of nutrient enrichment, the lake can exist only in a turbid state. As phosphate levels decline, alternate stable states are possible, depending on which way the system (marble) is pushed. If, for example, macrophytes and periphytic algae can be well established at intermediate nutrient levels, they can take in excess amounts of phosphorus (luxury uptake) that limits availability of phosphorus for phytoplankton and prevents their populations from increasing (and the clarity of the water from decreasing). The lower the level of nutrients in the water, the more stable the clear state becomes. If the model has conceived the system correctly, it demonstrates that the system's condition is a function not only of nutrient inputs, or even fish populations, but also of the state of populations of macrophytes and periphytic algae. Further, the system's future state is, in part, dependent on its present state, especially on how well established such populations of macrophytes and algae are and how much additional phosphorus they can absorb. Although this model is conceptual and theoretical, it does have some empirical support in studies of Swedish lakes that exhibit such alternative stable states (Blindow, Hargeby, and Andersson 1997).

Managing Freshwater Systems Through Riparian Zones

Riparian vegetation is the plant community adjacent to a body of water, such as a lake or stream. Riparian zones, aside from their potential importance as corridors that link populations in different areas, profoundly affect the quality of freshwater ecosystems because they can modify, dilute, or concentrate substances from terrestrial environments in the drainage basin. Thus, for good or ill, riparian zones are the link between an aquatic system and its terrestrial context. For streams and rivers, riparian zones as limited as 10 to 30 m in width can substantially moderate temperatures, stabilize banks, and provide essential material inputs to biotic communities. Riparian vegetation of similar widths (9 to 45 m) can substantially reduce inputs of sediments from the surrounding landscape (Osborne and Kovacic 1993). Finally, riparian vegetation, deliberately arranged as buffer strips along streams, lakes, or wetlands, can substantially reduce inputs of nutrients such as phosphorous and nitrogen from a surrounding and heavily fertilized agricultural landscape.

The quality of riparian vegetation is often especially critical to egg, larval, fry, and juvenile stages of fish because they have more narrow environmental tolerances than adults. For example, removal of riparian vegetation in the South Umpqua River of Oregon has been a contributing factor to declines in this river's chinook salmon (*Oncorhynchus tshawytscha*) population. Removal of riparian vegetation, primarily for logging and road construction, has contributed to increased erosion and subsequent siltation that covers gravel substrates needed for egg-laying habitat, with associated decreases in oxygen concentration and light penetration. Destruction of riparian vegetation increases evaporation from the stream, leading to reduced summer stream flows. In spring, runoff increases during peak flows, washing out deposits of gravel and debris from streambeds that are essential elements of salmon habitat. The most adverse effect of eliminating riparian vegetation is that summer water temperatures in some sections of the South Umpqua have risen above lethal levels for salmon (26°C) in recent years (Ratner, Lande, and Roper 1997). According to Ratner, Lande, and Roper, who conducted a population viability analysis (chapter 7) on this population of salmon, "if habitat degeneration continues at the historical rate . . . the population has a 100% probability of going extinct within 100 years" (Ratner, Lande, and Roper 1997). Ratner and her colleagues advocate closing roads along the river and its tributary streams and beginning a process of active riparian vegetation restoration as essential steps to maintain the South Umpqua chinook salmon.

In an experiment comparing grass and forested buffers, Osborne and Kovacic (1993) determined that both reduced nitrate and phosphorous concentrations in surface water and in shallow groundwater by up to 90%. On an annual basis, the forested buffers reduced nitrate concentrations more (range 40

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to 100%) than the grass buffers (range 10 to 60%), but were less effective than grass buffers at reducing phosphorus. Over time, both kinds of buffers "leaked" the nutrients they trapped, but such losses could be reduced by periodically harvesting the vegetation in the strips (Osborne and Kovacic 1993).

Managing Acidification

The most common direct method of restoring lakes suffering from acidification is a technique called ***liming***, the direct addition of lime (calcium carbonate, $CaCO_3$). Properly applied, liming restores the pH to a neutral or alkaline state, and normally leads to an increase in species diversity in the lake as well as an increase in the abundance of most species. However, liming does nothing to alter the existing input of acidic substances into the lake. If these inputs remain unaltered, the benefits of liming will be lost and the process will have to be repeated.

Managing Wetlands

Vegetative buffer strips adjacent to wetlands, even if relatively monotypic and composed of common, inexpensive grass species, remove nutrients, including nitrates and phosphates, from runoff and permit fewer nutrients to enter the wetland (Rickerl, Janssen, and Woodland 2000). An interesting and sometimes unexpected outcome of planting buffering vegetation is that it may actually increase the diversity of the plant community around the aquatic system. In South Dakota, three species—smooth bromegrass (*Bromus inermis*), orchardgrass (*Dactylis glomerata*), and alfalfa (*Medicago sativa*)—were planted as buffer species in experimental plots around wetlands. After establishment, the buffered communities had 29 additional plant species not found in the wetland itself or in uplands around unbuffered wetlands (Rickerl, Janssen, and Woodland 2000).

Coordinated management of lake-wetland complexes can produce more effective results for conservation than managing each system separately. Managers can reduce the inputs of phosphorus and other nutrients into a lake by maintaining or creating wetlands around it. Wetland vegetation and associated wetland systems absorb far greater quantities of nutrients, especially phosphorus and nitrates, from the lake's drainage basin than can terrestrial vegetation. Wetlands can remove up to 79% of total nitrogen, 82% of nitrates, 81% of total phosphorus, and 92% of sediment in drainage water (Chescheir, Skaggs, and Gilliam 1992).

Wetlands, as noted earlier, often have disproportionately high levels of species richness, compared with terrestrial habitats of similar area. Wetlands often demonstrate species-area relationships similar to those documented in island flora and fauna (chapters 4 and 5). As the size of a wetland increases, so does its species richness. Thus, the conservation value of a wetland increases with size (Findlay and Houlahan 1997). Because wetlands are often radically different than their surrounding landscape, successful management of wetland species may require management of landscape-level processes that extend far from the wetland's borders. For example, in southeastern Ontario (Canada) Findlay and Houlahan (1997) determined that wetland species richness in plants, herptiles (amphibians and reptiles), and birds was negatively correlated with the density of paved roads within 2 km of the wetland edge. Further, species richness of plants, herptiles, and mammals was positively correlated with the proportion of forest cover within the same distance of the wetland. Thus, a manager may be able to do as much to enhance biodiversity in a wetland by managing land-use processes as by managing the wetland itself.

Managing Biological Inputs to Aquatic Systems—Dealing with Invasive Species

Invasive species, both plant and animal, pose unique and particular problems for managers of aquatic systems. Some basic principles of managing invasive species have already been covered in chapter 7 and will not be repeated here. However, some management approaches are unique to aquatic species, especially plants.

Ashton and Mitchell (1989) note two basic strategies for the control of nonindigenous species: protection and intervention. Protectionist approaches are applicable in a variety of contexts and have been explored in chapter 7. Interventionist approaches are more species- and site-specific. There are six types of interventionist (control) techniques that can be especially successful against invasive aquatic plants. These are (1) manual removal; (2) mechanical control (using machines to mow, uproot, shred, or dredge out established plants); (3) chemical control (herbicides); (4) biological control (introduction of a specific parasite or predator to decimate the invader); (5) environmental manipulation (especially water-level manipulation); and (6) the direct use of the invasive species for some economic benefit (i.e., harvest) (Ashton and Mitchell 1989). Despite the daunting prospect of trying to eradicate an established invasive species, some such programs have succeeded. In successful control programs, the infestation was attacked early when the invasive plant was low in numbers and small in extent. Also, control efforts were successful when the invasive species was confined to one location. Under these conditions, all of the above techniques have been used effectively. Even the notorious carp (in this case, the grass carp, *Ctenopharyngodon idella*) has been put to good use as an agent of biological control to eradicate nonindigenous submerged plants (Ashton and Mitchell 1989).

Where invasive species are well established, some attempts at control, and even eradication, have been successful, but the range of effective techniques is more limited. Manual and mechanical removal are not practical when invasions become widespread, however, chemical and biological controls may still be effective. For example, an invasion of water hyacinth in Lake Hartbeespoort in The Republic of South Africa was eradicated with large-scale use of herbicides (fig. 9.11a). An infestation of the water fern *Salvinia molesta* was eradicated from Lake Moondarra in Australia through the introduction of another nonnative species, the Brazilian beetle or Salvinia weevil (*Cyrtobagous salviniae*) (fig. 9.11b). In the case of the beetle, environmental conditions also played an important role, with drought reducing populations of *Salvinia molesta* to low levels just prior to the beetle's introduction.

The dangers of biological control, especially of introducing a nonnative biological control agent like the Brazilian beetle to an African lake, are many, and have been reviewed in

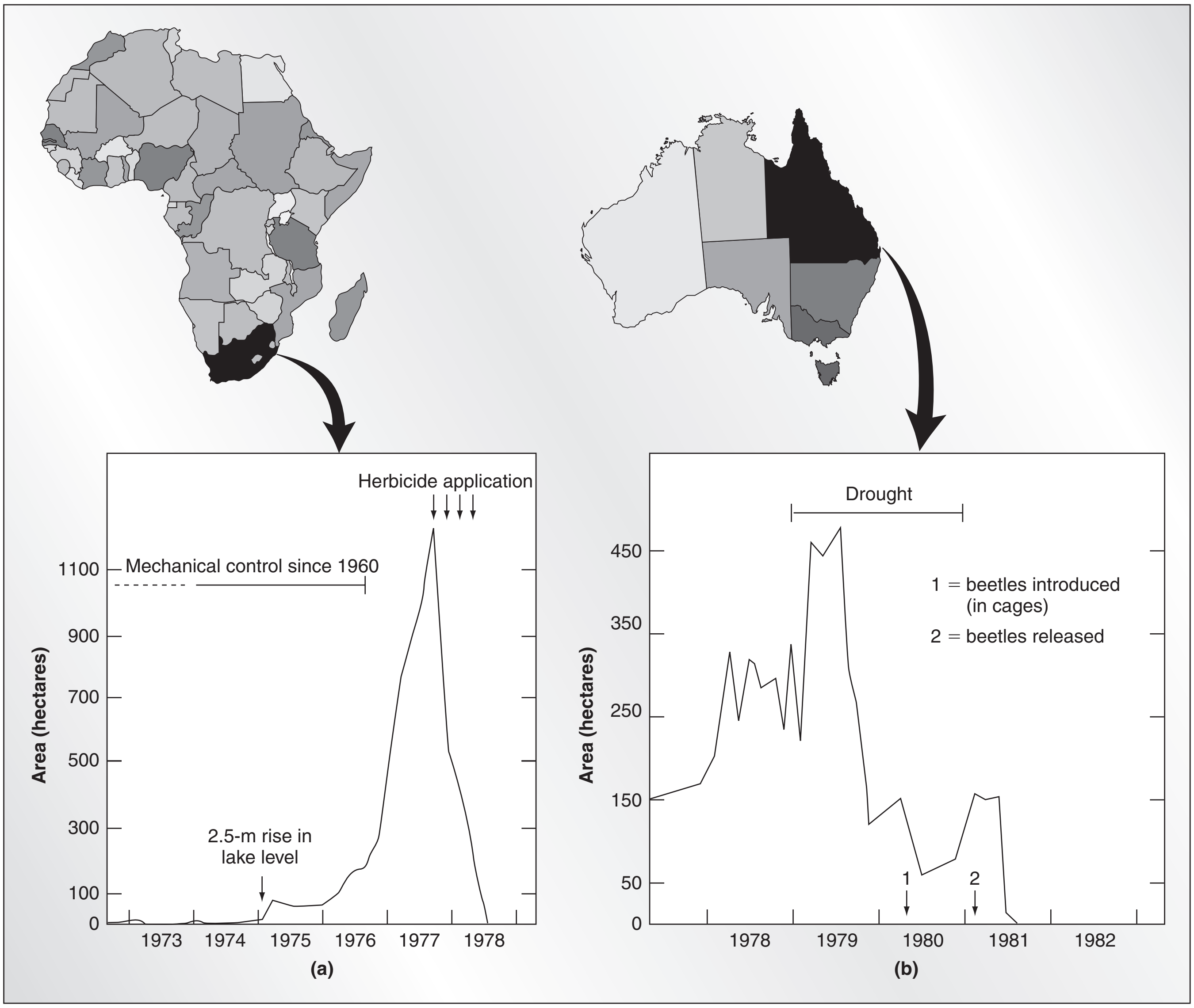

Figure 9.11

(a) Changes in the area covered by water hyacinth (*Eichornia crassipes*) on Lake Hartbeespoort, South Africa, before and after herbicide application. (b) Changes in the area covered by water fern (*Salvinia molesta*) on Lake Moondarra, Australia, before and after introduction of the beetle *Cyrtobagous salviniae.*

Adapted from Ashton and Mitchell (1989).

chapter 7. Risks in biological control can, however, be reduced where a native species can be used as the control agent. For example, to control the previously mentioned invasive aquatic weed, Eurasian watermilfoil, Sheldon and Creed (1995) evaluated the effects of a native North American aquatic weevil, *Euhrychiopsis lecontei*. In a carefully controlled experiment, Sheldon and Creed compared the growth of Eurasian watermilfoil, as well as 10 native aquatic species, in enclosures with and without weevils (fig. 9.12). They found 50% less Eurasian milfoil in enclosures with weevils than in those without weevils, but weevils had no significant effect on any native species.

POINTS OF ENGAGEMENT—QUESTION 1

What elements of Sheldon and Creed's study eliminate or reduce risks often associated with biological control, especially biological control using a nonnative control agent? Does their study contain protocols that could be applied more generally to biological control of invasive species?

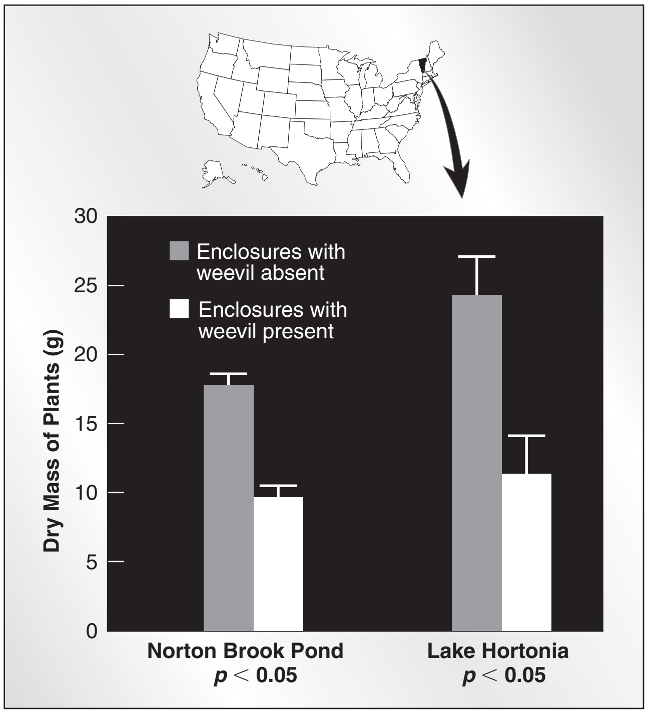

Figure 9.12
The effect of feeding by the native North American aquatic weevil *Euhrychiopsis lecontei* on Eurasian watermilfoil (*Myriophyllum spicatum*) in two Vermont lakes. Watermilfoil biomass is significantly lower where the weevil is present.

After Sheldon and Creed (1995).

Nonindigenous animal species are much more difficult to control, much less eradicate. Decades of chemical treatments, such as rotenone poisoning, or environmental manipulation (water drawdowns or complete drainage) to eradicate carp have usually had only short-term effects, if that, and have proved most effective at eliminating native species. The carp easily reestablished themselves in most cases, but the more desirable native species often did not. Mussels such as the Chinese clam (*Potamocorbula amurensis*), zebra mussel, and other invasive invertebrates have proved impossible to eliminate from aquatic environments once established, making preventionist approaches all the more important to maintaining the health of aquatic systems.

Legislation and Management for Freshwater Environments

The Wild and Scenic Rivers Act

In the United States, the most significant legislation protecting streams is the U.S. Wild and Scenic Rivers Act of 1968. Under this act, a stream or section thereof designated as a wild or scenic river is protected from any action by any federal agency that would adversely affect its water quality. Congress may also, by a special act, designate a section of a river as a National River, such as Missouri's Current River, and extend similar protection (Benke 1990). However, by 1990, less than 2% of U.S. streams (less than 100,000 km out of an estimated 5.2 million km) had been deemed of sufficient quality to merit such federal protection.

The Clean Water Act and Indices of Biotic Integrity

In the United States, the Water Pollution Control Act Amendments of 1972, outgrowths of the earlier Clean Water Act, adopted a visionary, biologically oriented approach to the assessment of national waters. The amendments directed the Environmental Protection Agency to "restore and maintain the physical, chemical, and biological integrity of the nation's waters" and to enhance "all forms of natural aquatic life" (Meybeck and Helmer 1989). Unfortunately, the law's vision of protecting the integrity and diversity of entire systems was lost in the convenience of a reductionistic approach that favored chemical standards and an emphasis on point source pollution (Karr 1991). The former was easier to apply and the latter was easier to clean up. Unfortunately, it is possible for fresh waters to meet standards relating to physical and chemical contaminants and still not be capable of sustaining functional ecosystems. Such systems, being dependent on processes, do not support diverse biological communities if interactions among organisms, and interactions between organisms and the surrounding physical environment, are not properly functioning. Many environmental impacts that degrade ecosystems are simply too diverse and too complex to be detected and understood by chemical assays.

To address this deficiency, a growing emphasis among conservationists has been the use of various indices of biotic integrity (IBI) as alternative, ecologically based measurements of water quality, particularly in streams. Although IBIs vary in detail, most follow similar basic principles and procedures. A particular taxon, say fish, is rated and scored in different attributes (table 9.1). The sum of the scores is then used to provide a summary value for the IBI that is associated with an "integrity class" ranking for the site that provides a summary index of community characteristics (table 9.2) (Karr 1991). Most such indices use three groups of attributes (technically, "metrics") to make their assessment. These are species richness and composition, trophic composition, and fish abundance and condition (Karr 1991). Expectations for the values of individual metrics are based on those found in an undisturbed, but otherwise similar, stream. Many conservationists advocate the use of the IBI over more traditional, chemically based measurements of individual elements or compounds (including pollutants and toxins) in streams because the IBI (1) reflects and focuses upon distinct attributes of biological systems, not simply chemical properties; (2) measures the sampled stream against a minimally disturbed system, thereby establishing a clear baseline and biological expectation; and (3) requires the incorporation of professional ecological judgment in evaluating the stream's condition, not simply a check for compliance in terms of specified elements, compounds, or toxins (Karr 1991). IBIs are strongly associated with independently derived measures of overall watershed

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Table 9.1 Metrics Used to Determine an Index of Biotic Integrity (IBI) for Fish Communities Ratings of 5, 3, or 1 are assigned to each measurement according to whether its value approximates, deviates somewhat from, or deviates strongly from the value of the same measurement at a comparable but relatively undisturbed site. Adapted from Karr 1991. Originally developed for midwest U.S.

METRICS	RATING OF METRIC 5	3	1
Species Richness and Composition			
1. Total number of native fish species	Expectations for metrics 1–5 vary with stream size and region.		
2. Number and identity of darter species (benthic species)			
3. Number and identity of sunfish species (water-column species)			
4. Number and identity of sucker species (long-lived species)			
5. Number and identity of intolerant species			
6. Percentage of individuals identified as green sunfish (tolerant species)	<5	5–20	>20
Trophic Composition			
7. Percentage of individuals as omnivores	<20	20–45	>45
8. Percentage of individuals as insectivorous cyprinids	>45	20–45	<20
9. Percentage of individuals as piscivores (top carnivores)	>5	1–5	<1
Fish Abundance and Condition			
10. Number of individuals in sample	Expectations for metric 10 vary with stream size and other factors.		
11. Percentage of individuals as hybrids (exotics, or simply lithophils)	0	0–1	>1
12. Percentage of individuals with disease, tumors, fin damage, and skeletal anomalies	<2	2–5	>5

condition (Steedman 1988), and are inexpensive, simple, and sensitive to environmental change. If continued and increasing use of IBIs can recapture the original ecosystem emphasis of the U.S. Clean Water Act and other water pollution laws by focusing attention on the ecological condition of freshwater systems, they may provide greater incentive and more valuable insight for managers to restore such systems to their original functions and properties, rather than merely meeting chemically prescribed standards.

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Table 9.2 An Example of Total Index of Biotic Integrity (IBI) Scores, Integrity Classes, and Associated Class Attributes for Fish Communities

TOTAL IBI SCORE*	INTEGRITY CLASS OF SITE	ATTRIBUTES
58–60	Excellent	Comparable to the best situations without human disturbance; contains all regionally expected species for the habitat and stream size, including the most intolerant forms, with a full array of age (size) classes; balanced trophic structure.
48–52	Good	Species richness somewhat below expectation, especially because of the loss of the most intolerant forms; some species are present with less than optimal abundances or size distributions; trophic structure shows some signs of stress.
40–44	Fair	Signs of deterioration include loss of intolerant forms, fewer species, highly skewed trophic structure (e.g., increasing frequency of omnivores and green sunfish or other tolerant species); older age classes of top predators may be rare.
28–34	Poor	Dominated by omnivores, tolerant forms, and habitat generalists; few top carnivores; growth rates and condition factors commonly depressed; hybrids and diseased fish often present.
12–22	Very Poor	Few fish present, mostly introduced or tolerant forms; hybrids common; disease, parasites, fin damage, and other anomalies are regularly observed.
†	No Fish	Repeated sampling finds no fish.

*The score is the sum of the 12 metric ratings. Sites with values between classes are assigned to the appropriate integrity class following careful consideration of individual criteria/metrics by informed biologists.

†No score can be calculated where no fish were found.

After Karr 1991

International and National Legislation for Wetlands

As noted in chapter 2, wetlands were one of the first cases in which international legislation, specifically the Ramsar Convention, focused on the protection of an ecosystem instead of a species. Recall that the Ramsar Convention obligated its signers to conduct land-use planning for wetlands and wetland preservation, to identify and designate at least one wetland as a "wetland of international importance," and to establish wetland nature reserves (Koester 1989). Canada's federal policy on wetland conservation provides one of the best national examples of implementing the ideals of Ramsar. The Canadian policy is a comprehensive federal plan that articulates strategies for sustainable use and management of the nation's wetlands. It aims to provide for the maintenance of overall wetland function on a national level; enhance and rehabilitate degraded wetlands; recognize wetland functions in planning, management, and economic decision making in all federal programs; secure and protect wetlands of national importance; use wetlands in a sustainable manner; and allow no net loss of wetlands on federal lands and waters (Rubec 1994). Although no policy is ever perfectly translated into practice, the Canadian wetlands policy has experienced remarkable success, primarily through its nonregulatory approach. Each Canadian province, following directives of federal policy, has developed its own public review and consultation process for wetlands conservation (Rubec 1994). Federal wetland directives led to the publication of a standardized manual, the *Wetlands Evaluation Guide* (Bond et al. 1992). With an estimated endowment of nearly one-quarter of the world's remaining wetlands, Canada's leadership in wetlands conservation policy is not only commendable but strategic.

Although Canada has provided a commendable example of integrating international wetlands conservation with national and provincial policies, other nations also have developed extensive wetlands conservation legislation. Wetlands conservationist Michael Williams, a native of the United Kingdom, considers the best example of national wetlands legislation to be that of the United States, which he asserts is "the most elaborate and complex legislation in place for the longest time" (Williams 1990). A number of U.S. legislative acts address wetlands conservation, and most lead to increasing preservation and restoration of

Table 9.3 Federal Legislation Affecting the Conservation of Wetlands in the United States

PROGRAM OR ACT	PRIMARY IMPLEMENTING AGENCY	EFFECT ON WETLANDS
Discouraging or Preventing Wetland Conversions		
Regulation		
Section 404 of the Federal Water Pollution Control Act (1972) amended as the Clean Water Act (1977)	U.S. Army Corps of Engineers, Department of Defense	Regulates activities that involve disposal of dredged or fill material
Acquisition		
Migratory Bird Hunting and Conservation Stamps (1934)	U.S. Fish and Wildlife Service (FWS)	Acquires or purchases easements with revenue from fees paid by hunters for Duck Stamps
Federal Aid to Wildlife Restoration Act	FWS	Provides grants to states for acquisition, restoration, and maintenance of wildlife areas
Wetlands Loan Act (1961)	FWS	Provides interest-free loans for acquisitions of and easements for wetlands
Land and Water Conservation Fund	Forest Service, Bureau of Land Management, FWS, National Park Service	Provides funds that can be used to aquire wetland wildlife areas
Water Bond Program (1970)	Agriculture Stabilization and Conservation Service, U.S. Department of Agriculture (USDA)	Leases wetlands and adjacent upland habitat from farmers for waterfowl habitat over 10-year period
U.S. Tax Code	Internal Revenue Service (IRS)	Provides tax deductions for donors of wetlands
Other General Policies or Programs		
Executive Order 11988 Floodplain Management (1977)	All agencies	Minimizes wetland loss and degradation from federal activities
Executive Order 11990 Protection of Wetlands (1977)	All agencies	Minimizes impacts on wetlands from federal activities
Coastal Zone Management Act (1972)	Office of Coastal Management	Provides funding (up to 80%) for state wetland protection initiatives associated with estuaries and other coastal zone habitats
Food Security Act (1985)	USDA	Withholds subsidies for agricultural improvements involving wetland conversion
Encouraging Wetlands Conversion		
U.S. Tax Code	IRS	Encourages farmers to drain and clear wetlands by providing tax deductions and credits for all types of general development activities
Payment-in-kind program	USDA	Indirectly encourages farmers to place previously unfarmed areas, including wetlands, into production

Adapted from Williams 1990.

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wetlands (table 9.3). For example, the 1985 Food Security Act contained a provision designed to arrest the process of draining wetlands on private agricultural lands before the last of these wetlands were lost. This provision, popularly known as "Swampbuster," denies most U.S. Department of Agriculture benefits to farmers who drain wetlands on their land. Swampbuster creates an eligibility requirement for farmers to receive commodity price supports, disaster payments, Farmers' Home Administration loans, and other benefits. Amended in 1990 as the Food, Agriculture, Conservation and Trade Act, the Swampbuster provision was supported in this amendment by the creation of the federal Wetland Reserve Program (WRP), which provides for payment of subsidies to farmers who remove croplands from production in former wetland areas and reestablish the land as wetlands. To enroll in WRP, the landowner's plan must include drainage alterations and the establishment of marsh plants on the enrolled site. The WRP was begun as a pilot program with a limited budget, and because the program's budget is small, so is its enrollment. In 1992, only 20,200 ha (20%) were enrolled in nine states out of 100,800 ha eligible for enrollment. Nevertheless, if even a fraction of all U.S. croplands enrolled in the program, the WRP would become the largest wetlands restoration program in U.S. history (Lant, Kraft, and Gillman 1995).

Despite an extensive network of wetlands conservation legislation, supported by national policies and executive orders (e.g., Executive Order 11990 of 1977) that make wetlands conservation a matter of national priority, wetlands loss in the United States continues, in part because (1) there is a lack of agency coordination in wetland conservation; (2) most legislation does not regulate private activity on private lands, which remain the greatest single source of wetland losses; and (3) some U.S. legislation still encourages, directly or indirectly, the draining of wetlands. For example, the U.S. tax code provides tax deductions and credits for farmers for many types of development activities, including draining wetlands (Williams 1990).

Setting Priorities for Conservation in Freshwater Habitats

The World Wildlife Fund–United States (WWF–U.S.) recently made a priority assessment of North American lakes and streams by region using two criteria: biological distinctiveness and conservation status of watersheds within a region (Abell et al. 2000). In ranking biological distinctiveness, WWF–U.S. gave priority to those regions that contained one or more systems that made important contributions to biodiversity at four different levels (globally outstanding, continentally outstanding, bioregionally outstanding, or nationally important). In ranking conservation status, regions were ranked as critical (intact habitat reduced to small, isolated patches with low probability of persistence over the next decade without immediate action); endangered (intact habitat of isolated patches of varying length with low to medium probability of persistence over the next 10 to 15 years without immediate or continuing protection or restoration); vulnerable (intact habitat remains in both large and small blocks, persistence is likely over next 10 to 20 years if the area receives adequate protection and restoration); relatively stable (disturbance and alteration in certain areas, but function linkages among habitats still largely stable, surrounding landscape practices do not impair aquatic habitat or could be easily modified to reduce impacts); and relatively intact.

Categories I–V were assigned on the basis of integration of these two criteria, with I being the most critical and V being the least critical (fig. 9.13). Following a triage philosophy of conservation, the greatest need for protection was assigned to globally outstanding areas in endangered and vulnerable status. Critical areas were considered too degraded and at risk to have high hopes of saving, and stable or intact systems were considered not to require immediate action. Among systems in the endangered and vulnerable categories, conservation priority declines as the importance of the system decreases in scope.

The WWF–U.S. prioritization system is far from perfect, but it is extremely useful at two levels. As a specific prioritization of aquatic conservation needs, the assessment uses objective criteria to identify key areas in need of immediate protection. As a method of conservation assessment, the ranking system can be adapted to other regions of the world or to smaller scales while preserving its intended purpose: focusing conservation efforts in areas that will reward the efforts with the greatest contribution to biodiversity. For example, conservation biologists working to manage or establish a system of local preserves may have no aquatic systems that are globally or continentally outstanding, but they may have systems that are outstanding at smaller scales, such as state or local levels. The need for such assessment, followed by appropriate management, is critical. Although the North American assessment found that Arctic lakes and rivers were, for the most part, intact and stable, there were no large temperate lakes or rivers that could be so described. The majority of temperate lakes and rivers were classified as endangered or critical (Abell et al. 2000).

To set management and conservation priorities, managers must understand the causes of habitat loss and their effects on aquatic diversity. Many aquatic and wetland species show dramatic shifts in distribution over relatively short time spans. Managers must determine if such changes represent the effects of habitat loss or environmental change or are simply random events. Making an accurate determination is critical to making an appropriate management response. But managers cannot make these determinations without systematic assessment and decision-making processes.

One approach to making such assessments is the use of **rule-based models** that evaluate possible mechanisms of distributional changes in species. Skelly and Meir (1997) used a rule-based approach to evaluate possible causes of changes in distributions of 14 species of amphibians across a landscape of 32 ponds in Michigan. Specifically, they attempted to explain changes using three different models: (1) an *isolation model* that assumed that changes in distribution were driven by distances between ponds (i.e., by dispersal abilities of the amphibians); (2) a *succession model* that assumed that distribution was determined by changes in vegetation in and around the ponds; and (3) a *null model* that assumed that changes were random events. Their basic data set was simple; namely, presence-absence data on 14 amphibian species based on annual surveys from 1967 to

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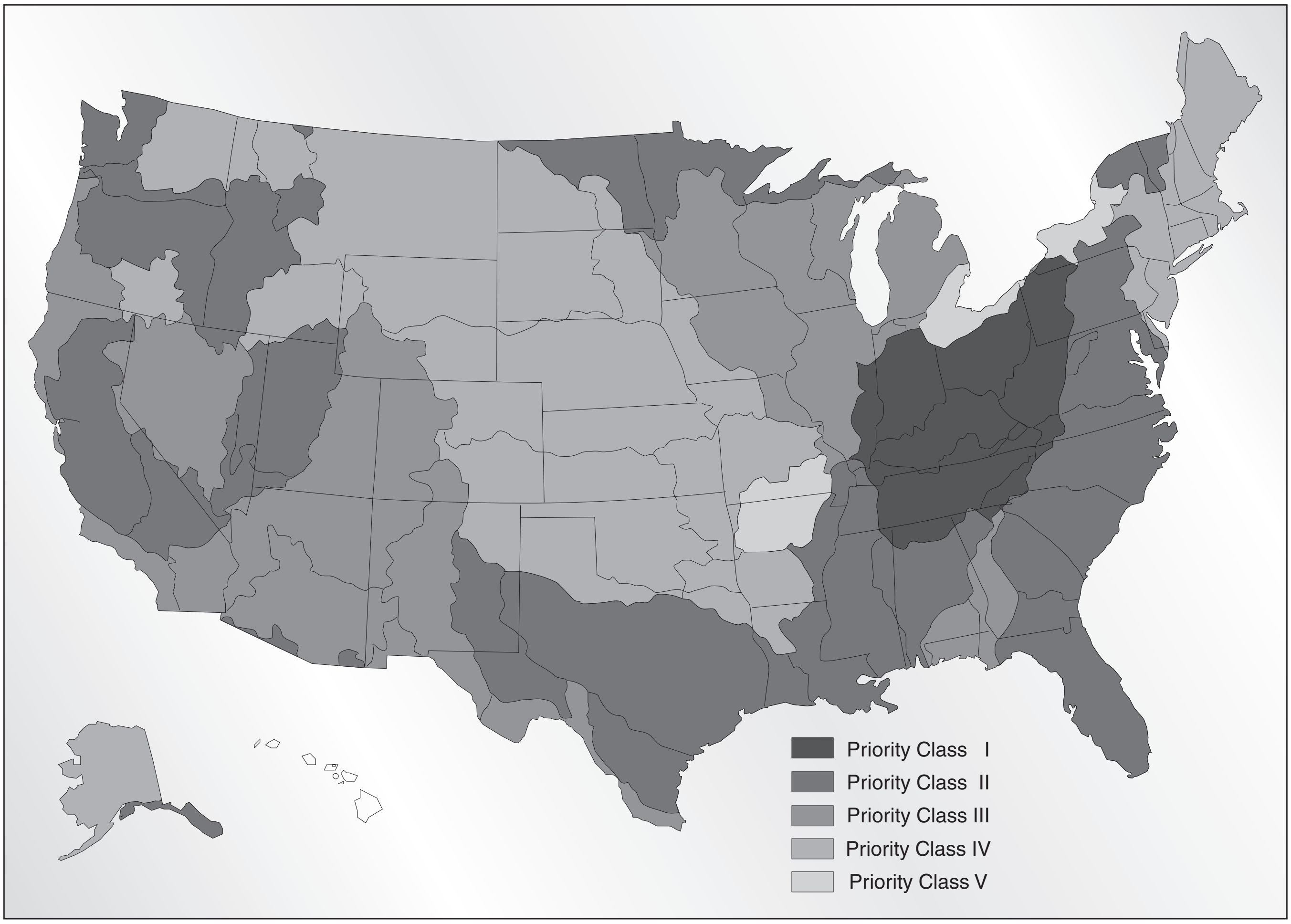

Figure 9.13
Priority categories for conservation of freshwater ecoregions in the United States. Prioritization is based on combined ranking of biological value (i.e., relative contribution to global biodiversity) and current management/conservation status. Conservation efforts will vary within the same priority category because of differences among watersheds in habitat, beta diversity, and resilience.

After Abell et al. (2000).

1974 and from 1988 to 1992. The underlying hypothesis of each model was used to divide the ponds into three classes based on (1) the distance from the pond to the nearest population of each species (isolation model), (2) the vegetational characteristics in and around the pond (succession model), or (3) random assignment of each pond to one of three classes (random model). For individual species, the succession model made fewer mistakes in predicting the occurrence of three species at individual ponds and was better at predicting species richness of amphibans at ponds (Skelly and Meir 1997).

These results suggested that the presence of amphibians in this landscape of wetlands could be best managed by managing the vegetation characteristics of the ponds, not by changing the distribution of ponds. Skelly and Meir note that the ability to explain a pattern with a rule-based model is not the same as showing causation between a factor and its effect. To accomplish that, managers would have to manipulate vegetation in and around the ponds experimentally and monitor amphibian response. What the rule-based approach does provide is insight about *which* experiments might be most useful to conduct. The authors conclude that "even relatively coarse information on presence and absence can be put to an . . . important use: as survey information accumulates it becomes a source of insight for managers interested in determining *why* species distributions are changing, not just *if* they are changing" (Skelly and Meir 1997). Rule-based models can be used in other contexts, but their application here shows how a manager, informed only by simple survey data, could use rule-based models to evaluate management actions and plan experiments to determine the causes of changes in species presence and distribution.

MARINE HABITATS AND BIODIVERSITY

It is beyond our scope to consider the multitude of marine habitats that contribute to earth's total biodiversity. However, we briefly review three that make disproportionately large contributions and face specific and significant threats from human activity. These are communities associated with coral reefs, bottom sediments, and hydrothermal vents.

Coral Reefs

Coral reefs have been called the tropical rain forests of the oceans. Worldwide, over 600 species of coral contribute to this remarkable habitat, and individual reefs may harbor up to 400 species of coral, 1,500 species of fishes, 4,000 species of mollusks, and 400 species of sponges (Hinrichsen 1997). Although the bulk of any coral reef is nonliving matter, the surface layer of living creatures is composed mostly of coral polyps. Relatives of jellyfish and anemones, the polyps have column-shaped bodies topped with stinging tentacles. These creatures secrete calcium carbonate as a metabolic product, and from such secretions fashion cup-shaped structures that serve as their homes and that they attach to one another. Over many years and generations of coral, these calcium carbonate secretions build a coral reef, each new generation enlarging the reef by building on the bodies of their ancestors.

Coral reefs are centers of marine biodiversity because they combine the elements of structure, nutrients, water quality, and light to create a favorable and productive environment for living things. Physically, the body of the reef provides a substrate and point of attachment for many species, especially more sedentary taxa such as crustaceans and mollusks. Even among more active species, the physical characteristics of the reef provide cavities for shelter and breeding. Upon this structure, high densities of prey species attract proportionally high densities of predators.

The coral polyps that build the reef constantly secrete calcium, an essential nutrient for photosynthetic organisms such as phytoplankton. Additional inputs of calcium come from the ongoing erosion and breakdown of dead corals that form the body of the reef. Because the reef forms in well-lit waters, light is available in combination with calcium and other nutrients, creating a favorable environment for photosynthesis to take place. Interacting with nutrient and light availability is a generally high water quality, produced in part by abundant populations of sponges on the reef's surface. Sponges, using the reef as a surface for support, circulate and cleanse the surrounding water through their own bodies, enhancing water quality, lowering turbidity, and allowing penetration of light to greater depths.

Benthic Communities

Of 29 nonsymbiont animal phyla known on earth, all but one have representatives in the ocean, and all of these have representatives in benthic communities. In fact, most of the diversity found in marine ecosystems consists of invertebrates that live in or on bottom sediments (Snelgrove 1999). We are only now beginning to appreciate the biodiversity of such communities. For example, 64% of polychaete (tubeworm) taxa identified in a recent deep-sea study were previously unknown to science (Grassle and Maciolek 1992). Given such ignorance, it is not surprising that we do not know the exact number of marine benthic species, but estimates have ranged from a low of 500,000 (May 1992) to a high of more than 10 million (Lambshead 1993). What is it about benthic habitats that leads to such high biodiversity?

There is enormous variability in benthic habitats and their associated communities, but some general patterns hold worldwide. Benthic habitats in extreme environments, such as estuaries, eutrophied areas, and high-energy regions with low organic content, have lower diversity than sediments in aquatic habitats without these characteristics (Snelgrove 1999). In addition, the diversity in sediment grain size is directly correlated with the diversity of the benthic community, probably because a greater diversity of sediment sizes naturally provides a higher diversity in sizes of food particles (Whitlatch 1977). Finally, diversity in seagrass bed sediments is higher than in adjacent sediments associated with open areas (Peterson 1979).

In shallow water, the distribution of benthic organisms is determined primarily by abiotic habitat features, including temperature, salinity, depth (which affects both light and pressure), surface productivity, and sediment dynamics. Many species have specific tolerances to temperature, salinity, and pressure because these factors affect their osmotic balance and the functioning of cellular enzymes. Despite poor swimming abilities and the lack of a central nervous system, the planktonic larvae of many benthic invertebrates show some ability to select favorable benthic habitat (i.e., they display habitat preference) (Butman, Grassle, and Webb 1988; Snelgrove 1999). It is not clear what environmental cue the larvae are responding to, although substrate organic content has been suggested (Butman 1987). What is demonstrable is that where most larvae end up, in terms of sediment type, is both adaptive and nonrandom (by definition, preferential).

Communities Associated with Hydrothermal Vents

A habitat like none other on earth is found in association with marine hydrothermal vents in some of the deepest parts of the sea, along the fissures and edges of tectonic plates. These habitats and their associated communities are a relatively recent discovery, first reported in 1977. Most benthic communities, both freshwater and marine, that exist below euphotic (lighted) depths must depend upon the input of organic matter from outside (allochthonous matter). Marine benthic communities around these vents, however, are unique in that the foundation of their productivity is bacteria that convert heat energy from the vent into chemical energy, analogous to the way in which photosynthetic organisms convert light energy into chemical energy. This process, known as chemosynthesis, provides a radical alternative to our traditional view of community production, structure, and function. Although the process may be new to human understanding, the hydrothermal vent communities appear to be very old, and extremely stable. They furnish habitats for relict species from the mesozoic era, including many species of crinoids and the most primitive living sessile barnacles (fig. 9.14) (Barry and Dayton 1991).

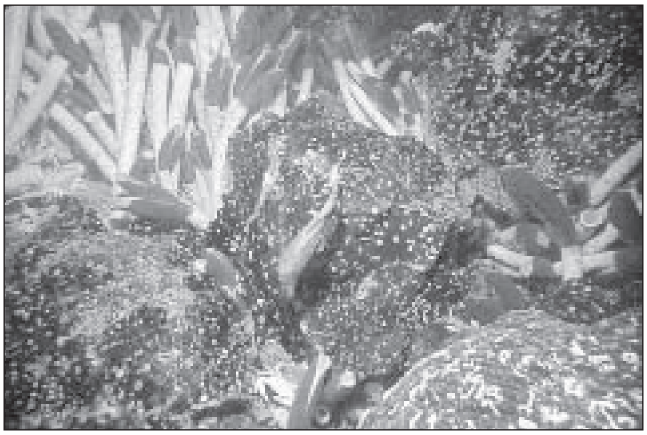

Figure 9.14
A hydrothermal sea vent community. Such communities are not only characterized by high biodiversity, but contain many unique "relict" marine species not found in other habitats. This photo, from the Galapagos Trench in the Pacific Ocean, reveals tube worms, vent fish, and Galapagos trench crabs.

CONSERVATION CHALLENGES OF MARINE HABITATS

Although problems of marine habitat and species preservation vary locally and regionally, the major threats to marine environments are consistent throughout the world. Some are similar or identical to threats facing freshwater environments, whereas others are unique to the marine system. The most important global threats include exploitation of commercial species, direct destruction of marine habitats, indirect degradation of marine habitats from land-based sources including eutrophication, pollution (primarily from radioactive wastes, heavy metals, and petroleum products), the degradation of coastal zones (from erosion, development, and habitat destruction), (VanDeVeer 2000), and nonindigenous species (Ruiz et al. 1997).

In the 1940s and 1950s, the emerging science of fisheries management perceived fish stocks as renewable resources that could be managed for a maximum sustainable yield (MSY), whose value could be calculated precisely by using estimates based on catch per unit effort (Ricker 1958). All that was thought to be required for a sustainable fishery was a reproductive surplus. Today the concept of MSY has all but disappeared from fisheries, along with many of the fish stocks mismanaged under its assumptions. The United Nations Food and Agriculture Organization (FAO) estimates that almost 70 percent of the world's marine stocks are fully to heavily exploited, overexploited, or depleted and in need of urgent conservation and management (UNFAO 1992). In U.S. fisheries alone, 45% of all species are considered overharvested (Ruckelshaus and Hays 1998). As fish biologists have learned more about fish populations, they have found that most such populations (1) show widely ranging cycles of high and low abundance, (2) do not necessarily show a strong correlation between recruitment and number of adults present, and (3) do not necessarily show advance warning of impending population decline or crash from overexploitation (Hilborn, Walters, and Ludwig 1995). The decline may be sudden, and stocks may not recover to harvestable levels in the short term even when given complete protection.

The effects of overexploitation on targeted commercial species are not surprising, but the effects on nontarget species can be equally devastating. The removal of prey species may severely reduce the populations of predator species, and not of fish only, but also of birds and mammals. The clearest examples of this effect have been seen in the decline of Peruvian seabirds following the decimation of the offshore anchovy fishery, and the decline of sea otter populations off the California coast following overfishing of abalones (Agardy 1997).

Some cases of this type have had legal as well as biological ramifications. For example, in 1998, a coalition of environmental organizations sued the North Pacific Fishery Management Council under the Endangered Species Act for failing to protect critical foraging habitat for the Stellar sea lion (*Eumetopias jubatus*) by allowing unregulated pollock (*Theragra chalcogramma*) fishing in the sea lion's main foraging areas (Stump 2000). Lack of food had previously been identified as a primary cause of the decline in sea lion populations, and pollock is a principal prey species of sea lions. The plaintiffs argued that it made no sense to allow unregulated fishing in critical foraging habitat, and violated the ESA's directive that required "reasonable and prudent alternative (RPA) measures" be taken to avoid inflicting "adverse modification" on the critical habitat of a species. A U.S. district court agreed and ordered the National Marine Fisheries Service to revise its regulations. Exactly what regulations will be imposed on the pollock industry is still being debated among the parties involved, but the debate has shifted from whether or not a problem existed to what must be done to solve it (Stump 2000).

Because the removal of a prey species can cause population declines in the predator, the removal of the predator can cause changes in prey populations, and those changes do not always lead to uniform or long-term increases (Goeden 1982). Overexploitation disrupts equilibria of many populations (Agardy 1997), and can make them more susceptible to declines associated with environmental and demographic stochasticity, such that stocks may continue to decline even after take is restricted or stopped altogether (Lauck et al. 1998). The take of nontargeted species in commercial fishing also continues to be a serious problem despite concern, attention, legislation, and supposedly improved technologies. In some fisheries, such as shrimp, the discarded biomass of by-catch exceeds the targeted catch worldwide (Agardy 1997). Species such as sea turtles, dolphins, sharks, rays, and benthic organisms continue to be affected as by-catch species.

Causes of Marine Habitat Degradation

The destruction of marine habitats can occur through a variety of means, most of which are associated with commercial fishing. One of the most obvious and deadly is the use of explosives, such as dynamite, to harvest coral reef species. A single blast can devastate hundreds or thousands of cubic meters of coral reef, destroying not only individual fish, but also the structure upon which the community depends. Destruction of physical reef structures instantly eliminates what may have taken hundreds or thousands of years for marine organisms to build (Agardy 1997).

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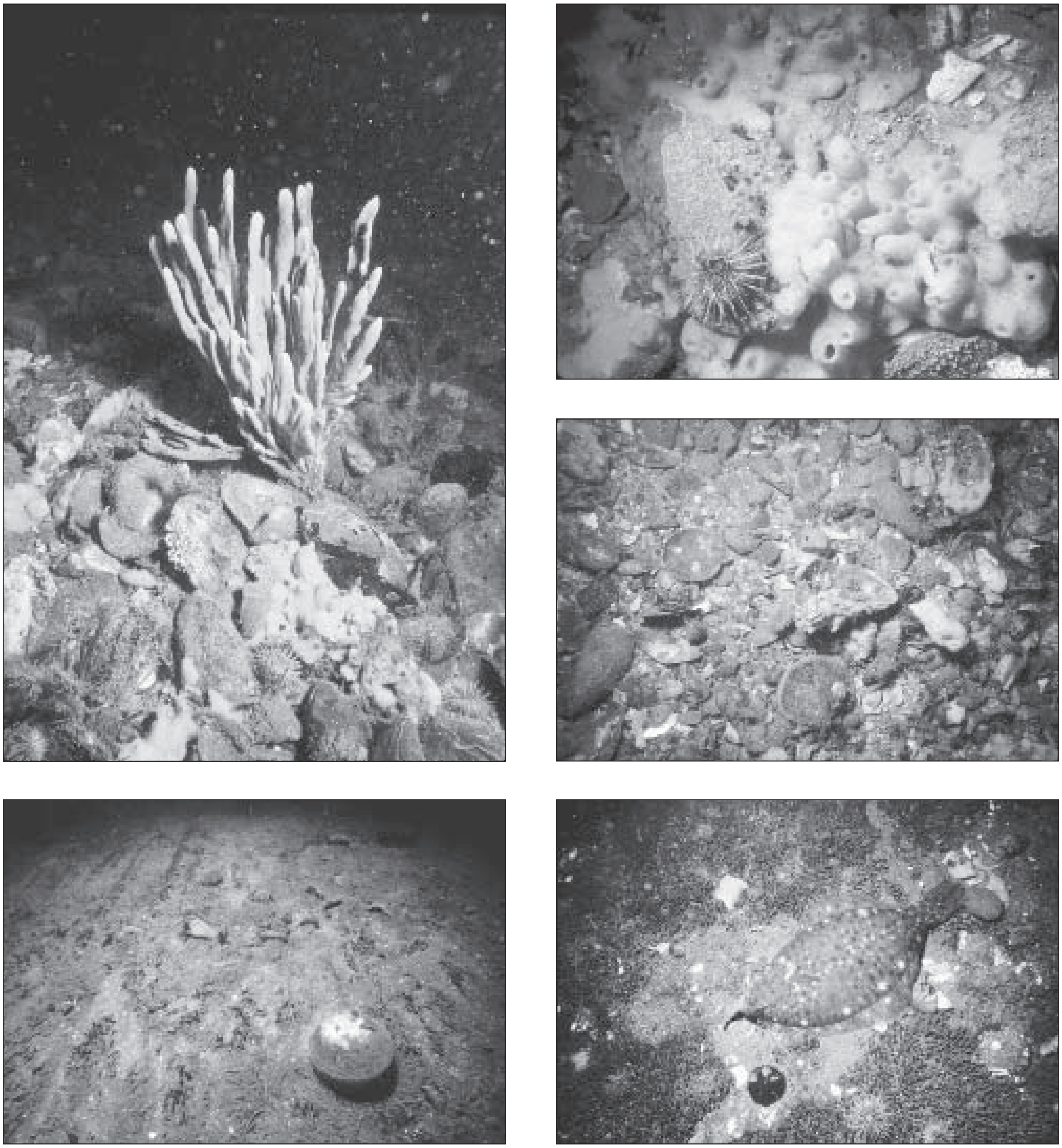

Figure 9.15
A portion of the Atlantic Ocean bottom before (top) and after (bottom) being swept by a trawling net. Prior to trawling, a complex and diverse community was present in and on the sediments, but trawling obliterated the community.
After Auster (1998).

The structure of benthic communities is significantly altered by the use of bottom trawling nets. Auster (1998) provides pictures of a site on the bottom of the Gulf of Maine off the east coast of the United States before and after bottom trawling (fig. 9.15). The top three photographs (before) reveal a complex and diverse assemblage of creatures, including tubeworms, sponges, and many other forms of life. The bottom two photographs (after) show the same spot after a trawl net was dragged across it. The complexity of the habitat has been obliterated, along with all its residents.

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Table 9.4 **A Classification of Fish Habitat Types on the Outer Continental Shelf of the Temperate Northwest Atlantic**

CATEGORY	DESCRIPTION	RATIONALE	COMPLEXITY SCORE*
1	Flat sand and mud	Areas with no vertical structure such as depressions, ripples, or epifauna.	1
2	Sand waves	Troughs provide shelter from current; previous observations indicate that species such as silver hake hold position on the downcurrent sides of sand waves and ambush drifting demersal zooplankton and shrimp.	2
3	Biogenic structures	Burrows, depressions, cerianthid anemones, hydroid patches; features that are created or used by mobile fauna for shelter.	3
4	Shell aggregates	Provide complex interstitial spaces for shelter; also provide a complex, high-contrast background that may confuse visual predators.	4
5	Pebble-cobble	Provide small interstitial spaces and may be equivalent in shelter value to shell aggregate, but less ephemeral than shell.	5
6	Pebble-cobble with sponge cover	Attached fauna such as sponges provide additional spatial complexity for a wider range of size classes of mobile organisms.	10
7	Partially buried or dispersed boulders	Partially buried boulders exhibit high vertical relief; dispersed boulders on cobble pavement provide simple crevices; the shelter value of this type of habitat may be lower or higher than previous types based on the size class and behavior of associated species.	12
8	Piled boulders	Provide deep interstitial spaces of variable sizes.	15

*Habitat complexity scores do not increase at a constant rate, but reflect cumulative effects of structural components added at each succeeding level.
After Auster 1998.

This vivid visual example of marine habitat destruction can be understood more generally through a conceptual model of the effects of fishing gear upon different marine habitats, such as might be found on a continental shelf. Consider eight different categories, ranging, at the simplest level, from flat sand or mud to the most complex, piled boulders (table 9.4). Auster (1998) assigned a "numerical complexity score" to each habitat category. Note that, as habitats become more complex, scores do not increase linearly. For example, category 6, pebble-cobble with sponge cover, receives 5 (not 1) additional points because it contains elements of all previous categories plus dense emergent epifauna. Category 7 receives 10 points for containing all the elements of category 6 plus 2 points for shallow boulder crevices and current refuges. Finally, category 8 receives an additional 3 points for its addition of deep crevices (Auster 1998). The effect of intensive fishing activity, primarily trawls and dredges, is to reduce habitat complexity by smoothing bedforms (habitat categories 1 and 2), removing epifauna (categories 3, 4, and 6) and removing or dispersing physical structures (categories 5, 7 and 8). Such a model predicts that the effect of fishing activity on habitat complexity is nonlinear (fig. 9.16). The more complex the original habitat, the greater the loss of complexity that results (Auster 1998).

Marine habitats are even more degraded from land-based sources. This indirect, but extensive degradation has multiple causative agents (table 9.5). Many of these, such as eutrophication, sedimentation, and thermal pollution, are proximity based relative to the source of the pollution, and thus have their greatest effects on coastal and estuarine environments. But others, such as radioactive wastes and persistent toxins, such as PCBs,

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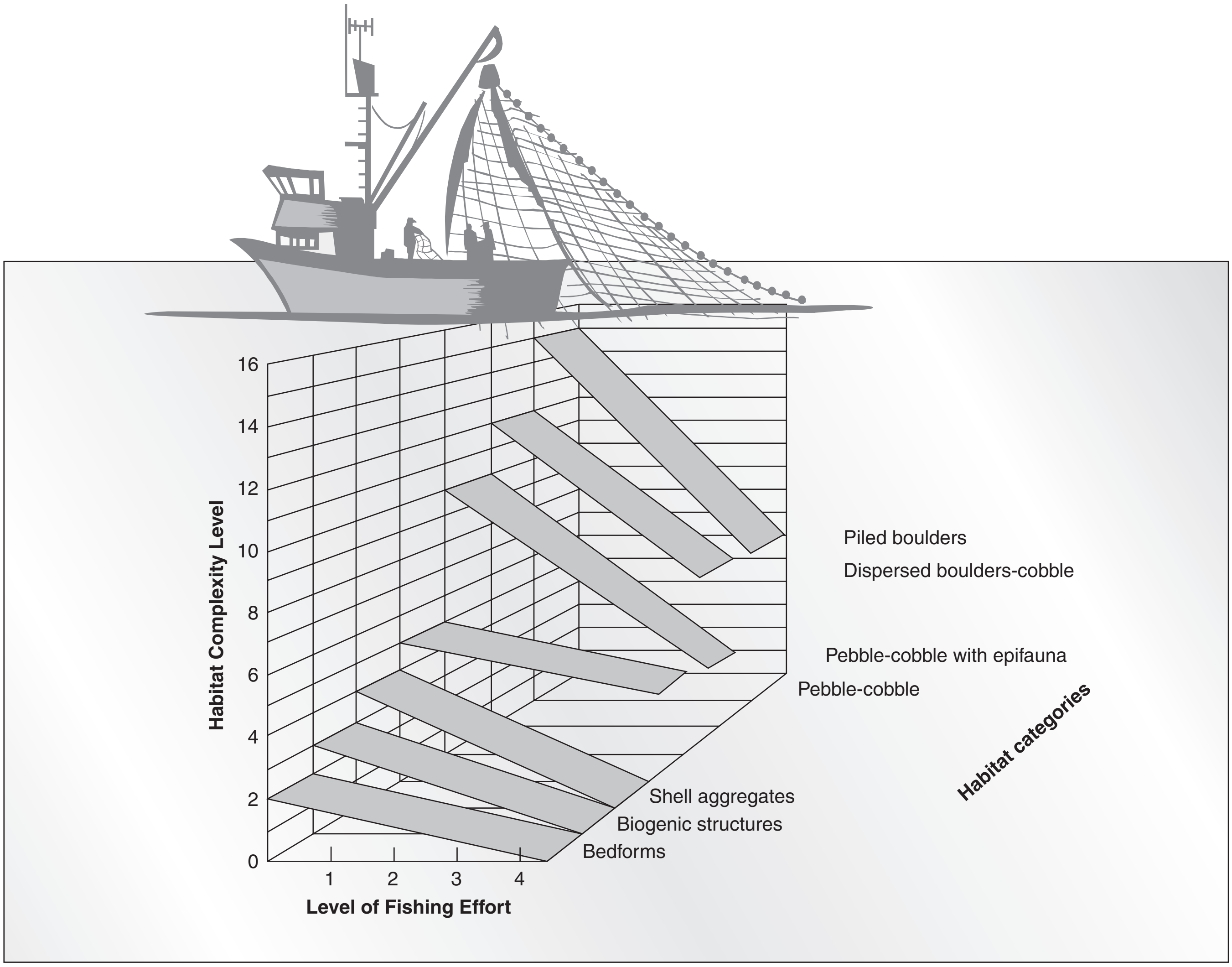

Figure 9.16
A conceptual model of the effects of fishing gear on seafloor habitat. Note that increases in fishing effort produce disproportionately greater reductions in habitat complexity in heterogeneous habitats than in simpler habitats.

Adapted from Auster (1998).

DDT, and similar or derivative compounds, travel long distances in ocean currents, or may be deposited far out to sea through atmospheric circulation patterns. Similarly, some kinds of military wastes, such as radioactive material or chemical weapons, may be deliberately transported long distances from shore before being deposited. These pollutants can cause habitat destruction and devastate populations thousands of miles from their source.

As in freshwater and terrestrial habitats, nonindigenous species pose a significant threat to the stability of marine communities and the habitats that support them. Historically, most invasions were by so-called fouling organisms that attached themselves to the hulls of ships (Ruiz et al. 1997). Today, as metal hulls have replaced wooden ones and the speed of ocean vessels has increased, these types of invaders have actually declined in importance, but four other means of invasion remain. These include (1) intentional releases of aquaculture, commercial or sport fishery, or bait species; (2) the connection of waterways through canals; (3) the release of species associated with the pet industry with other types of management practices; and (4) the release of organisms in the ballast water of ships. Of these, the last has often been the most destructive to native communities and habitats, perhaps because it is the least intentional yet introduces the largest volume of water into new areas.

The intentional releases of certain species have sometimes provided new and important sources of commercial and sport fishing or aquaculture. For example, the Pacific oyster (*Crassostrea gigas*) was transported from Japan to San Francisco Bay to establish an oyster fishery. Other planned introductions, however, have had unforeseen and sometimes devastating consequences. The connection of different marine environments by canals has allowed two-way invasions between

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Table 9.5 **Some Land-Based Pollutants That Degrade Marine Habitats and Ecosystems**

POLLUTANT	EFFECTS ON MARINE BIOTA
Herbicides	• Have serious effects at low concentrations. • May destroy or damage zooxanthellae in coral, free-living phytoplankton, algal, or seagrass communities. Basic food chain processes are destroyed or damaged.
Pesticides	• May selectively damage zooplankton or benthic communities (planktonic larvae are particularly vulnerable) and cause immediate or delayed death of vulnerable species. • May accumulate in animal tissues and affect physiological processes such as growth, reproduction, and metabolism.
Antifouling Paints and Agents	• May selectively damage elements of zooplankton or benthic communities. • Are prevalent in harbors, near shipping lanes, and in enclosed, poorly mixed areas with heavy recreational boat use.
Sediments and Turbidity	• May exceed or smother the clearing capacity of benthic animals, particularly filter feeders. • Reduce light penetration, likely to alter vertical distribution of plants and animals in shallow communities such as coral reefs. • May absorb and transport other pollutants.
Petroleum Hydrocarbons	• May cause local necrosis if organisms are briefly exposed, whereas long-term exposure eventually causes death. • Are detrimental to reproduction and dispersion. • Water-soluble hydrocarbons cause mucus production, abnormal feeding, changes in a wide range of physiological functions, and, with longer exposure, death. • Residual hydrocarbons may lead settling larvae to avoid affected areas, and thus block recolonization and repair.
Sewage and Detergent—Phosphates	• Have effects at very low levels. • Inhibit a wide range of physiological processes and increase vulnerability of affected biota to a range of natural and human-induced impacts. • Inhibit calcification (e.g., in corals and coralline algae).
Sewage and Fertilizers—Nitrogen	• Distort competition and predator/prey interactions in biological communities (i.e., coral reefs, which are characterized by low levels of natural nitrogen) because of increased primary production in phytoplankton and benthic algae. • Increased sedimentation because of increased detritus from planktonic communities. • Increased nutrient level in benthos from sedimentary organic material. • Favor the growth of some filter or detritus feeders (e.g., sponges and holothurians).
High- or low-salinity water—freshwater runoff, effluents (low-salinity water floats on top of water column; high-salinity water sinks, prior to mixing and dispersion)	• Species highly tolerant of the changed regime may alter biological communities, particularly in shallow, poorly mixed, or enclosed waters. • May affect settlement and physiology of shallow benthic and reef organisms. • May cause physiological stress.
High or low water temperature from industrial plant heating or cooling	• May cause physiological stress. • May affect settlement and physiology of shallow benthic and reef organisms.

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Table 9.5 *Continued*

POLLUTANT	EFFECTS ON MARINE BIOTA
Heavy Metals (e.g., Mercury and Cadmium)	• Accumulation has severe effects on filter feeders and species higher in the food chain. • May interfere with physiological processes such as the deposition of calcium in skeletal tissue. • May cause physiological stress.
Surfactants and Dispersants	• Most are toxic to marine biota. • Have synergistic effects when mixed with hydrocarbons: mixtures can be more toxic than individual components. • Can interfere with a wide range of physiological processes (e.g., photosynthesis).
Chlorine	• At low levels, inhibits external fertilization in some invertebrates (e.g., sea urchins). • Can be lethal to individual species.

Adapted from Kenchington 1990.

established communities in different areas, sometimes from radically different environments. Today the Mediterranean Sea has over 240 exotic species, and 75% are attributed to migration through the Suez Canal, primarily from the Red Sea (Ruiz et al. 1997).

The most extensive and often-used mechanism of invading species is through the ballast water of ships (Carlton 1985). One ship can carry more than 150,000 metric tons of ballast water for trim and stability, which it may dump in an estuary at the end of a voyage. In estuaries associated with major port systems, the amount of water dumped from foreign oceans can be staggering. For example, the port system of the Chesapeake Bay has been estimated to receive over 10,000,000 metric tons annually, and U.S. and Australian ports may receive over 79,000,000 metric tons each year. This amounts to more than 9 million liters of water per hour! At this rate of input, it is not surprising that estuaries appear to receive more exotic invaders than open oceans. For example, 212 nonindigenous species are known from San Francisco Bay, but fewer than 10 have been found along its adjoining outer coast (Ruiz et al. 1997).

Although invasions in terrestrial and freshwater systems are notorious for their devastating results on native species, marine communities appear to be more resistant to their effects. The U.S. Fish and Wildlife Service considers exotic species to be a significant cause of the decline of 160 native threatened or endangered species, but few of these are marine. In fact, there are relatively few recent extinctions of marine and estuarine species, and these extinctions did not appear to be caused by exotic species. Nevertheless, some exotic species have devasted native populations, marine environments, and commercial fisheries. The recent invasion of San Francisco Bay by the Chinese clam has altered marine communities in ways similar to the effects of the zebra mussel on freshwater systems. Chinese clams have become so numerically dominant, achieving densities of over 10,000 individuals/m^2, that they have replaced other benthic organisms, cleared plankton from overlying water, and eliminated seasonal plankton blooms (Snelgrove 1999). The invasion of the green crab (*Carcinus maenas*) along the northeastern U.S. coast has significantly reduced clam and mussel fisheries. A larger and more voracious predator than native U.S. crabs, the green crab can devastate local populations of oysters, clams, and other shellfish. The American comb jelly (*Mnemiopsis leidyi*) has unexpectedly contributed to a collapse of commercial fisheries in the Black and Azov Seas in Europe because it competes more effectively for the same food source (copepods) as native commercial fish (Ruiz et al. 1997).

Marine invasions are not as well studied or understood as those that occur in terrestrial habitats or in fresh water, so it is difficult to identify general trends or effects common to most invaders. There is some evidence that invading species decrease the abundance and evenness of remaining native species, decrease variation among communities (reduction in beta diversity, chapter 4), and alter gene flow within and among communities (Macdonald et al. 1989; Drake 1991; Ruiz et al. 1997). Overall, marine environments around island areas and estuarine environments appear to be more susceptible to invasion than do communities in open oceans.

The array and variety of threats to marine habitats means that there is no single strategy that can address all problems at once. However, one emerging strategy designed to address multiple threats is the concept of the marine protected area (MPA).

Marine Reserves: Management Context, Goals, and Strategies

All parks and reserves face the problem of defining appropriate biological boundaries that ensure the persistence of what the park is established to preserve. However, this problem is greater in aquatic environments, particularly in marine environments.

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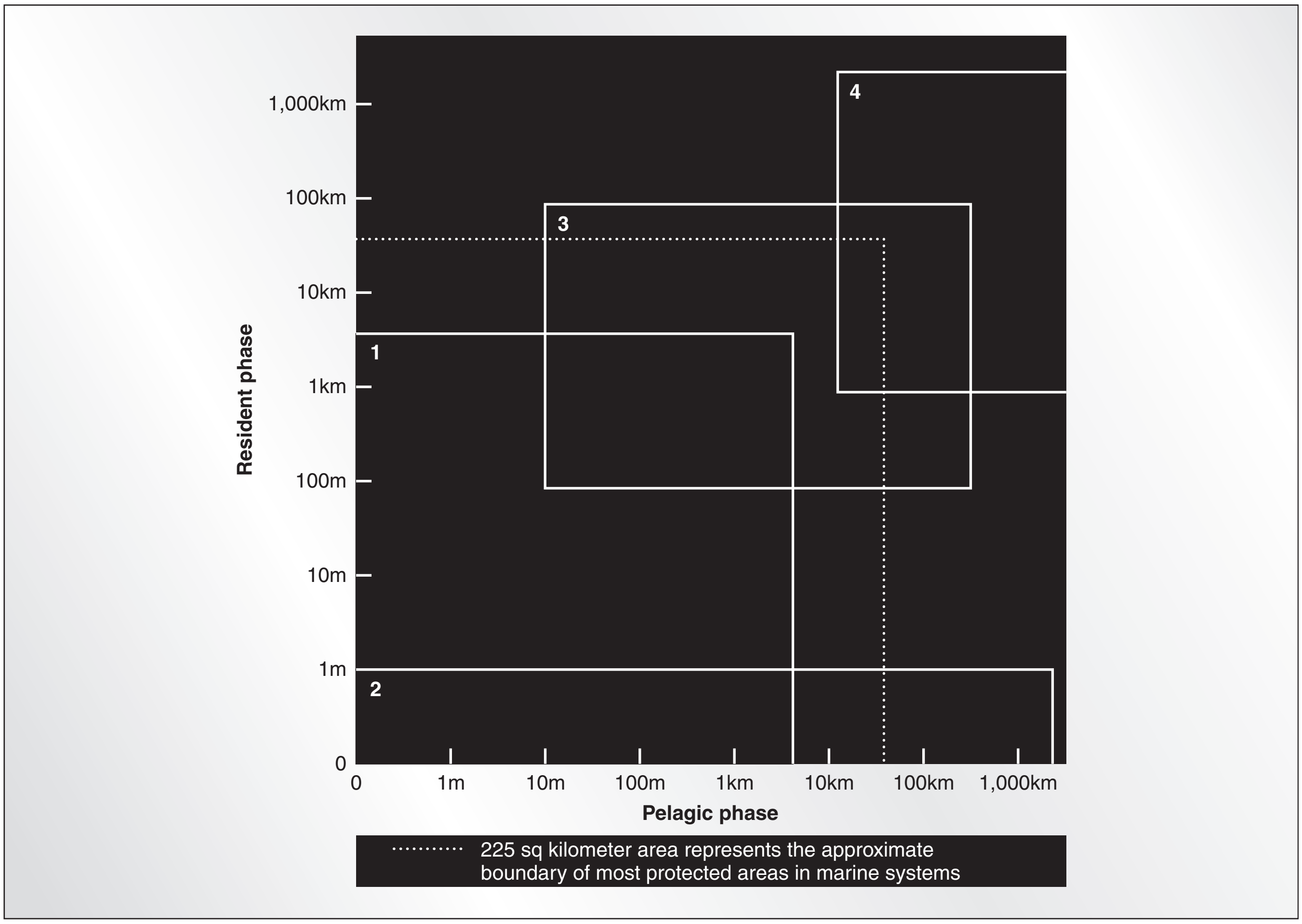

Figure 9.17

Four categories of life cycles characteristic of marine creatures, with respect to spatial scale. Box 1 represents species with no planktonic (drifting) phase and fixed or restricted movement in their adult phase. Box 2 represents species in which one phase is fixed and the other is planktonic or pelagic (open ocean). Box 3 represents species in which adults have large, defined territories but larvae are planktonic. Box 4 represents species in which phases of life are all planktonic or all pelagic.

After Kenchington (1990).

Land preserves are essentially two-dimensional, defined by their length and width on the earth's surface. Air may be a medium for flight and some passive dispersion, and contains essential elements and compounds for respiration and photosynthesis, but it is also relatively homogeneous. In contrast, marine reserves are three-dimentional, and their third dimension—the water column—is much more dynamic and critical to the marine community than is air in a terrestrial environment. In addition to plant and animal communities on the ocean floor, the water column itself contains communities of its own, perpetually drifting or swimming in and through it. Spores, eggs, and young of even the most sedentary species must use the water column for reproduction, dispersal, and development (Kenchington 1990). At most times and places, most photosynthesis, respiration, and transport of matter and energy take place within this water column, not on the seabed. Thus, in prescribing the boundaries of a marine reserve, one must consider carefully the properties of the water mass within such boundaries, because on these properties all life within the mass depends.

The water mass has enormous effects on issues of reserve scale. During early phases of development, most marine species have far greater dispersal distances than terrestrial species. Some remain highly mobile throughout life, whereas others become essentially immobile as adults. Kenchington (1990) identifies four basic life-history categories of marine creatures relevant to the question of spatial scale (fig. 9.17): (1) species with fixed or restricted movement in their adult phase, but no planktonic (drifting) phase (box 1); (2) species in which one phase is fixed and the other is planktonic or pelagic (box 2); (3) species in which adults have large, defined territories, but larvae are planktonic (box 3); and (4) species in which all phases of life are either planktonic or pelagic (box 4).

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POINTS OF ENGAGEMENT—QUESTION 2

Make a copy of figure 9.17. Now, with a dotted line, mark out a square within the figure, beginning at the origin of the *x* and *y* axes, that would correspond to a 100 km^2 (10 km $\times$ 10 km) marine reserve. Which category or categories of creatures are fully protected during all life-history phases within this hypothetical reserve? Which are only partially protected? Which category is least protected? What are the implications of your findings?

Marine conservation legislation and marine reserves are designed to meet three goals simultaneously: (1) protect marine and coastal biodiversity, (2) ensure that marine productivity is not undermined by uncontrolled exploitation, and (3) focus efforts for restoration of vital areas that may be presently degraded but have potential to support healthy marine ecosystems in the future (Agardy 1997). To these ends, marine reserves have been established worldwide with a variety of names, jurisdictions, and specific purposes. Within these reserves, areas closed to all types of marine fishing and harvesting are often designated as "harvest refugia" or "no-take zones." These are generally designed to protect a particular commercial stock or group of stocks from overexploitation. At large scales, "biosphere reserves," administered by the United Nations Educational, Scientific, and Cultural Organization (UNESCO), are usually divided into three zones. "Core" reserves are areas with little or no harvesting or other activities, "buffer" areas are those where limited harvest and other activities are permitted (Agardy 1999), and "transition" areas are zones that are least protected, and are administered with regulations most like those outside the reserve (Sobel 1993). At small scales, more limited reserves may be established to achieve a more limited set of conservation objectives, or even only one.

Efforts to establish marine reserves have varied in effectiveness according to region and country. There are 135 legally protected marine and coastal areas in the Greater Caribbean Basin alone (Dixon, Scura, and van't Hof 1995); France has 5 fully operational reserves; Spain has designated 21; and Italy has established 16. The United States has 12 designated marine reserves, administered under the National Marine Sanctuary Program (NMSP) and officially known as National Oceanic and Atmospheric Administration (NOAA) Marine Sanctuaries. The U.S. program has been criticized because its reserves are considered too small (less than 1% of U.S. territorial waters) and unprotected (less than 0.1% are no-take areas) (Agardy 1999). But the United States has established large marine reserves off the Florida Keys and the central California coast, and the NMSP has demonstrated a strong commitment to reserve persistence and effective protection. Within this variety of management goals, strategies, and national efforts, we can examine some specific case histories of individual marine reserves to better understand their role in conservation.

Ecosystem-Level Protection: Australia's Great Barrier Reef Marine Park

One of the best examples of a large marine reserve is Australia's Great Barrier Reef Marine Park (GBRMP), one of the world's premier protected areas, and part of the Biosphere Reserve and World Heritage Site programs. The Great Barrier Reef itself is a vast complex of some 2,900 individual reefs and 250 cays (low islands or reefs made of sand or coral) stretching along the continental shelf of northeast Australia from just south of the Tropic of Capricorn to the Torres Strait. The system possesses 71 genera of coral alone. The Great Barrier Reef was relatively inaccessible to humans until the 1960s. The GBRMP that attempts to preserve it is in many ways unique among marine preserves. The preserve was not established to stop or solve an existing problem or degradation of the reef, but was actually established in anticipation of future problems. In 1967, a private Australian firm filed an application for permission to take coral limestone from a part of the reef for use in the production of agricultural lime. The Wildlife Preservation Society of Australia perceived this application as setting a precedent for dangerous and destructive processes that could eventually destroy the reef. With other conservation groups joining the lead of The Wildlife Preservation Society, public outcry led to the refusal of the permit application by the provincial government (Queensland). Further controversies over offshore oil drilling in the reef area and outbreaks of the crown-of-thorns starfish (*Acanthaster planci* which destroyed reef corals) led to legislation that established the GBRMP (Kenchington 1990).

Today the GBRMP is a vast multiple-use area managed by establishing different zones within the park for different uses, through which it has successfully accommodated a variety of user groups (Agardy 1999) (fig. 9.18). However, even in this exemplary park there are serious problems. For all its size and jurisdictional power, the GBRMP authority that manages the park has no control over land-based inputs that pose significant threats to its coral reefs, commercial fish stocks, and endangered species. Its jurisdiction stops at the shoreline, and it cannot stop influxes of land-based sediments and chemical pollutants that pour into its aquatic system (Agardy 1999).

Tourist-Recreation Marine Reserves: The Bonaire Marine Park

Marine reserves are not the exclusive domain of large nations, nor are they established exclusively to protect fisheries or commercial stocks. The tiny Netherlands Antilles off the northern coast of Venezuela established the Bonaire Marine Park (BMP) around the island of Bonaire in the early 1980s. The Bonaire Marine Park is neither a vast, multiple-use area like the GBRMP nor a strictly no-take, closed marine reserve for scientific research and conservation. It belongs to a unique category that could be called "tourist-recreation reserves."

The BMP was established primarily to preserve the beauty of local marine resources for the enjoyment of snorkel and scuba divers, a mainstay of the island's tourist-driven economy (Dixon, Scura, and van't Hof 1995). Nearly 17,000 scuba

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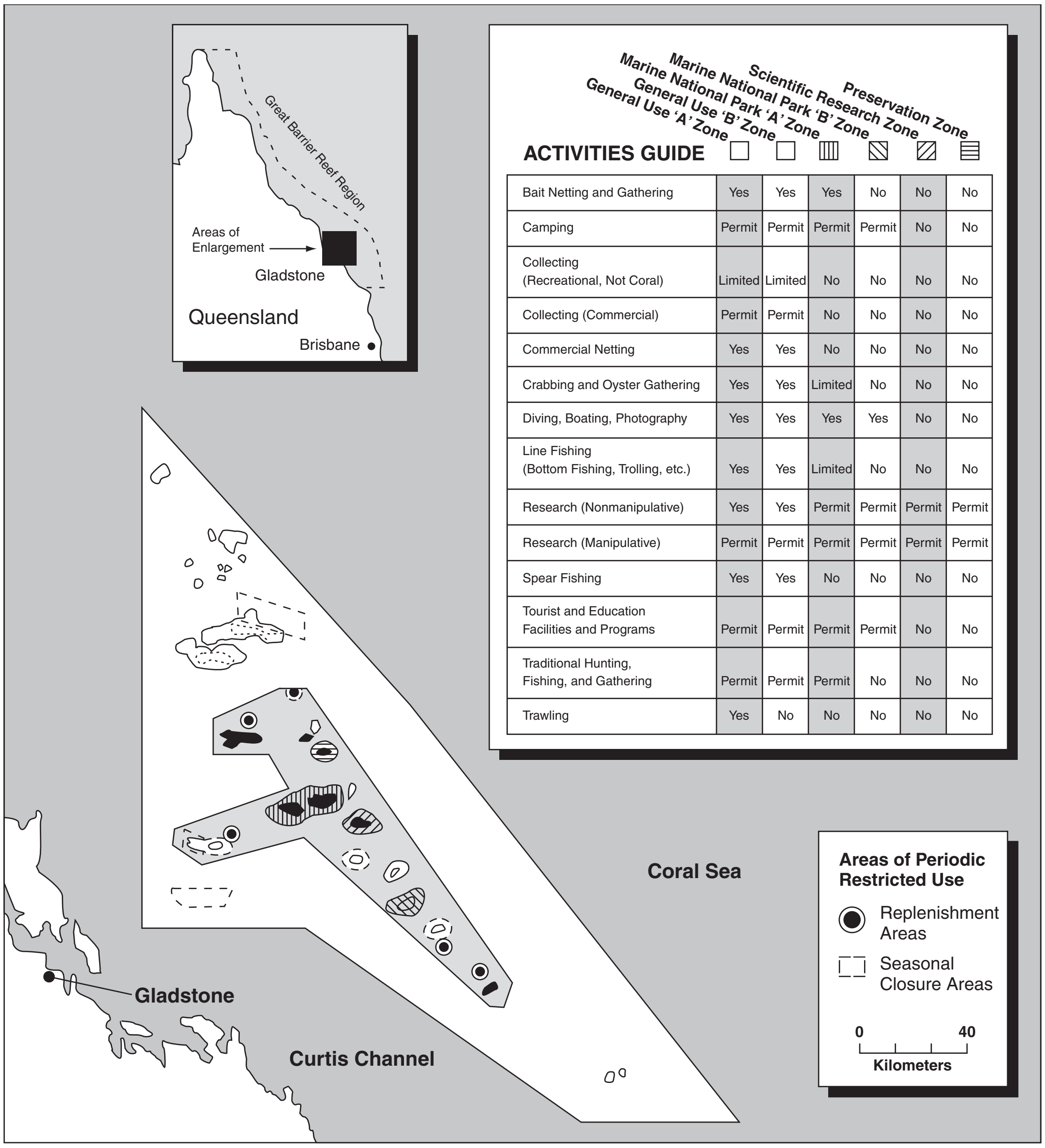

ACTIVITIES GUIDE	General Use 'A' Zone	General Use 'B' Zone	Marine National Park 'A' Zone	Marine National Park 'B' Zone	Scientific Research Zone	Preservation Zone
Bait Netting and Gathering	Yes	Yes	Yes	No	No	No
Camping	Permit	Permit	Permit	Permit	No	No
Collecting (Recreational, Not Coral)	Limited	Limited	No	No	No	No
Collecting (Commercial)	Permit	Permit	No	No	No	No
Commercial Netting	Yes	Yes	No	No	No	No
Crabbing and Oyster Gathering	Yes	Yes	Limited	No	No	No
Diving, Boating, Photography	Yes	Yes	Yes	Yes	No	No
Line Fishing (Bottom Fishing, Trolling, etc.)	Yes	Yes	Limited	No	No	No
Research (Nonmanipulative)	Yes	Yes	Permit	Permit	Permit	Permit
Research (Manipulative)	Permit	Permit	Permit	Permit	Permit	Permit
Spear Fishing	Yes	Yes	No	No	No	No
Tourist and Education Facilities and Programs	Permit	Permit	Permit	Permit	No	No
Traditional Hunting, Fishing, and Gathering	Permit	Permit	Permit	No	No	No
Trawling	Yes	No	No	No	No	No

Figure 9.18
Management zones in the Capricornia section of the Great Barrier Reef Marine Park, Australia.
After World Resources Institute et al. (1992).

divers visited Bonaire in 1991, and the number has been increasing at the rate of 9 to 10% annually. To accommodate divers within the marine park, Bonaire established a "snorkel trail," as well as a series of freestanding platforms throughout the reef area. Studies of the park show that tourism and conservation are interactive joint products of the marine park, but that use levels by tourists cannot increase indefinitely, even in a relatively "nonconsumptive" activity like diving. A "threshold" level exists in the park for diving pressure on reefs. Underwater areas around platforms that receive 4,000 to 6,000 dives per year begin to show signs of stress and wear, and both coral cover and species diversity begin to decline at this point. However, the distribution of funds from diving creates an environment that produces pressure to increase the number of divers. For most divers, diving at Bonaire is part of a prepaid travel package arranged with agents in the United States and Europe. As part of the arrangement, the diver receives "vouchers" that cover most expenses such as lodging, transportation, and food. Divers who come under these conditions often spend very little additional money. The locals are reimbursed for a portion of the vouchers by sending them back to the U.S. or European agents, but only after large commissions are deducted. As a result, income to locals from diver visitation may be marginal, and the economic benefit of each additional diver is important to

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residents. However, if increasing stress leads to a loss of world-class diving experiences at Bonaire, fewer visitors will come and total income will decline. Assuming that diving will continue at least at its present rate (the local economy has few other sources of income beyond subsistence agriculture and fishing), current suggestions to maintain the quality of the marine park include better distribution of divers, better diver education and training in "diver etiquette," and better regulation of underwater activities. However, as Dixon, Scura, and van't Hof (1995:142) noted, "These management measures do not *increase* the tolerance of marine systems to stress, rather they help to distribute the burden more evenly across the ecosystem. Such measures require both money and legal authority." Greater legal authority is possible, but local citizens have been reluctant to grant the park more regulatory authority than it already has. Locals have been especially reluctant to yield greater authority to regulate diving operators and cruise boats in the park, practices through which many local citizens make their living. Increasing revenues from divers may be an easier matter, as previous amounts charged to divers (U.S. $10) are only about half what diver surveys indicate as their average willingness to pay ($20) (Dixon, Scura, and van't Hof 1995).

The Bonaire Marine Park illustrates the dilemma of conflicting values that was addressed conceptually in chapter 3 (Values and Ethics in Conservation). If the real value of the marine resources is viewed as economic rather than intrinsic, then the resources themselves may be degraded even as economic revenues rise from fees for seeing and photographing these resources. It is possible that such degradation might have no adverse economic effects because divers would gradually become accustomed to the decreasing quality of the diving experience. Some marine conservationists have advocated that tourism and recreation should become the primary uses of the marine environment, the basis for appreciation and enjoyment of marine environments, and the foundation of long-term social and economic benefits for the local, national, and global community (Kenchington 1990). The experience of the Bonaire Marine Park shows that this optimism is premature, or perhaps misplaced altogether. Tourism can have a destructive effect on marine populations and habitats, and recreational use that is not well planned will lead to degradation of valued resources, conflicts between conservation values and economic interests, and little benefit to individuals in the local economy. In contrast, properly planned ecotourism can move beyond conflict, and even coexistence between conservation and economics, to a symbiotic relationship in which local citizens take responsibility and ownership of the resource and its values, marketing opportunities to enjoy the resource in profitable but nondestructive ways (Kenchington 1990). But in order for this to happen, practical management steps must be taken: (1) the use of the resource, even if nonconsumptive, must be restricted to a level that the resource can sustainably support; (2) the users must be optimally dispersed to avoid concentrations of use that could be destructive to the resource; and (3) where possible, the resource sites must be "hardened" by facilities and supporting structures that allow the sites to bear the level of use allowed without degradation.

Tourism and recreation will grow in importance as uses, values, and generators of economic wealth in human communities associated with marine environments. However, tourism and recreation do not exhaust the potential uses of marine resources or meet the needs of human populations for food. Ultimately, marine reserves may have an important role to play in commercial fishing as well as in tourism and research.

Marine Protected Areas and Commercial Fisheries

In 1982, most nations of the world adopted the conventions established at the United Nations Third Conference on the Law of the Sea (UNCLOS III). The most radical change in international law that emerged from this convention was the extension of national jurisdiction over territorial waters from the historic 12-nautical-mile standard to 200 nautical miles, a move estimated to place 90% of marine fishery resources within the jurisdiction of individual nations (Lauck et al. 1998). These enlarged areas of national jurisdiction, or exclusive econonic zones (EEZs) (Kaitala and Munro 1995) were seen as the saviors of international marine fishing. With this change in international maritime law, it was optimistically believed that the oceans' commercial fishing stocks would avoid becoming an example of Hardin's "tragedy of the commons" (Hardin 1968). More conservative harvesting policies of individual nations, backed by the power of international law, would lead to wise use based on national interest and local ownership of the fishery resource, resulting in long-term sustainability of marine fishery harvest.

These happy, hopeful visions have yet to come true. Despite the extension of territorial limits to 200 nautical miles and more exclusive use of fisheries stocks by individual nations, commercial fisheries have collapsed all over the world. One of the saddest and most dramatic failures of UNCLOS III occurred in what was historically one of the world's largest and most dependable commercial fisheries, the cod fishery of the Grand Banks of Newfoundland. In the early 1900s, the northern cod fishery was producing annual harvests of approximately 250,000 tons (Ruckelshaus and Hays 1998), but by the 1980s declining catches provoked the Canadian government to enforce drastic cuts. The stock still failed to recover, so the Canadian government instituted a 2-year moratorium on cod, but cod continued to decline even after the moratorium was in place. By 1996, the moratorium had become permanent (Lauck et al. 1998).

Lauck and colleagues (1998) argue that the answer to the problem of sustainable commercial fisheries may be the marine reserve. Far from being simply a means to enhance tourism or to preserve unique ecosystems or rare species, they assert that marine reserves should become the foundation of a new form of fisheries management that is based on a radical change of perspective. Namely, they argue we should abandon the concept that every available commercial fish stock should be exploited optimally and replace it with the strategy of "bet hedging." In other words, fisheries science should assume that high levels of uncertainty are a permanent and persistent dimension of estimating the size of fish populations and their future trends. If high uncertainty is taken as a given, then the optimal strategy is not to attempt to harvest a population wherever it occurs, but to harvest *some* of the populations at the predicted (but uncertain)

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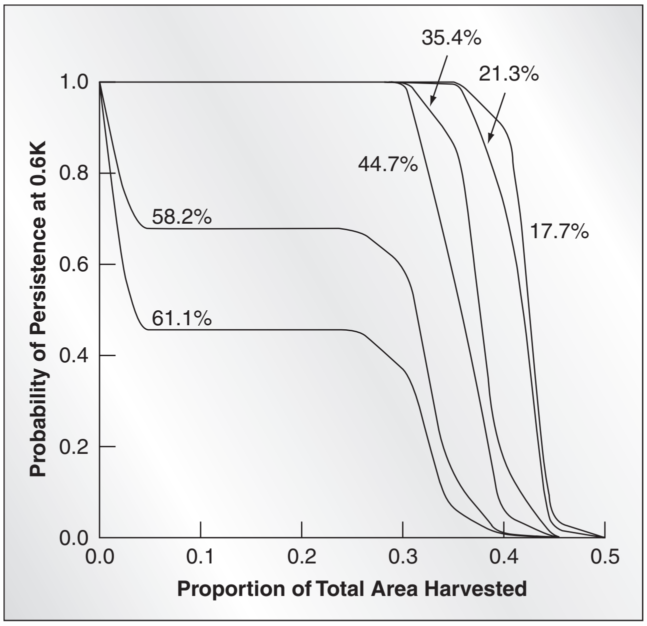

Figure 9.19

The probability of a fish stock remaining above 60% of its carrying capacity for 20 years depends on the fraction of area available for harvesting. In this simulation model, when more than 30% of the stock's total area is available for harvesting (i.e., outside the marine reserve), the probability of maintaining a population size that is $> 0.6\ K$ (K = carrying capacity) drops rapidly. Each line represents a different value for coefficient of variation associated with the average harvest (*CV* is defined as the standard deviation of the harvest fraction/mean of the harvest fraction).

After Lauck et al. (1998).

optimal level and leave a large portion unharvested as a protection against unforeseen declines in the harvested stock.

Lauck and colleagues articulate their ideas quantitatively in a model whose goal is to retain a fish population at more than 60% of its carrying capacity for at least 40 years (fig. 9.19). Through a series of equations that permit estimation of the proportion of the population available for harvest outside a closed area, they model the probability that the population could persist for the specified periods and levels. They assumed that half the available population outside the reserve was captured every year, but with coefficients of variation (the measure of uncertainty about the mean) assigned at six levels from 18 to 61%, and they varied the fraction of the total area available for harvesting (i.e., the size of the marine reserve) (Lauck et al.1998).

The results were dramatic. Even with a moderate amount of variation in the catch ($CV < 50\%$), the probability of the population persisting for 40 years dropped drastically when the amount of exploitable area became greater than 30%. If the catch percentage was more variable, the probability of the population's persistence was less than one (not certain) even if only 5% of the area was available for harvest. The probability of successfully protecting the stock of fish increased in the model if the harvest was reduced to lower levels, and at lower levels, more of the total area could be made available to fishing.

Two conclusions emerged from the model. First, "a reserve can simultaneously lead to stock protection and a higher level of catch," and "it is possible to maximize catch while protecting the stock" (Lauck et al. 1998). That is, Lauck and colleagues conclude that marine protected areas provide the "simplest and best approach to implementing the precautionary principle and achieving sustainability in marine fisheries" (Lauck et al. 1998).

Empirical data from marine reserves support their value in restoring fish populations. Russ and Alcala (1996) compared density and biomass of large predatory fish at two small marine reserves in the Philippines with two similar control sites. They found that the longer the reserve was protected from fishing, the greater the increase in density and biomass of large predatory fish (fig. 9.20). But they also noted that unregulated fishing within the reserves, even for a short time, eliminated gains in biomass and density that had taken years to achieve. Russ and Alcala (1996) conclude that "funding in support of marine reserves as fisheries management tools must be long-term, and . . . management measures used to implement and maintain marine reserves must be robust in the long term, i.e., on scales of decades."

POINTS OF ENGAGEMENT—QUESTION 3

Examine figure 9.21. Points above the diagonal line indicate species that increased in abundance after establishment of the reserve. Points below indicate species that were less abundant after reserve establishment. In your opinion, do these data support the assertion that marine reserves lead to increased populations of fish and invertebrates? Why or why not?

Not all marine areas will be placed in marine reserves. Most marine populations and their associated habitats will continue to be exploitable in open seas or in unprotected territorial waters. An alternative strategy to relieve the twin pressures of exploitation and degradation on these systems is that of mariculture, the intensive commercial cultivation of certain species in limited areas.

Mariculture—The Case History of the Giant Clam

Some forms of mariculture, such as the pearl industry and oyster farming, have been practiced successfully for centuries. Other forms are relatively recent developments. However, given an ever-accelerating human demand for marine creatures as food and for other products such as jewelry or decoration, it is certain that maricultural techniques will increase in size, scope, and diversity in the next decade. Like intensive agriculture in terrestrial landscapes, mariculture concentrates disturbance of the environment; increases, intensifies, and concentrates pollution; and reduces systems to the lowest possible levels of species diversity and ecological complexity, effectively eliminating most ecosystem services. Like intensive terrestrial

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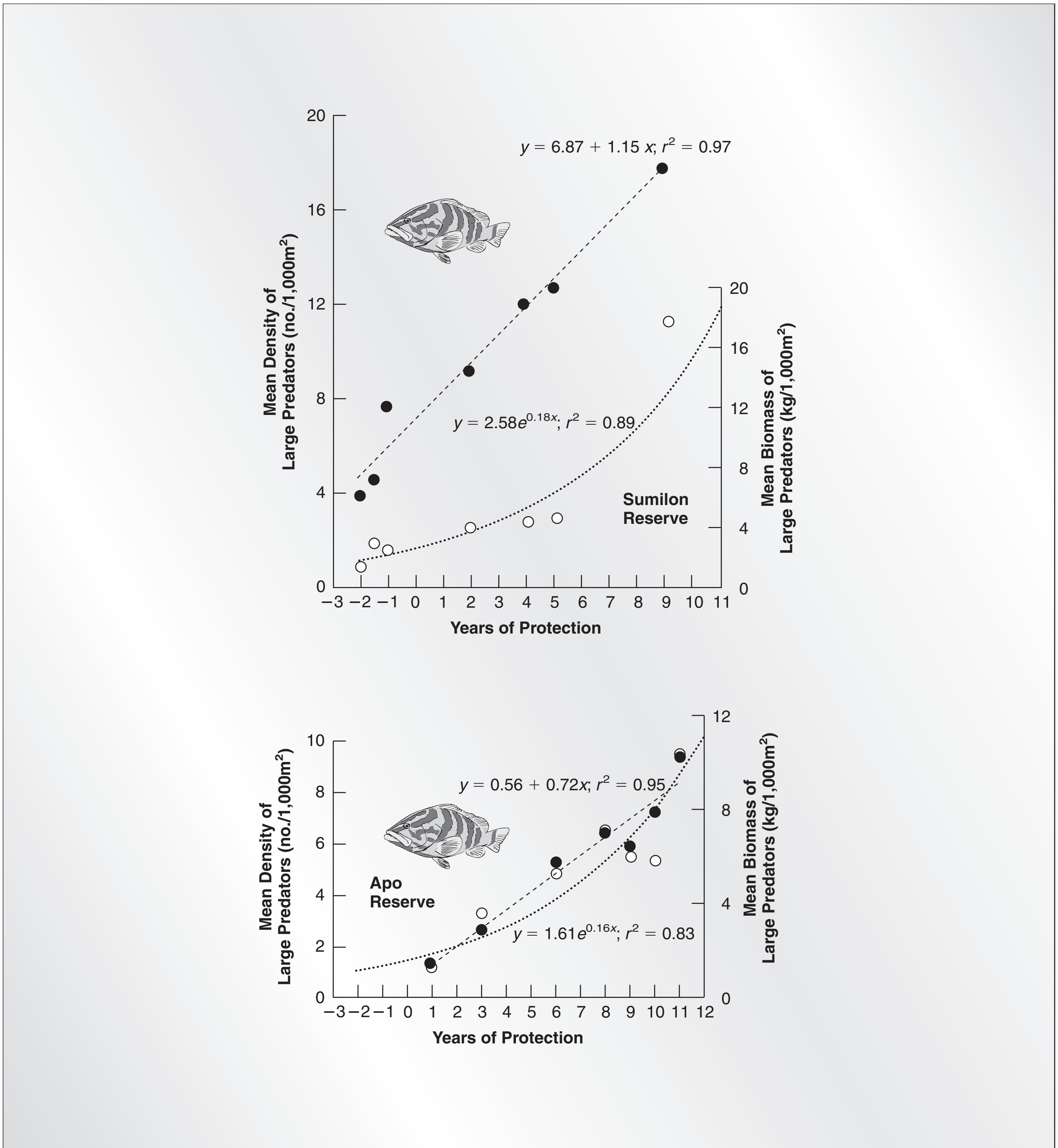

Figure 9.20

Changes in density (solid circles, dashed lines) and biomass (open circles, dotted lines) of large predatory fish at two small marine reserves in the Philippines, compared with two similar control sites. The longer the reserve was protected from fishing, the greater the increase in density and biomass of large predatory species.

Adapted from Russ and Alcala (1996).

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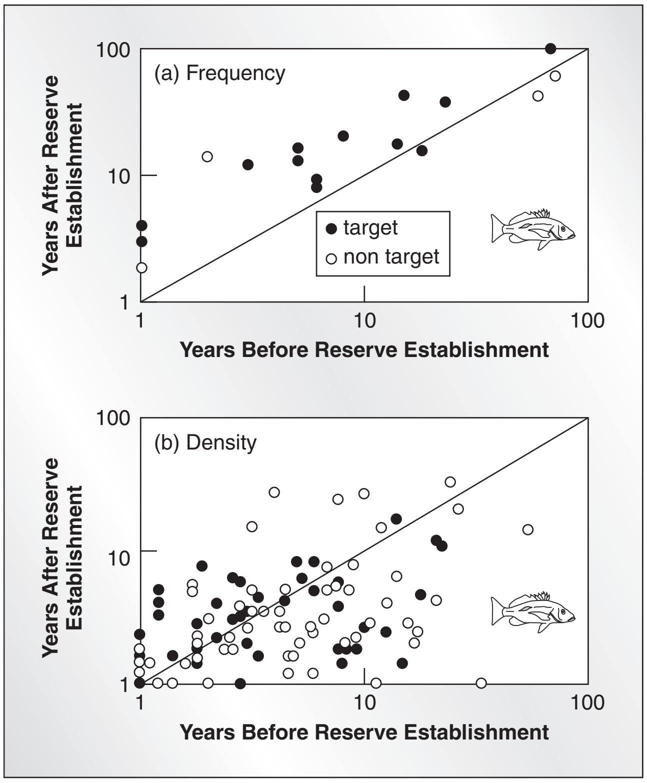

Figure 9.21
(a) Frequency of occurrence and (b) density of commercially targeted (solid circles) and nontargeted (open circles) of fish species before and after the establishment of marine reserves. Symbols above the diagonal lines indicate species that were more frequent or had higher densities after reserve establishment.

Data compiled and figures adapted from Ruckelshaus and Hays (1998).

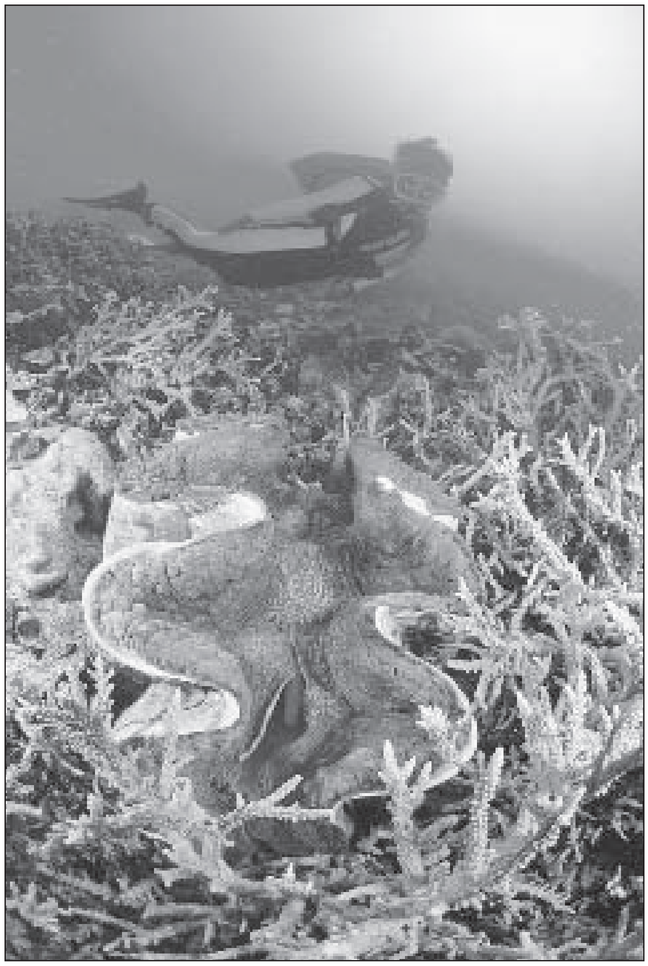

Figure 9.22
The giant clam (*Tridacna gigas*), an endangered species that has responded favorably to intensive mariculture.

agriculture, however, mariculture can also provide large per area, per effort yields of food and other products from the creatures subjected to its management. Because mariculture can be so effective and efficient, it can reduce the need to disturb or exploit natural systems and their populations, which may not be resilient to disturbance or exploitation even at very low levels. The case history of the giant clam illustrates the potential advantages of mariculture.

Giant clams (*Tridacna* spp. and *Hippopus* spp.) include nine species of marine clams that live in shallow tropical and subtropical waters, often on coral reefs, in the Indo-Pacific, primarily in the Indo-Malay region (fig. 9.22) (Lucas 1997). Only one species, *Tridacna gigas,* could truly be called “giant,” having a maximum shell length of 137 cm and a mass of about 500 kg (Lucas 1994). Other species range from 15 to 50 cm in length and average about 15 kg in weight. Nevertheless, one adult of even the smallest species would amply fill the average dinner plate, and a high demand for giant clams as food leads many to wind up there. Giant clams are limited to shallow waters because they live in a symbiotic relationship with microalgae known as zooxanthellae. The zooxanthellae, which are photosynthetic, use the clam’s mantle as a point of attachment, and from this substrate transfer some of the organic products of photosynthesis to their clam hosts. The clam fulfills its part of the symbiosis not only by acting as the substrate for the algae, but also by providing inorganic nutrients to the zooxanthellae and exposing them to sunlight in the shallow waters. The relationship can be considered essential for both organisms because the clam obtains many nutrients from these algae (Lucas 1997).

Because of their large size, their high value as food, and their accessibility in shallow waters, giant clams have been heavily exploited. This has led to a ban on international trade in clam products, bans on fishing for giant clams in marine reserves, limits on collection effort and harvestable size of clams outside of reserves, aggregation of remaining populations to facilitate reproduction, and replenishment of wild stocks with cultured clams. It is these “cultured clams” that deserve a more detailed examination.

After fertilization, the planktonic clam eggs are dispersed passively by ocean currents. Upon hatching, the clams develop into a free-swimming trochophores (fig. 9.23), which, in turn,

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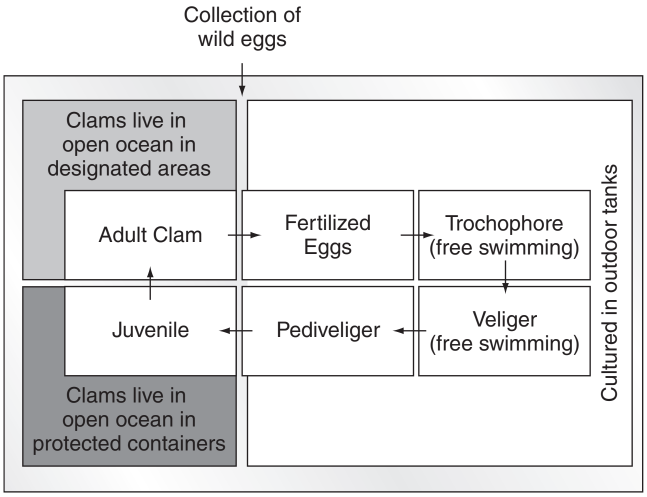

Figure 9.23
The life cycle of the giant clam (*Tridacna gigas*).

develop into small, filter-feeding, bivalved larvae called veligers. After increasing in size and developing a prominent foot, the veligers settle out of the current onto a reef surface, where they will grow and metamorphose. Although the clam may move slightly after settling, its initial location is likely to be its habitat for life.

Clam mariculture makes use of this life-history strategy by collecting eggs from wild clams or, more often, using eggs of existing domestic stock, and maintaining the hatching, larval, and juvenile stages in outdoor tanks. Juveniles at larger stages are moved into protective containers in the ocean, and larger individuals are later cultured without protection in the open sea. Amazingly, the mariculture of giant clams has no deleterious environmental effects. Even the feces produced by clams at high densities are so packed with algae (recall the clam's symbiotic relationship with the zooxanthellae) that they are rapidly and readily consumed by plankton-feeding fishes that take up residence, in abundance, around the clam colonies.

The mariculture of giant clams offers an environmentally friendly way to gain valuable resources from a fragile environment, the coral reef, while at the same time providing the means to supplement wild populations of clams with individuals raised in captivity. However, even this apparent success story cannot be accepted uncritically. Like sea turtle farming (chapter 3) (Ehrenfeld 1992), the mariculture of giant clams has drawbacks, some of which are the fruits of its own success. If effective, the increased supply of giant clams from mariculture can fuel increased demand for giant clams as food and ornaments, and encourage mariculture operators to remove additional quantities of eggs and adult clams from wild populations. In a climate of higher demand, pressure will increase to take clams directly from wild stocks. Consumers would not know the difference, and wild clams could be harvested with only a fraction of the time and effort needed to raise clams by mariculture. Poaching would become attractive, especially to individuals in the local culture who possess the skill to collect giant clams on their own. This last objection has been addressed, at least in part, through the development of a village-based, clam farming program in the Solomon Islands by the International Centre for Living Aquatic Resources Management Coastal Aquaculture Centre (Lucas 1997). Local villagers own and work in all stages of the mariculture enterprise, receiving the profits and sharing the risks directly. However, not every area where clam mariculture is practiced can expect to gain this degree of local ownership. In those cases, the potential and stimulus for poaching giant clams could be high.

Multiple and Conflicting Jurisdictions over Marine Resources

Lamenting the current state of marine environmental law and policy, W. M. von Zharen of the Texas Institute of Oceanography wrote, "the present management of the marine ecosystem is based on a series of regimes that are directed at the various parts rather than the whole and that are, as such, ineffectual" (von Zharen 1999). Marine conservationist Elliot Norse agreed, noting that a successful marine conservation strategy must be "cross-sectoral, embracing all categories of marine ecosystems and species, all types of human use, and all sources of threats" (Norse 1993:281). As we have already explored in our discussion of law and policy (chapter 2), international and national laws, and their respective interests, are often at odds in the conservation of marine resources and habitat. National jurisdictions over territorial waters, for example, do not always coincide with the distributions and movements of commercial fish populations, leaving these stocks vulnerable to depletion by international harvesting. Inputs of pollution from one country may be moved, through various currents and discharges, into the territorial waters of another country, where they degrade that nation's marine resources. And the discharge of ballast water from ships of distant countries into estuaries, bays, and coastal waters of another may transfer nonindigenous species that destroy local stocks of native marine creatures. Solutions to these problems are not possible without international cooperation and mutually enforced international conservation law.

The primary documents that serve as sources for an international conservation strategy are *Agenda 21* (United Nations 1992), the *Global Biodiversity Strategy* (World Resources Institute et al. 1992), and *Caring for the Earth: Strategy for Sustainable Living* (IUCN et al. 1991). Although these documents differ in details that are beyond the scope of this discussion, they agree that international strategies should include efforts to reduce population growth and the consumption and wasteful use of marine resources; the development of an open, nondiscriminatory, equitable, and environmentally sound international, multilateral trading system; and ratification of major UN documents establishing regional and global laws, policies, protocols, and organizations for marine ecosystem management, especially ratification of the third United Nations Convention on the Law of the Sea (UNCLOS III) (Norse 1993).

One attempt to develop more consistent patterns of international cooperation has been the work of the International Organization for Standardization (ISO), which developed out of the 1992 Earth Summit meetings (von Zharen 1999). The ISO has played a leading role in developing international and regional

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environmental management standards (EMSs) that attempt to establish consistent, internationally accepted protocols for managing resource use and pollution in marine environments. Core principles of the ISO include a commitment to environmental management as an organizational priority; identification of appropriate legislative and regulatory requirements; identification of the environmental aspects of an organization's activities, products and services; development of management processes for achieving objectives and targets; appropriate financial and human resources to achieve targets; assignment of clear procedures for accountability; establishment of a maintenance review and audit process; and development and maintenance of communication with interested parties (von Zharen 1999).

Management actions will differ in local context, but global strategies for protecting marine ecosystems endorsed by the World Resources Institute, the International Union for the Conservation of Nature, the United Nations Environmental Programme, and other international conservation organizations focus on three things.

1. Establish a commission on ecosystem restoration to provide technical guidance and help secure funding for nations seeking to restore the sustainability of their coastal and fresh waters.
2. Map, using GIS technology, all macroscopic structure-forming species including coral, oyster and worm reefs, kelp and seagrass beds, and mangrove forests that provide essential habitat for other species.
3. Develop a marine biogeographic scheme based on patterns of species endemism that can be used to establish a global system of marine protected and special management areas and use this scheme to establish a global network of marine parks (Norse 1993).

We know too little about aquatic habitats, especially the marine habitats that cover 71% of the earth's surface and fill more than 90% of the planet's livable volume. Yet we make extensive withdrawals of natural resources from these poorly understood systems. The more important problem is not that we know too little, but that we may know too little, too late.

Problems of degradation and destruction of aquatic habitats result from both unmanaged inputs and unconstrained exploitation. To restore aquatic habitats, we must control what we put in and reduce what we take out. In the next decade, the successful conservation of aquatic habitat will require (1) control of inputs to aquatic systems through management of land-use practices surrounding these systems; (2) the establishment of an extensive, well-defined, and properly enforced aquatic reserve system, consisting of designated lakes, rivers, and marine areas that preserve high levels of the global biodiversity of aquatic communities; (3) more aggressive, persistent, and comprehensive research efforts to understand the workings of aquatic systems, unfamiliar worlds in which we do not live and which, without great effort, we cannot even observe; (4) reduction and restriction of our use of aquatic resources; and (5) international cooperation, jurisdiction, and ownership of the problems of marine environments.

Visit our webpage at www.mhhe.com/conservation for case studies, animations, practice quiz questions, and additional readings to help you understand the material in this chapter. You'll also find active links to the following topics:

Extinction and Marine Habitats
Water Use and Management
Water Pollution
Red Tides
Coral Bleaching
Groundwater
Resources from the Sea
Fisheries
Impact of Humans on the Sea; Harvesting
Impact of Humans on the Sea; Pollution
Fisheries and Conservation Issues Concerning Teleosts

Reading assignment: Lauck, T., C. Clark, M. Mangel, and G. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8:S72–S78.

Questions

1. Compare and contrast the authors' concept of a marine reserve with more traditional views of the role of marine reserves in commercial fisheries.
2. In the appendix of this paper, the authors note a critical assumption of their model: "The reserve boundaries are set for harvesting but the stock moves smoothly across the boundary and fills the entire fishing ground."

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Identify a biological theory that supports this assumption. What alternative assumption is possible? Is there any support for the alternative in theory or specific knowledge of the natural history of harvested species?

3. Critics of Lauck et al. could argue that reducing the level of harvest achieves the same result as establishing a marine reserve. Why might these different strategies produce different outcomes? Which strategy is best at reducing risk to the fishery? Why?
4. Lauck et al. note an important cost of their strategy—enforcing the boundaries and protective regulations of the marine reserve. If you were the manager of a new reserve, how would you propose to pay for such costs? How would you persuade both conservationists and commercial fishers to support the plan with sufficient enthusiasm to pay some of the costs?

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