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Sustaining Biodiversity and Ecosystem Services in Soils and Sediments

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Vulnerability and Management of Ecological Services in Freshwater Systems

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Society obtains great benefits from properly functioning ecosystems in the form of provisioning (e.g., food), supporting (e.g., waste processing, sustained supplies of clean water), and enriching (e.g., recreation) services, all of which are provided at multiple scales and at no charge to society. Freshwater benthic ecosystems often play important and unique roles in providing many of these services (see Chapter 3, Table 3.1), but the number and magnitude of anthropogenic stressors that threaten these services is growing rapidly. Sustainable development, which "meets the needs of the present generation without compromising the ability of future generations to meet their own needs" (World Commission on Environment and Development 1987), depends on our ability to manage and maintain these ecosystems and the services they provide. In order to achieve this end, we need a better understanding of how benthic ecosystems function and are structured, as well as stronger integration of management with ecological studies. Having insulated ourselves from many natural ecosystems through technology, we often fail to appreciate the beneficial "workers" that sustain "nature's economy" upon which ecosystem services depend.

We now appreciate that degradation of freshwater sediments, which harbor the biota essential to benthic ecosystem processes, will in turn degrade water quality and a range of other services. We also understand that because of the strong linkage between freshwater ecosystems and the landscapes they drain (Giller & Malmqvist 1998), changes in land use and other activities in the catchment can contribute to such degradation. Many

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current water management practices, such as flood control, water diversion and detention, channelization, and irrigation, affect the hydrological cycle at local to catchment scales. Over the past several hundred years, humans have built thousands of kilometers of diversion canals, channels, and levees to divert water for society's use. Humans have drained wetlands for urban development and agriculture, and have dammed rivers for water abstraction and the generation of hydroelectric power. Although these activities are intended to provide certain important services to the human population, they also significantly degrade many other services, the values of which become evident only when they are lost or destroyed. The examples of the demise of the Aral Sea in Central Asia (Micklin 1992) due to the diversion of inflowing freshwater streams, and the ongoing threats from paper mill effluent to the species-rich and globally unique freshwater biota of Lake Baikal in southeast Siberia, are clear cases in point. On a larger scale, climate change, an unintended consequence of human activities, also alters the hydrological cycle, threatening freshwater habitats and organisms (and hence a range of services) throughout the world (Palmer et. al. 1997; Lake et al. 2000; Wall et al. 2001). The threats of such activities on sustainable development are clear.

The various types and importance of ecosystem services in fresh waters, and the role of benthic biodiversity in the delivery of these services, are presented in Chapter 3, along with a discussion of the balance between ecological and economic values. In this chapter, we will briefly review the various threats to freshwater benthic ecosystems and the important benthic species that help sustain ecosystem services. We also consider the vulnerability of these services, using a number of case studies to illustrate the cascading effects of overexploitation and the subsequent loss or degradation of other services. These case studies also illustrate how benthic organisms and the ecosystem services they perform can be used to enhance management and maintain the overall health and sustainability of freshwater systems.

Threats to Freshwater Systems

Threats to freshwater systems arise from a myriad of human activities, including channelization, groundwater pumping, diversion, dam building, pollution, human-induced climate change, and overexploitation of natural resources (e.g., Postel & Carpenter 1997; Malmqvist & Rundle 2002). Nearly all major rivers and lakes worldwide have large human population densities associated with them or within their drainage basins, usually sited there with relatively little thought to the availability of potable water. The growth of the human population and the mismatch between population growth and provision of, and accessibility to, water resources is an imminent concern (Cohen 1995). An estimated 1.8 billion people now live under a high degree of water stress in areas with limited supplies of potable water (Vörösmarty et al. 2000). This stress may continue to rise, with a projected population living in these areas estimated to be between 2.8 billion and 3.3 billion by 2025 (Engelman & LeRoy 1993, 1995; Cohen 1995).

Stressors and impacts that force changes in freshwater ecosystems can be classified into four major types of threat (Malmqvist & Rundle 2002): (1) complete ecosystem loss or destruction, (2) physical habitat alteration, (3) water chemistry alterations, and (4) modifications of species composition. Ecosystem loss or destruction is often associated with water withdrawal from the system (e.g., in the Alps, Ward et al. 1999) resulting from rapid urbanization and/or intensification of agriculture, and the associated water demand and lowering of water tables by extraction elsewhere. There is a strong correlation between population size and water withdrawal (Gleick 2001), and irrigation dominates water demand at the global level. Habitat alteration of the freshwater system can occur from both instream activities (including channelization, damming, and draining of wetlands) and catchment-related activities (such as deforestation, poor land use, and alteration of the riparian corridor). Changes in water chemistry result from pollution due to wastewater discharge, diffuse nutrient loading from agriculture runoff, acidification from atmospheric inputs, and the introduction of endocrine disruptors (Malmqvist & Rundle 2002). Introductions of exotic species may be direct or indirect (as discussed below). Extinctions are common, often due to overexploitation of the organisms themselves, habitat destruction (or loss of habitat to invasive species replacement), the loss of functions necessary for some life stage of a particular species, or the loss of a symbiont.

We have identified 14 major threats to the six major services provided by freshwater benthic systems (Figure 6.1). Each threat can impact more than one of the services, and many of these impacts are mediated through the benthos. In reality, each threat can be subdivided into a finer series of threats. For example, hydrologic modification can have effects through a decrease in peak flow, increase in low flows, change in timing of peak flows, changes in the rate of drawdown, and/or a decrease in flow variability, and so on. Each ecosystem service can be affected by several different threats, and different stressors may act synergistically. Eutrophication can increase biotic activity and thereby enhance the effect of metal contamination (for example, the mobility of mercury). Likewise, changes in water chemistry, mechanical disturbances to a system, or changes to the characteristics of the habitat can enhance the probability of successful species invasion (Jenkins & Pimm 2003), which in turn may decrease economic success based on a highly profitable food source for humans. Changes in the competitive balance between species can also ensue. One example of this phenomenon is the replacement of the sawgrass (*Cladium jamaicense*) communities in the wetlands of the Everglades in Florida, United States, by cattail species (*Typha latifolia* and *T. domingensis*) as a result of phosphorous and nitrogen loading from agricultural runoff (Newman et al. 1998). In areas of the 600,000–ha Everglades that have the highest phosphorous enrichment, cattails dominate, but in portions of the Everglades where phosphorous remains low, sawgrass still dominates. This shift in community structure directly resulting from human-caused changes in water chemistry is due to the fact that cattails are better able to assimilate nitrogen and phosphorous and to produce biomass.

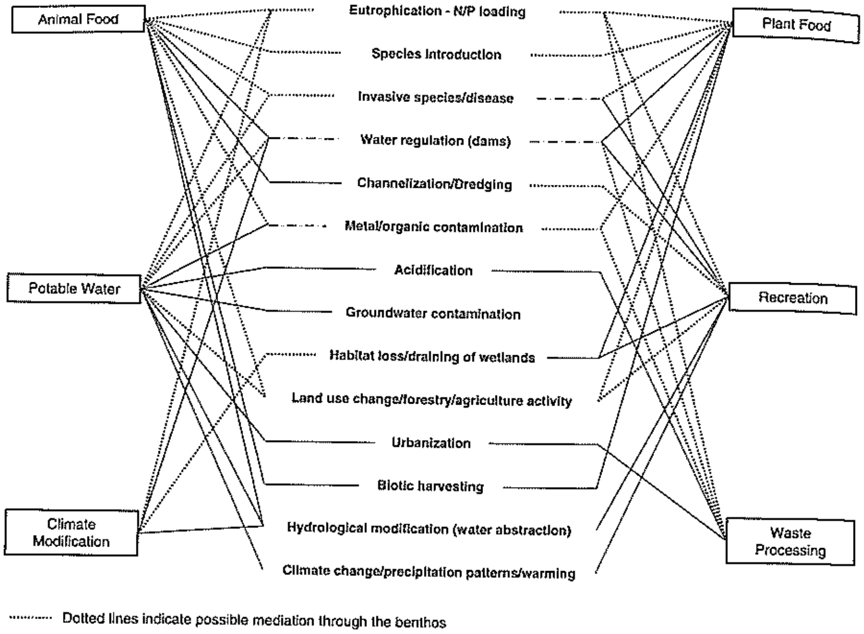

Figure 6.1. The interaction between six major ecosystem services, provided by freshwater systems, and fourteen potential threats in the freshwater domain. An explanation of the nature of the services is given in Chapter 3, Tables 3.1a–3.1e. Solid lines indicate the direct links between the major services and the various threats, and the dotted lines indicate links that may be mediated through the benthos.

The stressors described above in Figure 6.1 occur in all types of freshwater ecosystems; however, the magnitude and direction of their effects vary across ecosystems. Lakes and wetlands are susceptible to various stressors due to their slow turnover of water, their potential for accumulation of toxins and metals in their sediments, and their dependence on the quality and quantity of water inputs from inflow streams. The susceptibility of rivers and associated wetlands, on the other hand, is exacerbated by the downstream flow of water (and hence pollutants and sediments) and their longitudinal connectivity (upstream and downstream dispersal migration of many species). Almost any significant activity within a river catchment and throughout its drainage network may have the potential to exert effects for large distances upstream and downstream.

Freshwater ecosystems face different threats in different regions, depending largely on the economic activity and state of development. Water is abundant at high latitudes and in the wet tropics; however, in much of North and East Africa, Australia, and parts of North America, the availability of potable water is relatively scarce. Even in the more temperate countries with relatively high overall annual precipitation, major concentrations of population are often located in areas of lowest rainfall (such as Dublin and London), creating local water deficits that require large-scale engineering projects for water storage and/or transfer, as well as water regulation activities to overcome. Roughly 40 percent of the world's population that live in 80 dry, or partially dry, countries face serious periodic droughts (Cohen 1995); these pressures on water resources will be more pronounced in Africa and South America by 2025 (Vörösmarty et al. 2000). Plans to redirect water from uninhabited areas to population centers will create additional problems. Lakes in the developed world are threatened by eutrophication and lowered water tables due to groundwater abstraction, while in the undeveloped world, overexploitation of fish and invasion from exotic plants (e.g., the water hyacinth *Eichhornia crassipes*) are more problematic. Destruction of running water habitats is extensive in much of the developed world (because of flood control, drainage, clearing channels for transportation and transport of timber, and dredging), as well as in the developing world (largely due to dam construction and mining; see Covich et al., Chapter 3).

Waste disposal poses significant threats to many systems, as treated and untreated domestic and industrial waste leads to significant levels of eutrophication and to metal and other chemical contamination. Sedimentation and nonpoint source pollution result from changing land use such as deforestation, overgrazing, and intensification of agriculture. The degradation of riparian zones that often accompanies such intensification (as in the Netherlands, for example) also changes benthic ecosystem functions dramatically (Gregory et al. 1991). Even atmospheric pollution impacts aquatic ecosystems, as evidenced by acidification of freshwater systems throughout northern Europe, the northeastern United States, and Canada (Stoddard et al. 1999).

Anthropogenic threats and influences alter the balance of natural regulatory factors in freshwater systems such as energy supply and flow, organic and inorganic matter transport, hydrologic regimes, hydrologic and biogeochemical cycles, and water chemistry (Malmqvist & Rundle 2002). These anthropogenic factors change the structure of freshwater sediment, alter temperature regimes, and cause other environmental conditions to change beyond the normal levels of variation and extremes. Such changes will clearly impact species unless they possess certain traits that confer resistance or resilience to the environmental change.

Interaction of Threats and Ecosystem Disservices

There is frequently a trade-off between ecological and economic values associated with ecosystem services (see Covich et al., Chapter 3). In this context, the interconnections between services and threats provide an introduction to the concept of disservices. Exploiting one service can negatively affect, or in extreme cases completely eliminate,

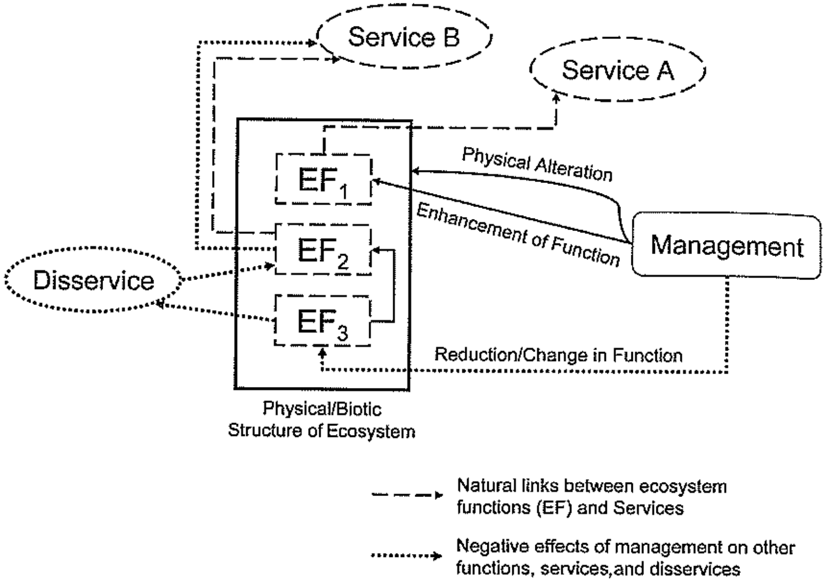

Figure 6.2. Conceptual diagram illustrating a disservice for humans, through the potential negative effect of implementation of management on an ecosystem function (EF$_1$) to enhance an ecosystem service (Service A). In this example, the physical alteration of the structure of the ecosystem through the management regime also leads to a reduction or change in function of EF$_3$. This in turn can act as a disservice to EF$_2$, hence causing a negative impact on Service B.

another service. The potential for disservice is exacerbated when society introduces a management process to enhance one particular ecosystem function, and hence one particular service, that unintentionally leads to a reduction or change in another ecosystem function. The net effect is to degrade a second, non-target, ecosystem service (Figure 6.2).

For example, regulating a river to obtain hydroelectric power has negative consequences on ecosystem services that depend on natural hydrologic regimes and free-flowing water. Natural rivers and streams are heterogeneous systems with flow patterns that vary over time, often in predictable patterns (Poff & Ward 1989). However, in regulated rivers, the purpose of management is to adjust this variation; the reduced seasonal and increased daily dynamics of flow in regulated rivers instead reflect the periods of electricity demand. Reduced spring floods and elevated winter discharge, and even high daytime/weekday flow and low nighttime/weekend flow often result (Malmqvist & Englund 1996). In addition to changing flow regimes, habitat loss, fragmentation, and (in heavily regulated systems) a general change from lotic (running water) to lentic (standing water), or even to dewatered conditions, can occur along some stretches of river. These flow alterations change river habitats and their biota, including sedimentary biota, fundamentally. For example, species richness and abundance of benthic macroinvertebrates are impacted (Ward & Garcia de Jalon 1991) which, given the clear role of such invertebrates in delivery of ecosystem services (see Covich et al., Chapter 3), will lead to degradation of such services (e.g., breakdown of wastes, support of fisheries, and maintenance of high water quality). Effects on migrations and stocks of anadromous salmonids, in turn, alter various services such as recreation. This is of significant concern, for instance, in Sweden (Malmqvist & Englund 1996; Jansson et al. 2000), where over 70 percent of the rivers are regulated, and also in the northern third of the Earth, where a majority of rivers are heavily influenced by river regulation (Dynesius & Nilsson 1994). Worldwide, the number of "large" dams (greater than 15 m) has increased approximately eightfold over the last 50 years and the total number of dams has risen to nearly 800,000 (Postel & Carpenter 1997; Rosenberg et al. 2000).

The introduction of exotic species further illustrates the concept of the interaction of threats and ecosystem disservices. Exotic species introductions create less visible but ecologically and sometimes economically important problems. Introductions of non-native fish to improve fisheries for sport or to provide protein for human consumption have led to the wholesale collapse of local biological communities and aquatic food webs. The negative impacts on ecosystem functions that rely on intact food webs, such as decomposition, biogeochemical cycling, and overall productivity, will likely affect water quality, other fisheries, and hence a number of other services. The introduction of a predatory cichlid into Gatun Lake in the Panama Canal (Paine & Zaret 1973) and the introduction of Nile Perch into the African rift valley lakes (Kitchell et al. 1997) are two cautionary cases. The zebra mussel (*Dreissena polymorpha*) is perhaps the most famous and pervasive invading freshwater exotic. Originally native to the Black and Caspian Seas, it spread throughout European waters during the 19th century, but it has only recently reached Ireland (Minchin et al. 2003). Discovered in 1988 in Lake St. Clair in the Great Lakes of the United States, it rapidly spread throughout the Great Lakes and Mississippi river basin (Ludyanskiy et al. 1993). There is a range of abiotic, biotic, direct, and indirect impacts of a zebra mussel introduction (MacIsaac 1996), but one of the greatest is the impact of biofouling (undesirable accumulation on artificial surfaces) associated with the settlement of the mussels. Water intake structures for municipal, industrial, and hydroelectric plants are extremely vulnerable to fouling if they draw intake water from an infested water body. Reaching densities of up to 334,000 mussels per square meter, the exotic mussels have significant ecological effects such as competitive exclusion of native unionid mussel species (Ludyanskiy et al.1993; Fitzsimons et al. 1995) and removal of phytoplankton, which results in the disruption of food webs (Karatayev et al. 1997). Theoretical estimates suggest that the native mussel population in Lake Erie can filter up to 14 times the entire lake and remove phytoplankton equivalent to 25 percent of primary production each day (Bronmark & Hansson 1998). On the other hand, this trait can be utilized in management of eutrophication problems as seen in the Netherlands. By efficiently filtering phytoplankton, these mussels are able to alter nutrient cycling patterns, transfer carbon and nutrients from the pelagic to the benthic zone through the build up of mussel biomass, reduce the concentration of suspended solids, and hence improve water clarity and increase macrophyte growth.

Given the various threats to ecosystem functioning in freshwater systems, one might ask why the problem is not worse. After all, large population centers are still supported by surface waters that continue to provide a number of ecosystem services. The answer lies in part with the level of technology and infrastructure we are able to bring to bear, such as wastewater processing, but also in the ability of the freshwater ecosystems and biological communities either to cope with a certain level of disturbance or to recover rapidly and restore function—that is, an innate resistance and/or resilience of the ecosystem. The question remains: What role do benthic biota play in reducing the impact of a threat? Specifically, how does benthic biodiversity influence ecosystem processes in freshwater systems and are there key taxa involved, the loss of which will have devastating consequences on ecosystem services? Overall, key taxa do influence ecosystem functioning; the presence of certain species can substantially influence the system (e.g., on decomposition) (Giller et al. 2004). Benthic studies, however, have generally focused on relatively low levels of species richness, and experimental studies have been at local scales (Covich et al. 1999; Covich et al. 2004). More research is needed to provide a comprehensive understanding of the various roles played by different benthic species and functional groups of species.

Management and Ecosystem Services

In this final section we present five specific case studies that illustrate, in detail, the interactions between threats and the impact on ecosystem services. We also provide examples of how some benthic ecosystem services themselves have been used to enhance management and contribute to the maintenance of the health of the freshwater ecosystems. The case studies differ in geographical location, type of freshwater system, and nature of the services and threats. The first case study highlights the Rhine and Meuse, major European rivers that have been subject to centuries of human interference leading to hydrological modifications and pollution and clear conflicts between the various ecosystem services they offer. Efforts at restoration management are reversing some of the more dramatic ecological changes. The second case study describes the Pantanal region, a huge natural wetland complex in South America that undergoes massive seasonal changes. Unlike the Rhine and Meuse rivers example, it is in a relatively undeveloped area. It offers a wide range of services to the native population and is a habitat to considerable biodiversity, yet the Pantanal is increasingly threatened from growing agriculture and mining. Lake Mendota, the third case study, provides a recreational service that was threatened by eutrophication. Here, management based on the ecological concept of the trophic cascade has been applied with some success. Like the Pantanal, the Everglades (the fourth case study) is a large wetland that provides a range of ecosystem services. Agricultural pollutants, including heavy metals, have compromised these services, illustrating the disservice phenomenon across terrestrial-aquatic boundaries. The final case study of the Catskill Mountains watershed shows the scale of watershed management that is needed to sustain water quality and provide potable water for New York City. This example illustrates how landscape management can obviate the need to replace natural ecosystem services with artificial technological processes, thus providing significant economic and ecological value.

Repairing Years of Abuse: The Impact of Management for Transport and Waste Disposal in the Lower Rhine and Meuse Rivers (Europe)

The Rivers Rhine and Meuse have served as vital European transport arteries for centuries, as well as sites for urban and industrial development and water resources. Thus, the two rivers are of considerable economic importance but have been subject to substantial anthropogenically derived changes over time. The River Rhine, a combined glacier-rainfall river, originates in Switzerland (2,200 m above sea level) and flows over 1,250 km through France, Germany, and the Netherlands with a drainage area of 185,000 km^2. In the Netherlands, it divides into three branches: Waal (65 percent of discharge), Lek (21 percent discharge), and Ijssel (14 percent discharge). The River Meuse is fed by rainwater, originates in France (410 m above sea level), and flows over 890 km through Belgium and the Netherlands, with a drainage area of 33,000 km^2. Both rivers flow into a lowland area where they form a river delta before entering the North Sea (van den Brink 1994). The earliest documented human influence on these rivers occurred in the Roman era and involved the construction of canals to regulate discharge into the Dutch Rhine tributaries (van Urk & Smit 1989) and embankments started in the Middle Ages. In the 18th century, the Rhine River floodplain was still tens of kilometers wide, and the river meandered and supported an extensive riparian forest. Large-scale river regulation began in the 19th century, with construction of dams and sluices for sea flood protection, dams for river regulation, and groins (breakwater boulder piles extending laterally into the river), weirs, and dykes to facilitate shipping. These changes impeded natural meandering and formation of side channels, cutoff channels, and oxbow lakes; consequently, the floodplain shrank dramatically (van den Brink 1994). Since then, nearly all the floodplain forests have been cut, the riparian forests have been largely removed, and the existing riparian areas have been degraded. The significant loss to the aesthetic and recreational services is self-evident.

The water quality of the main channels of both rivers has changed considerably since measurements began in the early 1900s, with increased levels of nutrients (nitrate and phosphate), salts (chloride, sodium, and sulphate), and heavy metals (cadmium, mercury, lead, and zinc) (van de Weijden & Middleburg 1989). In addition, increasing levels of organic micropollutants such as polychlorinated biphenyls (PCBs), para-aminohippuric acid (PAHs), insecticides, and herbicides have contaminated the sediments. The lower sections of the two rivers accumulate inputs from several countries upstream and are the most polluted. In the 1960s–1970s, oxygen levels were extremely low, which affected the abstraction and provision of quality drinking water. More recently, construction of sewage treatment plants has improved the Rhine, although the Meuse still suffers from low oxygen, particularly in summer (van den Brink 1994). As a result of thermal pollution from power plants and industries, water temperature in the lower Rhine and Meuse has risen by 2 to 4° C since 1900.

Not surprisingly, there have been dramatic changes in the biotic communities of the rivers. Plankton biomass in the river channels has increased, and is now dominated by a few ubiquitous centric diatoms and green algae (Admiraal et al. 1993). These add a considerable economic cost on filtration of the abstracted water. At present, the waters of the lower Rhine are dominated by sodium chloride instead of calcium bicarbonate (chloride levels increasing from < 20 mg/l in 1874 to > 200 mg/l in 1985; van den Brink et al 1990), which, together with the increased temperature, has created an environment that permitted the invasion of several exotic brackish-water and eurythermic macroinvertebrate species. These include exotic species introduced from North America and Eastern Asia and others that have immigrated from the Mediterranean and Ponte Caspian areas. One species is the benthic filter-feeding amphipod crustacean *Corophium curvispinum*, an invader originally from the southern Ponte Caspian area, which has expanded its range since 1900 from the rivers entering the Caspian and Black Seas via canals and rivers to western Europe, probably aided by shipping. It was first documented in the middle then lower Rhine in 1987, and within a couple of years increased explosively to become the most abundant species in the Rhine system. This species also reached the Belgian part of the River Meuse in 1981 and the Dutch part by the end of the 1980s. This invader has had a significant impact on the Rhine ecosystem (Neumann 2002). Its high fecundity, short generation time, and small size have led to massive densities (rising from $2/m^2$ in 1987 to $200,000/m^2$ in 1991 on stones of groins in the lower Rhine, van den Brink et al. 1993a), increased filter-feeding activity, and competition for food and space with other species, including other exotic invaders such as the amphipod crustacean, *Gammarus tigrinus,* and the zebra mussel, *Dreissena polymorpha. Gammarus tigrinus* invaded the lower Rhine in 1983, reducing abundance of the native amphipod *G. pulex. Dreissena* spp. invaded Europe from the Black Sea and Caspian Sea over two centuries ago, before the Industrial Revolution, but disappeared from the lower Rhine in 1960s due to the poor water quality and high levels of cadmium. Reductions in cadmium levels lead to *Dreissena polymorrpha*'s re-establishment in 1975 and its subsequent rapid population increase. However, the species has now dramatically declined since 1987 due to competition for space with the nonnative *Corophium* (van der Velde et al. 1994). Meanwhile, a number of native brackish-water crustaceans such as the benthic amphipod *Gammarus zaddachi* range more than 100 km upstream of their original distribution boundary, as a result of increased river salinity (van den Brink et al. 1990, 1993b).

The rivers' benthic community is now largely a pollution-tolerant one, with typical pollution-sensitive aquatic insects (ephemeropteran, trichopteran, and plecopteran species) having disappeared prior to 1940. Because the latter two families are involved in detrital breakdown, the decomposition process was likely affected. Species richness of macroinvertebrates declined from 83 around 1900 to 40 in 1987. The fish community was completely dominated by cyprinids (particularly roach) in the 1970s, and anadromous and rheophilous species declined or disappeared altogether (van der Velde et al. 1990). For example, the salmon (*Salmo salar*), was overexploited and became extinct despite large-scale restocking attempts, thus negatively impacting recreational services provided by the rivers. In addition, changes in the macroinvertebrate communities and the invasion of exotic species led to changes in the river food web structure and the diet of the major predatory fish (Kelleher et al. 1998).

Over the past two decades, various restoration management measures were implemented that began to reverse some of these impacts (Jungwirth et al. 2002). The Rhine Action Plan established by the Dutch government involved all the countries bordering the river and implemented various measures to restore water quality and habitat structure. Discharge of raw sewage and industrial wastes has decreased. The much-publicized Sandoz incident in 1986 (Lelek & Kohler 1990; Mason 1996), which involved huge inputs of insecticides following a major fire in a chemical plant in Switzerland, led to the closure of water diversion plants along the river and other controls and restrictions. Despite such setbacks, some evidence of success has been seen in the rediscovery of several benthic riverine species in the lower Rhine, including the net-spinning caddis fly *Hydropsyche conturbernalis,* the water bug *Aphelocheirus aestivalis,* the damselfly *Calopteryx slendens,* and the freshwater mussels *Anadonta anatina* and *Unio pictorum* (van den Brink et al. 1990). The number of fish species has increased, rising from a low of 12 in 1971 to 25 in 1987 (van der Velde et al. 1990). Further reduction of the pollution loads in the entire drainage basin has focused on nutrients, heavy metals, and organic micropollutants (such as PCBs and PAHs). Restoration of wetland vegetation, floodplain lake water quality, and, in particular, connections between the main channel, floodplain lakes, and side channels were suggested as being particularly important from a biodiversity perspective (van den Brink 1994). Indeed, the creation of permanently flowing secondary channels on the Rhine floodplain in 1994 showed that within five years these artificial secondary channels function well as an appropriate habitat for riverine species, including the more demanding rheophilic species (those that prefer to live in running water), and have thus contributed to the ecological value of the river (Simons et al. 2001). Jungwirth et al. (2002) give a number of other examples of similar river and floodplain restoration projects.

Wetland Protection to Preserve Biodiversity and to Enhance Food Production and Recreation: The Pantanal of South America

This enormous tropical wetland, the Pantanal of South America, is approximately the size of the state of Florida and is the fourth largest complex of wetland ecosystems in the world (Keddy 2000). Its basin covers approximately 138,000 km^2 in Brazil and 100,000 km^2 in Bolivia and Paraguay. It consists of numerous streams, lakes, and seasonally flooded swamps. The basin receives inflows from several large rivers (e.g., Rio Paraguay, Rio Petras, Rio Cuiaba) that flow southward to join the Rio Parana and then to become the Rio Plate in Argentina (see Por 1995 for further details). The river water that supplies it is primarily "clearwater" (*sensu* Sioli 1984), with little suspended material under pristine conditions. A unique feature of the Pantanal is that it experiences substantial changes in the area that is under water between wet and dry seasons each year, with as little as 10 percent of the area inundated during the dry season and as much as 70 percent during the four-to-six-month wet season. During the dry season, shallow, isolated water bodies develop aquatic communities that are characterized by high turbidity because of the density of bacteria and algae as well as black coloration in the water from humic materials released during decomposition. Nevertheless, these temporary aquatic ecosystems have no endemic or even rare species. This is because of the likelihood of extinction during occasional very dry periods followed by the certainty of the extensive mixing among aquatic and wetland ecosystems that follows flooding in the wet season.

The seasonal wet-dry cycle provides a wide range of ecosystem services of great ecological and economic value. There were a large number of indigenous people who cultivated wild water rice, hunted deer, and constructed artificial islands within the swamps on which to live (Moss 1998). Water supply, food production, and waste processing all still contribute important economic values to the region, and benthic communities play an important role. The Pantanal is characterized by a density of large vertebrates and unique food webs (Heckman 1998). In addition to providing habitat to endangered terrestrial and semi-aquatic species such as the spotted jaguar (*Panthera onca*), giant anteater (*Myrmecophaga tridactyla*), and giant river otter (*Pteronura braziliensis*), this vast region supports more than 40 species of wading birds and more than 400 species of fish. These species have high "existence values" for many people, and they maintain the complex pelagic and benthic food webs that are the basis of many ecosystem services. Recreational uses are also of major economic importance. Hunters, fishermen, and conservationists travel from all over the world to view and to exploit this exceptional biodiversity.

During the dry season, much of the unflooded matrix within the Pantanal wetland becomes a savanna used for grazing large herds of cattle that are supported by nutrient cycling in the sediments. The savanna is divided into a series of cattle ranches (based on several million zebu cattle and local breeds) that have been burned regularly by ranchers for the last 150 years. Deforestation by burning to create more grazing land has led to soil erosion and high rates of sedimentation (see Covich et al., Chapter 3 and Ineson et al., Chapter 9). In more recent years, nonnative grasses have been introduced to improve forage, and pesticides and fertilizer use has increased in an effort to support the growth of rice and soybeans. These increased chemical inputs have negative effects—such as bioaccumulation and eutrophication—as occur elsewhere in the world (Moss 1998). Gold mining predates ranching by about 100 years, and open-pit gold mines are still being established. Purification of gold ore utilizes mercury, which is then evaporated, and there is some evidence of mercury pollution affecting birds (as in the Everglades). Subregions within the basin (such as Nhecolandia, Brazil, the second largest of 11 subregions) are being studied with remote sensing to increase available data on land-use values. Meanwhile, threats from the watershed have also increased, and the rivers feeding the Pantanal now introduce chemical contaminants, nutrients, and sediment from increasing urban developments, agricultural operations, and mines. Seidl and Moraes (2000) estimate the annual total value of ecosystem goods and services to the Nhecolandia subregion is more than US$15.5 billion.

The conflict is clear in the Pantanal between the maintenance of natural provisioning, supporting, and enriching services and the increase of the delivery of artificial services through agriculture and exploitation of natural resources. It is quite remarkable that such a diverse and unusual animal assemblage exists, given that it is dependent on a food chain with a very important benthic base that itself is by no means unique in its diversity or nature. How long the Pantanal ecosystems can continue to provide the wealth of ecosystem services under the increasing effects of the various stressors is unknown.

Nutrient Cycling and Productivity of Lakes: Lake Mendota, Wisconsin, United States

Lakes are used for a variety of ecosystem services, but because of their enclosed nature and the slow turnover of their water, they are often susceptible to a variety of threats, among them the loss of ecosystem services and resulting disservices. Eutrophication, for instance, results in rapid growth of blue-green algae, which affect tastes and odors of drinking water. Algal blooms disrupt filtration processes during water abstraction and can be toxic, which may affect drinking water for municipalities. These issues stimulated intensive experimental and modeling studies to determine whether such changes were irreversible (Baerenklau et al. 1999; Wilson & Carpenter 1999).

Lake Mendota in Madison, Wisconsin, is one of the most thoroughly studied medium-sized (approximately 4,000 ha) lakes in North America (Kitchell 1992). In the early 1980s, the combined decline of walleye populations and lost recreational fishing, together with concerns over unpredictable eruptions of noxious and sometimes toxic blue-green algae (cyanobacteria), led to a research effort demonstrating that water quality and food web management could be integrated. The management processes developed here and elsewhere were based on the trophic cascade concept (Carpenter & Kitchell 1993), in which enhanced populations of top piscivorous predators that feed on planktivorous fish led indirectly to the reduction of algal densities through the release of zooplankton populations that feed on algae. This approach of using one ecosystem function (predation) to enhance another (herbivory) and hence increase an ecosystem service (provision of high-quality water) has been utilized in a number of countries. In the case of Lake Mendota, management issues to solve conflicting service provision included: (1) trade-offs between increased stocking for walleye and northern pike fishing or managing for bass or perch (distinct "goods" for different people); (2) effects of increased water clarity (following removal of algae by grazing zooplankton) on deep light penetration, which can result in increased growth of submerged aquatic plants (that provide critical habitat for juvenile fishes, but can become weedy and reduce dissolved oxygen in the littoral zone during late summer and winter when the dead plants decay); and (3) disadvantages of improved water quality (clear water with lower concentrations of dissolved nutrients), which made it difficult to fulfill the demand for recreational fishing.

These integrative studies led to new questions about how management can enhance ecosystem services in freshwater bodies: How are "distinct" ecosystems, with apparently clearly defined surface boundaries (e.g., small ponds, large lakes, and rivers), interconnected hydrologically over time and space? How might these linked ecosystems function and affect each other in predictable ways? Why must fisheries biologists add fertilizers to increase fish production in some locations (hatcheries, aquaculture ponds) when water-quality engineers are designing treatment plants to remove nutrients in other "downstream" locations (groundwaters, rivers, and lakes)? Is production of fish for food versus recreation a necessary trade-off? Or can aquatic ecosystems be managed to optimize complex production functions? Can natural processes of nutrient cycling and organic-matter breakdown provide supplemental services that could save construction of new treatment plants? Answers to such questions have emphasized that sedimentary deposits and the species that live in these substrates are key regulators of nutrient cycling and productivity of different forms of plants. These basic elements of nutrient cycling (bottom-up control) interact with the effects of open-water predators such as fishes (top-down control) to jointly influence entire food webs (Kitchell 1992; Carpenter & Kitchell 1993).

The Everglades: Coping with Heavy Metals and Ecosystem Disservice

The Everglades is a vast freshwater wetland that originally covered an area of more than 10,000 km^2 in south Florida, United States. It is part of a 100-km-long basin in which water flows along a gradual gradient of 3 cm/km from shallow Lake Okechobee to the mangroves lining Florida Bay. Exploitation of rich organic soils for agriculture, drainage for urban development, the construction of canals, and the impoundment of surface water for flood control and water storage have led to dramatic changes in flooding and fire regimes and nutrient inputs to the wetland. Because of draining and modifications in hydrologic regime, the area of the Everglades is now, in 2004, 35 percent of its original size.

The Everglades provides numerous ecosystem services for human well-being. Even in its much altered state, the Everglades filter polluted runoff from agricultural fields, yielding fresh, clean water for a variety of uses, including support of the estuarine ecosystems at its terminus. It harbors and produces a great quantity and diversity of wildlife, most notably alligators, crocodiles, the Florida panther, manatees, and a rich variety of aquatic birds. The fresh water it supplies to Florida Bay comes in a quality, quantity, and pattern of delivery that enables coastal ecosystems to provide their own suite of services. Finally, the Everglades provide aesthetic values, including recreation, to an audience that extends well beyond the boundaries of the United States.

Among the many changes to the Everglades that alerted scientists and resource managers to potential "ecosystem disservices," one that was particularly difficult to diagnose was the increase in concentrations of mercury in several species of vertebrates. Mercury contamination has been particularly pronounced for Everglades sport fishes; high levels have been detected in other vertebrates, including alligators, wading birds, and the Florida panther (Fink et al. 1999). Fear arose that agricultural pollutants introduced primarily into the north and eastern ends of the wetland were finding their way into and up the food chain, instigating a closer look at the mercury cycle in the Everglades. In fact, the emerging pattern of cause-and-effect is complex and, in some ways, very difficult to counteract.

Most of the mercury introduced to the Everglades comes from atmospheric sources, not from agriculture (Fink et al. 1999). Although some is from natural sources, such as volcanoes and outgassing from oceans, approximately 95 percent of the atmospheric mercury is released with coal combustion, waste incineration, and industrial processing (Krabbenhoft et al. 2003). Mercury in the atmosphere is primarily elemental mercury, which is relatively inert. Once deposited, it is subject to conversion to the more toxic methylmercury, a process performed primarily in an anoxic environment by sulfur-reducing bacteria, which are responsible for much of the organic carbon decomposition in the Everglades' sediments. An unusual feature in the Everglades' food chains is the dominance of periphyton over phytoplankton as the base of food chains (Browder et al. 1994). Periphyton is an assemblage of algae, bacteria, and associated microfauna that form a mat that overlies the surface sediments and often includes filamentous blue-green algae. Both mercury and methylmercury accumulate in periphyton, but it is still unclear how mercury becomes so concentrated in fishes near the top of the food chain. Complex interactions that change seasonally with fish diets (which include benthic invertebrates) and are affected by wetting cycles, fire, sunlight, total mercury concentrations, sulfate concentration, and levels of anoxia remain to be clarified (Gilmour et al. 1998;

Krabbenhoft et al. 2003). It is clear that in areas of nutrient enrichment, accumulation of biomass (often attributed to increased abundance and rates of growth of *Typha latifilia* and *T. domingensis*) increases, rates of microbial activity and decomposition increase, and there is an increased tendency for mercury methylation (Gilmour et al. 1998).

Through our use of the atmosphere to perform the service of waste mercury disposal, humans are compromising animal and human food chains in the Everglades. Atmospheric deposition of mercury to the Everglades is approximately double the rate in rural Wisconsin for example, but it is difficult to determine the source of this input. Although it may be possible to manipulate Everglades water levels and mercury release patterns to minimize formation of methylmercury, the parts of this wetland that are most affected are the parts with the most natural fire and water regimes. Maintaining an environment that can continue to produce sustainable populations of sport fish and wildlife may not be compatible with atmospheric release of waste mercury. This example of the Everglades' ecosystem demonstrates the extent to which freshwater systems are often compromised by the use of ecosystem services in other realms.

Clean Drinking Water: Managing the Catskill Mountains of New York City's Watershed to Provide High-Quality Water Supplies

One of the major success stories in the use of natural ecosystems to deliver vital ecosystem services is the use of a series of river-reservoir ecosystems located in the Catskill Mountains to provide water for New York City's nearly nine million people (Ashendorff et al. 1997). Three large reservoir systems (Croton, Catskill, and Delaware) containing 19 reservoirs, 3 controlled lakes, and numerous tributaries cover an area of 5,000 km^2 with a reservoir capacity of 2.2 $\times 10^9$ m^3. The US Environmental Protection Agency issued a "filtration avoidance status" in 1997 for five years in response to the city's request to upgrade their watershed management and enhance the capacity of natural ecosystems to maintain clean water. To avoid the potential expense of US$2–8 billion over 10 years to build new, larger filtration plants to meet drinking water standards, the city invested US$1–1.5 billion to restore natural ecosystem processes in the watershed (Ashendorff et al. 1997; Foran et al. 2000). The city agreed to construct a filtration plant if natural processes failed to meet EPA standards. Filtration is viewed as essential because chlorination is not completely effective in killing pathogens, particularly when there are high levels of suspended materials (Schoenen 2002).

New York City increased the capacity for natural nutrient retention and lower erosion by protecting riparian buffer zones along rivers and around reservoirs. Road construction within 30 m of a perennial stream and 15 m for an intermittent stream was prohibited. Non-point sources of nutrients and pesticides from stormwater runoff, septic tanks, and agricultural sources were also regulated. Water managers continued to monitor for protozoans, such as *Crytosporidium parvum* and *Giardia lamblia*, that cause cryptosporidiosis and giardiasis.

The city is now expected to save some US$300 million annually that would be necessary to run new filtration plants. The investment in natural capital reduced risks of contaminants, and the city can now focus on minimizing disinfectants at the final treatment stages. Although chlorination of drinking water is widely used, it can produce carcinogenic byproducts (e.g., chloroform, trihalomethane, and 260 other known chemicals) in drinking water, especially in ecosystems with high levels of organic matter (Zhang & Minear 2002).

Increasing effectiveness of natural ecosystem processes by watershed protection, restoration, and riparian management provides an example of how planners can cope with highly variable inputs that characterize this catchment (e.g., Frei et al. 2002). Boston, Seattle, San Francisco, and Greenville, South Carolina, are other examples where natural ecosystem services are used in conjunction with water treatment plants to ensure high-quality drinking water (O'Melia et al. 2000). This final case study illustrates the potential value of maintaining and enhancing natural ecosystem functioning in order to provide our vital ecosystem services.

Discussion and Conclusions

These case studies provide a spectrum of examples that demonstrate not only the ways in which ecosystem services are provided by freshwater benthic species, but also how they are vulnerable to human activities. The studies also provide some lessons that can be carried over into creating improved management of complex, interconnected ecosystems. A central feature of vulnerability of these benthic species is that, although freshwater is widely available, it is often extremely and unevenly distributed. Consequently, there are significant geographical disparities in the frequency and intensity of threats to the benthic biota and their associated ecosystem services. The trade-offs between ecological and economic values that are facing managers will be drastically different in the arid zones of Africa or India than in the arid western United States.

Trade-offs can be complex in wet or dry regions when exploitation of an ecosystem for one service eventually becomes a disservice relative to other needs. When managing for optimizing one service entails obstructing or even destroying the capacity to enjoy another service, either from the same ecosystem or from another ecosystem, planners must rationalize benefits from each service as well as the possibility of mitigation of effects in advance.

Managers often focus on a single problem and then seek to enhance a single ecosystem service to resolve the problem. For instance, designating the Catskill Mountains as a protected watershed for supplying New York City with fresh water provides a complex case study for other cities to consider. Will this approach establish a sustainable system for obtaining potable water without other unintended consequences? It is not clear what the effects of deflecting inflows for New York City's use will have on the Hudson River. Will the complexity of habitats that would have supported a greater number and diversity of fish and benthic infauna be affected by this alteration of flow? Will saline waters move farther upstream on the tidally altered portions of the Hudson River during droughts and thus affect other water supplies or certain benthic species' roles in providing other needed ecosystem services? Another poignant example of our inability to manage "single-service contracts" with freshwater aquatic ecosystems is the increased mercury contamination in the Everglades, now the scene of dramatic and expensive efforts to restore the suite of ecosystem services that it once provided. Restoring and preserving watersheds, redirecting wastewater to specially constructed wetland ecosystems, and guarding against the introduction of alien species are important goals—but complete analysis also requires comprehensive studies of inputs from the airshed. Mercury contamination from rainfall containing metals derived from burning fossil fuels persists as a major issue even if water pollution and hydrology can be managed to sustain the benthic biota. The Pantanal provides a positive example of a vast and complex landscape that continues to sustain high productivity in a mixture of wetland ecosystems that change shape and chemistry as wet and dry seasons alternate. Although the Pantanal is probably a fragile collection of interdependent ecosystems, and important parts may yet be lost to the threats that impinge on it, its example impresses on us the reality that assaults to a benthic community may ultimately be repairable. This is the hope for many of the severely stressed freshwater systems in Asia and Africa that have lost most of their most important natural provisioning and support ecosystem services (especially provision of potable clean water) through excessive inputs of pollutants. Generally, freshwater ecosystems are resilient to many kinds of short-term threats, once the perturbation stops and recovery becomes possible (Resh et al. 1988; Jansson et al. 1999). Much of this resilience and resistance can be attributable to the benthic community, which seems to provide a stabilizing interface between the physical environment and the nonbenthic community, and hence many of the services the freshwater ecosystems provide.

Risk analyses, to help balance our demands on valuable ecosystems more effectively, depend on the knowledge of what human activities are damaging, how such damage can be avoided, and the extent to which ecosystem services that are currently impaired can be restored. In order to offer such advice, we also need information on what governs the production of ecosystem services, the role of biodiversity in the sustainability and level of the services, and how production of services changes under altered conditions. Can we rank the threats in order to provide some guidance as to what actions are the most important to avoid and what are the most useful for beneficial restoration? We might speculate that geomorphic alteration is the most serious, as freshwater systems are not resilient to this sort of change. Chemical pollution and local extinctions can be more easily mitigated against and recovery is usually rapid. Large-scale watershed/catchment perturbations (such as changing land use) and resultant hydrochemical changes are far more significant again than local point source pollution. Invasive species may or may not be significant, depending on how they interact with the native communities and the scale of activity and population growth. Pulse disturbances (which occur over a reasonably limited spatial and temporal scale), be they hydrological (such as natural drought or flood) or chemical (such as pollution events), have limited long-term impact due to the high resilience of most freshwater systems. On the other hand, longer-term directed press disturbances (such as acidification, eutrophication, human-induced climate change, and hydrologic regulation) will have a greater impact on the ecological communities and hence on the provision of ecosystem services. The extent to which biodiversity provides some "insurance" against such changes is not clear at present, but the evidence from evolution suggests that some species may adapt to change while others may become extinct, thus, the provision of some ecosystem services may remain. For freshwater systems, however, this insurance is also at risk, as available information suggests that freshwater biodiversity has declined much faster over the past 30 years than either terrestrial or marine biodiversity. The greatest effects appear to be in the densely populated regions of the tropics (particularly South and Southeast Asia) and in dryland areas (Jenkins 2003). This complex linkage within and among ecosystems, like the example of the River Rhine, whose water quality has been improved enough to see the reappearance of many species of aquatic insects and fishes, will benefit from continued long-term monitoring and analysis of complex trade-offs inherent in management decisions.

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