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Ecosystem Services Provided by Freshwater Benthos

Alan P. Covich, Katherine C. Ewel, Robert O. Hall, Jr.,
Paul S. Giller, Willem Goedkoop, and David M. Merritt

The concept of ecosystem goods and services (Daily 1997; Heal 2000; Brismar 2002) conveys how natural processes such as biomass production and nutrient cycling are essential to the Earth's capacity for sustaining human populations. Here we examine how species diversity and ecosystem processes, which supply these goods and services to human societies, are mediated by sediment- or bottom-dwelling (benthic) organisms in fresh waters. Benthic invertebrates, microbes, and aquatic plants are widely distributed in fresh waters. Their ecology is well understood in many temperate-zone regions and the diversity of freshwater benthic communities is broadly documented (Bronmark & Hansson 1998; Giller & Malmqvist 1998; Thorp & Covich 2001). This biota includes some species that are widespread, functional generalists and others that are restricted in their distributions and are functionally specialized.

Sediment-dwelling plants and invertebrates provide numerous critical ecosystem services in fresh waters (Ewel 1997; Covich et al. 1999), yet economic valuation of associated ecosystem functions is rarely measured other than in shellfisheries production (Carpenter & Turner 2000; Odum & Odum 2000). What are the values of nonmarket goods and services derived from a lake or river or wetland? Relationships between species diversity, water resource allocations, and freshwater ecosystem services are being evaluated by ecologists and economists (Loomis 2000; Daily & Ellison 2002; National Research Council in press). Moreover, benthic biologists are beginning to determine how the loss of different species affects freshwater ecosystem functioning (Wall et al. 2001); to date, however, these experiments have primarily focused on small-scale, short-term studies of relatively few species (Giller et al. 2004; Covich et al. in press). Vulnerability of ecosystem services is increasing because of the elimination of many fresh-

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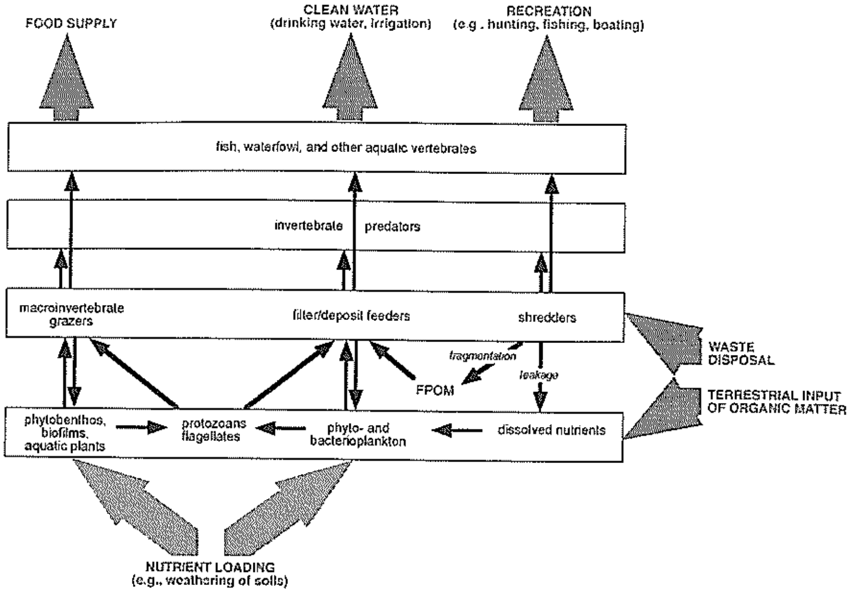

Figure 3.1. Schematic overview of a functional food web showing the linkages between food web processes and services provided by sediment and above-surface biota in freshwater ecosystems. Small black arrows indicate pathways for nutrient uptake and cycling from sediment-dwelling species to those in the open waters. Large gray arrows indicate major nutrient sources (inputs) and resulting ecosystem services (outputs) from biological processing in lakes and streams. FPOM = Fine Particulate Organic Matter.

water habitats and the accelerated rates of extinction among key species. Time for research on the ecological and economic importance of species is short (Everard & Powell 2002; Dudgeon 2003), and there is growing concern about losing these services following declines in species diversity (Davies & Day 1998; Moulton 1999).

In this chapter we outline the types and importance of freshwater ecosystem services. In particular, we discuss the role of benthic species in ecosystem processes such as productivity, nutrient transformations, and decomposition of organic matter (Figure 3.1). We also examine patterns of inter-connected ecosystem processes and ways to evaluate them. We briefly review how particular sediment-dwelling organisms can alter freshwater ecosystem services. We discuss three major categories of ecosystem services: provisioning, supporting, and cultural (Millennium Ecosystem Assessment 2003). Each of these categories is then illustrated with examples of how benthic species provide different ecosystem services. The vulnerability of ecosystem services in fresh waters is discussed in Chapter 6, where we consider the concept of disservice (or the exploitation of one ecosystem service that leads to a negative effect or elimination of a second service) and review several case studies.

Importance of Freshwater Ecosystem Services and Biodiversity

Ecosystem services in fresh waters depend on a range of different benthic species (Tables 3.1a–3.1e). For example, fish and shellfish yields depend heavily on sustained production of diverse benthic prey species (Huner 1995; New & Valenti 2000). Although only a few of the 390 species of crayfish native to North America are harvested for food, other crayfish species play major roles in ecosystem dynamics by linking sedimentary habitats with overlying waters through burrowing and mixing of sediments, nutrient cycling, breaking down dead organic matter, and grazing on submerged macrophytes (Covich et al. 1999; Hobbs 2001). Benthic invertebrates are essential prey for bottom-feeding fishes and aquatic mammals such as river otters and raccoons. Other freshwater ecosystem services include the breakdown of industrial and residential wastes by microbes and invertebrates (Geber & Bjorklund 2001; DeBruyn & Rasmussen 2002). Fresh waters dilute wastes, provide cooling waters for power generation and other industrial processes, as well as serve demands for recreational swimming, fishing, and boating (Postel & Carpenter 1997). The economic values of fisheries (New & Valenti 2000; Welcomme 2001) and recreational activities in fresh waters are well documented (Loomis 2000). Moreover, managers rely on monitoring services provided by benthic invertebrates by measuring changes in benthic species' presence and abundance to quantify indicators of water quality (Johnson et al. 1992; Clements & Newman 2002). These benthic species integrate local impacts over various time scales and provide important information on concentrations of dissolved oxygen, nutrients, and specific toxins. All these services are important for managerial decisions regarding water allocations (Postel & Carpenter 1997; Strange et al. 1999).

Benthic ecosystem services are sometimes considered a free resource (Mitsch & Gosselink 1993; Barbier et al. 1994; Acharya 2000). For example, clean drinking water supplies are derived from natural watersheds (Watson & Lawrence 2003). This essential ecosystem service is well studied by ecologists, economists, and environmental engineers. Clean drinking water can be naturally sustainable because of the role played by benthic species that carry out biofiltration, detoxification, and numerous processes that break down organic wastes in rivers, lakes, and groundwaters. Without this recycling by diverse microbes and benthic invertebrates, organic matter accumulates and leads to deoxygenation (through microbial respiration), which then causes rapid deterioration in water quality and often results in fish kills. The effectiveness of this natural "self-cleaning" ecosystem service is limited by the quantity, type, and rates of organic waste inputs that can be processed biologically under specific flow conditions and retention times (see Giller et al., Chapter 6). Thus, anthropogenic threats and influences

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Table 3.1a. Positive ecosystem service rankings (relative within fresh waters; not quantitative) for managed (flood-control reservoirs) and unmanaged lakes.

Explanation of service values:
(−3) = strong disservice; (0) = neutral; (3) = strong positive; n.a. = not applicable.

	Lakes: Unmanaged			*Lakes: Managed*		
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Service Rank*	*Biotic*	*Abiotic*
Provisional Services						
Food production						
Plant	0	n.a.	n.a.	0	n.a.	n.a.
Animal	2–3	***	*** flow-dependent	0–1	***	*** naturally flow-dependent
Other products						
Fuel/Energy	1	n.a.	***	1	n.a.	***
Fiber	0	n.a.	n.a.	0	n.a.	n.a.
Potable water	3	***	** dilution, sorption	0	n.a.	n.a.
Water quantity	3	n.a.	***	3	n.a.	***
Supporting Services						
Waste processing	2	***	*** dilution temperature	1	n.a.	n.a.
Climate modification C sequestration	0	n.a.	n.a.	0	n.a.	n.a.
Trace gas production	−1	***	* temperature	−1	***	*
Irrigation	3	n.a.	***	3	n.a.	***
Transport	3	*	***	3	*	***
Cultural Services						
Recreation	3	***	***	1 fish/boat/fowl	*	3
Aesthetic						

Asterisks indicate the relative importance of biotic and abiotic factors, from weak (*) to strong (***), in the provision of the associated good or service.

Table 3.1b. Positive ecosystem service rankings (relative within fresh waters; not quantitative) for rivers and waterways.

Explanation of service values:
(−3) = strong disservice; (0) = neutral; (3) = strong positive; n.a. = not applicable.

	Rivers: Unmanaged			*Waterways: Managed (Channelized)*		
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Service Rank*	*Biotic*	*Abiotic*
Provisional Services						
Food production						
Plant	0	n.a.	n.a.	0	n.a.	n.a.
Animal fish shellfish	2–3	*** decomposers, organic matter transformation, nutrient transformation (nitrification, etc.), intact food web	** trophic status, nutrient inputs, temperature	0–1	*** modified food web	*** chemical inputs, depth, geomorphology, topography, precipitation, trophic status, nutrient inputs, temperature
Other products						
Fuel/Energy	0	n.a.	n.a.	0	n.a.	n.a.
Fiber	0	n.a.		0	n.a.	n.a.
Potable water	3	*** nutrient cycling, decomposition, nitrification, phosphate liberation, DON, DOC	** residence time, depth topography	3	*** nitrification, phosphate liberation, DON, DOC	**

Table 3.1b. *(continued)*

Goods and Services	*Rivers: Unmanaged* Service Rank	*Rivers: Unmanaged* Biotic	*Rivers: Unmanaged* Abiotic	*Waterways: Managed (Channelized)* Service Rank	*Waterways: Managed (Channelized)* Biotic	*Waterways: Managed (Channelized)* Abiotic
Water quantity	2–3	*	***	3	* organic matter, moisture retention	* geomorphology
Supporting Services						
Waste disposal	3	*** nutrient cycling, decomposition	**	1–2	***	**
Climate modification	2	*** organic matter burial in sediments, decomposition	** Calcium carbonate deposition	1	** bacterial-based food webs enhance C loss (but still net C accumulation), CH_4 emission from manure	* moisture, complexing, etc.
C sequestration	1		**	1		
Trace gas production	−1					
Irrigation	1	n.a.	***	3	n.a.	***
Transport	3	***	**	1–2	*	***
Cultural Services						
Recreation	3	***	***	1 fish/boat/fowl	*	3
Aesthetic						

Asterisks indicate the relative importance of biotic and abiotic factors, from weak (*) to strong (***), in the provision of the associated good or service.

Table 3.1c. Positive ecosystem service rankings (relative within fresh waters; not quantitative) for managed and unmanaged wetlands.

Explanation of service values:
(−3) = strong disservice; (0) = neutral; (3) = strong positive; n.a. = not applicable.

Goods and Services	*Wetlands: Unmanaged* Service Rank	*Wetlands: Unmanaged* Biotic	*Wetlands: Unmanaged* Abiotic	*Wetlands: Managed* Service Rank	*Wetlands: Managed* Biotic	*Wetlands: Managed* Abiotic
Provisional Services						
Food production						
Plant	1	**	***	3	**	***
Animal	2	***	***	1	***	***
Other products						
Fuel/energy	0	n.a.	n.a.	0	n.a.	n.a.
Fiber	2	**	***	0	**	***
Potable water	3	***	***	0	n.a.	n.a.
Water quantity	0	n.a.	n.a.	−1	n.a.	***
Supporting Services						
Waste disposal	3	***	***	2	***	** application of manure
Climate modification						
C sequestration	0	n.a.	n.a.	0	n.a.	n.a.
Trace gas production	3	***	***	3	***	***
Irrigation	0	n.a.	n.a.	0	n.a.	n.a.
Transport	0	n.a.	n.a.	0	n.a.	n.a.
Cultural services						
Recreation	1	***	***	0	n.a.	n.a.
Aesthetic	2	**	***	2	***	***

Asterisks indicate the relative importance of biotic and abiotic factors, from weak (*) to strong (***), in the provision of the associated good or service.

Table 3.1d. Positive ecosystem service rankings (relative within fresh waters; not quantitative) for groundwater and abstraction.

Explanation of service values:
(−3) = strong disservice; (0) = neutral; (3) = strong positive; n.a. = not applicable.

	Groundwater: Unmanaged			*Abstracion: (Artificially Recharged)*		
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Service Rank*	*Biotic*	*Abiotic*
Provisional Services						
Food production						
Plant	0	n.a.	n.a.	0	n.a.	n.a.
Animal	0	n.a.	n.a.	0	n.a.	n.a.
Other products						
Fuel/energy	1		*** geothermal	1		*** geothermal
Fiber	0	n.a.	n.a.	0	n.a.	n.a.
Potable water	3	***	** percolation	3	***	*** infiltration (recharge)
Water quantity	3	n.a.	***	3	n.a.	***
Supporting Services						
Waste disposal	1	** bioremediation	** reverse wells	0	n.a.	n.a.
Climate modification	0	n.a.	n.a.	0	n.a.	n.a.
C sequestration	0	n.a.	n.a.	0	n.a.	n.a.
Trace gas production	0	n.a.	n.a.	0	n.a.	n.a.
Irrigation	3	n.a.	***	3	n.a.	***
Transport	0	n.a.	n.a.	0	n.a.	n.a.
Cultural Services						
Recreation	0	n.a.	n.a.	0	n.a.	n.a.
Aesthetic	1	* microbial mats, sulphur precipitation	geysers, springs	0	n.a.	n.a.

Asterisks indicate the relative importance of biotic and abiotic factors, from weak (*) to strong (***), in the provision of the associated good or service.

Table 3.1e. Positive ecosystem service rankings (relative within fresh waters; not quantitative) for prairie floodplain and drained wetlands.

The column on the left represents an intact ecosystem and the one on the right represents a managed ecosystem likely to be derived from the other. Explanation of service values:
(−3) = strong disservice; (0) = neutral; (3) = strong positive; n.a. = not applicable.

	Prairie Wetlands and Floodplain Forests			*Agricultural Crops on Drained Wetlands*		
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Service Rank*	*Biotic*	*Abiotic*
Provisional Services						
Food production						
Plant	0	n.a.	n.a.	3	**	***
Animal	2	***	**	2	***	**
Other products						
Fuel/energy	1	***	**	2	***	**
Fiber	0	n.a., no present-day use	n.a.	0	n.a.	n.a.
Potable water	3	**	***	−2	n.a.	***
Water quantity groundwater recharge flood mediation	2	n.a.	***	−1	n.a.	***
Supporting Services						
Waste disposal	0	n.a.	n.a.	0	n.a.	n.a.
Climate modification						
C sequestration	0	n.a.	n.a.	0	n.a.	n.a.
Trace gas production	1	***	***	0	n.a.	n.a.
Irrigation	0	n.a.	n.a.	0	n.a.	n.a.
Transport	0	n.a.	n.a.	0	n.a.	n.a.
Cultural Services						
Recreation	2	***	**	2	***	**
Aesthetic	3	***	**	1	**	**

Asterisks indicate the relative importance of biotic and abiotic factors, from weak (*) to strong (***), in the provision of the associated good or service.

can alter the balance of natural regulatory factors such as energy flow, organic matter transport, hydrologic regimes, biogeochemical cycles, and hydrochemistry (Palmer et al. 2000; Malmqvist & Rundle 2002). They change the structure of sediments, alter temperature regimes, and cause other extreme environmental conditions beyond normal levels of variation.

Misuse or overuse of one type of ecosystem service can lead to a negative effect on other important services and the biota and the ecosystem functions that underpin them (see Giller et al., Chapter 6). For example, soils are critical in the production of food and fiber, but overexploitation of terrestrial ecosystem services can diminish downstream services provided by sediment-dwelling systems. Runoff from intensive agricultural fields following heavy rains can contain excessive nitrogen because of the overuse of fertilizers or the accumulation of animal wastes. When these high-nutrient concentrations are combined downstream with nitrogen and phosphorus from sewage effluents and other sources, they cause excessive growth of aquatic plants and deoxygenation associated with eutrophication. Human health suffers from the poor water quality resulting from growth of toxic algal species (Burkholder 1998; Anderson et al. 2002) and increased abundance of disease pathogens in nutrient-laden rivers and estuaries. Furthermore, deoxygenation of nutrient-rich fresh waters results in increased ammonia, which is toxic to fish and many benthic invertebrates. The buildup of nitrate in groundwater can also pollute drinking waters and result in "blue babies" (methaemoglobinaemia) when infants drink contaminated water (Bouchard et al. 1992; Gupta et al. 2000; Mallin 2000). Thus, the provision of clean drinking water (through biotic treatment in ground waters and surface waters) is lost because of eutrophication (Brock 1985; Baerenklau et al. 1999; Boyle et al. 1999; Carpenter et al. 1999; Bockstael et al. 2000). Disservice results when ecosystems are poorly managed and positive natural processes are lost (see Giller et al., Chapter 6). Protection of catchments and good riparian and wetland management contributes to the maintenance of ecological processes and associated critical ecosystem services.

Analysis of Roles Played by Benthic Species

1. *Ecological evaluation of ecosystem service.* Society has alternative uses for fresh water, which are associated with competing demands for particular quantities and qualities of water. For example, in Central Asia, increased diversions of water from the Amu and Syr Darya Rivers expanded production of irrigated agriculture and other upstream uses beginning in the early 1960s, but resulted in major declines in fish production and water-based transportation after the Aral Sea partially dried and became more saline. The results included loss of aquatic species and endangerment of human health in and around what had been the fourth largest lake in the world (Williams 2002). Another example of these trade-offs for competing demands for fresh waters led to ecosystem degradation resulting from lower lake levels in Mono Lake, east of the Sierra Nevada Mountains of California. Demands for fresh water increased rapidly in the Los Angeles Basin and water was diverted from the Owens River in the Mono Lake Basin. These diversions to Los Angeles resulted in fewer breeding sites for migratory waterfowl and changes in lake food webs as salinity increased (Hart 1996). Local community action eventually restored the integrity of the lake ecosystem (Loomis 1987, 1995). These sorts of trade-offs require careful ecological evaluation of the full range of ways in which water allocations and species loss may alter ecosystem services. Ecologists and economists are beginning to quantify trade-offs among different uses of ecosystems influencing water quality and yield (Whigham 1997; Loomis et al. 2000). As is discussed below, more research is needed to evaluate how loss of species diminishes or eliminates critical ecosystem services.

2. *Economic evaluation of ecosystem services.* Many natural freshwater ecosystem processes have definable economic values (Abramovitz 1998; Pearce 1998) as well as the non-use, existence, and aesthetic values that must also be evaluated in ways that reflect the importance of protecting benthic species and their habitats. Methods to determine economic values include market pricing, contingent evaluation, cost-benefit analysis, consideration of replacement costs, and prices of substitute goods and services, if any (National Research Council in press). Values of ecosystem services such as the production of high-quality drinking water or storm mitigation (protection of river banks and lake shores by riparian vegetation) can be estimated by determining how much people are willing to pay for, or, if possible, to replace these services (Cleveland et al. 2001; Daily & Ellison 2002). The costs of comparable substitutes (e.g., in the form of engineered replacements for natural benthic ecosystems) provide one means to evaluate the economic values of some natural services provided by sediment-dwelling organisms. For example, building filtration plants to provide clean drinking water for New York City could cost from US$2 to 8 billion (Foran et al. 2000; O'Melia et al. 2000; Gandy 2002), while protection of the watershed's natural communities of benthic invertebrates and improved riparian management is likely to save many or all of the costs of building filtration plants (Daily & Ellison 2002). On-going studies of water quality and stream invertebrates by ecologists at the Stroud Water Research Center in Pennsylvania, USA, are documenting these ecosystem services (Bern Sweeney, personal communication 2003). Replacement costs of wetlands that provide natural filtration are also generally large (Mitsch & Gosselink 1993; Bedford 1996; Williams 1999) because of the complex nature of these ecosystem processes performed by numerous sediment-dwelling species of plants and animals. For example, more than US$500 million is being spent to restore 11,500 hectares along 90 km of the old river channel of the Kissimmee River Basin in Florida (Dahm et al. 1995; Toth et al. 1998). Services from the natural meandering river and its floodplain were lost in the 1960s when 167 km of the river was channelized and 21,000 hectares of wet-

lands were drained (Whalen et al. 2002). Other attempts to replace lost services with artificially constructed wetlands have had limited success, especially if native species and habitat structures are not included in the design (Zedler 2000; Bonilla-Warford & Zedler 2002; Stevenson & Hauer 2002). Similarly, as discussed in Chapter 6, attempts to restore ecosystem services provided by benthic organisms in European rivers (following industrial pollution, channelization, and dam building) continue to face serious constraints (Cioc 2002). In many cases there are no satisfactory and sustainable substitutes for natural ecosystem services.

Complexity of Natural and Managed Freshwater Ecosystems

Determining the total economic value of freshwater ecosystems is very difficult because some of their ecological functions have competing commercial values and others have primarily aesthetic or existence values. Studies that illustrate the importance of freshwater benthic ecosystems in providing essential services for sustainable human populations require a comprehensive perspective on evaluation of freshwater services that include both use and non-use values (National Research Council in press). The values of drinking water, freshwater fish, and shellfish, as well as recreational uses of rivers, lakes, and wetlands are very important to humans regardless of the methods used to estimate their market values. Indeed, "use values" derived from market pricing and the intrinsic "existence values" (estimated from surveys and nondirect methods) can be complementary and combined to document the need to maintain the biodiversity of fresh waters. Once species are lost, their economic values become abundantly clear to the general public but their natural services often cannot be fully restored or artificially replaced. Lessons from these failures can be extended to avoid similar future losses in other freshwater ecosystems.

Types of Freshwater Ecosystem Services

The goods and services provided to humans by freshwater benthic ecosystems may be classed as *provisioning services,* or products obtained from ecosystems, such as plant and animal food and fiber; *supporting services,* or services necessary for the production of all other ecosystem services, such as waste processing, the production of a sustained clean water supply, flood abatement, and climate moderation; and *cultural services,* or nonmaterial benefits obtained from ecosystems, such as aesthetics, education, and recreation (Millennium Ecosystem Assessment 2003). Besides natural waste treatment that enhances water quality, many freshwater ecosystems are critical habitats for certain life stages of marine and freshwater fishes, waterfowl, and other sources of human foods. Moreover, these benthic ecosystems provide critical habitat for many other species.

Understanding natural processes that contribute to ecosystem services is of immediate concern given the rates at which human activities are altering natural fresh waters. As human population densities increase further and new chemical compounds and technologies are developed, unanticipated consequences will have long-lasting impacts on freshwater benthic ecosystems (Malmqvist & Rundle 2002). If fresh waters are degraded under intensive exploitation, their natural processes can be diminished or lost completely. As native species are lost through local extinction and nonnative species are introduced into fresh waters, there is lively debate regarding trade-offs among different management alternatives. It is critical that decision makers understand how species can provide unique roles in cycling nutrients and in producing valuable commodities and services in many different types of fresh waters. Tables 3.1a–3.1e highlight the major goods and services under a number of major categories (including food production, water quality and quantity, waste disposal, climate modification, and recreation). The relative importance of services varies across the different freshwater ecosystems.

Groundwater

Provisioning Services. Groundwater supplies drinking, municipal, industrial, and irrigation water worldwide. The most important ecosystem service humans receive from groundwater is providing clean water for drinking. Although abiotic processes control water quantity through recharge, microbes are especially important in producing clean water. Microbial remediation of contaminated groundwater is another ecosystem service provided by sediment-dwelling organisms. Bioremediation of groundwater often benefits from injecting microbial assemblages into contaminated sites and encouraging bacterial growth with nutrient additions (Ghiorse & Wilson 1988; Baker & Herson 1994). For example, bacteria can remove nitrate or degrade recalcitrant organic contaminants. Groundwater supports a rich food web consisting of microbes and metazoan consumers (Marmonier et al. 1993). Because these groundwater species respond to chemical contamination, they can be used to identify polluted aquifers (Gounot 1994; Moeszlacher 2000). For example, the presence of certain flagellates and their grazing of bacteria may increase degradation rates of toluene (Mattison & Harayama 2001). However, little is known about the details of food web interactions in groundwater or subsurface flows in stream channels (hyporheic zones) that alter degradation and removal rates of contaminants (e.g., nitrate, organic compounds).

Lakes and Rivers

Provisioning Services. Benthic organisms in lakes and rivers provide food production mostly through the dependence of fish production on invertebrate prey and nutrient cycling. Globally about 8×10^6 tons of freshwater fish are harvested, with double that amount produced by aquaculture (FAO 1995). Productivity of these fisheries will, in part, depend upon benthic production directly (e.g., consumption of benthic invertebrates or aquatic plants) or indirectly (e.g., benthic mineralization of nutrients). For example, Chinese polyculture relies on benthic productivity for plant and mussel production for feeding carp. Productivity of deepwater ecosystems is often influenced by how tightly the upper waters are linked to nutrient cycling in the lower waters that are in contact with sedimentary sources of nutrients. This process of pelagic-benthic coupling is critical in determining how nutrients (or toxins) are stored in sediments and seasonally cycled into surface waters, where they are incorporated into algal production and then consumed by filter-feeding zooplankton and fishes. Several marine fisheries influence and depend upon production in freshwater ecosystems (e.g., anadromous salmon spawn and juveniles are reared in freshwater rivers and lakes).

Support Services. Benthic species maintain water quality via transformation of excess nutrients and organic pollutants. For example, stream organisms can rapidly take up and incorporate nitrogen into their biomass or produce ammonia or methane that enters the atmosphere, thereby lowering the loads of dissolved organic nitrogen (Alexander et al. 2000). Nutrients such as phosphorus in streams can be temporarily stored in sediments and the biota (Meyer & Likens 1979). Benthic bacteria permanently remove nitrogen via denitrification (e.g., Pind et al. 1997) as well as convert nitrogen from unusable to usable forms that can be taken up during plant growth. Invertebrates and microbes that are widely distributed in natural ecosystems also occur in sediments and biofilms found in water-treatment plants. Thus, the biological functions are similar, although the species and densities generally vary greatly between natural and artificial habitats and these communities respond primarily to nutrient loading (e.g., Kadlec & Knight 1996; DeBruyn & Rasmussen 2002). Other species of macroinvertebrates (such as stoneflies and caddisflies) that break down particular types of organic materials are restricted in their distributions. Many occur in pristine, unmanaged habitats where low levels of nutrients and high concentrations of dissolved oxygen are sustained by a diverse assemblage of plants and animals.

The breakdown of dead organic matter (detritus) is an ecosystem service provided by most freshwater benthic communities. The roles of benthic detritivores that transform and transfer nutrients are well documented (Wallace et al. 1996; Giller & Malmqvist 1998). Benthic organisms shred coarse sizes of organic matter into finer particles. Microbial species condition detritus, which facilitates use by the shredding invertebrates, and also decompose organic particles. Microbes also produce gases (CO_2, CH_4, N_2) that enter the atmosphere and dissolved forms of nutrients that enter the overlying waters. Dissolved nutrients increase the growth of algae and aquatic macrophytes, which in turn are consumed by herbivorous and omnivorous invertebrates and fishes, thus creating the basis for complex food webs (Covich et al. 1999; Crowl et al. 2001; Jonsson & Malmqvist 2003).

As previously discussed, water quality is maintained by a number of biotic processes that are associated with sedimentary habitats where benthic invertebrates play well-defined roles in ecosystem processes. The loss of certain species or their changes in abundance may impair ecosystem function and consequently ecosystem services. For example, findings from Coweeta Hydrologic Laboratory, a US National Science Foundation Long Term Ecological Research site in North Carolina, indicated that measures of stream water quality (associated with rates of detrital processing) declined when stream insects were experimentally eliminated from a stream. Sequential declines in aquatic insect biodiversity correlated with the changes in stream ecosystem processes. This study was the first field experiment to show that these measures of water quality correlated with ecosystem processes (Wallace et al. 1996). This research also showed specifically how physical and chemical impacts (which deplete invertebrate populations) may feed back to alter stream ecosystem processes. The ecosystem-scale evidence for this linkage in streams and rivers obtained from the research at Coweeta provided detailed information about specific ways in which ecosystem-level processes change following invertebrate removal. In these studies, many species of leaf-shredding invertebrates were known to process coarse leaf-litter inputs from riparian zones into smaller particles. To test the importance of this role of shredders in ecosystem function, the Coweeta researchers experimentally removed most stream-dwelling insects using low doses of insecticide, which lowered shredder secondary production to 25 percent of that of a nearby reference stream (Lugthart & Wallace 1992). Organic carbon export from the watershed decreased dramatically following the insecticide treatment (Cuffney et al. 1990). Leaf decomposition was twice as slow in the invertebrate removal stream, so standing stocks of leaf litter were much higher. In general, lower export of organic carbon from headwater streams may lower animal production in downstream food webs, where filter-feeding species may be facilitated by shredding species living upstream (Heard & Richardson 1995).

Studies at the Luquillo Experimental Forest in Puerto Rico (another US National Science Foundation Long Term Ecological Research site) further demonstrate the potential for a single species to have an impact on ecological functions. A freshwater shrimp (*Xiphocaris elongata*) is one of the few species of shredders that facilitates the uptake of suspended organic particulates by a filter-feeding species of shrimp (*Atya lanipes*), which co-occurs in some tropical headwater streams (Crowl et al. 2001). Loss of these species' functions of shredding and filter feeding would likely result in slower rates of leaf litter breakdown and less energy flow in the headwater food web. This loss of species that shred leaf detritus may be critical in tropical headwaters, where species of shredding insects are relatively rare and the functional redundancy among leaf shredders is relatively low (Covich et al. 1999; Dobson et al. 2002). Related research is beginning to identify the degree to which ecosystem services of rivers and other freshwater ecosystems are altered directly by physical and chemical impacts (e.g., low O_2, low pH, or high sedimentation) compared with being altered indirectly through the loss of key animal taxa (Jonsson & Malmqvist 2003).

Accumulation of organic matter can slow decomposition by microbial species and detritivorous invertebrates when dissolved oxygen is depleted by high rates of respiration, especially at warm temperatures. Deoxygenation subsequently results in displacement of numerous species that require high oxygen concentrations and replacement by other species that can tolerate the stressful conditions of low dissolved oxygen. This sequence of species substitutions typically results in a degraded stream community with nuisance and disease-transmitting characteristics as well as reduced capacity for providing critical ecosystem functions. For example, heavy pollution and deoxygenation in some urbanized streams around Rio de Janeiro eliminated Atyid shrimp, which previously filtered out suspended organic matter. Following this pollution and loss of freshwater shrimp in the streams, the increased densities of filter-feeding blackflies led to more biting insects due to the loss of the same ecological function (filtration of suspended organic matter) by the shrimp (Moulton 1999). Other benthic invertebrates directly serve as biocontrol agents by feeding upon vectors of diseases (e.g., aquatic insects and crustaceans that feed on certain species of mosquito larvae and snails) that are prevalent in tropical freshwater habitats. Field studies substantiate the widespread importance of benthic invertebrates as indicators of water quality and as functional regulators of important ecosystem functioning (Clements & Newman 2002).

Wetlands and Associated Freshwater Habitats

Among the most critical and scarce freshwater ecosystems are marshes, floodplains, and swamps. Although they cover only roughly 6 percent of the Earth's land surface and are most common in temperate and boreal regions, wetlands perform a wide range of ecosystem functions, many of consequence on a global scale. Most of these functions are related either directly or indirectly to the activities of the flora and fauna living in sediments. Wetlands occur where saturation or inundation often produces anaerobic sediments, limiting rooted plant diversity to only those species adapted to anoxic conditions (Ewel 1997; Brinson & Malvarez 2002). Seasonal and interannual patterns of hydrologic regime and water source (rain, groundwater, and/or riverine surface water) govern many of the characteristics of wetland ecosystems, including species diversity and primary productivity. Freshwater wetland types include wet meadows, fens, bogs, lake margins, floodplain forests and bottomland swamps, tropical peat swamps, and extensive boreal peatlands. All wetlands are flooded long enough to influence the types of biota able to inhabit the site and the character and rate of biogeochemical processes. The global diversity of wetlands derives from regional and local differences in hydrologic regime (especially duration of flooding but also water residence time and water chemistry), physical factors such as fire and storms, unique characteristics of the plant species inhabiting those wetlands, and the influence of the animals that visit and live in them.

These many types of wetlands often are connected to surface and subsurface waters. Their ecosystem services include cycling of nutrients, breakdown of organic matter, and filtering of sediments that otherwise would enter rivers (Naiman & Decamps 1997; Keddy 2000). Yet, these critical habitats are being lost at a rapid rate despite their recognized values and legal standing (Dahl et al. 1991; Bedford 1999; Brinson & Malvarez 2002). Threats to rivers, floodplains, and lakes are also increasing (see Giller et al., Chapter 6) and are likely to result in loss of their essential ecosystem services.

The draining of wetlands and other threats to freshwater ecosystems have given rise to local and regional programs aimed at reducing their loss and restoring them to natural levels of diversity (Zedler 2000; Mayer & Galatowitsch 2001). In some cases new wetlands are constructed in other areas to attempt to offset the loss of natural wetlands (Moshiri 1993; Kladlec & Knight 1996). These constructed wetlands for "mitigation banking" can provide some ecosystem services, but often lack the biodiversity as well as the hydrologic regime that characterize natural ecosystems. Successful management for the sustainability and reliability of ecosystem services remains uncertain.

Provisioning Service. Riparian wetlands often have higher concentrations of microorganisms, insects, and animals than adjacent ecosystems (Naiman & Decamps 1997), and in arid regions they may be the only forested natural vegetation, thereby providing valuable habitat for arboreal species (National Research Council 2002). Many terrestrial animals, both vertebrates and invertebrates, use wetlands during some portion of their lives, and 50 percent of the 800 species of protected migratory birds in America rely on wetlands for habitat and food resources associated with benthic production of invertebrates and aquatic plants (Wharton et al. 1982). For example, 50 to 80 percent of the duck populations in North America are produced in north-central prairie potholes. These ecosystems provide hunters with significant recreational opportunities of economic importance (Batt et al. 1989). Waterbirds use a range of habitats including ponds, swamps, lagoons, mudflats, estuaries, embayments, and open shores of lakes, rivers, and reservoirs. Wetlands flooded to average depths of 15 to 20 cm (fringe and depressional wetlands) accommodate the greatest richness and abundance of birds (Taft et al. 2002).

Beavers play an important role in wetland landscapes as ecosystem engineers, creating a tremendous expansion of wetlands that otherwise would not have existed. Beaver harvests have averaged 400,000 pelts per year over the past century in North America (Novak et al. 1987). Alligators are also harvested for their pelts and meat, generating over US$16 million in a single year in the state of Louisiana, USA (Mitsch & Gosselink 2000). Crayfish aquaculture has also become an important use of natural and created shallow marshes in North America, northern Europe, and Australia in recent years. *Procambarus clarkii* accounts for about 90 percent of the 60–70,000 tons of crayfish cultured annually for food in North America (Huner 1995).

Nearly all commercially harvested freshwater fish and shellfish species depend on fringe or riverine wetlands at some life stage (typically for spawning or for nursery habitat). Anadromous fishes are less reliant directly on freshwater marshes, but fry may use riverine marshes for protection. Plant foods are harvested from fringe, riverine, and depressional wetlands as well as from extensive peatlands. For instance, berries from boreal peatlands are an important and nutritious part of the diet typical of high-latitude human populations (Usui et al. 1994). The worldwide average annual harvest of blue-berries (*Vaccinium myrtillus*) was 157,128.6 million tons (1990–2002), with approximately 42,000 ha in production (FAO 2003). The total wild berry harvest in Finland can be as high as 10^9 kg per season for a market value of more than US$240,000 (Wallenius 1999). Rice production in managed wetlands plays an important role in world nutrition and in the global economy. About 596 million tons of rice are produced each year (86 percent of this is consumed by human populations), harvested from 1.6 million km^2 of wetlands (IRRI 2000).

Wetland timber is harvested for pulp and building materials; peat (partially decomposed organic material) for fuel and horticultural soil amendment; and herbaceous vegetation from marshes for livestock fodder, fuel, fiber, and other products. Harvesting may require lowering of water tables to facilitate access to and removal of materials, which may permanently alter species composition. Peat harvesting is often viewed as renewable, but recovery may take centuries or more. Peatlands cover 420 million ha globally, with the most extensive habitats located in Russia and Canada. Peat is used as fuel to generate electricity or for conversion to methanol or industrial fuels (Rydin et al. 1999; Mitsch & Gosselink 2000). It may also be used to remove toxic materials and pathogens from wastewater and sewage (Jasinski 1999). Wetland meadows of many kinds are used for harvesting fodder and grazing livestock throughout the world. In Scandinavia, wet meadows bordering lakes and rivers are some of the most productive areas for the production of livestock fodder (Nilsson 1999; Rosén & Borgegård 1999).

Supporting Service. Wetlands can recharge local and regional shallow groundwater water systems; small wetlands can be very important locally (Weller 1981). Many wetlands may also improve water quality by removing organic and inorganic materials from inflowing waters. Wetland vegetation takes up and stores nutrients and some toxic compounds, thereby removing them from rapid cycling. Where water levels fluctuate, microbial denitrification can reduce nitrogen loads.

Waste processing is a service most often attributed to wetlands, although it is generally restricted to a few kinds of wetlands that can treat only certain wastes under specific conditions. Generally, riverine and fringe wetlands treat non-point-source pollution, such as from agricultural fields, either directly through the uptake of nutrients, chemicals, and metals, or indirectly through the chemical transformation and processing of toxic compounds. For example, the freshwater tidal marshes of the Hudson River retain nutrients and result in denitrification when properly managed (Zelenke 1998). Depressional wetlands and extensive peatlands can substitute for tertiary wastewater treatment (e.g., Odum 1984; Ewel 1997), but the lack of control over waste processing has made construction of artificial wetlands more attractive (Ewel 1997). Wetlands created for further treatment of secondary sewage from major cities can remove up to 97 percent of the nitrogen delivered to them through a combination of uptake by plants and through denitrification (Costa-Pierce 1998).

The ability of wetlands to process wastes effectively depends on the rates of nitrogen, iron, manganese, sulfur, and carbon transformations that occur under increasingly low oxygen conditions in the sediments. Although wetlands maintain the widest range of oxidation-reduction reactions of any ecosystem, effective waste processing depends on appropriate ratios of many compounds. Overloading the system can compromise ecosystem functions. Waste processing and biological fixation of nitrogen relies on microbes such as *Azotobacter, Clostridium butyricum, Rhizobium* in root nodules, and cyanobacteria. Sediment-dwelling fauna affect surface and subsurface flows of water as well as stimulate microbial activity, even to the extent of changing the entire nature of a wetland. Beavers dam rivers, creating ponds and fringe wetlands, and alligators excavate cavities in wetlands in karst regions, such as the Florida Everglades (United States), facilitating the concentration of fish in patches of swamp wetlands during dry seasons.

Large expanses of wetlands (extensive peatlands in particular) are believed to affect global climate through the alteration of carbon dioxide and methane cycles. Burning peat as fuel further increases production of greenhouse gases such as carbon dioxide. Current global warming trends are likely to result in increased atmospheric trapping of greenhouse gases, in part because of the release of methane from boreal peat bogs. Wetlands contribute from 33 to 50 percent of the total annual methane production per year (100 teragrams; Whiting & Chanton 1993), mostly from boreal peatlands but approximately 25 percent from tropical and subtropical wetlands as well.

Cultural Services. Recreation such as bird watching, boating, fishing, and hunting are ecosystem services provided by many freshwater food webs that are supported by benthic organisms. In some areas, the recreational catch and value to the economy of recreational fishing outweigh the commercial catch because recreational fishermen spend nearly five times more per fish caught than commercial fishermen (DeSylva 1969). In South America, for example, the Pantanal provides many opportunities for ecotourism and recreational fishing in this enormous tropical wetland (approximately the size of the state of Florida). Its basin includes approximately 138,000 km^2 in Brazil and 100,000 km^2 in Bolivia and Paraguay (see Giller et al., Chapter 6). For four to six months of most years, some 70 percent of the land is inundated. Hunters, fishermen, and conservationists travel from all over the world to view and to exploit this exceptional biodiversity (Moraes & Seidl 1998). During the dry season, this wetland becomes a savanna used for grazing large herds of cattle.

Species Diversity and Ecosystem Services

In many regions, biodiversity is concentrated in specific "hot spots" of high species richness. For example, riparian areas and riverine wetlands typically maintain a much higher biodiversity than the proportion of the landscape that they occupy (National Research Council 2002). Large, ancient ecosystems such as Lake Baikal, the Amazon River, and the Pantanal wetland are other examples of especially diverse biotic communities. The seasonally flooded forests in the Amazon basin contain about 20 percent of the 4,000–5,000 estimated Amazonian tree species (Junk et al. 1989), and fish diversity in the Amazon Basin is exceptionally rich. The Pantanal contains more than 400 species of fish and many species of benthic invertebrates (see Giller et al., Chapter 6) in addition to providing habitat to endangered species such as the giant river otter (*Pteronura braziliensis*).

In the Santa Monica Mountains of Southern California, less than 1 percent of the total land area is comprised of wetlands but approximately 20 percent of the native vascular plant species have their primary habitat there (Rundel & Sturmer 1998). In Sweden, 13 percent (>260 spp) of the country's entire vascular plant flora occur along the Vindel River (Nilsson 1992). In France, 30 percent of the country's 1,386 vascular plant species occur along the Adour (Planty-Tabacchi et al. 1996). Approximately 28 percent of the threatened or endangered plants, 58 percent of threatened or endangered vertebrates and mussels, and 38 percent of threatened or endangered insects in the United States occur in wetlands (Niering 1988). Nevertheless, half of the world's wetlands are estimated to have been lost during the 20th century (Dahl 1990). More than half of this loss has been in the United States, and most resulted from conversion to agriculture and other land uses (Dahl et al. 1991).

Research Needs and Recommendations

Given the many services provided by benthic species living in a wide range of freshwater habitats, we must better understand how to maintain and protect these species and their associated processes. We suggest several areas that need more study to improve management of these critical services:

1. *Link fisheries production to sustainable models of harvest and management that avoid crashes and long-term breakdown of ecosystem functions.* There is an urgent need to strengthen the long-term collection of data on inland fisheries resources if a more complete understanding is to be achieved about the production of benthic invertebrates and determinants of high-quality water. The relationships between safe levels of water quantity and quality that ensure adequate habitats for freshwater species are poorly understood. Too often, minimum values of flow and dissolved oxygen are viewed as sufficient although they are often based on short-term data. In fact, these guidelines do not provide reliable, long-term sustainability. Including margins of error to enhance the "safe minimum levels" will increase reliability and minimize long-term species losses and impairment of benthic ecosystem services.
2. *Communicate results of large-scale, long-term monitoring programs to community-based organizations.* Major changes in water quantity and quality can encourage governmental agencies and local communities to generate alternative actions such as communities that conserve water for sustaining instream flow needs and fisheries that provide sustainable ecosystem services. Results of water-quality monitoring programs need to be translated into formats that enhance effective and informed responses from a wide range of stakeholders. Management groups need to include wide representation by both professional managers and general consumers of ecosystem services. Community-based ecosystem management approaches will also help to establish systematic data collection on the direct and indirect costs and benefits of fish stocking, introduction, and other "enhancement programs" to determine impacts of nonnative fish species on benthic biodiversity and ecosystem services. Programs such as the European Union's Freshwater Directive, the US Environmental Protection Agency's Community-Based Ecosystem management Program, and the Nature Conservancy's Sustainable Waters Initiative are recent examples of frameworks that are designed to incorporate a wide range of stakeholders in decision making. More of these partnerships and social networks are needed to resolve conflicts regarding evaluations and alternative uses of fresh water.

3. *Monitor and restore habitats in rivers, lakes, and wetlands.* Information on a wider range of chemical and biological measures is needed to detect changes in both surface water and groundwater that are essential to ecosystem services. Enhanced technologies such as remote sensing, wireless data transmission, and comprehensive modeling to develop spatial data are needed to monitor the connections among groundwater levels, stream and river flows, lake-level changes, and wetland distributions at large scales. This regional and cross-national monitoring can provide up-to-date information on changes in the locations, sizes, and types of lakes and wetlands, especially in response to climate changes and global changes in land use. Extreme fluctuations in runoff and erosion from widespread deforestation and related land uses are rapidly altering sedimentary conditions in many fresh waters that, in turn, will alter benthic habitats and associated ecosystem services. Restoration and establishment of hydrological monitoring stations are needed to improve the water-quality monitoring at the regional level using benthic invertebrates and diatoms. Even though there is increased recognition of the long-term effects of climate changes (global warming, cyclic changes in El Nino–Southern Oscillation and the North Atlantic Oscillation, etc.), the capacity to monitor stream flows and lake levels on large-scales within nested watersheds is limited and even diminishing in many regions. Integrated information on data regarding long-term changes in groundwater resources, including their distribution, quality, capacity, and use, is needed across a wide range of scales in different regions.
4. *Restore natural flow regimes.* Information on the number and locations of dams, including the thousands of dams less than 15 m in height that are not currently listed in international databanks, must be compiled and made widely available. These small dams greatly influence the peak flows, minimum low flows, and habitats available for benthic species. Additional studies of the effects of dam removal are needed to identify trade-offs for comparisons with more innovative management of water releases from reservoirs. Many small dams are being removed to provide more upstream habitat for fishes, but sediment releases during and after reservoir removal can still degrade benthic habitats for many years. Furthermore, some nonnative species can increase their distributions following dam removal if the struc-

tures previously served as barriers to dispersal. What ecosystem services are lost when dams are removed? How can these relatively short-term losses be minimized and long-term gains maximized? These and many other questions are being investigated as more dams are being phased out and removed.

5. *Consider additional measures of diversity.* Diversity measures have usually considered just the number of species and/or functional groups in studies of benthic ecosystem processes. This limited approach excludes consideration of the range of diversity elements that potentially affect ecosystem services because different size and age classes within species, as well as their relative abundances, food preferences, and positions within food webs, all can influence rates of processes. Anthropogenic disturbances can substantially change the evenness of species, distributions of abundance, and foraging behavior without associated changes in species richness. The question of whether these changes in evenness, independent of changes in species richness, can influence levels of ecosystem functioning is a necessary focus of future investigation.

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