Biodiversity Conservation in Running Waters

Identifying the major factors that threaten destruction of riverine species and ecosystems

J. David Allan and Alexander S. Flecker

Flowing waters contain a tiny fraction of the stored water in the biosphere, yet they are of great importance to our physical, chemical, and biological world. Rivers and streams play a critical role in the continuous water cycle and in the flux of minerals and nutrients from higher to lower land and eventually to the sea. They provide humankind with clean drinking water, harvestable plants and animals, routes of travel and transport, waste removal, and renewable energy. Flowing water also provides spiritual uplift and cleansing. Everywhere on Earth, from the smallest village to the largest metropolis, the life of people is intimately intertwined with fresh, and often flowing, water.

In the impending biodiversity crisis, much attention has focused on tropical moist forests, and there is growing interest in ocean conservation. Freshwater systems have received less attention, however, and rivers and streams perhaps least of all. As the issue of biodiversity conservation moves toward the crowded center stage of global issues, it is important to recognize that running waters harbor a diverse and unique panoply of species, habitats, and ecosystems, including some of the most threatened species and ecosystems on Earth and some of those having greatest value to human society.

The potential for recovery of damaged river ecosystems is considerable

In this article, we describe the biological diversity of running waters and its state of imperilment, and we identify six major factors that threaten the destruction of these species and ecosystems. Finally, although few steps are being taken to protect river ecosystems, their potential for recovery is considerable, and we close with a discussion of measures to enhance the health of flowing waters.

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The biological diversity of rivers and streams

Running waters present unique patterns of distribution of biological diversity among taxonomic groups and among regions. Overall, the information is woefully incomplete. Knowledge of the number of species dwelling in the streams and rivers of a region is more complete for vertebrates than for invertebrates, as in terrestrial systems. It is also more complete within the temperate zone than in to the tropics.

All the vertebrate groups include species adapted to running waters, but the fishes dominate freshwater vertebrate diversity worldwide. They are especially species-rich in the tropics, where the diversity of freshwater fishes is perhaps the last major void in global knowledge of vertebrate diversity.

Although invertebrate diversity is incompletely catalogued, generally it exceeds vertebrate diversity at any locale. In contrast with the fishes and terrestrial insects, the diversity of insects in tropical streams does not appear to exceed that found in temperate streams.

Last, higher plants have relatively few species in flowing waters. Plant diversity is associated mainly with diatoms and other algae, especially in smaller streams.

The diversity of fishes. Nearly one-half of the described vertebrate species of the world are teleost fishes. There are approximately 22,000 described species of teleosts (Page and Burr 1991), with perhaps 35,000 species as the eventual total. Approximately 100 new species of freshwater fishes are described each year, compared with perhaps 2 new bird species. More than 700 species of fishes are known from the fresh waters of North America (Page and Burr 1991), somewhat more than the number of bird species that breed in North America.

Due partly to geology and partly to behavior, freshwater fishes tend to become isolated within drainages, resulting in distinctive populations and subspecies. This isolation safeguards genetic diversity, which is important to the future evolution of species.

The geographical distribution of

north temperate zone fishes reveals a complex spatial mosaic in terms of species richness and species composition. So, for example, the eastern half of the United States is today much more diverse than the western half (Figure 1), and the Mississippi drainage alone contains almost as many species as all of Europe.

Such a pattern results in part from habitat complexity and area; but, in addition, it derives from the evolutionary history of individual taxa and from the opportunities for isolation and dispersal that depend so much on the location of land masses, mountains, and valleys. Moreover, two areas of roughly comparable species richness may differ substantially in species representation, body form, and overall ecology.

The diversity of invertebrates. Although some of the most conspicuous insects of running waters, such as the mayflies (Ephemeroptera), have attracted the interest of naturalists and taxonomists since the seventeenth century, until the past few decades little was known about freshwater invertebrates in virtually all taxonomic groups and regions. Substantial recent progress has provided a sufficient knowledge base to allow field biologists in North America and Europe to identify most individuals in the better-studied groups to genus and often to species. Even in the comparatively well-studied temperate zone, however, a complete taxonomic inventory is a formidable task. The great majority of ecological studies and surveys reflect the uneven level of knowledge, with some taxa itemized at the species level, whereas others routinely are catalogued at the level of family, order, or even phylum.

An intensive effort of almost two decades in a small German stream approximately 1 m wide and 4.5 km long, passing through meadow and woodland, provides an unusually complete list (Table 1). It includes 1044 invertebrate species, a number that is likely to increase with further study, but probably not greatly. It is difficult to say what fraction derives from other habitats, such as small impoundments and standing water, but this fraction is probably less than one-third. The compilation indicates that the greatest invertebrate diversity is located

Figure 1. The number of fluvial fish species in selected river systems of North and South America. Data sources: Canada, Scott and Crossman 1973; United States, Lee et al. 1980 and Sheldon 1988; South America, Welcomme 1990.

within a few groups, including several minute, interstitial phyla (Nematoda, Rotatoria, Annelida, and Turbellaria) and the highly diverse Diptera, especially the midge family Chironomidae. Unfortunately, these taxa are both the least well described and most difficult to identify. Studies of individual streams have rarely examined more than 100 taxa. Nonetheless, it seems certain that the number of invertebrate species in a section of temperate stream may exceed the number of fish species by an order of magnitude.

The diversity of plants. Flowering plants, mosses, and liverworts, a few species of encrusting lichens, the stoneworts, and other large algal species constitute the macrophytes or larger plants of flowing waters. Most of these plants can also be found in standing water and exhibit few adaptations to life in currents (Hynes 1970). The number of species of river-inhabiting macrophytes is not great, nor are they abundant in many settings. Species richness generally increases as one proceeds downstream, with cool, hard-bottom streams containing mostly bryophytes, and larger, soft-bottom rivers supporting angiosperms. Up to 20 species may occur where environmental conditions are favorable and

Table 1. Provisional faunal list of the Breitenbach River, Schlitz, Germany. Numbers of species occurring in each major group is shown in the second column. Subsequent columns give the breakdown of insects by order, family, and subfamily, showing the large contribution to species richness made by certain groups, particularly the Diptera.

Phylum or class	Species number	Order	Species number	Family	Species number	Subfamily	Species number
		Odonata	1				
Insecta	642	Ephemeroptera	16				
		Plecoptera	18				
Turbellaria	50	Megaloptera	2	Tipulidae	30		
		Planipennia	2	Limoniidae	86		
Gastrotricha	6	Coleoptera	70	Ptychopteridae	2		
		Trichoptera	57	Psychodidae	35	Tanypodinae	15
Nematomorpha	1	Diptera	476	Chironomidae	152	Diamesinae	8
				Dixidae	4	Orthocladiinae	88
Nematoda	125			Culicidae	2	Chironominae	41
				Thaumaleidae	3		
Rotatoria	106			Ceratopogonidae	61		
				Simuliidae	10		
Mollusca	12			Rhagionidae	2		
				Empididae	21		
Annelida	56			Dolichopodidae	50		
				Tabanidae	8		
Crustacea	24			Stratiomyidae	3		
				Ephydridae	2		
Hydracarina	22			Syrphidae	5		
Total	1044						

Data courtesy P. Zwick, Limnologische Flußstation des Max-Planck-Instituts für Limnologie, Schlitz, Germany.

varied (Haslam 1987).

Among the plants of running waters, it is the benthic algae that are most diverse. Also known as periphyton, these algae occur on all possible surfaces in running waters. Typically, there is an intimate association of algae with microbes and an extracellular organic matrix, to which the all-inclusive term *Aufwuchs* applies. Although most major algal groups are represented, the diatoms usually dominate the species list, especially in shaded rivers.

In a southern Ontario stream with a bottom of clay and detritus, Moore (1972) recorded 388 algal species, of which 83% were diatoms. Algal colonists sampled on glass slides at various sites in the United States exhibited similar proportions (Patrick 1961). Thus, it appears that several hundred species of algae, the bulk of which are diatoms, are typical of many streams, whereas the number of species of higher plants is roughly an order of magnitude lower.

Geographical pattern in diversity

Biological diversity invariably exhibits a geographic pattern, which can be characterized in the following ways:

- The total number of species increases logarithmically with area surveyed.
- In general, more species are found at low than high latitudes.
- Some regions, colloquially known as hot spots, contain high local diversity.
- A substantial fraction of the species in certain regions are highly localized.

The freshwater biota exhibits all of these aspects of biogeographic pattern.

The relationship between species richness and river size is documented in Figure 2. This figure also shows that individual large river systems of the tropics have higher recorded diversity than is found in the temperate zone. In addition, species richness increases more rapidly with increasing river size at low latitudes compared with high latitudes (Welcomme 1979). In excess of 3000 species of freshwater fish are estimated to occur in tropical South America (Moyle and Cech 1982), primarily associated with riverine habitats (Lowe-McConnell 1987). This number greatly exceeds the approximately 700 species that occur in the lakes and rivers of temperate North America and the 177 native species that are found in the inland waters of Canada (Scott and Crossman 1973).

Based on limited knowledge, it appears that stream-dwelling invertebrates are no more diverse in tropical than in temperate locales (Illies 1969, Patrick 1964). Indeed, stream-dwelling invertebrates have been cited as a principal exception to the rule that tropical diversity exceeds temperate diversity (MacArthur 1972). In contrast, a few studies have hinted at higher diversity of insects in tropical streams (McElravy et al. 1981, Stout and Vandermeer 1975). The evidence is still too thin to instill much confidence, and resolution requires additional and more thorough surveys.

Even less can be said about the diversity of plants in tropical rivers. However, tropical rivers appear unique in both their great floating islands of macrophytes (Junk 1985) and in containing the only two families of flowering plants that exhibit reproductive adaptation to life at high current velocities (Hynes 1970).

Recognition of areas of high local species diversity is of obvious importance to the protection of biological diversity. Understanding how such hot spots originate and are maintained is a considerable scientific challenge, however. Habitat complexity and the opportunity for lengthy isolation of subpopulations are likely to be important. In addition, the behavior and life history of a taxon may favor isolation and subsequent speciation. So, for example, the darters and minnows (particularly the genera *Etheostoma* and *Notropis*) have undergone great diversification in the small streams of North America, resulting in higher local diversity than is found in comparable streams of Europe (Mahon 1984).

Imperilment of the fauna of running waters

A substantial fraction of the rare and threatened species of North America are aquatic, and primarily freshwater, taxa (Table 2; Master 1990). Within North American fresh waters, fish, mollusks, and crayfish have received the most attention. Much less is known about the imperilment of many other groups.

An accurate description of the status of river-inhabiting organisms is difficult for several reasons. Not only are listings of threatened species far from complete, but they also are strongly biased toward vertebrates. In addition, the distinction between running waters and ponds or lakes is complicated by the refusal of many species to recognize such boundaries. However, in the following discussion we focus on taxa that primarily occupy lotic habitats.

The extent of the endangerment of North American freshwater fishes is well summarized by Williams et al. (1989), who categorize 103 species and subspecies as endangered, 114 as threatened, and 147 as deserving of special concern. The total represents roughly one out of three species and subspecies of North American fishes. This ratio is approximate, however, because although there is good agreement on the number of species of North America fishes, the number of subspecies and unique populations is subject to interpretation.

Comparison with a 1979 list adds a telling detail. Some 26 fish were deleted from the earlier list: 11 because of taxonomic revision, 5 because subsequent data proved the taxon to be more common than originally believed, and 10 because they went extinct over the decade. Not one species was removed from the listing because of successful recovery. Changes in status provide a similar view: more than three times as many fish taxa have declined versus improved (24 versus 7) in status since a previous assessment (Williams et al. 1989).

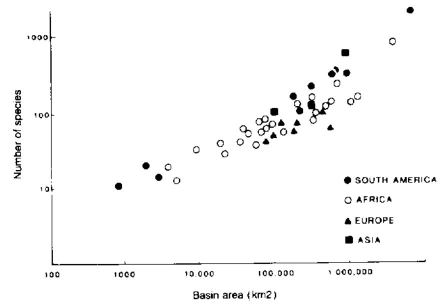

Figure 2. The number of fluvial fish species in river basins in relation to basin area (a useful correlate of the size and habitat complexity of a river system). The slope of the species-area relationship is 0.15 in northward-flowing Russian rivers, and for European, African, and South American rivers, respectively, the slope values are 0.24, 0.43, and 0.55. Data from Welcomme 1979, redrawn by Smith et al. 1988.

Documentation of imperilment and extinction of invertebrates is hampered by limited taxonomic knowledge and incomplete information on species' distributions. However, if the freshwater molluscs are any indication, the status of invertebrates is serious indeed.

North American river systems face catastrophic losses, which historically harbored an exceedingly high diversity of river snails (family Pleuroceridae) and mussels and clams (family Unionidae). The freshwater mussels of North America include 297 species and subspecies, of which 13 currently are extinct, 40 are endangered, 2 are threatened, and 74 are federal candidate species, for a total of 43% of the taxa (Neves 1992). This abundant and diverse fauna, which once served as an important food source for Native Americans and supported a commercial harvest for the manufacture of buttons, has been devastated by dam construction and degradation of water quality. Sadly, continuing habitat degradation and the impending invasion of the zebra mussel (*Dreissena polymorpha*) seem destined to eliminate all but a hardy minority.

No stream-dwelling insect currently is listed under the Endangered Species Act, although a substantial number are candidates for inclusion, and the Red List of the World Conservation Union includes a number of aquatic insect taxa (IUCN 1990). Inadequate knowledge of historic compared with present abundance and distribution, exacerbated by incomplete taxonomic information, limits ability to assess the rarity of insect taxa.

Few plants of running waters are considered to be imperiled, not surprisingly. The few species of higher plants that occur in rivers occupy a wide variety of habitats, which minimizes their vulnerability. For the algae, incomplete knowledge again prevents any assessment of their rarity. Only *Ptilimnium nodosum*, an annual herb in the parsley family, and *Zizania texana*, or Texas wild rice, are riverine plants currently listed as endangered.

Biotic impoverishment includes more than the loss of species. There are many instances where a river contains few or no endangered species and most of the native taxa still can be located, and yet the ecological integrity of the community has been seriously impaired. In two midwestern rivers where historical data existed, Karr et al. (1985) documented declining populations or local extirpations in 45–70% of the fish fauna.

Threats to biodiversity in running water

Many factors contribute to the extinction of a species, and often it is difficult to identify a single cause, due either to inadequacy of data or, often, because multiple factors play a role. The major causes of species loss in general have been described as the "sinister sextet" by Soulé (1991). Borrowing from his list and from studies of freshwater extinctions (Miller et al. 1989), we propose the following six factors as being of critical importance in lotic environments: habitat loss and degradation, the spread of exotic species, overexploitation, secondary extinctions, chemical and organic pollution, and climate change.

According to Miller et al. (1989), a total of three genera, 27 species, and 13 subspecies of North American fishes became extinct during the past century; of these extinct fishes, some 15 (40%) were primarily from flowing water habitats and two ascended streams to spawn. Although the evidence generally was anecdotal, Miller et al. were remarkably successful in assessing the factors that contributed

Table 2. Status of selected animal groups in North America, based on species (not subspecies), as of 15 April 1990. Ranks as developed by National Heritage Network of The Nature Conservancy; data are for global occurrences. (From Master 1990.)

	Terrestrial			Aquatic			
Number of US species ranked as:	Mammals	Birds	Reptiles	Amphibians	Fishes	Crayfishes	Unionid mussels
Extinct	1	20	0	3	18	1	12
Historical, possibly extinct	0	2	0	1	1	2	17
Critically imperiled	8	25	6	23	78	62	88
Imperiled	23	9	10	17	72	49	49
Rare, not imperiled	19	23	25	26	110	84	35
Widespread and abundant	330	628	251	153	549	106	73
Not yet ranked	62	55	9	3	24	9	26
Total	443	762	301	226	852	313	300
Extinct through rare as % of total	13	11	14	28	34	65	73

to species extinction. In 82% of these extinctions, more than one factor appeared to play a substantial role. Habitat loss and species introductions were about equally common (73% and 68% of cases, respectively), followed by chemical pollution (38%) and hybridization (also 38%, and often related to species invasions). Overharvesting contributed substantially to the demise of 15% of the losses, but these losses were exclusively large fishes of large lakes.

Habitat loss and degradation

The modification of flowing water environments by human activity has a long history. Moreover, as civilizations have advanced, so too have the ways by which humankind has harmed streams and rivers. Images of dams and deforestation of pristine wilderness might come first to mind, but agriculture and human settlements have long been at least as important forces modifying landscapes and waterways in most areas. Modern threats range from projects of massive dimension, whose effects are felt at distances of thousands of kilometers, to the most mundane and local alterations that nonetheless degrade habitats by in- dividually small but cumulatively significant increments.

Pharonic works. Giant water projects carried out in the twentieth century rank high among the great engineering marvels of history. Dams and diversions also represent some of the greatest threats to aquatic ecosystems. Although these great water projects often serve multiple purposes, the overriding economic importance of one use often stands out in each location. In the United States, dams and canals have been constructed primarily to irrigate farmland, especially in the arid west. In contrast, hydroelectric power generation dominates water resource development in Canada, where the total volume of diverted flow, if consolidated, would be the third largest Canadian river (Bocking 1987). China offers yet another example: the major justification for the proposed Three Gorges Dam is to reduce the risk of floods in the Yangzi plains, although hydroelectric generation also is an expected benefit (Fearnside 1988).

Developing countries seem likely to be the recipients of the next generation of massive water projects. Such projects are known in Brazil as pharonic works and, as Fearnside (1989) puts it, "Like the pyramids of ancient Egypt, these massive public works demand the effort of an entire society to complete but bring virtually no economic returns." Nonetheless, Brazil's hydroelectric planners have 80 dam projects under consideration, which would flood roughly 100,000 km^2 of Amazonia and likely disrupt a much larger area. As in the giant James Bay projects of Canada, consequences include relocation of indigenous peoples and disruption of their livelihoods. It remains to be seen whether environmental or economic considerations will call a halt to these grandiose plans.

Proponents of large-scale water development plans commonly insist that the environmental consequences are minimal (e.g., Roy and Messier 1989). In fact, adverse effects are well-documented (Hecky et al. 1984). Perhaps most important, case studies establish that some of the most serious issues emerge only after years to decades have elapsed, and they often are unanticipated. As Rosenberg et al. (1987) argue, we usually can assess damage after the fact, but our predictive capabilities still are rudimentary. As a consequence, much uncertainty surrounds the outcome of any large-scale disruption of ecological systems.

Numerous adverse effects are attributable to the placement of impoundments on river systems (Ward and Stanford 1987). Profound alteration of channel characteristics, habitat availability, and flow regime are perhaps the most fundamental changes, and these changes have serious consequences for the biota. Impoundments and dams are well known detriments to migratory species like salmon. Not only must adults surmount these barriers to reach spawning grounds, but young fish traveling downstream are subject to pressure damage from turbines as well as weakening by the greater swimming effort needed to compensate for the reduction in current due to reservoirs and withdrawals.

In addition to such direct effects, running water ecosystems experience a variety of subtle, unexpected consequences of altered habitat and flow. Even downstream of reservoirs, where flowing water superficially resembles a natural system, rivers regulated by dams differ from free-flowing rivers in many ways (Ward and Stanford 1987). Commercial fisheries have been damaged in inland waters important to native peoples and in coastal marine waters deprived of the spring flush of melt water that benefits productivity by inducing upwelling of nutrient-rich waters (Rosenberg et al. 1987). Water chemistry has been found to change, including increased acidity due to the decompositon of vegetation (Fearnside 1989) and mobilization of naturally occurring mercury (Rosenberg et al. 1987).

Land transformations and agriculture. Although major water projects are generally the most apparent of habitat alterations, various transformations of the landscape probably are the most widespread and potent threats to the well-being of lotic ecosystems. Draining of flooded areas, timber harvest, grazing of livestock, road building, spread of human settlement, and the intensification of agriculture are some principal forces behind changes in land use, with attendent consequences for hydrology, vegetation cover, and terrestrial-aquatic linkages.

Floodplains are a natural feature of large lowland rivers, a fact that is easy to forget in North America and Europe due to construction of dams, dikes, and levees to control flooding and permit agricultural use and human settlement of erstwhile floodplain areas. In unmodified large river systems, floodplains are sustained by flooding that exhibits considerable regularity in onset and duration (Junk et al. 1989). Biological productivity is enhanced by lateral exchanges between river and floodplain, and a highly diverse biota is adapted to use the habitats and resources of the river-floodplain biotope. Unfortunately, because these areas often are ideal for agriculture and settlement, intact floodplains have long vanished from all but a handful of major river systems, located exclusively in the tropics. Because the number of species in the great rivers of the tropics increases as one proceeds downstream, it is apparent that floodplains are essential to the maintenance of biodiversity (Welcomme 1979).

Timber harvest and deforestation have been shown to have profound effects on the ecology and hydrology of rivers, sometimes over great distances. Forest removal in the Himalayas has led to catastrophic flooding downriver, much to the detriment of India and Bangladesh. Indeed, a principal justification for preserving intact forested watersheds is to ensure quality water and minimize risk of flooding. Additionally, detailed studies of small headwater streams reveal a host of changes after deforestation. Among the most important effects, temperature and discharge fluctuate more widely, nutrient loss from terrestrial sources increases markedly, and the contribution of leaf litter to energy flow is greatly reduced. Fortunately, retaining even a minimal amount of forested land along river margins can do much to minimize these consequences.

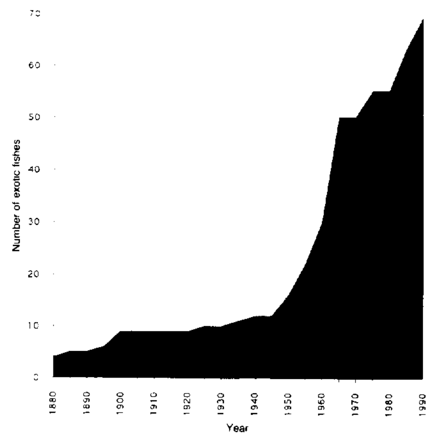

Figure 3. The number of introductions of exotic fish species to US freshwaters as of 1990. Translocations of fishes within the United States are not included. Data from W. R. Courtenay, 1992, Florida Atlantic University, Boca Raton.

Finally, we turn to the role of agriculture, which through a combination of direct and indirect effects contributes greatly to river modification. Degradation of physical habitat in streams and rivers usually has been the major cause of changes in the aquatic fauna wherever significant human settlement has occurred. Indeed, habitat alteration, including channel straightening and reduction of nearstream vegetation, continues to impair the ecological health of more streams than do toxic chemicals (Hughes et al. 1990). Collectively, these habitat alterations profoundly affect key qualities of the stream ecosystem. Streams with natural channel morphologies suffer less bank erosion and export fewer sediments. Streamside vegetation reduces both sediment and nutrient transport, which tend to be related because substantial nutrient loss from agricultural watersheds occurs in association with sediments. Shading by riparian forest canopy ameliorates temperature extremes, resulting in lower maximal values in summer and higher minimal values in winter (Karr and Schlosser 1978).

The hydrology of rivers and streams also has been greatly modified by the combination of drain tiles and channelization to enhance runoff after storms. Flood waters that normally recharge soils and aquifers are rapidly exported (or, in larger rivers, stored behind impoundments for other uses). As a consequence, water tables are lowered and summer base flows are reduced. Shrinkage of the riparian corridor and shifts in species composition are likely responses to this reduction in water availability (Smith et al. 1991). As habitats degrade, tolerant species increase their representation and altered communities become increasingly vulnerable to other threats, including population fragmentation and invasion by exotic species.

Species invasions

More than 160 species of exotic fishes from some 120 countries are listed on the international register kept by the Food and Agriculture Organization (FAO) of the United Nations, attesting to the global level of this problem (Bruton and van As 1986, Courtenay et al. 1984, Welcomme 1984). The common carp (*Cyprinus carpio*), probably the earliest fish species to be transferred into new habitats, provides an instructive example. It is believed to have originated in central Asia and has been reared in ponds in China and elsewhere in the Orient for many centuries. Carp probably reached Europe in the eleventh or twelfth century, aided by the gradual spread of pond culture. They were introduced into England before 1500, where they became so popular that Izaak Walton, writing in the mid-seventeenth century, referred to carp as the "queen of the rivers" (Eddy and Underhill 1974). Carp were later introduced into southern Africa in the early 1700s (Bruton and van As 1986) and to the New World in the mid 1800s (Courtenay et al. 1980). Indeed, the carp was brought to North America with such enthusiasm that "states anxiously awaited their quotas, and when a modest shipment of young carp arrived it might be greeted at the railway station by a brass band and paraded through town on its way to a river or pond" (Madson 1985). Thus, the common carp has been transformed from a fish of modest distribution in central Asia to a species of global status. In rivers of the United

Figure 4. The extent of overharvesting of fishes in South America is evident from the offerings at local fish markets. Several large-bodied species of pimelodid catfish (including *Sorubim lima* in the foreground) are displayed at this market at Asuncion, on the Paraguay River. Such fishes are rare in areas with a longer history of intensive harvest. Photo: G. R. Smith.

States, carp occupy habitat otherwise used by native species and increase water turbidity by their bottom-feeding habits.

Causes of species invasions. Reasons for the introduction of fishes, plants, and invertebrates into alien freshwater environments are many. During the nineteenth century and until about World War II, fish introductions were largely an outgrowth of colonialism and nostalgia by settlers in their newly adopted homelands for the familiar species and surroundings left behind (Welcomme 1984). Acclimatization societies proliferated in New Zealand in the late 1800s, augmenting the fauna with such zeal that of the 46 fish species now found in New Zealand, 20 are exotic (McDowall 1990).

Just why an exotic species succeeds or fails in a new environment remains an open question. Streams are highly variable environments, and invaders may serendipitously gain a foothold when conditions temporarily are favorable or the native fauna is reduced. Habitat alteration and degradation also may set the stage for successful invasion.

The establishment of exotic species in United States freshwaters is rising sharply (Figure 3). In 1920, only six fish species of exotic origin were established in United States waters; by 1945 just three more had been added. The big boom in fish introductions occurred after 1950. By 1980, some 35 exotics had become established and approximately 50 other exotic species had been recorded (Courtenay and Hensley 1980). Government agencies are responsible for 12 of these introductions, as sport fishes, for fish culture, and as agents of biological control. The aquarium fish culture industry accounts for the (unintentional) release of the remaining 23 species. These numbers refer only to fish brought in from outside the United States. The translocation of species within the country but outside their normal range is equally serious and often less appreciated.

Some of the most widely promoted exotics are popular sports fish. Alien and translocated North American species comprise more than 25% of the recreational fisheries catch of freshwater fish in the continental United States (Moyle et al. 1986), attesting to the pervasiveness of stocking efforts by government agencies. Programs aimed at eradicating nonsport native species exist in many parts of the United States; and, in some cases, efforts to purge native fishes to improve recreational stocks have been so extensive that extinctions of native species have occurred. The state of Oregon intentionally eradicated the endemic Miller Lake lamprey by using ichthyocides because it was a predator of stocked trout (Miller et al. 1989).

In recent years, introductions often have occurred for other purposes, such as aquaculture and biological control. Although fish culture employs relatively few species, they are among the most widely transferred fishes (Welcomme 1984). In the Third World, introductions associated with fish culture expanded considerably in the 1970s, as international development agencies promoted aquaculture as a protein source for rapidly expanding local human populations and for commerce.

Fishes also have been spread as biological control agents. The mosquitofish (*Gambusia affinis*) and guppies (*Poecilia reticulata*) now enjoy worldwide distribution due to mosquito control efforts. Tilapia and carp are commonly promoted to control aquatic weeds, many of which themselves are exotic (Shireman 1984).

Accidental introductions are of growing importance, due chiefly to the release/escape of aquarium pets and various means of hitchhiking. More than 1200 species of tropical aquarium species are shipped to various parts of the world, and as many as 6000 species may ultimately be of interest to the pet trade overall (Welcomme 1984). Most introductions of tropical fishes into the United States have occurred since 1960 (Figure 3), when techniques greatly improved for the live transport of pet fish.

Approximately 10% of exotic fish introductions have been unintended transfers (Welcomme 1984), such as small cyprinids that were included in shipments of juvenile carp species. Recently, exotic species carried in ship ballast water have been a focus of concern, due to invasions into the Laurentian Great Lakes of the zebra mussel and other species (Yount 1990). However, ballast water introductions are not new; although poorly publicized, hundreds of species of fishes and invertebrates have been introduced into marine and estuarine systems by what Carlton (1985) calls "international biotic conveyer belts."

Intercatchment water transfers

may also contribute to species translocations. This problem has been widespread in southern Africa, because almost all of the region's major river systems are connected by series of tunnels, pipes, and canals (Bruton and van As 1986). At least five fish species have invaded the Orange River from the Great Fish River, which before their connection had distinct faunas with high numbers of endemics. Fortunately, high-risk plans in North America that would link the Peace and Fraser drainages of the Pacific Northwest and that would link the Missouri-Mississippi with Hudson Bay drainages have not been implemented because of the concern over mixing of faunas.

Effects of invading species. Negative effects of exotics on native stream fauna have been implicated in a variety of geographical settings, most often from correlational analyses. An analysis of 31 case studies of fish introductions to stream communities found that 77% of the studies documented a subsequent decline in the native species (Ross 1991). Trout and some galaxiid species in New Zealand apparently are incompatible; formerly widespread populations of *Galaxias bulgaris* are now fragmented into remnant populations restricted to regions above barrier waterfalls inaccessible to trout (Townsend and Crowl 1991). In all likelihood, the present-day galaxiid distribution is a midcourse snapshot of the fate that has already befallen other native species in New Zealand. The New Zealand grayling (*Protroctes oxyrhynchus*), an endemic fish once so abundant that it was harvested by the cartload (McDowall 1990), precipitously declined after the introduction of brown trout and is now considered extinct.

Potential mechanisms whereby exotics affect native species include predation, habitat alterations, hybridization, and introductions of diseases or parasites (Taylor et al. 1984). Several authors have claimed that some of the best-documented cases of replacement of native fishes by introduced species are via predation (e.g., Ross 1991, Taylor et al. 1984). Surely the most spectacular and catastrophic effects of an introduced freshwater fish are now taking place in Lake Victoria, Africa, noted for its high diversity (perhaps 400 species) of colorful cichlid fishes. Introduction of the Nile perch, *Lates niloticus*, in the late 1950s resulted in a successful new fishery that earns needed foreign currency, but at great ecological and human cost. Many local people have lost a source of protein and of income, and the extinction of some hundreds of native species is in progress (Baskin 1992, Kaufman 1992).

Changes in habitat use by the native fauna may take place even if species extinction does not occur. Of the ten studies reviewed by Ross (1991) where resource use was examined, one-half found habitat shifts after fish introductions. For example, a variety of native species, including the Sacramento sucker, rainbow trout, California roach, and threespine stickleback, were displaced from deeper water habitats in the presence of the Sacramento squawfish, a predatory cyprinid introduced into the Eel River of California (Brown and Moyle 1991).

Invading species also affect native species by hybridization, which Miller et al. (1989) found to be a factor in 38% of the recorded extinctions of North American fish species. In most instances, some other factor apparently resulted in an initial decline, and hybridization was the final blow. Many native stocks of Pacific salmon have been influenced to an unknown extent by interbreeding with their hatchery-reared counterparts of different genetic makeup.

A host of diseases and parasites are associated with alien species, posing yet another threat to the invaded community. The introduction of resistant crayfish species from North America that carried a fungal parasite causing crayfish plague led to the destruction of native crayfish populations throughout Europe (Reynolds 1988). Of particular concern in fish are parasites that affect a wide variety of species such as the cestode *Bothriocephalus acheilognathi* (Bruton and van As 1986). In the Virgin River in the western United States, Asian tapeworm infections appeared in the woundfin (*Plagopterus argentissimus*), an endangered native species, after the exotic red shiner (*Notropis lutrensis*) invaded the river system (Deacon 1988).

The future promises a continuing spread of exotic species and mixing of faunas. As a consequence, the problems are likely to intensify, and managers of aquatic ecosystems increasingly will be confronted with a shifting mix of native and nonnative species.

Unfortunately, once exotic species are established they usually are impossible to eradicate. The Laurentian Great Lakes serve as one object lesson; in this example, managers have been comparatively successful in controlling sea lamprey populations, albeit at considerable cost and with the continual necessity to combat new arrivals. At the other extreme, by all accounts Lake Victoria is undergoing disasterous change at the moment. The ratio of successes and disasters to emerge from the ongoing mixing of the biota of running waters will reveal itself over the next years and decades, but an overall loss of biological diversity seems certain.

Overharvesting

There appear to be no instances of extinction of stream-dwelling taxa in the temperate zone due solely to overharvesting (Miller et al. 1989). Perhaps the closest example in temperate North America would be the threatened races of Pacific salmon. Generally, overfishing takes a back seat to habitat destruction, alteration of flow regime, and a host of other human disturbances (Nehlsen et al. 1991). In the tropics, however, fishes are exploited for both human consumption and for the lucrative First World pet trade, and there overharvesting is a much more serious threat.

There is ample evidence from marine and freshwater fisheries that as fishing effort increases, a fishing-up process occurs in which large, long-lived, prized species are replaced in the harvest and in the environment by smaller, fast-growing, less desirable species (Welcomme 1990). This process is particularly well documented in Africa, and there are signs it is beginning to occur in the neotropics. In South America, large individuals still are plentiful in areas where fishing pressure is modest (Figure 4), but not in heavily fished areas. For example, sharp declines in numbers have been reported for the largest species found in the Amazon near Manaus, and those large individuals brought to market come from greater and greater distances (Bayley and Petrere 1989). Similar shifts in fisheries have been reported for the lower Orinoco River in Venezuela and the Rio Magdalena in Colombia (Welcomme 1990).

Overfishing alone is unlikely to drive many species to global extinction, because economic forces generally cause a shift in effort before the complete collapse of a fishery takes place. Nonetheless, it is apparent that biological diversity is reduced when once-abundant species become too rare to be captured. In addition, the functioning of the aquatic communities and ecosystems unquestionably is greatly altered by the diminished presence of fish species with particular feeding habits, body sizes, and life cycles.

Although a number of the most common aquarium fish species are maintained by domestic breeding programs, the demand for novelty still creates pressures to collect from wild populations (Tudge 1990), and large numbers must be collected in order that a few individuals survive the long trip from rainforest stream to suburban home. As a consequence, the aquarium fish trade threatens some freshwater fish species with local extinction and significantly decreased abundance (McLarney 1988, Welcomme 1979).

Although the aquarium fish trade potentially can serve as a source of income to local people and be regulated against overharvesting, it does not appear that these goals are widely met. Even domestic breeding, which minimizes the demand for wild fish, poses other risks in the form of escaped exotics, which now comprise the majority of introduced fish species in North America.

Secondary extinctions

Secondary extinctions occur when the removal of one species has cascading effects throughout the species assemblage of the area, with the result that species unaffected by the original insult change in abundance and become undesirably rare or common. Such cascading effects often are mediated via food web connections, although there also are examples where the primary species affects habitat structure in a manner that influences other members of the community.

The local decline of such valuable and charismatic species as salmon, grizzly bears, and bald eagles is attributable to secondary effects of the opposum shrimp *Mysis relicta*, introduced as fish food into the great Flathead Lake and associated river systems of Montana (Spencer et al. 1991). Fishermen, grizzlies, and eagles all were beneficiaries of a successful prior introduction, the kokanee salmon *Oncorhynchus nerka*. The shrimp *M. relicta* was added to benefit this fishery, but it had quite the opposite effect. Evidently, the opposum shrimp consumed zooplankton that formerly were the principal prey of the kokanee. The shrimp were able to avoid becoming the kokanees' new prey by a behavioral adaptation; they migrate to deep waters during the day, thus minimizing their vulnerability to predators.

Collapse of the kokanee population soon affected bird and mammal populations that each autumn were attracted to lake tributaries to feed on the spawning salmon, their eggs, and carcasses. Bald eagles used these spawning runs as a pit stop on their southern migrations, resulting in spectacular concentrations that no longer take place. Whether eagle recruitment has been affected or individuals simply have moved elsewhere is uncertain, but it seems likely that an important resource that prepared birds for overwintering has disappeared. Declines also have occurred in other birds and mammals, including grizzly bears; and ecotourism has declined, with adverse effects on the local economy.

Chemical and organic pollution

Pollution of rivers and streams is one of the most visible threats to the ecological health of the system and to the survival of the biota. Nevertheless, it is doubtful that any river-dwelling species has been driven extinct by chemical pollution alone. For species with highly restricted ranges that are threatened by habitat degradation, however, chemical pollutants may well be a serious problem. Miller et al. (1989) estimated that chemical pollution played a role in 38% of the known North American extinctions.

Some spectacular success stories can be told of rivers that once were heavily polluted. The Thames River and estuary has undergone several cycles of deterioration and recovery (Gameson and Wheeler 1977). Comments as early as 1620 by the Bishop of London brought attention to the foulness of Thames water. Nonetheless, it was a good fishing river, providing a living for fishermen and food for the inhabitants of the city. By 1850, this era was ended by pollution from human and animal wastes, and the river became so foul that 1858 was known as the "Year of the Great Stink."

Advances in sewage treatment led to improved conditions into the first decades of the twentieth century, and some recovery of fish populations occurred. But by 1955 the increased volume of sewage had reduced water quality to an all-time low, odors released from anaerobic sections of the Thames again were a public nuisance, and a 70-kilometer section around London was devoid of any fish life except eels. These conditions spurred further improvements in the treatment of organic wastes, and within a decade the region around London again had sufficient oxygen for fish to survive passage. By 1973, some 62 species of fish were represented by more than a single capture within the river and estuary. This startling recovery of fish diversity in a decade and a half was paralleled by a similarly dramatic return of waterfowl, and, although the evidence is scanty, it appears that the invertebrate fauna have likewise recovered. The Thames thus provides a heartening example of the rapidity with which grossly polluted rivers can recover.

The Upper Sacramento River in California appears to be a similar story in progress. A spill into this high-quality trout stream of approximately 15,000 gallons of a highly toxic herbicide in July 1991 virtually sterilized some 60 km of river. Forecasts of long-term damage appeared in the media under headlines such as "Death of a River" (*Redding Record Searchlight* 1991). However, within ten weeks the algal and insect populations had undergone a remarkable recovery, and subsequent reports have focused on the Upper Sacramento River's recuperation.

Global climate change

The effect of global climate change on the biota of rivers and streams is the least predictable of the six factors considered. This unpredictability is due both to uncertainty regarding future climate scenarios and to the difficulty of anticipating the ecological consequences. Nonetheless, a number of potentially serious effects on lotic systems have been described (Regier and Meisner 1990). Adverse effects are likely to be most serious at middle and high latitudes, where the greatest climate change is expected to occur. In addition, the biota may be especially vulnerable in certain regions because of current temperature regimes and the lack of adequate escape routes to more suitable habitats.

Regier and Meisner (1990) identify three ecological links between future climates and freshwater fishes, which in all likelihood apply to the rest of the biota. Species ranges are likely to shift toward higher latitudes, and locales that previously supported species assemblages characteristic of cold waters will be replaced by warm-water species. The headwaters of mid-latitude streams generally support a cold-water fauna that will at least be reduced in extent if warmer climates prevail. Biota from warmer waters further downriver are expected to expand into headwaters, with a corresponding reduction in diversity within watersheds.

Changes in water quantity and quality also may be anticipated, although only approximately. Lower runoff and reduced stream flows are likely to occur due to increased evaporation and, locally, wherever climate change results in lower precipitation. Less habitat for fish and less dilution of pollutants are two obvious consequences. Potential changes in the severity and frequency of droughts and floods constitute another way that climate change might affect stream biota, although the causal linkages here are speculative.

Global species extinctions due to warming are unlikely to be common provided that routes exist that would allow dispersal to higher and cooler latitudes or altitudes. However, the fishes of the southern Great Plains of the United States provide a bleak example where species loss seems likely if significant warming occurs. Summer temperatures in these streams already are near the thermal tolerances of their inhabitants, and only a small increase would cause heat death. Equally important, virtually all Great Plains river systems drain from west to east or southeast, severely limiting the option of northward dispersal. At least 20 fish species of the Great Plains and southwest have ranges such that extinction could result from a several-degree warming (Matthews and Zimmerman 1990).

Recovery and restoration of running waters

Streams and rivers are unusual in at least one regard. Although all ecosystems have permeable boundaries, importing and exporting matter, energy, and organisms, the throughput in running water ecosystems is unusually high. Consequences include a natural cleansing ability and a regular supply of propagules delivered from upstream to downstream locations. Hence, streams and rivers are able to withstand a considerable amount of misuse and, once the misuse is halted, recovery occurs with a minimal amount of assistance. Even the physical dynamics of rivers tend toward a kind of equilibrium determined by climate, topography, and geology, although natural recovery of channel morphology takes a long time (Leopold et al. 1964). Because of this natural recovery capability of rivers, Gore (1985) argues that restoration of river ecosystems is best viewed as a process of recovery enhancement.

Pulse and press disturbances. Rehabilitation of physical habitat and improvement in water quality are the principal categories of stream restoration measures. Thus, efforts concentrate primarily on the mitigation of habitat degradation and chemical pollution. Species extinctions, the establishment of exotics, and potential climate-related changes are difficult or impossible to rectify. Nonetheless, much progress can be made, especially when the impairment of water quality can be traced to a limited number of discrete sources and appropriate technology brought to bear.

A recent review of more than 150 case studies of recovery in freshwater systems establishes that resilience varies with the type of disturbance, with biological attributes of the community, and with degree of isolation from a source of colonists (Niemi et al. 1990). The authors distinguish two types of disturbances: pulse events, which are of limited and definable duration, and press events, which are longer in duration. Typical examples of pulse events are chemical spills that are rapidly diluted, compared with press events such as habitat alteration by channelization.

Unsurprisingly, recovery generally was more rapid from pulse than from press disturbances. Especially for pulse disturbances, the recovery process depended on the opportunities for colonization and subsequent population growth, so the rapidity of organisms' life cycles, their dispersal capabilities, and the availability of refugia become significant rate controllers. Press disturbances generally were synonomous with habitat alteration. Recovery times of years to decades were common when habitat mitigation was accomplished; without intervention the recovery could be longer yet.

Habitat restoration measures. Habitat restoration is practiced mainly for game fish such as trout, for which a considerable body of knowledge has been developed. Within this restricted focus, the efficacy of such measures is well established. Wesche (1985) describes a number of physical structures designed to improve habitat for fish or the insects on which they feed. Generally speaking, the guiding principle of all such efforts is to reconstruct the stream channel to appear as much like an unmodified stream as possible, and the efforts usually result in greater numbers of invertebrates and fish. What appears to be lacking, however, is any comparable effort to provide for the habitat needs of the nongame fish that comprise the vast number of native species, much as one would want to protect the habitat needs of songbirds.

Petersen and Petersen (1992) outline a more general approach, aimed at the restoration of stream ecosystem function rather than reviving numbers of a particular sport fish, with the main focus always on restoring the physical habitat to as close to its unaltered state as feasible. This restoration strategy includes the construction of miniwetlands, meanders, riffle-pool sequences, and especially the maintenance of streamside vegetation in a buffer strip for some distance lateral to the channel. Buffer strips reduce sediment and nutrient input from the land surface, moderate temperature fluctuations, and help to maintain banks against erosion (Karr and Schlosser 1978). Figures for the desired width of buffer strips range from a few meters to 30 m (Gore and Bryant 1988); however, buffer strips of 5–10 m succeed in substantially reducing nutrient concentrations reaching streams, based on literature reviewed by Petersen Petersen (1992).

Conclusions

From the standpoint of biological diversity, rivers and streams are both rich in species and severely imperiled. The threats are many, but habitat degradation and species invasions rank highest, with the caveat that multiple factors often interact in a species' demise. Recognition of the extent of the problem clearly is a first step to responsible stewardship of running waters. Based on a Nationwide Rivers Inventory completed in 1982, only 2% (<100,000 km) of the 5.2 million km of streams in the contiguous 48 states have sufficient high-quality features to warrent federal protection status (Benke 1990). Clearly, running waters are in urgent need of both restoration and preservation.

Our ability to address these issues is limited partly by an inadequate knowledge base. Research directed at species description, inventories of abundance and distribution, ecosystem recovery, and interactions between river systems and their landscapes are just some of the areas demanding more effort.

Although rivers and streams are afforded some protection under the Wild and Scenic Rivers Act and some rivers occur within parks and other protected lands, protection benefits only a small fraction of the nation's rivers, and often quite short river stretches—the equivalent of forest fragments—rather than entire watersheds. A nationwide system of protected waters is urgently needed.

Last, we need stronger and more thoughtful policies aimed at species and ecosystem protection. Each of the six threats is driven by different forces, and specific countermeasures must be tailored. For example, tighter control over the aquarium trade and education of the fishing public and fisheries agencies on the effect of introduced species on native species are important steps to combat the spread of exotics. To counter the broad threat of degradation of riverine habitat, management and restoration efforts must address the ways that human activity transforms and gradually erodes aquatic habitat directly and indirectly via changes in land use within drainage basins. A tension exists between river conservation and other uses of the land and watershed, notably with agriculture and settlements. Riparian and stream conservation policies must include measures to control development along river corridors and to compensate land owners where other uses are forgone. However, it is probable that the actual costs of river protection are well compensated by the services that a healthy stream and riparian zone provide free of charge.

Because habitat quality is of such vital importance to the preservation of biodiversity, protective measures aimed at instream and near-stream habitat conditions will benefit both ecosystem function and the well-being of individual species. In this way, the imperilment of our freshwater biota is an important warning of how inadequately we are acting as stewards of river systems and the landscapes they drain.

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