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Freshwater biodiversity: importance, threats, status and conservation challenges

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ABSTRACT

Freshwater biodiversity is *the* over-riding conservation priority during the International Decade for Action – 'Water for Life' – 2005 to 2015. Fresh water makes up only 0.01 % of the World's water and approximately 0.8 % of the Earth's surface, yet this tiny fraction of global water supports at least 100 000 species out of approximately 1.8 million – almost 6 % of all described species. Inland waters and freshwater biodiversity constitute a valuable natural resource, in economic, cultural, aesthetic, scientific and educational terms. Their conservation and management are critical to the interests of all humans, nations and governments. Yet this precious heritage is in crisis. Fresh waters are experiencing declines in biodiversity far greater than those in the most affected terrestrial ecosystems, and if trends in human demands for water remain unaltered and species losses continue at current rates, the opportunity to conserve much of the remaining biodiversity in fresh water will vanish before the 'Water for Life' decade ends in 2015. Why is this so, and what is being done about it? This article explores the special features of freshwater habitats and the biodiversity they support that makes them especially vulnerable to human activities. We document threats to global freshwater biodiversity under five headings: overexploitation; water pollution; flow modification; destruction or degradation of habitat; and invasion by exotic species. Their combined and interacting influences have resulted in population declines and range reduction of freshwater biodiversity worldwide. Conservation of biodiversity is complicated by the landscape position of rivers and wetlands as 'receivers' of land-use effluents, and the problems posed by endemism and thus non-substitutability. In addition, in many parts of the world, fresh water is subject to severe competition among multiple human stakeholders. Protection of freshwater biodiversity is perhaps the ultimate conservation challenge because it is influenced by the upstream drainage network, the surrounding land, the riparian zone, and – in the case of migrating aquatic fauna – downstream reaches. Such prerequisites are hardly ever met. Immediate action is needed where opportunities exist to set aside intact lake and river

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ecosystems within large protected areas. For most of the global land surface, trade-offs between conservation of freshwater biodiversity and human use of ecosystem goods and services are necessary. We advocate continuing attempts to check species loss but, in many situations, urge adoption of a compromise position of management for biodiversity conservation, ecosystem functioning and resilience, and human livelihoods in order to provide a viable long-term basis for freshwater conservation. Recognition of this need will require adoption of a new paradigm for biodiversity protection and freshwater ecosystem management – one that has been appropriately termed 'reconciliation ecology'.

Key words: pollution, fisheries, overexploitation, dams, rivers, lakes, endangered species.

CONTENTS

I. INTRODUCTION

In December 2003, the United Nations General Assembly adopted resolution 58/217 proclaiming 2005 to 2015 as an International Decade for Action – 'Water for Life'. The resolution calls for a greater focus on water issues and development efforts, and recommits countries to achieving the water-related goals of the 2000 Millennium Declaration and of Agenda 21: in particular, to halve by 2015 the proportion of people lacking access to safe drinking water and basic sanitation. These are vitally important matters, yet their importance should not obscure the fact that the 'Water for Life' resolution comes at a time when the biodiversity and biological resources of inland waters are facing unprecedented and growing threats from human activities. The general nature of these threats is known, and they are manifest in all non-polar regions of the Earth, although their relative magnitude varies significantly from place to place. Identifying threats has done little, however, to mitigate or alleviate them.

This article explores why the transfer of knowledge to conservation action has, in the case of freshwater biodiversity, been largely unsuccessful. The failure is related to the special features of freshwater habitats – and the biodiversity they support – that makes them especially vulnerable to human activities. We start by elucidating why freshwater biodiversity is of outstanding global importance, and briefly describe instances where humans have caused rapid and significant declines in freshwater species and habitats. If trends in human demands for water remain unaltered and species losses continue at current rates, the opportunity to conserve much of the remaining biodiversity in fresh water will vanish before the 'Water for Life' decade ends. Such opportunity costs will be magnified by a significant loss in option values of species yet unknown for human use. In addition, these vital ecological and potential financial losses may well be irreversible. Importantly, effective conservation action will require a major change in attitude toward freshwater biodiversity and ecosystem management, including general recognition of the catchment as the focal management unit, and greater acceptance of the trade-offs between species conservation, overall ecosystem integrity, and the provision of goods and services to humans. At the same time, it is incumbent upon scientists to communicate effectively that freshwater biodiversity is *the* over-riding conservation priority during the 'Water for Life' decade and beyond; after all, water is the fundamental resource on which our life-support system depends (Jackson *et al.*, 2001; Postel & Richter, 2003; Clark & King, 2004).

II. FRESHWATER RICHES

Freshwater ecosystems may well be the most endangered ecosystems in the world. Declines in biodiversity are far greater in fresh waters than in the most affected terrestrial ecosystems (Sala *et al.*, 2000). What makes freshwater habitats and the biodiversity that they support especially vulnerable to human activities and environmental change? The main reason is the disproportionate richness of inland waters as a habitat for plants and animals. Over 10 000 fish species live in fresh water (Lundberg *et al.*, 2000); approximately 40 % of global fish diversity and one quarter of global vertebrate diversity. When amphibians, aquatic reptiles (crocodiles, turtles) and mammals (otters, river dolphins, platypus) are added to this freshwater-fish total, it becomes clear that as much as one third of all vertebrate species are confined to fresh water. Yet surface freshwater habitats contain only around 0.01 % of the world's water and cover only about 0.8 % of the Earth's surface (Gleick, 1996). Another way of looking at this is to ask: how many of the species described by scientists live in fresh water? The answer is around 100 000 out of approximately 1.75 million (Hawksworth & Kalin-Arroyo, 1995): almost 6 %, and an additional 50 000 to 100 000 species may live in ground water (Gibert & Deharveng, 2002). Given the rate at which humans are degrading fresh waters, it is literally true that, with regard to biodiversity loss and conservation, '… the medium is the message' (Stiassny, 1999).

Knowledge of the total diversity of fresh waters is woefully incomplete – particularly among invertebrates and microbes, and especially in tropical latitudes that support most of the world's species. Even vertebrates are incompletely known, including well-studied taxa such as fishes (Stiassny, 2002). Between 1976 and 1994, an average of 309 new fish species, approximately 1 % of known fishes, were formally described or resurrected from synonymy each year (Stiassny, 1999) and this trend has continued (Lundberg *et al.*, 2000). Among amphibians, almost 35 % of the global total of 5778 species has been described during the last decade (AmphibiaWeb, 2005). Regional discovery rates of new freshwater species vary: for example, Rainboth (1996) estimates that the Mekong drainage may support as many as 1000 fish species, more than twice the total given by earlier researchers, placing it third in the global ranking of rivers according to fish species richness. A more recent figure puts Mekong fish richness in the order of 1700 species (Sverdrup-Jensen, 2002). Clearly, the Mekong is one of a number of global 'hotspots' for river fish biodiversity (others include the Congo and Amazon) but, in general, freshwater hotspots receive less attention than their terrestrial counterparts (e.g. Myers *et al.*, 2000; see also Section V).

Adequate data on the diversity of most invertebrate groups in tropical fresh waters do not exist, but high levels of local endemism and species richness seem typical of several major groups, including decapod crustaceans, molluscs and aquatic insects such as caddisflies and mayflies (Dudgeon, 1999, 2000*c*; Benstead *et al.*, 2003; Strayer *et al.*, 2004). For instance, although it is incompletely known, the Mekong River fauna includes species-flocks of over 100 endemic molluscs, and a similar radiation has occurred in the Yangtze (Dudgeon, 1999, and references therein). Information on microbial biodiversity is fragmentary too, notwithstanding the crucial role of microbes in driving the biogeochemical cycles of the Earth. Most prokaryote taxonomic diversity remains unexplored (Torsvik, Øvreås & Thingstad, 2002; Curtis & Sloan, 2004). Recent genomic analyses (e.g. Zwart *et al.*, 2003) suggest that aquatic microbial biodiversity is considerably higher than inferred from classical, non-molecular evidence. Studies using a combination of approaches show that numerous protists (ciliates) may have restricted geographic distributions (Foissner *et al.*, 2003), implying they could be more speciose than supposed by researchers who assume they have cosmopolitan biogeographies (e.g. Finlay, 2002). It is likely that the richness of freshwater fungi and microalgae has been likewise underestimated (Johns & Maggs, 1997; Gessner & Van Ryckegem, 2003).

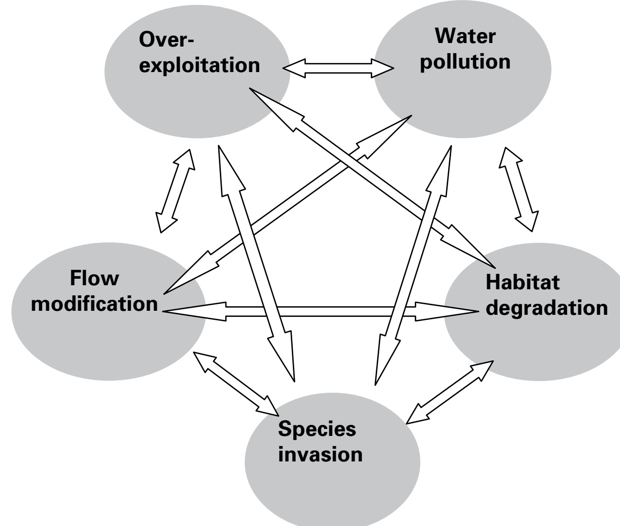

Fig. 1. The five major threat categories and their established or potential interactive impacts on freshwater biodiversity. Environmental changes occurring at the global scale, such as nitrogen deposition, warming, and shifts in precipitation and runoff patterns, are superimposed upon all of these threat categories.

III. MAJOR THREATS TO FRESHWATER BIODIVERSITY

The threats to global freshwater biodiversity can be grouped under five interacting categories (Fig. 1): overexploitation; water pollution; flow modification; destruction or degradation of habitat; and invasion by exotic species (e.g. Allan & Flecker, 1993, Naiman *et al.*, 1995; Naiman & Turner, 2000; Jackson *et al.*, 2001; Malmqvist & Rundle, 2002; Rahel, 2002; Postel & Richter, 2003; Revenga *et al.*, 2005). Environmental changes occurring at the global scale, such as nitrogen deposition, warming, and shifts in precipitation and runoff patterns (e.g. Poff, Brinson & Day, 2002, Galloway *et al.*, 2004), are superimposed upon all of these threat categories. Overexploitation primarily affects vertebrates, mainly fishes, reptiles and some amphibians, whereas the other four threat categories have consequences for all freshwater biodiversity from microbes to megafauna. Pollution problems are pandemic, and although some industrialized countries have made considerable progress in reducing water pollution from domestic and industrial point sources, threats from excessive nutrient enrichment (e.g. Smith, 2003) and other chemicals such as endocrine-disrupters are growing (e.g. Colburn, Dumanoski & Myers, 1996). Habitat degradation is brought about by an array of interacting factors. It may involve direct effects on the aquatic environment (such as excavation of river sand) or indirect impacts that result from changes within the drainage basin. For example, forest clearance is usually associated with changes in surface runoff and increased river sediment loads that can lead to habitat alterations such as shoreline erosion, smothering of littoral habitats, clogging of river bottoms or floodplain aggradation.

Flow modifications are ubiquitous in running waters (e.g. Dynesius & Nilsson, 1994; Vörösmarty *et al.*, 2000; Nilsson *et al.*, 2005). They vary in severity and type, but tend to be most aggressive in regions with highly variable flow regimes. This is because humans in these places have the greatest need for flood protection or water storage. That existing dams retain approximately 10 000 km^3 of water, the equivalent of five times the volume of all the world's rivers (Nilsson & Berggren, 2000), illustrates the global extent of human alteration of river flow. Water impoundment by dams in the Northern Hemisphere is now so great that it has caused measurable geodynamic changes in the Earth's rotation and gravitational field (Chao, 1995). Even some of the world's largest rivers now run dry for part of the year or are likely to do so as a result of large-scale water abstraction (Postel & Richter, 2003). Flow modifications are likely to be exacerbated by global climate change because greater frequency of floods and droughts, and consequent increased water-engineering responses, can be anticipated (Vörösmarty *et al.*, 2000). Although this matter will not be explored herein, impacts on river biota (fishes, for example) are likely to be severe (e.g. Dudgeon, 2000*a*; Xenopoulos *et al.*, 2005).

Widespread invasion and deliberate introduction of exotic species adds to the physical and chemical impacts of humans on fresh waters, in part because exotics are most likely to successfully invade fresh waters already modified or degraded by humans (e.g. Bunn & Arthington, 2002; Koehn, 2004). There are many examples of large-scale and dramatic effects of exotics on indigenous species (e.g. Nile perch, *Lates niloticus*, in Lake Victoria, the crayfish plague in Europe, salmonids in Southern Hemisphere lakes and streams: see Rahel, 2002), and impacts are projected to increase further (Sala *et al.*, 2000). Indirect impacts can arise from exotic terrestrial plants such as *Tamarix* spp. (Tamaricaceae), which alter the water regime of riparian soils and affect stream flows in Australia and North America (Tickner *et al.*, 2001).

The particular vulnerability of freshwater biodiversity also reflects the fact that fresh water is a resource for humans that may be extracted, diverted, contained or contaminated in ways that compromise its value as a habitat for organisms. In some instances, impacts have been sustained over centuries and, in the case of many of the major rivers of China, they have persisted for more than 4000 years (Dudgeon, 2000*a*). Indeed, some authors now believe it unlikely that there remain a substantial number of water bodies that have not been irreversibly altered from their original state by human activities (Lévêque & Balian, 2005). The extent of most freshwater systems is not confined to the wetted perimeter, but includes the catchment from which water and material are drawn (Hynes, 1975; see also Naiman & Latterell, 2005). Their position in the landscape (almost always in valley bottoms) makes lakes and rivers 'receivers' of wastes, sediments and pollutants in runoff. This is also true of seas and oceans, but inland water bodies typically lack the volume of open marine waters, limiting their capacity to dilute contaminants or mitigate other impacts.

In addition, in many parts of the world fresh water is subject to severe competition among multiple human stakeholders, to the point that armed conflicts can arise when water supplies are limiting and rivers traverse political boundaries (Poff *et al.*, 2003). There are 263 international rivers, draining 45 % of the Earth's land surface. That this area supports more than 40 % of the global human population is an indication of the scope of the issue (Bernauer, 2002; Postel & Richter, 2003; Clark & King, 2004). In the vast majority of disagreements over multiple uses of water, whether they are international or on a local scale, allocation of water to maintain aquatic biodiversity is largely disregarded (Poff *et al.*, 2003). In China and India, where approximately 55 % of the world's large dams are situated (W. C. D., 2000), hardly any consideration has been given to the downstream allocation of water for biodiversity (Poff *et al.*, 2003; Tharme, 2003).

IV. FRESHWATER BIODIVERSITY IN CRISIS

The combined and interacting influences of the five major threat categories (Fig. 1) have resulted in population declines and range reduction of freshwater biodiversity worldwide. Qualitative data suggest reductions in numerous wetland and water margin vertebrates (19 mammals, 92 birds, 72 reptiles and 44 fish species), while population trends indicate declines averaging 54 % among freshwater vertebrates (mainly waterfowl), with a tendency toward higher values in tropical latitudes (Groombridge & Jenkins, 2000; Loh, 2000). Furthermore, 32 % of the world's amphibian species now are threatened with extinction, a much higher proportion than threatened birds (12 %) or mammals (23 %), and 168 species may already be extinct (AmphibiaWeb, 2005). The well-known global decline of amphibians started during the 1950s and 1960s and has continued at the current rate of approximately 2 % per year, with more pronounced decreases in tropical streams (Houlahan *et al.*, 2000; Stuart *et al.*, 2004). This is close to the estimate of 2.4 % for declines in populations of freshwater vertebrates over the period 1970–1999 (Balmford *et al.*, 2002). These estimates are extremely alarming. Extinction rates of freshwater animals in North America, based on combined data sets for unionid mussels, crayfishes, fishes and amphibians, may even be as much as 4 % per decade – five times higher than species losses calculated from any terrestrial habitat (Ricciardi & Rasmussen, 1999). One third of the species in what was once the most diverse freshwater mollusc assemblage in the world (the Mobile Bay Basin in the

Table 1. IUCN Red List classifications for non-marine turtles in tropical Asia (including New Guinea). Around 90 species of non-marine turtles occur in this region. Classifications as Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) reflect a dramatic increase in threats due to overexploitation of turtles for food and the traditional Chinese medicine trade, with the consequence that over 80 % of the regional fauna is now threatened. Species classified as Data Deficient (DD) are poorly known but perceived to be under threat also (Van Dijk, 2000).

	IUCN Classification					
Year	CE	EN	VU	Total	%	DD
1996	5	9	23	37	41	18
2000	18	27	21	66	73	6
2003	19	31	23	73	81	6

south-eastern USA) have been driven to extinction by flow regulation and habitat alteration (Groombridge & Jenkins, 1998; see also Lydeard & Mayden, 1995); unionids are now regarded as the most imperilled of all organisms in North America (Strayer *et al.*, 2004). These limited data on extinction rates from one continent are believed to be indicative of a global freshwater 'biodiversity crisis' (Abell, 2002; see also Dudgeon, 1992; Kottelat & Whitten, 1996).

Rates of species loss from fresh waters in non-temperate latitudes are not known with any degree of certainty. They are likely to be high because species richness of many freshwater taxa (e.g. fishes, macrophytes, decapod crustaceans) increases toward the tropics. The drainage basins of many large tropical and subtropical rivers (e.g. the Ganges and Yangtze) are densely populated – with large dams, altered flow patterns and gross pollution from a variety of sources being the inevitable outcomes (e.g. Dudgeon, 2000*a*, 2002). For larger species in these rivers, the situation is parlous: the Yangtze dolphin (*Lipotes vexillifer* Miller) is probably the most endangered mammal on Earth (now numbering fewer than 100 individuals; Dudgeon, 2005), and the Ganges dolphin (*Platanista gangetica* (Roxburgh)) is 'Endangered' (IUCN, 2003). The crocodilian fauna of the Ganges and Yangtze likewise consists entirely of threatened or highly endangered species. Many other species of water-associated reptiles – a primarily tropical group – are gravely threatened (Gibbons *et al.*, 2000; Van Dijk, 2000), most particularly turtles (Table 1), as are large freshwater fishes in most rivers (e.g. Baird *et al.*, 2001; Carolsfeld *et al.*, 2004; Hogan *et al.*, 2004; see Table 2), and many freshwater fish stocks are over-fished to the point of population collapse (e.g. FAO, 2000; Dudgeon, 2002).

V. THE INFORMATION GAP

Populations of large vertebrates may not be accurate indicators of the status of all of freshwater taxa, but there are grounds for grave concern if their status were reflected in even 5 % of the total species complement. To date, however, there has been no comprehensive global analysis of freshwater biodiversity comparable to those recently completed for terrestrial systems (Myers *et al.*, 2000; Olson *et al.*, 2001). Existing data on the population status or extinction rates of freshwater biota are biased in terms of geography, habitat types and taxonomy; most populations and habitats in some regions have not been monitored at all. Even a basic global mapping of inland waters, classified by broad geomorphic categories, is lacking – and there are no global estimates of changes in the extent of lakes, rivers or wetlands (Balmford *et al.*, 2002).

Conservation efforts for freshwater biodiversity are constrained by the fact that most of the species in diverse communities are rare (e.g. Sheldon, 1988) and thus their natural histories tend to be poorly known. This means that even when reductions in overall species numbers are predictable, forecasting the identities of the affected taxa is not possible. Furthermore, the unreliability of estimates of species richness in individual river basins (e.g. the Mekong: see above) makes it virtually certain that regional national inventories, museum collections and taxonomic knowledge in many parts of the tropics are inadequate to document extinctions, and thus widespread undetected extinctions of inconspicuous species have already taken place (Harrison & Stiassny, 1999; Stiassny, 2002). The problem of species being misidentified, or not represented in collections, or listed incorrectly on protected species lists adds to the uncertainty (Kottelat & Whitten, 1996). One important implication of these various constraints is that, with the exception of a few well-known taxa in a limited number of countries (e.g. Ricciardi & Rasmussen, 1999; Strayer *et al.*, 2004), it is not possible to estimate or accurately project extinction rates of freshwater biodiversity using the approaches applied to terrestrial biota (Dirzo, 2001; Dirzo & Raven, 2003).

Globally, awareness of the need to conserve freshwater biodiversity seems limited. Between 1997 and 2001, only 7 % of papers in the leading journal in the field, *Conservation Biology*, was concerned with freshwater species or habitats (Abell, 2002). Most reported studies from northern temperate latitudes. This negligence is particularly acute in regions where biodiversity is both rich and highly threatened. A mere 0.6 % of papers in the conservation biology literature between 1992 and 2001 dealt with freshwater biodiversity in Asia (Dudgeon, 2003*b*), although this continent supports over half of the global human population, with consequent pressures on inland waters, and a very significant part of the world's biodiversity. Indonesia alone supports about 15 % of the word's species, and has more amphibians and dragonflies than any other country (Braatz *et al.*, 1992). The manifest knowledge impediment in Asia and elsewhere in the tropics limits both attempts to quantify the freshwater biodiversity crisis and the ability to alleviate it.

VI. CONSERVATION CHALLENGES

A significant challenge to freshwater biodiversity conservation results from the complexity imposed on fresh

Table 2. River fishes in Asia: threats and conservation status. All species listed are large, long-lived and/or migratory species that seem particularly susceptible to human impacts – especially overfishing.

Species (maximum weight or length)	IUCN classification	Range	Threats	Remarks	References
Chinese paddlefish *Psephurus gladius* (Martens) (~300 kg, possibly 500 kg; up to 3 m)	Critically endangered	Yangtze endemic	Mainly overfishing; also pollution.	Breeding migrations blocked by Gezhouba Dam (1981) following population collapse; close to extinction	Wei *et al.* (1997, 2004)
Chinese sturgeon *Acipenser sinensis* Gray (up to 500 kg)	Endangered	Yangtze and Pearl	Overfishing, pollution, spawning site degraded by Gezhouba Dam, habitat fragmentation	Population collapse caused genetic bottleneck; artificial propagation and release of juveniles since 1983	Wei *et al.* (1997, 2004); Zhang *et al.* (2003)
Yangtze sturgeon *Acipenser dabryanus* Duméril (over 16 kg; at least 1.3 m)	Critically endangered	Yangtze endemic	Mainly overfishing; also pollution; Gezhouba Dam blocked breeding migrations	Declining genetic diversity of wild populations between 1958 and 1999; large-scale artificial propagation not yet practiced; close to extinction	Wei *et al.* (1997, 2004); Wan *et al.* (2003)
Giant barb *Catlocarpio siamensis* Boulenger (~150 kg; may reach 300 kg)	Not listed	Mekong and Chao Phraya	Overfishing; few juveniles reach maturity	Protected by law in Cambodia	Rainboth (1996); Hogan *et al.* (2001)
Mekong giant catfish *Pangasianodon gigas* (Chevey) (exceeds 300 kg)	Critically endangered	Mekong endemic	Overfishing; navigation project in upper Mekong threatens spawning sites	Protected by law in Cambodia; artificial propagation and stocking in Thailand since 1985 depleting population and eroding genetic diversity	Kottelat & Whitten (1996); Hogan *et al.* (2001, 2004)
Isok barb *Probarbus jullieni* Sauvage (over 70 kg; up to 1 m)	Endangered	Mekong; formerly also rivers in Thailand and Malaysia	Overfishing in Mekong; elsewhere dam construction and habitat degradation	Populations of *Probarbus labeamajor* Roberts and *P. labeaminor* Roberts, endemic to the Mekong, are also declining	Rainboth (1996); Dudgeon (1999)
Freshwater whipray *Himantura chaophraya* Monkolprasit & Roberts (possibly up to 600 kg)	Vulnerable	Mekong, Chao Phraya, Fly and Mahakam	Overfishing; pollution and habitat degradation in Chao Phraya	Unconfirmed records suggest this stingray may be one of world's largest freshwater fish; a very poorly known species	Rainboth (1996); Hogan *et al.* (2004)

waters by catchment divides and saltwater barriers. As a result, low gene flow and local radiation lead – in the absence of human disturbance – to considerable inter-drainage variation in biodiversity and high levels of endemism (Table 3). This is especially notable among assemblages that evolved in isolated lakes on islands or mountains and inland plateaux such as the karstic regions of Burma and southwest China (Kottelat & Whitten, 1996). These and similar tropical uplands are poorly represented in existing protected-area networks (Rodrigues *et al.*, 2004). Ancient lakes such as Lake Baikal in Siberia and those in the East African Rift Valley support well-known species flocks of endemic crustaceans and fishes, but there are important radiations of cichlids, cyprinids, catfishes and other fishes, as well as frogs, crustaceans and molluscs, elsewhere in Africa (Table 3) and the world. For example, species flocks occur among Cyprinidae in the Philippines, Telmatherinidae on Sulawesi, and Balitoridae in China (Kornfield & Carpenter, 1984; Kottelat & Chu, 1988; Kottelat & Whitten, 1996). Virtually all of these radiations are severely endangered, as the examples from Africa illustrate (Table 3). At smaller geographic scales there is substantial species turnover (i.e. β-diversity) among drainage basins and water bodies, and many freshwater species have restricted ranges (e.g. Sheldon, 1988; Pusey & Kennard, 1996; Strayer *et al.*, 2004). These attributes combine with endemism to produce a lack of 'substitutability' among freshwater habitat units. This means that protection of one or a few water bodies cannot preserve all freshwater biodiversity within a region, or even a significant proportion of it.

In addition to conflicts arising from the multiple use of water, conservation of freshwater biodiversity is complicated by their landscape position as 'receivers' and the problems posed by high levels of endemism – and thus non-substitutability. Other features intrinsic to freshwater environments, especially rivers, also make them vulnerable to human impacts. Rivers are open, directional systems, and elements of their biota range widely using different parts of the habitat at various times during their lives. Fishes and other animals (from shrimps to river dolphins) use different habitats at different times, and longitudinal migrations may be an obligatory component of life histories especially if – as in many species – migration is associated with breeding (Welcomme, 1979). Longitudinal migrations may occur within the river, or from river to sea or lake and back, or from sea or lake to river and back. Such movements put animals at risk from stresses in various parts of their habitat at different times; long-lived species with low reproductive rates are likely to be the most vulnerable (Carolsfeld *et al.*, 2004). Dams in tropical regions are generally constructed without appropriate fishways or fish passes, or based upon designs that are suitable only for salmonids, and thus they obstruct fish migrations (Roberts, 2001). A dam on the lower course of a river prevents migratory fishes with an obligate marine phase in their life cycle from moving to and from the sea, creating the potential for activities in downstream reaches to impact upstream portions of the river by way of, for example, the nutrient transmission that occurs during spawning migrations of salmon (e.g. Naiman *et al.*, 2002 *a*; see also Pringle, 2001). Lateral migrations, between inundated floodplains or swamp forest and the main river channel, represent another axis of connectivity important for feeding and breeding in many fishes and other animals (Welcomme, 1979; Ward *et al.*, 2002; Carolsfeld *et al.*, 2004; Arthington *et al.*, 2005) that is dramatically altered by human activities.

VII. ARE TERRESTRIAL CONSERVATION STRATEGIES APPROPRIATE FOR FRESHWATER BIODIVERSITY?

Terrestrial conservation strategies tend to emphasize areas of high habitat quality that can be bounded and protected. This 'fortress conservation' is likely to fail for fresh waters (Boon, 2000) and may even be counterproductive (Moss, 2000; Dunn, 2003) for river segments or lakes embedded in unprotected drainage basins unless the boundaries are drawn at a catchment scale, which is virtually never the case (Naiman & Lattrell, 2005). This problem of boundary definition impedes sensible local management of freshwater biodiversity (but see Baird *et al.*, 2001) because protection of a particular component of river biota (and often habitat) requires control over the upstream drainage network, the surrounding land, the riparian zone, and – in the case of migrating aquatic fauna – downstream reaches (Pringle, 2001; Pusey & Arthington, 2003). Conservation action at the catchment scale, involving interconnected landscape units, is needed also for certain terrestrial taxa that undertake seasonal migrations, but the shortcomings inherent in fortress conservation are particularly acute for freshwater biodiversity.

The catchment scale is generally appropriate for all types of freshwater management of freshwater habitats (e.g. Pollard & Huxham, 1998; Moss, 2000), and it helps resolve the small-scale but damaging conflicts of interest among competing human demands. However, this approach can be problematic in practice, as relatively large areas of land need to be managed in order to protect relatively small water bodies. A promising approach could involve ecological management that integrates the requirements of terrestrial and freshwater environments. This will complicate the process of establishing appropriate boundaries for protected areas. However, from the freshwater perspective, it would have the added advantage of broadening the historic management approach that has been focused mainly on biodiversity and habitats within river channels, with dependent floodplains and their inhabitants receiving relatively little attention (Kingsford, 2000; Ward *et al.*, 2002). Large animals such as bear, swamp deer, rhinos, and elephants make seasonal use of riparian areas and floodplains for feeding or breeding (see Naiman & Décamps, 1997; Dudgeon, 2000 *b*; Naiman, Décamps & McClain, 2005). Maintaining proximity to water is essential for many large animals during the tropical dry season, which can be a period of severe ecological stress for herbivores. Effective preservation of biodiversity associated with freshwater habitats must therefore take account of the year-round habitat use and movements by terrestrial, riparian and amphibiotic fauna (e.g. frogs, water dragons and snakes, platypus, otters, and many water birds), as well as the needs of the strictly aquatic biota. Maintenance of some semblance of the natural flow variability and the flood/drought cycle of rivers and their floodplains, vernal pools, and water-level fluctuations in wetlands and along lakeshores, also will be essential.

VIII. THE IMPORTANCE OF ENVIRONMENTAL WATER ALLOCATIONS

There is growing awareness that maintenance of natural variability in flows and water levels is essential to underpin conservation strategies for freshwater or water-associated biodiversity and their habitats (Poff *et al.*, 1997; Richter *et al.*, 1997, 2003; Pollard & Huxham, 1998; Arthington & Pusey, 2003). The most straightforward water-engineering response is to provide a water regime (i.e. Environmental Water Allocations: EWA) that mimics natural variability and includes a range of flows – not just a minimum level (Fig. 2). Instead of being directed toward preservation of single species (such as salmon or trout), an EWA provides the flows required to sustain the entire riverine ecosystem including surface-groundwater systems (Arthington, 1998; Naiman *et al.*, 2002 *b*). Mimicking the natural flow regime is important because it influences aquatic biodiversity via several, inter-related mechanisms that operate over different spatial and temporal scales (Bunn & Arthington, 2002: see Fig. 2). The relationship between biodiversity and the physical nature of the aquatic habitat is likely to be driven primarily by large events that influence channel form and

Table 3. African lakes as an example of biodiversity threats and conservation status of fresh waters. Principal drivers of biodiversity decline throughout the region are assorted impacts arising from human population pressure as well as climate changes. Data are from Thieme *et al.* (2005), unless otherwise indicated.

Lake system (location)	Biodiversity features	Main threats	Remarks
Southern Eastern Rift soda lakes (including Nakuru, Magadi, Natron, Manyara and Eyadi) (Gregory Rift of Kenya and Tanzania)	Endemic radiation of phytophagous tilapiine fishes (*Oreochromis* spp.); globally important numbers of lesser flamingo (*Phoenicopterus minor*); primary production (dominated by *Spirulina platensis*) comparable to highest measured for any terrestrial plant community.	Numerous: soda mining; deforestation; agricultural and urban pollution; introduced species; climate change.	Soda mining in Lake Magadi extracts 0.5×10^6 t $NaCO_3$/year with effects on water quality and phytoplankton that impact flamingo and fish populations.
Lake Tana (Northern Highlands of Ethiopia)	Rich endemic fish fauna, including a globally outstanding species flock of piscivorous cyprinids (*Labeobarbus* spp.) and the only known African river loach (*Nemacheilus abyssinicus*); 15 planorbid snail species and an endemic sponge (*Makedia tanasesis*); exceptional regional diversity of resident wetland birds and Palearctic migrants.	Overfishing; water diversion.	Use of motorized boats opened access to deeper waters formerly free from fishing pressure; growing human populations resulted in heavy exploitation of fishes during spawning runs which, combined with use of fish poisons, appears unsustainable; stocks in the southern Lake Tana declining.
Western Equatorial crater lakes (including Barombi Mbo, Bermin, Ejagham and Kotto) (Cameroon)	Around 20 endemic tilapiine cichlids resulting in a per-area index of fish endemicity in these small lakes that is globally unrivalled; almost 60 frog species, $\sim$20 endemic to the lakes region; invertebrate diversity poorly known, but endemic sponge (*Corvospongilla thysi*) and atyid shrimp in Lake Barombi Mbo.	Deforestation and siltation; agricultural and urban pollution; water extraction; overfishing.	The small size of the Cameroonian crater lakes renders them particularly vulnerable to siltation due to land-use change or water extraction for agriculture and domestic use; lake level fluctuations in Lake Barombi Mbo have impacted fish breeding sites.
Bangwelo and Mweru Lakes system (D. R. Congo and Zambia)	Extremely rich fauna: over 100 fish species ($\sim$34 endemics); 37 mollucs (7 speceis endemic to Lake Mweru and lower Luapula River); 4 near-endemic frogs; 2 near-endemic dragonflies (*Aciagrion rarum* and *Monardithemis flava*) of conservation concern.	Overfishing; agricultural pollution.	Cichlid (mainly tilapiine) stocks greatly depleted in Lake Bangwelu by overfishing; drainage-basin degradation due to growing human populations, deforestation and land-use change; community-based co-management of fisheries and sustainable resource use being promoted in attempts to maintain productivity and ecosystem integrity.
Lake Upemba and upper Lualaba River system (D. R. Congo)	Aquatic fauna poorly known: at least 14 endemic fish species, 47 frog species (6 endemics); habitat also for the slender-snouted crocodile (*Crocodylus cataphractus*) and several wetland birds of conservation concern (e.g. the wattled crane, *Grus carunculatus*, and the black-faced waxbill, *Estrilda nigriloris*).	Mining; deforestation; agricultural pollution; overfishing.	Most of the human population is concentrated in the mining belt south of Lake Upemba, where mining, settlement, slash and burn agriculture, and overfishing have degraded aquatic systems; civil conflict plaguing D. R. Congo since 1996 has devastated human welfare and livelihoods; most conservation and research efforts have ceased.

Lake Malawi (Malawi and Mozambique)	Globally outstanding fish diversity including 400–800 cichlid species (99% endemic), a radiation of 17 deep-water clariid catfishes (*Bathyclarias* spp.) and many other endemic species; at least 30 mollusc species; richness in other taxa is likely also.	Localized overfishing; deforestation and siltation; eutrophication.	Extreme habitat specialization of many inshore cichlids makes them highly susceptible to over-fishing with fine-meshed nets; changes in fish communities are particularly obvious in along the densely-settled southern shores; spawning aggregations of large, endemic potamodromous cyprinids are heavily over-exploited.
Lake Rukwa (Tanzania)	About 60 fish species ($\sim$20 endemics), including two small endemic radiations of haplochromine cichlids and sucker-mouth (*Chiloglanis*) catfishes); large colonies of great white pelicans (*Pelecanus onocrotalus*) and white-winged terns (*Chlidonias leucopterus*), as well as large numbers of non-breeding wetland birds.	Land-use change; introduced species; overfishing.	Two introduced tilapias (*Oreochromis esculentus* and *Tilapia rendalli*) compete with the native tilapia (*O. rukwaensis*), but potential long-term impacts are as yet unstudied; declining fish stocks probably reflect increased fishing pressures from displaced immigrant fishers (many from Rwanda and Burundi); gold mining in the region poses the threat of mercury contamination of lake Rukwa.
Lake Tanganyika (Burundi, D. R. Congo, Zambia and Tanzania)	Globally outstanding diversity including $\sim$470 fish species, including endemic radiations of cichlids, mastacembelid spiny eels, claroteid and sucker-mouth catfishes, and latid perches, as well as a deep-water fish assemblage capable of tolerating periodic anoxia; invertebrate diversity is also quite exceptional with 74 endemic Ostracoda, 33 endemic Copepoda, and 17 genera and one family of endemic prosobrach snails.	Sedimentation; localized urban and agricultural pollution; overfishing; climate change.	Only one third of the lake shore has been thoroughly-sampled for fishes and many deep-water habitats are virtually unknown, so current species numbers of fish and especially other taxa certainly underestimate total diversity. O'Reilly *et al.* (2003) present compelling evidence that climate change (warming) has diminished productivity in the lake and contributed to decreasing fish yields.
Lake Turkana (Ethiopia and Kenya)	Around $\sim$50 fish species with 11 endemics; 3 endemic frogs and 2 threatened turtles (at least 1 endemic: *Pelusios broadleyi*); important site for 84 waterbird species, including 34 Palearctic migrants.	Drought (climate change?).	Declining fish catches attributed to falling lake levels and drying of the main fishery grounds; oil exploration ongoing in Rift Valley lakes, including Lake Turkana, since the 1980s; oil leakage or spills could have catastrophic effects.
Lake Victoria region (including Victoria, Kivu, Edward and George)	Globally outstanding aquatic diversity includes $\sim$600 endemic fish species in Lake Victoria, 60 endemics in Lakes Edward and George, and 28 endemics (19 cichlids) in Lake Kivu; over 60 frog species (15 endemics), 5 turtles, and two aquatic snakes are known from the region; 54 mollusc species (6 endemics).	Causation complex and not fully understood: overfishing, introduced species, land-use change and siltation; pollution from a variety of sources.	Concerns about declines in endemic cichlids in Lake Victoria raised in the 1980s following increases of introduced predatory Nile perch (*Lates niloticus*); losses appear serious although actual number of extinctions has yet to be determined (Harrison & Stiassny, 1999); visually-mediated sexual selection for male breeding coloration drives reproductive isolation in many lake cichlids, but increasing turbidity disrupts mate recognition by inshore species (Seehausen *et al.*, 1997).

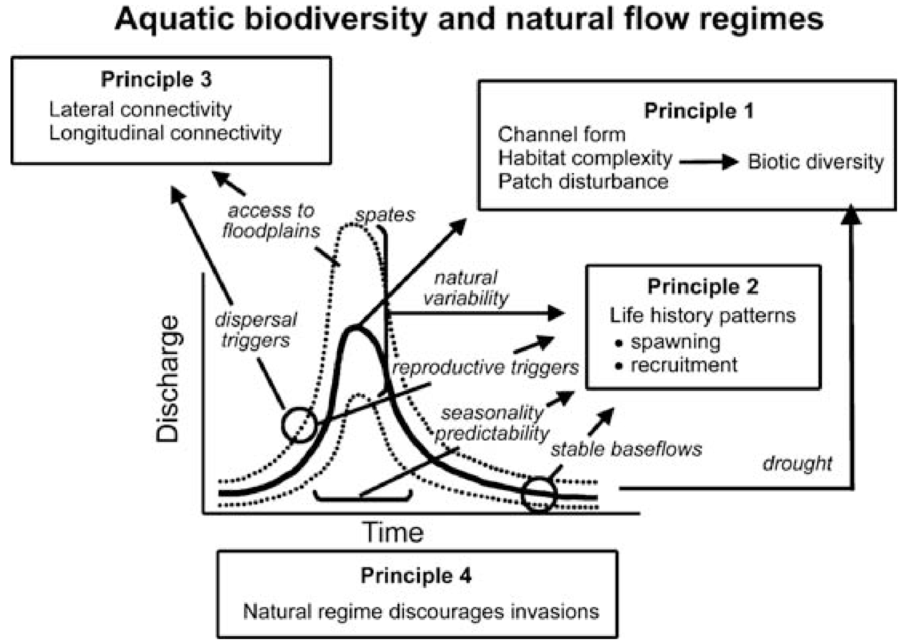

Fig. 2. Graphical representation of the natural flow regime of a river showing how it influences aquatic biodiversity via several, inter-related mechanisms (Principles 1–4) that operate over different spatial and temporal scales (redrawn from Bunn & Arthington, 2002). For further explanation, see text.

shape (Principle 1 in Fig. 2). However, droughts and low-flow events also play a role by limiting overall habitat availability and quality. Many features of the flow regime influence life-history patterns, especially the seasonality and predictability of the overall pattern, but also the timing of particular flow events (Principle 2). Some flow events trigger longitudinal dispersal of migratory aquatic organisms and other large events allow access to otherwise disconnected floodplain habitats (Principle 3). The native biota of rivers has evolved in response to the local flow regime. Catchment land-use change and associated water resource development inevitably lead to changes in one or more aspects of the flow regime resulting in declines in aquatic biodiversity via these mechanisms. Invasions by introduced or exotic species are more likely to succeed at the expense of native biota if the former happen to be adapted to the modified flow regime (Principle 4).

There are over 200 methods for assessing EWA (Tharme, 2003). The challenge is therefore to evaluate their relative merits and provide regionally relevant, hydro-ecological models (Benetti, Lanna & Cobalchini, 2004; Scatena, 2004). The main features of some of the more widely used approaches are given in Table 4. Because simplistic 'rules of thumb' about when and how much water should be allocated are confounded by the range of relationships between ecosystem integrity and flow characteristics, methodologies have been developed in Australia and southern Africa that are based on explicit links between these parameters (e.g. Arthington & Pusey, 2003; Arthington *et al.*, 2003; King, Brown & Sabet, 2003). This integrative approach to EWA has been used primarily for evaluating alternative water allocations within drainage basins where data are relatively scant or resources are too limited to allow detailed field investigations, with the results used to inform and improve subsequent EWA practices (Poff *et al.*, 2003). A new approach to water management – termed Integrated Water Resources Management (IWRM) – is now evolving into a process to reconcile the needs of humans and ecosystems through the development of holistic resource management (Wallace, Acreman & Sullivan, 2003). IWRM stresses the requirement for EWA to sustain the ecological integrity of fresh waters, and the biodiversity they support, while recognising and managing the trade-offs that will inevitably be generated as a result.

IX. THE VALUE OF FRESHWATER BIODIVERSITY

Freshwater biodiversity provides a broad variety of valuable goods and services for human societies – some of which are irreplaceable (Covich *et al.*, 2004*a*). The value of this biodiversity has several components: its direct contribution to economic productivity (e.g. fisheries); its 'insurance' value in light of unexpected events; its value as a storehouse of genetic information; and its value in supporting the provision of ecosystem services (e.g. cleaning water) (Pearce, 1998; Heal, 2000; Covich *et al.*, 2004*b*). Estimates of the full value of biodiversity need to account for each of these four components; to date, this has not been done. A number of fundamental questions still have to be answered (Loreau *et al.*, 2001), but substantial progress has been made in understanding the effects of biodiversity on the functioning

Table 4. Comparison of the four main types of environmental flow methods used worldwide to estimate environmental water allocations (EWA: adapted from King *et al*., 1999; Tharme, 2003). Riverine ecosystem components, data requirements (or resource intensity) and levels of application are indicated for each method.

Type	Riverine ecosystem components	Data requirements	Levels of application
Hydrological	Whole ecosystem, non-specific, or some components (e.g. fish: Tennant, 1976).	Primarily desktop; virgin/naturalised historical flow records; some use historical ecological data.	Reconnaissance level of water-resource developments, or as a tool within habitat simulation or holistic methodologies. Used widely.
Hydraulic rating	Instream habitat for target biota (e.g. Stalnaker & Arnette, 1976).	Desktop, limited field data; historical flow records. Discharge linked to hydraulic variables – typically single river cross section. Hydraulic variables (e.g. wetted perimeter) used as surrogate for habitat-flow needs of target biota.	Water resource developments where little or no negotiation is involved, or as a tool within habitat simulation or holistic methodologies. Used widely.
Habitat simulation	Models instream habitat for target biota (e.g. PHABSIM: Bovee, 1982; Stalnaker *et al*., 1995). May include channel form, sediment transport, water quality, riparian vegetation, wildlife, recreation and aesthetics.	Desktop and field data; historical flow records. Many hydraulic variables – multiple cross sections. Physical habitat suitability or preference data for target species.	Water resource developments, often large-scale, involving rivers of high conservation and/or strategic importance, and/or with complex, trade-offs among users, or as method within holistic approaches. Primarily used in developed countries.
Holistic	Whole river ecosystem; may also consider ground water, wetlands, floodplains, estuaries and coastal waters. Social dependence on ecosystems and related economic factors may be assessed (e.g. DRIFT: King *et al*., 2003; Benchmarking: Arthington, 1998).	Desktop and field data, plus historical flow and/or rainfall records; requires multidisciplinary teams of river scientists. Many hydraulic variables assessed at multiple cross sections. Biological data on flow- and habitat-related requirements of all biota and some/all ecological components; exotic species may be included in assessments of biodiversity implications (e.g. Arthington, 1998; Arthington *et al*., 2004). Hydro-ecological relationships and models increasingly used within holistic frameworks.	Water resource developments, typically large-scale, involving rivers of high conservation and/or strategic importance, and/or with complex user trade-offs. Simpler approaches (e.g. expert panels) often used where there are limited trade-offs among users, and/or time constraints. Used in developing and developed countries.

of terrestrial ecosystems (Hooper *et al*., 2005). However, the precise impacts of biodiversity change will vary with ecosystem type and the processes and properties considered (Giller *et al*., 2004; Hooper *et al*., 2005). Although much less is known about fresh waters than terrestrial ecosystems, there is evidence that ecosystem processes can be impacted by changes in biodiversity (Covich *et al*., 2004*a*). Invertebrates, for example, play multiple roles in the functioning of rivers (Wallace & Webster, 1996), and the presence of key species (Dangles *et al*., 2004), magnitude of species richness (Cardinale, Palmer & Collins, 2002; Jonsson & Malmqvist, 2003), and other attributes of communities (e.g. Dangles & Malmqvist, 2004) can affect rates of ecosystem processes. In addition, variability of process rates is likely to be increased when species are lost, even in situations where average rates remain unchanged (Dang, Chauvet & Gessner, 2005). In some cases it is possible to predict how different anthropogenic stresses will affect ecosystem functioning (Jonsson *et al*., 2002), but in most instances insufficient information is available to make informed predictions. Of particular concern is the decline in populations of large freshwater vertebrates (see Section IV) to a level whereby they become so scarce that their ecological roles are degraded to an extent that they might as well be extinct. Such functional extinctions, and associated reductions in ecosystem services, have been projected for a variety of land birds (Sekercioglu, Daily & Ehrlich, 2004) and may have already taken place in some freshwater ecosystems.

Appreciating the value of freshwater biodiversity is essential to ensure its well-being. It is certain that if scientists are unwilling or unable to place a value on 'free' ecosystem goods and services, then politicians and policy-makers will interpret this as 'zero value'. The resources apt to be protected are those that are appreciated. Water must no longer be a free or cheap resource – as it is still treated in most countries (Kingsford, 2000; Clark & King, 2004). Realistic economic valuations of water as a habitat for freshwater biodiversity, and the services that such biodiversity provides, will be an essential driver of any change in societal attitudes (Postel & Carpenter, 1997; Holmlund & Hammer, 1999; Postel & Richter, 2003; Clark & King, 2004). The first estimate of the global values of ecosystem goods (e.g. food in the form of fishes), ecosystem services (e.g. waste assimilation), biodiversity, and cultural considerations yielded a value of US$6579 $\times 10^9$/year for all inland waters (Constanza *et al.*, 1997). It exceeded the worth of all other non-marine ecosystems combined (US$5740 $\times 10^9$/year), despite the far smaller extent of inland waters. To provide an economic benchmark, the gross domestic product of the United States is US$9000 $\times 10^9$/year. Of course, all valuation estimates are subject to controversy (Pearce, 1998; Toman, 1998; Balmford *et al.*, 2002), but other approaches to assess values of freshwater systems (e.g. Barbier, Acreman & Knowler, 1997; Wilson & Carpenter, 1999, Woodward & Wui, 2001; Patterson, 2002) convey the same general message: inland waters have immense economic importance.

The value of inland waters is bound to increase as ecosystems become more stressed and their goods and services scarcer. However, there is a paucity of empirical data showing how the yield of goods and services derived by retaining habitats in a relatively undisturbed condition compares with that obtained when they are converted for human use (Balmford *et al.*, 2002; but see Hooper *et al.*, 2005). One of the few good examples assessed the value of pristine freshwater habitat of coho salmon (*Oncorhynchus kisutch* (Walbaum)) on the West Coast of Canada in relation to various alternative states of degradation (Knowler *et al.*, 2003). Even when only this single species was considered, retaining spawning and rearing streams in a pristine state produced annual values of US$940 to US$4980 per stream km, as measured by increased profits in the commercial fishery situated downstream. While fish conservation cannot be used as the sole index for assessing the relative value of different catchment management strategies, information of this type can help communicate the extent of the loss of benefit that accompanies degradation of freshwater ecosystems. For instance, income derived from the global sports fishing community provided an incentive to preserve the spawning habitat of marble trout (*Salmo marmoratus* Cuvier) in the Soca River, Slovenia, thereby generating an economic benefit of US$2.9 $\times 10^6$/year – equivalent to 44 % of all tourist revenues in the upper Soca region (Sullivan *et al.*, 2003). Likewise, sport fishing (albeit for exotic salmonids) in Lake Taupo, New Zealand, generates almost 10 % of the activity in the local economy, which is based largely on tourism and forestry (Anon, 2003). Freshwater biodiversity has particular importance for indigenous people in many parts of the world, who depend upon aquatic products and the seasonal flux of wetland conditions to support livelihoods. Examples include the Mesopotamian 'Marsh Arabs', who have been profoundly influenced by draining and ongoing restoration of riverine wetlands in Iraq (e.g. Richardson *et al.*, 2005), as well as societies on African River floodplains (e.g. the Dinka, Lozi and Tonga peoples: Tockner & Stanford, 2002), and communities in the Lower Mekong Basin (Choowaew, Chandrachai & Petersen, 1994). Amerindian communities in flooded forest (*varzea*) along the Amazon also use many products for handicrafts, medicines and food (Neves, 1995). These flooded forests have been calculated to generate a level of household income equivalent to US$2330/year (Sullivan, 2002), which highlights the importance of considering a wide range of stakeholders in environmental valuations and the development of effective conservation policies (Opschoor, 1998).

Freshwater biodiversity is also of immense direct importance to human health. Although many formerly devastating infections related to water (e.g. cholera, typhoid fever) are now largely in check, other water-borne diseases continue to be widely responsible for societal burdens and human misery. This is especially true in the tropics where water-borne diseases contribute to around 80 % of all illnesses. The figures for parasitic infections, which are expressed in terms of years of life lost to death or disability annually (DALY), speak for themselves (W.H.O., 2004): 46.5 million DALY due to malaria (although recent estimates of malarial incidence are more than 50 % higher: Snow *et al.*, 2005); 5.8 million due to lymphatic filariasis, 1.7 million due to schistosomiasis (bilharzia), and 0.5 million due to onchocerciasis (river blindness). The last of these has declined substantially as a result of research that allowed targeted control of the river-dwelling blackfly (Simuliidae) larvae that are obligatory hosts of this parasite (Lévêque *et al.*, 2003). Nevertheless, outbreaks of water-borne diseases continue to occur and can be greatly exacerbated by human alteration of hydrological regimes, as well as increases in the extent of irrigation ditches and channels and hence the availability of habitats for disease organisms and their vectors (e.g. de Moor, 1994). Habitat degradation, creation of 'ruderal' freshwater habitats, and simplification of natural species assemblages may foster mass proliferation of insect and mollusc vectors for infectious human diseases. If so, maintenance of natural freshwater communities and overall system integrity may contribute substantially to the alleviation of conditions for disease transmission.

It may be possible to meet human needs for water without loss of most inland-water species but, this will require implementation of environmental water allocations that mimic natural patterns of flow variability and include a range of flows – not just a minimum level (Poff *et al.*, 1997; Bunn & Arthington, 2002; see Fig. 2). For most freshwater systems and taxa, scientists can – at present – neither estimate the quantities of water that can be extracted nor the temporal changes in flow that can be tolerated. Maintenance of biodiversity is a critical test of whether water use or ecosystem modifications are sustainable, and this assumption underlies all use of freshwater organisms as biomonitors or indicators of habitat condition (e.g. Rosenberg & Resh, 1993; Karr & Chu, 1999). Preservation of all elements of freshwater biodiversity would guarantee that water use for humans is sustainable, and the magnitude of the threat to and loss of biodiversity is probably a reliable indicator of the extent to which current practices are unsustainable.

X. CONSERVATION OF FRESHWATER BIODIVERSITY IN THE REAL WORLD

Inland waters constitute a valuable natural resource, in economic, cultural, aesthetic, scientific and educational terms. Their conservation and management are critical to the interests of all nations and governments. Immediate conservation action is needed in some instances where opportunities exist to set aside 'pristine' lake and river systems in large protected areas. Realistically, it must be recognised that there are significant portions of the Earth's surface where it is almost inconceivable that any freshwater resource could be dedicated to the sole purpose of biodiversity conservation, with humans denied access or their use of the resource substantially limited. Even well-protected conservation areas can become focal points for tourism and recreational activities that may reduce habitat quality and biodiversity (Hadwen, Arthington & Mosisch, 2003). Thus, for most of the global land surface, trade-offs between conservation of freshwater biodiversity and human use of ecosystem goods and services are necessary.

If science is to be deployed in a manner that will secure commitment to the conservation of freshwater biodiversity from politicians and decision-makers, scientists will have to make some adjustments in attitude (e.g. Lévêque & Balian, 2005). In particular, reconsideration of what is regarded as acceptable forms of ecosystem management for biodiversity conservation will be required in the wider context of national development policies. We do not advocate abandoning attempts to check species loss but, in many situations, a compromise position of management for biodiversity conservation, ecosystem functioning and resilience, and human livelihoods will provide the most successful long-term basis for freshwater conservation (Moss, 2000). Furthermore, this approach is more likely to be achievable than idealistic prospects of 'win–win' situations between economic development and ecological management practices within which all species can be saved (Redford & Sanderson, 1992), or the alternative and discouraging view that conservation of biodiversity is fundamentally incompatible with economic development (Terborgh, 1999). An apparent lack of common ground between organisations committed to sustaining livelihoods and those concerned with biodiversity conservation might arise from different starting points and prioritisation of goals; if so, such differences must be recognised but they need not imply that attempts to combine the goals of conservation and meeting human needs should be regarded as futile (Adams *et al.*, 2004).

Data are insufficient to estimate accurately loss rates of freshwater biodiversity in many regions. An immediate, coordinated effort to assess global freshwater biodiversity, including identification of major hotspots, is mandated, and should involve partnerships among major non-government organisations, the United Nations, research institutions, and scientific societies. However, the current impediment of insufficient data should not be used as justification for preventing further losses. Nor does the broader community have to wait until all possible information is in hand before taking action. As the current trends in turtles, fishes and other taxa indicate, there are sufficient reliable data to show that the global crisis of freshwater biodiversity is now a calamity. Developing effective conservation and management strategies for freshwater biodiversity requires documenting declines and extinctions and understanding the underlying causes. Implementation of such strategies depends upon effective communication and engagement among scientists, politicians, non-government organisations and local communities (Poff *et al.*, 2003). Pragmatic approaches will be needed to ensure that attempts at communication between freshwater scientists and water-resource managers, as well as other stakeholders, contribute to planning and problem solving (Richter *et al.*, 2003; Bernhardt *et al.*, 2005) and do not become a dialogue of the deaf. This is a significant challenge as motivations of the broader community may be neither open nor fair. Conservation typically operates in a world where many players are characterized by dishonesty, self-interest, and hostility to nature, and where corporate interests often assume disproportionate importance (Stearns & Stearns, 1999; Meffe, 2001).

Emphatically, the importance of freshwater biodiversity to society must be communicated successfully to all. The threats to freshwater biodiversity are becoming sufficiently known among scientists, but are insufficiently incorporated within water development. Those making policy and management decisions affecting freshwater biodiversity and water resources need to apply the relevant scientific information, as far as this is available, and employ robust risk-assessment procedures, monitoring, and adaptive management (see Richter *et al.*, 2003; Revenga *et al.*, 2005). Ecologically-sustainable water management will only be achievable if concerns about ecology and biodiversity are treated with the same importance as other goals (such as engineering considerations) when water-resource developments are planned (Richter *et al.*, 2003). This will be a significant advance on the prevailing approach wherein ecological criteria are treated as compliance factors to be evaluated after a water-resource development plan has been completed. A first step in this process would be stipulation of ecosystem flow requirements (which inform EWA) so that water-resource managers can take account of these throughout the planning process.

While preservation of intact freshwater bodies and their biodiversity remains a priority, it is important to recognize the potential that partly degraded habitats may have to support significant portions of their original biodiversity. Rich aquatic communities can persist in some human-dominated landscapes (e.g. densely-populated Hong Kong: Dudgeon, 2003*a*), although certainly not in all situations (e.g. Singapore: Brook, Sodhi & Ng, 2003). Strategies are needed for managing and rehabilitating degraded ecosystems – even if they contain exotic species – in order to maximize the persistence of native biodiversity. In Chile, for example, freshwater management is mainly directed towards habitat protection for exotic salmonids. However, this approach contributes to the maintenance of ecosystem functioning and a good deal of indigenous biodiversity, although some native fishes are confined to places where salmonids do not do well (Soto & Stockner, 1995; Soto & Arismendi, 2005). There would certainly be strong opposition to removing salmonids from Chilean streams because most stakeholders view them as ecosystem goods of high value. In New Zealand also, the desire to preserve valuable fisheries based on exotic salmonids (see Section IX) has led to the development of habitat management plans (e.g. Anon, 2003) that incidentally protect elements of native biodiversity. Elsewhere, many important fresh- and brackish-water wetlands are largely man-made or human-dominated environments. Some – such as certain important Ramsar sites – host globally significant numbers of endangered water birds, thereby demonstrating that human alteration of ecosystems is not always incompatible with biodiversity conservation. In an attempt to move towards such 'win–win' solutions, Rosenzweig (2003) advocates an approach to enhancing species richness in human-dominated landscapes termed 'reconciliation ecology'. It is to such strategies that freshwater scientists should consider turning, where appropriate, rather than persisting only in attempts to preserve intact ecosystems in the face of burgeoning human pressure. Given the multiple and growing demands upon fresh waters, it can be anticipated that whatever principles emerge from reconciliation ecology will have direct relevance for conservation of freshwater biodiversity. While scientists may not yet have all the tools to ensure that biodiversity conservation and human use of fresh waters can be reconciled, Charles Elton, the 'father of animal ecology', was prescient when he wrote that we should be '... looking for some wise principle of co-existence between man and nature, even if it has to be a modified kind of man and a modified kind of nature. This is what I understand by conservation' (Elton, 1958; p. 145).

XI. CONCLUSIONS

(1) Fresh water makes up only 0.01% of the World's water and covers only 0.8% of the Earth's surface, yet this tiny fraction of global water supports at least 100000 species out of approximately 1.75 million – almost 6%. Not surprisingly, considering their landscape position and value as a natural resource, fresh waters are experiencing declines in biodiversity far greater than those in the most affected terrestrial ecosystems. These declines seem to be especially serious in some tropical latitudes, and particularly affect large fishes and other vertebrates.

(2) Freshwater biodiversity is *the* over-riding conservation priority during the International 'Water for Life' Decade for Action (2005 to 2015) and beyond. Assuming trends in human demands for water remain unaltered and species losses continue at current rates, the opportunity to conserve significant proportions of the remaining biodiversity in fresh water will vanish before the 'Water for Life' decade ends.

(3) Threats to global freshwater biodiversity fall into five categories: overexploitation; water pollution; flow modification; destruction or degradation of habitat; and invasion by exotic species. Their combined and interacting influences on biodiversity are now worldwide, and are exacerbated further by global-scale environmental changes such as nitrogen deposition and climate change. Knowledge of these threats is increasing among scientists but is insufficiently incorporated within water-resource development, and thus requires wider dissemination and emphasis.

(4) Inventories of freshwater biodiversity are incomplete in many parts of the world, especially the tropics, and rates of species loss may be higher than currently estimated. An immediate, coordinated effort to assess global freshwater biodiversity, including major hotspots, should be launched in partnership with major non-government organisations, the United Nations, research institutions and scientific societies. This exercise should take place in parallel with the ongoing development of strategies for the conservation and management of freshwater biodiversity.

(5) Fresh water is subject to severe competition among multiple human stakeholders, in many regions, and serious conflicts can arise when water supplies are limiting or traverse political boundaries. Conservation of biodiversity is complicated further by the landscape position of rivers and wetlands as 'receivers' of land use effluents, and the problems posed by endemism, limited geographic ranges and non-substitutability.

(6) Protection of freshwater biodiversity is perhaps the ultimate conservation challenge because, to be fully effective, it requires control over the upstream drainage network, the surrounding land, the riparian zone, and – in the case of migrating aquatic fauna – downstream reaches. Such prerequisites are hardly ever met, and will necessitate development of inclusive management partnerships at appropriate (drainage-basin) scales. The complicated issues associated with protected-areas design and management for fresh waters require energetic and imaginative attention from researchers.

(7) Water regimes influence aquatic biodiversity via several, inter-related mechanisms operating over a range of spatial and temporal scales. The maintenance of natural variability in flows and water levels is therefore essential to underpin conservation strategies for freshwater biodiversity and habitats. This requires establishing a hydrological regime that mimics natural variability in flows and water levels rather than focusing on minimum levels only. For most freshwater systems and taxa, scientists can – at present – neither estimate the quantities of water that can be extracted nor the temporal changes in flow that can be tolerated. Research on this matter of environmental water allocations is needed urgently. Furthermore, it is essential that provision of flows needed to preserve biodiversity be treated with the same importance as engineering concerns and other goals when water-resource developments are planned.

(8) Freshwater biodiversity provides a broad variety of valuable goods and services for human societies. Some are irreplaceable. Notwithstanding, there is a paucity of empirical data showing how the value of goods and services derived by retaining habitats in relatively natural conditions compares with that obtained when they are converted for human use. The uses of fresh water, including non-consumptive use, underscore the importance of considering the perspectives of a wide range of stakeholders in environmental valuation and in the development of effective conservation policies.

(9) Maintenance of biodiversity is a critical test of whether water use and ecosystem modifications are sustainable. Conservation strategies protecting all elements of

freshwater biodiversity would guarantee that water use for humans is sustainable while, in contrast, the magnitude of the threat to and loss of biodiversity is an indicator of the extent to which current practices are unsustainable.

(10) A mixture of strategies will be essential to preserve freshwater biodiversity in the long term. It must include reserves that protect key, biodiversity-rich water-bodies (especially those with important species radiations) and their catchments, as well as species- or habitat-centred plans that reconcile the protection of biodiversity and societal use of water resources in the context human-modified ecosystems. In parallel, scientists must more effectively communicate the importance and value of freshwater biodiversity to stakeholders and policy makers, so as to make certain that all available information on freshwater biodiversity is applied effectively to ensure its conservation.

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