Freshwater biodiversity conservation: recent progress and future challenges

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Abstract. Freshwater habitats occupy <1% of the Earth's surface, yet are hotspots that support ~10% of all known species, and ~ ⅓ of vertebrate species. Fresh waters also are hotspots for human activities that have led to widespread habitat degradation, pollution, flow regulation and water extraction, fisheries overexploitation, and alien species introductions. These impacts have caused severe declines in the range and abundance of many freshwater species, so that they are now far more imperiled than their marine or terrestrial counterparts. Here, we review progress in conservation of freshwater biodiversity, with a focus on the period since 1986, and outline key challenges for the future. Driven by rising conservation concerns, freshwater ecologists have conducted a great deal of research over the past 25 y on the status, trends, autecology, and propagation of imperiled species, threats to these species, the consequences of biodiversity loss for ecosystem functioning, metapopulation dynamics, biodiversity hotspots, reserve design, habitat restoration, communication with stakeholders, and weaknesses of protective legislation. Nevertheless, existing efforts might be insufficient to stem the ongoing and coming multitude of freshwater extinctions. We briefly discuss 4 important challenges for freshwater conservation. First, climate change will imperil both freshwater species and human uses of fresh water, driving engineering responses that will further threaten the freshwater biota. We need to anticipate both ecological and human responses to climate change, and to encourage rational and deliberate planning of engineering responses to climate change before disasters strike. Second, because freshwater extinctions are already well underway, freshwater conservationists must be prepared to act now to prevent further losses, even if our knowledge is incomplete, and engage more effectively with other stakeholders. Third, we need to bridge the gap between freshwater ecology and conservation biology. Fourth, we suggest that scientific societies and scholarly journals concerned with limnology or freshwater sciences need to improve their historically poor record in publishing important papers and influencing practice in conservation ecology. Failure to meet these challenges will lead to the extinction or impoverishment of the very subjects of our research.

Key words: endangered species, extinction, fresh water, limnology, climate change, North American Benthological Society.

Freshwater ecosystems provide vital resources for humans and are the sole habitat for an extraordinarily rich, endemic, and sensitive biota. Human demands on freshwater ecosystems have risen steeply over the past century (Fig. 1A–E), leading to large and growing threats to biodiversity around the world (Dudgeon et al. 2006; Fig. 2). As a result of this global crisis, documenting losses of biodiversity, diagnosing their causes, and finding solutions have become a major part of contemporary freshwater ecology. Here, we describe recent progress in freshwater conservation science, concentrating on the period since 1986 when *J-NABS* appeared; comment briefly on the past role and future potential of *J-NABS*, the North American Benthological Society (NABS), and other scholarly societies and journals concerned with freshwater sciences; and highlight a few areas that we think deserve special attention. Our treatment is necessarily brief and selective, focusing chiefly on streams, rivers, and lakes. We largely omit wetlands, even though they are ecologically important, biologically rich, and

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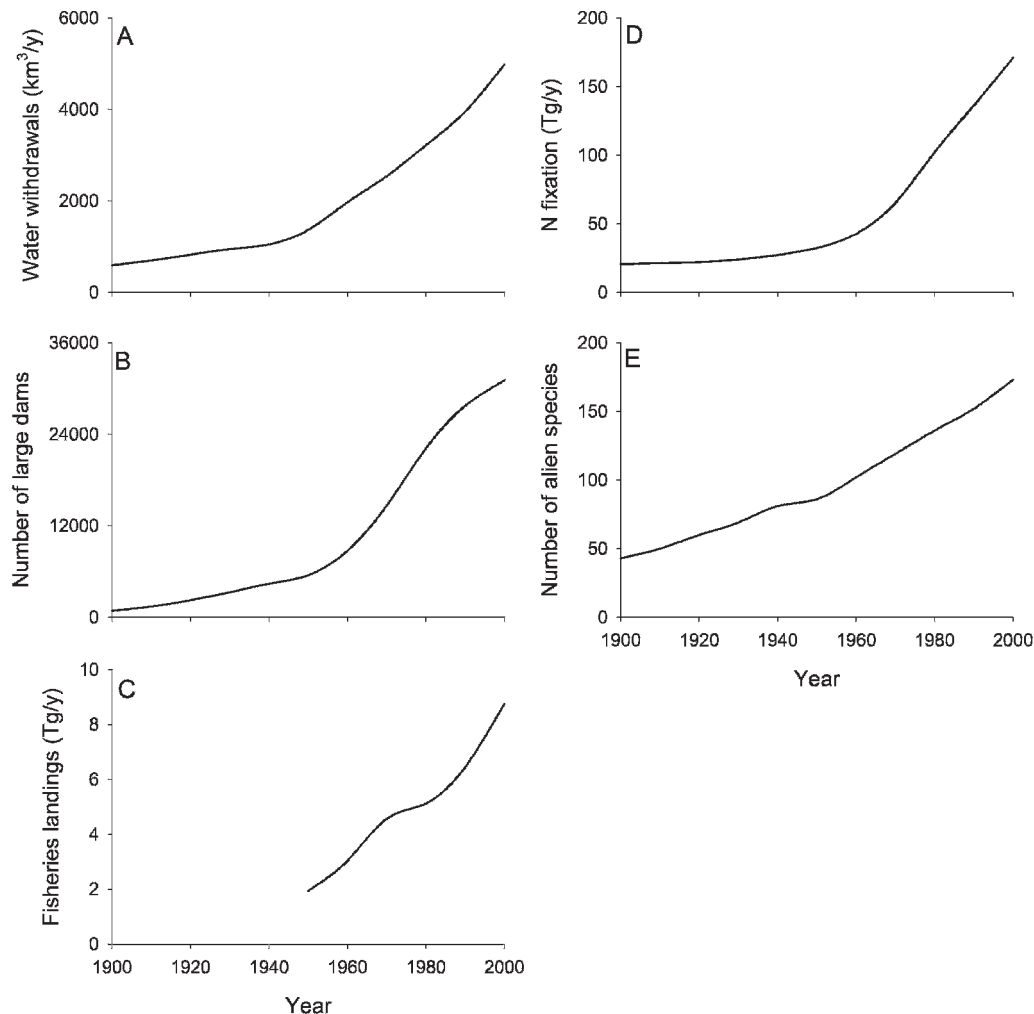
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FIG. 1. Five examples of rising human pressures on the world's freshwater ecosystems. A.—Global water withdrawals (after Gleick 1993). B.—Number of large (>15 m high) dams (International Commission on Large Dams 2008). C.—Fisheries landings from inland waters (Allan et al. 2005a). D.—Global inputs of anthropogenically fixed N. Input from all natural sources is ~110 Tg/y (Vitousek 1994, Galloway et al. 2008). E.—Number of known alien species in the Laurentian Great Lakes (Ricciardi 2006).

also imperiled by human activities (e.g., Brinson and Malvarez 2002, Junk 2002, Zedler and Kercher 2005).

The collision between humans and biodiversity in freshwater ecosystems

For millennia, humans have used fresh waters and their surroundings for drinking and irrigation water, waste disposal, transportation, power production, harvest of plants, fish, game, and minerals, and sites for homes, farms, and industries. In addition to the enormous direct economic value of these uses, ecosystem services provided by freshwater ecosystems have been estimated at $6.5 trillion USD/y, 20% of the value provided by all of the Earth's ecosystems (Costanza et al. 1997). Following the rapid growth of

the human population and the global economy over the past century, human uses of freshwater ecosystems have grown so steeply that they now produce large, widespread, negative ecological impacts (Fig. 1A–E). Humans now capture >50% of available freshwater runoff (Jackson et al. 2001), reservoirs trap 25% of the global sediment load before it reaches the oceans (Vörösmarty and Sahagian 2000), and several of the world's great rivers, including the Ganges–Brahmaputra, Yellow, Nile, and Colorado, have stopped flowing to the sea during dry periods (Postel 2000). River systems have been fragmented by ~1 million dams globally (Jackson et al. 2001), confined by levees, and dredged and straightened for navigation and flood control. Likewise, pervasive transformations of riparian zones and watersheds have
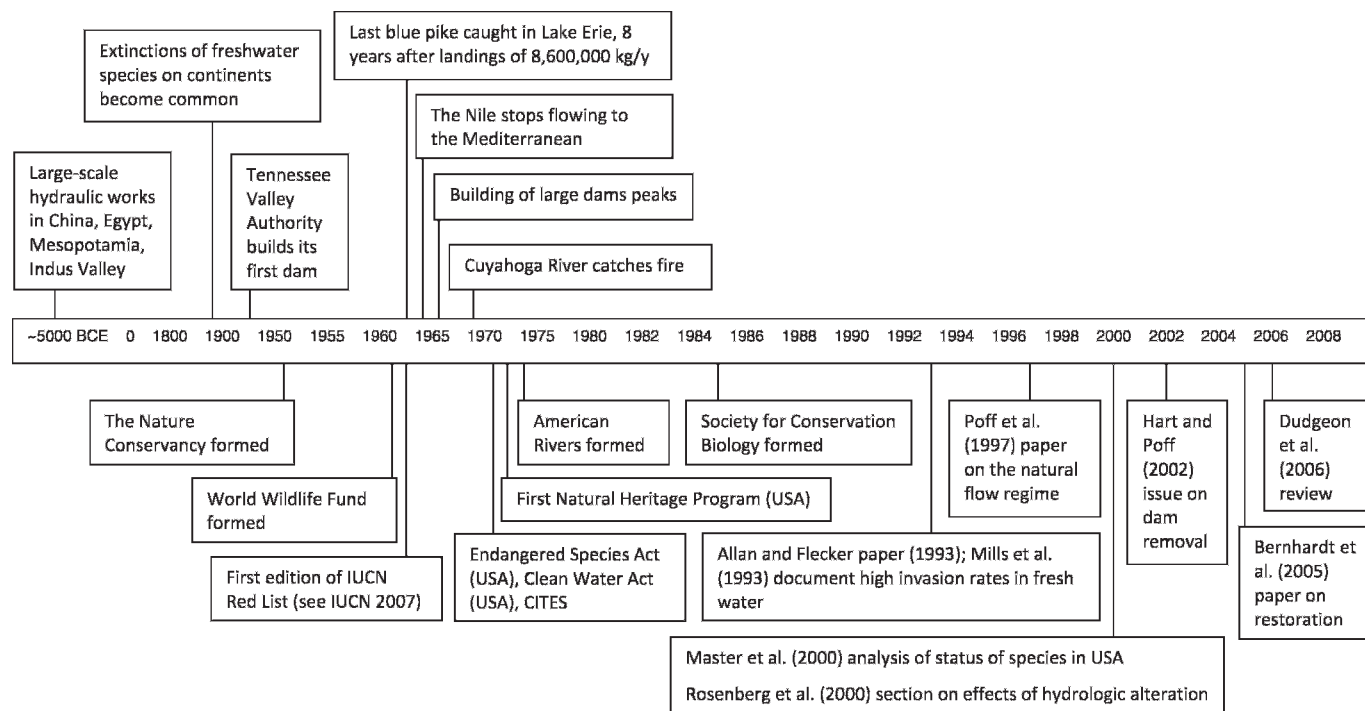
FIG. 2. A selective timeline of some major events in freshwater conservation ecology. Items listed above the timeline are examples of important events that led to the need for conservation action, from Anonymous (1969), Postel (2000), Baldwin et al. (2007), IUCN (2007), International Commission on Large Dams (2008), and Tennessee Valley Authority (2009). CITES = Convention on International Trade in Endangered Species, BCE = Before the Common Era.

altered inputs of water, nutrients, organic matter, and sediments to lakes and rivers. Excessive loading of nutrients and toxins from these landuse changes and point sources have eutrophied or poisoned many waters so much that they cannot support their natural biotic communities (e.g., Smith 2003, Polunin 2008, Smol 2008); indeed, pollution has eliminated all fish from 5% of the length of Chinese rivers (Dudgeon 1999). Freshwater fisheries around the world are seriously overexploited, and large freshwater fishes are in global decline (Allan et al. 2005a, Dudgeon et al. 2006). Humans have introduced hundreds to thousands of exotic species into fresh waters around the world (FAO 2008), dozens of which (water hyacinth, zebra mussels, Nile perch) have had large and long-lasting ecological impacts (Strayer 2009).

The biota of fresh waters is very much larger than would be expected from the area covered by freshwater habitats, although it has not yet been fully inventoried. The ~125,000 species of freshwater animals that have so far been described represent 9.5% of all known animal species on the planet (including ⅓ of all vertebrate species), even though fresh waters cover just 0.8% of the Earth's surface area (Dudgeon et al. 2006, Balian et al. 2008). Fresh waters as a whole are a hotspot for biodiversity (Fig. 3A, B).

When one considers the large proportion of the world's fresh waters that lie in recently glaciated regions, which have relatively low biodiversity and endemism, it is apparent that fresh waters in unglaciated regions can be much hotter spots of biodiversity than these global figures imply.

A few freshwater species have large geographic ranges, but the insular nature of freshwater habitats has led to the evolution of many species with small geographic ranges, often encompassing just a single lake or drainage basin (e.g., Benz and Collins 1997, Rossiter and Kawanabe 2000, Dudgeon et al. 2006, **Strayer 2006**[1]), resulting in biotas with high endemism and high species turnover between basins. Such high fragmentation and endemism reduces the ability of freshwater species to migrate freely across the landscape to reestablish local populations that have been extirpated or respond to climate change and makes them very sensitive to human impacts.

The collision between large and rising demands on fresh waters from humans and a rich and endemic freshwater biota has led to the extinction or imperilment of many species. The precise extent of this

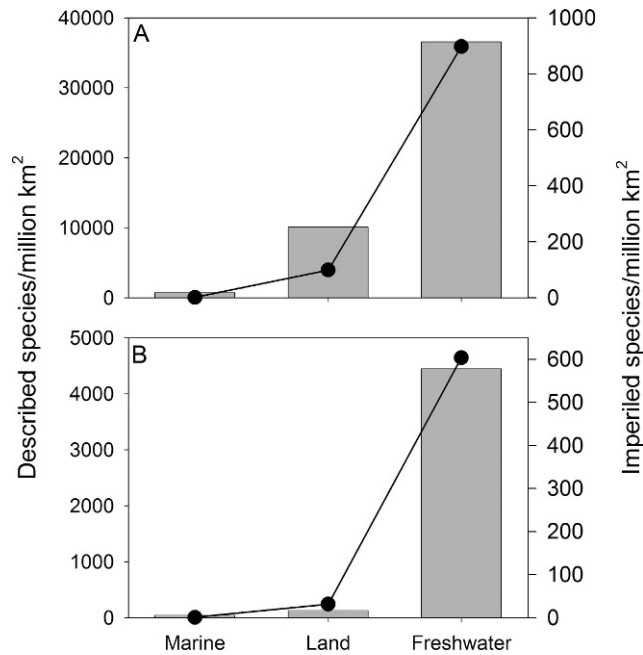[1] Boldface indicates paper was published in *J-NABS*

FIG. 3. The number of described (bars) and imperiled species (lines) of eukaryotes (A) and chordates (B) in fresh waters is much higher than would be expected from the area of the globe covered by freshwater habitats. This pattern holds true for chordates, which have been well inventoried, and for all eukaryotes, for which the data are very incomplete and probably biased. Numbers of described species are from Palmer et al. (1997), Groombridge and Jenkins (2002), and Balian et al. (2008). Imperiled species include species listed by IUCN (2007) in the following categories: extinct, extinct in the wild, critically endangered, endangered, and vulnerable.

imperilment is unknown, although we know that a great many species and populations have been affected and that continental freshwater biotas are nearly always far more imperiled than their terrestrial counterparts (e.g., Fig. 4A–D; Ricciardi and Rasmussen 1999, Master et al. 2000, Sala et al. 2000). In intensively developed areas, such as Europe and North America, it is not unusual for >⅓ of the freshwater species in a taxonomic group to be extinct or imperiled (Master et al. 2000, Kottelat and Freyhof 2007, Jelks et al. 2008). Globally, perhaps ~10,000 to 20,000 freshwater species already are extinct or imperiled as a result of human activities (**Strayer 2006**, IUCN 2007). Therefore, fresh waters are hotspots of endangerment as well as of biodiversity (Fig. 3A, B). Even in cases where species have not yet disappeared altogether, human activities have eliminated many populations and have caused a marked thinning of ranges that could reduce the future viability of many species (Strayer 2008).

Major Themes in Freshwater Biodiversity Research

Many of the early concerns about human impacts on freshwater ecosystems at least implicitly concerned biodiversity (e.g., loss of populations of fish or shellfish as a result of human activities: e.g., Ortmann 1909, 1924, van der Schalie 1938, Trautman 1957; irruption of nuisance species such as *Cladophora*, Cyanobacteria, and the sewage "fungus" *Sphaerotilus*: Hasler 1947, Hynes 1960, 1970), and attempts to restore or protect selected freshwater species by regulating harvests, controlling pollution, or restoring habitat have a long history (e.g., Tarzwell 1937). Nevertheless, it appears that practical work related to conservation was separated from the main body of freshwater ecology even at this early date: biodiversity conservation was scarcely mentioned in most limnology textbooks (e.g., Welch 1935, Ruttner 1963, Wetzel 1975). However, it was an important theme in Hynes' (1970) influential book on running-water ecology, perhaps because of Hynes' earlier experience with water pollution (Hynes 1960).

Nevertheless, freshwater biodiversity conservation came together as a distinct field only recently, after the emergence of conservation ecology as a distinct discipline in the 1980s (Fig. 2). Key drivers included the formation of the Society for Conservation Biology (1985; Fig. 2) and its journal *Conservation Biology* (1987), publication of widely used textbooks in this field in the 1990s (e.g., Primack 1993, Meffe and Carroll 1994, Caughley and Gunn 1996, Hunter 1996), and rapid growth of nongovernmental organizations (NGOs), such as The Nature Conservancy (Fig. 2), the World Wildlife Fund (Fig. 2), the International Rivers Network, and American Rivers (Fig. 2), that were concerned with protecting freshwater biodiversity. Legislation, such as the 1973 Endangered Species Act in the USA (Fig. 2), also was important in focusing attention and funding on imperiled freshwater species. Similar legislative frameworks exist in Canada, the European Union, and elsewhere. For example, the Endangered Species Scientific Commission of the People's Republic of China lists many aquatic vertebrates as Class 1 protected (i.e., threatened species that should not be exploited or traded) or Class 2 protected (threatened species that can be exploited or traded within quota limits). Several articles (e.g., Williams et al. 1989, Williams et al. 1993, Dudgeon 1992, Allan and Flecker 1993 [Fig. 2]) were important in defining and raising the profile of freshwater conservation ecology during these formative years.

The rapid expansion of conservation biology since 1980 has given rise to an extensive literature,

■ Extinct (GX, GH)
■ Critically imperiled (G1)
▨ Imperiled (G2)
▨ Vulnerable (G3)
□ Secure (G4, G5)

A. Birds and mammals   B. Freshwater fish   C. Freshwater insects   D. Crayfish and mussels
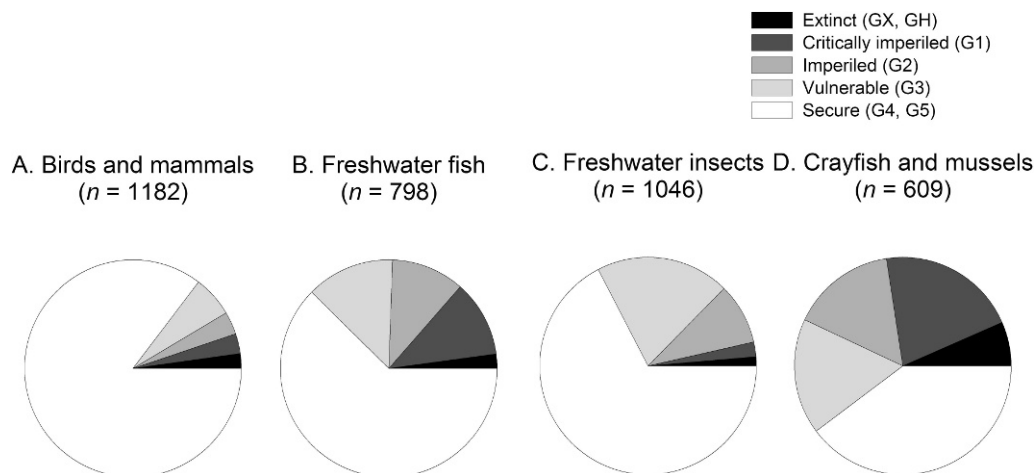(*n* = 1182)   (*n* = 798)   (*n* = 1046)   (*n* = 609)

FIG. 4.   Conservation status of birds and mammals (A), freshwater fishes (B), freshwater insects (C), and crayfish and mussels (D) in the US in the late 1990s (from Master et al. 2000), showing that freshwater animals, especially those that disperse poorly, are more highly endangered than their terrestrial counterparts. The number of species in each group (*n*) is given in parentheses. Freshwater insects includes only Odonata and Plecoptera. The conservation status of other freshwater insects was not assessed. Assessment codes are NatureServe designations.

involving a large number of specific subjects in research and management. As we detail below, freshwater scientists have participated in some, but not all, of these rapidly progressing areas. Here, we briefly describe areas of recent progress in freshwater biodiversity conservation.

Status assessment and study of specific threats

An enormous effort has recently gone into assessing the conservation status of imperiled species and identifying threats to their survival. This work has been motivated in large part by the requirement for such information prior to listing species for protection under the US Endangered Species Act, Canada's Committee on the Status of Endangered Wildlife in Canada (COWESIC), and similar programs in other jurisdictions. Although they do not often appear in technical journals such as *J-NABS*, these studies constitute a large proportion of all recent research on unionoid mussels, hydrobiid snails, and other taxa. At the global level, assessments of species status have been coordinated since 1963 and updated annually by the International Union for Conservation of Nature (IUCN) in their Red List (IUCN 2007; Fig. 2). Similar global assessments that include many freshwater taxa include the World Wildlife Fund (WWF) Living Planet Index (Loh et al. 2005), and the Global Amphibian Assessment (2006). Publications, such as Mills et al. (1993; Fig. 2) and Rosenberg et al. (2000; Fig. 2), highlighted specific threats to freshwater ecosystems, and Polunin (2008) recently provided an overview of leading threats. At the time of writing,

however, no global threat assessments have been made for any freshwater invertebrate group, nor has any integrated threat assessment of fresh waters comparable to that undertaken for marine ecosystems by Halpern et al. (2007) been done.

Consequences of biodiversity loss for ecosystem function

A large body of recent research has explored the links between biodiversity and ecosystem function (e.g., Hooper et al. 2005). Much of this work has focused on terrestrial plant communities, perhaps because they are experimentally tractable, but freshwater ecologists have made important contributions as well (e.g., Cardinale et al. 2002, Jonsson and Malmqvist 2003, McIntyre et al. 2007, Vaughn et al. 2007). Ecosystem function often depends on species richness and composition, but the size and nature of this effect depends on the identity of the species being gained or lost, the ecological process under consideration, and the characteristics of the ecosystem. Consequently, the effects of large anthropogenic biodiversity losses on ecosystem function in fresh waters still are unclear (McIntyre et al. 2007), even though they might be large.

Autecological studies of imperiled species

The desire to protect and manage populations of imperiled freshwater species has created a need for information on their life history, diet, genetics, physiology, and behavior. A large number of papers (e.g., **Jones and Neves 2002**, Foster and Soluk 2006,

Grobler et al. 2006, Keevin et al. 2007, and many others) have been published on these subjects over the past 25 y, and have added greatly to our knowledge of the biology of many imperiled species. The ultimate importance of many of these studies is difficult to assess because much of the information that they generated probably has not been used to inform conservation action or management interventions. We will return to this point later in the article.

Metapopulation theory and management

The conceptualization of a metapopulation as a series of connected populations (Levins 1969, Hanski and Gaggiotti 2004) has had enormous effects on community ecology and conservation biology and has focused attention on fragmentation and dispersal as key issues in species viability. Despite the facts that fresh waters are naturally fragmented into drainages, and that dams and other products of human activities have enormously increased habitat fragmentation (e.g., Nilsson et al. 2005), metapopulation ecology in fresh waters has lagged behind such work in other habitats. The research that has been done on freshwater metapopulations and fragmentation has yielded interesting results for conservation and suggests that fragmentation and the geometry of the drainage network can strongly affect the persistence of imperiled freshwater species and that extirpations and extinctions that will result from past fragmentation have not yet proceeded to completion (e.g., Fagan 2002, Fagan et al. 2002, Matthews and Marsh-Matthews 2007, Strayer 2008). Further work in this area probably would be fruitful and would yield insights that could be used to manage populations.

Identification of biodiversity hotspots and reserve design

Conservationists have spent much effort to identify geographic regions where species richness or endemism is high, and many such *hotspots* are now well known (Myers et al. 2000, Brooks et al. 2006). This information is used to prioritize areas for protection and as input to formal algorithms that develop optimal networks of protected areas that protect the most species using the least area (Sarkar et al. 2006). Freshwater conservation has lagged behind terrestrial conservation in these subjects, although a recent paper by Abell et al. (2008) describes an ongoing attempt to map global freshwater hotspots. Global biodiversity assessments frequently ignore freshwater species (e.g., Myers et al. 2000, Brooks et al. 2006, Kremen et al. 2008), despite the clear evidence that freshwater organisms are highly imperiled and that terrestrial hotspots do not always overlap with freshwater hotspots. Likewise, formal algorithms for designing optimal networks of protected sites rarely have been used for freshwater species (but see Linke et al. 2007, 2008).

Restoration ecology

The rising interest in protecting or managing natural ecosystems has been paralleled by a rapid rise in interest in using scientific knowledge to restore or rehabilitate damaged ecosystems, including the appearance of professional societies (Society for Ecological Restoration), journals (*Restoration Ecology*), and textbooks (Perrow and Davy 2002, Cooke et al. 2005, Falk et al. 2006). Interest in restoration or rehabilitation of freshwater ecosystems also has accelerated (e.g., Hart and Poff 2002 [Fig. 2], Buijse et al. 2005, National Research Council 2008). Restoration or rehabilitation of lakes rests on a firm scientific foundation (Cooke et al. 2005) and are routinely and successfully practiced. Scientific restoration and rehabilitation of running waters and wetlands is less well developed. Stream and wetland restoration are widely practiced, but many projects fail to achieve their objectives or are never adequately evaluated (Bernhardt et al. 2005 [Fig. 2], Palmer et al. 2007).

Coordination between scientists and other conservation stakeholders

Effective conservation depends on close communication between scientists and others interested in freshwater resources. Much has been written (e.g., **Pringle et al. 1993**, **Barbour et al. 2008**) about the importance of such communication and suggesting approaches for improving communication between scientists and stakeholders (e.g., government agencies, NGOs, journalists, environmental lawyers, concerned citizens). Our impression is that freshwater scientists work more frequently and comfortably with other stakeholders than they did 25 y ago. The discussion has moved from *whether* scientists should work with other stakeholders to *how* we best make these connections.

Assessment of weaknesses of protective legislation

Legislation to protect imperiled species has now been in place for long enough in many countries that it is possible to evaluate its effectiveness. An increasing and critical literature addresses the successes and shortcomings of such legislation, and authors have suggested modifications to improve its utility (e.g., Goble et al. 2005, Scott et al. 2005). Much of this analysis is very general, but some focuses

specifically on problems with freshwater species (e.g., Biber 2002).

Captive propagation and reintroduction

The longstanding practice of propagating game and food species for release into the wild recently has been adapted widely to imperiled species. Terrestrial birds and mammals still constitute the large majority of examples (Morell 2008), but some projects have involved fishes (e.g., Shute et al. 2005) and frogs (e.g., Banks et al. 2008), and recent progress in understanding the life history and juvenile ecology of unionoid mussels has allowed conservationists to propagate and introduce large numbers of these imperiled animals (Neves 2004). Successful application of captive propagation and reintroduction of any species, whether to a site from which the species was known historically or otherwise, requires careful consideration of genetic and ecological issues (e.g., Neves 2004, Araki et al. 2007). Attempts at reintroduction made without remedying the factors in the habitat that were responsible for the original extirpation of the target species usually are doomed to failure. Many reintroductions fail (Morell 2008), and their ultimate potential to contribute to freshwater conservation is not yet clear.

Recent Developments and Future Challenges

We close our brief survey of recent trends in freshwater biodiversity conservation by considering 4 areas in which current activities do not appear to be sufficient to meet the challenges that we will face in the coming decades. Efforts in these areas might need to be redoubled or refocused.

Emergence of climate change as a leading threat

When *J-NABS* began in 1986, very few conservationists recognized human-caused climate change as a threat to biodiversity. However, within a few years, it had appeared on the NABS agenda (Firth and Fisher 1992), and it now dominates discussions about the future conditions of and conservation planning in terrestrial, marine, and freshwater ecosystems (e.g., Heino et al. 2009, Poff et al. 2009).

Evidence for the beginnings of human-induced climate change in fresh waters already has appeared in the form of rising water temperatures, shorter periods of ice cover, and changes in the geographic ranges or phenology of freshwater animals (e.g., Ashizawa and Cole 1994, Magnuson et al. 2000, Parmesan 2006, Heino et al. 2009). Warmer temperatures will directly affect the metabolism of microbes, plants, and ectothermic freshwater animals, and could impact species that have narrow thermal tolerances (e.g., Nakano et al. 1996, Poff et al. 2001, Allan et al. 2005b). Climate change also will produce large hydrological changes, caused by changes in the amount and timing of precipitation, evapotranspiration, and glacial melting (Allan et al. 2005b, IPCC 2007). Many models also predict an increase in the frequency and severity of floods and droughts (IPCC 2007). As a result, the size and permanency of running and standing waters will change, with consequent changes in biodiversity.

Most climate change projections (IPCC 2007) predict that temperature increases in the tropics will be smaller than those further from the equator, so that impacts on tropical biodiversity might likewise be expected to be smaller. However, recent predictions from a model by Deutsch et al. (2008) suggest that tropical terrestrial species might be affected more seriously by rising temperatures than those closer to the poles because they are nearer their upper tolerance limits. These impacts are predicted to apply to fish and amphibians (Deutsch et al. 2008). A further potential outcome of global warming arises from the inverse relationship between body size in ectotherms and the temperature at which growth occurs, an important effect because in amphibians (and many aquatic invertebrates) larger body size at metamorphosis is associated with increased adult fitness (e.g., Semlitsch et al. 1988).

Given the insular nature of freshwater habitats, compensatory movements by organisms into cooler habitats further from the equator or at higher altitudes in response to climate change are often not possible, especially for the many fully aquatic species that cannot move through the terrestrial matrix separating potentially habitable sites. Even flying insects and amphibians might find their dispersal opportunities limited in human-dominated landscapes. These problems could be especially severe where drainage basins are oriented east–west, as in the US Great Plains (Matthews and Zimmerman 1990). One response to this problem would be translocation or *aided migration* of species of conservation significance from warmed water bodies to habitats within their thermal range (Hoegh-Guldberg et al. 2008). Actions, such as these, will be controversial for a variety of good reasons and might be costly and fraught with risk (e.g., Dodd and Siegel 1991). For instance, aided migration programs usually require detailed information about the species, which is available for only a tiny fraction of freshwater species imperiled by climate change; runs the risk of transferring diseases or causing genetic problems in the translocated species; and could lead

to large and uncontrollable ecological or economic problems similar to those caused by alien species (indeed, species that were deliberately translocated in the past are just as likely to have caused ecological or economic harm as those that were accidentally translocated; OTA 1993).

That climate change will strongly affect freshwater biodiversity over the coming century seems likely (Heino et al. 2009, Poff et al. 2009), but human responses to this climate change could cause effects that will be as large as or larger than the effects of climate change itself. Climate change will create or exacerbate water-supply shortages and threaten human life and property, effects that will encourage engineering solutions to these problems. These responses could include new dams, dredging, levees, and water diversions to enhance water security for people and agriculture and provide protection from floods. In addition, pressure is increasing to install new hydropower facilities on rivers to meet energy needs of developing countries or reduce dependence on fossil fuels. Such engineering responses will have large ecological impacts and could heighten the direct impacts of climate change. Impetus probably will be strong to rush these projects and circumvent the usual environmental reviews and regulations because many of these projects are likely to be designed and implemented following some disaster (e.g., similar to the responses to the 1927 flood in the Mississippi River, repeated devastating floods along the Yangtze, and the 2007 drought in Atlanta and the American Southeast). Projects conceived and constructed without adequate consideration of undesirable ecological effects can have severe impacts on freshwater biodiversity. Preventing damage from unnecessary or poorly designed engineering projects built in response to climate change will present freshwater conservationists with a series of challenges over the coming decades. Can we effectively encourage rational and deliberate planning of water projects *before* disasters strike? Will the knowledge and conservation concerns of freshwater ecologists be represented at the table when large engineering projects are planned? What are the most effective ways to reach policy-makers or a thirsty public?

The problem of urgency

The great improvements in information about the status of and threats to the freshwater biota (discussed above) have enabled us to foresee that the 21st century will be a time of crisis for the world's freshwater biota. We see 3 signs of this coming crisis. First, wholesale extinctions and endangerments of the freshwater biota are well underway in known biodiversity hotspots. For instance, in the Mobile River basin of the American southeast, 54 species of endemic mollusks are already extinct (Neves et al. 1997), and dozens more species of mollusks and fishes are seriously imperiled (i.e., ranked as G1 or G2 by NatureServe). Similar extinctions and endangerments, including the first human-caused extinction of a cetacean—the baiji (*Lipotes vexillifer*), a monotypic freshwater dolphin endemic to the Yangtze River (Turvey et al. 2007)—are occurring in the biodiverse Asian great rivers. Extinctions of spring-dwelling and groundwater species have accelerated as unsustainable water extraction has dried springs and aquifers with highly endemic biotas in arid regions around the world (e.g., Ponder 1986, Danielopol et al. 2003, Strayer 2006).

Second, we already have made the decisions that commit us to many more extinctions over the next few decades. The trajectories for human population growth, human water use, climate change, use of human-made nitrogenous fertilizers, invasions of alien species, numbers of dams and hydrologic alteration, overexploitation of fisheries, etc. are all rising sharply (Fig. 1A–E). They are projected to continue to rise into the near future, while sediments and toxins already en route from careless landuse practices will continue to find their way into rivers. For these and other reasons, stresses on freshwater ecosystems and their inhabitants are likely to rise significantly over the coming decades.

Third, human actions already taken probably have incurred a large unredeemed extinction debt (Tilman et al. 1994), although this debt is not yet well quantified (Strayer 2008). That is, even if human impacts on fresh waters remained unchanged into the future, many populations and species probably are no longer viable over the long term and will disappear.

Thus, a major advance in freshwater biodiversity conservation over the past 25 y is that we have gathered strong evidence that freshwater biodiversity loss is not a theoretical or future problem, but an ongoing and accelerating catastrophe. Surprisingly, however, this evidence has not had the effect one might have expected on the public, policy-makers, most conservation ecologists, and even freshwater ecologists (see below).

The urgency of the freshwater conservation situation highlights 3 specific issues that we will address briefly. First, *J-NABS* authors and freshwater ecologists in general have moved more into conservation work over the past 25 y (Fig. 5), but this modest shift seems unlikely to be sufficient to meet the demands of the impending global extinction crisis. If freshwater
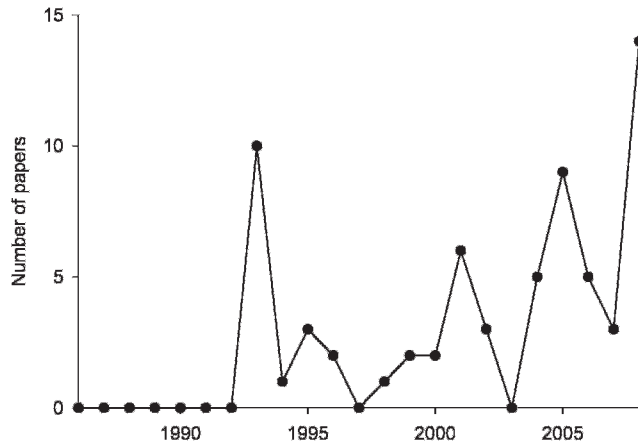
FIG. 5. Number of articles in *J-NABS* that appear in a Web of Science search using "conservation OR endangered" as the search term.

scientists are to be more effective in the conservation arena, we will need to move further, from doing research that is *useful* to doing work that is *used* by society (Rogers 2008). This step might entail 2 changes: 1) the direction of our research and 2) active collaboration with nonscientists to ensure that scientific knowledge is included effectively in societal decisions that affect freshwater biodiversity (Rogers and Breen 2003, Rogers 2008). Rogers' view of the need for much greater involvement in science of engagement rather than the more traditional science of discovery is complementary to, but more focused than, that advocated by Meffe (2001).

Second, it is easy to become fixated on the many gaps in knowledge about freshwater ecosystems, but the urgency of our present situation demands that we not allow uncertainty to be an excuse for inaction. We do often lack detailed knowledge of the life histories, environmental tolerances, ecological interactions, or even names of the species in imperiled freshwater ecosystems. These subjects are undoubtedly important and might be worthy of future research. However, given the severity of human impacts and rapid impoverishment of freshwater biotas, we must focus on the things that we do know and build management action on this strong foundation. Examples of such actions that could bring conservation gains for the freshwater biota are countless. We know that taking all of the water out of a river or producing a grotesque flow regime usually is bad for its inhabitants and that leaving some water in the river or restoring a more natural flow regime is often a sound course of action (Poff et al. 1997 [Fig. 2], Bunn and Arthington 2002). We know that better controls on the movement of alien species have the potential to

reduce substantially ecological and economic damages in the future. We know that continued overexploitation of fishes will destroy fishery stocks and can lead to large cascading changes in freshwater ecosystems (e.g., McIntyre et al. 2007). We know that inputs from poor land use and point sources of sediments, nutrients, and toxins that are orders of magnitude higher than natural loading rates extirpate species and alter ecosystem functioning and that reducing these inputs generally will improve ecological conditions. Delaying action until we have perfect knowledge will condemn many species to extinction and many freshwater ecosystems to irreparable degradation.

The 3rd issue concerns adaptive management, which sometimes is recommended as a useful tool for managing incompletely understood systems. In this approach, which has gained prominence over the past 25 y (Walters 1986, Williams et al. 2007), stakeholders agree on interim management actions, which are then adjusted as the response of the managed system is observed. Adaptive management has been used in fisheries and in the allocation of environmental flows, among other applications. We offer 2 cautionary comments about the use of adaptive management for freshwater biodiversity conservation. A common response to inadequate project funding (a nearly universal problem) is to focus resources on the project itself and reduce or even eliminate funding for subsequent monitoring and evaluation. However, the basic premise of adaptive management is that management actions are guided by information about the responses of the system. Thus, accurate information about system performance (in the case of biodiversity conservation, the status and trends of biological populations) is vitally important, and proposals to cut monitoring should be resisted. Without good monitoring, adaptive management cannot be adaptive. Moreover, the response of long-lived biota or slow factors that influence biodiversity (e.g., sediment routing, nutrient saturation, toxin concentrations) might change too slowly to be helpful in guiding adaptive management. In such cases, leading indicators of system performance (e.g., changes in physiological status or age structure of long-lived species) should be developed and tested to replace commonly used trailing indicators, such as population sizes or chemical concentrations.

The gap between freshwater ecology and conservation science

Because fresh waters are richer in species/area than terrestrial or marine habitats, and because those

TABLE 1. Number of papers cited from the 20 scholarly journals that were most cited in 2 recent textbooks on conservation biology (Groom et al. 2006, Hunter and Gibbs 2007), along with the number of citations to papers published in *J-NABS* and 2 other leading freshwater ecology journals.

Groom et al. (2006) (~2900 total citations)	Hunter and Gibbs (2007) (~1500 total citations)
Conservation Biology (261)	*Conservation Biology* (237)
Science (115)	*Science* (75)
Nature (92)	*Biological Conservation* (60)
Ecological Applications (89)	*BioScience* (42)
Ecology (83)	*Nature* (41)
Biological Conservation (81)	*Ecological Applications* (34)
BioScience (66)	*Annual Review of Ecology, Evolution, and Systematics* (25)
Proceedings of the National Academy of Sciences of the United States of America (41)	*Proceedings of the National Academy of Sciences of the United States of America* (24)
Trends in Ecology and Evolution (38)	*Trends in Ecology and Evolution* (21)
American Naturalist (35)	*Ecology* (16)
Annual Review of Ecology, Evolution, and Systematics (28)	*Biodiversity and Conservation* (14)
Biodiversity and Conservation (21)	*Wildlife Society Bulletin* (13)
Journal of Wildlife Management (19)	*Oryx* (12)
Oikos (17)	*Journal of Applied Ecology* (11)
Journal of Applied Ecology (15)	*Animal Conservation* (10)
Ecology Letters (13)	*Oikos* (10)
Environmental Management (11)	*American Naturalist* (9)
Journal of Animal Ecology (11)	*Environmental Management* (9)
Oryx (11)	*Journal of Wildlife Management* (9)
Wildlife Society Bulletin (11)	*Proceedings of the Royal Society B: Biological Sciences* (7)
J-NABS (3)	*J-NABS* (1)
Freshwater Biology (3)	*Freshwater Biology* (1)
Limnology and Oceanography (0)	*Limnology and Oceanography* (0)

species are more imperiled (Figs 3A, B, 4A–D), one might suppose that freshwater ecologists would have led the development of conservation biology and have come to dominate the science today. Despite several high-profile publications that clearly document the perilous state of freshwater biodiversity (e.g., Allan and Flecker 1993, Benz and Collins 1997, Master et al. 2000 [Fig. 2], Dudgeon et al. 2006), the freshwater biota is not especially well represented in contemporary conservation biology (amphibians are a notable exception), and we see no evidence that freshwater ecologists have been important in guiding the development of the field. For instance, 20% of IUCN-listed species are from fresh water, but only 8 to 12% of the species mentioned in leading textbooks (Macdonald and Service 2006, Primack 2006, Hunter and Gibbs 2007) are freshwater species, and many of these are species, such as waterfowl and semiaquatic mammals, that most freshwater ecologists probably would regard as terrestrial. Likewise, with a few exceptions, our impression is that concepts central to conservation biology have not always been widely or effectively used by freshwater conservationists, even though some of these topics (e.g., metapopulation dynamics, reserve design, integration of scientific knowledge with social and economic systems) seem highly relevant to freshwa-

ter conservation. In view of the importance of freshwater biodiversity, its critical and declining conservation status, and the potential to use freshwater science to illuminate conservation issues of general importance, freshwater ecologists should be helping to drive the field of conservation ecology, not merely following in the wake of terrestrial vertebrate and plant conservation.

Role of NABS and other freshwater scientific societies

Despite the obvious congruence in time and subject matter between the appearance of *J-NABS* and rise of conservation biology, NABS has not played a leading role in moving this important field forward, and *J-NABS* has not been a leading journal for the publication of papers on biodiversity conservation. To be sure, NABS meetings have included many presentations on conservation issues, including plenary talks, special sessions, and several specialized sessions on conservation-related subjects. Likewise, *J-NABS* certainly has published papers on conservation (Fig. 5). However, most of these papers have dealt with specialized technical issues (e.g., species status, autecology, or genetics) rather than general, theoretical, or conceptual problems, and few have been widely cited or could be said to have had much

influence outside the narrow confines of freshwater benthic science (Table 1).

The near-absence of citations to *J-NABS* in textbooks has 2 disturbing implications. First, it suggests that conservationists with something interesting to say do not think of *J-NABS* (or *Limnology and Oceanography* or *Freshwater Biology*) as a suitable outlet for their work, although the *J-NABS* Editorial Board would welcome such papers. Perhaps more disturbing, it appears that conservation practitioners do not consider the wealth of basic ecological information in these journals to be relevant to conservation.

It is not only NABS that has failed to provide adequate leadership in conservation of freshwater biodiversity. Other leading scientific societies and journals concerned with freshwater ecology (e.g., the American Society for Limnology and Oceanography, Societas Internationalis Limnologiae, Freshwater Biological Association) likewise have played largely marginal roles (Table 1). Instead, the lead in freshwater biodiversity conservation has been taken by the scientific societies that focus generally on conservation (e.g., the Society for Conservation Biology) or ecology (e.g., the Ecological Society of America), or by NGOs, such as the WWF, The Nature Conservancy (TNC), and NatureServe. For instance, WWF has been a leading player in the development of the Freshwater Ecoregions of the World (Abell et al. 2008), and TNC has actively promoted the development and implementation of environmental flow allocations (Richter et al. 2003).

We do not understand why the scientific societies concerned with freshwater ecology have not chosen to play a more central role in biodiversity conservation, although this decision might originate in the ancient split between basic limnology and applied conservation work that we noted earlier. Whatever its cause, the present approach seems inadequate to ensure the preservation of what now remains of the Earth's freshwater ecosystems and the biodiversity they support. We suggest that a higher level of engagement with conservation initiatives would draw more attention to the plight of the freshwater biota and improve the use and application of scientific information in biodiversity conservation. An additional outcome would be to place freshwater science at the heart of modern conservation biology and, perhaps, increase funding for freshwater conservation. Both NABS and the conservation community would benefit from closer mutual engagement, and the results of closer interaction can hardly be other than favorable for freshwater biodiversity. One thing is certain: a failure to act boldly now will lead to impoverishment or extinction of the freshwater biota and the very subjects of our research. Such an occurrence would be a tragic demonstration of the redundancy of our science.

Acknowledgements

Literature Cited

ABELL, R., M. L. THIEME, C. REVENGA, M. BRYER, M. KOTTELAT, N. BOGUTSKAYA, B. COAD, N. MANDRAK, S. CONTRERAS BALDERAS, W. BUSSING, M. L. J. STIASSNY, P. SKELTON, G. R. ALLEN, P. UNMACK, A. NASEKA, R. NG, N. SINDORF, J. ROBERTSON, E. ARMIJO, J. V. HIGGINS, T. J. HEIBEL, E. WIKRAMANAKE, D. OLSON, H. L. LOPEZ, R. E. REIS, J. G. LUNDBERG, M. H. SABAJ PEREZ, AND P. PETRY. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. BioScience 58:403–414.

ALLAN, J. D., R. ABELL, Z. HOGAN, C. REVENGA, B. W. TAYLOR, R. L. WELCOMME, AND K. WINEMILLER. 2005a. Overfishing of inland waters. BioScience 55:1041–1051.

ALLAN, J. D., AND A. S. FLECKER. 1993. Biodiversity conservation in running waters. BioScience 43:32–43.

ALLAN, J. D., M. PALMER, AND N. L. POFF. 2005b. Climate change and freshwater ecosystems. Pages 274–290 *in* T. E. Lovejoy and L. Hannah (editors). Climate change and biodiversity. Yale University Press, New Haven, Connecticut.

ANONYMOUS. 1969. The cities: the price of optimism. Time, 1 August. (Available from: http://www.time.com/time/magazine/article/0,9171,901182,00.html)

ARAKI, H., B. COOPER, AND M. S. BLOUIN. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100–103.

ASHIZAWA, D., AND J. J. COLE. 1994. Long-term temperature trends of the Hudson River – a study of the historical data. Estuaries 17:166–171.

BALDWIN, N. A., R. W. SAALFELD, M. R. DOCHODA, H. J. BUETTNER, AND R. L. ESHENRODER. 2007. Commercial fish production in the Great Lakes, 1867–2000. Great Lakes Fishery Commission, Ann Arbor, Michigan. (Available from: www.glfc.org/databases/commercial/commerc.php)

BALIAN, E. V., C. LÉVÊQUE, H. SEGERS, AND K. MARTENS. 2008. The Freshwater Animal Diversity Assessment: an overview of the results. Hydrobiologia 595:627–637.

BANKS, C. B., M. Y. N. LAU, AND D. DUDGEON. 2008. Captive management and breeding of Romer's tree frog *Chirixalus romeri*. International Zoo Yearbook 42:99–108.

BARBOUR, M. T., N. L. POFF, R. H. NORRIS, AND J. D. ALLAN. 2008. Perspective: communicating our science to influence public policy. Journal of the North American Benthological Society 27:562–569.

BENZ, G. W., AND D. E. COLLINS (EDITORS). 1997. Aquatic fauna in peril: the southeastern perspective. Special Publication 1. Southeast Aquatic Research Institute, Lenz Design and Communications, Decatur, Georgia.

BERNHARDT, E. S., M. A. PALMER, J. D. ALLAN, G. ALEXANDER, K. BARNAS, S. BROOKS, J. CARR, S. CLAYTON, C. DAHM, J. FOLLSTAD-SHAH, D. GALAT, S. GLOSS, P. GOODWIN, D. HART, B. HASSETT, R.

JENKINSON, S. KATZ, G. M. KONDOLF, P. S. LAKE, R. LAVE, J. L. MEYER, T. K. O'DONNELL, L. PAGANO, B. POWELL, AND E. SUDDUTH. 2005. Ecology – synthesizing US river restoration efforts. Science 308:636–637.

BIBER, E. 2002. The application of the Endangered Species Act to the protection of freshwater mussels: a case study. Environmental Law 32:91–173.

BRINSON, M. M., AND A. I. MALVAREZ. 2002. Temperate freshwater wetlands: types, status, and threats. Environmental Conservation 29:115–133.

BROOKS, T. M., R. A. MITTERMEIER, G. A. B. DA FONSECA, J. GERLACH, M. HOFFMANN, J. F. LAMOREUX, C. G. MITTERMEIER, J. D. PILGRIM, AND A. S. L. RODRIGUES. 2006. Global biodiversity conservation priorities. Science 313:58–61.

BUIJSE, A. D., F. KLIJN, R. S. E. W. LEUVEN, H. MIDDELKOOP, F. SCHIEMER, J. H. THORP, AND H. P. WOLFERT (EDITORS). 2005. Rehabilitating large regulated rivers. Archiv für Hydrobiologie Supplementband 155:1–738.

BUNN, S. E., AND A. H. ARTHINGTON. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

CARDINALE, B. J., M. A. PALMER, AND S. L. COLLINS. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415:426–429.

CAUGHLEY, G., AND A. GUNN. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts.

COOKE, G. D., E. B. WELCH, S. PETERSON, AND S. A. NICHOLS. 2005. Restoration and management of lakes and reservoirs. 3rd edition. CRC Press, Boca Raton, Florida.

COSTANZA, R., R. D'ARGE, R. DE GROOT, S. FARBER, M. GRASSO, B. HANNON, K. LIMBURG, S. NAEEM, R. V. O'NEILL, J. PARUELO, R. G. RASKIN, P. SUTTON, AND M. VAN DEN BELT. 1997. The value of the world's ecosystem services and natural capital. Nature 387: 253–260.

DANIELOPOL, D. L., C. GRIEBLER, A. GUNATILAKA, AND J. NOTENBOOM. 2003. Present state and future prospects for groundwater ecosystems. Environmental Conservation 30:104–130.

DEUTSCH, C. A., J. J. TEWKSBURY, R. B. HUEY, K. S. SHELDON, C. K. GHALAMBOR, D. C. HAAK, AND P. R. MARTIN. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the United States of America 105:6668–6672.

DODD, C. K., AND R. A. SEIGEL. 1991. Relocation, repatriation and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

DUDGEON, D. 1992. Endangered ecosystems: a review of the conservation status of tropical Asian rivers. Hydrobiologia 248:167–191.

DUDGEON, D. 1999. Tropical Asian streams: zoobenthos, ecology and conservation. Hong Kong University Press, Hong Kong, People's Republic of China.

DUDGEON, D., A. H. ARTHINGTON, M. O. GESSNER, Z.-I. KAWABATA, D. J. KNOWLER, C. LÉVÊQUE, R. J. NAIMAN, A.-H. PRIEUR-RICHARD, D. SOTO, M. L. J. STIASSNY, AND C. A. SULLIVAN. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163–182.

FAGAN, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83:3243–3249.

FAGAN, W. F., P. J. UNMACK, C. BURGESS, AND W. L. MINCKLEY. 2002. Rarity, fragmentation, and extinction risk in desert fishes. Ecology 83:3250–3256.

FALK, D. A., M. PALMER, AND J. ZEDLER (EDITORS). 2006. Foundations of restoration ecology: the science and practice of ecological restoration. Island Press, Washington, DC.

FAO (FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS). 2008. Database on introduction of aquatic species (DIAS). Food and Agriculture Organization of the United Nations, Rome, Italy. (Available at: http://www.fao.org/fishery/dias/1)

FIRTH, P., AND S. G. FISHER (EDITORS). 1992. Global climate change and freshwater ecosystems. Springer-Verlag, New York.

FOSTER, S. E., AND D. A. SOLUK. 2006. Protecting more than the wetland: the importance of biased sex ratios and habitat segregation for conservation of the Hine's emerald dragonfly, *Somatochlora hineana* Williamson. Biological Conservation 127: 158–166.

GALLOWAY, J. N., A. R. TOWNSEND, J. W. ERISMAN, M. BEKUNDA, Z. C. CAI, J. R. FRENEY, L. A. MARTINELLI, S. P. SEITZINGER, AND M. A. SUTTON. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320:889–892.

GLEICK, P. H. (EDITOR). 1993. Water in crisis. Oxford University Press, Oxford, UK.

GLOBAL AMPHIBIAN ASSESSMENT. 2008. Global amphibian assessment. International Union for Conservation of Nature and Natural Resources, Cambridge, UK. (Available from: http://www.globalamphibians.org).

GOBLE, D. D., J. M. SCOTT, AND F. W. DAVIS (EDITORS). 2005. The Endangered Species Act at thirty: Volume 1: Renewing the conservation promise. Island Press, Washington, DC.

GROBLER, P. J., J. W. JONES, N. A. JOHNSON, B. BEATY, J. STRUTHERS, R. J. NEVES, AND E. M. HALLERMAN. 2006. Patterns of genetic differentiation and conservation of the slabside pearlymussel, *Lexingtonia dolabelloides* (Lea, 1840) in the Tennessee River drainage. Journal of Molluscan Studies 72:65–75.

GROOM, M. J., G. K. MEFFE, AND C. R. CARROLL. 2006. Principles of conservation biology. 3rd edition. Sinauer Associates, Sunderland, Massachusetts.

GROOMBRIDGE, B., AND M. JENKINS. 2002. World atlas of biodiversity: earth's living resources in the 21st century. University of California Press, Berkeley, California.

HALPERN, B., S. HALPERN, S. WALBRIDGE, K. A. SELKOE, C. V. KAPPEL, F. MICHELI, C. D'AGROSA, J. F. BRUNO, K. S. CASEY, C. EBERT, H. E. FOX, R. FUJITA, D. HEINEMANN, H. S. LENIHAN, E. M. P. MADIN, M. T. PERRY, E. R. SELIG, M. SPALDING, R. STENECK, AND R. WATSON. 2007. A global map of human impact on marine ecosystems. Science 319:948–952.

HANSKI, I., AND O. E. GAGGIOTTI (EDITORS). 2004. Ecology, genetics, and evolution of metapopulations. Elsevier, Amsterdam, The Netherlands.

HART, D. D., AND N. L. POFF (EDITORS). 2002. A special section on dam removal and river restoration. BioScience 52:653–747.

HASLER, A. D. 1947. Eutrophication of lakes by domestic drainage. Ecology 28:383–395.

HEINO, J., R. VIRKKALA, AND H. TOIVONEN. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. Biological Reviews 84:39–54.

HOEGH-GULDBERG, O., L. HUGHES, S. MCINTYRE, D. B. LINDENMAYER, C. PARMESAN, H. P. POSSINGHAM, AND C. D. THOMAS. 2008. Assisted colonization and rapid climate change. Science 321:345–346.

HOOPER, D. U., F. S. CHAPIN, J. J. EWEL, A. HECTOR, P. INCHAUSTI, S. LAVOREL, J. H. LAWTON, D. M. LODGE, M. LOREAU, S. NAEEM, B. SCHMID, H. SETÄLÄ, A. J. SYMSTAD, J. VANDEMEER, AND D. A. WARDLE. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75: 3–35.

HUNTER, M. L. 1996. Fundamentals of conservation biology. Blackwell Science, Cambridge, Massachusetts.

HUNTER, M. L., AND J. P. GIBBS. 2007. Fundamentals of conservation biology. 3rd edition. Blackwell, Malden, Massachusetts.

Hynes, H. B. N. 1960. The biology of polluted waters. Liverpool University Press, Liverpool, UK.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ontario.

International Commission on Large Dams. 2008. Dams and the world's water. International Commission on Large Dams, Paris, France. (Available at: www.icold-cigb.net/images/PDF_EN/Dams%20&%20the%20World%20Water.pdf)

IPCC (International Panel on Climate Change). 2007. Climate change 2007: synthesis report. Intergovernmental Panel on Climate Change, Geneva, Switzerland. (Available from: http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf)

IUCN (International Union for Conservation of Nature and Natural Resources). 2007. 2007 IUCN Red List of threatened species. International Union for Conservation of Nature and Natural Resources, Cambridge, UK. (Available from: www.iucnredlist.org)

Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running. 2001. Water in a changing world. Ecological Applications 11:1027–1045.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Díaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33:372–407.

Jones, J. W., and R. J. Neves. 2002. Life history and propagation of the endangered fanshell pearlymussel, *Cyprogenia stegaria* Rafinesque (Bivalvia:Unionidae). Journal of the North American Benthological Society 21:76–88.

Jonsson, M., and B. Malmqvist. 2003. Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. Oecologia (Berlin) 134:554–559.

Junk, W. J. 2002. Long-term environmental trends and the future of tropical wetlands. Environmental Conservation 29:414–429.

Keevin, T. M., S. G. George, J. J. Hoover, B. R. Kuhaida, and R. L. Mayden. 2007. Food habits of the endangered Alabama sturgeon, *Scaphirhynchus suttkusi* Williams and Clemmer, 1991 (Acipenseridae). Journal of Applied Ichthyology 23:500–505.

Kottelat, M., and J. Freyhof. 2007. Handbook of European freshwater fishes. Kottelat, Cornol and Freyhof, Berlin, Germany.

Kremen, C., A. Cameron, A. Moilanen, S. J. Phillips, C. D. Thomas, H. Beentje, J. Dransfield, B. L. Fisher, F. Glaw, T. C. Good, G. J. Harper, R. J. Hijmans, D. C. Lees, E. Louis, R. A. Nussbaum, C. J. Raxworthy, A. Razafimpahanana, G. E. Schatz, M. Vences, D. R. Vietes, P. C. Wright, and M. L. Zihra. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science 320:222–226.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Linke, S., R. H. Norris, and R. L. Pressey. 2008. Irreplaceability of river networks: towards catchment-based conservation planning. Journal of Applied Ecology 45:1486–1495.

Linke, S., R. L. Pressey, R. C. Bailey, and R. H. Norris. 2007. Management options for river conservation planning: condition and conservation revisited. Freshwater Biology 52:918–938.

Loh, J., R. H. Green, T. Ricketts, J. Lamoreux, M. Jenkins, V. Kapos, and J. Randers. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 260:289–295.

Macdonald, D., and K. Service (editors). 2007. Key topics in conservation biology. Wiley–Blackwell, Oxford, UK.

Magnuson, J. J., D. M. Robertson, B. J. Benson, R. H. Wynne, D. M. Livingstone, T. Arai, R. A. Assel, R. G. Barry, V. Card, E. Kuusisto, N. G. Granin, T. D. Prowse, K. M. Stewart, and V. S. Vuglinski. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science 289:1743–1746.

Master, L. L., B. A. Stein, L. S. Kutner, and G. A. Hammerson. 2000. Vanishing assets: conservation status of U.S. species. Pages 93–118 in B. A. Stein, L. S. Kutner, and J. S. Adams (editors). Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York.

Matthews, W. J., and E. Marsh-Matthews. 2007. Extirpation of red shiners in direct tributaries of Lake Texoma (Oklahoma-Texas): a cautionary case history from a fragmented river-reservoir system. Transactions of the American Fisheries Society 136:1041–1062.

Matthews, W. J., and E. G. Zimmerman. 1990. Potential effects of global warming on native fishes of the southern Great Plains and the Southwest. Fisheries 15(6):26–32.

McIntyre, P. B., L. E. Jones, A. S. Flecker, and M. J. Vanni. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. Proceedings of the National Academy of Sciences of the United States of America 104:4461–4466.

Meffe, G. K. 2001. The context of conservation biology. Conservation Biology 15:815–816.

Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sinauer Associates, Sunderland, Massachusetts.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19:1–54.

Morell, V. 2008. Into the wild: reintroduced animals face daunting odds. Science 320:742–743.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nakano, S., F. Kitano, and K. Maekawa. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to global warming. Freshwater Biology 36:711–722.

National Research Council. 2008. Progress towards restoring the Everglades: the second biennial review, 2008. National Academies Press, Washington, DC.

Neves, R. 2004. Propagation of endangered freshwater mussels in North America. Journal of Conchology Special Publication 3:69–80.

Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity. Pages 43–85 in G. W. Benz and D. E. Collins (editors). Aquatic fauna in peril: the southeastern perspective. Lenz Design and Communications, Decatur, Georgia.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science 308:405–408.

Ortmann, A. E. 1909. The destruction of the fresh-water fauna in western Pennsylvania. Proceedings of the American Philosophical Society 48:90–110.

Ortmann, A. E. 1924. Mussel shoals. Science 60:565–566.

OTA (Office of Technology Assessment). 1993. Harmful nonindigenous species in the United States. Office of Technology Assessment, US Congress, Washington, DC.

Palmer, M., J. D. Allan, J. Meyer, and E. S. Bernhardt. 2007. River restoration in the twenty-first century: data and experiential

knowledge to inform future efforts. Restoration Ecology 15: 472–481.

PALMER, M. A., A. P. COVICH, B. FINLAY, J. GIBERT, K. D. HYDE, R. K. JOHNSON, T. KAIRESALO, P. S. LAKE, C. R. LOVELL, R. J. NAIMAN, C. RICCI, F. F. SABATER, AND D. L. STRAYER. 1997. Biodiversity and ecosystem function in freshwater sediments. Ambio 26: 571–577.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

PERROW, M. R., AND A. J. DAVY (EDITORS). 2002. Handbook of ecological restoration. Volumes 1 and 2. Cambridge University Press, Cambridge, UK.

POFF, N. L., J. D. ALLAN, M. B. BAIN, J. R. KARR, K. L. PRESTEGAARD, B. D. RICHTER, R. E. SPARKS, AND J. S. STROMBERG. 1997. The natural flow regime. BioScience 47:769–784.

POFF, N. L., P. L. ANGERMEIER, S. D. COOPER, P. S. LAKE, K. D. FAUSCH, K. O. WINEMILLER, L. A. K. MERTES, M. W. OSWOOD, J. REYNOLDS, AND F. J. RAHEL. 2001. Fish diversity in streams and rivers. Pages 315–349 in F. S. Chapin, E. Sala, and E. Huner-Sannwald (editors). Global biodiversity in a changing environment. Springer, New York.

POFF, N. L., J. D. OLDEN, AND D. L. STRAYER. 2009. Climate change and freshwater extinction risk. in L. Hannah (editor). Extinction risk from climate change. Island Press, Washington, DC (in press).

POLUNIN, N. V. C. (EDITOR). 2008. Aquatic ecosystems: trends and global prospects. Cambridge University Press, Cambridge, UK.

PONDER, W. F. 1986. Mound springs of the Great Artesian Basin. Pages 403–420 in P. De Deckker and W. D. Williams (editors). Limnology in Australia. W. Junk, Dordrecht, The Netherlands.

POSTEL, S. L. 2000. Entering an era of water scarcity: the challenges ahead. Ecological Applications 10:941–948.

PRIMACK, R. B. 1993. Essentials of conservation biology. Sinauer Associates, Sunderland, Massachusetts.

PRIMACK, R. B. 2006. Essentials of conservation biology. 4th edition. Sinauer Associates, Sunderland, Massachusetts.

PRINGLE, C. M., C. F. RABENI, A. C. BENKE, AND N. G. AUMEN. 1993. The role of aquatic science in fresh-water conservation – cooperation between the North American Benthological Society and organizations for conservation and resource management. Journal of the North American Benthological Society 12: 177–184.

RICCIARDI, A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions 12:425–433.

RICCIARDI, A., AND J. B. RASMUSSEN. 1999. Extinction rates of North American freshwater fauna. Conservation Biology 13:220–222.

RICHTER, B. D., R. MATTHEWS, AND R. WIGINGTON. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. Ecological Applications 13:206–224.

ROGERS, K. H. 2008. Limnology and the post-normal imperative: an African perspective. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 30: 171–185.

ROGERS, K. H., AND C. M. BREEN. 2003. The ecology-policy interface. Frontiers in Ecology and the Environment 1:49–50.

ROSENBERG, D. M., P. MCCULLY, AND C. M. PRINGLE (EDITORS). 2000. Global-scale environmental effects of hydrologic alterations. BioScience 50:746–823.

ROSSITER, N., AND H. KAWANABE (EDITORS). 2000. Ancient lakes: biodiversity, ecology, and evolution. Advances in Ecological Research 31:1–624.

RUTTNER, F. 1963. Fundamentals of limnology. English translation of 3rd edition. University of Toronto Press, Toronto, Ontario.

SALA, O. E., F. S. CHAPIN, J. J. ARMESTO, E. BERLOW, J. BLOOMFIELD, R. DIRZO, E. HUBER-SANWALD, L. F. HUENNEKE, R. B. JACKSON, A. KINZIG, R. LEEMANS, D. M. LODGE, H. A. MOONEY, M. OESTERHELD, N. L. POFF, M. T. SYKES, B. H. WALKER, M. WALKER, AND D. H. WALL. 2000. Biodiversity – global biodiversity scenarios for the year 2010. Science 287:1770–1774.

SARKAR, S., R. L. PRESSEY, D. P. FAITH, C. R. MARGULES, T. FULLER, D. M. STOMS, A. MOFFETT, K. A. WILSON, K. J. WILLIAMS, P. H. WILLIAMS, AND S. ANDELMAN. 2006. Biodiversity conservation planning tools: present status and challenges for the future. Annual Review of Environment and Resources 31:123–159.

SCOTT, J. M., D. D. GOBLE, AND F. W. DAVIS (EDITORS). 2005. The Endangered Species Act at thirty: Volume 2: Conserving biodiversity in human-dominated landscapes. Island Press, Washington, DC.

SEMLITSCH, R. D., D. E. SCOTT, AND J. H. K. PECHMANN. 1988. Time and size at metamorphosis related to adult fitness in Ambystoma talpoideum. Ecology 69:184–192.

SHUTE, J. R., P. L. RAKES, AND P. W. SHUTE. 2005. Reintroduction of four imperiled fishes in Abrams Creek, Tennessee. Southeastern Naturalist 4:93–110.

SMITH, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems: a global problem. Environmental Science and Pollution Research 10:126–139.

SMOL, J. P. 2008. Pollution of lakes and rivers: a paleoecological perspective. 2nd edition. Blackwell, Malden, Massachusetts.

STRAYER, D. L. 2006. Challenges for freshwater invertebrate conservation. Journal of the North American Benthological Society 25:271–287.

STRAYER, D. L. 2008. Freshwater mussel ecology: a multifactor approach to distribution and abundance. University of California Press, Berkeley, California.

STRAYER, D. L. 2009. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology (in press).

TARZWELL, C. M. 1937. Experimental evidence on the value of trout stream improvement in Michigan. Transactions of the American Fisheries Society 66:177–187.

TENNESSEE VALLEY AUTHORITY. 2009. Norris Dam. Tennessee Valley Authority, Knoxville, Tennessee. (Available from: http://www.tva.gov/sites/norris.htm)

TILMAN, D., R. M. MAY, C. L. LEHMAN, AND M. A. NOWAK. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

TRAUTMAN, M. B. 1957. The fishes of Ohio. 1st edition. Ohio State University Press, Columbus, Ohio.

TURVEY, S. T., R. L. PITMAN, B. L. TAYLOR, J. BARLOW, T. AKAMATSU, L. A. BARRETT, X. J. ZHAO, R. R. REEVES, B. S. STEWART, K. X. WANG, Z. WEI, X. F. ZHANG, L. T. PESSER, M. RICHLEN, J. R. BRANDON, AND D. WANG. 2007. First human-caused extinction of a cetacean species. Biology Letters 3:537–540.

VAN DER SCHALIE, H. 1938. Contributing factors in the depletion of naiades in the eastern United States. Basteria 3:51–57.

VAUGHN, C. C., D. E. SPOONER, AND H. S. GALBRAITH. 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. Ecology 88:1654–1662.

VITOUSEK, P. M. 1994. Beyond global warming – ecology and global change. Ecology 75:1861–1876.

VÖRÖSMARTY, C., AND D. SAHAGIAN. 2000. Anthropogenic disturbance of the terrestrial water cycle. BioScience 50:753–765.

WALTERS, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York.

WELCH, P. S. 1935. Limnology. McGraw–Hill, New York.

WETZEL, R. G. 1975. Limnology. W. B. Saunders, Philadelphia, Pennsylvania.

WILLIAMS, B. K., R. C. SZARO, AND C. D. SHAPIRO. 2007. Adaptive management: the U.S. Department of the Interior Technical Guide. Adaptive Management Working Group, US Department of the Interior, Washington, DC.

WILLIAMS, J. D., M. L. WARREN, K. S. CUMMINGS, J. L. HARRIS, AND R. J. NEVES. 1993. Conservation status of the freshwater mussels of the United States and Canada. Fisheries 18(9):6–22.

WILLIAMS, J. E., J. E. JOHNSON, D. A. HENDRICKSON, S. CONTRERAS-BALDERAS, J. D. WILLIAMS, M. NAVARRO-MENDOZA, D. E. MCAL-LISTER, AND J. E. DEACON. 1989. Fishes of North America endangered, threatened, or of special concern – 1989. Fisheries 14(6):2–20.

ZEDLER, J. B., AND S. KERCHER. 2005. Wetland resources: status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30:39–74.