Ecological Applications, 10(4), 2000, pp. 958–970

A FUTURE PERSPECTIVE ON NORTH AMERICA'S FRESHWATER ECOSYSTEMS

ROBERT J. NAIMAN[1] AND MONICA G. TURNER[2]

[1]*School of Fisheries, Box 355020, University of Washington, Seattle, Washington 98195 USA*
[2]*Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA*

Abstract. Fresh waters are central to society and to the environment. Nevertheless, ongoing and projected changes in the distribution, abundance, and quality of water resources and freshwater ecosystems represent a serious threat to the integrity of the environment as well as the vitality of human cultures. Nearly every country in the world experiences regular water shortages, agriculture uses most of the world's available fresh water, and most illnesses in developing countries result from waterborne parasites and pathogens. Unfortunately, often hidden in these and other depressing statistics are the needs of the environment for adequate water to maintain vibrant ecosystems. Understanding the abilities and limits of freshwater ecosystems to respond to human-generated pressures is becoming a central issue for cultures and a challenge for science. This article explores trends in alterations to freshwater ecosystems, discusses the ecological consequences of biophysical alterations expected to occur in the next 20–30 years, and identifies some of the major scientific challenges and opportunities to effectively address the changes. Topics discussed include altered hydrological regimes, biogeochemical cycles, altered land use, riparian management, life history strategies, and relations between climate change and water resource management.

Key words: disturbance; ecosystems; fresh water; global change; land use; water resource management.

INTRODUCTION

Freshwater ecosystems, touching nearly all aspects of the natural environment and human culture, act as integrators and centers of organization within the landscape. Their roles in providing natural resources, such as fish and clean water, are well known, as are their roles in providing transportation, energy, waste assimilation, and recreation. Unfortunately, human societies have exploited the natural benefits provided by fresh waters for centuries without understanding how these systems maintain their vitality (Gleick 1993, Naiman et al. 1995). Today, with ever increasing demands being made on fresh waters by an exponentially increasing human population, a basic understanding of the trends in resource use, the ecological consequences of multiple system alterations, and the identification of major research challenges is essential for formulating sound management and policy decisions (NRC 1998, Postel 1998).

In addition, changes to land cover and use, and how societies view the land and its resources, can no longer be divorced from aquatic systems (Naiman et al. 1998*a*, *b*, Dale et al. 2000). Indeed there are strong and intimate links between terrestrial and aquatic systems that shape the character and productivity of the environment over multiple spatial and temporal scales. Alterations to disturbance regimes and spatial patterning associated with the terrestrial landscape have important, long-term consequences for aquatic ecosystems.

The objectives of this article are threefold. First, we examine status and trends in significant categories of change that ultimately affect freshwater ecosystems. Second, we discuss the ecological consequences of changes expected to occur in the next two to three decades. Finally, we identify several of the major scientific challenges and opportunities for effectively addressing the expected changes. This latter objective, by necessity, links climate, land, and fresh water.

STATUS AND TRENDS

There are five major categories of change affecting freshwater ecosystems (Naiman et al. 1995, 1998*b*). These are human demography, resource use (especially as it affects environmental quality), patterns of water consumption, technology development, and social organization. Collectively, these result in one or more of the following types of changes: physical restructuring of aquatic ecosystems, introduction of exotic species, discharge of toxic substances, or overharvesting of resources (Rapport and Whitford 1999).

Human demography.—Projected changes in the world's population are well known (Turner et al. 1990, Cohen 1995). The world's population likely will likely

Manuscript received 7 December 1998; revised 26 April 1999; accepted 15 September 1999. For reprints of this Invited Feature, see footnote 1, p. 939.

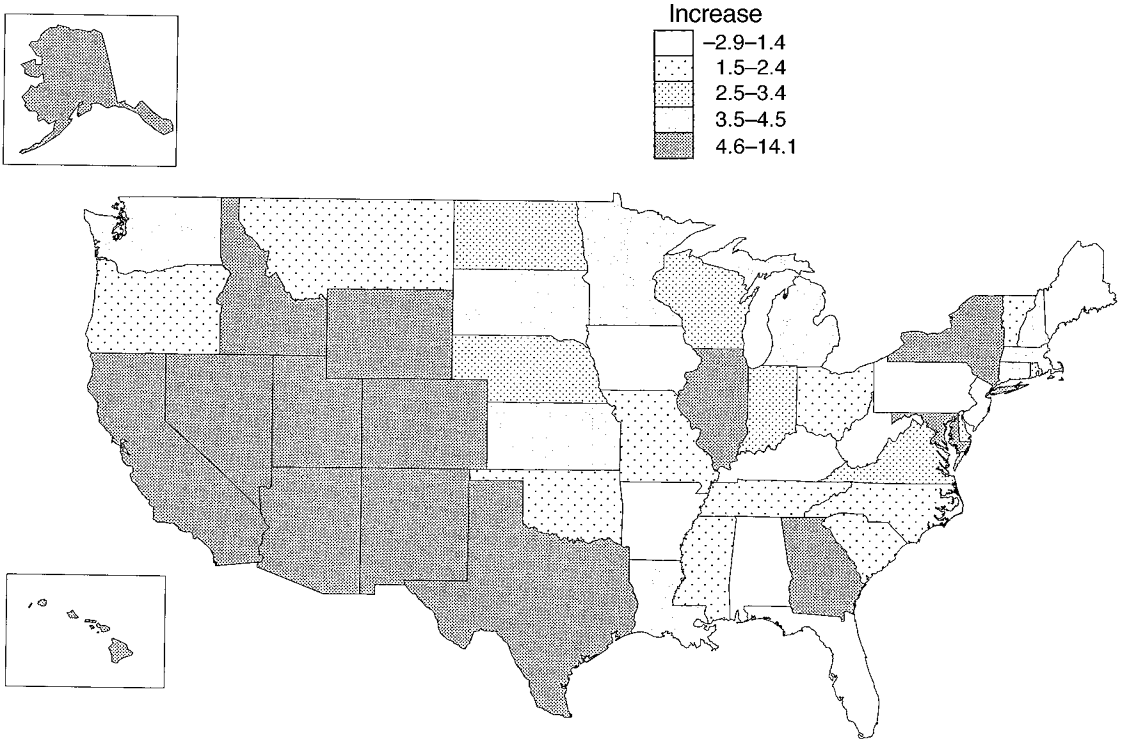

FIG. 1. Projected average annual rate of natural increase in population (increase per 1000 population) for the United States, by state, between 1995 and the year 2025. Population change reflects births minus deaths plus net migration. (Data are from the U.S. Department of Commerce, Bureau of Census, Population Division [PPL-47], 1997.)

increase by ~50% in the next 50 years or so, ~90% of the increase will be in developing countries, and as much as 60% of the population may reside in urban centers (WRI 1997).

In the United States, the pattern of population growth continues to be stronger in most of the western and southern states, while the national population is expected to increase by 27% from 275 million in the year 2000 to 350 million by year 2030 (U.S. Department of Commerce 1997). All states will have more people but in some states the increases will be significant (Fig. 1). California, Texas, and Florida will gain >6 million persons, while 12 states (all in the West with one exception) will experience >4% increase in population size. Thus, although the per capita rate of population growth in the United States is relatively low, the number of individuals to be added to the population in coming decades is substantial. All but one of these states already experience severe water-based environmental challenges.

Resource use.—The distribution of major land uses in the United States reflects a complex pattern of historical conversion of native lands, especially forests and grasslands, to human-dominated lands (Turner et al. 1998, Dale et al. 2000). The area occupied by forests continues to decline even though large-scale conversion to agriculture has diminished. This continued decline in forests may be attributed to urban and suburban expansion. Nevertheless, resource use resulting in land use change represents an enormous uncontrolled experiment in the ways habitat changes influence the movement of water, nutrients, and sediments from land to fresh waters.

Today <5% of the original forests remains in the lower 48 states, croplands now occupy ~16% of the land base, nearly 50% of the wetlands and 70% of the riparian forests have been converted to other uses, nearly half the land is cultivated or grazed by livestock, and ~3% of the land is in urban settings (Turner et al. 1998). Although the percentage of area in urban setting seems low, urban centers have disproportionate impacts on the environment. Overall, changes in drainage and erosion accompanying all forms of land use changes have had, and will continue to have, substantial effects on freshwater ecosystems (NRC 1992, 1998, Naiman et al. 1995).

Changes to freshwater resources have been equally severe. The Nationwide Rivers Inventory estimates a total of 5.2×10^6 km of streams in the contiguous United States, but only 2% (<10 000 km) have sufficiently high-quality features to be considered relatively natural rivers and thus worthy of federal protection (Benke 1990). In North America (north of Mexico), in Europe, and in the republics of the former Soviet Union, 77%

of the runoff from the 139 largest rivers is strongly or moderately affected by fragmentation of the river channel by flow regulation, interbasin diversion, and irrigation (Dynesius and Nilsson 1994). As a result of these and numerous other changes related to exploitation, exotic introductions, pollution, and erosion, there is a general malaise in freshwater fisheries to the point that they are in serious decline throughout the nation (Hilborn et al. 1995, Postel and Carpenter 1997). Approximately 39% of the native fishes are considered to be extinct, threatened, or endangered (Stein and Flack 1997).

Water consumption.—In the United States water consumption has doubled in the last 40 years, and over the next few decades this consumption will increase dramatically, especially for agriculture where ~1000 Mg (1000 metric tons) of water are required to produce 1 Mg of grain (Powledge 1984, Pimentel et al. 1997, Postel 1998). Globally, Postel (1998) has estimated that the volume of irrigation water annually available to crops (as soil moisture) would need to increase by 2050 km^3 over current demand to meet agricultural needs in the year 2025, the equivalent of the annual runoff of 24 Nile Rivers or 110 Colorado Rivers.

Not only is agricultural consumption excessive but so is household consumption, with a typical family of four in the United States requiring about 1300 L/d (of which only 3% is used for cooking and drinking). In contrast, the corresponding consumption rate in developing countries is only 300 L/d per family (Powledge 1984), uncomfortably close to Gleick's (1998) estimate of a minimum human water requirement of 200 L/d per family. The United States alone has built more than two million dams to support this use. Reservoirs have become a significant component of the nation's hydrologic cycle because they have the capacity to store an amount of water equal to three years' annual runoff from the nation's landscapes (Graf 1993). The nature and severity of water constraints remain ill-defined, largely because of national inadequacies in governmental coordination, data collection and management, and effective application of knowledge, thereby hampering the development of appropriate water and agricultural strategies (NRC 1998, Postel 1998).

Technology development.—History provides many examples of how the emergence of new technologies has profoundly affected societal use of the landscape (Headrick 1990). Inventions such as powerful pumps, labor-saving machinery, and herbicides and pesticides, have fundamentally altered agriculture and forestry; construction of highways and river locks forever altered the transportation and use of essential goods; and medical advances have reshaped the age structure and size of human populations (Dale et al. 2000). New technologies continue to emerge, and some will have strong influences either on the distribution of human populations or on land use.

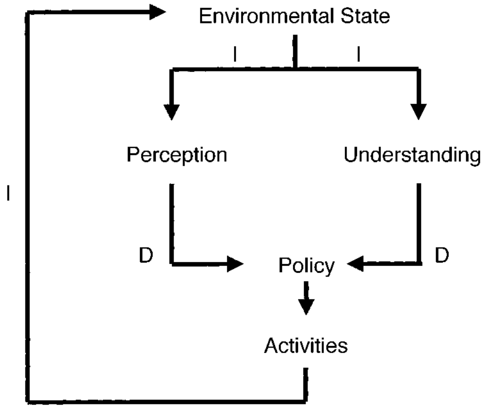

FIG. 2. Conceptual diagram showing interrelationship and feedbacks between environmental state (or condition), public perception and understanding, formulation of governmental policy, and resultant policy activities that ultimately affect environmental conditions. Abbreviations are: I, Influences; D, Determines.

As one looks to the future, there are numerous technologies on the horizon that promise to change land and water use in fundamentally significant but unspecified ways. For example, advances in telecommunications promise to change the ways business is conducted and thereby influence patterns of human settlement. In addition, emerging technologies targeted at improving resource production (e.g., food and fiber) and water efficiency promise to make more intensive use of increasingly scarce land and water resources. Consider managed forests. These will be cut on shorter rotations, plantation areas will increase, and additional uses will be found for fiber that is not currently utilized.

Social organization.—A comprehensive discussion of this subject is beyond the scope of this article but some discussion is fundamental to understanding how ecological systems have been changed in the past and will be changed in the future. The variety of attitudes, traditions, and perceptions of North American people are embodied in their cultures and institutions, which ultimately shape the character of freshwater systems. There are at least 22 federal agencies, and scores of state and local agencies, which have responsibilities for the hydrological cycle, often with dramatically different perspectives (NRC 1998). Environmental conditions directly influence perceptions about freshwater availability and resources, and those perceptions determine much of the policy related to environmental regulation (Fig. 2). In turn, policies directly influence the future environmental state. Unfortunately, attitudes and traditions, as well as institutional missions, are highly resistant to change. Effectively resolving most freshwater issues means finding better ways to communicate between people and organizations (Naiman et al. 1998*b*, NRC 1998). We return to this subject later in the article.

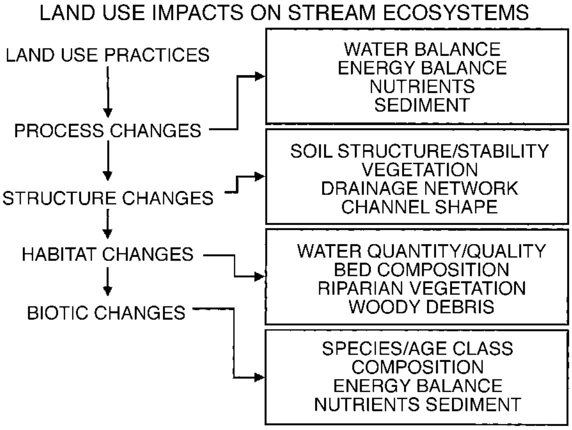

FIG. 3. Hierarchical impacts caused by land use practices on the structure and dynamics of streams, with some specific examples of each in the boxes to the right.

CONSEQUENCES

The ecological consequences of past and projected changes in the above five categories are as varied as the categories themselves. The only things that can be said with certainty are that the ecological responses will be pervasive, affecting every aspect of the environment, and that they will be played out in ways and at scales that will be difficult to predict. Unless there are sustained improvements in how issues are addressed, how information is processed into knowledge, and how wisdom is inserted into policy decisions, one can expect that variation and uncertainty will be the norms (Walters 1997, Naiman et al. 1998*a*).

So what are some of the major ecological consequences that one may expect to see in the next two to three decades? As Rapport and Whitford (1999) have stated so clearly, projected changes to aquatic ecosystems will be manifested by a ''distress syndrome'' indicated by reduced biodiversity, altered primary and secondary productivity, increased prevalence of disease, reduced nutrient cycling efficiency, increased dominance of exotic species, and increased dominance by smaller, shorter lived opportunistic species. For ease of presentation, we provide seven wide-ranging examples (land use change, disturbance regimes, ultraviolet [UV] radiation, life history phenology, pollution, exotic invasions, and cumulative effects) of how human activities may affect freshwater ecosystems.

Land use change.—We use the phrase ''land use'' in the sense of Turner et al. (1998) to accommodate changes in land cover and use. The ecological consequences of changing land use are complex because changing land use practices also influence ecosystem-scale structure and processes that, in turn, influence habitat and communities (Fig. 3). Embedded at each scale are concomitant alterations to water, sediment, energy, and nutrient balances, to community structure and species demography, and to overall aquatic system integrity (Innis et al. 2000).

Land use influences freshwater systems by directly altering the composition and structure of the natural flora and fauna, changing disturbance regimes, fragmenting the land into smaller and more diverse parcels, and changing the juxtaposition between parcel types. Collectively, these changes result in alterations in the relative abundance of habitat types, a reduction of native biodiversity, changes in the natural patterns of environmental variation that are needed to sustain a variety of species, and augmentation of nitrogen and phosphorus loads (Turner et al. 1999). Perhaps the latter point is the best documented. There are numerous studies either relating questionable land uses to increasing nutrient loads or ecologically proper land uses to the maintenance of acceptable water quality (Peterjohn and Correll 1984, Cole et al. 1993, Hunsaker and Levine 1995, Bolstad and Swank 1997, Johnson et al. 1997).

Disturbance regimes.—The type, intensity, duration, timing, and spatial pattern of disturbance shape the characteristics of populations, communities, and ecosystems. Disturbances may be natural (e.g., wildfire, storms, floods, grazing) or induced by human actions (e.g., fire suppression, flow regulation, fragmentation). However, the human-induced regimes differ so radically from natural regimes that all levels of system organization are affected (Poff et al. 1997, Dale et al. 2000). Consider fire suppression. Average fire size and severity have increased in a variety of temperate ecosystems, due in part to the legacy of increased fuel loads and the encroachment of shade-tolerant late-successional species. These effects of fire suppression are pronounced in ecosystems that would typically experience frequent fires of low intensity, such as the pine and scrub communities in the southeastern coastal plain, chaparral along the Pacific coast, and the pine forests of the Southern Rocky Mountains. Fire suppression during the past century has lengthened the fire return interval and altered successional pathways (e.g., Glitzenstein et al. 1995, Linder et al. 1997). Where fire suppression was effective, the resulting increase in the amount and connectivity of fuel, both vertically and horizontally, has made these systems conducive to larger and more intense fires. The effects of these more severe fires include greater plant mortality, and shifts in species composition and vegetation structure may result. The implications for freshwater systems are significant. Fire suppression results in changing land cover and soil properties, pulsed erosion, altered biogeochemical cycles and nutrient retention, and severely degraded habitat for aquatic organisms.

Altered flow regimes are another pervasive type of artificial disturbance (Poff et al. 1997). Whereas, historically, there were regular patterns (or at least identifiable periods with increased probabilities) for ex-

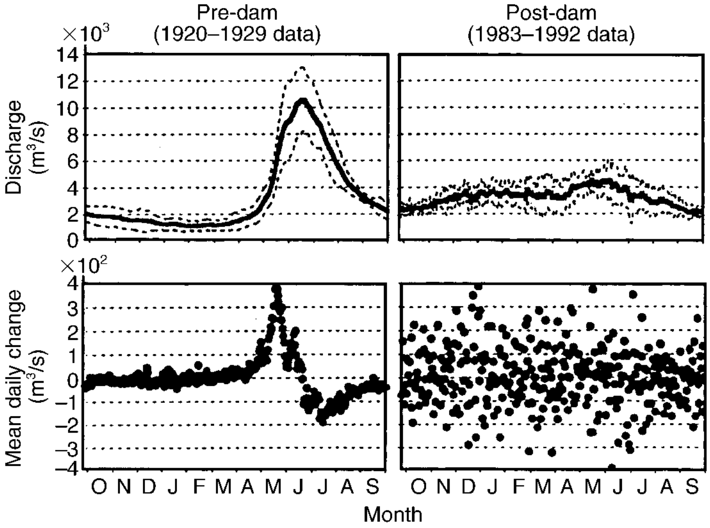

FIG. 4. Effect of upstream dams on discharge of the Hanford Reach of the Columbia River, Washington, USA (from Stanford et al. 1996).

treme flows, today the timing of flows is often substantially different (Fig. 4). Critical components of the flow regime affected by discharge regulation are magnitude, frequency, duration, timing, and rate of change. Organisms queuing reproduction, migration, or feeding to flow patterns especially are affected. At the opposite hydrologic extreme is flow stabilization, often found below certain types of dams, that results in artificially constant and faunistically simple environments.

Huston (1994) postulated that there are predictable interactions between frequency of disturbance, community productivity, and biodiversity (Fig. 5), and Pollock et al. (1998) provided empirical evidence for that relationship in riparian wetlands. Fundamentally altering the disturbance regime, results in system-level shifts that are ultimately expressed as biodiversity. Overall biodiversity may be increased by new or more frequent disturbances, allowing exotic species to colonize, or it may be decreased by less frequent disturbances (such as fire suppression or stabilized flow) which exclude both native and exotic species. Indeed, the virtual elimination of fire from once fire-maintained ecosystems and the reduction or elimination of flooding from many river systems have altered not only biodiversity but also successional pathways (e.g., Linder et al. 1997).

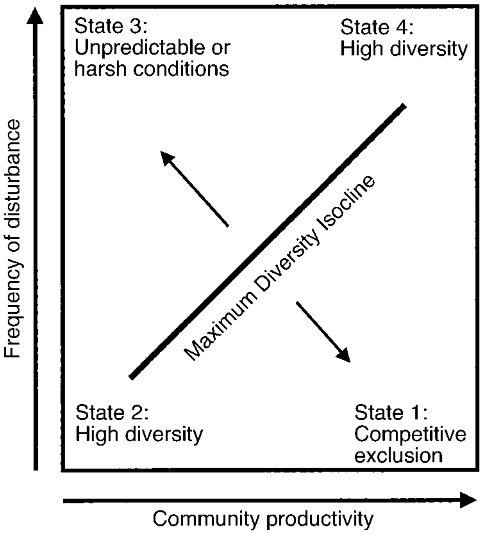

FIG. 5. Theoretical relationship between frequency of disturbance, community productivity, and species diversity. Adapted from Huston (1994).

UV radiation.—The chemical reactions responsible for stratospheric ozone depletion are extremely sensitive to temperature. Greenhouse gases warm the Earth's surface but cool the stratosphere, and therefore affect ozone depletion (Shindell at al. 1998). Increased concentrations of greenhouse gases are thought to be responsible for the large increase in the Arctic and Antarctic ozone losses observed in recent years, and which are expected to increase in the future (Rex et al. 1997, Shindell et al.1998).

What does this atmospheric change mean for freshwater ecosystems? Ozone depletion increases the amount of UV-B and UV-A radiation reaching the water surface, and it is known that UV radiation can be harmful to aquatic organisms (Williamson 1995). Fortunately, dissolved organic carbon (DOC) has strong attenuation effects on the depth of penetration of UV radiation. However, there is a strong dependence of the 1% attenuation depth on DOC concentrations below 1–2 mg/L with penetration depths exceeding several meters. This suggests that waters with low DOC concentrations may be very sensitive to small changes in DOC concentrations (Williamson et al. 1996). For example, it has been shown that high UV radiation levels in lakes with low DOC concentrations modify the spawning depth, hatching success, and recruitment of freshwater

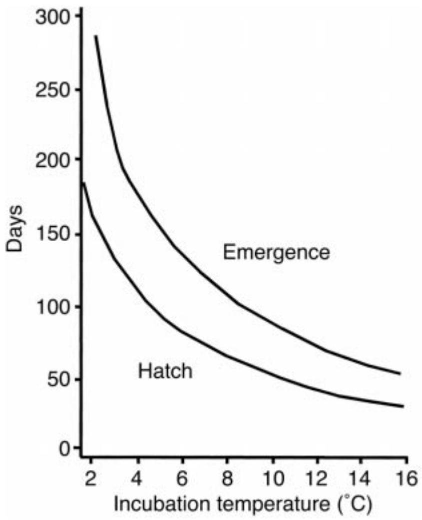

FIG. 6. Average hatching and emergence times in relation to ambient incubation temperatures for five species of Pacific salmon (*Onchorhynchus* spp). Adapted from Beacham and Murray (1990).

fishes (Williamson et al. 1997). These studies, although alarming, are somewhat difficult to interpret for future decades. This is because others have shown that the numerous dams being constructed have increased the residence time of water on the land, and thereby contributed to increased DOC concentrations (Vörösmarty et al. 1997). Nevertheless, there are many fresh waters with naturally low DOC concentrations that are susceptible to pervasive system-level damage from increasing doses of UV radiation, but the effects are hard to quantify, often severely harming organisms at sensitive life history stages.

Life history phenology.—Aquatic organisms have evolved within a range of natural environmental variation, adapting their life history traits (age at reproduction, fecundity, movements, and so forth) to key environmental attributes such as temperature, light, oxygen, and food. Alterations from optimal conditions for these key variables result in a variety of responses at the individual and population levels. These may include decreases in population sizes, growth, age, and size at reproduction, fecundity, and survivorship (Ward 1992).

Temperature is probably the most important environmental variable for aquatic organisms since it determines not only metabolic rates and food requirements, but also controls developmental processes. Even small alterations to water temperatures can have far-reaching effects. For example, altering the egg incubation temperature for salmonids by only 1–3°C can either accelerate or retard hatching and emergence by weeks to months depending on the basic temperature range (Fig. 6), as well as significantly influence fry size and survivorship (Beacham and Murray 1990). Further, temperature tolerances for the formation of viable eggs are much narrower (usually just a few degrees) than that for developmental tolerances which are, in turn, narrower than temperature tolerances for normal reproductive behavior (Gerking 1981).

Temperature effects on organisms can be insidious, making them exceedingly difficult to quantify. Consider the effects of a deep release reservoir on downstream organisms (Fig. 7). These cold waters result in a delayed maximum, winter warming, seasonal constancy, summer cooling, and diurnal constancy, all of which have differing effects on the life history of the organism and, in many cases, eventually leading to species elimination (Ward 1976).

Pollution.—Pollution comes in an increasingly bewildering array of forms: toxic organic compounds such as atrazine and hormone inhibitors, heavy metals, fertilizers, and even toxic algal blooms (Naiman et al. 1995). The 1995 Toxic Release Inventory (TRI) reports that 630 000 Mg of toxic chemicals were released into waters of the United States, 120 000 Mg were transferred to wastewater treatment plants, and ∼631 000 Mg were released into the air, of which some unspecified portion eventually moves to fresh waters (USEPA 1997). No integrated understanding of polluting compounds exists, especially for synergistic effects. De-

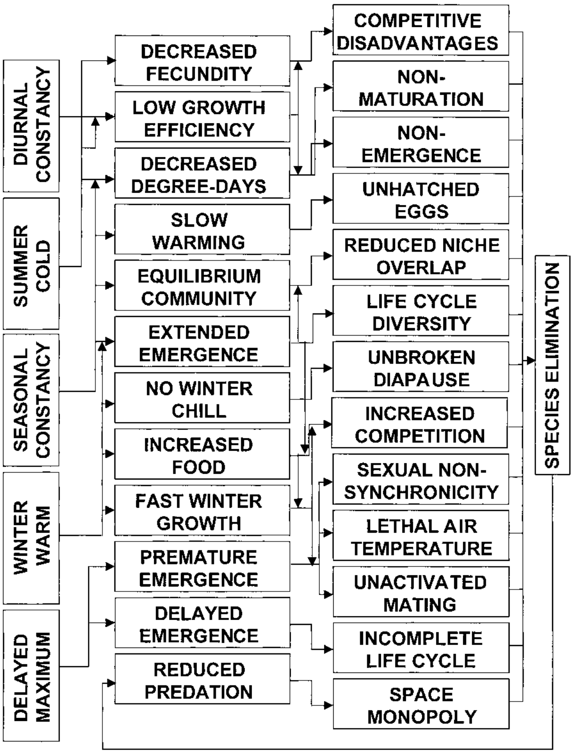

FIG. 7. Synergistic effects of thermal modifications found below deep release dams on the life history characteristics and population dynamics of aquatic invertebrates. Modified from Ward (1976).

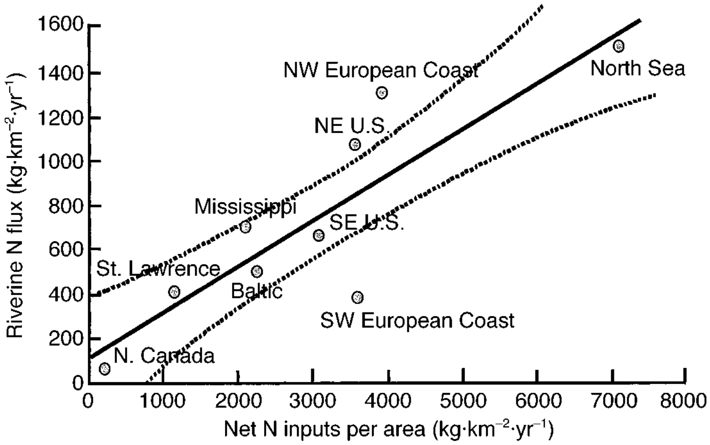

FIG. 8. Comparison of nitrogen export by regional rivers to nitrogen inputs per unit area for selected areas of North America and Europe. Modified from Howarth et al. (1996).

spite the Clean Water Act and other federal regulations, pollutants are increasing nationally, and environmental quality and integrity are decreasing, as exemplified in recent contaminant surveys of the Mississippi River drainage (Meade 1995) and reviews of nonpoint sources of nitrogen and phosphorus (Carpenter et al. 1998).

An especially acute pollution issue, with national and international consequences now and into the future, is associated with nitrogen. Human activities have doubled the rate of nitrogen entering the soil, water, and atmosphere, and that rate is continuing to climb. Recently, Vitousek et al. (1997) showed that there are increased global concentrations of the greenhouse gas nitrous oxide in the atmosphere as well as regional increases in other forms of oxides of nitrogen that drive the formation of photochemical smog. Also associated with the increased nitrogen loading are losses of calcium and potassium from soils, acidification of soils and fresh waters from nitric acid, and greatly increased export of nitrogen to estuaries and the coastal zone where it is a major pollutant (Fig. 8). They also suggest that the increase in nitrogen and its cycling rate may result in losses of biological diversity, especially among organisms adapted to low-nitrogen soils and water, and may contribute to long-term declines in coastal fisheries. Further, it has been suggested by Asner et al. (1997) that the nitrogen supply may eventually lead to a decoupling of the carbon and nitrogen cycles and perhaps even a loss of nitrogen limitation in terrestrial systems. The potential disappearance of terrestrial nitrogen limitation would mean increased N-fluxes to aquatic systems. Based on the estimated projections of nitrogen deposition by Galloway et al. (1994) for early in the next century, the consequences could be especially severe in North America, Europe, and Asia.

Exotic invasions.—The homogenization of the world's fauna and flora is an increasingly perplexing issue with multiple, synergetic consequences. Thousands of exotic plants and animals, as well as pathogens, are already established in North America and hundreds of others arrive annually. About 15% of the total have caused widespread problems that are proving to be ecologically serious as well as costly to remedy (Simberloff 1996).

Ecological impacts include domination (e.g., red mangrove, Asian salt cedar), disruption (e.g., zebra mussel, feral hogs), epidemics (e.g., chestnut blight fungus, balsam woolly adelgid), competition (e.g., European brown trout), and hybridization (e.g., mallard ducks, rainbow trout). Other examples abound. Overall, introduced organisms pose initially hidden but eventually monumental problems. The harmful effects are often subtle and surreptitious but the eventual impacts on the natural environment are real, and sometimes disastrous and irreversible, as when native species disappear. On a general level, exotic species often are encouraged by the destruction, fragmentation, and alteration of natural habitat. Sadly, government regulations remain woefully insufficient to meet the challenge.

Cumulative effects.—Incremental changes when added to other past, present, or reasonably foreseeable future impacts can result in significant environmental changes. The concept is relatively simple to understand whereas, in practice, it is exceedingly difficult to quantify even in apparently straightforward cases (Reid 1998). Quantifying cumulative effects is important because of the increasing number and variety of environmental impacts.

The difficulty of quantification is evident in the following example for Pacific salmon (Fig. 9). Let's assume that two adult salmon (a spawning pair) produce 2000 eggs. Further, if there is a 20% survival rate to the juvenile stage, a 10% survival to smoltification, and a 5% survival over several years at sea, then two adult salmon will return to spawn again. However, if the survivorship is reduced by only 2% at the juvenile and smolt stages and by only 1% at the sea stage, then only one adult salmon will return, leading to eventual

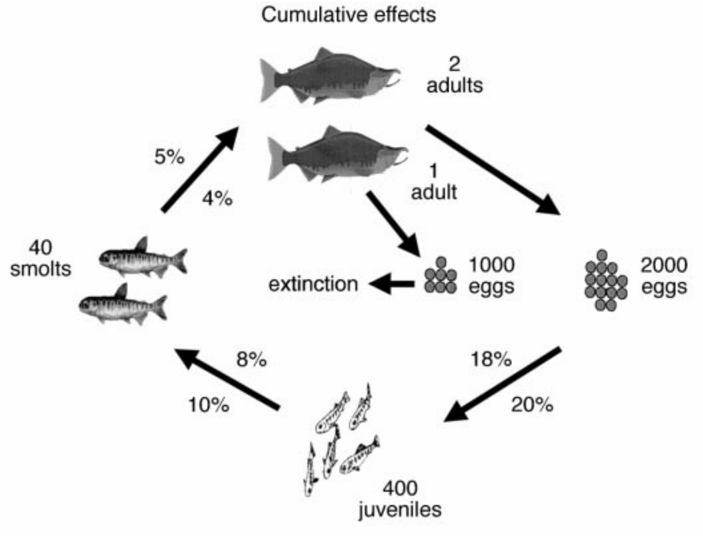

FIG. 9. Illustration of cumulative effects associated with different life stages of Pacific salmon. It is possible to increase population size, or drive the population to extinction, by only slight changes in survivorship at each life history stage. See *Consequences: Cumulative effects* for full explanation.

extinction if the trend continues. The scientific difficulty is in determining if there are statistically significant declines in survivorship at a given life history stage. It is estimated that studies of survival and abundance for salmonids may require 20–30 years to provide an 80% chance of detecting a 50% change. Studies of age and size at important life history stages may require 8–10 years to provide an 80% chance of detecting a 5–15% change (Lichatowich and Cramer 1979). Subtle changes, as in this example, illustrate the scientific difficulties as well as the ecological and managerial consequences being faced in literally thousands of similar cases.

The overall consequence of these and other changes is that the historic characteristics of watershed processes, such as the movements of water and other materials, have been significantly altered (Fig. 10). Today, precipitation contains quantities of pollutants capable of altering ecosystem processes while land use practices change runoff, sediment, and chemical regimes, roads and other structures modify the landscape's ability to regulate water movements, and resource extraction alters the timing, magnitude, and duration of water-based disturbance regimes.

CHALLENGES AND OPPORTUNITIES

Considering the magnitude of the changes already having taken place, and those that are projected to occur in the next two decades, the challenges facing ecologists, resource managers, and decision makers are daunting while the opportunities are unlimited. For example, challenges related to information management, cultural diversity, technology, institutional organization, public responsibility, and education are essential for progress that, unfortunately, can be only lightly treated in our discussion. Here we focus on processes at the watershed and landscape scales that require better understanding if progress is to be made in the ecological arena for fresh waters.

A basic need is the incorporation of ecological principles into aquatic resource use and management decisions. Specifying ecological principles, such as those related to time, place, species, disturbance, and scale, and understanding their environmental and social implications, are essential steps on the path to sustainability (see Dale et al. 2000). Developing and communicating ecological principles, goals, and guidelines for terrestrial and aquatic resources enhances the wisdom of human choices by elucidating the consequences of those choices for ecological systems. For example, it is now known that there are fundamental reasons why some management approaches fail, while others succeed (Schueler 1996, Baskerville 1997, Walters 1997, Naiman et al. 1998*a*). These reasons fall into four categories: (1) weakness in the models (of the mind or in a computer); (2) expense and risk in adaptive management experiments; (3) protection of self-interests; and (4) conflicts related to divergent institutional and personal values. Understanding and managing the biocomplexity of the world's ecosystems, however, remains a major goal for science (Colwell 1998).

Ecologists need to clearly articulate what is known with certainty about freshwater systems, to identify and prioritize key voids in knowledge that impede understanding and issue resolution, and to recognize their dependence on advances in other disciplines. For example, consider these needs in terms of disturbance patterns, human population demography, landscape structure and fragmentation, and resource substitutability.

All ecological systems are influenced by the dynamics of disturbance and succession, although the spatial

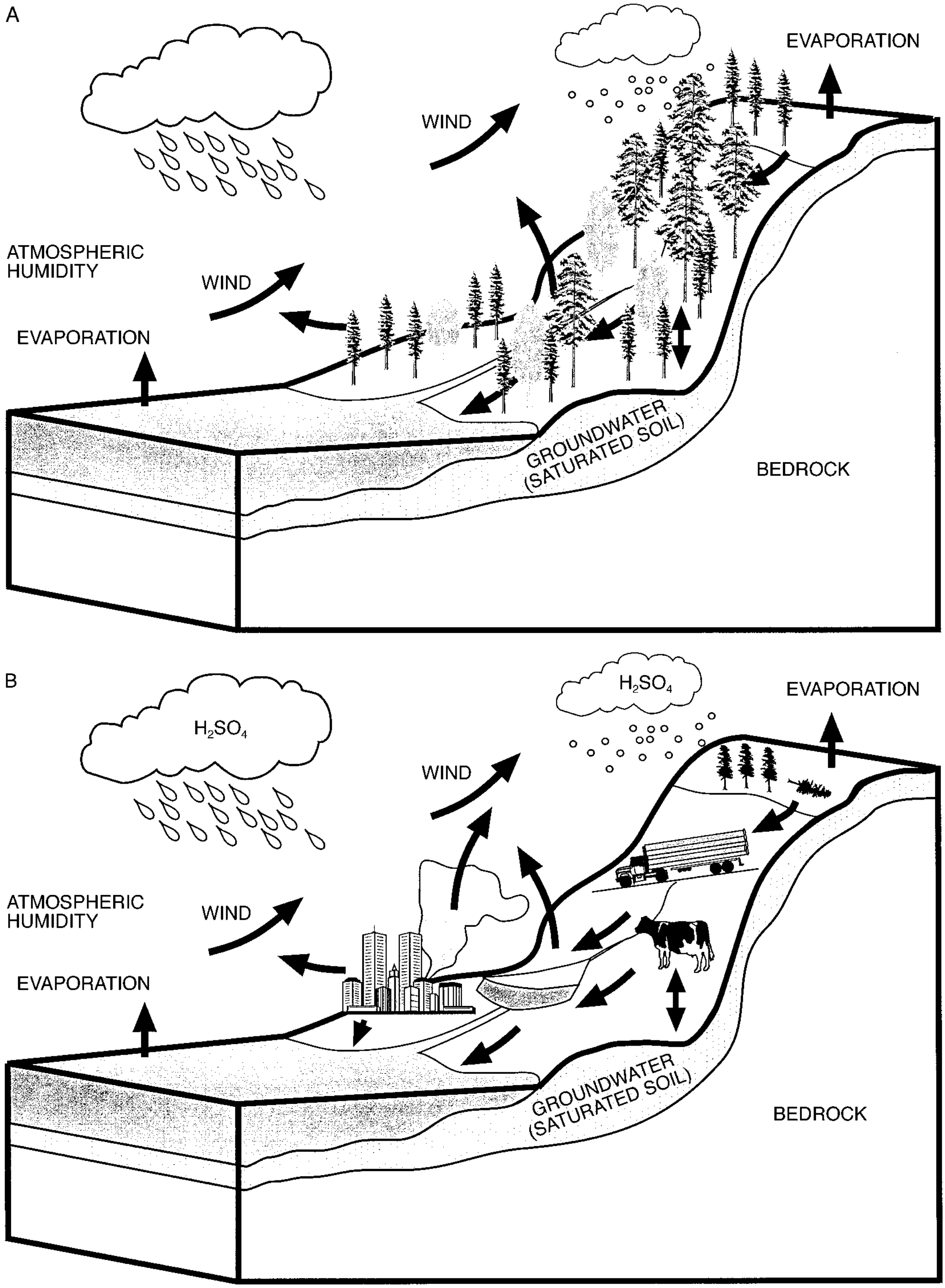

FIG. 10. (A) Pervasive changes have occurred to hydrologic cycles and material transport as a result of (B) human-induced changes to the atmosphere and watersheds in this century. Long-range transport of materials, changing land cover and use, altered climate regimes, and water quantity and availability are acting in concert to shape the freshwater issues of the next century.

and temporal scales vary widely among ecosystems (Pickett and White 1985, Glenn-Lewin et al. 1992). It is well known that some ecosystems require regular disturbances for the maintenance of function or species diversity. The unusual juxtaposition of two disturbances may result in qualitative changes to ecological systems (Paine et al. 1998, Sparks et al. 1998), and large infrequent disturbances may produce qualitatively different responses than disturbances of lesser magnitude (Romme et al. 1998, Turner et al. 1998). However, humans have substantially modified the frequency, intensity, duration, and extent of natural disturbance regimes in many areas, often with unintended effects (e.g, Ogden et al. 1998, Sparks et al. 1998).

Now it is known with certainty that many disturbances (fires, storms, floods) are strongly influenced by climate. Examples include fire size and frequency related to El Niño and persistent high pressure ridges in the Pacific Northwest (Swetnam and Betancourt 1990, Johnson 1992), among others. Also, disturbance size, frequency, and intensity have varied considerably with past changes in climate (Clark 1990). Climate change during the last century appears to drive increased fire frequency and extent, especially in high-elevation or boreal areas little affected by fire suppression. Fire frequency and annual area burned are predicted to continue to increase under most global climate change scenarios with important consequences for aquatic systems.

But what are the key scientific impediments to making reliable predictions about the ecological consequences of altering disturbance regimes? First, there is the need to predict disturbance regimes from climate projections. Knowing climate variability, especially the frequency of extreme events (e.g., very dry or very wet years), is key for predicting changes in disturbance regimes. At the same time, there are needs for improved projections of climate changes at local to regional scales as well as quantifying the relationship between climate change and the frequency and intensity of storms. Second, there is the need to understand relationships between specific disturbances and aquatic ecosystem processes. One example might be the long-term effects of altered fire frequency on net carbon storage in the terrestrial setting and its flux to aquatic systems. Information on the frequency, aerial extent, and carbon storage consequences of disturbance is a high priority for improving spatial modeling and could be used immediately in the current generation of models (Schimel et al. 1997). Finally, it remains extremely difficult to quantitatively detect altered disturbance regimes. Given the spatiotemporal variability in disturbance regimes, how much change must occur before it can be detected? In addition, how can one predict interactions among multiple disturbance regimes (e.g., cumulative effects)? The salmon example used earlier in this article provides a sobering example of the difficulties involved.

The demography of human populations presents substantial challenges and opportunities for predicting land use patterns. Land use change is the leading cause of habitat loss and fragmentation for terrestrial as well as aquatic systems (Skole et al. 1994, Turner et al. 1994, Sinclair et al. 1995). The total land area dedicated to human uses has increased dramatically to the point that nearly all the habitable land and most of the water is dedicated to human use (Richards 1990, Postel et al. 1996, Pringle 1999). It is known, for example, that:

1) Historical rates of deforestation in some regions of the United States were as great as observed in the tropics today (Iverson 1991).

2) Humans introduce new ecosystem types, often at the expense of natural communities.

3) The conversion of land to urban settings tends to leave a long-lasting impression on the landscape and it's aquatic ecosystems.

4) Legacies of past land and water use on contemporary ecological communities and processes are ubiquitous (Foster 1992, Wallin et al. 1994, Soranno et al. 1996, Pearson et al. 1998).

5) Human populations, the ultimate drivers of land and water changes, will continue to increase substantially, especially in developing countries.

The challenges and opportunities are squarely centered on understanding the complex drivers related to landscape change (see Fig. 2), and understanding the links between land use and aquatic systems. This means projecting spatial patterns of future human settlement and land use patterns, predicting with reasonable certainty the ecological responses to dynamic land use change, understanding the linkages and consequences of these changes to freshwater systems, and developing approaches and tools to increase confidence in predictions (not only the ecological consequences but also the feedbacks on human land use dynamics).

Presently, the ability to predict landscape structure two to three decades into the future is fraught with great uncertainty. One fruitful approach is to rely more on scenarios rather than on specific predictions. There are major limitations on modeling land use change (which require interdisciplinary efforts), on modeling disturbance regimes (which depend on climate regimes and human behavior), and on linking terrestrial changes to aquatic responses. Both modeling activities have high uncertainty associated with them and understanding terrestrial–aquatic linkages is still underdeveloped. Along with this is the necessity to quantify nonlinearities and thresholds that exist in important relationships such as between climate, disturbance, and successional processes, between fragmentation and connectivity, and between interactions among multiple environmental drivers. An example of such an approach is the Land-Use Change and Analysis System (LUCAS) (Berry et al. 1996, Turner et al. 1996). In modeling environments, such as LUCAS, which couples social, economic, and environmental considerations, the risk of undesirable future conditions can be assessed by exploring alternative land management scenarios to simulate future conditions (Wear et al. 1996, 1998).

Traditionally, as economic incentives grow, lower grade resources or previously unexploitable resources are substituted for the exhausted ones. In the case of water, however, there are compelling reasons to believe this will be impossible or dauntingly expensive (Postel 1992, 1999, Cohen 1995, Postel and Carpenter 1997). Well known examples include desalination (Postel and Carpenter 1997), wastewater treatment, long-range transport and irrigation, and nonconventional agriculture (Cohen 1995), all of which are economically and energetically costly as compared to natural processes. In addition, there are the environmental consequences of altering hydrologic regimes that are in excess of the technological costs. The key point is that societies are running up against hard limits in water supplies not only for human use but also for environmental needs. Water appears to be becoming the most limiting factor, in a Liebig sense, for human and nonhuman populations. The limits are occurring directly (water limits on human population or industry), or indirectly as competition for water between humans and the environment (leading to critical levels of biotic impoverishment), severely limiting widespread substitutability as a viable option for the long term.

CONCLUDING REMARKS

As the next century approaches, there are substantial challenges and opportunities awaiting ecologists to provide not just *good* science but *useful* science that is actively *used* in the decision-making process (e.g., NRC 1992, 1998, Gunderson et al. 1995, Lubchenco 1998, Pringle 2000 and others). Even though the fundamental roles of science are not changing, there is an ever-increasing expectation that achieving societal goals (e.g., clean water, productive fisheries, or healthy rivers) will be outcomes of the scientific process. Immediate challenges are to craft better watershed protection and management plans based on sound scientific principles (Dale et al. 2000), to develop seamless processes which allow effective decisions to be made and implemented regardless of spatial scale or jurisdiction (Gunderson et al. 1995, NRC 1998), to ensure that emerging legislation (i.e., the Clean Water Act and Endangered Species, among others) have the breadth, integration, and scientific basis to effectively meet future challenges (McKnight et al. 1996), and to provide the educational tools necessary to meet the tasks (NRC 1996, Firth 1998). Accomplishing these challenges means having to understand the variety and magnitude of environmental changes, how the changes interact to produce new environmental states, and what is needed to resolve specific environmental and societal issues as they arise. These are challenges and opportunities, not only for ecologists, but for all citizens committed to a vibrant future.

ACKNOWLEDGMENTS

We thank S. R. Carpenter, P. L. Firth, and Kevin H. Rogers for comments that substantially improved the manuscript. Formulation of ideas contained in this article benefited from discussions with many colleagues and students; we truly appreciate their willingness to share perspectives and information. Financial support was provided by the U.S. Man and the Biosphere Program, the A.W. Mellon Foundation, the Pacific Northwest Research Station of the U.S. Forest Service, and the National Science Foundation.

LITERATURE CITED

Asner, G. P., T. R. Seastedt, and A. R. Townsend. 1997. The decoupling of terrestrial carbon and nitrogen cycles. BioScience **47**:226–234.

Baskerville, G. L. 1997. Advocacy, science, policy, and life in the real world. Conservation Ecology **1**(1):9[on line: ⟨http://www.consecol.org/vol1/iss1/art9⟩].

Beacham, T. D., and C. B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Transactions of the American Fisheries Society **119**:927–945.

Benke, A. C. 1990. A perspective on America's vanishing streams. Journal of the North American Benthological Society **9**:77–88.

Berry, M., B. C. Hanzen, R. L. MacIntyre, and R. O. Flamm. 1996. LUCAS: a system for modeling land-use change. IEEE Computational Science and Engineering **3**:24–35.

Bolstad, P. V., and W. T. Swank. 1997. Cumulative impacts of landuse on water quality in a southern Appalachian watershed. Journal of the American Water Resources Association **33**:519–533.

Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications **8**:559–568.

Clark, J. S. 1990. Fire and climate change during the last 750 years in northwestern Minnesota. Ecological Monographs **60**:135–169.

Cohen, J. E. 1995. How many people can the Earth support? W.W. Norton, New York, New York, USA.

Cole, J. J., C. L. Peierls, N. F. Caraco, and M. L. Pace. 1993. Nitrogen loading of rivers as a human-driven process. Pages 141–157 *in* M. J. McDonnell and S. T. A. Pickett, editors. Humans as components of ecosystems. Springer-Verlag, New York, New York, USA.

Colwell, R. 1998. Balancing the biocomplexity of the planet's living systems: a twenty-first century task for science. BioScience **48**:786–787.

Dale, V. H., S. L. Brown, R. Haeuber, N. T. Hobbs, N. J. Huntly, R. J. Naiman, W. E. Riebsame, M. G. Turner, T. J. Valone. 2000. Ecological principles and guidelines for managing the use of land. Ecological Applications **10**:639–670.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science **266**:753–762.

Firth, P. L. 1998. Fresh water: perspectives on the integration of research, education, and decision making. Ecological Applications **8**:601–609.

Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. Journal of Ecology **80**:753–772.

Galloway, J. N., H. Levy, II, and P. S. Kasibhatla. 1994. Year

2020: consequences of population growth and development on deposition of oxidized nitrogen. Ambio **23**:120–123.

Gerking, S. D. 1981. The contribution of the desert pupfish (*Cyprinodon nevadensis*) to fish reproduction in stressful environments. Pages 335–356, *in* R. J. Naiman and D. L. Soltz, editors. Fishes in North American deserts. John Wiley & Sons, New York, New York, USA.

Gleick, P. H., editor. 1993. Water in crisis. Oxford University Press, New York, New York, USA.

Gleick, P. H. 1998. Water in crisis: paths to sustainable water use. Ecological Applications **8**:571–579.

Glenn-Lewin, D. C., R. K. Peet, and T. T. Veblen, editors. 1992. Plant succession. Chapman and Hall, New York, New York, USA.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. The effects of fire regime and habitat on tree dynamics in North Florida longleaf pine savannas. Ecological Monographs **65**: 441–476.

Graf, W. L. 1993. Landscapes, commodities, and ecosystems: the relationship between policy and science for American rivers. Pages 11–42 *in* Sustaining our water resources. National Academy Press, Washington, D.C., USA.

Gunderson, L. H., C. S. Holling, and S. S. Light, editors. 1995. Barriers and bridges to the renewal of ecosystems and institutions. Columbia University Press, New York, New York, USA.

Headrick, D. R. 1990. Technology change. Pages 5–67 *in* B. L. Turner, III, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and R. B. Meyer, editors. 1990. The Earth as transformed by human action. Cambridge University Press, Cambridge, UK.

Hilborn, R., C. J. Walters, and D. Ludwig. 1995. Sustainable exploitation of renewable resources. Annual Review of Ecology and Systematics **26**:45–67.

Howarth, R., et al. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. Biogeochemistry **35**: 75–139.

Hunsaker, C. T., D. A. Levine. 1995. Hierarchical approaches to the study of water quality in rivers. BioScience **45**:193–203.

Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK.

Innis, S., R. J. Naiman, and S. R. Elliott. 1999. Indicators and assessment methods for measuring the ecological integrity of semi-aquatic terrestrial environments. Hydrobiologica (*in press*).

Iverson, L. R. 1991. Forest resources of Illinois: what do we have and what are they doing for us? Illinois Natural History Survey Bulletin **34**:361–374.

Johnson, E. A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, UK.

Johnson, L. B., C. Richards, G. Host, and J. W. Arthur. 1997. Landscape influences on water chemistry in Midwestern streams. Freshwater Biology **37**:193–208.

Lichatowich, J. A., and S. Cramer. 1979. Parameter selection and sample sizes in studies of anadromous salmonids. Oregon Department of Fish and Wildlife Information Report Series, Fisheries Number 80–1, Portland, Oregon, USA.

Linder, P., B. Elfving, and O. Zackrisson. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. Forest Ecology and Management **98**:17–33.

Lubchenco, J. 1998. Entering the century of the environment: a new social contract for science. Science **279**:491–497.

McKnight, D., D. F. Brakke, and P. J. Mulholland, editors. 1996. Freshwater ecosystems and climate change in North America. Limnology and Oceanography **41**(5):815–1149.

Meade, R. H., editor. 1995. Contaminants in the Mississippi River, 1987–92. U.S. Geological Survey Circular 1133, United States Government Printing Office, Washington, D.C., USA.

Naiman, R. J., P. A. Bisson, R. G. Lee, and M. G. Turner. 1998*a*. Watershed management. Pages 642–661 *in* R. J. Naiman and R. E. Bilby, editors. River ecology and management: lessons from the Pacific Coastal Ecoregion. Springer-Verlag, New York, New York, USA.

Naiman, R. J., J. J. Magnuson, and P. L. Firth. 1998*b*. Integrating cultural, economic and environmental requirements for fresh water. Ecological Applications **8**:569–570.

Naiman, R. J., J. J. Magnuson, D. M. McKnight, and J. A. Stanford, editors. 1995. The freshwater imperative: a research agenda. Island Press, Washington, D.C., USA.

NRC (National Research Council). 1992. Restoration of aquatic systems: science, technology and public policy. National Academy Press, Washington, D.C., USA.

NRC (National Research Council). 1996. Freshwater ecosystems: revitalizing educational programs in limnology. National Academy Press, Washington, D.C., USA.

NRC (National Research Council). 1998. New strategies for America's watersheds. National Academy Press, Washington, D.C., USA.

Ogden, J., L. Basher, and M. McGlone. 1998. Fire, forest regeneration and links with early human habitation: evidence from New Zealand. Annals of Botany **81**:687–696.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises: everything else is business as usual. Ecosystems **1**:535–545.

Pearson, S. M., A. B. Smith, and M. G. Turner. 1998. Forest patch size, land use, and mesic forest herbs in the French Broad River Basin, North Carolina. Castanea **63**:382–395.

Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology **65**:1466–1475.

Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Pimentel, D., J. Houser, E. Preiss, O. White, H. Fang, L. Mesnick, T. Barsky, S. Tariche, J. Schreck, and S. Alpert. 1997. Water resources: agriculture, the environment and society. BioScience **47**:97–106.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience **47**:769–784.

Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in forested and emergent wetlands—a test of biodiversity theory. Ecology **79**:94–105.

Postel, S. L., 1992. Last oasis: facing water scarcity. W. W. Norton, New York, New York, USA.

Postel, S. L. 1998. Water for food production: will there be enough in 2025? BioScience **48**:629–637.

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

Postel, S. L., and S. Carpenter. 1997. Freshwater ecosystem services. Pages 195–214 *in* G. C. Daily, editor. Nature's services. Island Press, Washington, D.C., USA.

Postel, S. L., G. C. Daily, and P. R. Ehrlich. 1996. Human appropriation of renewable freshwater. Science **271**:785–788.

Powledge, F. 1984. The magnificent liquid of life. National Wildlife **22**:7–9.

Pringle, C. M. 2000. Threats to U.S. public lands from cumulative hydrologic alterations outside of their boundaries. Ecological Applications **10**:971–989.

Rapport, D. J., and W. G. Whitford. 1999. How ecosystems respond to stress. BioScience **49**:193–203.

Reid, L. M. 1998. Cumulative watershed effects and watershed analysis. Pages 476–501, in R. J. Naiman and R. E.

Bilby, editors. River ecology and management: lessons from the Pacific Coastal Ecoregion. Springer-Verlag, New York, New York, USA.

Rex, M., et al. 1997. Prolonged stratospheric ozone loss in the 1995–96 Arctic winter. Nature **389**:835–838.

Richards, J. F. 1990. Land transformation. Pages 163–178 *in* B. L. Turner, III, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews and R. B. Meyer, editors. 1990. The Earth as transformed by human action. Cambridge University Press, Cambridge, UK.

Romme, W. H., E. E. Everham, L. E. Frelich, M. Moritz, and R. E. Sparks. 1998. Are large infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems **1**:524–534.

Schimel, D. S., VEMAP Participants, and B. H. Braswell. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecological Monographs **67**:251–271.

Schueler, T. R. 1996. Crafting better urban watershed protection plans. Watershed Protection Techniques **2**:1–9.

Shindell, D. T., D. Rind, and P. Lonergan. 1998. Increased polar stratospheric ozone losses and delayed eventual recovery owing to increasing greenhouse-gas concentrations. Nature **392**:589–592.

Simberloff, D. 1996. Impacts of introduced species in the United States. Consequences **2**(2):13–24[on line: 〈http://www.gcrio.org/CONSEQUENCES/introCON.html〉].

Sinclair, A. R. E., D. S. Hik, O. J. Schmitz, G. G. E. Scudder, D. H. Turpin, and N. C. Larter. 1995. Biodiversity and the need for habitat renewal. Ecological Applications **5**:579–587.

Skole, D. L., W. H. Chomentowski, W. A. Salas, and A. D. Nobre. 1994. Physical and human dimensions of deforestation in Amazonia. BioScience **44**:314–322.

Soranno, P. A., S. L. Hubler, S. R. Carpenter, and R. C. Lathrop. 1996. Phosphorus loads to surface waters: a simple model to account for spatial pattern of land use. Ecological Applications **6**:865–878.

Sparks, R. E., J. C. Nelson, and Y. Yin. 1998. Naturalization of the flood regime in regulated rivers. BioScience **48**:706–720.

Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration rivers. Regulated Rivers: Research & Management **12**:391–413.

Stein, B. A., and S. R. Flack. 1997. 1997 Species report card: the state of U. S. plants and animals. The Nature Conservancy, Arlington, Virginia, USA.

Swetnam, T. W., and J. L. Betancourt. 1990. Fire-southern oscillation relations in southwestern United States. Science **249**:1017–1020.

Turner, B. L., III, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and R. B. Meyer, Editors. 1990. The Earth as transformed by human action. Cambridge University Press, Cambridge, Cambridge, UK.

Turner, B. L., III., W. B. Meyer, and D. L. Skole. 1994. Global land use/land cover change: toward an integrated program of study. Ambio **23**:91–95.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems **1**:511–523.

Turner, M. G., S. R. Carpenter, E. J. Gustafson, R. J. Naiman, and S. M. Pearson. 1998. Land use. Pages 37–61, *in* M. J. Mac, P. A. Opler, P. Doran, and C. Haecker, editors. Status and trends of our nation's biological resources. Volume 1, National Biological Service, Washington, D.C., USA.

Turner, M. G., D. N. Wear, and R. Flamm. 1996. Land ownership and land-cover change in the southern Appalachian Highlands and the Olympic Peninsula. Ecological Applications **6**:1150–1172.

U. S. Department of Commerce. 1997. Demographic state of the nation: 1997. Special Studies Series P23–193, Bureau of the Census, Washington, D.C., USA.

USEPA (Environmental Protection Agency). 1997. Environmental Monitoring and Assessment Program (EMAP). Draft Research Plan, Office of Research and Development, Washington, D.C., USA.

Vitousek, P. M., J. D. Aber, R. H. Howrath, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications **7**:737–750.

Vörösmarty, C. J., K. P. Sharma, B. M. Fekete, A. H. Copeland, J. Holden, J. Marble, and J. A. Lough. 1997. The storage and aging of continental runoff in large reservoir systems of the world. Ambio **26**:210–219.

Wallin, D. O., F. J. Swanson, and B. J. Marks. 1994. Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. Ecological Applications **4**:569–580.

Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. Conservation Ecology **1**(2): 1[on line: 〈http://www.consecol.org/vol1/iss2/art1〉].

Ward, J. V. 1976. Effects of thermal constancy and seasonal temperature displacement on community structure of stream invertebrates. Pages 302–307, *in* G. W. Esch and R. W. McFarlane, editors. Thermal Ecology II. National Technical Information Service, Springfield, Virginia, USA.

Ward, J. V. 1992. Aquatic Insect Ecology. John Wiley & Sons, New York, New York, USA.

Wear, D. N., M. G. Turner, and R. O. Flamm. 1996. Ecosystem management with multiple owners: landscape dynamics in a Southern Appalachian watershed. Ecological Applications **6**:1173–1188.

Wear, D. N., M. G. Turner, and R. J. Naiman. 1998. Land cover along an urban–rural gradient: implications for water quality. Ecological Applications **8**:619–630.

Williamson, C. E. 1995. What role does UV-B radiation play in freshwater ecosystems? Limnology and Oceanography **40**:386–392.

Williamson, C. E., S. L. Metzgar, P. A. Lovera, and R. E. Moeller. 1997. Solar ultraviolet radiation and the spawning habitat of yellow perch, *Perca flavescens.* Ecological Applications **7**:1017–1023.

Williamson, C. E., R. S. Stemberger, D. P. Morris, T. M. Frost, and S. G. Paulsen. 1996. Ultraviolet radiation in North American lakes: attenuation estimates from DOC measurements and implications for plankton communities. Limnology and Oceanography **41**:1024–1034.

WRI (World Resources Institute). 1997. World resources: 1996–1997. World Resources Institute, Washington, D.C., USA.