

Protecting Freshwater Ecosystems in the Face of Global Climate Change

Stacey Combes, Ph.D.

Department of Biology, University of Washington

FRESHWATER ECOSYSTEMS HAVE BEEN critical to sustaining life and establishing civilizations throughout history. Humans rely on freshwater systems not only for drinking water, but also for agriculture, transportation, energy production, industrial processes, waste disposal, and the extraction of fish and other products. As a result of this dependence, human settlements worldwide are concentrated near freshwater ecosystems, with over half of the world's population living within 20 km of a permanent river (Small and Cohen, 1999).

In addition to humans, an enormous array of plants, animals, and microorganisms depend on freshwater ecosystems for their survival. Although freshwater ecosystems contain only 0.01% of the Earth's water and cover a small fraction of the planet's surface, rivers, lakes and wetlands harbor a disproportionately high fraction of the Earth's biodiversity. Freshwater fishes alone account for over one-fourth of all living vertebrate species. (McAllister et al., 1997).

Because freshwater ecosystems continuously channel precipitation from the surrounding landscape through the interconnected lakes, rivers, and wetlands that lie below, they can be surprisingly sensitive to distant activities. Increasing human water needs and extensive land alteration has contributed to the decline of countless freshwater species. Freshwater biodiversity is now more threatened than terrestrial biodiversity, and the projected mean future extinction rate of North American freshwater animals is about five times higher than for terrestrial animals, and comparable to predicted extinction rates for tropical rainforest communities (Ricciardi and Rasmussen, 1999).

The long-term protection of freshwater species is largely dependent upon identifying the underlying physical processes of freshwater systems that are most vulnerable to change, and determining how changes in these physical features might affect the resident flora and fauna. For this purpose, it is useful to divide freshwater ecosystems into rivers, lakes, and wetlands. In this chapter, rivers and streams are considered to be channelized bodies of water that generally display continuous flow, and lakes are relatively still bodies of water that can be either connected (through rivers, streams, etc.) or isolated from other bodies of water. Wetlands (also known as marshes, swamps, fens, bogs,

floodplains, or depressions) are areas where the water table is at or near the surface, and vegetation is submerged for at least part of the year. Many, although not all, wetlands are connected to or interact strongly with lakes and rivers.

Because freshwater ecosystems are sensitive not only to water temperature, volume, and flow, but also to variability in these factors, rivers, lakes and wetlands are expected to display a wide variety of changes in response to global climate change. The purpose of this chapter is to provide information and strategies for designing and managing reserves that will allow freshwater ecosystems to withstand and/or adapt to climate change. The chapter begins with a review of current threats to freshwater ecosystems and some of the observed and predicted effects of global climate change on these systems. Next, general suggestions are presented for designing and managing freshwater reserves to increase resistance and resilience to climate change. The chapter concludes with a discussion of methods for selecting and implementing specific adaptation strategies to accommodate global climate change in freshwater ecosystems.

Current Threats to Freshwater Ecosystems

Because freshwater ecosystems depend strongly on physical features such as water quantity, quality and flow, many of the threats to these ecosystems involve activities that alter fundamental physical characteristics. Freshwater ecosystems throughout the world are threatened by human activities that directly alter system hydrology, such as construction of physical barriers to flow, water extraction, and filling or draining of shallow habitats. Pollution of waterways with toxic substances and excessive nutrients, as well as destructive land use practices in areas surrounding freshwater ecosystems, lead to reductions in water quality. While the above threats directly affect physical features of freshwater ecosystems, the introduction of exotic species primarily affects native biota. The invasion of freshwater ecosystems by non-native species is rapidly becoming one of the most serious threats to freshwater communities. Overexploitation of animals associated with freshwater ecosystems, particularly freshwater fishes, is also a continuing problem. Finally, penetration of harmful UV-B radiation into water bodies is increasing in many areas due to interactions between a number of anthropogenic factors, and a range of negative impacts on freshwater communities may result.

Alteration of hydrology

PHYSICAL BARRIERS TO FLOW

Humans have constructed a variety of physical barriers, including dams, levees and dikes, to prevent flooding, generate power, supply water for irrigation or municipal water supplies, and provide recreational opportunities. Dams have been built on every continent except Antarctica; they are prevalent in developed countries and their rate of construction is increasing rapidly in developing nations. Dams have traditionally been viewed as an environmentally-friendly and sustainable means of ensuring water supply, controlling floods, and generating power without polluting the environment. However, retaining water and altering its natural flow can lead to large changes in aquatic and terrestrial habitats, both above and below dams.

Initial flooding above dams to create reservoirs can result in massive losses of terrestrial habitat; for example, India lost approximately 479,000 hectares of forest land to various river valley projects from 1950-1975 (Goldsmith and Hildyard, 1984). Stagnation and low flow rates in reservoirs can lead to large changes in water temperature, including variations in seasonal peak temperatures and a reduction in natural temperature variation (Baron et al., 2003). Silt that is normally carried down rivers accumulates behind dams, and costly removal procedures are sometimes necessary to ensure that dams remain functional. In addition, the decomposition of flooded vegetation above dams may release significant quantities methane and other greenhouse gases, particularly in tropical areas where plant biomass is high (McCully, 1996); the magnitude of this greenhouse gas release compared to fossil fuel burning has been widely debated (Rudd et al., 1993; Gagnon and Chamberland, 1993; Fearnside, 1997).

Dams also cause dramatic changes in downstream flow regime, where seasonal, dynamic flows are replaced by steady water release for energy production, or intermittent large releases to lower reservoir levels. The temperature variability of water released from the bottom layer of reservoirs is low compared to that of natural stream flows, and oxygen content may be reduced. The loss of natural silt in released water can lead to a range of damaging effects downstream, including changes in chemical composition, river bank erosion, and massive habitat loss and erosion in coastal deltas and floodplains.

Finally, dams pose a significant barrier to diadromous fish and other migrating animals. In the Brazilian Amazon, where many fish undergo long-distance migrations during the rainy season, 79 dams are either planned or currently in existence (Pringle et al., 2000), and hydroelectric development is considered to be the greatest threat to Amazonian fisheries in the near future (Bayley and Petrere, 1989; Goulding et al., 1996). On the Columbia River in the northwestern United States, 19 major dams have already contributed to the extinction of at least 106 local stocks of pacific salmon (McGinnis, 1994).

Humans also build obstructions such as levees and dikes to prevent water from flowing laterally over river banks during high flows—in this way, land adjacent to rivers can be developed with less risk of seasonal flooding. However, these barriers disrupt connections between rivers and valuable floodplain habitats, which serve as refugia and spawning grounds for many animals, and are often sites of high biodiversity.

WATER DIVERSION/WITHDRAWAL

In order to meet the agricultural and municipal water needs of a growing population, large quantities of water are diverted or withdrawn directly from rivers, lakes, or the underlying water table. A large proportion of the world's population is currently experiencing water stress, and human water needs are expected to increase dramatically in the coming decades due to projected population growth and increased development (Vörösmarty et al., 2000).

Withdrawal of water for human needs can reduce the total amount of water available to aquatic biota (resulting in low stream flows and declining lake levels), reduce seasonal

variability in flows, and lead to large losses of habitat, particularly valuable edge habitats that are used for spawning or rearing (Tyedmers and Ward, 2001). Withdrawal of groundwater for agriculture in adjacent areas can completely dry up valuable wetlands, even if the habitat itself is protected (McDowall, 1984). Water that is withdrawn from freshwater systems is often returned in the form of household wastewater, agricultural runoff, or industrial cooling water, with reduced quality (increased pollutants, changes in nutrient load) and altered temperature.

FILLING OR DRAINING SHALLOW HABITATS

Wetlands throughout the world have been filled or drained for development or agriculture (Brinson and Malvarez, 2002; Junk, 2002). These habitats have traditionally been regarded as useless in their natural state, and many countries have provided subsidies to encourage the conversion of wetlands to agricultural land. Thankfully, the valuable ecosystem services that wetlands provide, including water purification, groundwater recharge, and flood control, are becoming more widely appreciated (National Research Council, 1995).

Invasive species

Apart from direct alterations of system hydrology, the most serious threat to freshwater ecosystems in many areas is the presence of invasive, non-native species. Invaders are often adaptable generalists who breed and disperse quickly, endangering native species through highly efficient competition, predation, or habitat alteration.

DELIBERATE INTRODUCTIONS

The deliberate introduction of non-native species for commercial or recreational fishing is widespread; for example, approximately 80% of the alpine lakes in the western United States have been stocked with non-native fish (Bahls, 1992). In many areas, lakes and streams are continuously re-stocked to maintain populations. Although these fisheries generate enormous income, the effects on freshwater communities can be devastating. Hundreds of native fish species in North America are threatened, and competition or predation by non-natives is the primary threat to many of these species (Allan and Flecker, 1993; Schindler, 2001). In Lake Victoria, increased predation and competition due to the introduction of the Nile perch and several non-native tilapiine species (in addition to ongoing environmental changes in the lake), led to the extinction of up to 200 endemic cichlid species within a few decades (Ogutu-Ohwayo, 1990; Witte et al., 1992).

ACCIDENTAL INTRODUCTIONS

Many species are introduced to and spread throughout freshwater ecosystems accidentally—for example, non-native species can be attached to boats or transported in ballast or bilge water. The zebra mussel, which is native to Europe, was accidentally introduced to the Great Lakes in 1986 through ballast water. It has altered water chemistry through highly efficient filter feeding, outcompeted populations of native mussels, and fouled boats, docks, and power plant intakes, costing millions of dollars in damage (Cooley, 1991; Effler et al., 1996; Nalepa et al., 1996). Several species of native mussels, clams,

and commercially important fish are threatened directly or indirectly by its presence (Nalepa et al., 1996; Roberts, 1990).

Non-native plants can also cause damage to aquatic ecosystems. The water hyacinth, which is native to the Amazon River, has been introduced to freshwater ecosystems on several continents, including Africa and North America. It grows on the surface of water, blocking light, decreasing oxygen levels, and changing water chemistry (Gopal, 1987). Entire food webs have been altered as a result, and fish populations have been reduced or eliminated in some areas (Gowanloch, 1945; Timmer and Weldon, 1967). In the United States, water hyacinth has spread to rivers, lakes and lagoons throughout the country, forming dense mats that block canals and drainage pipes, prevent swimming and boating, and impair waterway navigation (Buker, 1982). In Lake Victoria, water hyacinth “hot spots” have persisted near areas of urban, industrial, and agricultural pollution, despite efforts to eradicate the floating vegetation (Lake Victoria Environmental Management Project, 2003)

Pollution

Freshwater ecosystems are polluted by a variety of human activities, from large-scale agriculture and industry to everyday behaviors, such as driving cars and fertilizing lawns. Large quantities of pollution often enter freshwater systems from point sources, such as industrial or municipal sewage outflows; for example, 23.4 billion tons of sewage and industrial waste was dumped into the Yangtze River in 2001, threatening human health and the survival of the endangered Yangtze River dolphin (Young, 2002). Thus, the focus on protecting water quality in many countries has been on preventing point source pollution (i.e. U.S. Clean Water Act of 1972). However, nonpoint source pollution is far more significant in many cases. Airborne pollutants can enter the atmosphere and travel long distances, entering lakes and waterways in otherwise pristine locations. Pollutants dissolved in runoff from the surrounding landscape may account for the greatest source of pollution in many freshwater ecosystems—for example, it has been estimated that 80% of the nutrients (nitrogen and phosphorus) that pollute U.S. waterways derive from nonpoint sources such as agricultural and urban runoff (Shaw and Raucher, 1993).

NUTRIENT POLLUTION

Runoff from fertilizers used in commercial agriculture or private yards adds large amounts of nitrogen and phosphorus to freshwater ecosystems. This can be especially problematic in lowland areas and in lakes or rivers with developed shores. The added nutrients lead to excess growth of algae (which is sometimes toxic), resulting in reduced water clarity and light penetration. Because of this increased primary productivity, the activity of decomposing, oxygen-consuming bacteria increases and oxygen levels decline. Shifts in the food web and alterations in bottom-water habitat can lead to changes in species composition and distribution. For example, the density, distribution and relative abundance of aquatic plants can change after eutrophication (Schmieder, 1997), and valuable fish species are often replaced by less desirable fauna that can tolerate low oxy-

gen levels (Egerton, 1987). Natural eutrophication is a normal state in the succession of lakes as they age, but polluted runoff has led to early eutrophication and changes in the community structure of many naturally oligotrophic (nutrient-poor) lakes.

TOXIC POLLUTION

Toxic pollution in freshwater ecosystems can devastate local biota and endanger human food sources. Most toxic pollution derives from industry (i.e. dioxin, PCBs) or agriculture (pesticides such as DDT and toxaphene). Heavy metals, such as arsenic, zinc, selenium, and mercury are also released from mining and other industrial activities. Heavy metals and toxic compounds can become volatilized in warmer parts of the globe, enter the atmosphere, and re-condense in cooler areas, often contaminating pristine sites and indigenous food supplies (Dewailly et al., 1989; Kidd et al., 1995; Wania and Mackay, 1993). These pollutants cause massive mortality events, such as fish kills, and are found in concentrations considered unsafe for human consumption in many aquatic animals, such as freshwater mussels (Lau et al., 1998). Because many pollutants accumulate in fatty tissues, they are magnified in the food chain and can reach concentrations in fish-eating birds and mammals that are up to 10 million times higher than those found in polluted water (Schindler et al., 1995).

Acid rain containing high levels of sulfuric and nitric acids is also a serious threat to many freshwater ecosystems, particularly lakes at high altitudes and latitudes. These pollutants enter the air mainly through the burning of fossil fuels, are transported atmospherically to distant parts of the globe, and are finally released into freshwater ecosystems through precipitation. In lakes susceptible to acidification (where acids are not readily neutralized by the soil or water), lake pH is lowered dramatically, and species composition and abundance can change as a result (Schindler et al., 1985; Wright and Schindler, 1995).

Land use

Destructive land use practices that result in vegetation loss anywhere within the drainage basin of a river can have negative impacts on freshwater ecosystems. The forests and native plant communities surrounding lakes, rivers, and wetlands help protect water quality and quantity by filtering and storing runoff. Changes in land use brought about by agriculture and urbanization (such as deforestation, chemical fertilization, and paving) lead to increased runoff with higher levels of nutrients and other pollutants. In addition, more sediments are washed into the system and water turbidity rises, with negative impacts on fish, filter feeders, aquatic plants, and bacteria (Baron et al., 2003; Megahan et al., 1992).

The vegetation immediately surrounding water bodies (i.e. riparian or floodplain vegetation) is particularly important to freshwater ecosystem health, as it shades water bodies (regulating water temperatures and providing thermal refugia) and supplies organic material such as falling leaves, insects, and woody debris to freshwater systems. The deforestation of Amazonian floodplains is considered to be one of the major forces behind

the decline of Amazonian fisheries, as deforestation in these seasonally flooded areas has led to massive erosion, increased sediment load, and a decrease in large, woody debris in the river (Goulding et al., 1996). Although its function has not been studied extensively in tropical rivers, large, woody debris has been shown to play numerous important roles in temperate river systems, including altering flow to create habitat heterogeneity (i.e. stepped channels and deep pools) and helping to determine river channel form and stability. Woody debris also has a long residence time in most water bodies, and provides substrate, food, and shelter for a wide range of plants and animals (Bilby and Bisson, 1998; Petts, 2000).

Overexploitation

Fish and shellfish harvests have declined sharply in the last few decades, and in many cases this decline is due to commercial or recreational overexploitation of these resources (Naiman et al., 1995). Overharvesting of aquatic species has occurred repeatedly in freshwater ecosystems throughout the world, in part because high levels of natural population variability can mask the effects of overexploitation until population declines are severe and irreversible (Ludwig et al., 1993). Attempts to bolster declining populations, such as with the release of hatchery fish, often exacerbate the problem (Hilborn, 1992; Meffe, 1992). Species inhabiting lakes can be particularly vulnerable to overexploitation in areas where there is not continual recruitment from populations outside the lake (Abell et al., 2002).

Hunting or extermination of mammals associated with freshwater ecosystems (i.e. beavers, muskrats) can affect not only the biological community, but also the physical structure of freshwater ecosystems, as the activities of some species lead to flooding and the creation of important wetland habitats. Hunting in tropical rivers and floodplains can add additional pressure to endangered species such as manatees, turtles, river otters and caiman (Junk, 2002).

Exposure to Ultraviolet-B radiation

Exposure to high levels of Ultraviolet-B (UV-B) radiation can have a range of harmful effects on living organisms, and damage to the ozone layer has caused an increase in UV-B radiation of up to 50% in some alpine areas (Schindler et al., 1996). Although the ozone layer protects both terrestrial and aquatic ecosystems from much of the sun's UV-B radiation, some aquatic animals may be more vulnerable to the radiation that reaches the Earth's surface because they have historically been afforded a high level of protection by natural characteristics of the waters they inhabit (Williamson, 1995). UV-B radiation generally only penetrates the top layer of water bodies; the depth of UV-B penetration depends on water clarity and on the concentrations of dissolved organic carbon (DOC) and/or chromophoric dissolved organic matter (CDOM), which are derived from the breakdown of plant materials or dead organisms.

Animals living in clear or shallow bodies of water, those that are sessile or can't sense UV-B radiation, and those that are restricted to the upper layer of water during the day-

time (i.e. small zooplankton taking refuge from downward migrations of predators) may be particularly vulnerable to increases in UV-B radiation (Williamson, 1995). Primary productivity has decreased as a result of increased UV-B radiation in some cases, but productivity could also increase, depending on whether the system is nutrient or grazer-limited (Williamson, 1995). Many vertebrates, including amphibians, lay transparent eggs with little UV-B protection in bodies of water (Hansen et al., 2002). UV-B radiation can reduce hatching success, retard larval growth rates, and cause morphological abnormalities in amphibians, and increased exposure to UV-B has been implicated as a possible factor in (although not the sole cause of) recent worldwide declines in amphibian populations (Blaustein et al., 1996; Blaustein and Wake, 1995; Gardner, 2001). However, the danger of UV-B radiation in freshwater ecosystems remains site-specific; for example, 85% of the potential amphibian breeding sites sampled in the U.S. Pacific Northwest are protected by naturally-occurring levels of DOC in the water (Palen et al., 2002).

The threat of UV-B exposure may be magnified by other human-induced stresses. For example, CDOM derived from healthy, forested drainage basins is far more effective at attenuating UV-B than colorless DOC from other sources (Schindler et al., 1996), and deforestation decreases the input of CDOM to freshwaters. In addition, acidification of lakes causes a decline in DOC concentrations, and thus UV-B radiation may actually be responsible for many of the negative effects attributed to lake acidification (Schindler et al., 1996).

Anticipated and Observed Effects of Climate Change on Freshwater Ecosystems

Human activities within the last century have led to a dramatic rise in atmospheric concentrations of carbon dioxide and other gases that contribute to the greenhouse effect. Within the next century, carbon dioxide concentrations are expected to rise to levels at least twice as high as those present in pre-industrial times, and global climate is expected to change in a number of ways as a result. This climate change will primarily affect freshwater ecosystems through changes in water temperature, quantity, and quality (Shuter and Meisner, 1992), as well as through changes in the timing and duration of flows. Some of the expected physical and biological effects of climate change will affect all freshwater ecosystems, while others are specific to rivers, lake or wetlands.

Physical effects common to all freshwater ecosystems

TEMPERATURE CHANGES

There is widespread consensus that the greenhouse effect will lead to a global rise in air temperature, with mean surface temperatures increasing 1.5 to 5.8_ C by the year 2100 (Houghton et al., 2001). Temperatures are expected to increase more at higher latitudes, and in many of these regions the effects of global warming have already been documented; in Canada, mean air temperatures, water temperatures, and evaporation have all increased in the past 20-30 years (Schindler, 2001), and ice cover durations over lakes and rivers have decreased over the entire northern hemisphere by almost 20 days since the mid-1800's (Magnuson et al., 2000).

However, in most cases, the effects of global warming on air and water temperatures are likely to be far more complicated than a gradual increase in average temperatures. In many regions, daily minimum air temperatures have increased more than daily maximum temperatures, leading to a reduction in the diurnal temperature range (Easterling et al., 1997). Both observational studies and models of future climate change suggest that there will be more hot summer days and fewer cold waves (Easterling et al., 2000). Regionally, temperatures are likely to become more variable, and this increased variability (i.e. a 1°C increase in the standard deviation of temperature) will lead to a far greater frequency of extreme temperature events than a similar change in the mean temperature would (Meehl et al., 2000).

Rising temperatures are generally expected to lead to an increase in glacial melting, although increased winter precipitation could compensate for ice loss in some areas (Arnell et al., 2001). Many simulations suggest that glacier melting will depend strongly on the rate of temperature change; for example, Oerlemans et al. (1998) predicted that in the absence of increased precipitation, a rise of 0.4°C per decade would eliminate nearly all of their study glaciers by 2100, while a rise of 0.1°C per decade would only lead to a 10-20% loss of glacier volume. Tropical glaciers may be especially sensitive to global warming, as the equilibrium line between ice accumulation and melting is more sensitive to changes in air temperature (due to the lack of seasonality in tropical temperatures), and because glacial melting is significant year-round (Kaser et al., 1996).

PRECIPITATION CHANGES

Since 1900, surface precipitation has generally increased in mid- and high-latitude areas, and decreased in the tropics and subtropics (Easterling et al., 2000). Current models of global climate change suggest that annual precipitation is likely to increase further in high and mid-latitudes and most equatorial regions, but decrease in the subtropics (Carter et al., 2000). However, predicted regional changes in precipitation are far less certain, and in many areas, the size of predicted precipitation changes due to global warming are small compared to those due to natural multi-decadal variability (Arnell et al., 2001).

However, even slight changes in average precipitation could lead to substantial increases in the variability of precipitation events; because the size of precipitation events is not normally distributed about the mean, a change in average precipitation will also cause a change in variability (Meehl et al., 2000). Climate change models predict that global warming will generally lead to more extreme events, such as heavy 1-day and multi-day precipitation (Easterling et al., 2000), and an increase in the frequency of extreme rainfall has been observed in the United States and the UK (Karl and Knight, 1998; Osborn et al., 2000). In addition, most countries that have experienced a significant increase or decrease in precipitation also experienced a disproportionate change in the amount of precipitation falling during extreme precipitation events (Easterling et al., 2000). Tropical storm intensity has increased, and is expected to increase further in some areas, such as southwest Asia (Anderson et al., 2002), but in other areas tropical storm frequency and intensity is expected to remain the same or decline (Easterling et al., 2000).

WATER QUANTITY AND FLOW CHANGES

Although precipitation is one of the main factors determining water availability and flow, other factors such as evaporation, soil moisture, groundwater recharge, and glacial and snowmelt are also critical. Evaporation is generally expected to increase due to increasing mean temperatures. However, the exact amount of evaporation that will occur at a given site is determined by a host of other factors, including soil characteristics, the amount of water available, vegetation cover, and plant transpiration (which is affected by temperature and atmospheric carbon dioxide concentrations; Arnell et al., 2001). Soil moisture will depend on soil characteristics and the magnitude of local precipitation changes, and soil infiltration and water-holding capacity will in turn determine the volume of run-off. For example, drier soils often shows reduced water infiltration, and less extreme freezing events can reduce water infiltration in limestone soils (Boix-Fayos et al., 1998); reduced water infiltration could lead to greater run-off and an increase in flooding events. Groundwater recharge is affected by both the amount of precipitation and the duration of the recharge season, as well as by evaporation and soil moisture (Arnell et al., 2001). Although climate change is likely to lead to some changes in groundwater recharge, freshwater ecosystems that primarily receive input from groundwater are likely to experience smaller changes in water temperature and quantity than those dominated by precipitation.

Water flows depend primarily on precipitation in tropical and arid regions. In tropical river systems, seasonal heavy rainfall events already surpass the natural infiltration rates of soil, leading to high sediment input and dangerous levels of pesticide runoff from agricultural lands (Pringle, 2000); increased extreme rainfall events in these areas could lead to further water quality problems. In higher latitude regions, temperature changes will affect water flow through changes in snowmelt and the form of falling precipitation. In large parts of eastern Europe, European Russia, central Canada, and California, a major shift in streamflow from spring to winter has already been observed, because elevated temperatures cause precipitation to fall as rain rather than snow (Dettinger and Cayan, 1995; Westmacott and Burn, 1997). Similarly, glacier-fed rivers, lakes and wetlands (in temperate and tropical regions) may experience increased flows due to glacial melting, even in the absence of increased precipitation (Arnell et al., 2001).

Many models predict that extreme water flow events such as floods are likely to increase, due to heavier individual rainfall events (Reynard et al, 1998) or increased overall precipitation (Panagoulia and Dimou, 1997). Some models also predict seasonal shifts in peak flooding seasons (Saelthun et al., 1998). Finally, models of climate change suggest that hydrological droughts should increase in frequency, but this has only been observed in some areas, such as Hungary and China (Easterling et al., 2000). The effects of climate change on low flow conditions appear to be sensitive to the storage capacity of the system; basins with little groundwater storage capacity may experience more frequent droughts because they do not benefit as much from winter groundwater recharge (Arnell et al., 2001).

WATER QUALITY CHANGES

The input of chemicals, sediments, organic matter, nutrients and pollutants to freshwater ecosystems are all likely to be affected by climate change. Both simulations and direct observations indicate that increased precipitation can increase water alkalinity via enhanced weathering and input of base cations to streams or lakes (Avila et al., 1996; Sommaruga-Wögrath et al., 1997). Intense storm events following prolonged dry periods can lead to increased flushing of sediments or nitrates into water bodies (Arnell et al., 2001).

Rising temperatures and changes in precipitation are likely to cause changes in the biomass, production, and composition of terrestrial communities surrounding lakes, rivers and wetlands (Carpenter et al., 1992). These changes may affect the supply of organic matter to freshwater systems, shading and light (including UV-B) penetration, as well as the characteristics of runoff entering the system (i.e. DOC and nutrient concentrations, sediment load). Rising temperatures and evaporation may cause an increase in fires in some regions (this has been documented already in Canada; Schindler et al., 1990). Fires in regions surrounding water bodies could lead to increased nutrient input (from burnt vegetation) leading to eutrophication, increased sediment load, reduced input of organic matter (DOC, woody debris), and reduced protection from winds.

Water pollution could be affected in many ways by climate change. Increased volatilization of pesticides, PCBs, and heavy metals in warm and warming regions with condensation elsewhere will lead to increased pollutant loads in water bodies at higher latitudes and altitudes. Increased runoff could lead to increased pollution from agricultural and urban sources, while decreased water levels could lead to concentration of pollutants from point sources and the atmosphere (Schindler, 2001). Increased glacial melt has been shown to increase the concentrations of pollutants in glacial-fed streams and lakes by releasing organic pesticides and PCBs deposited in glacial ice during earlier decades when pollution levels were higher (Blais et al., 2001).

INCREASING HUMAN WATER NEEDS AND EXTRACTION

Rising air temperatures and evaporation are likely to contribute to increasing human water use and water shortages. By far, the largest proportion of current and predicted future water use is for agricultural irrigation; in 1995, 67% of all water withdrawals and 79% of all water consumed worldwide was used for agriculture, whereas municipal, or domestic, use represents only about 9% of withdrawals (Arnell et al., 2001).

Based on predicted population increases and development scenarios, water withdrawals are expected to increase 23-49% over 1995 levels by the year 2025 (Raskin et al., 1997). Municipal water withdrawals may be offset by declining per capita usage in some countries, and increases in water usage by the industrial sector in developing countries (particularly in Asia and Latin America) may be partially ameliorated by greater industrial efficiency (Arnell et al., 2001). Agricultural water usage, on the other hand, is expected

to increase due to higher evaporation rates and because larger areas of land are likely to be under cultivation (to feed an growing human population). Areas where agriculture accounts for a large portion of the GNP and water is already scarce (i.e. many African countries) are likely to be hardest hit by climate-associated water shortages (Smith and Lenhart, 1996). Alterations in the way that water is priced (i.e. reducing agricultural water subsidies) could play an important role in promoting more efficient water use and thus decreasing human water needs and extraction.

Biological changes common to all freshwater ecosystems

EFFECTS ON PHYSIOLOGY AND LIFE HISTORY

Temperature change alone is known to affect a range of physiological processes and life history traits. Higher ambient temperatures increase the metabolic demands of many animals; for example, even at sub-lethal temperatures, warming would lead to a several-fold increase in the energy requirements of lake trout (*Salvelinus namaycush*) (McDonald et al., 1996). The effects of higher metabolism on growth may depend on food availability. In zooplankton with an adequate food supply, increased temperatures lead to a dramatic rise in feeding, assimilation, growth, and reproductive rates (Schindler, 1968), and local species richness can increase as a result (Stemberger et al., 1996). Increased temperatures can also lead to a rise in the frequency of toxic algal outbreaks, and in their toxicity to other animals (Hallengraeff, 1993).

Temperature affects body size in many aquatic animals; increased rearing temperature causes a reduction in body size at a given developmental stage in over 90% of cold-blooded, aquatic animals studied (Atkinson, 1995). Temperature also determines the sex of offspring in the American alligator (*Alligator mississippiensis*) and several groups of turtles (Conover, 1984). In one population of painted turtles (*Chrysemys picta*), offspring sex was shown to be highly correlated with mean July air temperatures; statistical analyses indicate that a 2°C rise in air temperatures would drastically skew sex ratios, and a 4°C rise would virtually eliminate all males from the population (Janzen, 1994). The phenology, or timing of life history events, is also affected by ambient temperature; for example, breeding migrations and spawning dates have begun to occur earlier in several species of amphibians as a result of climate warming (Beebee, 1995).

Life history traits are intricately linked with water quantity and seasonal flow in numerous aquatic animals. In tropical rivers, many fish undergo feeding and spawning migrations of several thousand kilometers that are dependent on predictable, seasonal flooding events (Junk, 2002), and extreme flow levels may be necessary for maintaining populations of a number of other species (Poff and Ward, 1989; Poff et al., 1997). On the other hand, intense flooding can scour streambeds, displacing organic matter, bottom-feeding organisms, and small fish fry, and substantial increases in flood frequency could cause a shift in species composition, possibly eliminating many species (Poff et al., 1997).

The timing and duration of the breeding season in wading birds that frequent freshwater wetlands is strongly tied to water levels (Butler and Vennesland, 2000), and could be af-

ected by either increases or decreases in precipitation and water table levels. Frogs are particularly sensitive to decreased precipitation; low precipitation in Puerto Rico has been correlated with drastic declines in frog populations (Stewart, 1995), and the extinctions of four frog species in Costa Rican cloud forests have been linked to a series of severe population declines following extreme El Niño-associated droughts (Pounds et al., 1999). Some inhabitants of seasonal wetlands, such as fairy shrimp, are entirely dependent on precipitation-filled, ephemeral vernal pools to complete short, highly-specialized life cycles (Eriksen and Belk, 1999).

EFFECTS ON COMMUNITY COMPOSITION AND DYNAMICS

Climate warming is likely to alter the composition of many communities, as different species will have different thermal tolerances and interactions between species may intensify as a result of reduced resources and habitat availability. In algae, thermal tolerance can affect the outcome of competition for nutrients and alter community composition (Rhee and Gotham, 1981). Where water levels or the size of suitable thermal habitats decreases, biotic interactions (including human overexploitation) may intensify as a result of increased densities of aquatic animals. For example, caddisfly competition in streams that is usually limited to the summer season persisted year-round in years when drought eliminated normal winter density reductions (Feminella and Resh, 1990). Climate change may affect motile vs. non-motile species differently, leading to differences in species distribution; in the marine intertidal zone, vertical distribution of marine invertebrates is tightly correlated with temperature, whereas the distribution of motile species is not (Huey et al., 2002).

In temperate or high-elevation tropical systems, where water temperatures are currently cool, climate warming is expected to facilitate the spread and establishment of non-natives, especially those from warmer climates (Stachowicz et al., 2002). Once thermal barriers to invasion are removed, native species may be displaced by invaders with a competitive advantage, such as warmwater, omnivorous fish with fast life cycles (Carpenter et al., 1992). Natural high flows help minimize the success of non-native fish by removing species that are poorly adapted to dynamic river environments; the restriction of flooding by reservoirs has already helped facilitate the proliferation of exotic fish in many river systems (Baron et al., 2003). Reduced flooding due to climate change could similarly allow non-native fish to become established in areas where the current flow regime would otherwise exclude them. Several species of exotic marine invertebrates may benefit from warming temperatures at higher latitudes, as earlier recruitment in warmer years helps them gain a competitive advantage over native species (Stachowicz et al., 2002); a similar breeding strategy may be present in invasive freshwater invertebrates.

Migration may be the only option for many animals that cannot adapt to increasing temperatures. During past eras of climate change, most plants and animals displayed range shifts, rather than morphological change, in response to changing environmental conditions (Noss, 2001). However, the rate of warming expected in the next 100 years is over ten times higher than warming after the last ice age (De Groot and Ketner, 1994), and it

is unknown whether plants and animals will be able to migrate quickly enough to keep up with climate change (Malcolm and Markham, 2000). Meta-analyses indicate that hundreds of plant and animal populations have already shown highly significant, non-random changes in range boundaries, in the direction expected to result from climate change (Parmesan and Yohe, 2003), and temperature is known to affect geographic distribution of fish, diatoms, and other aquatic animals (Meisner and Shuter, 1992; Reynolds, 1984).

Unfortunately, the ability of many freshwater species to migrate is restricted by bodies of water that preclude migration or that don't allow movement in the correct direction. Migration is impossible from many isolated lakes and wetlands, and numerous major river systems run from east to west, precluding latitudinal migration. In the southwest and southern Great Plains (USA), nearly all major river systems run from east to west, and these systems contain some of the hottest free-flowing water on Earth. Many native species in these areas are already living near their thermal tolerance limits, and the combination of increased warming and the lack of northern migration routes could cause extinctions of up to 20 species of endemic fish (Matthews and Zimmerman, 1990).

Even where migration is possible, it is unlikely that entire communities and ecosystems will be transplanted intact. Species differ in their levels of tolerance of environmental change, and in their abilities to adapt or migrate in response. Differences in sensitivity to temperature change are likely to alter community dynamics. For example, communities composed of several species of *Drosophila* that were allowed to migrate between different thermal habitats did not simply shift to new zones when temperatures were increased to simulate global warming (Davis et al., 1998). Interactions between species and with parasites introduced to the system altered the relative abundance of species in different thermal zones in ways that were non-intuitive and difficult to predict. Thus, simple "climate mapping", or assuming that species range boundaries will shift smoothly with changes in temperature, oversimplifies the effects that climate change may have on communities.

Effects of climate change on lakes

PHYSICAL EFFECTS ON LAKES

Increased mean surface temperatures are likely to lead to increased water temperatures and evaporation in many lakes, in both temperate and tropical areas (Schindler, 2001; Zinyowera et al., 1998). If precipitation does not increase enough to compensate, this could lead to reductions in outflow and/or lake volume. Important spawning and rearing habitat near the edges of lakes (Tyedmers and Ward, 2001) would be lost if lake levels declined, and lake characteristics based on water outflow could change dramatically: Lakes that currently supply outflow to downstream systems may become endorheic (with no outflow), and endorheic freshwater lakes may become saline (Schindler, 2001). The African Great Lakes are particularly sensitive to climatic effects on outflow, as current outflow is small (i.e. only 6% of water input to Lake Tanganyika leaves as riverine outflow), and even minor declines in precipitation (10-20%) are expected to completely close these basins (Bootsma and Hecky, 1993).

Changes in mean air temperatures have been shown to increase water temperatures in both temperate and tropical lakes, resulting in a range of physical and biological effects. Water temperatures in Lake Tanganyika, a deep tropical lake in East Africa, have risen by 0.2 °C at the lake bottom and 0.9 °C at 100 meters since 1913 (Verburg et al., 2003). Although the resulting change in the temperature gradient is relatively small, the vertical gradient in water density (which depends on temperature) has tripled. This sharpened density gradient has reduced annual mixing, which normally supplies nutrients from decomposition on the lake bottom to surface waters. The lack of nutrients in the upper layers of the lake has led to a 70% reduction in primary productivity since 1975 and an increase in water clarity and light penetration (Verburg et al., 2003).

Temperate lakes display sharper thermal gradients and larger seasonal changes in water temperature than tropical lakes. Lakes at higher latitudes and altitudes currently experience seasonal thermal stratification, in which they are covered by ice in the winter (with cool, relatively constant temperatures below), and develop a thermal gradient (thermocline) in the summer as surface waters warm up. Increased ambient temperatures have led to an earlier onset of thermal stratification, longer ice-free periods, and deeper thermoclines (thus smaller bottom layers) in many temperate lakes (Schindler et al., 1990). In addition, longer periods of thermal stratification with little vertical mixing results in reduced oxygen concentrations near the bottom of lakes.

Lake chemistry may be affected by climate change in a number of ways. Drought and decreased groundwater flow may make some lakes more susceptible to acidification, as groundwater often contains acid-neutralizing chemicals important to lake buffering (Schindler, 2001). However, the overall pH and chemical balance of lakes may be affected by temperature and precipitation changes in ways that are site-specific and difficult to predict; a number of European alpine lakes that experienced a 1_ C increase in temperature over 10 years actually displayed an increase in pH, as well as trends in sulfate and nitrogen concentrations that were opposite to trends in atmospheric deposition of these compounds (Sommaruga-Wögrath et al., 1997). These changes are most likely explained by increased biological activity and enhanced weathering of surrounding substrates due to high precipitation.

Concentrations of colored DOC, which derives from surrounding vegetation and provides the greatest protection from UV-B radiation, has been shown to decline in high latitude lakes as a result of climate warming, reduced streamflows, and lowered water tables (Schindler et al., 1996). Lake acidification (which can itself be caused by climate change) will exacerbate this effect (Schindler et al., 1996). Conversely, increased precipitation should increase DOC concentrations, and vegetation shifts due to climate warming (such as altitudinal shifts in the tree line) may protect higher lakes by increasing DOC concentrations (Palen et al., 2002).

Finally, the physical effects of climate change on temperate lakes can be synergistic and complex. For example, lakes at the Experimental Lakes Area in the boreal forests of

northwestern Ontario experienced an average increase in air temperature of 2°C over 20 years (Schindler et al., 1990). This resulted in an increase in mean and maximum water temperatures, an ice-free period that was 20 days longer, and an 30% increase in evaporation. The area experienced below-average precipitation and reduced runoff into lakes. More frequent fires caused a rise in nutrient input, which combined with higher temperatures to increase phytoplankton abundance and diversity. Reduced terrestrial input to the lakes (because of fires and clear-cutting) reduced DOC concentrations and led to clearer lakes with less protection against UV-B radiation. Increased solar penetration and higher winds (due to the loss of trees) led to deeper thermoclines and a reduction in bottom habitat (Schindler et al., 1990).

BIOLOGICAL EFFECTS ON LAKES

Although the effects of climate warming on the biotic communities of tropical lakes has received little attention, large decreases in primary productivity due to climate warming (Verburg et al., 2003) are likely to have a significant impact on the rest of the food chain. In temperate lakes, the radical physical changes in lake chemistry and thermal stratification resulting from climate change can have a range of effects on biological communities. As temperate freshwater fisheries play an important economic role in many countries, a great deal of research into the effects of climate change on freshwater ecosystems has focused on temperate freshwater fish.

Temperate fish can be divided into three major guilds according to their “fundamental thermal niche”, or the temperature at which they choose to spend most of their time and at which they experience optimal growth, activity levels and swimming performance (Shuter and Meisner, 1992): coldwater fish such as salmon and trout (with an optimal temperature around 15° C), coolwater fish such as perch (with an optimal temperature around 24° C), and warmwater fish such as carp and catfish (with an optimal temperature around 28° C).

Seasonal thermal stratification in lakes allows all three guilds to co-exist because of variations in life history strategies (Shuter and Meisner, 1992). In the winter, cool- and warmwater fish are inactive, and cold water fish are active but experience little growth. Temperatures are optimal and growth rates highest for coldwater fish in the spring and fall, while the summer is optimal for cool- and warmwater fish. During the summer, the upper layers of the lake become too hot for coldwater fish and they are restricted to the cooler bottom layer, where oxygen levels are low and competition for food is fierce.

Because climate warming leads to longer periods of thermal stratification, coldwater fish will be restricted to these bottom layers for longer periods of time, and deeper thermoclines brought about by climate change may reduce the area of bottom layers and further intensify competition for food (Shuter and Meisner, 1992). Climate change may also lead to shorter spring and fall seasons, when temperatures are optimal for coldwater fish. An overall rise in water temperatures will lead to increased metabolic demands, but coldwater fish will generally have reduced access to prey. Warmer temperatures may

make winter slightly more favorable, but not enough to compensate for losses during other seasons (Shuter and Meisner, 1992). Overall, coldwater fish are likely to experience decreased growth rates and increased heat mortality (Tyedmers and Ward, 2001).

Some populations may be able to adapt to thermal changes; a shift in preferred temperature from 15° C to 20-21° C has been observed in one population of lake trout (*Salvelinus namaycush*) in Canada (Sellers et al., 1998), and other populations of coldwater fish display adaptive behavior, in which they spend most of their time in coldwater refugia but make occasional feeding forays into warmer water (Snucins and Gunn, 1995). However, the majority of coldwater fish populations are likely to experience range shifts, with contractions near the low-latitude and low-altitude limits of their current range, and expansions to higher latitudes if migration is possible. Suitable habitat for coldwater fish in the continental United States may decline by as much as 50% (Eaton and Scheller, 1996), and range contractions of coldwater species could eliminate some of the world's most valuable fisheries (Schindler et al., 1990).

Conversely, however, climate warming and changes in thermal stratification may have positive effects on cool- and warmwater species, reducing winter kills, lengthening the growth season, and increasing available habitat, both locally and regionally, if poleward migration is possible (Shuter and Meisner, 1992). If lakes are not nutrient-limited, productivity is likely to increase (due to increased primary productivity and growth rates); overall fish catch may increase, but there are likely to be changes in the relative abundance of fish species (Tyedmers and Ward, 2001).

Finally, although most studies examine the effects of climate change on only a few species of fish, negative effects on one species can have an impact on the entire community. For example, a summer kill of planktivorous herring in a Wisconsin (USA) lake reduced predation on zooplankton by 50%, which led to an increase in large zooplankton and intensified zooplankton grazing, causing a substantial reduction in phytoplankton abundance (Kitchell, 1992). In addition, while many studies concerning lake water level focus on the effects of declining levels, rising water levels due to regional or seasonal increases in precipitation could also have negative impacts. In Lake Baikal, for example, the construction of a dam along with increased precipitation led to a 1.5 meter rise in the level of the lake, and a subsequent decline in fish biodiversity and production (Izrael et al., 1992).

Effects of climate change on rivers

The effects of climate change on rivers are likely to vary widely depending on latitude. Temperate rivers, like temperate lakes, will be affected primarily by temperature changes, while changes in precipitation timing and quantity could have dramatic effects on tropical rivers.

PHYSICAL EFFECTS ON RIVERS

Increases in air temperature will strongly influence water temperature in many rivers (particularly smaller rivers and streams) because the surface to volume ratio of rivers is

high (Tyedmers and Ward, 2001). Increasing air temperatures will result in warmer water throughout rivers, from the headwaters to the mouth, as well as reduced oxygen levels. Rivers that are fed primarily by groundwater will be buffered against increasing seasonal variability in temperature (as groundwater temperature generally equals average annual air temperature), and may serve as thermal refugia in some areas, supplying relatively cooler water during hot seasons and warmer water during cold seasons.

Temperate rivers experience seasonal thermal cycles similar to temperate lakes, with uniform cold temperatures in winter (sometimes accompanied by ice cover) and longitudinally stratified temperatures in summer, with lower temperatures at groundwater-fed headwaters and higher temperatures downstream (Shuter and Meisner, 1992). High latitude rivers are already experiencing shorter periods of ice cover and earlier ice break-up (Magnuson et al., 2000), and many of the beneficial functions of ice jams (river scouring, changes in river channel morphology, flooding of riverine wetlands) may be compromised.

Flow regime is a critical component of river ecosystems. Mean flow may increase or decrease depending on changes in average precipitation, evaporation, soil moisture, and groundwater recharge, but seasonal shifts in flow may be more significant to freshwater ecosystems (Carpenter et al., 1992). Many rivers will experience altered timing or duration of high and low flows due to changes in seasonal variability of precipitation, frequency of extreme precipitation events, and timing of snowmelt. Spring snowmelts are likely to occur earlier due to warming, and winter flows are likely to increase in areas where winter precipitation falls as rain instead of snow. A shift in peak flows from spring/summer to winter will reduce the cooling effect of snowmelt on summer river temperatures (Tyedmers and Ward, 2001).

Where precipitation increases, stream flows may increase in volume and floods may become more frequent. Extreme flooding events and landslides could remove important woody debris from rivers and destabilize river channels (Carpenter et al., 1992). Where precipitation decreases, stream flow volume may also decrease, and reductions in runoff will lower the concentrations of DOC and organic matter in rivers. Increased evaporation could also lead to reduced streamflow, even in the absence of precipitation changes. Summer and ephemeral streams in arid regions (which provide critical habitat for many animals) are more vulnerable to drying up. A reduction in natural flooding events could eliminate many of the beneficial physical effects of seasonal flooding, such as creating floodplain habitat, displacing exotic plants, and determining river channel form.

BIOLOGICAL EFFECTS ON RIVERS

In tropical rivers, variations in air and water temperature are generally small, and water temperature is mainly regulated by shade and rainfall, rather than by cool groundwater refugia. The rainy and dry seasons of the tropics lead to large, predictable seasonal variations in precipitation and annual flooding of adjacent grasslands and forests, which provide abundant food and breeding grounds for fish. Thus, the life histories of tropical

river fish are more strongly affected by changes in water level than by changes in temperature (Meisner and Shuter, 1992). As the rainy season draws to a close and floodplains dry up, members of the “whitefish” guild, who are sensitive to reduced oxygen levels, retreat to the main river channel with the receding floodwaters. “Blackfishes”, who are more tolerant of or adapted to low oxygen levels, remain in marginal floodplain habitats that become disconnected from the river and may even dry up completely (Welcomme, 1979). Some of these species, such as the lungfishes, are able to aestivate (coocon in the mud) and breathe air when their water supply evaporates.

Climate change may affect the both the timing and extent of flooding in tropical rivers, although these effects are currently difficult to predict and will vary regionally. According to some estimates, the tropics will experience the smallest change in temperature, but the largest changes in precipitation, with rainfall becoming more variable, both within and between years (Houghton et al., 2001). Changes in floodplain dynamics will directly affect fish populations and fisheries yield, as growth rates and overall fish catch is correlated with the area of flooded land (Meisner and Shuter, 1992; Welcomme and Hagborg, 1977).

Fish communities in temperate rivers will experience effects similar to those in temperate lakes. Coldwater fish that are restricted to cool refugia at headwaters during the summer will experience increased competition, reduced growth, and possible range shifts (Shuter and Meisner, 1992). Warmer water and decreased oxygen content at headwaters may have negative impacts on eggs and larvae often placed there (Carpenter et al., 1992). Diadromous stocks that migrate long distances during the peak of summer may experience higher rates of pre-spawning mortality because of increased metabolic needs and disease outbreaks (Tyedmers and Ward, 2001). Even in stocks that do not perform summer migrations (such as the Adams River sockeye salmon) climate change is likely to result in a net population decline due to reduced juvenile emergence, growth and survival (Henderson et al., 1992). Some invertebrates in northern rivers require a prolonged period of exposure to nearly 0°C water, followed by spring warming, in order for eggs to hatch. The release of warmer water in the winter from dams has resulted in massive local extinctions of invertebrates for tens of kilometers downstream (Lehmkuhl, 1974), and overall river warming would be expected to have a similar effect.

Effects of climate change on wetlands

PHYSICAL EFFECTS ON WETLANDS

Increased air temperatures are likely to have a drying effect on many wetlands, unless increased precipitation compensates for evaporation. Shallow and ephemeral habitats, such as depressional wetlands (with no channelized flow in or out) or wetlands in arid areas could be lost entirely, especially if precipitation declines and groundwater is extracted for human needs (Gitay et al., 2001). Overall, a drier climate is likely to lead to contractions and loss of wetland habitat, as well as increased habitat fragmentation. Conversely, increased precipitation could lead to flooding, expansion and deepening of wetland habitat, and increased connectivity. However, increased precipitation or ex-

treme flooding may also lead to an increased input of sediment and pollutants, and could destroy some wetlands if vegetation or other important habitat features are completely submerged.

Arctic and subarctic bogs located over permafrost could suffer dramatic changes in hydrological regime if rising temperatures lead to permafrost melting and wetland drainage. Increased decomposition in thawed northern peat bogs, as well as the increased risk of catastrophic fires due to drier peat, could release large amounts of carbon dioxide into the atmosphere, contributing to further global warming (Gorham, 1991)

Coastal freshwater wetlands are particularly sensitive to extreme high tides resulting from an increase in storm frequency or magnitude; these high tides can carry salts inland to salt-intolerant vegetation and soils, and could lead to the displacement of freshwater flora and fauna by salt-tolerant species (Michener et al., 1997). Rising sea levels could destroy coastal freshwater wetland communities as saline water invades, especially if these communities cannot shift inland due to development or dikes (Tyedmers and Ward, 2001). Salt water inundation of coastal freshwater wetlands is expected to cause significant loss of wetland habitat in Australia and elsewhere (Gitay et al., 2001).

BIOLOGICAL EFFECTS ON WETLANDS

Ephemeral, depressional wetlands, especially those in arid areas, often harbor rare species that would be lost if these areas dry up. For example, several endemic species of fairy shrimp in California (USA) that are already severely threatened by habitat loss (Belk and Fugate, 2000) could disappear if reduced precipitation and increased evaporation eliminates their shallow, vernal pool habitats.

Small, temporary wetlands are the most numerous types of wetlands in many landscapes, and are often used by more species than permanent ponds (Gibbs, 1993; Semlitsch et al., 1996; Semlitsch and Bodie, 1998). The drying and loss of wetlands would reduce not only the number and size of available ponds, but also increase inter-pond distance (Gibbs, 1993; Semlitsch and Bodie, 1998), lowering the chances of amphibian recolonization, since adult frogs are generally only capable of traveling 200-300 m (Sjogren, 1991; Skelly et al., 1999). Drying and loss of wetlands would also reduce habitat connectivity on a regional scale, endangering migrating birds that depend upon a network of wetlands along their migration route (National Research Council, 1995).

Wetlands in areas with increased precipitation might suffer fewer negative effects, and may even benefit from increased wetland area and connectivity. However, some rare species that are adapted to drier, ephemeral wetlands may not be able to compete with invading species adapted to wetter habitats (National Research Council, 1995), and wading birds that require shallow water to feed may experience reduced access to feeding areas (Butler and Vennesland, 2000). Wetter, more permanent wetlands would support more fish, which prey on vulnerable tadpoles and invertebrates that usually inhabit seasonal wetlands with less predation pressure (Semlitsch and Bodie, 1998).

General Considerations for Designing and Managing Freshwater Reserves to Withstand Climate Change

The likelihood that individual species or communities will be able to persist in the face of global climate change depends to a large degree on how resistant (able to withstand change) and resilient (able to recover from change) they are (Noss, 2001). Because there is still a great deal of uncertainty associated with climate change predictions (especially predictions of precipitation changes), and interactions between physical and biological features of freshwater ecosystems can be complex and non-intuitive, focusing on increasing system resistance and resilience is a far better approach than trying to plan for a specific set of predicted changes. Many common considerations in designing and managing ecosystem reserves, such as preserving biodiversity and minimizing outside stresses, will also help increase the resistance and resilience of communities to climate change. Additional considerations that are unique to freshwater ecosystems will become increasingly important in buffering systems against growing climatic and water extraction pressures.

Preserve habitat heterogeneity and biodiversity

Both species and habitat diversity increase resistance and resilience to climate change, as diversity provides a greater range of stress tolerances and adaptive options (Chapin et al., 1997). Diverse communities that have redundant species within functional groups should be more resistant to climate change because there are likely to be differences in environmental sensitivity among members within each group; functional group richness also appears to increase resistance to environmental change (Noss, 2001). High biodiversity areas may also become important as sources for re-colonizing damaged sites or colonizing new ones as the effects of climate change become more severe (De Groot and Ketner, 1994).

In aquatic systems, high biodiversity is often found in older or isolated habitats, in sink-holes, caves or underground habitats, and in areas with high habitat heterogeneity—especially dynamic habitats with seasonal changes in water level (i.e. river floodplains of seasonal wetlands; Abell et al., 2002). Many of these areas also harbor rare species, such as endemic species that have evolved in and remain restricted to a particular habitat (i.e. communities of endemic cichlid fish in African rift lakes), relict species that were restricted to isolated habitats after previous range contractions (i.e. cold stenothermic fish that were isolated to high latitude lakes after the last ice age), or species that are highly adapted to unusual environments (i.e. cave-dwelling fish and invertebrates). In protecting some of these high biodiversity sites, rare or vulnerable species may also be protected (often a primary consideration in reserve design). Protecting rare species, especially those that are charismatic, can assist in drawing public attention and funding to conservation efforts, but strategies aimed solely at protecting one species may detract from the more desirable goals of protecting ecosystem function (Junk, 2002) and increasing resistance and resilience to climate change.

Areas where natural physical barriers separate biota (i.e. impassable waterfalls), and transition zones between different habitats or ecosystems may also harbor high biodi-

versity (Abell et al., 2002). Protecting transitional zones has the added benefit of accommodating possible range shifts due to climate change, and can help preserve diverse habitat types. Protecting a variety of potential habitats may help increase resistance and resilience in vulnerable species; for example, protecting an array of natural ponds with a wide range of sizes and hydroperiods will help ensure that amphibians have access to suitable breeding sites regardless of climatic variation (Semlitsch, 2002). If possible, replicate sites of a particular habitat type should be protected to safeguard against the complete loss of critical species or communities if one site is damaged beyond repair by an extreme climatic event (Markham and Malcolm, 1996; Roberts et al., 2003).

Although diverse communities may be more resistant and resilient to climate change, it is important that high biodiversity not be used as the sole criterion in selecting sites for conservation. An equally important goal is protecting communities that perform valuable “ecosystem services” (Kareiva and Marvier, 2003), such as relatively low-diversity wetlands that provide flood protection, water filtration and other services that are likely to become increasingly important as climate variability and extreme events increase. Protecting sites with lower biodiversity also helps maintain functioning ecosystems over broader regions of the globe, and preserves distinct evolutionary lineages that can provide fuel for future evolutionary innovation (Kareiva and Marvier, 2003). Preserving sites harboring high biodiversity can still be a valid conservation goal in many areas, and diversity indices can be extremely useful in choosing between different sites *within* a habitat type (rather than using biodiversity indices as an absolute guide in choosing *between* different habitats). However, considering ecosystem services and other potentially beneficial features of low diversity sites is an important aspect of planning for climate change.

Protect physical features rather than individual species

Aquatic ecosystems differ from many other ecosystems in that they are usually governed by “bottom-up” rather than “top-down” dynamics—in other words, much of ecosystem function is determined by basic physical features such as water flow, channel morphology, and nutrient balance, rather than by species assemblages (Moss, 2000). Protecting flow patterns, water quality, and water quantity will go a long way towards protecting biodiversity in freshwater habitats (Abell et al., 2002), whereas conservation efforts that focus solely on preserving particular species or groups of species without considering wider physical features of the system may be doomed to failure. In many cases, the function of a species in a freshwater ecosystem is actually more important than its identity; for example, plants are essential components of some aquatic habitats (i.e. floodplain vegetation and aquatic plants in shallow lakes), but the exact species of plant may be less important than the physical features it provides (Moss, 2000).

The physical features of rivers, lakes and wetlands are expected to undergo a number of changes as a result of climate warming and precipitation variability. Removing barriers to water flow, maintaining healthy, forested river basins, and reducing the input of nutrients and toxic substances will increase the likelihood that freshwater ecosystems will be able to adjust to climate change. For example, removing levees and other barriers to the

lateral expansion of rivers could prevent the loss of critical edge habitats and the species that depend on them, by allowing new floodplains to be established if average river flows increase or extreme precipitation events become common.

Preserve habitat connectivity to allow access to migration routes and thermal refugia

Connectivity is an important feature of many freshwater ecosystems, as it can help preserve flow regimes, promote ecological integrity, and allow migrating animals to move between different habitats at various life history stages. Connectivity is important not only between different freshwater habitats (i.e. between rivers, lakes, and wetlands), but also along the length of rivers, and between freshwater habitats and subterranean systems or groundwater sources (Abell et al., 2002). Maintaining connectivity will become even more important in some areas as the effects of climate change increase, because connectivity may provide animals with access to thermal refugia, or allow them to migrate to more suitable habitats.

Although some species may be able to adapt to climate change in their current habitats, warmer waters will force other species to move into cool, thermal refugia, where temperatures remain below their thermal tolerance limits and metabolic demands are lower. Many species (i.e. coldwater fish) already rely on thermal refugia at certain times of the year, and these species are likely to become even more dependent on these refuges for year-round survival. Headwaters of rivers and any areas where temperature-buffered groundwater enters a system should be protected, and vegetation over bodies of water should be maintained to provide cooling. Maintaining or increasing connectivity between cool refugia and the rest of an ecosystem should be considered, as this may help provide additional species with access to these areas.

In many cases, where thermal refugia do not exist or other climate-related changes make an animal's environment uninhabitable, the only option may be migration to more suitable habitats. Because migration of aquatic animals is already severely limited by the direction of connections between water bodies, preserving or improving the possible migration corridors that do exist may be important in some cases. Rivers and other aquatic ecosystems that allow movement in the north-south direction, as well as freshwater systems spanning altitudinal gradients are particularly valuable migration corridors. In addition, areas near the current range limit of species should be protected (in the direction of expected migration; Markham and Malcolm, 1996). Consideration should be given to protecting areas that are currently not of interest, but that species are likely to migrate into, or marginal habitats (i.e. areas that are too cold for most species) that are likely to be improved by climate warming.

Although maintaining connectivity between habitats and ecosystems may have a number of beneficial effects in terms of allowing native species to adapt to climate change, the increasing threat of invasion by exotic species (see section 3.4) makes connectivity in aquatic systems a more complicated issue. Because invasion by exotic species can potentially have devastating effects on ecosystems, the risks of invasion should be weighed

on a site-by-site basis against the vulnerability of native populations to climate change, and the necessity and feasibility of migration to other habitats. In cases where species are particularly sensitive to temperature changes and are likely to experience local extinctions due to thermal stress, and where migration corridors leading to more suitable habitats exist, the benefits of connectivity may outweigh the risks of invasion. In other areas, however, the risks of invasion may be so severe that allowing one sensitive species to be lost would be preferable to endangering the entire community.

Protect sites from human pressures and exotic species

Protecting reserves from outside stresses (particularly stresses that tend to reduce diversity) will become increasingly important as local climates become more variable, because stressed systems display reduced resistance and resilience to change (Noss, 2001). Human stresses, such as overexploitation and poor land use practices, should be reduced as much as possible. In choosing between a group of candidate sites for new reserves, it may sometimes be advisable to avoid sites that are already severely degraded or likely to be subject to intense human pressure (Roberts et al., 2003), although restoration of some ecosystem functions is possible (see section 3.6).

It is also critical to increase efforts to prevent access of invading species to reserves, and to eliminate or control harmful non-native species already present. Many systems are likely to become more vulnerable to invasions, as thermal barriers that previously excluded invaders will be removed, and communities that are already stressed by climate change are invaded by warmer-adapted species (Carpenter et al., 1992; Schindler, 2001). Even in sites that are well-protected from all other stresses, non-native species can wreak havoc on biological communities; for example, native fish populations in the nearly pristine Blindekloof River in South Africa have been nearly devastated by invading largemouth bass (Skelton et al., 1995).

Unfortunately, in some systems, preventing access of motile, invasive species may conflict with the goal of maintaining connectivity to allow seasonal or climate-induced migrations. Isolating vulnerable habitats from other freshwater ecosystems may be feasible in some cases, but building barriers that disrupt flow to prevent access of exotic species may do more harm than good. In cases where the risk of invasion is relatively low and migration is important to resident species, maintaining current levels of connectivity while enacting careful monitoring of ecosystems (to allow early, aggressive management responses to invaders) may be a suitable approach.

Manage entire watersheds and regulate extractive water use

Freshwater ecosystems are intricately connected to their drainage basins, and downstream or lowland rivers, lakes and wetlands can be extremely sensitive to distant, upstream disturbances. Deforestation, agriculture, and other pressures on terrestrial communities that drain into water bodies can alter the quality, quantity, and temperature of water in all freshwater systems downstream of the disturbance.

Because freshwater ecosystems are so intricately connected to one another and to the terrestrial systems that surround them, common reserve considerations such as reserve size and buffer zones are less applicable. For example, Kruger National Park in South Africa is a very large reserve that protects significant downstream portions of the rivers that flow through it; however, populations of several species of fish that are protected within the park have declined as a result of upstream activities outside of the reserve (Skelton et al., 1995). Although reserve size and buffer zones may be applicable in limited, small-scale cases (i.e. no-take fishing areas and buffer zones to protect seasonal breeding grounds in Lake Tanganyika; Abell et al., 2002), protected habitat patches will generally provide only short-term solutions. Freshwater reserves will not be secure unless upstream threats are removed by managing (or in rare cases protecting) the entire drainage basin (Moss, 2000).

Managing entire watersheds rather than simply protecting aquatic elements or habitat patches will become increasingly important as the effects of climate change intensify and are magnified by interactions with human stresses. Human population growth is likely to lead to increased deforestation, agriculture, industrial development, and urbanization within watersheds. Models of land use and climate change in South Africa predict that abrupt, future changes in local land use will have a far greater impact on freshwater hydrology than gradual effects of climate change (Schulze, 2000). Importantly, the stresses caused by these habitat alterations often exacerbate the effects of climate change. For example, deforestation near freshwater ecosystems eliminates cooling, vegetative cover over streams and reduces the input of large, woody debris. The loss of shading further increases water temperatures that are already rising due to global warming, and the lack of large, woody debris eliminates in-stream refugia. In addition, the loss of forest cover may lead to increased terrestrial and aquatic evaporation, and reduced soil moisture and water infiltration. During heavy precipitation events, streams already experiencing unusually high flows would receive increased runoff due to low soil infiltration, as well as increased inputs of sediments and pollutants.

Perhaps even more important than projected increases in habitat alteration are the dramatic projected increases in human water extraction. Population growth will lead to increased water extraction for agricultural irrigation, direct consumption, and industrial development. Increasing human water extraction is likely to be one of the primary stresses on freshwater ecosystems in coming years, and is expected to greatly outweigh global warming in affecting water supply through at least 2025 (Vörösmarty et al., 2000). Increasing human water demands on freshwater ecosystems that are particularly sensitive to climate change are likely to lead to more frequent water shortages and conflicts over water use. For example, Egypt relies on the Nile river basin for over 95% of its national water budget. Based on one scenario of global climate change, models predict that a modest decline in precipitation (20%) and rise in air temperature (4°C) would nearly halt flow of the Nile (98% flow reduction; Strzepek et al., 1996), and human demands would be likely to outweigh ecosystem needs in determining the fate of the re-

maintaining water. Clearly, management schemes aimed at protecting freshwater ecosystems from climate change must take human water needs into account, and attempt to manage the timing and magnitude of water extractions.

Restore degraded sites and consider performing active interventions in response to climate-induced threats

Because freshwater ecosystems are strongly influenced by activities in the surrounding landscape and increasing amounts of water are being extracted for human needs, most drainage basins have already experienced some degree of degradation. Restoration of degraded sites holds great promise for freshwater ecosystems, in terms of both improving the ecological integrity of damaged systems (thus increasing resistance and resilience to future change), and providing tools to smooth the recovery of ecosystems from future damage caused by climate change (McCarty and Zedler, 2002). Successful restoration techniques include neutralizing acidified lakes and rivers by applying lime (Schindler, 1997; Appleberg, 1998), and restoring the hydrology of wetlands by removing impediments to flow (Gilbert and Anderson, 1998). Exotic species such as predatory game fish have been successfully removed from some freshwater systems (McNaught et al., 1999), but in many cases, controlling aquatic community composition has proven difficult (McCarty and Zedler, 2002). All of the ecosystem problems mentioned above could potentially be caused or exacerbated by climate change (i.e. lake acidification, changes in hydrology, invasions of exotic species), and lessons learned from current restoration projects can help guide future responses to climate change. However, it is important to keep in mind that restoration efforts are unlikely to be successful after certain thresholds of damage have been crossed, such as the collapse of fisheries or permanent cultural eutrophication of lakes (McCarty and Zedler, 2002).

Rather than attempting to restore systems after they have already been degraded by climate change, it may be possible to perform active interventions to ameliorate the effects of climate change or to directly protect vulnerable species. Adding to water tables below drying wetlands or draining excess water from flooded habitats has been proposed (De Groot and Ketner, 1994), and inter-basin transfers of water have been suggested as a possible adaptation to climate change in Africa and South America (Pringle, 2000; Smith and Lenhart, 1996). However, interbasin transfers result in the intermixing of diverse faunal communities that were previously isolated, and may have unforeseen effects on native communities (Davies et al., 2000). In addition, tropical rivers and lakes (for which many of these projects have been proposed) are particularly vulnerable to the negative effects of interbasin transfers (Pringle, 2000). Flow conditions below dams could possibly be manipulated to relieve some of the negative effects of climate change, for example by releasing bursts of water to simulate flooding events (Middleton, 1999; Vaselaar, 1997) or releasing water from multiple reservoir layers to control temperature (McCarty and Zedler, 2002). However, although these actions may help alleviate some of the negative effects of climate change on systems already impacted by dams, erecting dams solely to control water flows would cause far more damage to the ecosystem than the original alteration in flow regime caused by climate change.

Some of the more controversial suggestions put forward for helping species and communities adapt to climate change involve transplantation of animals. Although protecting severely threatened species *ex situ* (i.e. in zoos or aquaria) until a suitable habitat for reintroduction becomes available (Noss, 2001) is a sound idea, using artificially-aided dispersal to move aquatic creatures over watershed boundaries to cooler waters (Gitay et al, 2001) could lead to the extinction of existing fauna, as the transplanted species would be pre-adapted to warming waters and could have a range of unanticipated effects on the native community. Similarly, the often-devastating effects that non-native fisheries stocking can have on native fauna would seem to make introducing better-adapted non-native species to replace waning stocks (Gitay et al, 2001) a bad idea. Transplanting vulnerable species to new, created habitats where no native community exists (i.e. uninhabited, enclosed basins) would eliminate the risk of damaging existing biotic communities (McCarty and Zedler, 2002), but creating functioning, self-sustaining ecosystems from scratch is likely to prove difficult. Re-introduction of species to their native habitat may be a useful approach in cases where an extreme weather event destroys existing populations (De Groot and Ketner, 1994).

Use adaptive management strategies to maintain flexibility

Because many aspects of climate change are unpredictable and climatic variability is likely to increase, it is critical to maintain flexible conservation goals and strategies. Rather than striving to maintain current distributions of species and preserve current ecosystems, managers should allow for and even assist in the adaptation of species and communities. Static management practices with fixed policies designed to protect particular species should be changed to adaptive management strategies aimed at protecting ecosystem processes (Markham and Malcolm, 1996).

Adaptive management is based upon the recognition that uncertainty is inherent in all natural processes, and the expectation that management practices will change over time (Parma et al., 1998). Passive adaptive management involves adjusting management practices based on what is learned from the results of past practices, but learning about the underlying system is not an explicit goal. In contrast, active adaptive management is somewhat like performing a (hopefully) well-designed experiment; it involves forming multiple hypotheses about how the system will respond (to climate change and/or management practices), choosing strategies to systematically test and learn about the underlying hypotheses, monitoring systems closely to evaluate responses, and adapting future management practices based on what was learned about the system. The rationale behind this approach is that we cannot hope to understand the complex systems we are supposed to be managing without experimenting on them (Parma et al., 1998). Management practices in which a single (often arbitrary) strategy is chosen teach us little about the underlying system, and it is often impossible to know exactly what aspects of the strategy led to its ultimate failure or success.

Obviously, there are some cases where experimenting with the response of a system is not an option; some strategies may be irreversible, or may be too risky if populations are

already endangered (Parma et al., 1998). However, adopting active adaptive management practices now, while the effects of global climate change are only beginning to be felt in many areas, may provide enough time to learn about the underlying processes governing how a particular system responds to change, and provide an understanding of how to best manage the system in the face of global climate change.

Selecting and implementing adaptation strategies for your particular location

The previous section illustrates some of the conflicts that may arise in choosing a management strategy to sustain freshwater ecosystems in the face of global climate change. For example, should the focus be on protecting high-diversity sites that are more likely to be resistant to climate change, or on protecting low-diversity sites that perform ecosystem services that will become more valuable as climate change continues? Should connectivity between habitats be maintained or even increased to allow migration, or should habitats be isolated to prevent invasion by exotic species? Applying a general list of conservation goals (such as those discussed in section 3) blindly to a freshwater ecosystem ignores the specific strengths and weaknesses of the system, and does not account for the relative importance of various threats. Performing a careful, site-specific analysis that takes all known factors into account and evaluates how to best meet conflicting goals is likely to be the best approach to designing a successful adaptation strategy.

Characterize and monitor species/systems that are most vulnerable to climate change to determine the scale of conservation needs

One of the most important steps in selecting an adaptation strategy for climate change is to characterize which life history stages, species, communities, or physical features in your location are most vulnerable to changes in average climate, changes in climate variability, or extreme events (Solomon, 1994). This can help determine the scale of management that is necessary. For example, if only one species of coldwater fish in a series of lakes is declining and the rest of the community appears to be resistant to climate change, a small-scale conservation strategy such as protecting thermal refugia and maintaining potential migration corridors to pristine lakes at higher altitude may be sufficient. However, if increased precipitation and runoff from deforested, agricultural lands is causing a dramatic increase in sediment load and nutrient content, along with large-scale changes in species composition, distribution and abundance, a more ambitious basin-wide management plan may be called for.

Attempting to predict which species will be most vulnerable to climate change before large effects are observed can be very useful, as initiating careful monitoring before effects are noticeable will provide a baseline against which future changes can be compared. While predicting exactly how species will respond to change can be difficult, numerical methods that combine assessments of climatic sensitivity (thermal tolerance, etc.) with general vulnerability (life history traits, current knowledge of the species, taxonomic uniqueness, overexploitation) may help highlight species for further consideration (Her-

man and Scott, 1994). Identifying and protecting keystone species is also important in order to prevent cascading effects that would alter the entire community (Noss, 2001).

Performing careful and continuous monitoring of both biological and physical indicators of change is critical, as reactions to climate change can be delayed in many plants and animals. For example, directly monitoring the water table and hydrology of temperate wetlands may be critical in preventing habitat loss, because by the time the vegetation shows a response to environmental change it may already be too late to save the system (Solomon, 1994).

Develop strategies for protecting freshwater ecosystems while dealing with increasing human water needs

A serious potential threat, and one unique to aquatic ecosystems, is the anticipated rise in human water needs, mainly due to population growth and increasing development. Pressures caused by water extraction and climate change will almost certainly interact, exacerbating the effects of climate change on ecosystems and possibly increasing human water needs further due to increased temperatures and evaporation. Proposed adaptation strategies for human water resource management include “demand-side” adaptations, such as price incentives for conserving water, enforceable water efficiency standards, and increased irrigation efficiency, as well as less environmentally-friendly “supply-side” adaptations, such as building more dams (Arnell et al., 2001). The Intergovernmental Panel on Climate Change recommends using Integrated Water Resource Management (IWRM) to adapt to increasing water resource demands (Arnell et al., 2001). In this process, all stakeholders are included in potential considerations of supply- and demand-side actions before a decision is made, and the situation is continuously monitored and re-evaluated. Unfortunately, IWRM does not consider maintaining aquatic ecosystem function as one of the goals of water management (i.e. aquatic ecosystems are not considered a “stakeholder”); environmental damage is only included as a potential negative side effect of some actions.

A vast improvement over this water management strategy in terms of maintaining ecosystem health is ecologically sustainable water management, which strives to protect the ecological integrity of freshwater ecosystems while meeting current and future human needs for water (Richter et al., 2003). This strategy has been applied primarily in cases where one or more large dams already exist on a river and there are conflicts between increasing human water extraction and ecosystem flow needs, a problem that is likely to become more common in the future due to climate change. Methods of addressing water conflicts commonly include altering patterns of surface and groundwater extraction, increasing efforts to improve water efficiency, and changing temporal patterns of water release from dams. All stakeholders are involved in the process of estimating ecosystem flow requirements (seasonal base flows, high and low flows, rates of rise and fall), determining current and future human water needs, identifying incompatibilities (i.e. in seasonal or regional needs), and collaboratively searching for solutions. A critical component of this management strategy in terms of adapting to climate

change is the inclusion of short-term management experiments (i.e. injecting treated wastewater back into groundwater reserves) to test the effectiveness of various management options as climate change continues to alter water flows, ecosystem needs, and human water demands. The method also calls for the development of an on-going adaptive management strategy to continuously monitor and respond to ecosystem changes.

This method has proven effective in many cases, such as in the management of the Green River Dam in Kentucky, USA (Richter et al., 2003). This dam was managed to provide recreational opportunities in the reservoir during the summer and water storage capacity to protect against flooding during the winter. As a result, large quantities of water were released from the dam during the fall, which biologists believed were disrupting downstream prey aggregations and dispersing mussel larvae during the fall breeding season. After examining ecosystem and human needs and identifying the incompatibilities (mainly related to the large outflow of water in the fall), the management of the dam was altered to release a steady, low volume of water throughout the fall, along with big bursts in November coinciding with natural storm events. The reservoir level was still lowered before the winter, when large storms could cause flooding, and the new schedule provided a more natural flow regime for downstream wildlife (Richter et al., 2003). This case provides an especially “tidy” example of ecologically sustainable water management (particularly because human water extraction was not a major issue), but the method has also proven effective in far more complicated cases where multiple governing bodies were involved and the goals of various stakeholders differed widely (Richter et al., 2003).

Perform Integrated River Basin Management to buffer systems against climate change and provide a basis for long-term conservation

Although a primary goal of ecologically sustainable water management is maintaining the ecological integrity of freshwater systems, the main focus is on managing the water itself. As described in [section 3.22](#), freshwater ecosystems depend on more than just the water they contain—rivers, lakes and wetlands are intricately connected to all of the terrestrial systems within the drainage basin surrounding them. To protect freshwater ecosystems that are showing large-scale changes in response to climate change, or systems that are likely to be vulnerable (due to land alteration or other anthropogenic stresses), the entire drainage basin must be managed.

One-sided decisions to adopt fixed river basin management plans are likely to fail if unexpected climatic changes occur. For example, the tri-nation development authority in charge of the Senegal River basin in the Sahel region of West Africa initiated a plan several decades ago to convert large areas of the river basin to irrigated rice production, in an effort to reduce the countries’ dependence on foreign imports. Two dams were constructed to provide irrigation water, but during the 1960’s, the Sahel began to experience a severe and long-term drought that current climate models suggest may be permanent (Venema et al., 1997), constraining the amount of water available for flooded rice paddy agriculture. Over the last several decades, the basin has suffered increasing desertifica-

tion, due in part to climate change and in part to the abandonment of cleared rice paddies. As a result of water shortages and river basin degradation, large numbers of local residents have migrated to urban areas. Proposed changes in river basin use include switching from industrial rice production back to local, village-based agriculture utilizing cereal and grain crops with low irrigation needs, as well as a more ambitious plan to convert areas of the basin to agro-forestry, which involves mixed vegetable production within plots of reforested land; this reforestation would help lower air and water temperatures, and halt desertification. The reforestation plan also recruits unemployed urban residents in an attempt to reverse recent patterns of massive demographic shifts to urban areas (Venema et al., 1997).

In order to avoid the necessity of restoring river basins that have been severely degraded by climate change and failed management, the basin-wide needs of ecosystems and local communities should be considered, as well as the potential impacts of future climate change, before enacting any management plan. Integrated River Basin Management (IRBM) is a method of balancing basin-wide ecosystem needs with human water resource needs to achieve economic, social, and environmental goals. One of the major problems with basin-wide management is that many river basins cross national boundaries; worldwide, there are 261 major transboundary rivers that drain 45% of the Earth's surface, account for 80% of the planet's river flow by volume, and are home to 40% of the world's population (WWF, 2002). Transboundary rivers can make water management more difficult, but management of these systems is essential to future economic and political stability.

With IRBM, the needs and expectations of all "water stakeholders" (local community members, civil authorities, water and fishery resource managers, scientists and conservationists, and representatives of the private sector) from all countries are assessed jointly, a basin-wide authority is created, monitoring methods are developed, and an adaptive management plan is initiated (WWF, 2002). Decisions can be made locally, but must be in accordance with basin-wide strategy. Key aspects in determining the success or failure of IRBM are actively promoting public involvement (through appropriately-scaled local discussions suited to the target audience) and ensuring sustainable funding for the basin-wide authority (often through water taxes, reductions in water subsidies, or international funding programs). Because it employs adaptive management strategies, IRBM is able to continuously respond to the effects of climate change. In addition, because management is basin-wide, IRBM provides the ability to protect climatic refugia and areas that are particularly vulnerable to climate change, as well as to minimize damaging land use practices and other human stresses that are known to interact with and exacerbate the effects of climate change.

Although system-wide conservation can present difficulties in terms of reaching consensus, and can be costly and slower to achieve noticeable results than local campaigns to preserve endangered species, system-wide approaches ultimately conserve the functional value of the river basin and provide a sustainable basis for future conservation

(Moss, 2000). Successful IRBM in Costa Rica, in which fossil fuel taxes and payments from a private hydro-electric plant compensate upstream landowners for the maintenance and restoration of forest cover, has improved water quality and quantity for downstream towns, farms, and industries, and reduced sediment accumulation at the hydro-electric plant (WWF, 2002). In South Africa, IRBM led to the creation of the Working for Water Programme, a massive project that protects biodiversity while creating jobs for 18,000 people clearing invasive, water-hungry plants from several river basins.

Within a managed river basin, priority should be given to protecting upstream sub-basins and headwaters; these areas serve as thermal refugia, providing cool, oxygen-rich groundwater to many species not found downstream, and are often the destination of migratory fish and other animals (WWF, 2002). In addition, upstream areas affect the flow regime and water quality of all areas further downstream, and are often less degraded and easier to protect (Skelton et al., 1995). It is also important to protect side channels and backwaters, which serve as refugia and spawning grounds for a range of animals, and provide corridors to important floodplains (Sedell et al., 1990). Finally, other downstream areas should also be protected, as these areas are necessary for the migration of diadromous species, possess abundant water resources, and are often more productive and species-rich than upstream areas. However, downstream areas are also more frequently subjected to human pressures such as water extraction and land use, so protecting these areas may involve restoration or creative approaches to resource management (WWF, 2002).

Protect entire freshwater ecoregions to preserve the ecological and evolutionary driving forces of biodiversity

Freshwater ecoregion conservation (ERC) involves protecting relatively large units of water and surrounding land that contain distinct assemblages of natural communities sharing many of the same conditions (Abell et al., 2002). These ecoregions are defined by the similarity of the communities and conditions contained within them, and can include one or more drainage basins. Many freshwater ecoregions encompass a number of basins and cover vast tracts of land, such as the Amazon River and Flooded Forests ecoregion and the Yangtze Rivers and Lakes ecoregion (Abell et al, 2002).

The main difference between freshwater ecoregion conservation and IRBM is that ecoregion conservation focuses primarily on preserving biodiversity, while IRBM emphasizes balancing environmental, economic, and social needs. In addition, ecoregion conservation is often applied to areas of high-biodiversity importance, in order to preserve these exceptional areas while addressing and analyzing the ecological and evolutionary driving forces of biodiversity. Because of its focus on protecting high-diversity communities and ecosystems (which are likely to be more resistant and resilient), and because the large scale of ecoregion conservation allows managers to control most non-climatic stresses affecting freshwater ecosystems, ERC is particularly well-suited to buffer systems against the effects of climate change. Additional benefits of an ecoregion approach include the ability to address the conservation needs of wide-ranging species or species that require

particularly large areas of habitat, and the ability to address threats that operate across an entire ecoregion with a single, coherent approach (Abell et al., 2002).

In relation to climate change, freshwater ecoregion conservation may provide the most comprehensive and holistic approach to providing adaptation options (thermal refugia, migration routes, etc.) and minimizing anthropogenic stresses, thereby allowing regions of paramount importance in biodiversity to resist, recover from, and/or adapt to global climate change. However, because many river basins throughout the world are heavily populated, a more balanced approach (such as IRBM) that considers socioeconomic factors in adaptive management of river basins may be more likely to provide long-term protection; as human water demands increase and human populations experience more direct effects of climate change and extreme climatic events, interest in protecting ecosystems is likely to wane and management schemes with the sole goal of protecting freshwater ecosystems and biodiversity may lose support. Ideally, IRBM could be applied to more heavily populated or degraded basins within a freshwater ecoregion, but overall management of the region could be guided by ecological principles aimed at increasing resistance and resilience to climate change, thus combining the benefits of the two approaches. Ultimately, however, any management strategy for dealing with global climate change will simply buy time until either rapid, anthropogenic climate change ceases or species are no longer able to adapt and massive extinctions result. Management strategies can only provide long-term protection of freshwater ecosystems if the root causes of climate change are addressed and solutions are enacted on a global scale.

Literature Cited

- Abell, R., Thieme, M., Dinerstein, E., and Olson, D. 2002. A Sourcebook for Conducting Biological Assessments and Developing Biodiversity Visions for Ecoregion Conservation. Volume II: Freshwater Ecoregions. World Wildlife Fund, Washington, D.C., USA, 201 pp.
- Allan, J.D., and Flecker, A.S. 1993. Biodiversity conservation in running waters. *BioScience* 43:32-43.
- Anderson, D.M., Overpeck, J.T., and Gupta, A.K. 2002. Increase in the Asian southwest monsoon during the past four centuries. *Science* 297:596-599.
- Appleberg, M. 1998. Restructuring of fish assemblages in Swedish Lakes following amelioration of acid stress through liming. *Restoration Ecology* 6:343-352.
- Arnell, N., Liu, C., and others. 2001. Chapter 4: Hydrology and water resources. Pages 191-233 *In* McCarthy, J., O. Canziana, N. Leary, D. Dokken, and K. White (Eds.). *Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.
- Atkinson, D. 1995. Effects of temperature on the size of aquatic ectotherms: exceptions to the general rule. *Journal of Thermal Biology* 20(1/2): 61-74.
- Avila, A., Neal, C., and Terradas, J. 1996. Climate change implications for streamflow and streamwater chemistry in a Mediterranean catchment. *Journal of Hydrology* 177:99-116.
- Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. *Northwest Science* 66: 183-193.
- Baron, J.S., Poff, N.L., Angermeier, P.L., Dahm, C.N., Gleick, P.H., Hairston, N.G. Jr., Jackson, R.B., Johnston, C.A., Richter, B.D., and Steinman, A.D. 2003. Sustaining healthy freshwater ecosystems. *Issues in Ecology* 10:1-16.

- Bayley, P.B., and Petrere, M. 1989. Amazon fisheries: assessment methods, current status and management options. *Canadian Special Publications in Aquatic Sciences* 106:385-398.
- Beebee, T.J.C. 1995. Amphibian breeding and climate change. *Nature* 374:219-220.
- Belk, D. and Fugate, M. 2000. Two new Branchinecta (Crustacea: Anostraca) from the southwest United States. *The Southwestern Naturalist* 45(2): 111-117.
- Bilby, R.E., and Bisson, P.A. 1998. Function and distribution of large woody debris. Pages 324-346. *In* Naiman, R.J. and R.E. Bilby. *River Ecology and Management*. Springer-Verlag, New York, USA.
- Blais, J.M., Schindler, D.W., Muir, D.C.G., Sharp, M., Donald, D., Lafrenière, M., Braekevelt, E., and Strachan, W.M.J. 2001. Melting glaciers: A major source of persistent organochlorines to subalpine Bow Lake in Banff National Park, Canada. *Ambio* 30(7):410-415.
- Blaustein, A.R., Hoffman, P.D., Kiesecker, J.M., and Hays, J.B. 1996. DNA repair and resistance to solar UV-B radiation in eggs of the red-legged frog. *Conservation Biology* 10:1398-1402.
- Blaustein, A.R., and Wake, D.B. 1995. The puzzle of declining amphibian populations. *Scientific American* 272:52-57.
- Boix-Fayos, C., Calvo-Cases, A., Imeson, A.C., Soriano Soto, M.D., and Tiemessen, I.R. 1998. Spatial and short-term temporal variations in runoff, soil aggregation and other soil properties along a Mediterranean climatological gradient. *Catena* 33:123-138.
- Bootsma, H.A., and Hecky, R.F. 1993. Conservation of the African Great Lakes: a limnological perspective. *Conservation Biology* 7:644-656.
- Brinson, M.M., and Malvarez, A.I. 2002. Temperate freshwater wetlands: types, status, and threats. *Environmental Conservation* 29(2): 115-133.
- Buker, G.E. 1982. Engineers vs. Florida's green menace. *The Florida Historical Society Quarterly* April:413-427.
- Butler, R.W., and Vennesland, R.G. 2000. Integrating climate change and predation risk with wading bird conservation research in North America. *Waterbirds* 23(3): 535-540.
- Carpenter, S.R., Fisher, S.G., Grimm, N.B., and Kitchell, J.F. 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* 23: 119-139.
- Carter, T.R., Hulme, M., Crossley, J.F., Malyshev, S., New, M.G., Schlesinger, M.E., and Tuomenvirta, H. 2000. Climate Change in the 21st Century—Interim Characterizations based on the New IPCC Emissions Scenarios. *The Finnish Environment* 433, Finnish Environment Institute, Helsinki, Finland, 148 pp.
- Chapin III, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., and Tilman, D. 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500-504.
- Conover, D.O. 1984. Adaptive significance of temperature-dependent sex determination in a fish. *American Naturalist* 123(3): 297-313.
- Cooley, J.M. 1991. Zebra mussels. *Great Lakes Research* 17(1):1-2.
- Davies, B.R., Snaddon, C.D., Wishart, M.J., Thoms, M.C., and Meador, M. 2000. A biogeographical approach to interbasin water transfers: implications for river conservation. Pages 431-444. *In* P.J. Boon, B.R. Davies, and G.E. Petts (Eds.). *Global Perspectives on River Conservation: Science, Policy and Practice*. John Wiley & Sons, Inc., West Sussex, UK.
- Davis, A.J., Lawton, J.H., Shorrocks, B., and Jenkinson, L.S. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* 67(4): 600-612.
- De Groot, R.S. and Ketner, P. 1994. Sensitivity of NW European species and ecosystems to climate change and some implications for nature conservation and management. Pages 28-53. *In* Pernetta, J., R. Leemans, D. Elder, and S. Humphrey (Eds.). *Impacts of Climate Change on Ecosystems and Species: Implications for Protected Areas*. The World Conservation Union (IUCN), Gland, Switzerland.
- Dettinger, M.D., and Cayan, D.R. 1995. Large-scale forcing of recent trends toward early snowmelt runoff in California. *Journal of Climate* 8:606-623.
- Dewailly, E.A., Nantel, J.P., Weber, J.P., and Meyer, F. 1989. High levels of PCBs in breast milk of Inuit women from Arctic Quebec. *Bulletin of Environmental Contamination and Toxicology* 43:641-646.
- Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, M.J., Razuvayev,

- V., Plummer, N., Jamason, P., and Follard, C.K. 1997. Maximum and Minimum Temperature Trends for the Globe. *Science* 277:364-367.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., and Mearns, L.O. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068-2074.
- Eaton, J.G., and Scheller, R.M. 1996. Effects of climate warming of fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41(5): 1109-1115.
- Effler, S.W., Brooks, C.M., Whitehead, K., Wagner, B., Doerr, S.M., Perkins, M.G., Siegfried, C.A., Walrath, L., and Canale, R.P. 1996. Impact of zebra mussel invasion on river water quality. *Water Environment Research* 68(2):205-214.
- Egerton, F.N. 1987. Pollution and aquatic life in Lake Erie: early scientific studies. *Environmental Review* 11(3):189-205.
- Eriksen, C.H., and Belk, D. 1999. Fairy shrimps of California's puddles, pools, and playas. Mad River Press, Eureka, California, USA, 196 pp.
- Fearnside, P.M. 1997. Greenhouse-gas emissions from Amazonian hydroelectric reservoirs: the example of Brazil's Tucuruí Dam as compared to fossil fuel alternatives. *Environmental Conservation* 24(1): 7-19.
- Feminella, J.W., and Resh, V.H. 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. *Ecology* 71:2083-2094.
- Gagnon, L., and Chamberland, A. 1993. Emissions from hydroelectric reservoirs and comparison of hydroelectricity, natural gas and oil. *Ambio* 22(8):568-569.
- Gardner, T. 2001. Declining amphibian populations: a global phenomenon in conservation biology. *Animal Biodiversity and Conservation* 24(2):25-44.
- Gibbs, J.P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. *Wetlands* 13:25-31.
- Gilbert, J. J. 1996. Effect of temperature on the response of planktonic rotifers to a toxic cyanobacterium. *Ecology* 77: 1174-1180.
- Gilbert, O.L., and Anderson, P. 1998. *Habitat Creation and Repair*. Oxford University Press, New York, USA, 288 pp.
- Gitay, H., Brown, S., Easterling, W., Jallow, B., and others 2001. Chapter 5: Ecosystems and their goods and services. Pages 235-342. *In* McCarthy, J., O. Canziana, N. Leary, D. Dokken, and K. White (Eds.). *Climate Change 2001: Impacts, Adaptation, and Vulnerability*. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Goldsmith, E., and Hildyard, N. 1984. *The Social and Environmental Effects of Large Dams, Vol. I*, Waderbridge Ecological Centre, UK, 287 pp.
- Gopal, B. 1987. *Water Hyacinth*. Amsterdam: Elsevier Science Publishers. 471 pp.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probably responses to climatic warming. *Ecological Applications* 1:182-195.
- Goulding, M., Smith, N.J.H., and Mahar, D.J. 1996. *Floods of Fortune: Ecology and Economy along the Amazon*. Columbia University Press, New York, USA, 193 pp.
- Gowanloch, J.N. 1945. Economic importance of the water hyacinth, *Eichhornia crassipes*, in management of water areas. *Transactions of the 10th North American Wildlife Conference* 10:339-345.
- Hallengraeff, G. M. 1993. A review of toxic algal blooms and their apparent global increase. *Phycologia* 32: 79-99.
- Hansen L.J., Fabacher D.L., and Calfee R. 2002. The role of the egg jelly coat in protecting *Hyla regilla* and *Bufo canorus* embryos from ultraviolet B radiation during development. *Environmental Science & Pollution Research* 9(6):412-416
- Henderson, M.A., Levy, D.A., and Stockner, J.S. 1992. Probably consequences of climate change on freshwater production of Adams River sockeye salmon. *GeoJournal* 28(1):51-59.
- Herman, T.B., and Scott, F.W. 1994. Protected areas and global climate change: assessing the regional or local vulnerability of vertebrate species. Pages 13-27. *In* Pernetta, J., R. Leemans, D. Elder, and S. Humphrey *Impacts of Climate Change on Ecosystems and Species: Implications for Protected Areas*.

- The World Conservation Union (IUCN), Gland, Switzerland.
- Hilborn, R. 1992. Hatcheries and the future of salmon in the Northwest. *Fisheries* 17:5-8.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., and Xiaosu, V. (Eds.). 2001. *Climate Change 2001: The Scientific Basis*. Intergovernmental Panel on Climate Change: Working Group I. Cambridge University Press, Cambridge, UK, 881 pp.
- Huey, R.B., Carlson, M., Crozier, L., Frazier, M., Hamilton, H., Harley, C., Hoang, A., and Kingsolver, J.G. 2002. Plants versus animals: Do they deal with stress in different ways? *Integrative and Comparative Biology* 42(3): 415-423.
- Izrael, Y., Anokhin, Y., and Eliseev, A.D. 1997. Adaptation of water management to climate change. Pages 373-392. *In* Laverov, N.P. (Ed.). *Global Changes of Environment and Climate: Collection of Selected Scientific Papers*. The Federal Research Program of Russia, Russian Academy of Sciences, Moscow, Russia.
- Janzen, F.J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Sciences* 91:7487-7490.
- Junk, W.J. 2002. Long-term environmental trends and the future of tropical wetlands. *Environmental Conservation* 29(4): 414-435.
- Kareiva, P., and Marvier, M. 2003. Conserving biodiversity coldspots. *American Scientist* 91(4):344-351.
- Karl, T.R., and Knight, R.W. 1998. Secular trends of precipitation amount, frequency and intensity in the United States. *Bulletin of the American Meteorological Society* 79:231-241.
- Kaser, G., Hastenrath, S., and Ames, A. 1996. Mass balance profiles on tropical glaciers. *Zeitschrift für Gletscherkunde und Glazialgeologie* 32:75-81.
- Kidd, K.A., Schindler, D.W., Muir, D.C.G., Lockhart, W.L., and Hesslein, R.H. 1995. High concentrations of toxaphene in fishes from a subarctic lake. *Science* 269:240-242.
- Kitchell, J.F. (Ed.). 1992. *Food Web Management: A Case Study of Lake Mendota*. Springer-Verlag, New York, USA, 553 pp.
- Lake Victoria Environmental Management Project. 2003. Water hyacinth "hot spots" in Lake Victoria. Available on-line at http://www.lvemp.org/L_Whats%20new/Wh_hot%20spots.htm
- Lau, S., Mohamed, M., Tan Chi Yen, A., and Su'ut, S. 1998. Accumulation of heavy metals in freshwater molluscs. *Science of the Total Environment* 214: 113-121.
- Lehmkuhl, D.M. 1974. Thermal regime alterations and vital environmental physiological signals in aquatic systems. Pages 216-222. *In* Gibbons, J.W., and R.R. Sharitz (Eds.). *Thermal Ecology*. Atomic Energy Commission Symposium Series, CONF-730505, Augusta, GA, USA
- Ludwig, D., Hilborn, R., and Walters, C. 1993. Uncertainty, resource exploitation, and conservation: Lessons from history. *Science* 260:36.
- Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T., Assel, R.A., Barry, R.G., Card, V., Kuusisto, E., Granin, N.G., Prowse, T.D., Stewart, K.M., and Vuglinski, V.S. 2000. Historical trends in lake and river cover in the Northern Hemisphere. *Science* 289:1743-1746.
- Malcolm, J.R., and Markham, A. 2000. Global warming and terrestrial biodiversity decline. A report prepared for the WWF. Available on-line at http://www.panda.org/downloads/climate_change/speedkills_c6s8.pdf
- Markham, A., and Malcolm, J. 1996. Biodiversity and wildlife: Adaptation to climate change. Pages 384-401. *In* Smith, J., N. Bhatti, G. Menzhulin, R. Benioff, M. Campos, B. Jallow, F. Rijsberman, M. Budyko, and R. Dixon (Eds.). *Adapting to Climate Change: An International Perspective*. Springer-Verlag, New York, USA.
- Matthews, W.J., and Zimmerman, E.G. 1990. Potential effects of global warming on native fishes of the southern Great Plains and the southwest. *Fisheries* 15(6):26-32.
- McAllister, D.E., Hamilton, A.L., and Harvey, B. 1997. Global freshwater biodiversity: Striving for the integrity of freshwater ecosystems. *Sea Wind* 11:1-140.
- McCarty, J.P., and Zedler, J.B. 2002. Restoration, ecosystem. Pages 532-539. *In* Mooney, H.A. and J.G. Canadell (Eds.) *The Earth System: Biological and Ecological Dimensions of Global Environmental Change*, Vol. 2. John Wiley & Sons, Inc., Chichester, UK.

- McCully, P. 1996. *Silenced Rivers: The Ecology and Politics of Large Dams*. Zed Books, New Jersey, USA, 350 pp.
- McDonald, M. E., Hershey, A. E., and Miller, M. C. 1996. Global warming impacts on lake trout in Arctic lakes. *Limnology and Oceanography* 41: 1102-1108.
- McDowall, R. M. 1984. Designing reserves for freshwater fish in New Zealand. *Journal of the Royal Society of New Zealand* 14(1): 17-27.
- McGinnis, M.V. 1994. The politics of restoring versus restocking salmon in the Columbia River. *Restoration Ecology* 2(3): 149-155.
- McNaught, A.S., Schindler, D.W., Parker, B.R., Paul, A.J., Anderson, R.S., Donald, D.B., and Agbeti, M. 1999. Restoration of the food web of an alpine lake following fish stocking. *Limnology and Oceanography* 44:127-136.
- Meehl, G.A., Karl, T., Easterling, D.R., Changnon, S., Pielke Jr., R., Changnon, D., Evans, J., Groisman, P.Y., Knutson, T.R., Kunkel, K.E., Mearns, L.O., Parmesan, C., Pulwarty, R., Root, T., Sylves, R.T., Whetton, P., and Zwiers, F. 2000. An introduction to trends in extreme weather and climate events: observations, socioeconomic impacts, terrestrial ecological impacts, and model projections. *Bulletin of the American Meteorological Society* 81(3):413-416.
- Meffe, G.K. 1992. Techno-arrogance and halfway technologies: Salmon hatcheries on the Pacific Coast of North America. *Conservation Biology* 6:350-354.
- Megahan, W.F., Potyondy, J.P., and Seyedbagheri, K.A. 1992. Best management practices and cumulative effects from sedimentation in the South Fork Salmon River: An Idaho case study. Pages 401-414. *In* Naiman, R.J.(Ed.). *Watershed Management: Balancing Sustainability and Environmental Change*. Springer-Verlag, New York, USA.
- Meisner, J.D., and Shuter, B.J. 1992. Assessing potential effects of global climate change on tropical freshwater fishes. *GeoJournal* 28(1): 21-27.
- Michener, W.K., Blood, E.R., Bildstein, K.L., Brinson, M.M., and Gardner, L.R. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7:770-801.
- Middleton, B. 1999. *Wetland Restoration, Flood Pulsing, and Disturbance Dynamics*. Wiley, New York, USA, 388 pp.
- Moss, B. 2000. Biodiversity in fresh waters—an issue of species preservation or system functioning? *Environmental Conservation* 27(1): 1-4.
- Naiman, R.J., Magnuson, J.J., McKnight, D.M., and Stanford, J.A. (Eds.). 1995. *The Freshwater Imperative: A Research Agenda*. Island Press, Washington, D.C., USA, 165 pp.
- Nalepa, T.F., Harston, D.J., Gostenik, G.W., Fanslow, D.L., and Lang, G.A. 1996. Changes in freshwater mussel community of Lake St. Clair: from Unionidae to Dreissena polymorpha in eight years. *Journal of Great Lakes Research* 22(2):354-369.
- National Research Council 1995. *Wetlands: characteristics and boundaries*. National Academy Press, Washington, D.C., USA, 307 pp.
- Noss, R. F. 2001. Beyond Kyoto: Forest management in a time of rapid climate change. *Conservation Biology* 15(3): 578-590.
- Oerlemans, J., Anderson, B., Hubbard, A., Huybrechts, P., Johannesson, T., Krap, W.H., Schmeits, M., Stroeven, A.P., van der Wal, R.S.W., Wallinga, J., and Zuo, Z. 1998. Modeling the response of glaciers to climate warming. *Climate Dynamics* 14:267-274.
- Ogutu-Ohwayo, R. 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fishes* 27:81-96.
- Osborn, T.J., Hulme, M., Jones, P.D., and Basnet, T.A. 2000. Observed trends in the daily intensity of United Kingdom precipitation. *International Journal of Climatology* 20:347-364.
- Palen, W.J., Schindler, D.E., Adams, M.J., Pearl, C.A., Bury, R.B., and Diamond, S.A. 2002. Optical characteristics of natural waters protect amphibians from UV-B in the U.S. Pacific Northwest. *Ecology* 83(11): 2951-2957.
- Panagoulia, D., and Dimou, G. 1997. Sensitivity of flood events to global climate change. *Journal of Hydrology* 191:208-222.

- Parma, A. M. et al. 1998. What can adaptive management do for our fish, forests, food, and biodiversity? *Integrative Biology* 1(1): 16-26.
- Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.
- Petts, G.E. 2000. Wood in world rivers. *FBA News* 12:1-2.
- Poff, N.L., and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46(1):805-818.
- Poff, N.L., Allen, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B., Sparks, R., and Stromberg, J. 1997. The natural flow regime: A new paradigm for riverine conservation and restoration. *BioScience* 47:769-784.
- Pounds, J.A., Fogden, M.P.L., and Campbell, J.H. 1999. Biological responses to climate change on a tropical mountain. *Nature* 398:611-615.
- Pringle, C.M. 2000. River conservation in tropical versus temperate latitudes. Pages 371-384. *In* Boon, P.J., B.R. Davies, and G.E. Petts (Eds.). *Global Perspectives on River Conservation: Science, Policy and Practice*. John Wiley & Sons, Inc., West Sussex, UK.
- Pringle, C.M., Scatena, F.N., Paaby-Hansen, P., and Núñez-Ferrera, M. 2000. River conservation in Latin America and the Caribbean. Pages 41-77. *In* Boon, P.J., B.R. Davies, and G.E. Petts (Eds.). *Global Perspectives on River Conservation: Science, Policy and Practice*. John Wiley & Sons, Inc., West Sussex, UK.
- Raskin, P., Gleick, P., Kirshen, P., Pontius, G., and Strzepek, K. 1997. *Water Futures: Assessment of Long-Range Patterns and Problems*. Background Report for the Comprehensive Assessment for the Freshwater Resources of the World. Stockholm Environment Institute, Stockholm, Sweden, 78 pp.
- Reynard, N.S., Prudhomme, C., and Crooks, S.M. 1998. The potential impacts of climate change on the flood characteristics of a large catchment in the UK. Pages 320-332. *In* Proceedings of the Second International Conference on Climate and Water, Espoo, Finland, August 1998. Helsinki University of Technology, Helsinki, Finland.
- Reynolds, C.S. 1984. *Ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge, U.K., 384 pp.
- Rhee, G.-Y. and Gotham, I. J. 1981. The effect of environmental factors on phytoplankton growth: temperature and the interactions of temperature with nutrient limitation. *Limnology and Oceanography* 26: 635-648.
- Ricciardi, A., and Rasumssen, J.B. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* 13:1220-1222.
- Richter, B.D., Matthews, R., Harrison, D.L., and Wigington, R. 2003. Ecologically sustainable water management: Managing river flows for ecological integrity. *Ecological Applications* 13(1): 206-224.
- Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Possingham, H.P., Ruckelshaus, M., and Warner, R.R. 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* 13(1): S199-S214.
- Roberts, L. 1990. Zebra mussel invasion threatens U.S. waters. *Science* 249:1370-1372.
- Rudd, J.W.M., Harris, R., Kelly, C.A., and Hecky, R.E. 1993. Are hydroelectric reservoirs significant sources of greenhouse gases? *Ambio* 22(4):246-248.
- Saelthun, N.R., Aittoniemi, P., Bergstrom, S., Einarsson, K., Johannesson, T., Lindstrom, G., Ohlsson, P.-O., Thomsen, T., Vehriläinen, B., and Aamodt, K.O. 1998. Climate change impacts on runoff and hydropower in the Nordic countries. *Nordic Council of Ministers, TemaNord* 1998:552, 170 pp.
- Sellers, T.J., Parker, B.R., Schindler, D.W., and Tonn, W.M. 1998. The pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian Shield lakes with respect to temperature, dissolved oxygen, and light. *Canadian Journal of Fisheries and Aquatic Sciences* 55:170-179.
- Schindler, D. W. 1968. Feeding, assimilation and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. *Journal of Animal Ecology* 37: 369-385.
- Schindler, D.W. 1997. Liming to restore acidified lakes and streams: A typical approach to restoring dam-

- aged ecosystems? *Restoration Ecology* 5:1-6.
- Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 18-29.
- Schindler, D.W., Mills, K.H., Malley, D.F., Findlay, D.L., Shearer, J.A., Davies, I.J., Turner, M.A., Linsey, G.A., and Cruikshank, D.R. 1985. Long-term ecosystem stress: The effects of years of experimental acidification on a small lake. *Science* 22:1395-1401.
- Schindler, D.W., Beaty, K.G., Fee, E.J., Cruikshank, D.R., DeBruyn, E.R., Findlay, D.L., Linsey, G.A., Shearer, J.A., Stainton, M.P., and Turner, M.A. 1990. Effects of climate warming on lakes of the central boreal forest. *Science* 250: 967-970.
- Schindler, D.W., Kidd, K.A., Muir, D.C.G., and Lockhart, W.L. 1995. The effects of ecosystem characteristics on contaminant distribution in northern freshwater lakes. *Science of the Total Environment* 160/161: 1-17.
- Schindler, D.W., Curtis, P.W., Parker, B.R., and Stainton, M.P. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature* 379: 705-708.
- Schmieder, K. 1997. Littoral zone - GIS of Lake Constance: a useful tool in lake monitoring and autecological studies with submersed macrophytes. *Aquatic Botany* 58: 333-346.
- Schulze, R.E. 2000. Modeling hydrological responses to land use and climate change: A southern African perspective. *Ambio* 29(1):12-22.
- Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A., and Hawkins, C.P. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. *Environmental Management* 14: 711-724.
- Semlitsch, R.D. 2002. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64: 615-631.
- Semlitsch, R.D., and Brodie, J.R. 1998. Are small isolated wetlands inexpendable? *Conservation Biology* 12:1129-1133.
- Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., and Gibbons, J.W. 1996. Structure and dynamics of an amphibian community: Evidence from a 16-year study of a natural pond. Pages 217-248. *In* Cody, M.L. and J.A. Smallwood (Eds.). *Long-term Studies of Vertebrate Communities* Academic Press, San Diego, California, USA.
- Shaw, W.D., and Raucher, R.S. 1993. Recreation and tourism benefits from water quality improvements: An economist's perspective. Pages 3-19-3-33 *In* EPA. *Clean Water and the American Economy—Proceedings: Surface Water*, Vol. 1. EPA 800-R-93-001a. Environmental Protection Agency, Office of Water, Washington, D.C., U.S.A.
- Shuter, B.J., and Meisner, J.D. 1992. Tools for assessing the impact of climate change on freshwater fish populations. *GeoJournal* 28(1): 7-20.
- Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: The case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnaean Society* 42:135-147.
- Skelly, D.K., Werner, E.E., and Cortwright, S. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80:2326-2337.
- Skelton, P. H., Cambray, J. A., Lombard, A., and Benn, G. A. 1995. Patterns of distribution and conservation status of freshwater fishes in South Africa. *South African Journal of Zoology* 30(3): 71-81.
- Snucins, E., and Gunn, J.M. 1995. Coping with a warm environment: behavioral thermoregulation by lake trout. *Transactions of the American Fisheries Society* 124:118-123.
- Small, C., and Cohen, J.E. 1999. Continental physiography, climate and the global distribution of human population. Pages 965-971. *In* Proceedings of the International Symposium on Digital Earth. Chinese Academy of Science, Beijing China. Available on-line at http://www.ideo.columbia.edu/~small/PDF/ISDE_SmallCohen.pdf
- Smith, J.B., and Lenhart, S.S. 1996. Climate change adaptation policy options. *Climate Research* 6:193-201.
- Solomon, A.M. (1994). Management and planning of terrestrial parks and reserves during climate change. Pages 1-12. *In* Pernetta, J., R. Leemans, D. Elder, and S. Humphrey (Eds.) *Impacts of Climate Change on Ecosystems and Species: Implications for Protected Areas*. The World Conservation Union (IUCN), Gland, Switzerland.

- Sommaruga-Wögrath, S., Koinig, K.A., Schmidt, R., Sommaruga, R., Tessadri, R., and Psenner, R. 1997. Temperature effects on the acidity of remote alpine lakes. *Nature* 387: 64-67.
- Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., and Osman, R.W. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences* 99(24): 15497-15500.
- Stemberger, R. S., Herlihy, A. T., Kugler, D. L., and Paulsen, S. G. 1996. Climate forcing on zooplankton richness in lakes of the northeastern United States. *Limnology and Oceanography* 41: 1093-1101.
- Stewart, M.M. 1995. Climate driven population fluctuations in rain forest frogs. *Journal of Herpetology* 29(5):437-446.
- Strzepek, K.M., Yates, D.N., and El Quosy, D.E.D. 1996. Vulnerability assessment of water resources in Egypt to climatic change in the Nile Basin. *Climate Research* 6:89-95.
- Timmer, C.E., and Weldon, L.W. 1967. Evapotranspiration and pollution of water by water hyacinth. *Hyacinth Control Journal* 6:34-37.
- Tyedmers, P., and Ward, B. 2001. A review of the impacts of climate change on BC's freshwater fish resources and possible management responses. *Fisheries Centre Research Reports* 9(7): 1-12.
- Vasalaar, R.T. 1997. Opening the flood gates: the 1996 Glen Canyon Dam experiment. *Restoration & Management Notes* 15:119-125.
- Venema, H.D., Schiller, E.J., Adamowski, K., and Thizy, J.-M. 1997. A water resources planning response to climate change in the Senegal River basin. *Journal of Environmental Management* 49:125-155.
- Verberg, P., Hecky, R.E., and Kling, H. 2003. Ecological consequences of a century of warming in Lake Tanganyika. *Science* 301:505-507.
- Vörösmarty, C.J., Green, P., Salisbury, J., and Lammers, R.B. 2000. Global water resources: vulnerability from climate change and population growth. *Science* 289:284-288.
- Wania, F., and Mackay, D. 1993. Global fractionation and cold condensation of low volatility organochlorine compounds in polar regions. *Ambio* 22:10-18.
- Welcomme, R.L. 1979. *Fisheries ecology of floodplain rivers*. Longman, London, UK, 317 pp.
- Welcomme, R.L., and Hagborg, D. 1977. Towards a model of a floodplain fish population and its fishery. *Environmental Biology of Fishes* 2:7-24.
- Westmacott, J.R., and Burn, D.H. 1997. Climate change effects on the hydrologic regime within the Churchill-Nelson River Basin. *Journal of Hydrology* 202:263-279.
- Williamson, C.E. 1995. What role does UV-B play in freshwater ecosystems? *Limnology and Oceanography* 40(2): 386-392.
- Witte, F., Goldschmidt, T., Wanink, J., van Oijen, M., Goudswaard, K., Witte-Maas, E., and Bouton, N. 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* 34:1-28.
- Wright, R.F., and Schindler, D.W. 1995. Interaction of acid rain and global changes: effects on terrestrial and aquatic ecosystems. *Water, Air, and Soil Pollution* 85:89-99.
- WWF. 2002. *Managing water wisely: Promoting sustainable development through integrated river basin management*. Available on-line at <http://www.panda.org/downloads/freshwater/managingwaterwiselyeng2.pdf>
- Young, E. 2002. Yangtze river pollution at dangerous levels. *New Scientist Online* 13:20. Available on-line at <http://www.newscientist.com/news/news.jsp?id=ns99991802>
- Zinyowera, M.C., Jallow, B.P., Maya, R.S., and Okoth-Ogendo, H.W.O., and others. 1998. Africa. Pages 30-84. *In* Watson, R.T., M.C. Zinyowera, R.H. Moss, and D.J. Dokken (Eds.) *The regional impacts of climate change; An assessment of vulnerability, A special report of IPCC Working Group II*. Cambridge University Press, Cambridge, UK.