Aquatic ecosystems
& Global climate change

Potential Impacts on Inland Freshwater and Coastal Wetland Ecosystems in the United States

Prepared for the Pew Center on Global Climate Change

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Foreword *Eileen Claussen, President, Pew Center on Global Climate Change*

Aquatic ecosystems are critical components of the global environment. In addition to being essential contributors to biodiversity and ecological productivity, they also provide a variety of services for human populations, including water for drinking and irrigation, recreational opportunities, and habitat for economically important fisheries. However, aquatic systems have been increasingly threatened, directly and indirectly, by human activities. In addition to the challenges posed by land-use change, environmental pollution, and water diversion, aquatic systems are expected to soon begin experiencing the added stress of global climate change.

"Aquatic Ecosystems and Global Climate Change" is the seventh in a series of Pew Center reports examining the potential impacts of climate change on the U.S. environment. It details the likely impacts of climate change over the next century on U.S. aquatic ecosystems. Report authors, Drs. N. LeRoy Poff, Mark Brinson, and John Day, Jr. find:

- Increases in water temperatures as a result of climate change will alter fundamental ecological processes and the geographic distribution of aquatic species. Such impacts may be ameliorated if species attempt to adapt by migrating to suitable habitat. However, human alteration of potential migratory corridors may limit the ability of species to relocate, increasing the likelihood of species extinction and loss of biodiversity.

- Changes in seasonal patterns of precipitation and runoff will alter hydrologic characteristics of aquatic systems, affecting species composition and ecosystem productivity. Populations of aquatic organisms are sensitive to changes in the frequency, duration, and timing of extreme precipitation events, such as floods or droughts. Changes in the seasonal timing of snowmelt will alter stream flows, potentially interfering with the reproduction of many aquatic species.

- Climate change is likely to further stress sensitive freshwater and coastal wetlands, which are already adversely affected by a variety of other human impacts, such as altered flow regimes and deterioration of water quality. Wetlands are a critical habitat for many species that are poorly adapted for other environmental conditions and serve as important components of coastal and marine fisheries.

- Aquatic ecosystems have a limited ability to adapt to climate change. Reducing the likelihood of significant impacts to these systems will be critically dependent on human activities that reduce other sources of ecosystem stress and enhance adaptive capacity. These include maintaining riparian forests, reducing nutrient loading, restoring damaged ecosystems, minimizing groundwater withdrawal, and strategically placing any new reservoirs to minimize adverse effects.

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Executive Summary

Climate change of the magnitude projected for the United States over the next 100 years will cause significant changes to temperature regimes and precipitation patterns across the United States. Such alterations in climate pose serious risks for inland freshwater ecosystems (lakes, streams, rivers, wetlands) and coastal wetlands, and they may adversely affect numerous critical services they provide to human populations.

The geographic ranges of many aquatic and wetland species are determined by temperature. Average global surface temperatures are projected to increase by 1.5 to 5.8°C by 2100 (Houghton et al., 2001), but increases may be higher in the United States (Wigley, 1999). Projected increases in mean temperature in the United States are expected to greatly disrupt present patterns of plant and animal distributions in freshwater ecosystems and coastal wetlands. For example, cold-water fish like trout and salmon are projected to disappear from large portions of their current geographic range in the continental United States, when warming causes water temperature to exceed their thermal tolerance limits. Species that are isolated in habitats near thermal tolerance limits (like fish in Great Plains streams) or that occupy rare and vulnerable habitats (like alpine wetlands) may become extinct in the United States. In contrast, many fish species that prefer warmer water, such as largemouth bass and carp, will potentially expand their ranges in the United States and Canada as surface waters warm.

The productivity of inland freshwater and coastal wetland ecosystems also will be significantly altered by increases in water temperatures. Warmer waters are naturally more productive, but the particular species that flourish may be undesirable or even harmful. For example, the blooms of “nuisance” algae that occur in many lakes during warm, nutrient-rich periods can be expected to increase in frequency in the future. Large fish predators that require cool water may be lost from smaller lakes as surface water temperatures warm, and this may indirectly cause more blooms of nuisance algae, which can reduce water quality and pose potential health problems.

Warming in Alaska is expected to melt permafrost areas, allowing shallow summer groundwater tables to drop; the subsequent drying of wetlands will increase the risk of catastrophic peat fires and the release of vast quantities of carbon dioxide (CO_2) and possibly methane into the atmosphere.

In addition to its independent effects, temperature changes will act synergistically with changes in the seasonal timing of runoff to freshwater and coastal systems. In broad terms, water quality will probably decline greatly, owing to expected summertime reductions in runoff and elevated temperatures.

These effects will carry over to aquatic species because the life cycles of many are tied closely to the availability and seasonal timing of water from precipitation and runoff. In addition, the loss of winter snowpack will greatly reduce a major source of groundwater recharge and summer runoff, resulting in a potentially significant lowering of water levels in streams, rivers, lakes, and wetlands during the growing season.

The following summarizes the current understanding regarding the potential impacts of climate change on U.S. aquatic ecosystems:

1 Aquatic and wetland ecosystems are very vulnerable to climate change. The metabolic rates of organisms and the overall productivity of ecosystems are directly regulated by temperature. Projected increases in temperature are expected to disrupt present patterns of plant and animal distribution in aquatic ecosystems. Changes in precipitation and runoff modify the amount and quality of habitat for aquatic organisms, and thus, they indirectly influence ecosystem productivity and diversity.

2 Increases in water temperature will cause a shift in the thermal suitability of aquatic habitats for resident species. The success with which species can move across the landscape will depend on dispersal corridors, which vary regionally but are generally restricted by human activities. Fish in lowland streams and rivers that lack northward connections, and species that require cool water (e.g., trout and salmon), are likely to be the most severely affected. Some species will expand their ranges in the United States.

3 Seasonal shifts in stream runoff will have significant negative effects on many aquatic ecosystems. Streams, rivers, wetlands, and lakes in the western mountains and northern Plains are most likely to be affected, because these systems are strongly influenced by spring snowmelt and warming will cause runoff to occur earlier in winter months.

4 Wetland loss in boreal regions of Alaska and Canada is likely to result in additional releases of CO_2 into the atmosphere. Models and empirical studies suggest that global warming will cause the melting of permafrost in northern wetlands. The subsequent drying of these boreal peatlands will cause the organic carbon stored in peat to be released to the atmosphere as CO_2 and possibly methane.

5 Coastal wetlands are particularly vulnerable to sea-level rise associated with increasing global temperatures. Inundation of coastal wetlands by rising sea levels threatens wetland plants. For many of these systems to persist, a continued input of suspended sediment from inflowing streams and rivers is required to allow for soil accretion.

6 Most specific ecological responses to climate change cannot be predicted, because new combinations of native and non-native species will interact in novel situations. Such novel interactions may compromise the reliability with which ecosystem goods and services are provided by aquatic and wetland ecosystems.

7 Increased water temperatures and seasonally reduced streamflows will alter many ecosystem processes with potential direct societal costs. For example, warmer waters, in combination with high nutrient runoff, are likely to increase the frequency and extent of nuisance algal blooms, thereby reducing water quality and posing potential health problems.

8 The manner in which humans adapt to a changing climate will greatly influence the future status of inland freshwater and coastal wetland ecosystems. Minimizing the adverse impacts of human activities through policies that promote more science-based management of aquatic resources is the most successful path to continued health and sustainability of these ecosystems. Management priorities should include providing aquatic resources with adequate water quality and amounts at appropriate times, reducing nutrient loads, and limiting the spread of exotic species.

Overall, these conclusions indicate climate change is a significant threat to the species composition and function of aquatic ecosystems in the United States. However, critical uncertainties exist regarding the manner in which specific species and whole ecosystems will respond to climate change. These arise both from uncertainties about how regional climate will change and how complex ecological systems will respond. Indeed, as climate change alters ecosystem productivity and species composition, many unforeseen ecological changes are expected that may threaten the goods and services these systems provide to humans.

I. Introduction

Freshwater ecosystems and coastal wetlands are essential contributors to the diversity and productivity of the biosphere. Freshwater ecosystems and coastal wetlands are incredibly diverse and productive, providing many tangible and intangible goods and services to human civilization and welfare (see Table 1). Yet these systems are increasingly imperiled by human activity. In the United States, a global center of freshwater biodiversity (Table 2), the extinction rate for freshwater species equals or exceeds that for species in other ecosystem types, including tropical rain forests (Ricciardi and Rasmussen, 1999).

Table 1

Goods and Services Provided by Rivers, Streams, Lakes, Freshwater Wetlands, and Coastal Wetlands

	Streams and Rivers	Lakes and Ponds	Freshwater Wetlands	Coastal Wetlands
Water supply				
Drinking, cooking, washing, and other household uses	X	X	—	—
Manufacturing, thermoelectric power generation, and other industrial uses	X	X	—	—
Irrigation of crops, parks, golf courses, etc.	X	X	X	—
Aquaculture	X	X	X	X
Supply of goods other than water				
Fish	X	X	X	X
Waterfowl	X	X	X	X
Clams, mussels, other shellfish, crayfish	X	X	X	X
Timber products	X	—	X	—
Nonextractive benefits				
Biodiversity	X	X	X	X
Flood control	X	X	X	—
Transportation	X	X	—	X
Recreational swimming, boating, etc.	X	X	X	X
Pollution dilution and water quality protection	X	X	X	X
Hydroelectric generation	X	—	—	—
Bird and wildlife habitat	X	X	X	X
Enhanced property values	X	X	X	X
Coastal shore protection	—	—	—	X

Modified from Postel and Carpenter (1997).

Table 2

Global Significance of U.S. Freshwater Species

	Number of Described U.S. Species	Number of Described Species Worldwide	Percentage of Known Species Worldwide found in U.S.	U.S. Ranking Worldwide in Species Diversity
Fishes	801	8,400	10	7
Crayfishes	322	525	61	1
Freshwater mussels	300	1,000	30	1
Freshwater snails	600	4,000	15	1
Stoneflies	600	1,550	40	1
Mayflies	590	2,000	30	1
Caddisflies	1,400	10,560	13	1
Dragonflies and damselfies	452	5,756	8	uncertain
Stygobites (cave fauna)	327	2,000	16	1

From Master et al. (1998).

Because water flows downhill, aquatic ecosystems occupy low points on the landscape and filter materials that move via gravity from the terrestrial environment. Accordingly, pollutants and fertilizers flowing off the landscape accumulate in these systems, impairing their health. Humans often modify the physical structure of these systems for commerce, agriculture, and recreation, resulting in habitat destruction, one of the major stresses on the integrity of contemporary freshwater ecosystems. Further, these ecosystems are harmed by direct appropriation of freshwater for human consumption, a problem that is likely to grow in the future (Postel, 2000; Vörösmarty et al., 2000). Coastal wetlands also receive the pollutants and eroded silts from human activities on land via freshwater inputs. Likewise, they experience direct habitat loss from coastal development and erosion exacerbated by reduced river inflows.

Humans are altering the global climate through the release of greenhouse gases (Wigley, 1999; NAST, 2000; Houghton et al., 2001). Average global surface temperatures are projected to increase by 1.5 to 5.8°C by 2100 (Houghton et al., 2001), but increases may be higher in the United States (Wigley, 1999). This projected change in climate will place additional pressure on already-stressed freshwater and coastal ecosystems. Although aquatic systems are generally viewed as resilient and able to maintain a healthy and self-sustaining condition despite large year-to-year variation in hydrologic and temperature conditions, rapid climate change may impose new environmental regimes that will exceed the limits of the resilience of aquatic ecosystems. Even though aquatic ecosystems have historically experienced elevated temperatures similar to those projected for the next 100 years, the projected rate of change falls outside the natural range of variation and is therefore unprecedented (Peters, 1989). Moreover, the extent of fragmentation of the landscape in which aquatic ecosystems are situated is unprecedented historically (Dale, 1997). These systems are increasingly isolated and disconnected, making adjustment to rapid climate change through animal and plant dispersal very problematic. Thus, climate change clearly represents an additional, significant threat to aquatic ecosystems, one that will interact in complex ways with existing human-caused stresses (Carpenter et al., 1992; Firth and Fisher, 1992; Lake et al., 2000; Lodge, 2001; Poff et al., 2001).

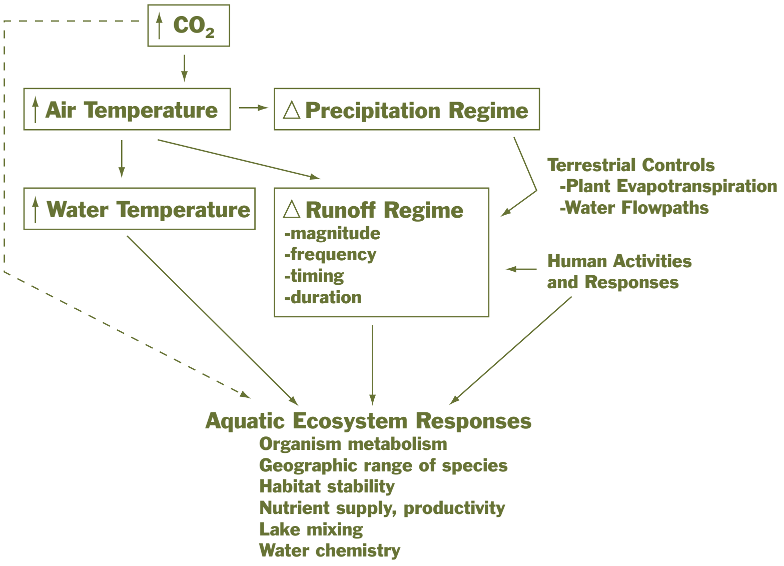
This report focuses on the implications of climate change for freshwater ecosystems (streams, rivers, lakes, wetlands) and coastal wetlands in the United States. Where appropriate, examples from outside the United States are used. Estuarine and blue-water ecosystems will be covered in a future Pew Center report.

II. Climate, Environmental Drivers, and Aquatic Ecosystems

The ecological consequences of climate change will largely depend on the rate and magnitude of change in two critical environmental drivers: (1) temperature and, (2) water availability from precipitation and runoff. These factors regulate many ecological processes in aquatic ecosystems, both directly and indirectly (Figure 1). Average temperatures are predicted to increase across North America, but more markedly at higher latitudes (Wigley, 1999). Some areas of the continent will become wetter and some drier, and the variability in the timing and quantity of precipitation will also change, altering patterns of runoff to aquatic ecosystems. Although the precise

Figure 1

CO_2, Climate, and Ecological Processes



Linkages between atmospheric increases in CO_2 and environmental drivers of temperature and precipitation that regulate many ecological processes and patterns in inland freshwater and coastal wetland ecosystems. Solid arrows indicate direct responses; dashed arrow indicates direct effects of lesser known importance.

geography of these regional shifts is uncertain at present because of limitations in climate forecasting (Box 1), changes in the fundamental character of many aquatic ecosystems in response to a changing climate are highly probable.

Temperature directly controls many vital life processes, and a change in the thermal regime (e.g., extreme temperatures, their duration, and seasonal rates of temperature change) can directly regulate rates of growth and reproduction for species. Since individual aquatic and wetland species are adapted to a specific range of temperatures, global warming will shift the potential geographic ranges of species to the north, or to higher elevation in mountain regions. Likewise, the more southerly (or lower-elevation) part of the present geographic range of many species will become unsuitable. The availability of species to move into expanded ranges will depend on the availability of habitat and the ability of species to move along dispersal corridors, which will vary for the different types of aquatic ecosystems considered here.

Box 1

Regional Projections and Uncertainties of Temperature and Precipitation Change

The general circulation models (GCMs) used to predict climate change are currently unable to provide the level of detail needed to predict local or regional responses of aquatic ecosystems to climate change (Wigley, 1999). Indeed, GCMs diverge significantly in their regional projections of temperature and precipitation change. The most consistent projections among the many models are obtained for winter temperature-change patterns, because many models show a greater warming in higher latitudes. The models diverge substantially in their regional projections of precipitation changes, particularly those for summer and fall. The most certain projection is, therefore, that colder regions are likely to warm faster, and this will directly alter runoff patterns by decreasing the amount of winter precipitation that falls as snow, causing earlier runoff in river basins currently characterized by snowmelt hydrographs.

Regional predictions of runoff are even more uncertain, because runoff is sensitive to the interaction of precipitation, temperature, evaporation, and plant transpiration. Different GCMs can produce very different projections of regional runoff. For example, Frederick and Gleick (1999) report estimated change in runoff for 18 water resource regions in the United States using two contrasting GCMs. These models agreed in only four of 18 cases that runoff would change in the same direction for 1990-2030, and in only nine of 18 cases that runoff would change in the same direction for 1990-2090. In many cases of agreement about the direction of change, the magnitude of change was very different. The most consistent results for the 1990-2090 projections were for substantial increases in annual runoff for the arid southwestern United States. They concluded that arid lands are most sensitive to modest changes in runoff and that a shift in mountainous watersheds from snow to rain would significantly alter seasonal patterns of water availability.

The volume of water in an aquatic ecosystem directly influences ecological processes by determining the amount of available habitat and many aspects of water quality. The regional pattern of precipitation and runoff dictates how the volume of water in an aquatic ecosystem changes over time. Because climate naturally varies from region to region (e.g., arid West versus humid East), the hydrologic regime (the seasonal pattern of magnitude, frequency, duration and timing of runoff) also varies among regions (Box 2). Seasonal variation in water volume strongly influences what kinds of species can flourish in an aquatic system. Therefore, a change in regional climate that alters the existing hydrologic regime has the potential to greatly modify habitat suitability for many species and cause significant ecological change (even if the thermal regimes remain unchanged).

Box 2

The Water Cycle and Aquatic/Wetland Ecosytems

Precipitation in excess of evapotranspiration either flows downhill as surface runoff or percolates into the soil and moves as groundwater into aquatic ecosystems. Runoff and groundwater transport nutrients and sediments into inland freshwater ecosystems, and, eventually, to coastal wetlands. The quantity and timing of runoff directly influence habitat conditions and regulate water quality. Thus, the hydrologic cycle is a determinant of many ecosystem attributes, and an alteration in hydrology can have numerous, cascading ecological effects.

The magnitude, frequency, duration, and timing of runoff over time are known as the "flow regime" in streams and rivers, and the "hydroperiod" in lake margin and wetland ecosystems. Three aspects of the water cycle are of fundamental importance in understanding the structure and function of aquatic ecosystems. First, the amount of water determines livable habitat for aquatic organisms. In addition, more water often translates into more contact with the terrestrial environment (shoreline, floodplain), which increases nutrient supply and influences the types of food available to aquatic organisms. Second, the rate at which water moves through a system has a tremendous influence on the rates at which ecosystem processes occur and on the kinds of organisms that can live in them. For example, lakes and wetlands have low flow-through rates compared to streams and rivers; consequently, nutrients are retained longer and system productivity tends to be higher. Third, the timing of hydrologic inputs to aquatic ecosystems is critical for creating and maintaining seasonal habitats and for supplying sediment and nutrients predictably. In many systems, aquatic organisms are adapted to specific timing of high and low water levels, and extreme flow levels may be needed to maintain certain species within the community (Poff and Ward, 1989; Poff et al., 1997). Consequently, a change in the timing or seasonality of hydrologic inputs can severely alter aquatic ecosystems.

III. Responses of Aquatic Ecosystems to Climate Change

A. Streams and Rivers

Stream and river ecosystems comprise both the actual aquatic (in-channel) environment and the associated floodplain or riparian system. The expected impacts of climate change on these ecosystems will depend on how thermal and streamflow regimes deviate from present conditions. The amount of deviation will reflect both the regional and local setting of the ecosystem.

Changes in Temperature

An increase in air temperature due to global warming will translate directly into warmer water temperatures for most streams and rivers, thereby altering fundamental ecological processes and species distributions. Streams and rivers are relatively shallow, turbulent, and well-mixed systems, meaning they exchange heat and oxygen easily with the atmosphere. Therefore, they will become warmer under projected climate change (Eaton and Scheller, 1996). A warming of water temperatures by, for example, 4°C in present-day ecosystems would represent a northward latitudinal shift in thermal regimes of about 680 kilometers (422 miles), and this would have serious consequences for aquatic ecosystems (Sweeney et al., 1992).

The life processes of many aquatic organisms are temperature-dependent. Warmer water can increase growth rates and stimulate ecosystem production. For example, aquatic invertebrates at the base of the food web (e.g., aquatic insects) may mature more rapidly, albeit to a smaller size, and reproduce more frequently (see Arnell et al., 1995). Assuming no change in food resources, invertebrate production of streams and rivers may increase, potentially yielding more food for fish. However, higher water temperatures will also increase the rate of microbial activity and thus the rate of decomposition of organic material, which may result in less food being available for invertebrates and ultimately fish (Meyer and Edwards, 1990). In either case, warmer water holds less dissolved oxygen, so water quality will be reduced for organisms such as invertebrates and fish that have a high oxygen demand.

For many species, even modest increases in temperature can have dramatic effects that are not necessarily intuitive. For example, in far northern rivers, many aquatic invertebrates require prolonged periods of near 0°C in winter followed by a rapid rise in spring temperature to cause eggs to hatch. The construction of dams that release slightly warmed water during the winter (i.e., water that does not freeze) has been documented to cause massive local extinctions of invertebrate species for tens of kilometers downstream (Lehmkuhl, 1974). Thus, warmer winter temperatures under global warming could induce similar changes in river diversity and related productivity.

Species at the southern limits of their geographic distributions will face local extinction unless they migrate. The ability to migrate to thermally suitable habitat will depend on the dispersal mode of the species and the availability of suitable migration corridors (Sweeney et al., 1992). Many species may simply move upstream, because headwaters are generally cooler than downstream reaches. However, warmer headwaters could result in the disappearance of species that already are restricted to cool headwaters. So, although upstream movement may work well for some species, an overall reduction in biodiversity in many watersheds can be expected, as cool-adapted headwater species lose critical habitat.

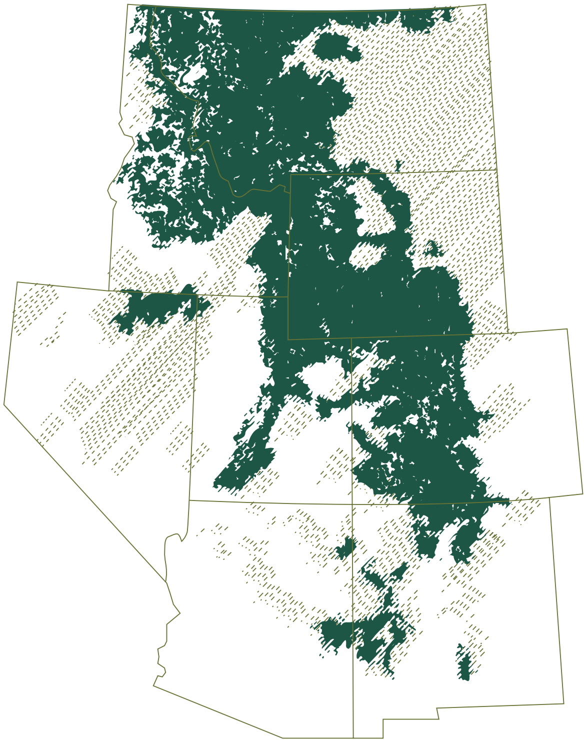
This situation could be ameliorated if species lacking thermal refuges within a watershed could migrate northward to more suitable habitat. In prehistoric periods of climate change, many aquatic species were able to disperse and find thermal refuges. For example, during the late Pleistocene glaciation of about 10,000 years ago, fish moved from north to south in the Mississippi River Basin (Briggs, 1986). Unfortunately, stream and river systems are now highly fragmented owing to human alteration of landscapes (e.g., dams and reservoirs, deforestation, diversion of water for offstream uses such as irrigation and urban development), so migration corridors along many stream channels are restricted (Allan and Flecker, 1993). Some species may avoid this problem by overland dispersal. For example, most aquatic insects have winged adult stages, although some of these species are poor fliers (e.g., mayflies) and would most likely not be successful, particularly in harsher regions such as the arid West. Purely aquatic species like fish and amphibians are expected to have many problems because the overland route is not an option for them, and not all waterways connect to higher latitudes. For example, fish of lowland streams in the desert Southwest and in the southern Great Plains occupy streams and rivers that predominantly drain west and east, providing no opportunity for northward migration. As many as 20 native fish species in these regions are likely to become extinct under a few degrees of warming (Matthews and Zimmerman, 1990; Covich et al., 1997).

The effect of climate warming on fish has received much attention, because many are highly valued game fish. In one study, Eaton and Scheller (1996) estimated increases in maximum weekly water temperatures in streams across the continental United States in response to an average air temperature increase of about 4°C, which is well within the range of projected elevated temperature for the United States over the next century. Their analysis revealed that thermally suitable habitat for 57 species that require cold or cool water (including game fish, such as trout, salmon, and perch) would decline by about 50 percent. Habitats for many fish requiring warm water were also predicted to decline slightly, although the habitats for some species like largemouth bass and carp, which can flourish in extremely warm water, would increase.

Trout and salmon will be particularly vulnerable to warming. For example, in streams of the Rocky Mountain region, an increase in air temperature of only 1°C is predicted to reduce suitable stream habitat for trout by 7-16 percent, and a 3°C increase would reduce habitat by 42-54 percent (Keleher and Rahel, 1996; Rahel et al., 1996; Figure 2). Remnant populations may hold out in locales where local groundwater effluent

Figure 2

Projected Geographic Contraction of Rocky Mountain trout



Future potential distribution of stream segments that could support cold-water trout (dark shading) and habitat loss (light shading) in the Rocky Mountains given a 3°C warming in July air temperatures.

Source: Keleher and Rahel (1996).

continues to provide cool-water refuges in warm summer months or thermally suitable hatching sites for eggs (Meisner, 1990). However, over time, even groundwater will warm, and those remnant populations would decline. Ranges for cold-adapted species may expand northward or to higher elevations, where very cold temperatures now limit population growth (Clark et al., 2001).

At the northern or high elevation end of current distributional ranges, conditions should improve for trout, because of the favorable warming of very cold surface waters (Meisner et al., 1988). In Alaska, winter water temperatures are likely to increase by several degrees Celsius, eliminating extensive ice cover and allowing invasion of cool-water species and the range expansion of seasonally migratory species such as salmon and trout (Poff et al., 2001).

Commercially important salmon in the Pacific Northwest may also be harmed. During the middle Holocene (6,000 to 9,000 years ago), when temperatures in the Pacific Northwest were 1-2°C warmer and the climate was drier, the very large populations of salmon in some rivers in the region appear to have been depressed (Neitzel et al., 1991). The current depressed populations of Pacific salmonids (due to habitat degradation, barriers to migration, commercial harvest, genetic dilution from hatchery fish, hydrologic alteration, and variable ocean conditions) make them particularly vulnerable to a warmer and drier climate. For example, warmer temperatures and reduced streamflows in the Columbia River Basin may increase mortality of juvenile coho salmon or create thermal barriers for migration of adult salmon (Mote et al., 1999). Juvenile mortality may also increase during periods of warmer spring-summer water temperatures, when warm-water fishes are more efficient predators. Petersen and Kitchell (2001) estimate that inter-annual variation in summer water temperatures up to 2°C from 1933-1996 has caused predation rate on juvenile salmon by one predator species to vary by up to 100 percent. Populations of sockeye salmon in Alaska, however, may potentially benefit from a warming of sea-surface temperatures, which favor increased ocean productivity. This pattern has been observed during bouts of natural climatic variation over the last 300 years (Finney et al., 2000).

Changes in Precipitation and Runoff Regimes

A modified seasonal pattern of runoff in streams and rivers in response to climate change will alter species composition and ecosystem productivity. The seasonal pattern of precipitation falling on a watershed is translated into surface runoff that feeds into streams and rivers. In ecological terms, the extremes of runoff are critical events that influence species composition and the productivity of aquatic and wetland communities (Resh et al., 1988; Poff et al., 1997; Meyer et al., 1999). Streams in the northern tier of states and in much of the mountainous West have snowmelt runoff regimes characterized by a predictable period of high flow in late spring followed by a predictable period of late summer, fall, and winter baseflow. By contrast, in the deserts of the Southwest, winter flows are very variable; summer flows are usually very low because of lack of rainfall, but intense monsoonal thunderstorms can create flash flooding. In the eastern United States, precipitation is generally high enough to sustain year-round flow in streams. Thus, knowledge of the particular regional changes in streamflow regimes brought about by climate change is critical to anticipating ecological impacts. Some projections are reasonably well supported and others need to be considered as possible scenarios to evaluate the range of ecological concerns related to a changing climate.

Early Snowmelt Runoff

One major consequence of global warming will be a shift from spring peak flows to late winter peaks in snowmelt-dominated regions (Frederick and Gleick, 1999). Many of the life history characteristics (e.g., reproductive strategies) of both aquatic and riparian species have evolved to avoid or take advantage of the predictable high spring flows in these ecosystems. For example, many fish in snowmelt streams time their reproduction so their young can avoid stressful spring peak flows. Some species lay eggs in the fall that hatch before snowmelt runoff. High winter flows associated with rain or rain-on-snow events can scour the streambed and destroy these eggs (Erman et al., 1988; Montgomery et al., 1999). In streams of the Sierra Nevada in California, native trout that lay eggs in the late spring are favored in years when large winter floods occur, whereas non-native trout that lay eggs in the fall are favored in years when high flows do not occur until the spring, after the young have emerged from the stream gravel (Strange et al., 1992). Further, increased streamflow and associated increases in water velocities during winter and spring could reduce the number of salmon successfully returning from the sea because these fish rely on accumulated energy reserves to reach upstream spawning areas (Hinch et al., 1995). Cottonwood trees provide important riparian habitat for many terrestrial animals along streams throughout the West, and their ability to successfully reproduce and replace themselves along streams and rivers depends on high spring flows from snowmelt that inundate floodplain habitat (Rood and Mahoney, 1990; Auble et al., 1994). A warmer climate that reduces the magnitude of spring flows could have broad impacts throughout this region.

Another significant consequence of a shift from snow to rain in high elevation or northern basins is the reduction in streamflow in late summer. This is expected even if winter precipitation increases in northern latitudes as projected, because excess precipitation will not be stored as snow, which provides a source of runoff to sustain late summer baseflow in arid highlands (see Frederick and Gleick, 1999). Lower summer baseflows translate into less instream habitat for invertebrates and fish. Further, less water in the stream channel means less water flowing into stream-side groundwater tables, which are important for sustaining riparian tree communities (Stromberg et al., 1996; Scott et al., 1999). These ecosystems are likely to experience very significant changes in species composition and productivity.

Increased Precipitation Variability

Some climate change models predict possible increases in the intensity of rainfall on fewer rain days (Kattenberg et al., 1996), as has already been observed for precipitation data in the United States over the last century (Karl et al., 1996). The implications for streams and rivers are significant. For example, in a historical reconstruction of flood histories for upper Mississippi River tributaries over the last 7,000 years, Knox (1993) found that small shifts in temperature (1-2°C) and precipitation (10-20 percent) caused sudden changes in flood magnitude and frequency. Because the transport and storage of nutrients and pollutants depend on flow, an increase in floods would probably result in more silt and pollutants entering streams and rivers. The corresponding degradation in water quality could lead to a loss of sensitive stream species (Waters, 1995). Further, floods scour the streambed and displace stored organic carbon (food resources for many species), bottom-dwelling organisms, and small fish fry. A well-developed empirical literature suggests that a substantial increase in flood frequency would cause a shift in species composition and perhaps eliminate many species (see Poff et al., 1997).

Reduced Streamflows

Even if flooding increases in magnitude and frequency, earlier snowmelt and higher temperatures could still result in lower summer streamflow in many areas. In addition, some areas could become generally drier. Periods of low flow in streams and rivers are particularly stressful for aquatic and riparian ecosystems. The drying of streams into isolated pools crowds organisms and results in reduced dissolved oxygen levels. In arid regions, periods of prolonged low flows are common, but even in these streams, rewetting is critical to maintaining high diversity. Prolonged dry periods could selectively eliminate biota that require wetter conditions (Larimore et al., 1959; Boulton et al., 1992; Stanley et al., 1997). In more humid regions characterized by greater annual precipitation, such as the eastern United States, periods of no flow are less common. Accordingly, increasing the duration of no-flow periods in these streams would represent a large deviation from usual conditions and thus be very damaging ecologically. One previous analysis has suggested that a 10 percent decline in annual runoff in eastern streams that have little groundwater inputs could result in nearly half of these small streams ceasing to flow in some years (Poff, 1992). Reduced water depths may not only eliminate habitat for aquatic organisms but also increase the vulnerability of sensitive species (e.g., amphibians) to harmful ultraviolet radiation (Kiesecker et al., 2001).

Many aquatic communities in large rivers are partially dependent on riparian floodplains, either for nursery habitat for fish or for seasonal export of nutrients from floodplain wetlands to the river (Meyer and Edwards, 1990; Sparks et al., 1990; Bayley, 1995). If these floodplains become disconnected from the main rivers because of reduced streamflows, aquatic productivity and diversity may decline.

B. Lakes

Lakes are very vulnerable to climate change. The historical record clearly indicates that during previous periods of climate change, the distribution of lakes changed dramatically as the balance among precipitation, evapotranspiration, and runoff shifted (Street and Grove, 1979).

Many of the physical and chemical features of lake ecosystems depend on the depth of the lake, the amount of heat it absorbs from and releases to the atmosphere, the supply of nutrients to the lake from the watershed, and the retention time of water in the lake. Together, these factors determine the thermal characteristics and dissolved oxygen availability in the lake, which influence habitat suitability for species and the lake's seasonal and annual ecosystem productivity. Because of differences in size and geographic variations in temperature and watershed runoff among lakes, they provide a very wide range of habitats for freshwater species. Predicting the consequences of climate change for any particular lake is dependent on an understanding of how species composition in that lake will change (Carpenter, 1988; Lodge, 2001).

Changes in Temperature

Warming of lakes will increase the potential for production of nuisance algae, a phenomenon that will be exacerbated where predatory fish are eliminated due to loss of suitable thermal habitat. As lakes warm in the spring and summer, they develop a less dense upper layer and a cool, more dense lower layer of water. The upper layer has high oxygen levels even into late summer, because winds mix the waters to expose them to the air. Because of high light levels, the surface waters are very productive, especially where watershed nutrient supply is high. The lower layer is colder and does not mix with the atmosphere. Dead organic material (phytoplankton, zooplankton, etc.) from the productive surface waters falls into these deep waters, where bacteria and other bottom-dwelling organisms consume them and deplete oxygen in the lower depths. The depletion of oxygen means that, by late summer, these deep waters may become marginal habitats for many invertebrates and fish.

This condition of oxygen starvation is exacerbated in those lakes that have a high natural or human-caused supply of nutrients. Indeed, human activity has resulted in significant runoff of nitrogen and phosphorus into most lakes in North America, which are now much more productive (eutrophic) than they would be in the absence of human activities (Carpenter et al., 1998). If large and productive lakes warm too much, they may have insufficient oxygen in deeper, cool water in late summer to support large game fish. Whole-lake experiments have shown that when key predatory fish species are eliminated, smaller fish increase in abundance and reduce zooplankton populations, thereby allowing algae to proliferate (Carpenter and Kitchell, 1993). This cascade of effects can directly result in a decrease in water clarity.

Predicting the effects of altered thermal regimes on fish is complex (Stefan et al., 1995). In many studies, the effects of a doubling of CO_2 on aquatic thermal regimes have been modeled to evaluate responses of individual fish species whose thermal preferences are reasonably well known. In large, deep lakes (e.g., many of the Great Lakes), suitable thermal habitats are expected to increase for almost all fish. Not only will fish thriving in warmer waters benefit, but cold-adapted fish will probably also benefit from a slight warming of deep, cold waters which are expected to retain sufficient oxygen even under a doubling of CO_2 and a temperature increase of 3.5°C (Magnuson et al., 1997). In smaller and shallower lakes, by contrast, the entire lake volume is likely to warm significantly, and fish requiring cold water (especially large, predatory fish) will suffer from a reduction in habitat. Oxygen concentrations will decline in these warmed waters, further degrading deep-water habitat during the stressful summer months. Even larger lakes, if shallow, could experience a substantial warming and loss of oxygen from the lake bottom, especially if human pollution is substantial, as in Lake Erie (Blumberg and DiToro, 1990). In very small, eutrophic lakes, by contrast, prolonged ice cover prevents the lake from absorbing oxygen from the atmosphere, and depletion of dissolved oxygen in winter often causes die-backs in fish populations. In these lakes, climate warming may enhance survival of fish in winter (Fang and Stefan, 2000).

In a thorough study, Stefan et al. (2001) simulated the effects of a doubling of CO_2 on 27 lake types (defined by combinations of three categories of depth, area, and nutrient enrichment) across the continental United States and examined the responses of fish species to projected changes in lake temperature and dissolved oxygen. They found that suitable habitat would be reduced by 45 percent for cold-water fish and 30 percent for cool-water fish, relative to historical conditions (before 1980). Shallow and medium-depth lakes (maximum depths of 4 meters and 13 meters, respectively) were most affected. Habitat for warm-water fish was projected to increase in all lake types investigated.

Because warmer waters support more production of algae, many lakes may become more eutrophic due to increased temperature alone, even if nutrient supply from the watershed remains unchanged. Warm, nutrient-rich waters tend to be dominated by nuisance algae, so water quality will decline in general under climate change (see also Murdoch et al., 2000). The possible increase in episodes of intense precipitation projected by some climate change models implies that nutrient loading to lakes from storm-related erosion could increase. Further, if freshwater inflows during the summer season also are reduced, the dissolved nutrients will be retained for a longer time in lakes, effectively resulting in an increase in productivity. These factors will independently and interactively contribute to a likely increase in algal productivity.

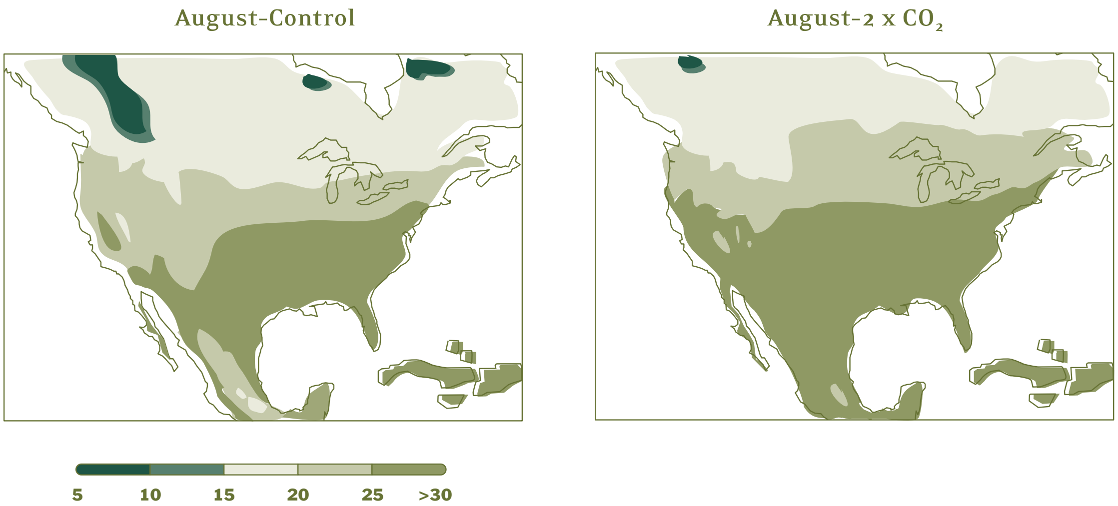
Hostetler and Small (1999) assessed the sensitivity of lakes across all of North America to climate change using models that simulate seasonal thermal evolution in response to atmospheric forcing. Their models project that under CO_2 doubling, future water temperatures would increase substantially because of increased atmospheric temperatures and reduced winter ice cover. Regional variation in warming would be significant, with surface water temperatures in midwestern and southern lakes and reservoirs increasing by up to 7°C in summer (Figure 3). Many lakes and reservoirs would have surface water temperatures exceeding 30°C, which would be ecologically significant. They found the magnitude of warming to be similar for both deep and shallow lakes within a region.

Changes in Watershed Runoff

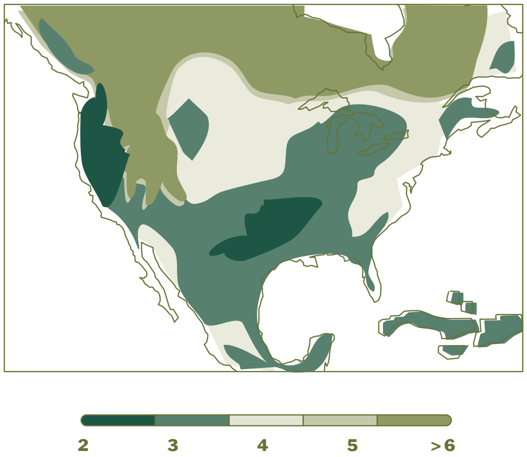
Altered stream inflows into lakes can cause complex ecosystem responses in lakes by changing lake depth and modifying water temperatures. One of the most direct effects will be reduced lake levels, although areas that become wetter could have higher lake levels. Even large lakes are vulnerable. Indeed, the extent of potential lake-level declines in

Figure 3

Ten-Year Average Lake Temperatures (°C) simulated using the Canadian Climate Center Atmosphere Ocean General Circulation Model (CGCM1) as input data



Summer (June-August) differences
(2 x CO_2 minus control)



Source: Hostetler and Small (1999).

some of the Great Lakes is projected to exceed the rate of change projected for sea-level rise (Chao, 1999). Permanent lowering of lake levels will expose more shoreline, possibly harming productive littoral (near-shore) zones and coastal wetlands of the Great Lakes (Magnuson et al., 1997). Many of these lake-fringing wetlands may become isolated, reducing habitat for fish that require wetlands for spawning and nursery habitat (Brazner and Magnuson, 1994). The effects of water-level reductions in smaller lakes could be equally profound.

A more subtle and indirect effect of reduced stream inflows is potential lake warming. Inflowing streams transport dissolved organic carbon (DOC) from the terrestrial landscape into lakes. Aside from its importance as a nutrient, DOC absorbs the light energy passing through the lake's water column. A reduction in the delivery of DOC to lakes allows light to penetrate more deeply into the water column, thereby heating the lake to greater depths. Thus, if streamflows are reduced (e.g., in summer), warmer (and less-oxygenated) water may extend to deeper levels in lakes. This reduces the cool-water habitat refuge of deep water that many fish require. Additionally, ultraviolet light can penetrate more effectively in surface waters where DOC is reduced. This harmful light can diminish algal productivity in surface waters, further clarifying the water, which allows light to penetrate even deeper and heat the lake (Schindler et al., 1990).

Evidence of this effect of reduced inflows on lake ecosystem processes was documented empirically in western Ontario, Canada, between 1969 and 1989, a period of low precipitation, high evaporation, and subsequent low stream inflow to lakes. Lakes were not flushed as often with new water, and concentrations of chemicals in both lakes and streams increased. DOC levels dropped as well. As a result, dissolved oxygen levels dropped and some fish stocks were threatened (Schindler et al., 1990; 1996).

Range Expansions and Contractions of Lake Species

Warming of lakes will allow fish and other aquatic species that are currently restricted in their distribution by very cold water temperatures to expand their ranges (Mandrak, 1989). Under a doubling of CO_2, range expansions of warm-water species can be expected, maybe up to 500 kilometers north on average (Eaton and Scheller, 1996). However, the rate and extent of migration will depend on availability and access to dispersal corridors. Successful dispersal of fish depends on the degree to which lakes are interconnected via streams and the kinds of physical barriers that may exist in connecting streams

(Magnuson et al., 1998; Hershey et al., 1999; Olden et al., 2001). In many glaciated regions, lakes are interconnected by streams and species are able to move across the landscape.

In general, fishery yields decrease with increasing latitude (Regier et al., 1990), and because warming of northern lakes will increase available habitat for warm-water fish, these lakes may support a more diverse and productive fishery (Carpenter et al., 1992). However, the importance of interactions among new mixes of species is unknown, especially when large predatory species are included in the mix (Rouse et al., 1997; see above section for discussion on the consequences of introducing large predators).

C. Freshwater Wetlands

Shallow freshwater wetlands are already stressed as ecological transition zones between aquatic and upland terrestrial ecosystems, making them particularly sensitive to changes in temperature and precipitation. Freshwater wetlands have been extensively altered by humans. More than half of the wetlands in the lower 48 states have been converted to other uses since the mid-1700s (NRC, 1995). Many of those that have not been converted exist in a degraded condition because of the cumulative effects of altered flow regimes, removal of timber, and deterioration of water quality due to human development and encroachment (NRC, 1992). Because freshwater wetlands provide many critical goods and services (see Table 1), they have become highly valued by large sectors of society; yet human activity still threatens these sensitive ecosystems. Climate change is expected to further stress wetlands, because increasing temperatures will affect species growth and reproduction, and altered water regimes will change soil and vegetation conditions (Burkett and Kusler, 2000; Winter, 2000).

Freshwater wetlands provide habitat for species that have adapted to widely varying soil moisture and chemical conditions. Purely wetland species are often habitat specialists that can survive nowhere else on the landscape. Further, wildlife populations are increasingly using wetlands as refuges as humans modify other types of ecosystems (Calhoun, 1999). For this and other reasons, wetlands are very important contributors to biodiversity and wildlife in most landscapes (Brinson and Verhoeven, 1999).

The driving force of wetland ecosystems is the hydrologic regime, because it regulates the “wetness” of the wetland. The patterns of water depth, and the duration, frequency, and seasonality of flooding together constitute a wetland’s hydroperiod, which determines its vegetation composition, habitat for aquatic organisms, and other ecosystem characteristics (see Box 2). Viewing wetlands according to hydroperiod is perhaps the best way to consider potential effects of climate change. For example, in floodplain swamp forests, trees such as bald cypress are indicative of long periods of flooding. A shorter hydroperiod under drier conditions will allow species that are not as tolerant of prolonged soil saturation and oxygen deprivation to invade. By contrast, a longer hydroperiod normally results in tree death and eventual replacement by aquatic plants.

Carbon dioxide enrichment has the potential to alter species composition in some wetland types, independently of hydrologic or temperature changes. Some groups of plants are more responsive to higher CO_2 concentrations than others because of fundamental physiological differences. Marshes on the Chesapeake Bay, where most relevant studies have taken place, show quite striking increases in photosynthesis when CO_2 levels are raised. These studies suggest that, over the long term, the more responsive plant species may eventually crowd out the less responsive ones (Arp et al., 1993). However, there are many caveats, not the least of which is the difficulty of scaling up from individual plant responses to whole ecosystem responses, where many variables other than just CO_2 are important. In addition, it is difficult to generalize about the effects of CO_2 on wetlands because of uncertainty about changes in other important factors such as water use efficiency, insect and fungal damage, and soil bacterial activity (Thompson and Drake, 1994). Therefore, broad-scale generalizations of the effect of CO_2 enrichment on wetland communities are not currently feasible (Marsh, 1999).

Responses to CO_2 enrichment are further masked by human-caused enrichment by nitrogen and phosphorus. It is common for aggressive plants (including non-native invasive species) to dominate when excess nutrients are available. Indeed, in low-fertility sites such as bogs and some lake shorelines, nutrient enrichment is known to favor weedy, aggressive species that can outcompete the native dominant species as well as rare and endangered species (Wisheu and Keddy, 1992). In these settings, additional CO_2 enrichment may contribute to the loss of sensitive species and thus reduce regional plant biodiversity.

Effects of Altered Water Regime

The vulnerability of wetlands to a drying climate depends, in large part, on the sources of their water supply. The dominant sources of water to wetlands are precipitation, surface flows, and groundwater discharge (Brinson, 1993). As a general rule, wetlands that are fed mainly by precipitation are the most likely to lose wetland characteristics in a drying climate. Groundwater-driven sites that have large volumes of available water stored in aquifers will have the greatest resistance to climate change (Winter, 2000). The responses of surface-flow wetlands will be somewhere between those types.

Wetlands dominated by precipitation are already at the “dry end” of the spectrum of wetland types. They tend to occur in flat landscapes with low soil drainage in humid climates, such as parts of the eastern United States and Alaska. If the climate were to dry, these wetlands would contract, resulting in the loss of locally unique species such as orchids and insectivorous plants characteristic of acidic peat bogs. Plant species less tolerant of flooding would dominate, and, over time, soils would dry to the point that they would no longer support the nutrient cycling processes unique to wetland soils. Peat-based wetlands would be especially hard-hit as the highly organic soils undergo oxidation and subsidence, thus altering drainage patterns, topography, and exposure to fire. In a more humid climate, precipitation-dominated wetlands could expand, assuming no barriers from competing land uses.

The hydroperiods of many wetlands are driven by surface waters such as adjacent rivers and lakes. Climate change that alters hydrologic regimes of rivers and lakes will have ecological impacts on these wetlands. For example, a reduction in the frequency or magnitude of high flows that inundate the floodplain would tend to dry out floodplain wetlands, isolate them from the adjacent stream or river, and replace wetland plant species with more terrestrially adapted species (Johnson et al., 1976; Auble et al., 1994). Floodplain wetlands along rivers with a snowmelt hydrology may be particularly harmed, because peak flows from seasonal snowmelt may disappear (see earlier section on streams and rivers). Analogues of this effect are seen below dams on impounded rivers, where reservoirs store flood flows and thus “shave” downstream flood peaks, transforming floodplain forests to species adapted to drier conditions (Auble et al., 1994).

Lake fringe wetlands also tend to be driven by surface water, responding to both seasonal and interannual variations in lake water levels. Multiannual cycles cause the position of these types of wetlands to migrate back and forth across shallow shorelines (Keough et al., 1999). Their susceptibility to climate change will depend largely on shoreline morphology. For example, deepening of water under a wetter climate would eliminate some wetland plant species, especially in areas where the shoreline is too steep to allow plants to become established. Lower water levels would require that plants become established further lakeward, but this could only happen if protective barrier beaches form along the shoreline (Kowalski and Wilcox, 1999). This is of particular importance for the Great Lakes, where lake levels might drop significantly under projected climate change (Chao, 1999; NAST, 2000).

Groundwater is the principal water supply for many wetlands. If climate becomes wetter, rising water tables will expand wetland areas and make existing wetlands even wetter. Under a drier climate, the opposite will occur. For example, declines in water tables in the prairie pothole region of the Dakotas will cause many seasonal wetlands that typically remain flooded well into the summer to dry out weeks earlier. This is the most important region in North America for breeding waterfowl. Using models that calibrate waterfowl populations and pond numbers to the Palmer Drought Severity Index and general circulation models (GCMs), Sorenson et al. (1998) predicted that breeding bird populations would be reduced to about 50 percent of present long-term averages in response to reduced precipitation and temperature increases of up to 4°C.

Drawdown of water for human uses provides additional insight into the effects of a drier climate on groundwater-dominated wetlands. In the northern Tampa Bay area of Florida, peat-based cypress domes have dried out because of drawdown for human consumptive use. This has caused the peat to oxidize and collapse, resulting in more destructive fires, invasion of weedy upland plants, and abnormally high tree-fall (Rochow, 1994). Other factors come into play for wetlands in arid climates, most of which receive groundwater as their dominant source. For example, riparian cottonwood forests in the arid West have died as a result of groundwater pumping (Scott et al., 1999). These human-induced changes, however, typically occur much more abruptly than those expected from a drier climate. Further, because many groundwater-supplied wetlands are supported by large aquifers, these wetland types may be affected less by climate change than wetlands supplied by precipitation and surface water (Winter, 2000). However, if conditions become drier, there is likely to be increased human demand for groundwater (Frederick and Gleick, 1999), which could negatively affect these wetland types.

Changes in Temperature

Extensive regions throughout boreal and arctic zones of Alaska and Canada are covered by wetlands made up of organic-rich soils underlain with permafrost. The warming predicted for these regions will increase the depth at which the ground stays frozen (i.e., lower the permafrost table), resulting in drainage that will expose the peat to the atmosphere, thus increasing the rates of organic decomposition and the release of CO_2 and methane (Gorham, 1991). Given the probability of increased fire frequency and intensity that accompanies drier conditions, more peat will tend to burn under a warmer climate. Carbon dioxide and methane generated from these sources would stimulate a positive feedback to global warming (Gorham, 1991).

Groundwater-dominated wetlands, or fens, are also an important habitat for many rare species of plants and animals. Because groundwater travels slowly through subsurface pathways, it is buffered from atmospheric temperature extremes. Thus, the thermal regimes of fens are much cooler in the summer and warmer in the winter than adjacent surface waters. Many fens support wetland plant and animal species that normally occur in abundance only much farther north, where summer water temperatures are cooler (Cooper, 1996). These species were probably once common in the southern end of their current ranges when the climate was cooler, but they are now isolated. Thus, a change in future climate that eventually warms groundwaters will cause a loss of these species from the southern end of their ranges.

Plant and Animal Movements in a Changing Climate

The geographic distributions of plants and animals living in freshwater wetland ecosystems may shift in response to a changing climate. Because the types of wetlands defined above occur in all climates (except those dominated by precipitation), transformation to a warmer and drier (or wetter) climate in a particular region will produce conditions that already exist for wetlands in a similar climate at a different geographic location (Michener et al., 1997). For example, silver maple/ash/elm forests of the upper Midwest could be replaced by cypress/tupelo swamps, currently limited to the Southeast and along the Mississippi Valley. Treeless tundra wetlands of the Alaska North Slope permafrost could be replaced by black spruce peatlands with discontinuous permafrost. In each case, colonization by wetland plants and animals could be determined by the addition of species that migrate to their more favorable climatic conditions elsewhere and the removal of species that become locally extinct because of changing environmental conditions. Species that survive the changed conditions have traits that are suited to the new environment. To some extent these traits allow predictions of survival under future environmental conditions (Keddy, 1992).

If all species had instantaneous dispersal powers in response to climate change, and enough was known about the tolerances of individual species, it might be possible to predict with great accuracy the responses of species to changing climate. However, such predictions are precluded by many confounding factors, including formidable barriers to migration (both natural and human-caused, such as dams and dikes), changes in frequency and seasonality of fires, and modification of water quality. Species vary greatly in their abilities to disperse, so the success of plants and animals in colonizing suitable habitats under a changing climate will be highly variable. Many recently introduced, non-native species have expanded rapidly across the landscape, and analysis of their mode of colonization may allow insight into which native species may be best able to disperse successfully under a changing climate (Galatowitsch et al., 1999). These invaders may be expected, however, to interfere with the gradual spread of indigenous wetland plants, because the invaders are able to rapidly expand their range and to monopolize available space and nutrients before indigenous plants can arrive (Galatowitsch et al., 1999). Further, the proliferation of these exotic species is favored by human activities unrelated to climate change (e.g., altered hydrology, nutrient loading, and sedimentation). For some wetland species, geographic barriers are so formidable that they are unlikely to be overcome in the time frame projected for climate change. For example, the flora of alpine wetlands, restricted to the highest peaks in the continental United States, are particularly vulnerable, because an increase in temperature will eliminate species that require cold thermal regimes (Halpin, 1997).

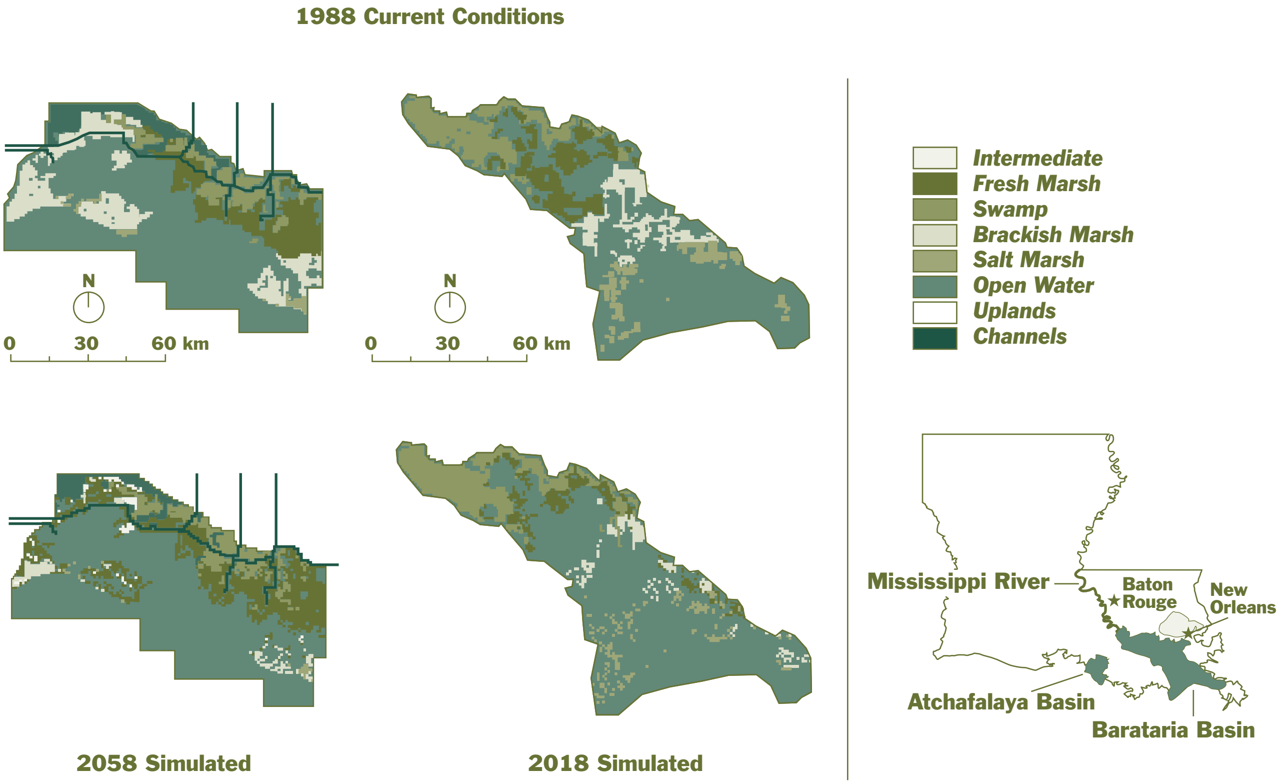
D. Coastal Ecosystems

Potential changes in temperature and hydrologic regimes projected to occur over the next 100 years will most likely lead to loss of coastal wetlands, deterioration of water quality, and disruptions in fisheries. Sea-level rise, sediment starvation, and changing species composition in coastal wetlands all threaten the sustainability and resilience of these systems. Coastal wetlands and estuaries are among the most productive ecosystems on earth (Day et al., 1989). The high productivity of these systems is related to the inputs of freshwater and to the fluctuating water levels caused by the ocean tides. Freshwater inputs to estuaries deliver not only nutrients that support high production, but also large quantities of suspended sediments, which are critical to the accretion of wetland soils that allow plants to avoid permanent inundation by the sea. In addition, the mixing of freshwater and seawater in estuaries creates water circulation patterns that tend to retain nutrients, which further enhances coastal ecosystem productivity. Coastal wetlands support dense populations of animals, many of them migratory and of great commercial value (see Table 1). The movements of many migratory aquatic animals (e.g., crabs, fish) to deeper sea water are regulated by estuarine salinity, which changes as freshwater inflows mix with tidal salt water. Temperature conditions are also an important environmental cue for migration. Further, water temperature regulates many ecological processes and the distribution of many coastal wetland species.

Coastal wetland ecosystems are also among the most altered and threatened natural systems. Important impacts include increased nutrient loading leading to eutrophication, direct loss through habitat destruction, changes in hydrology, introduction of toxic materials, and changes in species composition due to over-harvest and introduction of new species (Day et al., 1989; Mitsch and Gosselink, 1993; Neumann et al., 2000). Most coastal wetland loss has been due to draining and filling. In some coastal states, such as California, almost all coastal wetlands have been lost. In the largest coastal ecosystem in the United States, the Mississippi Delta, restriction of river sediment input is largely responsible for massive wetland loss (Figure 4). Coastal eutrophication is a growing problem because of increasing inputs of nutrients from

Figure 4

Landscape Model Simulations of parts of the Mississippi Delta showing the importance of riverine input to the future development of the delta



The two maps on the right show the Barataria Basin, a sub-estuary of the Mississippi that does not receive riverine input because of the presence of river levees. The two maps on the left show the Atchafalaya Basin, a sub-estuary that receives about 30 percent of the total flow of the Mississippi River. In each case, the upper map presents actual habitat coverage in 1988, while the lower maps shows future conditions as simulated by the landscape model (Box 3). The different colors represent different coastal wetland habitat types as indicated by the legend. The 2018 simulation of the Barataria Basin shows that much of the wetlands of the basin will disappear due to a combination of subsidence and sea-level rise. For the Atchafalaya Basin, the three blue lines entering the maps from above are river channels. The left channel is a small local river, while the two right channels are the two mouths of the Atchafalaya River. The 2056 simulation dramatically shows the effects of high riverine input in two ways. At the two mouths of the river, new wetlands are created as sediments from the river are deposited in the shallow bay. In addition, the existing wetlands are stable in strong contrast to the high wetland loss in the Barataria Basin.

Source: Images provided by Dr. Enrique Reyes, Coastal Ecology Institute, Louisiana State University. More information on the landscape models can be found at www.lsu.edu/guests/wwwcei.

agriculture, industry, and human populations. The combined effects of climate change, wetland loss, and eutrophication will be worse for wetlands than the impacts of these individual stresses acting alone.

Coastal wetland plants thrive in a relatively harsh intertidal environment characterized by alternate flooding and draining of salt marshes with associated waterlogging of soils, depletion of oxygen, and production of natural toxins that inhibit plant growth. To cope with these harsh conditions, plants have a number of adaptations, including the production of aerial roots and submerged tissues that allow them to capture oxygen needed by the roots. But these adaptations are suitable only as long as the average water level remains relatively constant. Accordingly, coastal wetlands exist within a fixed elevational range, where the frequency and duration of inundation by seawater are relatively constant (McKee and Patrick, 1988). Because plants become progressively more stressed and ultimately die if they are inundated for too long (Mendelssohn and McKee, 1988), an increase in water levels due to sea-level rise can severely stress the integrity of coastal wetland ecosystems.

Sea-level rise over the last several decades has reportedly led to salinity intrusion and wetland loss in a number of coastal areas around the world and in the United States, including Long Island (Clark, 1986), the mid-Atlantic region (Kana et al., 1986; Hackney and Cleary, 1987), Chesapeake Bay (Stevenson et al., 1988), and the Mississippi Delta (Salinas et al., 1986; Conner and Day, 1989; Day et al., 2000). Since sea-level rise over the last century is two to nine times lower than the projected 20-90 centimeters of sea-level rise expected over the next 100 years (Neumann et al., 2000), there is great concern for the potential loss of coastal wetlands in the United States and globally. The projected rise in sea levels under global climate change will certainly place these productive and important ecosystems under additional stress, with the very likely result of extensive dieback of plants residing in the current intertidal zone. For example, a 0.5 meter rise in sea level would inundate about 12,000 square kilometers (about 4,600 square miles) of coastal wetlands, most of which would likely be lost (Neumann et al., 2000).

Vertical Accretion: Key to Wetland Survival

For coastal wetlands to persist in the face of projected sea-level rise, the soil surface must accrete vertically at a rate two to nine times that observed over the last century. During periods of sea-level rise, coastal wetlands can persist only when they accrete soil vertically at a rate at least equal to water-level rise (Cahoon et al., 1995a). A number of studies have shown that coastal marshes are indeed able to accrete at a rate equal to the historical rate of sea-level rise (1-2 millimeters per year; Gornitz et al., 1982) and persist for hundreds to thousands of years (Redfield, 1972; McCaffey and Thompson, 1980; Orson et al., 1987). Given that sea level is projected to increase up to two to nine millimeters per year over the next 100 years, soil accretion will have to occur at a much higher rate than that observed over the last century. In the Mississippi Delta, for example, where there is sufficient sediment input from the river, accretion rates greater than 10 millimeters per year have been measured (Day et al., 2000). Such accretion rates are possible in other systems as well, if sufficient sediment is available.

The rate at which accretion occurs is a function of the combination of the inputs of both inorganic and organic material to the soil. Organic material is mostly derived from the growth of plant roots, whereas inorganic material is mostly supplied in the form of sediments that come from either the sea or freshwater sources. Riverine sediments are generally more important because their input is more frequent and they contain nutrients that enhance organic soil formation. Many rivers emptying into coastal estuaries now carry only a fraction of the inorganic sediment that they did historically. For example, sediment discharge to the Mississippi Delta has decreased by over 50 percent since 1860, largely due to the building of Missouri River dams, which capture and store the suspended sediment in the river water, resulting in a significant loss of coastal wetlands (Kesel, 1989).

Given these reduced sediment loads, one management strategy to offset sea-level rise and promote continued coastal wetland productivity is to actively use existing riverine sediments rather than letting most of them flow out to sea. An example of this is given for the Mississippi Delta in Box 3. Although wetlands are able to migrate inland as sea levels rise, in many cases barriers of human development exist that preclude effective migration. Also, rapid increases in elevation often characterize the uplands bordering coastal wetlands, which means that upland migration could support only a small fraction of the wetlands expected to be lost to rising sea levels.

The Impacts of Changes in Freshwater Input to Coastal Systems

Changes in freshwater runoff to coastal wetlands will alter the availability of sediment needed to accrete soils as sea levels rise. For much of the U.S. coast, most GCMs agree that winter and spring rainfall will increase, although there is disagreement among models as to whether precipitation will increase or decrease in summer and fall (Wigley, 1999). Thus, there is the potential that freshwater discharge to coastal systems will increase during some seasons but decrease during others. Increased freshwater input

Box 3

The Mississippi Delta: A Case Study of Accelerated Sea-Level Rise

Deltas can serve as models for studying the effects of accelerated sea-level rise because most deltas are currently undergoing a high rate of relative sea-level rise (RSLR), the total change in the level of the sea relative to the land surface (Day and Templet, 1989). This is due to a combination of change in the volume of water in the oceans (eustatic sea-level rise) and movement of the land surface. Deltas naturally sink as the soft sediments deposited on them by rivers consolidate and compress under their own weight. Essentially, deltas and their associated wetlands are subsiding, often at a faster rate than they are being built up by addition of organic and inorganic soil formation. Where the sediment supply from rivers has been greatly reduced, the rate of buildup is less than RSLR. Because of this, the wetlands experience more flooding. For example, while the current rate of sea-level rise is between 1 and 2 millimeters per year (Gornitz et al., 1982), the RSLR in the Mississippi Delta is about 10 millimeters per year (Baumann et al., 1984). Other deltas such as the Nile, Rhone, and Ebro also have high rates of RSLR (L'Homer, 1992; Stanley and Warner, 1993; Ibañez et al., 1996).

In the Mississippi Delta, the effects of the interaction of a high rate of RSLR and human management can be seen. Landscape simulation models of the delta show the effects of RSLR with and without riverine input of inorganic sediments that contribute to vertical soil accretion, which is necessary to maintain the viability of coastal wetland plants (Martin et al., 2000; Reyes et al., 2000). These landscape models use hydrologic submodels to move water, salt, nutrients, and sediments over an area divided into several thousand individual cells. Each cell has its own submodels of plant production and soil formation. Decision rules are used to determine if there will be land loss or gain based on salinity and flooding. The models successfully duplicated historical patterns before being used for future simulations. In the Barataria and Terrebonne coastal basins, which are isolated from the Mississippi River and its nourishing sediment supply, there are high rates of loss of coastal wetlands (Figure 4). In the Atchafalaya coastal basin, which receives direct input of river water, land loss has been very low and wetland area is projected to increase over the next half-century (Figure 4). Day et al. (1997) concluded that the riverine input to the Mississippi Delta wetlands is important in allowing these wetlands to survive accelerated sea-level rise.

Most of the wetlands along the Atlantic and Gulf coasts are not associated with sinking deltas; therefore, they will become inundated more frequently because of eustatic sea-level rise over the next century, similar to that now being experienced by wetlands in the Mississippi Delta because of RSLR. Therefore, comparable vertical accretion rates will be needed to keep these coastal marshes intact. This means that the rate of accretion for most Gulf and Atlantic marshes would have to increase by 2-9 millimeters per year above current rates. Studies in the Mississippi Delta suggest that active management of sediment-laden riverine inputs could be employed to sustain coastal wetlands. It is likely that sufficient sediments and nutrients exist for this purpose, but management must ensure that these are trapped by marshes and not transported out to sea.

As with any large-scale ecosystem manipulation, there are inherent uncertainties in the outcome. In the Mississippi Delta, current evidence suggests that river diversions that bring sediment to coastal marshes can be carried out without detrimental impacts on water quality (Lane et al., 1999). However, there is a risk that such diversions of water may contribute to a degradation of water quality, mainly by encouraging nuisance algal blooms. As more information is gathered over the coming years, the ecological consequences of large-scale sediment management should become more clear. But information currently available suggests that introduction of sediment-laden water into coastal wetlands results in increased accretion, which can help these wetlands survive accelerated sea-level rise.

can have both beneficial and detrimental impacts on coastal systems. The benefits associated with vertical soil accretion have already been highlighted. An additional benefit could be an increase in fisheries production in coastal systems (Nixon, 1988). This could result because the nutrients in freshwater flowing into estuaries stimulate primary production, which in turn increases the energy available for organisms on which fish forage. In the Mississippi Delta, these diversions add sediments that increase accretion, lower salinity to combat saltwater intrusion, and benefit fisheries and wildlife. There is concern, however, that diversions will lead to algal blooms because of the added nutrients (see next paragraph) and that they will add pollutants, which may severely affect organisms in these areas. Thus, diversions will have to be studied and managed carefully to avoid problems. On the other hand, decreased freshwater inputs are likely to lead to less accretion, lowered productivity, and saltwater intrusion.

One potential negative impact associated with an increase in freshwater runoff to coastal ecosystems is an excessive increase in nutrients. There is already considerable evidence that agricultural runoff and wastewater from human activity in tributary watersheds are degrading many coastal ecosystems. Nuisance algal blooms and low oxygen in bottom waters kill fish and shellfish, as has been well documented in the Chesapeake Bay (Kemp et al., 1992; Harding and Perry, 1997) and off the coast of Louisiana in the so-called Gulf Dead Zone (Rabalais et al., 1996). The increased runoff will also lead to problems with toxic pollutants (e.g., heavy metals, organic chemicals) if there are high levels of these chemicals in the runoff.

Several suggested changes in environmental management have been made to reduce high nutrient loading to streams and coastal waters. For the Mississippi River basin, for example, these recommendations include changes in farming practices, use of buffer strips along steams, protection of wetlands to improve water quality, and reduction of nitrate in river water by diversions in the Mississippi Delta (Mitsch et al., 1999).

The Effects of Higher Temperatures on Coastal Vegetation and Fisheries

With a warming of waters in coastal wetlands, substantial shifts in species composition are expected. One important likely result of increasing temperatures along the southeast U.S. coast will be a northward migration of mangroves, which will replace salt marshes. Mangroves are tropical coastal forests that are frost-intolerant. Chen and Twilley (1998) developed a model of mangrove response to the frequency of freezes. They found that when freezes occurred more often than once every eight years, mangrove forests could not survive. At a frequency of 12 years, mangroves replaced salt marsh. Along the Louisiana coast, freezes historically occurred about every four years. By the spring of 2001, however, a killing freeze had not occurred for 13 years, and small mangroves are found over a large area. If this warming trend continues, mangroves will spread even further, over much of the northern Gulf and part of the South Atlantic coast.

Because mangroves have many of the same ecological functions as salt marshes (high productivity, habitat for wildlife and fish, sites of nutrient uptake, etc.), a switch in U.S. coastal wetlands from salt marshes to mangroves might not change ecosystem function. However, if the climate becomes more variable, with frost-free periods interspersed with occasional hard freezes, it could be more difficult for either marshes or mangroves to survive, resulting in a loss of wetland habitat. Further, mangrove forests are more prone to damage by hurricanes than are marshes, so the stability of coastal ecosystems might diminish as mangroves spread (discussed further below).

Global climate change and sea-level rise can influence coastal fisheries in a number of ways. Approximately 70 percent of the U.S. fisheries' catch is derived from estuarine-dependent species, and their young are therefore dependent on suitable habitat. Rising sea levels that lead to destruction of coastal wetlands can have direct negative consequences for coastal fisheries. More indirect effects could result from wetland loss that leads to shoreline erosion, which, by adding fine sediments to the water column, would reduce water clarity and thus interfere with feeding ability. Many shellfish species also use coastal wetlands as an important habitat; therefore, they are vulnerable to wetland loss caused by sea-level rise.

Fish and shellfish species that use coastal wetlands as nursery habitat are also sensitive to temperature conditions. As climate warms, many species will be forced to shift their geographic ranges northward toward suitable thermal rearing environments for their young (Kennedy, 1990). The continued production of coastal fisheries will then be partially dependent on these species finding coastal environments containing functional nursery habitats at the higher latitude. Juvenile shellfish and fish rely on environmental cues for migration out to the sea, and these cues might be masked by changes brought on by the direct and indirect consequences of climate change. For example, large changes in freshwater inputs could also alter salinity gradients and estuarine circulation patterns that are important cues for migratory fish and shellfish. Changes in coastal ocean circulation patterns caused by changes in freshwater inputs and temperature may lead to changes in the regional patterns and spatial distribution of production as well as variability in naturally fluctuating stocks such as herring and sardines (e.g., Southward et al., 1988), thus affecting national and local economies. How offshore waters will respond to climate change is poorly understood (Francis, 1990).

Potential Changes in Storm Intensity, Frequency, and Track

The frequency, track, duration, and intensity of storms and hurricanes might also change with global climate change (Knutson et al., 1998; McCarthy et al., 2001). There is some empirical evidence that the frequency of Atlantic hurricanes increases with increasing sea-surface temperatures (Raper, 1993), although the uncertainty in such predictions is high. In addition, with warmer sea-surface temperatures, hurricanes might reach higher latitudes more often. Storms may also be accompanied by greater rainfall intensity (Wigley, 1999). Increases in hurricane intensity predicted by the models, however, fall within the range of natural interannual variability and of uncertainties of current studies (Henderson-Sellers et al., 1998; Wigley, 1999).

In general, long-term changes in the frequency, intensity, timing, and distribution of strong storms would most likely alter the species composition of coastal marshes, as well as the rates of important ecosystem processes such as nutrient cycling and primary and secondary productivity (Michener et al., 1997). For coastal systems of the southeastern United States, there could be both positive and negative effects. For example, hurricanes greatly increase the rate of soil accretion in marshes, thereby helping to offset accelerated sea-level rise (Cahoon et al., 1995b). Runoff generated by hurricanes introduce freshwater and nutrients that can enhance coastal wetland productivity (Conner et al., 1989). In the arid areas of south Texas, freshwater input can also have a stimulatory impact by reducing salinity and its attendant stresses (Conner et al., 1989).

On the negative side, hurricanes can reduce the structural complexity of coastal forested wetlands such as mangroves and tidal freshwater forested wetlands (Rybczyk et al., 1995; Stone and Finkl, 1995). The locations with the highest probability of hurricane landfall are south Florida and the Mississippi Delta. The coastal ecosystems of south Florida are dominated by mangroves and, if warming continues, the

Mississippi Delta will become increasingly dominated by mangroves. This trend, combined with increased hurricane frequency, would reduce the structure of these forests and destroy some of them. Freshwater forested wetlands (swamps) of the Mississippi Delta are slowly degrading and disappearing because increased flooding from rising water levels has largely eliminated the establishment and growth of young trees. Hurricanes can also cause tree loss; for example, Rybczyk et al. (1995) reported that nearly 10 percent of trees in a swamp forest in Louisiana were blown down during the passage of Hurricane Andrew in 1992. An increase in hurricanes would amplify the kind of damage resulting from the interaction between rising water levels and hurricanes and would hasten the loss of forests in the Mississippi Delta and elsewhere. High runoff from hurricanes can also lead to excessive nutrient loading and eutrophication problems. For example, record runoff from Hurricane Floyd into the Pamlico Sound estuary in North Carolina led to water quality problems (Paerl et al., 2000).

IV. Limits to Ecosystem Adaptation and the Importance of Human Adaptation

For many reasons, the ability of aquatic ecosystems to adapt to climate change is limited. Expected rates of climate change are probably too great to allow adaptation through natural genetic selection. Many types of habitat will be diminished or possibly lost entirely (e.g., alpine wetlands). Animals and plants will need to disperse northward or to higher elevations, but aquatic species differ greatly in their dispersal abilities, so not all species will be able to move to hospitable habitat. Further, most high-quality aquatic habitats are now spatially isolated (due to human activities), making successful dispersal even more difficult. The extinction of many local species can be expected across all aquatic ecosystem types. Many surprises are also expected as species migrate across the landscape and come into contact with new species for the first time, particularly exotic species that humans have introduced outside their historical ranges.

In general, there is strong scientific consensus that aquatic ecosystems are vulnerable to projected climate change. However, the amount of ecosystem alteration directly attributable to climate change will be difficult to ascertain, because other powerful agents of global change (e.g., human activities, exotic species) will continue to independently and interactively degrade aquatic ecosystems (Carpenter et al., 1992; Firth and Fisher, 1992; Grimm, 1992; Arnell et al., 1995; Lodge, 2001; Poff et al., 2001; Schindler, 2001).

One critical uncertainty in projecting future aquatic ecosystem response to a changing climate is how humans will interact with these ecosystems as climate changes. Human activities have severely modified many aquatic ecosystems with actions such as diversion, groundwater pumping, and the building of dikes, levees, and reservoirs, all of which have modified natural processes and increased the vulnerability of aquatic ecosystems to additional stress associated with climate change. Cumulatively, these alterations fragment the aquatic landscape and make dispersal between ecosystems more difficult.

A rapidly changing climate introduces uncertainty in water resource management and therefore threatens aquatic ecosystems if they are not adequately considered in human adaptation to climate change (Frederick and Gleick, 1999). To date, the needs of aquatic ecosystems have not generally been adequately represented in the formulation of environmental policy, especially the need for water quantity and timing that can sustain aquatic biodiversity and productivity (Baron et al., in press). Thus, a challenge for human society will be to adapt in ways that minimize damage to these important ecosystems. Human activities should maximize the potential for adaptation of these ecosystems by minimizing such present environmental stresses as pollution, habitat destruction, fragmentation, and exotic species introduction. These and other actions could enhance aquatic and wetland ecosystems, regardless of whether climate changes with the projected magnitude or not. Climate change offers additional incentives to implement more science-based management of aquatic resources; this could be considered "climate change insurance." Examples of such policies would include the following:

- Maintain riparian forests that shade streams and rivers to ameliorate increased temperature and contribute to the maintenance of existing habitat quality.
- Reduce nutrient loading to rivers, lakes, and estuaries. Protecting healthy wetlands and restoring degraded wetlands to enhance nutrient uptake will reduce nutrient loading.
- Locate any new reservoirs only off-channel so as not to disrupt the natural downstream flow of water and sediments critical to riverine ecosystems. Passage of sediment to estuaries is also critical for the accretion of soil in coastal wetlands, which are threatened with inundation by rising sea levels.
- Restore aquatic and wetland ecosystems to the maximum extent possible. On heavily managed ecosystems, such as regulated rivers and wetlands, some semblance of the natural flow regimes or hydroperiods should be restored, where feasible, to promote ecosystem resilience to climate change and other stressors.
- Minimize groundwater pumping for irrigation, human consumption, etc., that removes water from aquatic and wetland ecosystems.

Human society depends on inland freshwater and coastal wetland ecosystems to provide reliable goods and services. These ecosystems' abilities to continue doing so in the future under climatic stress will require that scientists and policy-makers turn more attention to the role that humans can play in minimizing the risk to these important systems.

V. Conclusions

1 Aquatic and wetland ecosystems are very vulnerable to climate change. The metabolic rates of organisms and the overall productivity of ecosystems are directly regulated by temperature. Projected increases in temperature are expected to disrupt present patterns of plant and animal distribution in aquatic ecosystems. Changes in precipitation and runoff modify the amount and quality of habitat for aquatic organisms, and thus, they indirectly influence ecosystem productivity and diversity.

2 Increases in water temperature will cause a shift in the thermal suitability of aquatic habitats for resident species. The success with which species can move across the landscape will depend on dispersal corridors, which vary regionally but are generally restricted by human activities. Fish in lowland streams and rivers that lack northward connections, and species that require cool water (e.g., trout and salmon), are likely to be the most severely affected. Some species will expand their ranges in the United States.

3 Seasonal shifts in stream runoff will have significant negative effects on many aquatic ecosystems. Streams, rivers, wetlands, and lakes in the western mountains and northern Plains are most likely to be affected, because these systems are strongly influenced by spring snowmelt and warming will cause runoff to occur earlier in winter months.

4 Wetland loss in boreal regions of Alaska and Canada is likely to result in additional releases of CO_2 into the atmosphere. Models and empirical studies suggest that global warming will cause the melting of permafrost in northern wetlands. The subsequent drying of these boreal peatlands will cause the organic carbon stored in peat to be released to the atmosphere as CO_2 and possibly methane.

5 Coastal wetlands are particularly vulnerable to sea-level rise associated with increasing global temperatures. Inundation of coastal wetlands by rising sea levels threatens wetland plants. For many of these systems to persist, a continued input of suspended sediment from inflowing streams and rivers is required to allow for soil accretion.

6 Most specific ecological responses to climate change cannot be predicted, because new combinations of native and non-native species will interact in novel situations. Such novel interactions may compromise the reliability with which ecosystem goods and services are provided by aquatic and wetland ecosystems.

7 Increased water temperatures and seasonally reduced streamflows will alter many ecosystem processes with potential direct societal costs. For example, warmer waters, in combination with high nutrient runoff, are likely to increase the frequency and extent of nuisance algal blooms, thereby reducing water quality and posing potential health problems.

8 The manner in which humans adapt to a changing climate will greatly influence the future status of inland freshwater and coastal wetland ecosystems. Minimizing the adverse impacts of human activities through policies that promote more science-based management of aquatic resources is the most successful path to continued health and sustainability of these ecosystems. Management priorities should include providing aquatic resources with adequate water quality and amounts at appropriate times, reducing nutrient loads, and limiting the spread of exotic species.

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