CHAPTER SEVENTEEN

Climate Change and Freshwater Ecosystems

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To date, about 17,000 species exclusive of
fish have been described in freshwater sys-
tems, and this is considered a gross under-
estimate because of the large number of
undescribed species, particularly the small
sediment fauna (Abell et al. 2000; Palmer
et al. 2000). The most diverse groups (in-
cluding estimated undescribed species)
include the microbes and algae. Among
the freshwater invertebrates, global spe-
cies richness is highest in the nematodes
and rotifers, insects, crustaceans, annelids,
and mollusks, respectively (Palmer and
Lake 2000). Many freshwater wetlands are
extremely speciose, with over 2000 spe-
cies at a site, with rivers and lakes typically
harboring 80–1400 species and ground-
water regions generally fewer than 150.

Some 41 percent of the 28,000 known
fish species live in fresh water and about 1
percent of the remainder spend part of
their lives in fresh water (Moyle and Cech
1996). East African rift valley lakes indi-
vidually contain several hundred cichlid
species and have attracted the attention of
evolutionary biologists fascinated by their
functional specialization and adaptive ra-
diation. Lake Baikal, an ancient lake and
the world's largest by volume, has many
endemic species (65 percent of animals,
35 percent of plants; Burgis and Morris
1987). North America is rich in both ver-
tebrate and invertebrate freshwater species
(Allan and Flecker 1993), including nearly
one-third of the world's described fresh-
water mussels and over 60 percent of the
world's described freshwater crayfish
(Master et al. 1998). Unfortunately, North
America's freshwater environments have
been identified as among those most
threatened (Abell et al. 2000).

Extinction rates of freshwater fauna are extremely high. Ricciardi and Rasmussen (1999) documented current extinction rates of 0.4 percent per decade for freshwater fish, 0.1 percent for crayfish, and 0.8 percent for gastropods. Assuming extinction rates will continue to increase at the same rate as they have in the past century, Ricciardi and Rasmussen estimated future rates of 2.4 percent, 3.9 percent, and 2.6 percent for these same groups, respectively. These data compare to much lower current and future extinction rates for most terrestrial fauna (e.g., birds = 0.3 percent now, 0.7 percent future). The threats to freshwater fauna fall into several broad categories: nutrient enrichment, hydrological modifications, habitat loss and degradation, pollution, and the spread of invasive species. A changing climate and increasing levels of UV light pose additional risks that superimpose upon existing threats. The combination of rapid land-use change, habitat alteration, and a changing climate is viewed as a particularly serious challenge to aquatic ecosystems (Carpenter et al. 1992; Meyer et al. 1999; Lake et al. 2000). This is one example of the synergies that appear to be all too common between climate forcing and other stressors.

THE IMPORTANCE OF FRESHWATER AND FRESHWATER ECOSYSTEMS

Surface fresh waters are a small fraction of global water. Freshwater lakes constitute 0.009 percent of water in the biosphere, and rivers are one hundred–fold less by volume (Wetzel 2001). By contrast, polar ice and glaciers make up 2.08 percent of the global total. Because the freshwater supply is unevenly distributed over land surfaces and threatened by contamination in many places, the real supply is even less than these small numbers indicate. It has been estimated that humans appropriate roughly one quarter of the global renew-able freshwater supply (Postel et al. 1996), and further population growth will cause this fraction to grow substantially (Vörös-marty et al. 2000), placing increasing pressure on freshwater ecosystems.

Healthy freshwater ecosystems provide vital ecosystem services to human societies (Naiman et al. 1995; Gleick 1998; Carpenter and Lunetta 2000), including the provision of clean water for drinking, for agriculture, for fisheries, and for recreation (Table 17.1). While the value of such ecosystem services is not easy to quantify in economic terms (Toman 1997), the impact of the loss of such services is often deeply felt. Many regions in the world have insufficient clean water to meet even the minimal demands for human survival (Postel 1997; Gleick et al. 2002), some countries are experiencing an increase in water-borne diseases (Sattenspiel 2000), while others are experiencing rapid declines in freshwater fishery yields (WRI 2000).

Maintenance of a diverse freshwater biota may be key to the retention of services provided by freshwater ecosystems (Covich et al. 1997; Palmer et al. 1997, 2000). Assemblages that are diverse may be able to utilize resources more efficiently, resulting in more productive systems; or they may offer "insurance" against ecosystem collapse in the face of disturbance (Loreau et al. 2001; Cardinale et al. 2002; Naeem 2002). Human actions that harm ecosystem health thus may also threaten human health and require costly replacement of damaged ecosystem services. For example, the city of New York has embarked on a watershed protection plan based on land acquisition at a cost of approximately $300 million, to prevent the need to construct a several-billion-dollar filtration system (Featherstone 1996), demonstrating the economic value of an undamaged freshwater resource.

The remainder of this chapter reviews the most likely and best anticipated impacts of future climate change on freshwater biodiversity, with an emphasis on

Table 17.1. Goods and Services Provided by Freshwater Ecosystems

Goods and Services	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

Source: Poff et al. (2002); modified from Postel and Carpenter (1997).

mid- and high-latitude regions, where effects are expected to be most severe.

CLIMATE CHANGE AND THE HYDROLOGIC CYCLE

Freshwater ecosystems will naturally be sensitive to changes in the hydrologic cycle, and these are difficult to predict. A warmer climate will result in greater evaporation from water surfaces and greater transpiration by plants, which will result in a more vigorous water cycle. However, whether rainfall will increase or decrease in a particular region is uncertain, and surface waters will decline even if precipitation increases, if evapotranspiration (ET) increases by a greater amount. General cir-

culation models (GCMs) are not yet able to reliably predict how precipitation and water levels will change at the local or regional level (Wigley 1999; NAST 2000), although downscaling and regional modeling efforts are in progress in many parts of the world in order to predict localized impacts of climate change (Neff et al. 2000; Polsky et al. 2000). There is still a great deal of uncertainty in climate change forecasts (Elzen and Schaeffer 2002; Forest et al. 2002; Heal and Kristrom 2002). For example, while earlier projections called for declines in levels of the Great Lakes of one meter or more (Mortsch and Quinn 1996), more recent models predict both increases and decreases, and of generally lesser magnitude (Lofgren et al. 2002). Frederick and Gleick (1999) examined
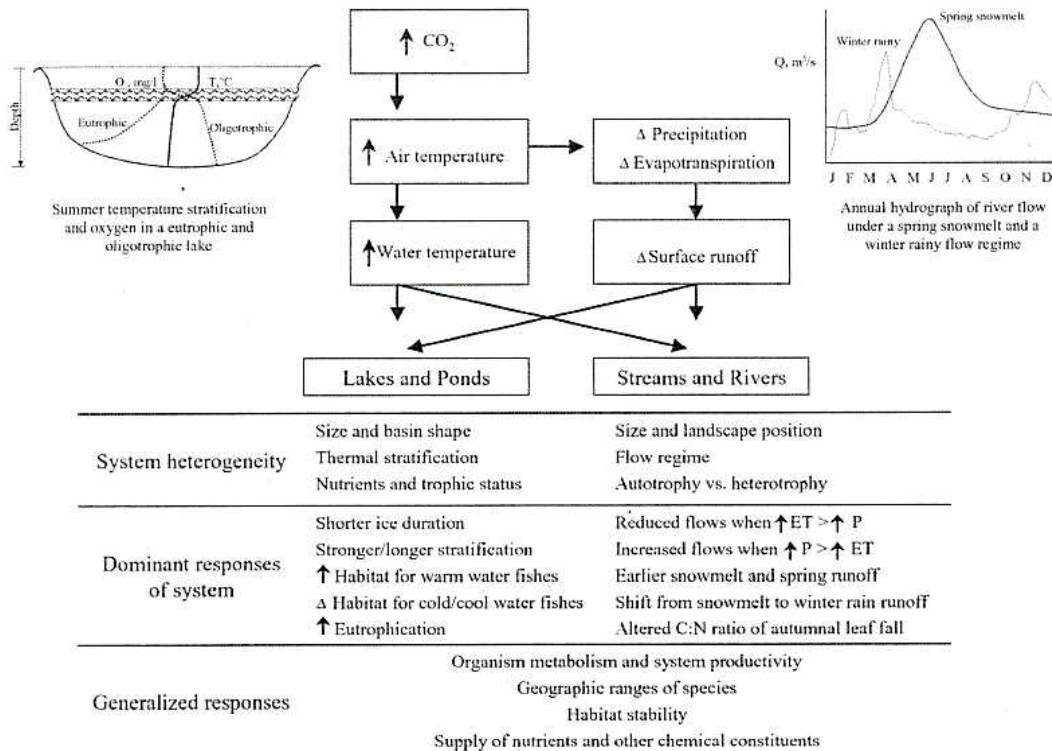
System heterogeneity	Size and basin shape	Size and landscape position
	Thermal stratification	Flow regime
	Nutrients and trophic status	Autotrophy vs. heterotrophy
Dominant responses of system	Shorter ice duration	Reduced flows when $\uparrow ET > \uparrow P$
	Stronger/longer stratification	Increased flows when $\uparrow P > \uparrow ET$
	$\uparrow$ Habitat for warm water fishes	Earlier snowmelt and spring runoff
	Δ Habitat for cold/cool water fishes	Shift from snowmelt to winter rain runoff
	$\uparrow$ Eutrophication	Altered C:N ratio of autumnal leaf fall
Generalized responses	Organism metabolism and system productivity	
	Geographic ranges of species	
	Habitat stability	
	Supply of nutrients and other chemical constituents	

Figure 17.1. Linkages between atmospheric increases in CO_2 and environmental drivers of temperature and precipitation that regulate many physical and ecological processes in lakes and ponds (left) and rivers and streams (right). Studies of climate change impacts on lakes have emphasized responses to warming, which are affected by vertical temperature stratification. Studies of climate change impacts on rivers have emphasized responses to altered flow regime, including changes to magnitude, frequency, duration, and timing of discharge events. Some biological responses shown at the bottom of the figure are general.

runoff for 18 water resource regions of the United States using two contrasting GCMs and found that predictions often were in disagreement. The two models predicted the same direction of change in runoff in only 9 of the 18 regions, and where the direction was similar, often the magnitude was not. Perhaps the greatest single challenge in evaluating aquatic ecosystem response to future climate change is the considerable uncertainty regarding the local and regional responses of the hydrologic cycle.

IMPACTS ON FRESHWATER ECOSYSTEMS

In general, analyses of impacts on lakes have emphasized responses to changing temperature, while analyses of rivers and streams have emphasized changes to the amount and timing of flow (Fig. 17.1). The approach of this review is similar, although clearly some impacts of climate warming, such as higher metabolism and productivity, and poleward range shifts, are very general. In addition, forested streams are highly dependent upon inputs of terrestrial organic matter, especially leaf fall, for their energy supply, and so shifts in terrestrial vegetation and changes in leaf chemistry provide another, quite intricate set of pathways by which stream biota and ecosystems can be affected. Due to space limitations, wetlands are not included in this review. However, those wetlands dependent upon surface runoff (rather than groundwater) are especially sensitive to drying, and coastal wetlands to saltwater intrusion due to rising sea levels (IPCC

2001; Pearsall, this volume). Melting of permafrost, drying of peat, and resultant release of methane and CO_2 are of special concern not only because of the loss of many small boreal wetlands, but also because peat-accumulating wetlands are a carbon sink that could become a carbon source and positive feedback under future climate warming.

Lakes and Ponds

Freshwater lakes range in size from Lake Baikal, the deepest (1620 m maximum depth) and largest (23,000 km^3 by volume) lake, and the Laurentian Great Lakes, with a collective volume of 24,620 km^3, to literally millions of small lakes that dot glaciated landscapes and are usually less than 10 m in depth (Wetzel 2001). Subarctic lakes and prairie potholes are usually very small and shallow. Differences among lakes in surface area, depth, latitude and elevation, and water residence times are all factors that will influence their response to climate change. The more than 36,000 dams over 15 m high in operation worldwide have a combined maximum impoundment volume of approximately 8400 km^3, about seven times the volume of natural river water (Vörösmarty et al. 1997), and millions of farm ponds add substantially to the extent of standing fresh water.

Lakes can be classified according to their vertical temperature profile and the seasonality of that profile. During summer at mid-latitudes, lakes of sufficient depth typically develop thermal stratification due to the density difference between warmer and cooler water, resulting in a warm layer (the epilimnion), a cold and deep layer (the hypolimnion), and a zone of rapid temperature change in between known as the thermocline. The epilimnion is oxygenated and biologically productive, while the hypolimnion may experience oxygen limitation due to decomposition of organic matter raining down from

above. Climate interacts with lake basin shape and wind (which affects the depth of mixing of surface waters) to determine the strength and duration of thermal stratification.

PHYSICAL EFFECTS

The duration of ice cover for northern hemisphere lakes provides one of the strong signals of global climate change over the past 150 years (Magnuson et al. 2000; IPCC 2001). On average, from 1846 to 1995 the freeze date was 8.7 days later and the ice breakup 9.8 days earlier (Fig. 17.2). As well, the inter-annual variability in freeze dates, thaw dates, and ice duration has increased (Kratz et al. 2001). Climate-induced shortening of ice duration will affect evaporation rates and lake metabolism (IPCC 2001).

Future climate change will directly affect lake ecosystems through warmer temperatures and changes to the hydrologic cycle. However, the heterogeneity of lake types and locations will interact with
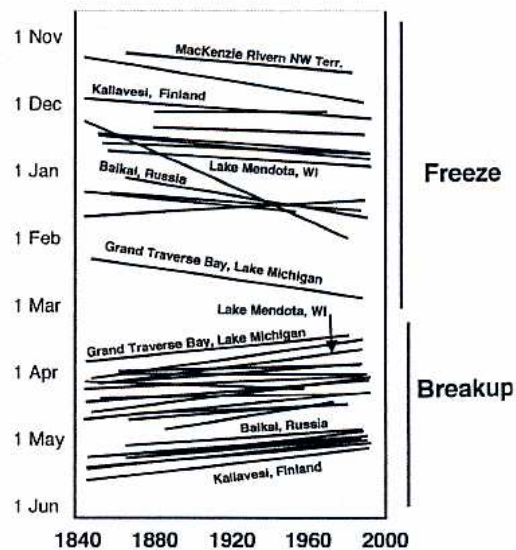

Figure 17.2. Historical trends in freeze and breakup dates of lakes and rivers in the Northern Hemisphere; 37 of the 39 trend slopes are in the direction of warming. Source: IPCC (2001); modified from Magnuson et al. (2000).

climate drivers in diverse ways. Lake size and depth, exposure to wind, and latitude or altitude will determine the existence, strength, and duration of thermal stratification, and therefore the seasonal amount of cold-, cool-, and warm-water habitat available. The water supply to lakes may be differently affected by future climate change depending on whether the water originates from glacier, snowmelt, rain-fed, or groundwater-fed sources. Water supplied by glaciers and snowmelt may increase initially but decrease in the long run, while small wetlands and prairie pothole lakes are examples of systems that may simply disappear depending on the balance between precipitation and evapotranspiration. Increases in evapotranspiration brought about by higher temperatures, longer growing seasons, and extended ice-free periods, unless offset by equal or greater increases in precipitation, are likely to result in reduced lake levels and river inputs. In cases where precipitation and evapotranspiration both increase, lake levels might change little but water residence time in lakes would be expected to be shortened.

IMPACTS ON BIOTA

The freshwater biota is dominated by cold-blooded organisms, and in general ectotherms increase their metabolism with increase in temperature until they approach their upper temperature tolerances. Rates generally increase by a factor of $2-4$ with each $10°C$ increase in water temperature, up to about $30°C$ (Regier et al. 1990). In a review of approximately 1000 studies of macroinvertebrate production, Benke (1993) estimated a $3-30$ percent increase in production for each $1°C$ increase in temperature. Thus while there may be complex and unpredictable changes in species composition, an overall increase in system productivity is likely to be a common response to climate warming.

A strong case can be made that future climate warming will alter the extent of habitat available for cold-, cool-, and warm-water organisms depending upon region, and result in range expansions and contractions (Fig. 17.3). Species at the

Figure 17.3. Ten-year average lake temperatures simulated using the Canadian Climate Center Atmosphere Ocean General circulation model as input data. *Source:* Poff et al. (2002); based on Hostetler and Small (1999).

August–Control   **August – 2x CO₂**

10   15   20   25   >30
Lake Temperature °C
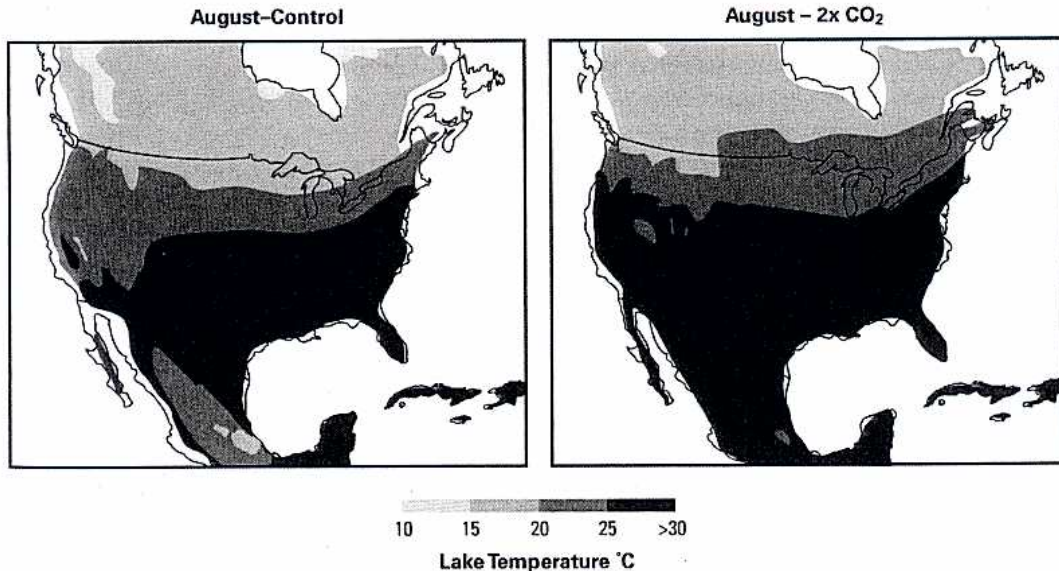
southern extent of their geographical distribution (in the north temperate zone) will shift northward and face local extirpation at their southern limit, while expanding at the northern limit of their range. It is estimated that a 4°C warming results in a 640-km northward latitudinal shift in thermal regimes for macroinvertebrates (Sweeney et al. 1992) and a roughly 500-km northward shift for smallmouth bass and yellow perch. While useful as a first-order approximation, such projections assume that water temperatures warm about as much as air temperatures (valid for shallow, well-mixed systems), that dispersal corridors are available, and that other system effects including biological interactions are unaltered. While many aquatic insects have aerial dispersal, fish and other organisms that require an aquatic dispersal corridor may lack the opportunity to disperse, due to the isolated nature of some lakes, dams that block connecting rivers, and land divides that separate basins such as the Laurentian Great Lakes from the Nelson and Mackenzie basins of Canada.

The effect of climate warming on lakes is further complicated by their thermal stratification. In large deep lakes such as Lakes Huron, Superior, and Michigan, a warming of 3.5°C is expected to increase suitable thermal habitat for warm-water fishes that occupy the epilimnion during summer. Cold- and cool-water fishes of the hypolimnion are also expected to benefit, because slight warming will promote metabolic activity yet remain well within thermal tolerances (Magnuson et al. 1997). In contrast, smaller and shallower lakes may experience sufficient loss of cool hyoplimnetic volume that fish requiring cold water (many top predators) may experience reduced habitat. In eutrophic (high nutrient input) lakes with a restricted area of hypolimnion, bottom waters may become depleted in oxygen due to the decomposition of algae and other organic matter that settle out of surface waters. As climate warming reduces the volume of the hypolimnion and increases the productivity of surface waters, oxygen depletion in the deep waters may become more severe.

A simulation study by Stefan and colleagues (2001) incorporated much of this complexity by exploring how 27 lake types (3 categories each of depth, area, and productivity) responded to a temperature change expected under a doubling of CO_2. Based on projected changes in temperature and hypolimnetic oxygen availability they forecast an overall 45 percent decrease in habitat for cold-water and 30 percent for cool-water fish, with greatest impact in lakes of shallow and medium depth. Warm-water fish benefited in all lake types, however.

While it is tempting to imagine these effects as simple adjustments, with some winners offsetting some losers, it is important to stress that the biological consequences of altered species assemblages are difficult to forecast and unlikely to be benign. Temperature also sets the northern range limit for harmful invasive species such as the zebra mussel (Strayer 1991), and so a northward range expansion seems highly probable. Given the well-established negative impacts of invasive species on freshwater ecosystems (Allan and Flecker 1993), native biodiversity may be adversely affected by such range shifts.

Eutrophication results from excessive nutrient inputs, promoting high biological production of algae and a preponderance of nuisance algae including the blue-green algae or Cyanobacteria (Carpenter et al. 1998). Water clarity and quality are reduced, deep and bottom waters may become anoxic from excessive decomposition, and some blue-green algae release toxins. Due to human activities, many more lakes today receive excessive nutrients from their catchments and from internal recycling, and warming is expected to increase lake productivity (IPCC 2001). However, because climate-influenced processes have interacting, seasonal, and

often opposing effects (Magnuson et al. 1997; Schindler 1997), the relation between eutrophication and climate change is complex. A longer period of summer stratification will increase the likelihood of summer anoxia below the thermocline, while a shorter ice duration will reduce the likelihood of winter anoxia (Stefan and Fang 1993). More nutrients likely will be delivered to lakes by their catchments under wetter climates, and less under dryer climates, which in the latter case will result in longer water residence times (Schindler et al. 1996) and increase the importance of internal recycling. Light penetration will increase if less dissolved organic carbon (DOC) is exported from catchments into lakes, as is expected under drier conditions, and this could result in increased primary production at greater depths. These complex and offsetting interactions make it extremely difficult to predict how lake ecosystems will respond to alternative climate scenarios (Lathrop et al. 1999; IPCC 2001).

The three-way interactions among lake acidification, UV-B radiation, and climate warming, termed a "triple whammy" by Schindler (1998), are an instructive example of complex system responses. Lakes with low buffering capacity, including many north temperate lakes, experience lowered pH due to acid deposition, resulting in a number of biological and chemical changes including reduced DOC and greater water clarity. Climate warming potentially can limit the supply of buffering cations via reduced river inflow, which exacerbates the acidification process. DOC affects water clarity, especially in boreal lakes receiving DOC that is colored with dissolved humic material, and climate-induced reductions in streamflow can reduce DOC inputs to lakes. Thus acidification and climate warming interact to increase water clarity. This in turn influences the depth to which damaging UV-B radiation is able to penetrate. UV-B radiation, which has increased due to the re-

duction in stratospheric ozone, can directly damage the biota via molecular damage and oxidative stress (Häder et al. 2003), as well as furthering the depletion of DOC by accelerating the photolysis of organic macromolecules (Wetzel 2001) in yet another aspect of positive feedback. The ultimate effects of increased water clarity are difficult to state, because it potentially allows algal photosynthesis to occur at greater depth while permitting harmful UV-B radiation to reach greater depths as well.

Unexpected, synergistic effects are well illustrated by several of the previous examples. In one of the most thoroughly investigated areas of climate change and freshwater ecosystem response, future warming interacts with lake size and depth, position, and nutrient status to determine changes in temperature and oxygen in epilimnetic and hypolimnetic waters, thereby influencing habitat available to cold-, cool-, and warm-water fishes. Warming interacts with system connectedness and taxon dispersal capability to determine the opportunity for range shifts, and it will not be surprising if already successful invasives turn out to be best able to exploit opportunities and adversely affect native species. Warming may interact with human augmentation of nutrient supply to increase the extent of eutrophic waters, although complexities abound when we try to foresee the consequences. In some boreal lakes, acidification may interact with decreases in DOC due to reduced streamflows to increase water clarity, allowing the higher incidence of UV-B light to cause photolytic damage at greater depth than before. Clearly, shifting ranges and species substitutions are only the beginning of the anticipated impacts.

Rivers and Streams

Running waters contain only about 1 percent by volume of the fresh water occur-

ring in lakes, but they are enormously important for transport of water and dissolved and suspended materials. Some 20 large rivers (less than 2000 km in length) contribute a major share of riverine export of water to oceans; the Amazon alone contributes 15 percent of the total (Allan 1995). As with lakes, the vast majority of running waters comprises small rivers, streams, and tributaries of larger systems. Stream order designates the smallest, permanent stream as first-order, the confluence of two stream of order n creates a stream of order n + 1, and so on. Of the approximately 5,200,000 km of rivers in the United States, nearly 50 percent are first-order, and the total for first- through third-order combined is just over 85 percent. Examples of large rivers include the Allegheny (seventh-order), the Columbia (ninth-order) and the Mississippi (tenth-order). Stream order, latitude and elevation, the relative contributions of surface water to groundwater, seasonal timing of precipitation and evapotranspiration, and additional variables of the drainage basin likely will influence response to climate change.

The ecology of rivers varies with their size (order) and landscape setting (Vannote et al. 1980). Lower order and headwater streams tend to derive much of their energy as organic matter inputs from the terrestrial ecosystem, and in forested locations they may have a closed canopy, low light levels, and stable flows. Larger and higher-order rivers tend to be more integrative of upstream influences, open to the sun, and periodically connected to their floodplains, at least in low-lying areas and where human engineering is minimal. Dams alter flow regimes and upstream–downstream connectivity, and many populated rivers receive a wide variety of contaminants along their lengths.
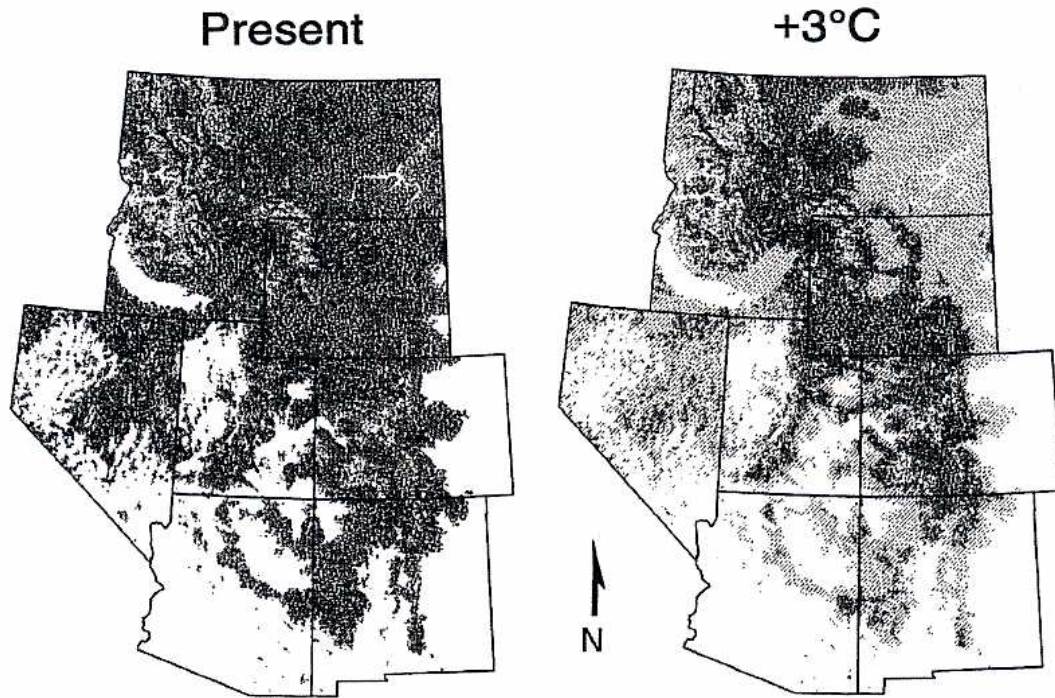
PHYSICAL EFFECTS

Streams and rivers respond rapidly to changes in air temperature because they are relatively shallow and well-mixed. Thus, future warming can be expected to directly increase the seasonal water temperatures of most running water ecosystems, with greater effects at more northerly (poleward) latitudes. Warm-season river temperatures usually closely approximate air temperatures, typically with a time lag of weeks or less, although streams and smaller rivers with a large component of groundwater or meltwater may be considerably cooler than summer air temperatures, corresponding to mean annual air temperature for the region. While small streams receiving glacier, snowmelt, or groundwater can experience substantial day–night temperature fluctuations, larger rivers are thermally stable over the 24-hour cycle due to the volume of water, and show little or no temperature profile, due to vertical mixing. Unlike lakes, the distribution of heat in river water is very uniform vertically.

River flow or discharge (m^3/s) typically is variable on intra-annual, inter-annual, and very long time scales, and although some groundwater-fed systems are highly stable, they are the exception. Variability in the magnitude, duration, frequency, timing, and rate of change of river flows collectively characterizes the flow regime of a river (Poff et al. 1997) and varies with region due to the influence of climate, vegetation, and geology on river flow (Poff and Ward 1989). The flow regimes of rivers already are altered by a number of human actions, most notably dams, which often regulate and stabilize river flows, and land-use change, which often causes more rapid runoff from land to receiving stream systems and makes flow more responsive to rainfall extremes.

Climate change is expected to significantly alter flow regimes as well as the total volume of river runoff by changing precipitation, evapotranspiration, and their relative magnitude. Precipitation falling on watersheds is translated into stream runoff by direct overland flow and by ground-

Present

+3°C

N

Figure 17.4. Present and 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: Poff et al. (2002); based on Keheler and Rahel (1996).

water flow. In humic, vegetated regions the majority of runoff follows subsurface pathways, and the majority of precipitation returns to the atmosphere as evapotranspiration. On average in the United States, about one-third of precipitation becomes stream runoff. Thus, how climate change alters terrestrial vegetation and its transpiration rates will influence runoff, even where seasonal shifts in precipitation do not occur. For example, in well-vegetated humid regions, summer flows are low even though precipitation may equal that in winter (Benke et al. 2000). In the winter rainfall area of southeastern Australia, rains have shifted to spring, and the associated increase in plant transpiration is causing a "green drought" in which streamflows are reduced while the surrounding terrestrial vegetation flourishes (P. S. Lake, personal communication). Whether due to climate change or other fluctuations, this example demonstrates how seasonal shifts in the timing of rainfall can influence the amount of water in streams.

Expected changes in regional flow regime change are uncertain due to inability to predict changes in the balance between precipitation and evapotranspiration; nevertheless, some outcomes are expected with reasonably high certainty. Glacier-fed streams are likely to experience an increase in discharge for years to decades, followed by declines. Warmer temperatures will cause a shift from winter snow to rain and snow, or primarily rain, depending upon latitude. As a result, streamflows will reflect earlier spring snowmelt or the transition to a variable winter flow regime in response to rain. In regions that currently experience a mix of rain and snow during winter, floods often result from "rain on snow" events, when snow and frozen ground cause much of the land to behave as an impervious surface, and so rainfall produces immediate and extreme runoff. In some areas of

Canada a shift in dominant mode of precipitation from snow to rain has already been observed (Frederick and Gleick 1999). The location of a watershed relative to the ocean may mediate its response to climate change, however. For example, high-latitude maritime watersheds currently receive less precipitation as snow compared to inland watersheds, which are therefore more vulnerable to earlier runoff as snow shifts to rain (Loukas and Quick 1999).

The magnitude and timing of runoff is a critical factor influencing the aquatic biota and ecosystem processes (Poff et al. 1997). Variation in flow regime among watersheds is believed to maintain high regional diversity, because different combinations of frequency, magnitude, duration, and timing of flow influence the variety of habitat conditions afforded. Thus, changes in flow regimes in response to climate change can have profound effects on aquatic ecosystems.

BIOLOGICAL IMPACTS

Rapid climate change has many negative implications for the biodiversity of rivers and streams. On a global scale, the vulnerability of stream systems appears to increase as one moves from the tropics to the poles (Poff et al. 2001), where disproportionately greater warming will occur, along with associated dislocations of the hydrologic cycle.

In general, streams are coolest in the headwaters, and a warming will tend to push species upstream to find thermally optimal habitats. However, small streams are effectively like the tops of mountains, in that once these cool-water refuges are warmed there is no escape route for individuals or populations that are trapped there. Thus, stream networks in low-gradient, lowland areas are more vulnerable to climate warming than are those in areas with high topographic relief. Aquatic organisms in mountainous areas have the potential to move upstream to higher-altitude refuges that may remain thermally suitable during the course of climate change; however, the overall extents of the species' ranges will contract. This is seen for trout in the Rocky Mountain region (Fig. 17.4).

Climate change may cause extinction at several taxonomic levels. At the species level, those species that are highly restricted in their geographic distribution or that are very specialized ecologically (and thus occupy narrow habitat types) are vulnerable to global extinction. This is true for fish (Angermeier 1995; Poff et al. 2001), where there are regional differences in the proportional occurrence of specialized species (Poff et al. 2001). It is also probably true for invertebrates such as mussels, whose biology is closely tied to host fish species and whose habitat is greatly diminished by river regulation (Duncan and Lockwood 2001).

Particular geographic locations are especially vulnerable. For example, fish in the southern Great Plains and the desert Southwest of the United States cannot move northward because those streams and rivers tend to run west and east. With just a few degrees of warming, up to 20 native fish species in these regions are at risk of extinction (Matthews and Zimmerman 1990; Covich et al. 1997).

If related species with particular ecological traits are more sensitive to climate change, then higher levels of taxonomic diversity may also be threatened. For example, because darter species in genera of the family Percidae are uniformly small, are ecologically specialized, and generally have narrow geographic ranges, they appear vulnerable as a group to extinction (Poff et al. 2001).

Even if species do not go extinct, reduction in regional abundances can result in biodiversity loss at the population genetic level. Streams and rivers are naturally relatively isolated due to watershed divides, and within-watershed genetic differ-

entiation has occurred for many groups. Severe isolation has led to speciation, as with the galaxiid fishes of New Zealand (e.g., Allibone and Townsend 1997). Many salmonid fish species that migrate to the sea have developed a high affinity for particular watersheds, where environmental conditions vary, leading to local adaptation, meaning genetic differentiation at the subpopulation level. A change in climate that causes the elimination of a subpopulation results in some loss of genetic variation from the larger species population.

The production of salmon and other high-value fishes that spend part of their lives in fresh water may be vulnerable to climate change. Beamish and colleagues (1999) document a synchrony between climate indexes and both Pacific salmon and Pacific sardines that may have occurred for centuries, and is well established for the past 100 years. This raises the possibility that global warming will result in large and abrupt changes in abundance, termed regime shifts, in commercially important species. Within the river ecosystem, used for spawning and rearing of juveniles, bioenergetic models predict that warmer spring-summer temperatures will result in higher predation rates by important piscivores of juvenile salmon (Petersen and Kitchell 2001). Increased mortality of juvenile coho salmon in the Columbia River basin may result from warmer temperatures and reduced streamflows, and thermal barriers may impede the migration of adult salmon (Mote et al. 1999). On the other hand, populations of sockeye salmon in Alaska appear to benefit from a warming of surface sea temperatures, observed as bouts of natural climatic variation over the past 300 years, apparently due to increased ocean productivity (Finney et al. 2000). Anadromous fishes potentially will be affected by climate change impacts to both marine and freshwater environments.

Streams draining forested landscapes and with forested riparian zones derive much of their energy as organic matter inputs from the terrestrial environment (Allan 1995). Leaves and leaf fragments, termed coarse particulate organic matter (CPOM), are quickly colonized by fungi and bacteria, and subsequently consumed by a wide variety of invertebrates. Climate change is likely to affect the processing of detritus and functioning of the microbial-shredder food web linkage in complex ways. Altered carbon-to-nitrogen ratios of the leaves likely will reduce palatability, temperature changes will affect leaf processing rates, and floods may export leaf matter before it can be processed (Rier and Tuchman 2002; Tuchman et al. 2002, 2003). Figure 17.5 illustrates that these interactions are complex and potentially offsetting, making the overall impact of climate on this important energy supply difficult to predict.

In their natural state, river networks typically are connected systems in which biota can move during periods of rapid environmental change. Indeed, in previous bouts of climate change, such movements have been critical to sustained species survival for fishes (e.g., Briggs 1986) and aquatic invertebrates such as stoneflies (Zwick 1981). In the contemporary landscape, rivers are fragmented by a variety of human activities (Allan and Flecker 1993; Dynesius and Nilsson 1994) and species and populations are less capable of moving easily along river corridors. This isolation poses one of the largest threats to aquatic biodiversity during climate change (Poff et al. 2001, 2002).

SUMMARY

Human demands for freshwater quantity and quality now pose severe threats to freshwater biodiversity, and human demands are projected to increase dramatically (Postel et al. 1996; Vörösmarty et al. 2000). The multiple human stressors of
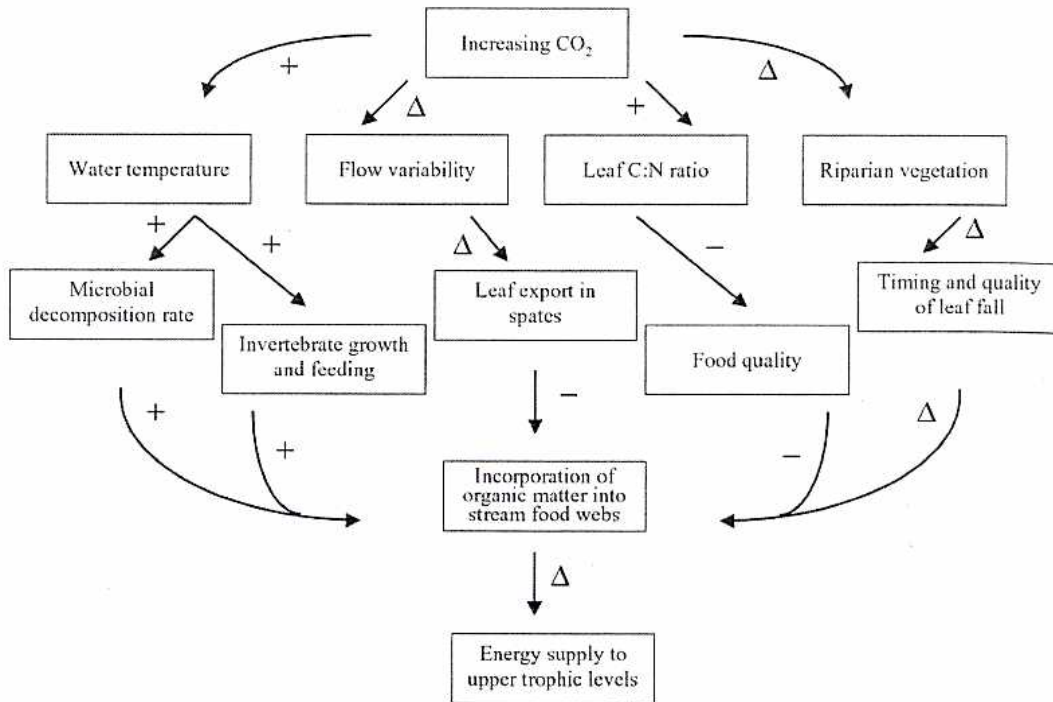
Figure 17.5. A rise in atmospheric CO_2 is expected to have complex effects on organic matter inputs, especially leaf fall, which is a principal energy supply to small streams. A warmer climate will increase most rate processes, increased hydrologic variability may adversely affect the retention and thus processing of organic matter, a higher carbon to nitrogen ratio of leaves is expected to reduce palatability, and climate change may cause shifts in the composition of riparian species. Source: Based on studies by Rier and Tuchman (2002) and Tuchman et al. (2002, 2003).

freshwater ecosystems (Allan and Flecker 1993; Palmer et al. 2000) will interact with future climate change (Schindler 2001; Poff et al. 2002) to further compromise the biodiversity and function of freshwater ecosystems. Physical impacts due to the direct effects of warming and altered hydrology are understood in broad outline but are manifested differently across lakes, ponds, rivers, and streams owing to system heterogeneity including size, depth, landscape position, latitude, and many additional factors (see Fig. 17.1). Higher biological rates of metabolism, growth and production are expected to be widespread in temperate and boreal regions, because the majority of organisms of freshwater ecosystems are ectotherms. Biological responses often are unpredictable due to the complexity of the system, including nonlinear responses, sometimes offsetting interactions, and the importance of exceptional, stochastic events. The potential for negative synergies is of special concern. The impacts due to warming of lakes depend on depth, which determines the extent of the hypolimnion, and lake productivity, which influences oxygen depletion in deep waters.

Poleward range shifts are expected to be a very general response in river and stream biota, although both natural and manufactured migration barriers are widespread and north–south dispersal corridors may be absent. Invasive species also will undergo range shifts, posing a risk to native biodiversity in regions they have not yet colonized. The combined effects of climate change on the food webs of forested streams, which are highly dependent upon organic matter inputs of terrestrial origin, are difficult to predict due to the offsetting nature of multiple pathways of impact (see Fig. 17.5).

A number of studies have evaluated changes in available habitat for fishes due to climate warming. This is more straightforward in streams, which are well mixed and track air temperature closely, than in lakes, where thermal stratification and depth affect the relative change in habitat for cold-, cool-, and warm-water fishes. Rivers and streams will experience altered flow regimes due to changes in both precipitation and evapotranspiration. Because water budgets depend on the balance of these terms and both are difficult to predict at the catchment or regional scale, it usually is uncertain whether streamflows will increase or decrease, and in what season. However, spring runoff is likely to occur earlier and snowmelt runoff regimes change to winter rainy regimes, a trend already observed in some locations.

Mitigation and adaptation measures need far more investigation before they can be described with confidence. Many mitigation measures likely will require addressing interacting stressors of human origin. Invasive species pose potent threats to native biodiversity and continue to be facilitated by fish and wildlife agencies and habitat degradation. Removal of riparian vegetation in farmland warms streams by as much as 3–5°C (Abell and Allan 2002), and riparian tree plantings likely would lower stream temperatures by a similar amount. Dams and inhospitable habitat create barriers to dispersal by aquatic organisms that will need dispersal corridors to cope with changing temperatures. Acid deposition is expected to interact with climate-induced changes in delivery of dissolved organic carbon to boreal lakes to enhance water clarity and permit damaging UV-B rays to penetrate to greater depth. It may be easier to deal with the already existing sources of negative synergies, than with climate change itself. Freshwater ecosystems will adapt to climate change as they have adapted to land-use change, acid rain, habitat degradation, and multiple forms of pollution. Unfortu-nately, that adaptation is likely to entail a diminishment of native biodiversity.

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