Chapter 8

NATURAL ECOSYSTEMS II. AQUATIC SYSTEMS

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INTRODUCTION

There is growing public awareness that concentrations of several greenhouse gases (e.g. carbon dioxide, methane, and chlorofluorocarbons) are increasing in the atmosphere and much of this increase is attributed to anthropogenic sources (Hansen and Sato 2001, Hansen et al. 2001, 2002). Relationships between ozone depletion, global warming, and linkages with El Niño-Southern Oscillation (ENSO) climate dynamics add further complexity. Several studies conclude that climate change over the last 100 years has exceeded the natural range of variability and has been caused at least in part by anthropogenic changes (Crowley 2000). The directionality, magnitude, rate, and causes of any future climatic changes are all topics of ongoing research.

For inland drainage basins in western United States, the relationship between warmer climate and altered precipitation is of utmost importance because of the arid to semi-arid nature of this Intermountain region, and the increasing need for fresh water by a rapidly growing human population. However, there remain persistent uncertainties regarding the linkages between global warming and changes in patterns of precipitation in general. The hydrologic and ecological implications of climate change are perhaps the least understood of the wide array of potentially important future impacts. The combined effects of warmer water and extreme floods and droughts that are considered likely in some forecasts will alter inland aquatic ecosystems over the next 50 years, especially because the demand for freshwater by human populations is growing regionally (Coutant 1981, Carpenter et al. 1992, Covich 1993, Grimm 1993, Grimm et al. 1997, McKnight and Covich 1997, Meyer et al. 1999, Murdoch et al. 2000, Postel 2000, Jackson et al. 2001, Poff et al. 2002).

A group of geologists, hydrologists, and ecologists met in February, 2000 in Salt Lake City, Utah to discuss different climate scenarios and examine some well-documented historic changes in climate. The group discussed the potential effects of climatic variability and change on aquatic ecosystems in the Rocky Mountains and Great Basin. This chapter is a synthesis of the material and views presented at the Salt Lake workshop and extensive review of the relevant literature discussing climate-change effects on aquatic ecosystems.

A major goal of this chapter is to summarize important points needed to understand ways in which large-scale, long-term dynamics of climate would affect inland aquatic ecosystems. A second goal is to provide examples and case studies that illustrate general relationships of how climate change has already affected aquatic species and ecosystems in the Rocky Mountain/Great Basin (RMGB) region. A third goal is to identify gaps in current understanding that need more study in order to improve future forecasts regarding the expected consequences of climate change on freshwater ecosystems.

CURRENT AND FUTURE STRESSES AFFECTING RMGB AQUATIC SYSTEMS

As commented in the other chapters, climate-change effects will interact with other stresses now affecting the sectors, or those likely to affect them in the decades ahead. Several influential ones are now besetting aquatic systems in the RMGB region.

Human Populations and Transfers of Scarce Water Resources

Social changes will influence how any climatic changes affect freshwater ecosystems. Climatic effects can only be observed in conjunction with changes in land use that alter interconnected hydrologic, geomorphic, and biological responses to climatic variables. Thus, increased understanding of the effects of future climate change must be coupled with better understanding and integration of the likelihood of increased demands for high-quality freshwater resources. These demands for drinking water, irrigated agriculture, industrial coolants, and dilution of treated sewage and industrial effluents will continue to increase and add more stress to aquatic ecosystems.

Predicting responses of species and ecosystems to climatic changes is also complicated by complexity of the terrain in the region. Yet, assessing how future climatic change may alter aquatic ecosystems is especially important because of these close connections between aquatic habitats and rapidly growing human populations. Resource management by private owners, state and federal agencies, and research strategies for understanding and adapting to climatic changes will require enhanced coordination. This region relies on groundwater, large reservoirs, water diversions for irrigation, and many types of regulated river flows and interbasin water transfers to maintain reliable sources of water for human uses. The combined effects of these managed flows on natural aquatic habitats are extensive. Urban development, road construction, overgrazing, and irrigated agriculture have affected infiltration, overland flow, and evapotranspiration. These changes have altered the seasonal patterns of discharge, caused declines in some river flows, draining of wetlands, and loss of aquatic habitats (Hirsch et al. 1990, Postel 2000, Vorosmarty et al. 2000).

Under warmer climate conditions these regulated flows in some large rivers may be managed to reduce variability in seasonal discharge and water temperatures, and to minimize effects of any increased frequencies of floods and droughts (Meyer et al. 1999). In other rivers, the addition of adverse effects from climate change may further disrupt ecosystem dynamics. Dams already have altered natural flow regimes and affected the ability of native species to compete with non-native species (Poff et al. 1997, 2002). Effects of dams may already be greater than any expected effects from climate change. Currently dams are responsible for fragmenting fluvial ecosystems in much of the western United States and their impacts on river discharge is several times greater than impacts anticipated as a result of climate change (Graf 1999).

Although water resources are abundant in a few locations (near large rivers, deep lakes, and reservoirs), the recent rapid increases in human populations have already overappropriated water resources (Naiman and Turner 2000, Jackson et al. 2001). This region contains some of the fastest growing cities in North America. For example, urban and suburban growth in Las Vegas, Denver, Albuquerque, Salt Lake City and surrounding areas is dependent on water transfers from remote locations and reallocation from agricultural uses. Several towns (e.g., Clover Creek and Rush Valley) are using much of the available water supplies south of the Great Salt Lake so that groundwater use is increasing faster than recharge of aquifers. In other areas deeper drilling for well water is occurring to support expansion of irrigated farming and population growth. Very rapid growth of populations in the cities of the region continues to create increased demand for high-quality, freshwater resources. During the next century these demands will continue to increase.

Moreover, aquatic habitat degradation from eutrophication of rivers and reservoirs (from both point and non-point sources of nutrients), and atmospheric acid deposition may combine to lower water quality and reduce habitat availability for fish and wildlife as a consequence of rapid human population growth in urban centers. In rural areas the increased demand for water to irrigate crops (Postel 2000) and the potential for overgrazing rangelands (Armour et al. 1991, Trimble and Mendel 1995, Kauffman et al. 1997) will further stress drainage basins.

Thus, any effects from future changes in precipitation and temperature may be accelerated and accentuated by associated increased demands for freshwater from human population growth. These combined effects from climate change and human population growth will be difficult to distinguish. Trends in both climate change and landscape change can occur gradually so that detection and identification of each of these sources of change will be problematical.

Incursion of Nonnative Species

Throughout North America the present distributions of native aquatic species have been greatly modified through competitive displacement by introduced non-native species, and by habitat loss resulting from rapidly expanding human populations and homogenization of fish faunas (Rahel 2000). Recent studies report 92 introduced non-native fish taxa (foreign and native transplants) in the Great Basin, and 64 and 102 in the Upper Colorado River and the Lower Colorado River Basins, respectively (Fuller et al. 1999). These introduced fishes compete with native species and also disrupt food webs by having a major effect on invertebrate prey species. In the Intermountain West, many of the introduced forms are adapted to relatively warm water temperatures. They have usurped the lower, warmer stream reaches and restricted the native species to the higher-elevation, colder reaches. Increasing water temperatures would allow the exotics to move to higher elevations and further impact the natives.

Currently, many native species that occur in inland waters are listed as endangered, and rapid changes in climate may further degrade their habitats. Plans for managing these endangered forms need to consider how extreme climatic events, human population growth, and exotic species interact to affect their chances for survival. The additional stress on aquatic species and ecosystems induced by climate change may generate renewed interest in better managing rivers, lakes, wetlands, and floodplains for the preservation of threatened and endangered species. The potential for significant economic consequences resulting from global warming may lead to more large-scale, long-term planning and ecosystem management. This integrated approach could minimize local extinctions of already threatened forms. But much remains unclear about how this interdisciplinary integration may be accelerated to enhance management options.

Past and Current Climate Variability

Climatic variability influences water budgets of drainage basins and affects a diversity of streams, rivers, ponds, lakes, springs, and wetlands in the RMGB region (Winter 1981, 1989, Hostetler 1995, Hostetler and Giorgi 1995, Hostetler and Small 1999). Current and historic data demonstrate that these regional aquatic ecosystems are subject to large interannual variations in climatic variables, and have changed greatly over geologic time scales. These major shifts in precipitation, temperature, and wind have altered species distributions, ecosystem productivity, and foodweb structure.

The biotic responses to abrupt climatic shifts are especially well documented by paleoecological studies of lake sediments with relatively fine temporal resolution determined with various dating methods (Benson et al. 1990, Fritz 1996, Reheis 1999, Battarbee 2000, Saros and Fritz 2000). Shifts in species of plant and animal fossils are preserved in lake sediments throughout the region. For example, remains of different species of chironomid midges are used to interpret paleotemperatures. Diatom species reflect shifts in salinity and alkalinity that were altered by changes in temperatures, evaporation, and precipitation.

Fluctuating lake levels have occurred in many of these closed drainage basins over the last 50,000 years (Benson and Thompson 1987, Benson et al. 1990, Lall and Mann 1995). Increases in lake levels and the subsequent linkage among lakes were followed by decreases in lake levels and isolation of populations that were exposed to different salinities and temperatures so that organisms evolved adaptations to different aquatic environments over many thousands of years (Galat and Robinson 1983, Dickerson and Vinyard 1999a, Herbst 1999).

The region's aquatic systems are also highly variable on the shorter time scale of the contemporary climate. The area is largely semi-arid, and arid and semi-arid climates are among the most variable, globally. The region is also influenced by the El Niño-Southern Oscillation (ENSO) climate variability (Molles and Dahm 1990, Cayan and West 1993, Cayan et al. 1998, 1999). Currently, there are marked year-to-year variations in snow accumulation that are altered by ENSO patterns. For example, snowpack depths were 30% lower during the 1996 La Niña event than in the previous winter in the Jemez Mountains of northern New Mexico, the southernmost area of this Rocky Mountain/ Great Basin region (Baker et al. in press).

Spatial Variability

The great latitudinal, elevational, and geomorphic variability of the region produces a collage of aquatic habitats. Varying combinations of water temperatures, flow rates, sediment loads, nutrients, other dissolved materials, and water depths (habitat permanence) produce a wide range of habitat quality for aquatic species. Habitat quality, fragmentation, and connectedness within drainage networks influence distributions of fishes, associated food-web components, and ecosystem processes.

As is well known, distributional patterns of precipitation and temperature are influenced by the topographic relief of drainage basins. Fluvial and alluvial geometry, in turn, affects the weathering of basins and is responsive to climate change (Schumm 1977, Howard et al. 1994, Montgomery and Buffington 1997, Whipple and Tucker 1999, Whiting et al. 1999). The extensive, heterogeneous topographic relief of high mountains and broad valleys within this large geographic region results in complex temperature regimes, uneven precipitation, and exposure to high winds. Snow can occur during most any month at high elevations; and precipitation is characteristically different from north to south, and to some degree from east to west. The timing of snowfall and snow melt in this complex terrain varies across latitude and elevation resulting from differences in slope, aspect, geology, vegetational cover, and land use.

The hydrology reflects regional precipitation, evapo-transpiration, vegetative cover, catchment runoff, river regulation, and land use. The combination of high winds and complex terrain results in deep snow accumulation in some locations and snow removal in other locations. These topographic features create a complex mosaic of habitats with variously sized and shaped drainage basins. Many mountains are characterized by rain shadows and rapid runoff. Thus, because of the complex mountainous terrain there are multiple sources of landscape-level variability that alter local weather patterns within subregions.

Although considerable long-term data exist for temperature, precipitation, and wind for some areas (Baron 1992), there is a general lack of data from higher elevations and non-agricultural areas (Hirsch et al. 1990, Williams et al. 1996, Stokstad 1999). Aquatic ecosystems could be especially vulnerable to any increased frequencies of extreme events, as predicted in some climate-change scenarios, because this region is generally characterized by relatively low mean annual precipitation and by widespread occurrence of floods and droughts. Although there are several large rivers and thousands of permanent lakes (especially in the mountainous areas) that provide critical habitat for native species and for recreational uses, there are also less persistent habitats such as shallow ponds, vernal pools, and various types of wetlands that provide important habitat diversity. All of these aquatic habitats could be altered by persistent climatic shifts in precipitation, evaporation, wind, and temperature. Individual species will respond in different ways by altering population densities and community composition, and will likely be influenced by several physical and chemical variables.

Wetlands in the Rocky Mountains and Great Basin are relatively scarce except in riparian areas, and these species-rich habitats are likely to be sensitive to climatic change. Of the six physiographic types of wetlands defined by Winter (2000), the mountainous and the broad interior drainage basins that dominate this large semi-arid region are highly vulnerable to climate change because their groundwater sources are often limited or negligible. In general, the shallower the water depth and the more dependent the water source on direct precipitation, the more likely these wetland habitats will be vulnerable to climatic change (Winter 1989, 2000).

Over time, the aquatic biota of the Rocky Mountain/Great Basin region has evolved adaptations to survive in this climatic and habitat variability—in some cases broad tolerance ranges to cope with wide swings in water temperatures, depths, chemistry, etc.; in other cases genetic changes that best adapt organisms to local habitat conditions. The effects of climate change on the aquatic species, communities, and ecosystems will depend on their abilities to respond to changing conditions. Almost certainly, some species will be more adaptable than others, and community and ecosystem compositions will change.

As a consequence of the region's habitat variability and the many differences in geological terrain, drainage basins, water resources, and aquatic habitats, RMGB aquatic systems are likely to respond to climate changes at different rates (Hurd et al. 1999). Freshwater ecosystems may be altered by interannual changes in the frequencies and intensities of short-term extreme events. These events may reset the geomorphic template in fluvial ecosystems. Their frequency and intensity can result in very different impacts. For example, some populations of freshwater fishes or invertebrates in different microhabitats can adapt physiologically or behaviorally to changes in water temperatures or discharges that occur seasonally or over decadal time scales. Similarly, plant species and vegetative communities that cover the drainage basins may respond to climatic shifts at different rates and in different ways from aquatic species. But a sequence of severe droughts could cause widespread mortality and lead to wildfires and a major restructuring of drainage basins.

The challenges which the aquatic biota will face in adapting to climate change in an already variable environment will be exacerbated further by the newer stresses of human alterations of water resources—eutrophication, acidification, soil erosion and associated siltation, and water diversion and regulation—and by competition with intrusive, nonnative species. This complex of stresses makes assessment of climate-change effects highly problematic and raises a host of questions needing intensive research: How will changes in climate alter persistence and function of the current biota? Will species move to other habitats and can they disperse as conditions change? Will nonnative species compete more aggressively and displace native species? Will ecosystem functions change if the populations become fragmented and biotic composition changes? These and many other questions need to be answered if the effects of climate change on Rocky Mountain/Great Basin aquatic ecosystems are to be understood and predicted.

ASSESSMENT PROCEDURES

Subregional Scenarios

For purposes of this assessment of aquatic ecosystems, the RMGB region was divided into northern and southern subregions for three reasons. The first is the great latitudinal, and thus climatic, extent of the region. The second is the fact that the southern portion has a predominantly summer monsoonal precipitation pattern while the northern portion has a more Mediterranean seasonal distribution. And third, the evidence presented in Chapters 3 and 4 suggested that climatic changes predicted by general circulation models (GCMs), and resulting hydrologic changes, may have started to appear during the 20th century in the northwestern two-thirds of the region but not in the southeastern third.

The subregions are separated by an east-west line running approximately through central Utah and central Colorado. The southern subregion thus includes the southern halves of Utah and Colorado, and the northern New Mexico portions of the RMGB region. The northern subregion includes virtually all of the Great Basin, and those portions of the Rocky Mountain system north of central Utah and central Colorado.

This subdivision could draw attention to potential survival strategies of some species in response to rising temperatures. In the next century, if temperatures increase in the southern subregions, differences in orientation among rivers are likely to be important because drainage basins with a predominantly north-south directionality may provide some potential for northward movement by many aquatic species that require cooler-water habitats. Such movements could occur where dams, steep terrain, and the isolated locations of some reservoirs, lakes, and wetlands did not prevent species from moving into thermal refugia.

Different sets of scenarios are posed for the subregions (Table 8.1). Rising temperatures are posed for both, especially in winter. Increased precipitation is posed for both, primarily in winter in the north, and summer in the south. A number of authors are projecting increases in summer-monsoonal moisture in the southern portion of the Intermountain West. These climatic changes would be expected to reduce (northern) or eliminate (southern) montane snowpacks, alter stream temperatures and seasonal hydrographs; and in the south reduce soil infiltration and increase evaporation.

Table 8.1

Climate-change Scenarios and Hydrologic Responses for RMGB Aquatic Ecosystems

Scenario and Consequences	Northern Subregion	Southern Subregion
Precipitation	Increased winter precip., especially rain	Reduced winter rain, increased summer rain
Temperature	Warmer fall, winter, spring	Warmer winter, late summer
Expected Hydrologic Consequences	Reduced snowpacks	Snowpacks eliminated
	Earlier peak spring flows	Reduced peak spring flows
	Increased annual and base flows	Reduced annual and base flows
	Reduced summer flows	Reduced infiltration
	Increased flood magnitudes	Reduced flood magnitudes
	Increased baseflow temperatures	Increased evaporation

The Need for Model Development

Effective projections of the impacts of climate change on RMGB aquatic ecosystems can best be made with well-structured models. Developing models that simulate the effects of climate change on aquatic biotas is complicated by the fact that climate influences the organisms both by shaping the hydrology, and by affecting such environmental variables as water temperature and chemistry. The latter affect the organisms' physiologies, subsequently their population processes, and ultimately such biotic interactions as predation and competition which structure community composition. Hence the needed models will be complex structures that couple climatic inputs, hydrology, and biotic processes within aquatic systems. Such models do not presently exist, and thus cannot facilitate this assessment. But it seems useful to review some of the data needs and complexities that will affect development of such models.

Increasingly sophisticated models simulate global and regional scenarios related to directional changes in temperatures and precipitation (see reviews by Henderson-Sellers 1994, Leavesley 1994, 1999). Shifts in mean, annual global temperatures and precipitation remain difficult to forecast, especially at seasonal and regional levels (Mahlmen 1997, Reiners 1998, Ojima et al. 1999). But current general circulation models (GCMs) predict some increase in mean, annual global temperatures and changes in global precipitation over the next century. These directional changes are expected to alter regional patterns of evaporation and precipitation and thereby alter regional hydrology, especially the frequencies and intensities of floods and droughts (Arnell 1994, 1996, Lins and Slack 1997a, b, Easterling et al. 2000).

Statistical downscaling (SDS) models are being linked to GCMs and runoff models to generate regional and basin-level predictions of climate and precipitation runoff (Xu 1999a, 1999b). This approach appears to be more accurate than previous approaches because GCMs do not include effects of surface features and land-surface processes that influence runoff in mountainous basins (Wilby et al. 1999, Hay et al. 2000, Wilby et al. 2000). Other enhancements may come from use of artificial neural networks (ANN) for spatial interpolations of data used in SDS models (Snell et al. 2000). The combined applications of ANN and SDS are likely to provide more useful predictions to hydrologists and aquatic ecologists working in complex terrain if sufficient long-term data are available at enough locations within the region.

During the last several decades more attention has focused on models of how climate change beyond the range of natural variability can cause aquatic species (especially fishes) to respond to rapid and persistent shifts in temperature (e.g. Coutant 1981, Beitinger et al. 2000, Schlosser et al. 2000, Carline and Machung 2001, Isaak and Hubert 2001). Distributional and phenological changes of species are increasingly being documented. Some biological changes may be linked to extreme climate events (Easterling et al. 2000, Hughes 2000) that can trigger hydrologic and geomorphic responses which, in turn, modify the ecology of entire drainage basins. Because of these concerns, numerous studies have focused on how climate change may affect inland waters and associated biota (Gleick 1986, Molles and Dahm 1990, Hostetler 1991, Carpenter et al. 1992, Firth and Fisher 1992, Grimm 1993, McKnight et al. 1996, Cushing 1997, Meyer et al. 1999, Murdoch et al. 2000, Poff et al. 2002). These studies have identified important physical relationships among hydrologic and geomorphic variables that affect aquatic ecosystems. Researchers attempting to evaluate effects of future climate change on hydrology and precipitation confront challenges similar to those addressed by workers who are evaluating the effects of other on-going sources of disturbance on aquatic communities.

Studies dealing with distributions of biodiversity in aquatic ecosystems (Vannote and Sweeney 1980, Hawkins et al. 1995, Poff 1997, Vinson and Hawkins 1998, Lowe and Hauer 1999, 2000, McKee and Atkinson 2000) incorporate physical factors in their analyses including climate-driven variables such as temperature and discharge variability. Although variability in these physical variables is known to have seasonal and interannual effects on natural ecosystems, the understanding of how directional change or extreme variability in climate can alter biotic communities and ecosystem dynamics is still inadequate. A comprehensive approach is needed to integrate the more narrowly focused, short-term studies into a context of climate variability. For example, use of multivariate approaches to examine complex relationships between changing distributions of aquatic organisms and climate trends and variability is needed to succeed research that has previously been concerned only with eutrophication or ecotoxicology.

Several characteristics of aquatic systems complicate the development of climate-change models. One such complication is that species- and community-level dynamics are less predictable than the overall ecosystem functions of productivity, nutrient cycling, and decomposition. Rates of ecosystem functions are likely to respond to various combinations of climatic driving forces such as precipitation, temperature, and wind. Climatic variables may often drive mean rates of change in nutrient uptake, storage, and cycling. These climatic driving forces influence, but often do not control, population dynamics and some community relationships. The linkages among physical variables and biotic communities even for current climatic conditions are locally complex and not yet highly predictable. Streams, rivers, ponds, lakes, springs, and wetlands constitute broad continua of conditions where many aquatic species are adapted to wide ranges of conditions. Other species are more specifically adapted to narrow ranges of conditions, and must migrate within a bounded landscape in search of new locations if their environment changes.

Local terrain and other physical features greatly influence the composition of biotic communities so that species-specific responses to climate change remain uncertain. For example, models of energy balance and water balance for lake ecosystems are based on physical parameters. These models generally are useful for predicting when ice forms and melts on lakes (Magnuson et al. 2000, Prowse and Beltaos 2002) and when lake levels rise or fall (Winter 1981, 1989 Wurtsbaugh and Berry 1990). However, the consequences of having shallower, warmer waters or longer periods of open water and increased light penetration into a lake are not as predictable. Warmer waters generally stimulate faster rates of growth and production, but how these rates alter species-specific functions are not well known.

A related complication involves the size of a water body. As the size of a river, lake, or wetland increases, the hydrologic and ecological connections are more complex and some types of predictions are more uncertain. For example, snow melt and runoff from mountainous terrain are predictable with several types of hydrologic models (Band et al. 1996, Leavesley 1999, Baron et al. 2000). How the stream fishes respond to earlier peak flows or warmer summer waters, however, is not clear. In the RMGB region, deep lakes have predictable density and thermal stratification that result in more thermal refugia for organisms. However, stratification may result in biologically important differences in dissolved oxygen until the lakes again mix completely and increase exposure to atmospheric oxygen. Increased salinity can further accentuate stratification in lakes and large rivers so that species distributions become more variable over time and space and thus more difficult to predict competitive outcomes.

Larger, shallow-water ecosystems are often mixed by wind-driven currents and these create more spatial and temporal complexity. Such habitat complexity provides microhabitats for numerous species and increases food-web complexity. But again at the ecosystem level, these larger aquatic habitats may allow more predictable biotic responses to climate change in terms of major functional relationships. At the ecosystem level, size of lakes and rivers can influence the number of trophic levels in food webs or the complexity of energy flows through these food webs (Post et al. 2000). Species-level changes in microbes, phytoplankton, zooplankton, and fish within complex food webs, as responses to climate changes, are less predictable (e.g., Keleher and Rahel 1996, Rahel et al. 1996, Taniguchi et al 1998, Jager et al. 1999, Petchey et al. 1999).

As a third characteristic related to the latter two, aquatic-ecosystem responses are likely to be spatially and temporally linked at larger spatial scales. These interconnections can produce significant time lags associated with variable flow velocities among different standing- and flowing-water ecosystems. Although aquatic ecosystems have distinct boundaries and attributes, they are also linked to important sources of atmospherically and terrestrially derived inputs of water, nutrients, and toxins. In general, connected networks of rivers, streams and lakes integrate many physical and chemical aspects of their drainage basins that influence their biotic communities (Hynes 1970, Likens and Borman 1974, Power 1995). Standing waters of lake ecosystems have residence times, temperatures, and chemical attributes that reflect complex surface and groundwater dynamics within their drainage basins (Winter 1999, 2000, 2001). These ecosystems are also interconnected as chains of lakes and reservoirs within topographically controlled drainage networks (Hutchinson 1967, Hasler, 1975, Taub 1984, Baron 1992, Kling et al. 2000). Linkage by groundwater connections provides a continuum of internal interactions within a hierarchy of nested watersheds and varied rates of flow (Kratz et al. 1991, 1997, Winter et al. 1998).

Thus, any ecosystem-level or biotic-community-level responses to climate changes are likely to be complex and characterized by lags and thresholds that are challenging to model if only certain types of discrete systems are analyzed. Clearly, temporal and spatial scales are critical considerations in developing models for the aquatic systems of a region as large and diverse as the RMGB.

ASSESSMENT OF POTENTIAL EFFECTS

While we do not yet have models that permit comprehensive simulations of climate-change effects on RMGB aquatic ecosystems, we can make reasonable projections on the effects of changing climate variables on ecosystem components, based on the extensive aquatic literature for the region. These are proposed in the following sections, subdivided by climatic and hydrologic variables.

Precipitation and Hydrology

The major effects of precipitation on aquatic ecosystems are its influences on hydrology. The amount of precipitation determines the amount of water resources for the organisms, and its seasonality influences seasonal fluctuations to which the organisms adapt their life cycles. In the RMGB region, 85% of stream flow results from the melting and run-off of montane snowpacks (Dahm and Molles 1991, Barry 1992), and hence the stream hydrographs are intimately linked to the timing, form, and amount of montane precipitation, and to the timing of snowmelt. Any changes in seasonal distribution of precipitation, evaporation, or temperature are likely to affect the timing and amounts of flow.

The scenarios of Table 8.1 project higher temperatures and precipitation for both the northern and southern subregions, similar to the scenarios posed for the region in Table 3.8 of Chapter 3. Increased precipitation should add to the existing resources as long as the increase exceeds the higher evapotranspiration resulting from higher temperatures. Nash and Gleick (1993) concluded that a temperature increase of 4°C (7.2°F) would require a 15-20% increase in precipitation just to maintain annual run-off in the Colorado River basin at historical levels. Increased streamflow increases habitat and oxygen content, while reduction concentrates dissolved chemicals and facilitates increased temperatures.

This region has numerous seeps, springs, and groundwater-fed rivers and lakes. Habitat persistence is determined by the quantity of precipitation and by the ratio of infiltration to groundwaters and runoff to surface waters. These relationships of groundwater flows and runoff to surface waters and below-surface waters (hyporheic) are critical for defining types of biotic communities along a gradient of permanence and vulnerability to climatic changes (Winter 2000).

Current climate-change models for this region all suggest reduction in (or possible elimination of) snowpacks by 2080 to 2100. Spring peak flows during snow melt are forecasted to be lower and possibly earlier than currently observed, and reduction in snowpack would limit the quantity of snowmelt that provides the source of surface and groundwater for aquatic habitats. Any long-term change in the seasonal distributions of rain or snow (or rain on snow that results in rapid runoff and flooding) will likely alter aquatic ecosystems, especially where and when other environmental factors such as acid and nutrient deposition shift in their effects (Baron and Campbell 1997, Bowman and Steltzer 1994).

Earlier spring snow melt and increased frequencies of rain-on-snow events will greatly alter the timing of peak flows and patterns of species reproduction and survival. The timing and number of floods greatly alter wetland and floodplain habitats as well as nutrient transfers. More extreme floods and droughts would increase mortality of fishes and many types of invertebrates. More rapid runoff and higher peak floods would alter bank erosion and sediment transport. Increased sedimentation of fine particulates and infilling of rocky substrata (embeddedness) would limit fish spawning and result in loss of some species. Biotic communities would almost certainly change in species composition, dominance, and foodweb structure.

Precipitation and Water Chemistry

Retention of organic matter that provides food resources for detritivores will be altered under different seasonal patterns and magnitudes of flow alterations. During prolonged low-flow conditions, accumulation and decomposition of organic matter will lead to decreases in dissolved oxygen, especially if water temperatures are also increased. Lower dissolved oxygen and warmer waters will stress many species of fish and invertebrates and increase mortality, particularly in late summer.

Changes in water balances within catchments result from both shifts in precipitation, evaporation, evapotranspiration, and water diversions or inter-basin transfers. Together with geologic composition and land use, these hydrologic changes greatly alter salinity of inland waters. The Great Basin region is characterized by salt lakes and mineral-rich springs and soils that are derived from climatic changes and soil weathering during the Pleistocene (Lall and Mann 1995). Within the last several decades, increased salinization of soils and stream runoff has created water-quality problems in many areas of western North America. Changes in lake levels and persistence of riparian vegetation, playas, and other wetlands are all indicators of large-scale responses to hydrologic conditions that influence salinity, especially in closed basins with internal drainage. Closed basins accumulate salts in solution or in sediments over time. During periods of rapid evaporation, brines form that limit biotic diversity in closed basins with internal drainage. Open basins with out-flowing rivers transport salts out of the drainage area.

Changes in salinity along with other associated water-quality effects (warmer waters, decreased dissolved oxygen, and increased nutrients) have generally had major effects on biotic distributions in inland waters (Williams 1998, Murdoch et al. 1999, Koop and Grieshaber 2000). Physico-chemical variables restrict biotic distributions because of the physiological limitations among different species. Only a few species are well adapted for highly variable changes in salinity (i.e., euryhaline), and most species are limited to narrow ranges (stenohaline).

For example, as salinity fluctuates in response to variations in precipitation and evaporation, invertebrate communities in many deep lakes and shallow vernal pools change rapidly to exploit new conditions (Galat and Robinson 1983, Galat et al.1988, Stephens 1990, Wurtsbaugh and Berry 1990,Williams 1998). Shallow-water habitats that vary in salinity are often characterized by low species diversity but high productivity. These habitats provide essential food resources for wading birds and migratory waterfowl that consume large numbers of invertebrate prey (Wollheim and Lovvorn 1995, 1996). Such highly mobile consumer species disperse prey species among similar habitats that vary in temporal persistence. These prey species produce resistant stages or encapsulated eggs during their relatively short life spans that are well adapted for bird transport.

In total, changes in amounts and seasonal variations in aquatic environments associated with precipitation and temperature change would undoubtedly produce significant changes in aquatic biotas.

Temperature

General circulation models predict that climates will warm over the next 50 to 100 years at a rate much faster than in the recent past. The Rocky Mountain/Great Basin region is expected to be one of the warmer areas relative to global trends. Recently, these projections have included higher temperature increases (Houghton et al. 2001). Mean annual temperatures in many locations have increased during the last decade.

Because most aquatic species are ectothermic —a few species of aquatic birds and mammals are exceptions—and assume the body temperatures of their environments, an extensive history of research has examined the effects of temperature variations on aquatic ecosystems and individual species, and provides a basis for projecting global-warming effects.

General System Effects

Temperature is biologically important for aquatic organisms because it directly affects metabolic rates, growth, and reproduction. The potential impact of rapidly changing water temperatures is great in inland waters because the fish and invertebrates living in these waters lack physiological abilities to regulate their body temperatures. They rely on behavioral thermal regulation by moving into specific microhabitats with different thermal regimes. Depending upon their location and their mobility, many species can seek out different water temperatures where they attempt to optimize their growth and reproduction. Generally, species that are restricted to narrow ranges of temperatures (stenotherms) can persist only in relatively stable environments such as spring-streams or very deep lakes. Species with wider ranges of temperature tolerances (eurytherms) are more commonly found in shallow streams, lakes and ponds. Aquatic species differ greatly in their thermal preferences and tolerances: cold stenotherms are well adapted to waters just above freezing and are often limited by distinct upper thresholds while warm stenotherms are limited by lower and upper thresholds in water temperatures. These physiological differences led Magunson et al. (1979) to propose that various species use locations with particular thermal regimes as a resource within their habitat just as food types and sizes are essential resources within a species' niche.

If the warming trends of the 20th century continue, species already at the southern limits of their temperature tolerances will experience warmer waters than they can tolerate, especially during late summer. Thus, at southern margins of distribution, the maximal temperatures will likely affect some species. At the northern edges of distributions, there may be changes in lengths of growing seasons, and shifts in patterns of growth and reproduction. Warmer waters create constraints for aquatic species because metabolic demands for dissolved oxygen increase but solubility of oxygen decreases. In general, these constraints are likely to increase for some species, especially if temperature increases are extreme (Vannote and Sweeney 1980, Sarvivo, V.S. 1983, Cox and Rutherford 2000a, b).

Effects on Fishes

The thermal niches of fishes are well studied and widely used to determine how different species interact and compete for certain locations within their physiological niche requirements (Magnuson and DeStasio 1996). Coldwater fish species such as trout and salmon are the dominant components of food webs throughout the Rocky Mountain/Great Basin region. Any decline in coldwater fish abundance will have a cascade of ecological effects. These species are also especially well studied in terms of their thermal tolerances (De Staso and Rahel 1994, Taniguchi et al. 1998, Poff et al. 2000). Some of the earliest work on the effects of water temperature on trout distributions emphasized the limiting effects of cold water because growth and recruitment can be severely reduced at high elevations and latitudes. Later studies considered variable temperatures and related factors such as dissolved oxygen (Scarnecchia and Bergersen 1987).

Because of their intolerance to warm water temperatures, coldwater fishes are likely to be restricted to higher elevations if climate warming occurs. Reduction in the geographic distribution of coldwater fishes and fragmentation of remaining populations into isolated, high-elevation enclaves is anticipated as an important effect of climate warming. Based on current regional distributions of trout during the summer, Keleher and Rahel (1996) used a Geographic Information System approach to project loss of geographic range under different warming scenarios for the Rocky Mountains. Increases of 1, 2, 3, 4, and 5°C (1.8, 3.6, 5.4, 7.2, and 9.0°F) in mean July air temperatures were projected to reduce the geographic area containing suitable habitat by 17, 36, 50, 62, or 72% respectively.

Other studies used a 21°C (37.8°F) maximum water temperature as the current limit of distribution of trout in the North Platte River drainage basin, and found similar projections for reductions in stream lengths that would contain thermally suitable habitat (Rahel et al. 1996). The potential for habitat fragmentation was evaluated in the North Platte drainage where the present-day distribution of trout habitat that extends over 4,000 km (1,488 mi) of interconnected, thermally suitable streams would be broken up into many smaller, isolated enclaves with a 3°C increase in summer water temperatures (Rahel et al. 1996).

In addition to reduced suitable habitat, it is likely that climate warming will cause coldwater fishes to be replaced by warmwater species such as minnows and suckers. Laboratory experiments demonstrate competitive dominance of trout over minnows in cold water (4-20°C, 7.2-36°F) , while minnows begin to compete successfully from 22 to 24°C (39.6-43.2°F) and dominate at 26°C (46.8°F, Taniguchi et al. 1998). Physiological adaptation by trout to warmer waters is unlikely because they are currently excluded from warmer waters at low elevations, at least in part by competition with warmwater species.

Even among the coldwater species of trout, climate warming may favor non-native species such as brook trout, brown trout, or rainbow trout at the expense of native species such as cutthroat or bull trout in some habitats within the Rocky Mountain region. In laboratory studies, brook trout tolerated warm water temperatures better than Colorado River cutthroat trout in terms of survival and bursts in swimming speeds associated with successful predation. When matched for body size, brook trout and Colorado River cutthroat trout were equal competitors for food and space at 10°C (18°F), but brook trout were superior competitors at 20°C (36°F, De Staso and Rahel 1994). In this area it is likely that warming would favor nonnative salmonids over native cutthroat trout and bull trout.

In other locations within this region various subspecies have different thermal tolerances. The temperature preferences and current distributions of the federally listed native species are increasingly well documented. For example, the native Colorado greenback cutthroat trout possibly can expand its range to upper and lower elevations under warmer water conditions wherever non-native fishes can be eliminated (Young and Harig 2001). The Lahontan and Bonneville cutthroat trout may also be able to increase their geographic ranges under warmer climates if non-native species of trout are restricted from competing with the natives.

Studies of the projected long-term increases in mean, annual air temperatures from GCMs in other regions provide some insight regarding the effects of warmer air temperatures on groundwater and on groundwater-fed streams relative to trout distributions during summer. Meisner (1990) concluded that habitat restrictions are likely in some low-elevation and low-latitude waters, where fishes such as brook trout (*Salvelinus fontinalis*) are limited by their upper thermal physiological limits for growth and reproduction. Although not yet examined, lethal effects on young-of-the year might also occur as a result of extremely warm temperatures during late summer. These "bottlenecks" for survival limit persistence of those species that require cold waters. There may be some thermal refugia in deeper springs and groundwater-fed rivers, and in deep, stratified lakes where cooler waters are spatially distributed (Eaton et al. 1995, Eaton and Scheller 1996). The size and extent of these local refugia may be very limited and may increase vulnerability to predators and diseases.

However, Meisner (1990) pointed out that climate warming could result in some positive effects in populations at high altitudes and/or latitudes. Naturalized populations of introduced brook trout in western North America could increase their range of suitable habitats if higher water temperatures occur. The difficulty is that they may expand into habitats of native species such as the endangered Colorado greenback cutthroat trout (Young 1998, Behnke 1992).

Effects on Invertebrates

Aquatic invertebrates which provide food for fishes and wading birds in upper trophic levels are also known to have distinct thermal requirements. Water temperatures clearly alter individual growth and reproductive rates. The timing of reproduction and allocation of energy into egg production are influenced by water temperature. For example, aquatic insects are among the most widely distributed invertebrate groups. They live over a wide range of thermal regimes with some species adapted to very warm waters such as thermal springs (Pritchard 1991). But in North America, most aquatic insect species are found in cold or intermediate ranges of temperature (see Ward and Stanford 1982, Sweeney et al. 1992, Hershey and Lamberti 2001 for reviews). Similarly, a few species of freshwater crustaceans can tolerate high water temperatures while many more occur in cooler waters. Some amphipod crustaceans occur in relatively warm waters. For example, *Hyalella azteca* lives in waters up to 33-34°C in Devil's Hole, Nevada while *Gammarus lacustris* lives in cold alpine waters.

Gammarus lacustris occurs over a wide geographic range including altitudinal and elevational differences in annual thermal regimes, and varies greatly in such reproductive traits as egg size and number (France 1992, Wilhelm and Schindler 2000). If montane-lake waters warm, *G. lacustris* reproduction is predicted to shift along a continuum from a few large eggs to many small eggs. Warming of high-elevation lakes will result in a shorter life cycle and increased egg production in *G. lacustris* which could increase density of this species (Wilhelm and Schinder 2000). Such an increase could alter interactions with amphipod food resources in the benthic and planktonic communities as well as predators such as fish.

Generally, many aquatic species track seasonal temperatures to optimize their survival. For example, field studies show that *Hyalella azteca* has a 20°C threshold for induction and termination of reproductive resting stages. These crustaceans move from warmer, shallow waters to cooler, deeper water as individuals mature (Panov and McQueen 1998). Other species are restricted to cooler waters (*Gammarus minus* occurs only in waters below 20°C, see Covich and Thorp 2001 for review). Zooplanktonic crustaceans such as *Daphnia pulex* and *D. galeata* are likely to respond by altering their foraging, food-web dynamics, and life histories. One hypothesis being tested is that warmer waters will provide an environment that favors smaller zooplankton over larger species because of metabolic constraints on swimming and bioenergetics (Achenbach and Lampert 1997, Beisner et al. 1997).

If extreme temperatures occur more frequently in the future, the effects of climate change will likely alter many shallow-water aquatic communities through increased physiological stress due to both warmer and more fluctuating temperatures (Sarvivo 1983, Lagerspetz 2000). In addition, reduced volumes due to higher evaporation and evapo-transpiration rates could result in rapid loss of habitat (Winter 1989, 1999). Increased temperatures reduce the solubility of dissolved oxygen while simultaneously increasing metabolic rates and physiological demands for more dissolved oxygen by aquatic invertebrate species. In addition, rates of microbial growth and decomposition also increase and require more dissolved oxygen. Over time, the indirect effects of increased temperatures on growth and reproduction can be as important as the direct effects of high lethal temperatures because mortality results in fewer individuals surviving to reproduce.

Biotic distributions are likely to shift in response to climatic changes but how food-web dynamics and ecosystem productivity will be altered is not known. A decline of species diversity can generally be predicted in sites where there is a persistent increase in high temperatures or in those with highly fluctuating temperatures (Hogg and Williams 1996). These two sets of environmental extremes create major barriers to dispersal for most aquatic species.

Effects on Riparian Vegetation

Light, temperature, and flow regimes affect which plants can compete for space along stream banks. Native riparian plants provide shade (as well as leaf litter and woody organic inputs) that influence water temperatures. A diverse community of trees along streams can alter the invertebrate community by the timing, quantity, and quality of litter inputs to the stream, and can reduce bank erosion and maintain substrates suitable for fish spawning and benthic prey (Kennedy et al. 2000). The frequency and magnitude of flooding greatly influences seed germination and recruitment of new individuals into these populations. Changing hydrologies associated with climate change will almost certainly alter the distributions and compositions of these zones, and consequently their influences on stream ecosystems.

Conclusions and Needs for Further Study

Currently, aquatic ecosystems within the heterogeneous landscapes of the Rocky Mountains/Great Basin region support a high diversity of species (Cushing 1997, Grimm et al. 1997, Hauer et al. 1997, Leavesley et al. 1997, Melack et al. 1997, McKnight and Covich 1997). Many biotic communities have undergone post-Pleistocene changes in species composition along riparian zones, wetlands, floodplains, springs, rivers, and lakes. The most recent post-glacial changes shifted from a wet, pluvial climate to an arid or semi-arid climate throughout most of the region. This series of natural climatic changes has created a mosaic of different habitats occupied by a very diverse biota (Herbst and Blinn 1998, Dickerson and Vinyard 1999b, O'Brien and Blinn 1999, Kulkoyluoglu and Vinyard 2000, Shepard et al. 2000).

Climate change will almost certainly alter these systems, in many cases very fundamentally. And some of the changes can be predicted, at least qualitatively, with a high level of probability. For example, in the two subregions considered, climatic forecasts of 2 to 4°C (3.6-7.2°F) increases in temperatures over the next century are likely to result in different impacts on freshwater ecosystems from north to south. Some of the future changes in aquatic ecosystems resulting from this warming can be anticipated, especially for the southern subregion. These effects will likely include an earlier spring peak flow driven by more rapid snowmelt. Warmer springs are expected to extend the growing seasons of some species of fishes and invertebrates and alter food-web dynamics. Warmer water temperatures in streams and their combined input to lakes and reservoirs may alter lake stratification by mid to late summer. Warmer surface waters (epilimnion) and slightly warmer bottom waters (hypolimnion) of stratified lakes will likely alter phytoplankton and zooplankton community structure and productivity by increasing metabolic rates and shifting competitive and feeding relationships.

Higher water temperatures may well shift the distributions of cold-water species northward and to higher elevations. At the same time those temperatures are likely to favor warm-water species, many of which are nonnatives, and which are likely to compete more stringently with species that are now threatened or endangered.

Moreover, climate change is likely to interact with several current trends that will either continue to change incrementally or could shift in unexpected ways in the next century as human population growth and management decisions change. Thus climatic change is likely to have several cumulative and possibly synergistic effects as warmer waters, more extreme precipitation (droughts and floods), and increased demand for water resources by a growing human population combine their influences. Warmer and more nutrient-rich waters (from various human effluents) will likely modify many different types of aquatic ecosystems by accelerating nutrient cycling and increasing primary and secondary productivity while at the same time impacting individual species. Increased erosion (from overgrazing, streambank erosion, and road construction) during extremely high peak flows will alter stream substrates and lead to changes in benthic communities and fish distributions.

However, firm quantitative predictions await the development of coupled hydrologic and ecosystem models, and increased information on many aspects of the RMGB aquatic ecosystems. Many locations lack basic data as a result of the uneven distribution of climatic monitoring stations and limited, long-term biotic sampling. Although studies exist for some locations near urban centers, limits on extrapolation among many different ecosystems within this very large region prevent definitive analysis.

To an unknown degree, constituent species have not yet been discovered and described. For example, Hershler (1998) collected aquatic snails in a survey of springs from 500 sites in the Great Basin. He found 58 new undescribed species of *Pyrgulopsis* that occur in a wide variety of thermal and saline spring-fed waters. Endemism is extreme and 22 of these new species are known from only a single site. Kulkoyluoglu and Vinyard (2000) collected 14 species of ostracodes from 24 springs and found nine species not previously reported for Nevada. Little is known of the population ecology of these species or how they might respond to warmer or drier climates in the future. Additional new species continue to be found (Hershler et al. 1999). Equally important are gaps in conceptualization and understanding of how these dynamic biotic communities and ecosystems function. Knowledge of local and regional biodiversity and of likely biotic responses to climatic change is limited. Careful monitoring of the few groups that are relatively well studied is essential.

In total, climate change as projected in Table 8.1 will in all probability fundamentally alter RMGB aquatic ecosystems. Some of those changes can be predicted qualitatively on the basis of existing research. But concerted research effort is needed to provide the additional information required for quantitative predictions of those changes.

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