IMPACTS OF CLIMATE CHANGE ON AQUATIC ECOSYSTEM FUNCTIONING AND HEALTH[1]

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ABSTRACT: We review published analyses of the effects of climate change on goods and services provided by freshwater ecosystems in the United States. Climate-induced changes must be assessed in the context of massive anthropogenic changes in water quantity and quality resulting from altered patterns of land use, water withdrawal, and species invasions; these may dwarf or exacerbate climate-induced changes. Water to meet instream needs is competing with other uses of water, and that competition is likely to be increased by climate change. We review recent predictions of the impacts of climate change on aquatic ecosystems in eight regions of North America. Impacts include warmer temperatures that alter lake mixing regimes and availability of fish habitat; changed magnitude and seasonality of runoff regimes that alter nutrient loading and limit habitat availability at low flow; and loss of prairie pothole wetlands that reduces waterfowl populations. Many of the predicted changes in aquatic ecosystems are a consequence of climatic effects on terrestrial ecosystems; shifts in riparian vegetation and hydrology are particularly critical. We review models that could be used to explore potential effects of climate change on freshwater ecosystems; these include models of instream flow, bioenergetics models, nutrient spiraling models, and models relating riverine food webs to hydrologic regime. We discuss potential ecological risks, benefits, and costs of climate change and identify information needs and model improvements that are required to improve our ability to predict and identify climate change impacts and to evaluate management options.
(KEY TERMS: aquatic ecosystems; anthropogenic change; climate change; instream flow; riparian zones; surface water hydrology; water quality; water temperature.)

INTRODUCTION

Human societies require the goods and services supplied by healthy aquatic ecosystems, which are sustainable, maintain ecological structure and func- tion over time, and continue to meet societal needs and expectations (Meyer, 1997). Maintaining biological diversity and providing other essential goods and services such as clean water and fish protein depends on basic ecosystem processes such as nutrient uptake and cycling, primary and secondary production, decomposition, and food web interactions. Primary productivity and inputs from the watershed support food webs yielding fish for both recreational and commercial uses. Removal of nutrients by biological uptake purifies the water and protects downstream ecosystems. Rates of these vital processes are impacted by water temperature as well as the range and temporal pattern of discharge, all of which may be altered in a changed climate.

Freshwaters are rich in biological diversity, and a large part of the fauna is under threat of extinction because of human activities (Naiman *et al.*, 1995). A changing climate may intensify these threats in many ways, such as the spread of exotic species, further fragmentation of species populations because of thermal constraints, and human responses to a changing climate (e.g., additional pressure to build flood control or water supply reservoirs). Sensitivity to climate change may differ in natural versus managed aquatic ecosystems. For example, regulated rivers may experience less variability in flow caused by climate change than would unregulated rivers (because control structures are present), but there may be greater competition for a limited quantity of water resulting from indirect influences of climate (such as increased demand for power to supply air conditioning). Hence

the impacts of climate change are set in the broader context of intensifying human disturbance of the landscape.

Water to meet the needs of aquatic ecosystems is competing with other uses for water. Two decades ago the Water Resources Council completed its second National Water Assessment, presenting a nationally consistent evaluation of the current and projected water use and supply information by region (WRC, 1978). This assessment identified serious water resource problems, including preservation of fish and wildlife habitat and other instream needs for water such as freshwater recruitment to estuaries and maintenance of riparian vegetation and floodplain wetlands. Using relatively simple screening techniques (Tennant, 1976), the WRC quantified instream flow needs for fish and wildlife as a percentage of total streamflow in 1975 (Table 1). Instream flow requirements for maintenance of aquatic ecosystems place significant unmet demands on total streamflow. The lack of integrated water quantity and quality management was identified as a special problem, which continues today despite recurring calls for such a management plan. Although methods for determining instream flow needs have improved significantly since the last WRC assessment, and minimum instream flows have been increased in many areas through environmental regulations, competition over limited water resources remains a serious stress to aquatic ecosystems (e.g., HBSI, 1998). Postel et al. (1996) estimate that humans currently appropriate 54 percent of runoff that is geographically and temporally accessible to them. This competition is likely to be intensified by climate change. Hence climate-induced changes must be assessed in the context of existing demands for a limited supply of water and massive human-induced changes in water quantity and quality that have resulted from altered patterns of land use, water withdrawal, and species invasions. Climate change effects may be dwarfed or exacerbated by these other forces of change.

Many analyses of the effects of climate change on freshwater ecosystems have been published in the past decade. Here we review these studies as they relate to the on-going regional assessment of the effects of climate change on water resources in the United States. We review ecological benefits and costs that have been identified and explore approaches that offer promise in assessing impacts of climate change. We conclude with a discussion of what is needed to improve our ability to predict and identify impacts of climate change and to evaluate management options.

TABLE 1. Estimated In-Stream Flow Requirements to Meet the Needs of Fish and Wildlife and Total Use as a Percentage of Total Streamflow in 21 Water Resource Regions (from Volume 2, Table IV-11,WRC, 1978). Total streamflow is calculated as 1975 streamflow + 1975 consumption - 1975 groundwater overdraft.

Water Resources Region (from Figure I-1, WRC, 1978)	Instream Use/Total Streamflow (percent)	Total Use/ Total Streamflow (percent)
New England	88	89
Mid-Atlantic	85	87
South Atlantic-Gulf	81	83
Great Lakes	85	88
Ohio	89	90
Tennessee	94	95
Upper Mississippi	82	94
Lower Mississippi	79	86
Souris-Red-Rainy	60	62
Missouri	60	87
Arkansas-White-Red	71	83
Texas-Gulf	68	101
Rio Grande	48	136
Upper Colorado	64	84
Lower Colorado	111	225
Great Basin	59	125
Pacific Northwest	80	84
California	45	82
Alaska	95	95
Hawaii	62	70
Caribbean	72	79
ENTIRE NATION	79	87

REGIONAL ASSESSMENTS OF THE IMPACT OF CLIMATE CHANGE ON AQUATIC ECOSYSTEMS

Earlier analyses of the impact of climate change on aquatic ecosystems were founded on expected climate trends in an atmosphere richer in CO_2 (warmer, somewhat higher precipitation that is more variable in both space and time) and insights from previous ecological research (e.g., Carpenter et al., 1992, Firth and Fisher, 1992). Papers in Firth and Fisher (1992) explored the effects of a 2-5°C warming in the next century on freshwater ecosystems. Effects identified include: alterations in emissions of greenhouse gases such as methane (Harriss and Frolking, 1992); shifts in distributions of aquatic insects whose development and generation times are highly sensitive to temperature (Sweeney et al., 1992); altered plant assemblages in riparian zones and altered rates of organic matter

supply, decomposition and exchanges occurring at the terrestrial-aquatic interface (Meyer and Pulliam, 1992); changes in sediment loading and channel morphology (Ward et al., 1992); and elimination of some fish species, particularly in drainages oriented east-west rather than north-south (Carpenter et al., 1992).

The impacts of climate change on North American water resources have been more recently assessed at a regional level by the Intergovernmental Panel on Climate Change (Shriner et al., 1998, summarized by Mulholland and Sale, 1998) and by a group of limnologists, hydrologists, and climatologists for eight physiographic regions in North America based on an analysis of historical trends and climate change predictions for each region (McKnight and Covich, 1997, Leavesley et al., 1997). These assessments are reviewed in this section. They were largely based on climate models with CO_2 concentration doubled as a step function and without aerosol forcing. Including aerosol effects or ramping up CO_2 concentration would likely reduce the climate changes predicted (Houghton et al., 1996).

Analyses of recent hydrological trends have indicated that precipitation and streamflow have increased over the last 50 years for much of the U.S., particularly in autumn and winter (Lettenmaier et al., 1994; Lins and Michaels, 1994). Some portions of Canada are experiencing earlier spring snowmelt (Burn, 1994) and decreased summer low flow (Anderson et al., 1991). Coupled with these climate-related changes, loss of wetlands from agriculture and urban expansion are producing changes in the hydrological characteristics of many drainage basins. These include increases in maximum river discharges resulting from reduced storage capacity for flood waters and reductions in groundwater recharge and minimum discharges.

Changes in hydrologic variability (frequency and magnitude of extreme events) are likely to have a greater potential to impact water resources in many regions than changes in mean annual conditions (Gleick, 1990). Several doubled CO_2 simulations with global climate models have indicated an increase in the magnitude of rainfall events, particularly for central and northwest North America, even with small changes in mean annual rainfall (Cubasch et al., 1995; Mearns et al., 1995). Few model simulation analyses, however, have addressed the issue of variability in daily precipitation, and increases in the frequency or severity of extreme hydrologic events are plausible but highly uncertain at this time (Karl et al., 1995). Greater hydrologic variability could pose large problems for the management of water resources in populated regions in terms of both quantity (e.g., flood control, water allocations during droughts) and quality (e.g., increases in sediment and

contaminant loading during floods, reduction in assimilation capacity for effluents during droughts).

Predictions of increasing air temperature are made with greater confidence than predictions of hydrologic change (Shriner et al., 1998). The direct effects of increasing temperatures on aquatic ecosystems will be both positive and negative. Species-specific habitat requirements for temperature and dissolved oxygen are sufficiently well known for many game fish species so that likely responses to changing climates can be predicted (Coutant, 1990). In general, climatic warming will produce a general shift in species distributions northward, with extinctions and extirpations of cold-water species at lower latitudes and range expansion of warm-water and cool-water species into higher latitudes. Eaton and Scheller (1996) project that the suitable habitat for cold-water and cool-water fish species would be reduced by over 50 percent in streams of the conterminous U.S. by summer mean air temperature increases of 2-6°C derived from simulations of a doubled CO_2 climate model. In contrast, a 4°C increase in mean air temperature is projected to expand the ranges of smallmouth bass and yellow perch northward across Canada by about 500 km (Shuter and Post, 1990).

Human demands for water are expected to increase under a warmer climate, exacerbating current management problems. Increasing demands for irrigation and industrial cooling water under a warmer climate would conflict with the increasing demands for municipal water supplies resulting from urban growth. Higher water temperatures will reduce the efficiency of cooling systems and could make it increasingly difficult to meet regulatory requirements for downstream water temperatures, particularly during summer heat waves (Miller et al., 1993). Improved management of water infrastructure, pricing policies, and demand-side management of supply have the potential to mitigate some of the impacts of increasing water demand (Frederick and Gleick, 1989).

Arctic and Sub-Arctic North America

Both historic records (instrument record, tree rings, ice cores, and diatom chronologies) and model predictions for Alaska indicate temperature increases and some increases in precipitation (Rouse et al., 1997). These climate shifts have and will continue to result in profound changes in freshwater ecosystems mediated through effects on permafrost, nutrient delivery, and length of growing season. Increased rates of decomposition and increased water residence time are predicted to increase primary and secondary productivity, yet it is not clear that these increases in

production will be adequate to make up for the increased metabolic demand of higher temperatures for fishes (Rouse *et al.*, 1997). Top predators (grayling and lake trout) appear particularly vulnerable to climate change, and reductions in their abundance would likely have effects throughout the food web. In addition, reduction in ice-jams on rivers are predicted to result in loss of river delta lakes.

Climatic warming could result in substantial changes in the mixing properties of many high-latitude and mid-latitude lakes (Hostetler and Small, 1999) which, in turn, would produce large effects on deep-water dissolved oxygen concentrations and on primary productivity via effects on nutrient supplies and exposure of phytoplankton to light. Although these effects are expected to be highly dependent on the morphometric characteristics of individual lakes and are difficult to predict, at high latitudes the effects are likely to result in higher primary productivity.

The abundant peatlands in this region are vulnerable to changes in water table depth influenced by permafrost melting and altered water balances. A changing climate can shift them from a net sink to a net source for CO_2. Aquatic ecosystems in this region appear particularly vulnerable to climate change.

Laurentian Great Lakes and Precambrian Shield

Historical records and climate predictions for this region indicate a climate growing warmer and wetter (Magnuson *et al.*, 1997). Since 1911 spring air temperatures have increased by 0.11°C per decade, periods of ice cover have grown shorter, and annual precipitation has increased by 2.1 percent per decade. Changes such as these will alter lake mixing regimes (e.g., longer periods of summer stratification), reduce lake levels (because of excess evaporation), and shorten water residence time, all of which will have profound effects on ecosystem processes. For example, dissolved organic carbon (DOC) concentrations are predicted to decrease because of reduced runoff from drier catchments, resulting in increases in water clarity, thermocline depth, and productivity. Changes in the seasonality of runoff may also affect water quality. Extended droughts in boreal regions have been shown to result in acidification of streams due to oxidation of organic sulfur pools in soils (Schindler, 1997).

Potential water level changes in the Great Lakes are of particular concern because of their great economic and social importance. Analyses conducted as part of the Great Lakes-St. Lawrence Basin Project by Environment Canada suggest declines in water levels of from 0.2 to 2.5 m in the Great Lakes under several

doubled CO_2 climate change scenarios (Mortsch and Quinn, 1996; Mortsch and Mills, 1996). These water level changes were based on climate change scenarios from models that produced global temperature increases that are at least twice as large and precipitation changes that are generally greater than the most recent climate change simulations that include effects of aerosols. Nonetheless, although highly uncertain at this time, the potential declines in Great Lakes water levels could have large negative effects on wetlands, fish spawning, recreational boating, commercial navigation, and municipal water supplies in the Great Lakes.

In deep, thermally-stratified lakes in the mid and high latitudes, including the Great Lakes, winter survival, growth rates, and thermal habitat for fish generally increase under doubled CO_2 climate simulations, although these predictions do not take changes in oxygen into account (Magnuson and DeStasio, 1996). Dissolved oxygen below the thermocline is predicted to decrease (Magnuson *et al.*, 1997). In smaller mid-latitude lakes and reservoirs, however, warming may reduce habitat for many of the cool-water and cold-water species because deep-water thermal refuges in summer are not present or become unavailable as a consequence of declines in dissolved oxygen concentrations (Stefan *et al.*, 1996). Thermal habitat area is predicted to increase for warm-water and cool-water species, but decrease for cold-water species, with greatest changes in more productive lakes. Hence, invasions of warm-water fishes and extirpations of cold-water species are predicted to increase in this region. Aquatic ecosystems in this region are clearly sensitive to climate change.

Rocky Mountains

Because of high spatial and temporal variability of weather patterns, climate predictions for this region are tenuous, although a warming climate is generally predicted. Hauer *et al.* (1997) discuss consequences of this general warming. Potential lowering of the elevation of timberline will increase the amount of organic matter being supplied to food webs from outside the stream as riparian vegetation increases shading and litter inputs. In addition, altered temperature regimes along rivers could impact aquatic insect distributions. One likely consequence of a warmer climate is increasing fragmentation of cold-water fish habitats in headwaters and potential shifts in the competitive dominance of introduced salmonid species. Alpine lakes in this region are generally oligotrophic and naturally fishless; food webs are sensitive to increases in nutrient loading, siltation, and

temperature, all of which could be expected with a changing climate. Likely shifts in the hydrologic regime toward earlier and higher winter and spring flows and lower summer flows could exacerbate the stresses resulting from changes in population and land use and lead to water quality and quantity problems. Impacts of climate change in this region are occurring in the context of and seem dwarfed by extensive anthropogenic impacts resulting from rapid population growth and introductions of exotic species.

Mid Atlantic and New England

Climate predictions suggest warmer and somewhat drier conditions in this region, which is characterized by dense human populations, extensive land use alterations, and abundant freshwater ecosystems. Hence, impacts of climate change must be considered in the context of existing anthropogenic stressors. Both negative and positive impacts of climate change have been predicted; although bioaccumulation of contaminants may increase, there may be less episodic acidification during snowmelt (Moore et al., 1997). Bog ecosystems in the region, which are dependent upon rainwater inputs, appear most vulnerable to predicted changes in climate.

Southeastern U.S.

Freshwater ecosystems in this region are characterized by extensive abundant wetlands and high biodiversity. Climate change scenarios indicate warming with possible increases in annual precipitation and greater clustering of storms (Mulholland et al., 1997a), although some show declines in summer precipitation in this region (Shriner et al., 1998). Changes likely to occur in freshwater ecosystems include (Mulholland et al., 1997a): increased rates of production and nutrient cycling with higher temperature and longer growing season; reduction in habitat for cool-water species, such as brook trout and many aquatic insects; more extensive summer deoxygenation in reservoirs (Chang et al., 1992); greater summer drying of wetland soils resulting in greater fire threat; and expansion of subtropical species northward, some of which are nuisance exotics (e.g., Melaleuca). These climate change effects are likely to exacerbate current patterns of anthropogenic stress, such as increased urbanization and demands for increased water storage capacity and increasing loadings of waste heat from power production.

Pacific Coast and Western Great Basin

Analyses of long-term climate records and climate predictions suggest warming with less precipitation falling as snow and increased winter rainfall (Melack et al., 1997; Shriner et al., 1998). This could result in increased river flows in winter and spring in the Pacific Northwest, but decreased runoff during summer because of the lower soil moisture levels predicted in some climate change scenarios (Shriner et al., 1998). In saline lakes of the region, increased incidence of meromixis (permanent stratification) and reduced productivity are linked to reductions in streamflow. Altered runoff regimes, increased sediment loads, and decreased channel stability are predicted to reduce benthic diversity in glacial-fed rivers and reduce growth rates of economically important aquatic species such as salmon.

Great Plains

There is a diversity of aquatic ecosystems in this region: playas, prairie pothole lakes, ox-bow lakes, springs, ephemeral streams, large rivers, and reservoirs. The region has a strong east-west gradient in precipitation and temperature, an historical record of major droughts, and considerable human alteration of aquatic ecosystems (dams, dikes, channelization). In the mid-latitude regions of North America, the amount and seasonal timing of runoff could change dramatically as a result of shifts in the form of precipitation and in the timing of snowmelt (Shriner et al., 1998). River and reservoir systems that rely on snow or glacier melt during the spring and summer periods of high agricultural and municipal demand and low precipitation may have critical supply-demand mismatches. The Great Plains and Prairie regions of the U.S. and California have been shown to be particularly vulnerable in this regard (Cohen et al., 1989; Gleick, 1993).

Lake levels and wetland distributions are highly sensitive to changes in precipitation and evaporation. Lakes in dry evaporative drainage basins and the semi-permanent prairie sloughs in the north-central U.S. (fed primarily by ground water, precipitation, and spring snowmelt) are among the most sensitive to changes in climate that produce drier conditions. Water level and extent of open water in prairie potholes are predicted to be reduced in a $2xCO_2$ climate with substantial negative effects on waterfowl since prairie wetlands produce 50-80 percent of the total North American duck population (Covich et al., 1997). Predicted warming of surface waters in the western and northern Great Plains could lead to increasing

salinity and to extinction of endemic fish species already close to their lethal thermal limits. In addition, increased human demands for water and potentially higher shallow groundwater temperatures could alter the fauna of unique springs in the region and greatly reduce the area of wetted channel in ephemeral streams (Covich et al., 1997).

Arid Southwest

The climate of this region is variable and unpredictable, yet its aquatic ecosystems are particularly sensitive to changes in quantity, timing, and variability of precipitation and stream flow (Grimm et al., 1997). Many aquatic ecosystems in this region are isolated with high rates of endemism. Rapidly expanding human populations will exacerbate reductions in water availability resulting from climate warming. These changes threaten loss of riparian vegetation and salinity-mediated species invasions leading to food web alterations.

Patterns of Predicted Impacts. Several patterns of change are common among these regional analyses. (1) All regions are predicted to experience warmer conditions, although the extent of temperature change varies considerably. Expected changes in precipitation are more variable, with some regions (Northwest, Southeast, Great Lakes) predicted to be wetter and others (New England) predicted to be drier. (2) These climate-induced changes are occurring in the context of massive anthropogenic alterations of water quantity, quality, sediment and nutrient loads, and exotic species. Climate change effects may be dwarfed or exacerbated by these other forces of change. In addition, the direct effects of climate change are complicated by indirect effects of human actions in response to a changing climate (construction of flood control or water supply reservoirs). (3) Water to meet the instream needs of aquatic ecosystems is competing with other uses of water, and that competition is likely to be intensified by climate change. (4) Changes in hydrologic variability (frequency and magnitude of extreme events) and seasonality appear likely to have a greater impact on aquatic ecosystems in many regions than changes in mean annual conditions. (5) Many of the predicted changes in aquatic ecosystems (e.g., DOC and nutrient loading) are a consequence of the effects of a changing climate on terrestrial ecosystems. Hence, assessing changes in terrestrial-aquatic linkages is a critical component of a climate change assessment. Shifts in vegetation composition and hydrology of riparian zones are particularly critical.

The regions described above differ in their vulnerability to climate change as a consequence of the extent of climate change predicted and the context of other anthropogenic stressors. If we were to attempt to array these various regions according to their vulnerability to projected climate change, aquatic ecosystems in the Arctic, Great Lakes, and Great Plains (especially prairie potholes) regions appear most vulnerable. Although aquatic ecosystems in the arid southwest are clearly vulnerable to changing precipitation, the nature of predicted climate change in that region is not apparent from the analyses reviewed. The context of extensive anthropogenic alteration and uncertainties of climate change predictions in the other regions complicate predictions of the impact of climate change on aquatic ecosystems.

A change in water temperature is the most likely effect of climate change in most regions, and this change will have secondary effects on water quality parameters (e.g., dissolved oxygen) and biotic processes, as described above in the discussion on each region. Changes in thermal regime pose threats to a broad range of higher level population and community interactions, ranging from direct mortality from acute temperature stress, chronic bioenergetic stresses, and shifts in the balance of interspecies competition as habitat space for some species is reduced. Thermal refugia are a critical component of aquatic ecosystems that are difficult to capture using current climate models.

Patterns are also apparent in the properties of different aquatic ecosystems that are vulnerable to a changing climate (Table 2). Wetlands are particularly sensitive to changes in their water balance resulting in reduced areal extent, increased vulnerability to fire, and altered rates of exchange of greenhouse gasses. The changes identified in lakes are associated with altered mixing regimes, delivery of nutrients and DOC from the watershed, availability of thermal refuges, and alteration of population sizes of the top predators with cascading effects on lower trophic levels. In streams, the changes are closely linked with climate impacts on the riparian zone, species-specific thermal tolerances, and alterations in flow regime.

RISKS AND BENEFITS FOR
AQUATIC ECOSYSTEMS

The studies reviewed above have identified potential risks and benefits of climate change for aquatic ecosystems. Increasing competition for water in stream channels will lead to escalating conflicts between aquatic ecosystems and societal demand for

TABLE 2. Some Properties of Different Aquatic Ecosystems that are Particularly Sensitive to Climate Change.
Changes in these properties could alter aquatic ecosystem functioning and health.

Lakes	Streams	Wetlands
Mixing Regime	Flow Regime	Altered Water Balance Leading to Wetland Losses
Nutrient and DOC Inputs	Sediment Transport/Channel Alterations	Fire Frequency
Habitats Meeting Temperature and Oxygen Requirements	Nutrient Loading and Rates of Nutrient Cycling	Altered Rates of Exchanges of Greenhouse Gases
Productivity	Fragmentation and Isolation of Cold Water Habitats	Vegetation Species Composition
Top Predator Changes Leading to Trophic Cascades	Altered Exchanges with the Riparian Zone	Reproductive Success of Many Animal Species
Abundance of Cold-Water and Warm-Water Fish Species	Life History Characteristics of Many Aquatic Insects	Sensitivity to Invasion by Tropical Exotic Species

water. For regions where increases in runoff variability or more prolonged drought conditions are associated with climate change, the pressure to build water supply reservoirs will be great. These structures would further fragment and alter lotic ecosystems. If altered river flows require a 20 percent increase in reservoir storage capacity to meet irrigation demands, costs to maintain current irrigated acreage could exceed $200 billion (Postel, 1999). Threats to freshwater biodiversity from climate change include fragmentation of cold-water habitats, loss of glacial relict populations, invasion and spread of exotic species, and alteration of parasite loads. Extended periods of low flow will lead to water quality degradation and potential reductions in wasteload allocations.

A recent assessment of the impacts of changing water temperatures on the economic yield from recreational fisheries concluded that changes in cool-water and cold-water fisheries could lead to economic losses ranging from $85-320 million per year (Abt Associates, 1995), although these estimates are uncertain because the extent of any tradeoff from cold-water to warm-water fisheries is unknown. Flow alterations were not formally considered in the analysis, but they would likely escalate calculated losses. Fisheries benefits expected in a warmer climate include increased productivity of warm-water fisheries and aquaculture as well as reduced winter fish kill.

VULNERABILITY TO CLIMATE CHANGE
IN DIFFERENT HYDROLOGIC REGIMES

Streamflow is considered by ecologists as a master variable (Minshall, 1988; Poff and Ward, 1989; Power

et al., 1995) that integrates many important environmental conditions and limits the distribution and abundance of riverine species. Many fundamental ecological processes are influenced by temporal flow variation: availability and persistence of habitat; species access to habitat needed for specific life stages; rates of uptake, transformation, and flux of nutrients and organic matter; and the strength of competition and predation. Thus, temporal variation in flow is viewed as an environmental template upon which ecological processes and patterns are expressed (Poff and Ward, 1990; Townsend and Hildrew, 1994).

Temporal variation in streamflow occurs naturally within a watershed in response to seasonal and inter-annual climate variation. Natural hydrologic regimes also vary among watersheds because of regional variation in climate, geology, lithology, and vegetative cover. Hydrologists have long recognized geographic variation in hydrologic regimes, and in the past few years, ecologists have also become interested in these patterns because they indicate how ecological organization may be constrained by landscape setting (Resh et al., 1988; Poff and Ward, 1989; Poff, 1996; Richards, 1990; Hughes and James, 1989; Jowett and Duncan, 1990). Indeed, a few ecological studies have shown that among-watershed variation in the ecological organization of stream communities can be explained in terms of the natural patterns of hydrologic variability (Scarbrook and Townsend, 1993; Biggs, 1995; Poff and Allan, 1995; Clausen and Biggs, 1997; Richards et al., 1997).

An important implication of this research is that ecological organization in a stream or river will reflect the adjustment of the biota to the natural pattern of hydrologic variation over long (evolutionary) time periods. Species without the attributes that allow

them to exploit the prevailing environmental regime are selected against. For example, some species require flooding at a specific time of year at least every few years to reproduce and sustain their populations, and in the absence of such high flows, they do not sustain their populations. Similarly, ecosystem processes such as nutrient exchange with the floodplain or input of woody debris will reflect the temporal pattern of flows that allow lateral communication between the main channel and the banks and side channels (see Poff et al., 1997).

Thus, ecological interactions and ecosystem function are expected to differ among streams and rivers that have different hydrologic regimes. For example, streams draining highly porous soils have high infiltration and minimal overland flow during rain events; they are relatively stable hydrologically, especially when compared to streams draining catchments with impervious or shallow soils or with much exposed bedrock. Streams in the same climatic region may differ in geology and thus flashiness, which can influence ecological properties such as species abundance or community composition (Strayer, 1983; Scarsbrook and Townsend, 1993; Poff and Allan, 1995).

One approach for identifying mechanistic linkages between climate and aquatic ecosystem properties involves monitoring one system over time periods that include considerable hydrologic variability. A recent study in Switzerland examining ecosystem metabolism in streams over several years has shown that floods depressed primary productivity and ecosystem respiration for considerable periods of time afterward, particularly in winter (Uehlinger and Naegeli, 1998). Earlier, a multi-year study of macroinvertebrate communities following floods of varying magnitude in an Arizona desert stream showed that recovery of biomass and species composition was rapid and not strongly affected by the magnitude or frequency of floods, and that drying of the streambed during extended droughts had greater impacts on the community than floods (Boulton et al., 1992).

The ecological response to a modification in natural flow regime depends on how the regime is altered relative to the historical regime. That is, ecological responses to a change in flow regime will depend on the local hydrologic template. For example, a system that is historically very variable can be severely disrupted by stabilizing the hydrologic regime (Ward and Stanford, 1983). This is a pattern that is common in perennial streams of the desert Southwest (e.g., Meffe, 1984; Minckley and Deacon, 1991). Similarly, a system that has historically experienced predictable, seasonal flooding, such as snowmelt-dominated streams and rivers, may show dramatic changes in community composition and ecosystem function if the

seasonal resets are eliminated, as has been documented for the loss of riparian trees along western watercourses (Auble et al., 1994).

Projected climate change can be viewed as another form of anthropogenic environmental alteration that will modify the ecological organization of streams and rivers (Grimm, 1993; Poff et al., 2000). Once again, the nature of the response should reflect the extent to which flow components are changed relative to the prevailing conditions. For example, a system characterized by extremely flashy and variable flows would not likely show much response to a climate change that exacerbated this already harsh regime. However, a climate change shift to more perennial and stable flows would be expected to elicit great response (see Poff, 1992).

USING MODELS TO ASSESS THE IMPACT OF CLIMATE CHANGE

One approach to assessing the impact of climate change is to use models to examine the impact on aquatic ecosystems of alterations in those properties identified as vulnerable to climate change. Rivers and streams are particularly sensitive to variations in flow, and here we focus on models that have been used to examine the impact of changing flow regime (e.g., as experienced below dams) on aquatic species and ecosystems. These models should prove useful in evaluating potential effects of climate change.

Instream Flow Modeling

The first models of instream flow needs were based on a habitat evaluation approach (e.g., Tennant, 1976; Stalnaker, 1993; Stalnaker et al., 1995). Although quantitative, these habitat-based methods are limited by making simplifying assumptions about biotic-abiotic relationships, by failing to consider hydraulic conditions associated with ecologically critical high flows, and by focusing on only one or a few species. More recent instream flow assessment methods have employed population modeling, either in a lumped parameter mode (e.g., Bartholow et al., 1993; Cheslak and Jacobson, 1990) or with individual-based approaches (Jager et al., 1993, 1997). These population models allow more detailed examination of the biotic and abiotic interactions of fish and their environment.

Other modeling approaches recognize that the performance of individual species is embedded in a community or ecosystem context, and thus environmental

conditions that sustain the ecosystem will sustain individual species. These newer, holistic approaches view rivers as intractably complex systems where among-species interactions and species responses to abiotic environmental conditions vary dynamically over space and time. Species have differing and often opposing environmental needs; therefore it is not possible to determine a single optimum environmental condition for all species in the ecosystem. A shifting balance of favorable and unfavorable environmental conditions through space and time is required to sustain the whole ecosystem. For example, extreme conditions such as occasional droughts and floods are critical to sustaining species diversity and dominance in both aquatic and riparian communities (see reviews by Resh et al., 1988; Poff et al., 1997).

Detailed responses of all species to shifting conditions cannot be accurately modeled; however, the environmental regime can be. Thus the guiding framework for these newer approaches to flow analysis is to describe the natural environmental regime, usually in terms of the natural flow regime (e.g., Richter et al., 1996; Poff et al., 1997), although other environmental drivers such as temperature and sediment flux are also used. In these models, the integrity of riverine ecosystems varies in response to the deviation of the prevailing flow regime from the pre-impaired state. The natural regime is characterized in terms of the magnitude, frequency, duration, seasonal timing, and rate of change of flows that have demonstrable effects on aquatic habitat and ecological processes. These quantities can be assessed using simple techniques that evaluate deviations from historical values (Richter et al., 1996). This holistic approach has been at least partially implemented in several rivers for a variety of purposes: recovery of endangered fish species (Glen Canyon, Arizona, by Collier et al., 1997; Green River, Utah, by Stanford, 1994; Pecos River, New Mexico, by Robertson, 1997), restoring riparian plant communities (Olman River, Alberta, Canada, by Rood et al., 1995; Owens River, California, by Hill and Platts, 1998), enhancing native fish communities (Putah Creek, California, by Moyle et al., 1998), and restoring ecosystem function through channel-floodplain connections (Kissimmee River, Florida, by Toth, 1995). In principle, this approach could be used to assess the extent of hydrologic alteration resulting from climate change. By using projected changes in precipitation and temperature to drive hydrologic models calibrated to particular watersheds, future hydrographs could be generated and compared with historical streamflow records. In this way, a regional sensitivity analysis could be performed to assess regions where streams and rivers are most threatened by climate change (Poff, 1992).

Models of Nutrient Uptake Related to Hydrodynamic Properties

The linkage between nutrient cycling and the hydrologic properties of stream ecosystems is central in the development of the nutrient spiraling model, one of the primary organizing concepts in stream ecology (Webster and Patten, 1979; Newbold et al., 1981, 1983; Elwood et al., 1983). The nutrient spiraling model was developed to quantify the simultaneous processes of nutrient cycling by biota and the downstream transport of nutrients via water flow. Spiraling of nutrients is one of the important ecosystem services provided by streams because it purifies water for downstream uses. The intensity of nutrient cycling can be quantified by the spiraling length, defined as the average distance traveled by a nutrient atom in completing one cycle through the ecosystem (Newbold et al., 1981). Spiraling length is a measure of the efficiency with which the available nutrient supply is utilized by biota, with shorter spiraling lengths indicating higher nutrient utilization efficiency and presumably greater biological productivity for a given nutrient supply. Alternatively, spiraling length can be viewed as a measure of the retentiveness of stream ecosystems for nutrients, with shorter spiraling lengths indicating greater nutrient retentiveness.

Newbold et al. (1982, 1983) have shown theoretically that uptake length, the component of spiraling length that quantifies the distance traveled by a nutrient atom in water prior to uptake by biota, is directly related to the downstream flux of nutrients in water and to water velocity, and is inversely related to nutrient uptake rate per unit area. Therefore, hydrologic changes that increase stream discharge or water velocity without commensurate increases in biological uptake increase uptake length and reduce nutrient retention efficiency. Hydrologic changes that reduce biological uptake rates per unit area, such as reductions in algae, bryophytes, or debris dams and associated detritus caused by scouring floods, also increase uptake length. Debris dams and the accumulation of organic detritus within and behind them appear to be particularly important for nutrient retention in streams because they reduce water velocity as well as increase rates of nutrient uptake by organisms associated with detritus. Field investigations of nitrogen and phosphorus spiraling have verified the importance of water velocity and detritus storage as determinants of nutrient uptake length and nutrient retention (Mulholland et al., 1985; Munn and Meyer, 1990; D'Angelo et al., 1991). Determination of changes in spiraling length or uptake length with changes in hydrologic regime both within a system and across systems can be a useful approach for understanding

how climate changes might influence nutrient retention and productivity in streams. Measurement of nutrient uptake length involves experimental injections of nutrients at low concentrations to streams (Stream Solute Workshop, 1990).

Recently, spiraling models have been revised to consider the exchange of water and solutes between surface and subsurface (hyporheic) zones in lotic ecosystems (Kim et al., 1992; Bencala et al., 1993). Field studies have shown that the hyporheic zone is an important zone of nutrient cycling in streams (Triska et al., 1989; Findlay et al., 1993; Jones et al., 1995; Wondzell and Swanson, 1996). Spiraling models that explicitly incorporate hyporheic exchange show that nutrient spiraling lengths are shorter and nutrient retention greater in streams with larger hyporheic zones and greater surface-subsurface water exchange (Mulholland and DeAngelis, in press). Results from a comparative field study supported this prediction (Mulholland et al., 1997b). The size of the hyporheic zone and rates of surface-subsurface water exchange are functions of stream channel morphology, hydrologic regime, and sediment properties. Because climate is a strong determinant of stream morphology and hydrology, impacts of climate change on streams are likely to be manifested by changes in hyporheic properties and, as a consequence, by changes in nutrient spiraling.

Changes in nutrient flux resulting from changes in nutrient loading to streams and rivers also will alter nutrient uptake and spiraling lengths. Further, nutrient flux in streams and rivers is important because it represents the loading to lakes, estuaries, and oceans. Climate change is likely to affect nutrient loading primarily through its effect on runoff. In general, nutrient loading increases with runoff, particularly in human-dominated landscapes (Lewis and Grant, 1979; Alexander et al., 1996). Thus, increases in runoff due to increased precipitation are likely to increase nutrient loading, whereas reductions in runoff should reduce nutrient loading to streams and rivers.

Models of Bioenergetic Response

Bioenergetics modeling of the growth of fish and other organisms is another assessment tool that is available to study climate change, especially the effects of changing temperature regimes (e.g., Railsback and Rose, 1999). Van Winkle et al. (1997) used bioenergetics modeling and an individual-based population model of rainbow trout to study the effects of increased temperature on growth and reproductive success. Jager et al. (1999) used a similar approach to evaluate the combined effects of temperature and

hydrologic change. Such modeling approaches provide valuable insights into potential climate change effects.

Models Relating Riverine Food Web Structure to Climate and Hydrologic Regime

In addition to the direct effects of temperature and flow on organisms and ecological processes, indirect effects mediated through food web interactions have also been observed. For example, in Mediterranean climates, spring blooms of Cladophora appear to be more common in non-regulated rivers than in rivers with stabilized flows because winter floods reduce grazer populations in non-regulated rivers. In rivers with stabilized flow, grazer populations are maintained through the winter, and their grazing pressure reduces the likelihood of spring blooms (Power, 1992). Indirect effects of climate variability have also been observed; occasional extreme temperatures that lead to fish kills can have long-lasting impacts because they result in cascading effects throughout the food web (Carpenter et al., 1992). Relative strengths of year classes can be related to weather conditions during spawning and early life, and variations in year classes of top predators can alter food web structure at lower trophic levels (Carpenter et al., 1992).

Modeling the complexity of the interaction between food webs and hydrologic regime is in its infancy (Power et al., 1995). Very simple food web models suggest that there will be more trophic levels in a river with variable flow than in one with stabilized flow (Power et al., 1995). More complex dynamic models are needed to develop useful predictions of the impacts of changes in hydrologic regime on endangered species, nuisance species, fisheries yields, and overall health of the aquatic ecosystem. Development of these models requires a better understanding of the mechanisms linking physical environmental variables (temperature, flow regime, channel geomorphology) and species performance, including their impact in complex food webs (Power et al., 1995).

INFORMATION NEEDS

The ability to predict climate change impacts on water resources and to plan for adaptation and amelioration is still hindered both by the lack of good predictions of future climate at regional scales and by a lack of fundamental understanding of many of the effects of climate variability on the physical, chemical, and biological characteristics of aquatic ecosystems.

We are limited by availability of both data and models. More extensive data sets and better models are needed linking hydrologic regime with ecosystem processes (productivity, nutrient dynamics, food web interactions), with ecological interactions (predation, species invasions), and with water quality. The documented loss of stream gaging sites (down 22 percent since 1971; Stokstad, 1999) is antithetical to the need for hydrologic data, which are vital to an assessment of the impact of climate change on aquatic ecosystems. In addition to bolstering existing stream gaging sites, ecological monitoring needs to be added to the networks monitoring physical and chemical properties of water bodies, and the sampling frequency of monitored sites should be increased to capture the short-term variations that are so critical to determining transport in flowing waters. The sites and ecological populations and processes most likely to be early warning systems for ecological change should be identified and included in these networks.

The impacts of climate change may not be gradual. Monitoring and experimental data should be examined for the existence of thresholds of ecological change. Do systems change slowly with respect to temperature or hydrologic alteration until some threshold is reached, after which there are dramatic changes in state? Does variability increase as thresholds are approached? Improving our ability to assess the impact of climate change on aquatic ecosystem functioning and health requires continued improvements in both ecological monitoring and modeling: development of better regional climate models; development of models linking climate variability and ecological processes at the population, community, and ecosystem level; and integrated assessments of the potential impacts and viable response options for alternative climate futures.

ACKNOWLEDGMENTS

LITERATURE CITED

Abt Associates, 1995. Ecological Impacts from Climate Change: An Economic Analysis of Freshwater Recreational Fishing. U.S. Environmental Protection Agency, Office of Policy, Planning and Evaluation, EPA 230-R-95-004.

Alexander, R. B., P. S. Murdoch, and R. A. Smith, 1996. Streamflow-Induced Variations in Nitrate Flux in Tributaries to the Atlantic Coastal Zone. Biogeochemistry 33:149-177.

Anderson, J., S. Shiau, and D. Harvey, 1991. Preliminary Investigation of Trend/Patterns in Surface Water Characteristics and Climate Variations. In: Using Hydrometric Data to Detect and Monitor Climatic Change, G. Kite and K Harvey (Editors). Proceedings of NHRI Workshop, National Hydrology Research Institute, Saskatoon, Saskatchewan, Canada, pp. 189-201.

Auble, G. T., J. M. Friedman, and M. L. Scott, 1994. Relating Riparian Vegetation to Present and Future Streamflows. Ecological Applications 4:544-554.

Bartholow, J. M., J. L. Laake, C. B. Stalnaker, and S. C. Williamson, 1993. A Salmon Population Model with Emphasis on Habitat Limitations. Rivers 4:265-279.

Bencala, K. E., J. H. Duff, J. W. Harvey, A. P. Jackman, and F. J. Triska, 1993. Modelling Within the Stream-catchment Continuum. In: Modelling Change in Environmental Systems, A. J. Jakeman, M. B. Beck, and M. J. McAleer (Editors). John Wiley and Sons, New York, New York, pp. 163-187.

Biggs, B. J. F., 1995. The Contribution of Flood Disturbance, Catchment Geology and Land Use to the Habitat Template of Periphyton in Stream Ecosystems. Freshwater Biology 33:419-438.

Boulton, A. J., C. J. Peterson, N. B. Grimm, and S. G. Fisher, 1992. Stability of an Aquatic Macroinvertebrate Community in a Multiyear Hydrologic Disturbance Regime. Ecology 73:2192-2207.

Burn, D. 1994, Hydrologic Effects of Climate Change in West-Central Canada. Journal of Hydrology 160:53-70.

Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell, 1992. Global Change and Freshwater Ecosystems. Annual Review of Ecology and Systematics 23:119-139.

Chang, L. H., S. F. Railsback, and R. T. Brown, 1992. Use of a Reservoir Water Quality Model to Simulate Global Climate Change Effects on Fish Habitat. Climatic Change 20:277-296.

Cheslak, E. F. and A. S. Jacobson, 1990. Integrating the Instream Flow Incremental Methodology with a Population Response Model. Rivers 1:264-288.

Clausen, B. and B. J. F. Biggs, 1997. Relationships Between Benthic Biota and Hydrological Indices in New Zealand Streams. Freshwater Biology 38:327-342.

Cohen, S. J., L. E. Welsh, and P. Y. T. Louie, 1989. Possible Impacts of Climate Warming Scenarios on Water Resources in the Saskatchewan River Sub-Basin. CCC Report No. 89-9, Atmospheric Environment Service, National Hydrology Research Centre, Saskatoon, Saskatchewan, 87 pp.

Collier, M. P., R. H. Webb, and E. D. Andrews, 1997. Experimental Flooding in the Grand Canyon. Scientific American 276:82-89.

Coutant, C. C., 1990. Temperature-Oxygen Habitat for Freshwater and Coastal Striped Bass in a Changing Climate. Transactions of the American Fisheries Society 119:240-253.

Covich, A. P., S. C. Fritz, P. J. Lamb, R. D. Marzolf, W. J. Matthews, K. A. Poiani, E. E. Prepas, M. B. Richman, and T. C. Winter, 1997. Potential Effects of Climate Change on Aquatic Ecosystems of the Great Plains of North America. Hydrological Processes 11:993-1021.

Cubasch, U., J. Waszkewitz, G. Hegerl, and J. Perlwitz, 1995. Regional Climate Changes as Simulated Time-slice Experiments. Climatic Change 31:273-304.

D'Angelo, D. J., J. R. Webster, and E. F. Benfield, 1991. Mechanisms of Stream Phosphorus Retention: An Experimental Study. Journal of the North American Benthological Society 10:225-237.

Eaton, J. G. and R. M. Scheller, 1996. Effects of Climate Warming on Fish Thermal Habitat in Streams of the United States. Limnology and Oceanography 41:1109-1115.

Elwood, J. W., J. D. Newbold, R. V. O'Neill, and W. Van Winkle, 1983. Resource Spiraling: An Operational Paradigm for Analyzing Lotic Ecosystems. *In:* The Dynamics of Lotic Ecosystems, T. D. Fontaine III and S. M. Bartell (Editors). Ann Arbor Science, Ann Arbor, Michigan, pp. 3-27.

Findlay, S., D. Strayer, C. Goumbala, and K. Gould, 1993. Metabolism of Streamwater Dissolved Organic Carbon in the Shallow Hyporheic Zone. Limnology and Oceanography 38: 1493-1499.

Firth, P. and S. G. Fisher (Editors), 1992. Global Climate Change and Freshwater Ecosystems. Springer-Verlag, New York, New York, 321 pp.

Frederick, K. D. and P. H. Gleick, 1989. Water Resources and Climate Change. *In:* Greenhouse Warming: Abatement and Adaptation, N. J. Rosenberg, W. E. Easterling III, P. R. Crosson, and J. Darmstadter (Editors). Resources for the Future, Washington, D. C., pp. 133 -143.

Gleick, P. H., 1990. Vulnerability of Water Systems. *In:* Climate Change and Water Resources, P. E. Waggoner (Editor). John Wiley and Sons, New York, New York, pp. 223-240.

Gleick, P. H., 1993. Water in Crisis. Oxford University Press, Oxford, United Kingdom, 473 pp.

Grimm, N. B., 1993. Implications of Climate Change for Stream Communities. *In:* Biotic Interactions and Global Change, P. M. Kareiva, J. G. Kingsolver, and R. B. Huey (Editors). Sinauer Associates Inc., Sunderland, Massachusetts, pp. 292-314.

Grimm, N. B., A. Chacon, C. N. Dahm, S. W. Hostetler, O. T. Lind, P. L. Starkweather, and W. W. Wurtsbaugh, 1997. Sensitivity of Aquatic Ecosystems to Climatic and Anthropogenic Changes: The Basin and Range, American Southwest and Mexico. Hydrological Processes 11:1023-1041.

Harriss, R. C. and S. E. Frolking, 1992. The Sensitivity of Methane Emissions from Northern Freshwater Wetlands to Global Warming. *In:* Global Climate Change and Freshwater Ecosystems, P. Firth and S. G. Fisher (Editors). Springer Verlag. New York, New York, pp. 48-67.

Hauer, F. R., J. S. Baron, D. H. Campbell, K. D. Fausch, S. W. Hostetler, G. H. Leavesley, P. R. Leavitt, D. M. McKnight, and J. A. Stanford, 1997. Assessment of Climate Change and Freshwater Ecosystems of the Rocky Mountains, USA and Canada. Hydrological Processes 11:903-924.

HBSI (Hagler Bailly Services, Inc.), 1998. Water and Climate Change: A National Assessment of Regional Vulnerability. U.S. E.P.A., Work Assignment 121, 68-W6-0055. Washington D.C.

Hill, M. T. and W. S. Platts, 1998. Restoration of Riparian Habitat with a Multiple Flow Regime in the Owens River Gorge, California. Fisheries 23:18-27.

Hostetler, S. W. and E. E. Small, 1999. Response of North American Freshwater Lakes to Simulated Future Climates. Journal of the American Water Resources Association 35(6):1625-1637.

Houghton, J. J., L. G. Meiro Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell (Editors), 1996. Climate Change 1995: The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, 584 pp.

Hughes, J. M. and B. James, 1989. A Hydrological Regionalization of Streams in Victoria, Australia, With Implications for Stream Ecology. Australian Journal of Marine and Freshwater Research 40:303-326.

Jager, H.I., H. E. Cardwell, M. J. Sale, M. B. Bevelheimer, C. C. Coutant, and W. Van Winkle, 1997. Modelling the Linkages Between Flow Management and Salmon Recruitment in Rivers. Ecological Modelling 103:171-191.

Jager, H. I., D. L. DeAngelis, M. J. Sale, W. Van Winkle, and D. D. Schmoyer, 1993. An Individual-Based Model for Smallmouth Bass Reproduction and Young-of-the-Year Dynamics in Streams. Rivers 4:91-113.

Jager, H. I., W. Van Winkle, and B. D. Holcomb, 1999. Would Hydrologic Climate Changes in Sierra Nevada Streams Influence Trout Persistence? Transactions of the American Fisheries Society 128:222-240.

Jones, J. B., Jr., S. G. Fisher, and N. B. Grimm, 1995. Nitrification in the Hyporheic Zone of a Desert Stream Ecosystem. Journal of the North American Benthological Society 14:249-258.

Jowett I. G. and M. J. Duncan, 1990. Flow Variability in New Zealand Rivers and Its Relationship to In-Stream Habitat and Biota. New Zealand Journal of Marine and Freshwater Research 24:305-317.

Karl, T. R., R. W. Knight, and N. Plummer, 1995. Trends in High-frequency Climate Variability in the 20th Century. Nature 377: 217-220.

Kim, B. K. A., A. P. Jackman, and F. J. Triska, 1992. Modeling Biotic Uptake by Periphyton and Transient Hyporheic Storage of Nitrate in a Natural Stream. Water Resources Research 28: 2743-2752.

Leavesley, G. H., K. Turner, F. A. D'Agnese, and D. McKnight, 1997. Regional Delineation of North America for the Assessment of Freshwater Ecosystems and Climate Change. Hydrological Processes 11:819-824.

Lettenmaier, D. P., E. F. Wood, and J. R. Wallis, 1994. Hydroclimatological Trends in the Continental United States, 1948-1988. Journal of Climate 7:586-607.

Lewis, Jr., W. M. and M. C. Grant, 1979. Relationships Between Stream Discharge and Yield of Dissolved Substances from a Colorado Mountain Watershed. Soil Science 128:353-363.

Lins, H. F. and P. J. Michaels, 1994. Increasing U.S. Streamflow Linked to Greenhouse Forcing. EOS Transactions 75:281-283.

Magnuson, J. J. and B. T. DeStasio, 1996. Thermal Niche of Fishes and Global Warming. *In:* Global Warming – Implications for Freshwater and Marine Fish, C. M. Wood and D. G. MacDonald (Editors). Society for Experimental Biology Seminar Series 61, Cambridge University Press, Cambridge, U.K., pp. 377-408.

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn, 1997. Potential Effects of Climate Changes on Aquatic Systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrological Processes 11:825-871.

McKnight, D. and A. Covich (Editors), 1997. Regional Assessment of Climate Change and Freshwater Ecosystems. Hydrological Processes 11:819-1067.

Mearns, L. O., F. Giorgio, L. McDaniel, and C. Shields, 1995. Analysis of Daily Variability of Precipitation in a Nested Regional Climate Model: Comparison with Observations and Doubled CO2 Results. Global and Planetary Change 10:55-78.

Meffe, G. K., 1984. Effects of Abiotic Disturbance on Coexistence of Predator and Prey Fish Species. Ecology 65:1525-1534.

Melack, J. M., J. Dozier, C. R. Goldman, D. Greenland, A. M. Milner, and R. J. Naiman, 1997. Effects of Climate Change on Inland Waters of the Pacific Coastal Mountains and Western Great Basin of North America. Hydrological Processes 11:971-992.

Meyer, J. L., 1997. Stream Health: Incorporating the Human Dimension to Advance Stream Ecology. Journal of the North American Benthological Society 16:439-447.

Meyer, J. L. and W. M. Pulliam, 1992. Modifications of Terrestrial-aquatic Interactions by a Changing Climate. *In:* Global Climate Change and Freshwater Ecosystems, P. Firth and S. G. Fisher (Editors). Springer Verlag. New York, New York, pp. 177-191.

Miller, B. A. *et al.*, 1993. Sensitivity of the TVA Reservoir and Power Supply Systems to Extreme Meteorology. Report No. WR28-1-680-111, Tennessee Valley Authority, Knoxville Tennessee, 166 pp.

Minckley, W. L and J. E. Deacon (Editors), 1991. Battle Against Extinction: Native Fish Management in the American West. University of Arizona Press, Tucson, Arizona.

Minshall, G. W., 1988. Stream Ecosystem Theory: A Global Perspective. Journal of the North American Benthological Society 8:263-288.

Moore, M. V., M. L. Pace, J. R. Mather, P. S. Murdoch, R. W. Howarth, C. L. Folt, C. Y. Chen, H. F. Hemond, P. A. Flebbe, and C. T. Driscoll, 1997. Potential Effects of Climate Change on Freshwater Ecosystems of the New England/Mid-Atlantic Region. Hydrological Processes 11:925-947.

Mortsch, L. and F. Quinn, 1996. Climate Change Scenarios for Great Lakes Basin Ecosystem Studies. Limnology and Oceanography 41:903-911.

Mortsch L. D. and B. N. Mills (Editors), 1996. Great Lakes-St. Lawrence Basin Project Progress Report No. 1: Adapting to the Impacts of Climate Change and Variability. Environment Canada, Burlington, Ontario, 160 pp.

Moyle, P. B., M. P. Marchetti, J. Baldrige, and T. L. Taylor, 1998. Fish Health and Diversity: Justifying Flows for a California Stream. Fisheries 23:6-15.

Mulholland, P. J., G. R. Best, C. C. Coutant, G. M. Hornsberger, J. L. Meyer, P. J. Robinson, J. R. Stenberg, R. E. Turner, F. Vera-Herrera, and R. Wetzel, 1997a. Effects of Climate Change on Freshwater Ecosystems of the South-Eastern United States and the Gulf Coast of Mexico. Hydrological Processes 11:949-970.

Mulholland, P. J. and D. L. DeAngelis (In Press). Effect of Surface/Subsurface Exchange on Nutrient Dynamics and Nutrient Spiraling in Streams. *In:* Streams and Ground Waters, J. B. Jones, Jr. and P. J. Mulholland (Editors). Academic Press, San Diego, California.

Mulholland, P. J., E. R. Marzolf, J. R. Webster, D. R. Hart, and S. P. Hendricks, 1997b. Evidence that Hyporheic Zones Increase Heterotrophic Metabolism and Phosphorus Uptake in Forest Streams. Limnol. Oceanogr. 42:443-451

Mulholland, P. J., J. D. Newbold, J. W. Elwood, L. A. Ferren, and J. R. Webster, 1985. Phosphorus Spiralling in a Woodland Stream: Seasonal Variations. Ecology 66:1012-1023.

Mullholland, P. J. and M. J. Sale, 1998. Impacts of Climate Change on Water Resources: Findings of the IPCC Regional Assessment of Vulnerability for North America. Water Resources Update, Universities Council on Water Resources, Issue No. 112 (Summer 1998).

Munn, N. L. and J. L. Meyer, 1990. Habitat-Specific Solute Retention in Two Small Streams: An Intersite Comparison. Ecology 71:2069-2082.

Naiman, R. J., J. J. Magnuson, D. M. McKnight, and J. A. Stanford, 1995. The Freshwater Imperative. Island Press, Washington D.C., 165 pp.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon, 1983. Phosphorus Dynamics in a Woodland Stream Ecosystem: A Study of Nutrient Spiralling. Ecology 64:1249-1265.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and W. Van Winkle, 1981. Measuring Nutrient Spiralling in Streams. Canadian Journal of Fisheries and Aquatic Sciences 38:860-863.

Newbold, J. D., R. V. O'Neill, J. W. Elwood, and W. Van Winkle, 1982. Nutrient Spiralling in Streams: Implications for Nutrient Limitation and Invertebrate Activity. American Naturalist 120:628-652.

Poff, N. L., 1992. Regional Hydrologic Response to Climate Change: An Ecological Perspective. *In:* Global Climate Change and Freshwater Ecosystems, P. Firth and S. G. Fisher (Editors). Springer-Verlag, New York, New York, pp. 88-115.

Poff, N. L., 1996. A Hydrogeography of Unregulated Streams in the United States and an Examination of Scale-Dependence in Some Hydrological Descriptors. Freshwater Biology 36:101-121.

Poff, N. L. and J. D. Allan, 1995. Functional Organization of Stream Fish Assemblages in Relation to Hydrological Variability. Ecology 76:606-627.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg, 1997. The Natural Flow Regime. BioScience 47:769-784.

Poff, N. L, P. L. Angermeier, S. D. Cooper, P. S. Lake , K. D. Fausch, K. O. Winemiller, L. A. K. Mertes, M. W. Oswood, J. Reynolds, and F. J. Rahel (In Press). Global Change and Stream Fish Diversity. *In:* Future Scenarios of Global Biodiversity, O. E. Sala, F. S. Chapin, and R. Huber-Sannwald (Editors). Springer-Verlag.

Poff, N. L. and J. V. Ward, 1989. Implications of Streamflow Variability and Predictability for Lotic Community Structure: A Regional Analysis of Streamflow Patterns. Canadian Journal of Fisheries and Aquatic Science 46:1805-1818.

Poff, N. L. and J. V. Ward, 1990. The Physical Habitat Template of Lotic Systems: Recovery in the Context of Historical Pattern of Spatio-Temporal Heterogeneity. Environmental Management 14: 629-646.

Power, M., 1992. Hydrologic and Trophic Controls of Seasonal Algal Blooms in Northern California Rivers. Archiv für Hydrobiologie 125:385-410.

Power, M., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton, 1995. Hydraulic Food Chain Models. BioScience 45:159-167.

Postel, S., 1999. Pillar of Sand. W. W. Norton and Co., New York, New York, 313 pp.

Postel, S. L., G. C. Daily, and P. R. Ehrlich. 1996. Human Appropriation of Renewable Fresh Water. Science 271:785-788.

Railsback, S. F. and K. A. Rose, 1999. Bioenergetics Modeling of Stream Trout Growth: Temperature and Food Consumption Effects. Transactions of the American Fisheries Society 128:241-256.

Resh, V. H., A. V. Brown, A. P Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. Wissmar, 1988. The Role of Disturbance in Stream Ecology. Journal of the North American Benthological Society 7:433-455.

Richards, R. P., 1990. Measures of Flow Variability and a New Flow-Based Classification of Great Lakes Tributaries. Journal of Great Lakes Research 16:53-70.

Richards, C., R. J. Haro, L. B. Johnson, and G. E. Host. 1997. Catchment and Reach-Scale Properties as Indicators of Macroinvertebrate Species Traits. Freshwater Biology 37:219-230.

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun, 1996. A Method for Assessing Hydrologic Alteration Within Ecosystems. Conservation Biology 10:1163-1174.

Robertson L., 1997. Water Operations on the Pecos River, New Mexico and the Pecos Bluntnose Shiner, A Federally-Listed Minnow. U.S. Conference on Irrigation and Drainage Symposium 1996, pp. 407-421.

Rood, S. B., J. M. Mahoney, D. E. Reid, and L. Zilm, 1995. Instream Flows and the Decline of Riparian Cottonwoods Along the St. Mary River, Alberta. Canadian Journal of Botany 73:1250-1260.

Rouse, W. R., M. S. V. Douglas, R. E. Hecky, A. E. Hershey, G. W. Kling, L. Lesack, P. Marsh, M. McDonald, B. J. Nicholson, N. T. Roulet, and J. P. Smol, 1997. Effects of Climate Change on the Freshwaters of Arctic and Subarctic North America. Hydrological Processes 11:873-902.

Scarsbrook, M. R. and C. R. Townsend, 1993. Stream Community Structure in Relation to Spatial and Temporal Variation: A Habitat Templet Study of Two Contrasting New Zealand Streams. Freshwater Biology 29:395-410.

Schindler, D. W., 1997. Widespread Effects of Climatic Warming on Freshwater Ecosystems in North America. Hydrological Processes 11:1043-1067.

Shriner, D. S., R. B. Street, R. Ball, D. DíAmours, K. Duncan, D. Kaiser, A Maarouf, L. Mortsch, P. Mulholland, R. Neilson, J. A. Patz, J. D. Scheraga, J. G. Titus, H. Vaughan, and M. Weltz, 1998. North America. *In:* The Regional Impacts of Climate Change, An Assessment of Vulnerability, R. T. Watson, M. C. Zinyowera, and R. H. Moss (Editors). Special Report of International Panel on Climate Change Working Group II, Cambridge University Press, Cambridge, United Kingdom, pp. 253-330.

Shuter, B. J. and J. R. Post, 1990. Climate, Population Viability and the Zoogeography of Temperate Fishes. Transactions of the American Fisheries Society 119:316-336.

Stalnaker, C. B., 1993. Fish Habitat Evaluation Models in Environmental Assessment. *In:* Environmental Analysis, The NEPA Experience, S. G. Hildebrand and J. B. Cannon (Editors). CRC Press, Inc., Boca Raton Florida, pp. 145-163.

Stalnaker, C., B. L. Lamb, J. Henriksen, K. Bovee, and J. Batholow, 1995. The Instream Flow Incremental Methodology: A Primer for IFIM. Biological Report No. 29, National Biological Service, U.S. Department of the Interior, Fort Collins, Colorado.

Stanford, J. A., 1994. Instream Flows to Assist the Recovery of Endangered Fishes of the Upper Colorado River Basin. Biological Report No. 24, National Biological Service, U.S. Department of the Interior, Washington, D.C.

Stefan, H. G., M. Hondzo, X. Fang, J. G. Eaton, and J. McCormick, 1996. Simulated Long-Term Temperature and Dissolved Oxygen Characteristics of Lakes in the North-Central United States and Associated Fish Habitat Limits. Limnology and Oceanography 41:1124-1135.

Stokstad, E, 1999. Scarcity of Rain, Stream Gages Threatens Forecasts. Science 285:1199-1200.

Strayer, D. L., 1983. The Effects of Surface Geology and Stream Size on Freshwater Mussel (Bivalvia, Unionidae) Distribution in Southeastern Michigan, U.S.A. Freshwater Biology 13:253-264.

Stream Solute Workshop, 1990. Concepts and Methods for Assessing Solute Dynamics in Stream Ecosystems. Journal of the North American Benthological Society 9:95-119.

Sweeney, B. W., J. K. Jackson, J. D. Newbold, and D. H. Funk, 1992. Climate Change and the Life Histories and Biogeography of Aquatic Insects in Eastern North America. *In:* Global Climate Change and Freshwater Ecosystems, P. Firth and S. G. Fisher (Editors). Springer Verlag. New York, New York, pp. 143-176.

Tennant, D. L., 1976. Instream Flow Regimens for Fish, Wildlife, Recreation and Related Environmental Resources. *In:* Instream Flow Needs, J. F. Orsborn and C. H. Allman (Editors). American Fisheries Society, Bethesda, Maryland, pp. 359-373.

Townsend, C. R., and A. G. Hildrew, 1994. Species Traits in Relation to a Habitat Templet for River Systems. Freshwater Biology 31:265-276.

Toth, L. A., 1995. Principles and Guidelines for Restoration of River/Floodplain Ecosystems – Kissimmee River, Florida. *In:* Rehabilitating Damaged Ecosystems (Second Edition), J. Cairns (Editor). Lewis Publishers/CRC Press, Boca Raton, Florida, pp. 49-73.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, G. W. Zellweger, and K. E. Bencala, 1989. Retention and Transport of Nutrients in a Third-Order Stream in Northwestern California: Hyporheic Processes. Ecology 70:1893-1905.

Uehlinger, U. and M. W. Naegeli, 1998. Ecosystem Metabolism, Disturbance, and Stability in a Prealpine Gravel Bed River. Journal of the North American Benthological Society 17:165-178.

Van Winkle, W., K. A. Rose, B. J. Shuter, H. I. Jager, and B. D. Holcomb, 1997. Effects of Climatic Temperature Change on Growth, Survival, and Reproduction of Rainbow Trout: Predictions from a Simulation Model. Canadian Journal of Fisheries and Aquatic Sciences 54:2526-2542.

Ward, J. V. and J. A. Stanford, 1983. The Intermediate Disturbance Hypothesis: An Explanation for Biotic Diversity Patterns in Lotic Ecosystems. *In:* Dynamics of Lotic Ecosystems, T. D. Fontaine and S. M. Bartell (Editors). Ann Arbor Science, Ann Arbor Michigan, pp. 347-356.

Ward, A. K., G. M. Ward, J. Harlin, and R. Donahoe, 1992. Geological Mediation of Stream Flow and Sediment and Solute Loading to Stream Ecosystems Due to Climate Change. *In:* Global Climate Change and Freshwater Ecosystems, P. Firth and S. G. Fisher (Editors). Springer Verlag. New York, New York, pp. 116-142.

Webster, J. R., and B. C. Patten, 1979. Effects of Watershed Perturbation on Stream Potassium and Calcium Dynamics. Ecological Monographs 49:51-72.

Wondzell, S. M. and F. J. Swanson, 1996. Seasonal and Storm Dynamics of the Hyporheic Zone of a 4th-order Mountain Stream. II. Nitrogen Cycling. Journal of the North American Benthological Society 15:20-34.

WRC (U.S. Water Resources Council), 1978. The Nation's Water Resources: 1975-2000 (Vol. 2). U.S. Government Printing Office, Washington D.C.