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SENSITIVITY OF AQUATIC ECOSYSTEMS TO CLIMATIC AND ANTHROPOGENIC CHANGES: THE BASIN AND RANGE, AMERICAN SOUTHWEST AND MEXICO

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ABSTRACT

Variability and unpredictability are characteristics of the aquatic ecosystems, hydrological patterns and climate of the largely dryland region that encompasses the Basin and Range, American Southwest and western Mexico. Neither hydrological nor climatological models for the region are sufficiently developed to describe the magnitude or direction of change in response to increased carbon dioxide; thus, an attempt to predict specific responses of aquatic ecosystems is premature. Instead, we focus on the sensitivity of rivers, streams, springs, wetlands, reservoirs, and lakes of the region to potential changes in climate, especially those inducing a change in hydrological patterns such as amount, timing and predictability of stream flow.

The major sensitivities of aquatic ecosystems are their permanence and even existence in the face of potential reduced net basin supply of water, stability of geomorphological structure and riparian ecotones with alterations in disturbance regimes, and water quality changes resulting from a modified water balance. In all of these respects, aquatic ecosystems of the region are also sensitive to the extensive modifications imposed by human use of water resources, which underscores the difficulty of separating this type of anthropogenic change from climate change. We advocate a focus in future research on reconstruction and analysis of past climates and associated ecosystem characteristics, long-term studies to discriminate directional change vs. year to year variability (including evidence of aquatic ecosystem responses or sensitivity to extremes), and studies of ecosystems affected by human activity. © 1997 by John Wiley & Sons, Ltd.

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INTRODUCTION

The Basin and Range, Southwest and Mexico Region (hereafter, BRSWM) encompasses a wide band of mountain and lowland in western North America from the state of Oregon (48° N) in the US south to Oaxaca (18° N) in Mexico (Fig. 1 in Leavesley *et al.*, 1997). The region includes all of the major North American deserts, and is in general bordered by and dotted with mountainous terrain. This wide range of topographic relief (Plate 1 in Leavesley *et al.*, 1997) strongly influences both the horizontal and vertical spatial distribution of precipitation. Precipitation in subalpine watersheds of mountain ranges (many over

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3000 m) is often 4–10 times higher than in the adjoining basin lowlands. Except for the often ephemeral outflows of lowland springs, perennial streams in this area arise at high elevation.

The value to humans of aquatic resources in arid and semi-arid regions such as the BRSWM is obvious. Less often considered are the values of aquatic ecosystems as foci of biodiversity. Springs and stream–riparian ecosystems in the BRSWM support a high diversity of plant and animal life that are dependent on these oases of water and food resources in the arid and semi-arid surroundings. Biodiversity in Mexico ranks fifth globally; this is probably owing to its varied topography and climate, but also, in part, to the high degree of endemism associated with isolated aquatic ecosystems. The importance of BRSWM aquatic ecosystems, both as water resources and as foci of biodiversity, argues for the need to understand fully their dynamics in a changing climate, as well as with changing pressure from expanding human populations.

Variability and unpredictability are characteristics of the region's hydrology and climatology. Neither hydrological nor climatological models for the region are sufficiently developed to describe the magnitude or direction of change in response to increased carbon dioxide; thus, an attempt to predict specific responses of aquatic ecosystems is premature. The objectives of this paper are to highlight the key features of BRSWM aquatic ecosystems that are likely to be most sensitive to climate change, to discuss the interaction of climate change with anthropogenic change that is already occurring, to review briefly the current status of climate and hydrology models as applied to the region, and to provide a few recommendations for future research that will be crucial for understanding these interactions in this particular region.

HYDROCLIMATOLOGY OF THE REGION

Temperature

The amplitude of the annual temperature cycle of the BRSWM increases from south (range =< 5°C) to north (range = 25°C) as a result of changes in source regions for the air masses that affect the BRSWM. Mean January temperatures range latitudinally from over 25°C in the extreme south to −5°C in the north; July temperatures vary in response to elevation to a greater extent than to latitude and range from 15 to 20°C in high plateaus and mountains to 35–40°C in hot desert lowlands (Plates 3 and 4 in Leavesley *et al.*, 1997).

Precipitation

The climate of the BRSWM ranges from semi-arid to arid, with locally mesic climates occurring at high elevations. Annual precipitation varies considerably both in space and time throughout the region. In the northern area, winter and early spring precipitation delivered by cyclonic storms originating in the Pacific dominates. Annual precipitation ranges from 250 to 750 mm. Precipitation increases sharply at the north-eastern boundary of the region with up to 1500 mm annually over the higher elevations of the western humid and subhumid slopes of the Rocky Mountains (Price, 1979; Plate 2 in Leavesley *et al.*, 1997). The southern area is predominantly arid and precipitation is dominated by monsoonal flows that carry moisture from the Gulf of Mexico. Average annual precipitation for the area ranges from below 100 mm in the Mohave and Sonoran deserts to as much as 800 mm in the western Sierra Madre in Mexico. Annual rainfall seldom exceeds 250 mm in the valleys, where long dry periods extending to 150–210 days have been recorded in Hermosillo, Mexico (Ibarra *et al.*, 1995). The southernmost part of the region is mainly humid to tropical with average annual precipitation reaching 2000 mm.

Runoff

Because of the wide range of land use, temperature, vegetation cover and sources of runoff (i.e., snowmelt, direct rainfall), runoff variability is very pronounced on both regional and subregional scales. According to Bedinger and Sargent (1989), 'most of the region's runoff is generated by precipitation occurring on the intermediate elevations of the higher basin areas and the lower parts of the mountains'. The scarcity of protective vegetation cover, high temperatures and low antecedent soil moisture at low altitudes combine to produce maximum rates of evaporation in lowlands. Consequently, runoff is lower in the region's valleys

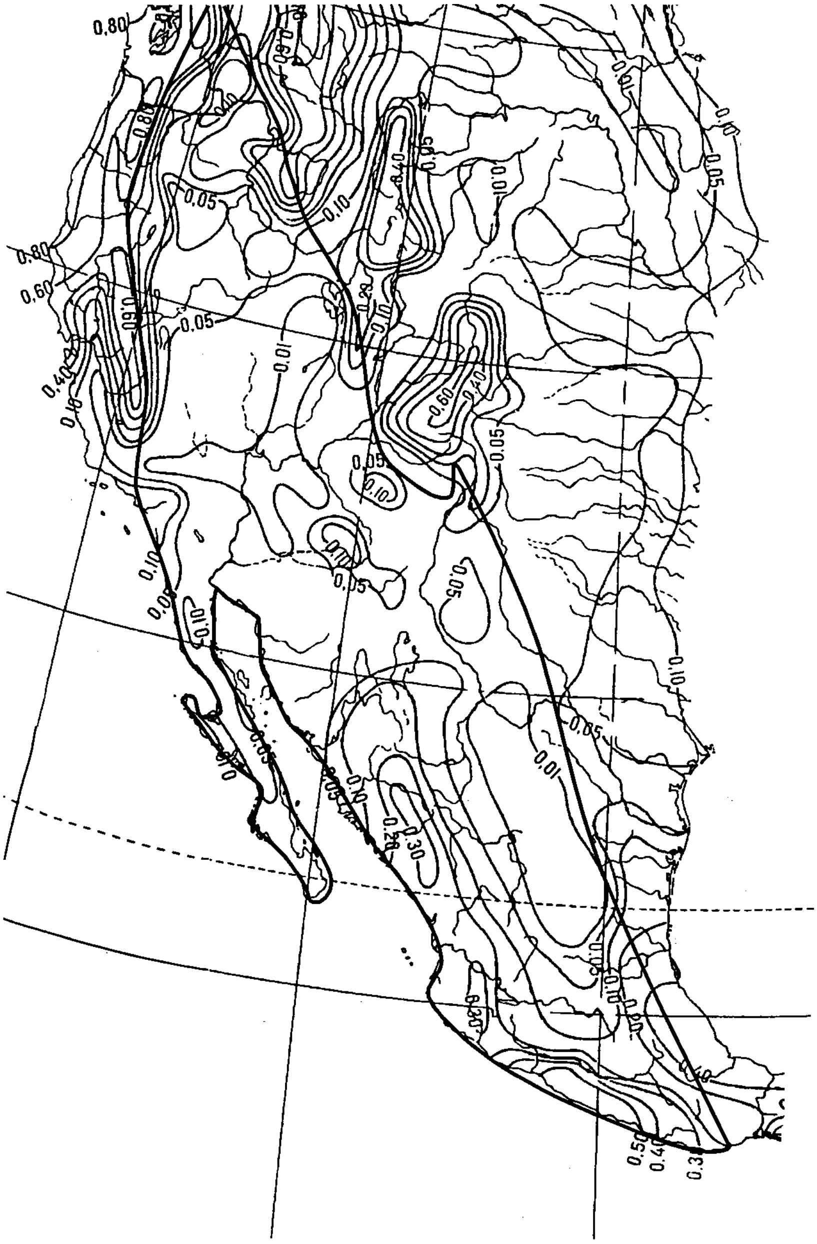

Figure 1. Map of western North America showing runoff ratios (runoff/precipitation) in the Basin and Range, Southwest and Mexico region (enclosed by thick line)

compared with its mountains, and is but a small fraction of precipitation. Runoff ratios (RO/P) are as low as 0·01 in some endorheic basins of northern Mexico and generally do not exceed 0·2 throughout the lowlands in much of the region (Figure 1). Furthermore, because most of the watersheds and subwatersheds in the region are characterized by high length to width ratios, mountain fronts play an important role in recharging the underlying aquifers, especially from spring snowmelt. This recharge represents an additional contribution of mountain precipitation to lowland stream flow within the BRSWM (Price, 1979).

Because of the combined effects of the above characteristics, average annual runoff in the southern part of the BRSWM varies between 2·5 mm in lowland desert areas to 50 mm at higher elevations. In contrast, average annual runoff in the northern BRSWM varies from 20 mm in the valleys to 125 mm at the highest mountain elevations.

OVERVIEW OF AQUATIC ECOSYSTEMS

A diversity of aquatic ecosystems can be found in the BRSWM, especially when elevational transects are considered. Nevertheless, certain region-wide generalities are consistent with its water-poor nature. Few natural lakes occur in the BRSWM, yet the region contains some of the largest reservoirs in North America. All large rivers in the region are impounded. Other natural aquatic ecosystems of the BRSWM are isolated, temporary waters are common (such as ephemeral and intermittent streams, tinajas and playas), and nearly all sizable aquatic ecosystems are stressed by the increasing demands for urban and agricultural water supplies. Ecotones such as riparian zones are particularly evident in the BRSWM because they represent zones where starkly contrasting ecosystems meet (Fisher, 1995).

Springs, Streams and Rivers

Streams and rivers of the BRSWM are spring fed or are derived from runoff (snowmelt in the north, rainfall in the south) from montane regions bordering these arid and semi-arid environments (Price, 1979; Minshall *et al.*, 1989). Perennial, large rivers of the region support much lower mean annual flows than those in more mesic regions with comparably sized catchments (Table I). The tendency for low flows is exacerbated by consumptive use throughout the basins. Prior to extensive impoundment, most rivers exhibited extreme variation in discharge over annual, decadal and longer time-scales. Mid-sized streams of the region that have not been impounded retain their ‘flashy’ hydrological characteristics. Many are spatially intermittent, flowing in summer only in bedrock-dominated segments where shallow alluvium permits surface flow. In general, constrained channel reaches with minimal sediment deposition are commonly gaining segments (i.e. discharge increases with downstream flow) of the streams where groundwater emerges into the channel. Conversely, unconstrained reaches with depositional features are sections of stream where groundwater recharge occurs and stream flow decreases. Springs sustain their permanent flow through aquifer discharge in high elevation montane regions and, in some smaller catchments of desert lowlands, by way of connection to artesian or other underground waters.

Table I. Comparison of largest rivers of the BRSWM with the Illinois River and the Columbia River, in terms of basin area and annual discharge. Colorado River discharge is at Hoover Dam (almost no runoff from the Colorado River reaches its mouth)

River	Basin area (km^2)	Annual discharge ($\times 10^6$ m^3)
Río Santiago	33 800	2100
Río Fuerte	36 600	5900
Río Yaqui	70 000	2800
Río Nazas	85 500	1700
Río de las Balsas	106 000	13 900
Snake River	267 000	40 000
Río Grande/Bravo	457 000	18 000
Colorado River	629 000	10 000
Comparison:		
Illinois River	65 527	18 300
Columbia River	668 000	230 000

High *in situ* primary production, the paucity of perennial flow, and the importance of disturbance are general attributes of streams in this dryland region. Lotic ecosystems of the northern BRSWM exhibit high rates of primary production and many may be autotrophic (i.e.$P_G > R$; Minshall, 1978; Cushing, 1996). High levels of solar radiation reaching the stream surface, through discontinuous riparian canopy cover, promotes generally high rates of aquatic primary production (Cushing and Wolf, 1984; Cushing, 1996). This feature is even more strongly expressed in the hot desert portions of the region, where high annual temperatures, long growing seasons and wide channels (with nearly year-long light saturation) result in high rates of both primary and secondary production (Busch and Fisher, 1981; Fisher *et al.*, 1982; Fisher and Gray, 1983; Jackson and Fisher, 1984). The food base in streams of both subregions is algae and aquatic macrophytes, with collector–gatherers feeding primarily on autochthonous detritus (Fisher and Gray, 1983; Gaines *et al.*, 1989).

Streams and rivers of the BRSWM are subjected to intense natural disturbance. Hydrological extremes, of both flood and drought, are the principal disturbance agents. Flash floods in the hot deserts of south-western USA (and presumably, in the more southerly desert regions) shape channel morphology, scour and deposit sediment and remove both instream and riparian biota (Fisher *et al.*, 1982; Grimm and Fisher, 1989; Stromberg *et al.*, 1993). Hot desert streams are also subject to extensive drying. Drying results in stranding and concentration of biota and loss of surface water. In some cases, hyporheic flow persists beneath the dry sediment surface (Stanley and Valett, 1992; Stanley and Boulton, 1995). In the northern subregion of the BRSWM, rain on snow events or thunderstorms can generate catastrophic floods. The few long-term databases on discharge for these ecosystems suggest an average of 3–4 years between such severe spates (Cushing and Gaines, 1989), compared with a more frequent occurrence in the south (for example, 2–9 flash floods per year occur in dry and wet years, respectively, in Sycamore Creek, Arizona; Grimm, 1993).

Lakes, Reservoirs and other Lentic Ecosystems

Standing water of the intermountain West are varied in geographical setting, basin origin and present day limnological conditions. The relatively few natural lakes or other open waters are of four types: large saline lakes that are remnants of far more extensive late-Pleistocene limnetic systems, temporary waters of desert basin lowlands (playas), montane/subalpine lakes and terminal wetlands with annual inundation but strong seasonality.

Many lakes of the BRSWM are closed, and lake levels therefore reflect the imbalance between annual precipitation and evaporation. They are thus sensitive to climate variability that would be of minor influence in systems with outflows (Cole, 1974; Hostetler and Giorgi, 1995). The size, depth and salinity of large saline lakes exhibit substantial temporal fluctuations caused by climate. For example, the area of Utah's Great Salt Lake, the largest saline lake in the region, more than doubled over 26 years between a drought and flood period (Stephens, 1990). Thermal stratification is limited in Great Salt Lake and many other lowland lakes because they are so shallow.

Hundreds of lowland valleys throughout the Great Basin, Mohave, Chihuahuan and Sonoran deserts can hold shallow, ephemeral lakes or *playas* (Snyder, 1962; Mifflin and Wheat, 1979). Some playas lie in the relict basins of late-Pleistocene pluvial lakes. Others are hydrologically isolated and have small watersheds, thus they have no geological record of limnetic permanence. The existence of lakes in these valleys depends on local (watershed) precipitation, playa surface evaporation (Hartland-Rowe, 1972) and, except in endorheic basins (especially prevalent in the Great Basin and north-central Mexico), alluvial hydrological drainage (Snyder, 1962).

Permanent montane lakes in the Great Basin/Mojave (northern) portion of the BRSWM lie at elevations of 2800 m or more. These lakes, which are essentially snowmelt- or spring-fed ponds, are found in isolated central mountain ranges, are generally no more than a few hectares in surface area, and have small watersheds such as those of cirque basins. These characteristics lead to high hydrological variability. Inflows peak during spring runoff and, in some, outflow may occur for only a few weeks of the year. The ponds display transient stratification as local convective storms produce regular episodes of severe wind shear and thorough mixing.

Montane lakes are more abundant in the southern BRSWM (Mexico). Most of these lakes are warm polymictic and exhibit minimal seasonal variation in temperature. Seasonal variation in other limnological properties is coupled to wet–dry seasons and dilution and evaporative concentration of solutes. Like lakes in the northern subregion, these lakes are very sensitive to changes in water input. For example, endorheic Lake Patzcuaro has exhibited extensive variation in level on both 10^3-year and 10^1–10^2-year time-scales (Chacón, 1993; O'Hara, 1993).

The few wetlands in the region include highly seasonal freshwater wetlands and saline marshes (Hofstetter, 1983). Wetlands associated with the littoral zones of lakes are poorly developed, owing to large excursions in lake level that result from variation in inflows (as in the northern terminal lakes). Riverine marshes, or ciénegas, were common in the south-western USA and northern Mexico until the mid-1800s, but these have all but vanished (Hendrickson and Minckley, 1984).

In addition to the natural lentic systems, many reservoirs, ranging in size from small stock ponds to some of the largest in North America, such as those of the lower Colorado River (Lakes Powell, Mead, Mohave and Havasu), are found in the BRSWM. The reservoirs of the Colorado River have conventional warm monomictic pelagia with largely familiar, cosmopolitan plankton biotas, yet are set within an arid climate and desert landscape. Many reservoirs are highly productive, with consequent hypolimnetic oxygen depletion during stratification. Intra- and inter-annual drawdowns of the reservoirs for irrigation and flood control can greatly reduce, or even dry up, shallow reservoirs. Additionally, the frequent water level fluctuations associated with the storage and use of water restrict the development of littoral zone plants and their associated animal communities.

PAST CLIMATE CHANGE AND ANTHROPOGENIC CHANGE

Climate

The geological record of climate since the last glacial maximum (21 000 years ago) indicates that the central and northern portions of the BRSWM were affected by relatively large climatic changes, i.e. shifts in the average climate (e.g. Thompson *et al.*, 1994). These late-Pleistocene climate changes have been associated with changes in synoptic-scale atmospheric circulation, characterized primarily by a southward displacement of the polar jet stream (westerly storm track) over western North America that was forced by the height and thermal effects of the Laurentide Ice Sheet (e.g. Kutzbach and Guetter, 1986; COHMAP Members, 1988). The climatological effect of the displaced storm track was a general enhancement of moisture throughout the Great Basin (Thompson *et al.*, 1994). Geological evidence from the southern portions of the Basin and Range (e.g. Van Devender *et al.*, 1987) suggests that the region was affected less by these late-Pleistocene climate changes than it was by Holocene climatic variability resulting, for example, from ENSO (El Niño–Southern Oscillation) events or from atmospheric circulation patterns associated with anomalous pressure patterns in the eastern Pacific (Enzel *et al.*, 1989, 1992; Ely *et al.*, 1993). More recent climate variations and flood events in the Southwest (e.g. the past 500 years) have also been attributed to anomalous circulation patterns (Redmond and Koch, 1991; Ely *et al.*, 1994). Interannual variation in stream flow over the historical record (past 50 years) has also been linked to both El Niño and La Niña events in the American Southwest (Molles and Dahm, 1990; Kahya and Dracup, 1994).

Anthropogenic Changes in Aquatic Ecosystems

Although the region includes some of the large rivers in the US and Mexico, these rivers are not large enough to meet the ever increasing, and rather fluctuating, demand for water. Rapid growth of urban areas, agriculture and industry, especially in the second half of this century, has placed significant stress on the region's water resources. Although the USGS water use estimates for 1985 (Solley *et al.*, 1988) indicate a 10% drop in freshwater consumption from 1980 levels, they remain at double the 1950 estimates.

One of the most obvious anthropogenic changes is the extensive impoundment of rivers to capture mountain runoff for municipal use, irrigation and hydroelectric power generation throughout the BRSWM.

Impoundment and diel, seasonal and interannual variation in water releases from these reservoirs have greatly altered the dynamics of the rivers below them (Ward and Stanford, 1979, 1983). Impoundment creates lentic ecosystems where none previously existed, and these ecosystems are now a common, if incongruous, feature of the desert landscape. Artificial control of surface water, whether for instream or offstream (diversion) uses, affects both the quantity and the quality of freshwater. The thermal properties of reservoirs can be influenced by the changing area–depth characteristics resulting from such controls. Additionally, return flow from irrigation diversion introduces pesticides and nutrients into the aquatic system.

The near-full utilization of surface water resources in the region has fostered an increasing reliance on groundwater resources. Until recently, groundwater and surface water were treated as two distinct resources. Consequently, continued groundwater pumping caused a significant drop in the water levels of several floodplain aquifers, leading to noticeable changes in the flow patterns of some perennial streams. In some cases, such as the Santa Cruz River of southern Arizona, perennially flowing stream reaches became intermittent or ephemeral (Arizona Department of Water Resources, 1995).

The Santa Cruz River is a striking example of anthropogenically induced changes in freshwater ecosystems, and a detailed examination of its history provides a good illustration of the effects of human manipulation on rivers in arid regions such as the BRSWM. Average annual precipitation in the 22 200 km^2 basin is 450 mm. The river flows southwards towards Mexico from its headwaters at the San Rafael Valley (south-eastern mountains of Arizona, altitude 2800 m), then flows westwards in Mexico for 56 km, and re-enters the US 10 km east of Nogales. In Mexico, most of the perennial flow of the river is captured by wells from the aquifer directly connected to the stream. Some of the captured water is returned to the stream through effluent discharge from Nogales.

Recently (May 1995), and under the title 'The Way We Were', the *Tucson Citizen* newspaper published a photograph dating to the late 1800s of a recreational lake called Silver Lake near Tucson, Arizona. The lake was an artificial lake generated by diverting water from the nearby perennial Santa Cruz River. Today the lake and, of course, the river reach are both dry because of the effect of groundwater pumping from the underlying floodplain aquifer. After 1940, the high rate of urban and agricultural development in the Tucson basin and subsequent lowering of the groundwater table (100 m below the river bed) caused further changes in stream characteristics. The elimination of marshes and wet meadows, which occupied short perennial reaches, resulted in the longitudinal expansion of arroyos, thus connecting the stream reaches into a continuous channel along the 80 km reach in the Tucson basin. Channel degradation continues as the result of floodplain development. In some areas the channel bed has been lowered four metres below its 1940 level.

According to the Arizona Department of Water Resources (1995), a wetter weather cycle starting in 1960, declining groundwater pumping in the past decade and, most importantly, the establishment of the Nogales treatment plant, are all contributing factors to the observed recovery of groundwater levels in the upper Santa Cruz Basin. This recovery has resulted in the establishment of a cottonwood–willow (*Populus fremonti* and *Salix goodingii*) riparian community along the river north of the Mexican border. Unlike the historical Santa Cruz, however, the flow in the river is derived primarily from treated effluent.

Where they occur, natural lakes are also used for water supply. In the southernmost portion of the BRSWM in Mexico, most lakes and reservoirs have experienced greatly decreased storage volumes over the past 20 years. Most of this is a result of increased demand by both a rapidly expanding population and, perhaps more importantly, a great increase in economic growth. Water demand in Mexico is closely tied to the economy. Fluctuations in the volume of Lake Chapala, Mexico over a 60-year period provide an excellent example of the difficulty in separating the magnitude of change wrought by human consumptive water use from climatic effects on hydrology.

Lake Chapala is possibly the oldest (middle Pleistocene; Clements, 1963) North American large lake. It lies in an east–west valley at 1524 m elevation. Its watershed is large (basin : lake area = 47), from which it derives nearly two-thirds of its water input, the remainder coming from direct rainfall (Limón and Lind, 1990). Changes in Lake Chapala brought about increased human demand are superimposed on climate-driven variation. In 1990, the volume of Lake Chapala was approximately one-fourth the mean long-term volume. Between 1974 and 1982, direct rainfall inputs to the lake increased slightly, but riverine inputs decreased by 45%. Lake volume declined by 40%. Limón *et al.* (1989) proposed that increased water use in the river basin, and not climate change, was responsible.

The decline in Lake Chapala's storage volume between 1974 and 1983 was coincident with the economic expansion produced by the demand for Mexican oil. With the crash of the oil market in 1982 the decline in lake storage volume stopped for five years, but the lake did not recover. The decline resumed in 1987 and continued to the minimum of record in 1990. As needs for water are no longer met by the natural lakes of the region, a large expenditure on reservoir construction and groundwater extraction is underway. Anthropogenic change, rather than climate variation, is especially implicated in lake level decline, since the years considered were characterized by a large number of warm episodes (El Niño-like conditions), which, at least in the American Southwest, have been linked to increased rainfall and runoff (e.g. Molles and Dahm, 1990).

Water quality deteriorated in Lake Chapala during the period of storage volume decline. As a result of the combined effects of reduced riverine inputs, control of releases through the outflow and relative increase in output to evaporation, the concentration of total dissolved solids increased by over 100%, and phosphorus increased by almost 400% (Limón *et al.*, 1989). However, this increase in salts did not produce increased algal growth and eutrophication. As the lake level declined, resuspension of sediments increased and light limitation prevented algal blooms. Because of concern over the diminished water supply experienced in the 1970s and 1980s, extra effort was taken to protect the quality of existing supplies; a series of 16 secondary waste water treatment plants were constructed around Lake Chapala between 1985 and 1992.

The examples from Lake Chapala and the Santa Cruz River clearly illustrate the tremendous changes in aquatic ecosystems that have occurred as a result of population pressure. Distinguishing between changes in aquatic ecosystems of the BRSWM caused by climate and those attributable to other anthropogenic effects will be difficult, especially against a background of high natural variability. Even if montane lakes of Mexico were sensitive to climate change, it is likely that the pressures from human populations have already induced changes in their structure and functioning that preclude detection of past responses to climate change. This may be true of permanent lentic ecosystems throughout the BRSWM. On the other hand, many temporary or smaller permanent systems are, by definition, on the brink of existence; their sensitivity is extreme and the record of a changed climate will be clearly indicated by their persistence. Finally, because of the pervasive effect of humans on naturally variable rivers like the Santa Cruz, it is unlikely that BRSWM rivers and streams will readily serve as sensitive bellwethers of climate change in the future. Rather, climate change will most likely be superimposed upon the substantial modifications of lotic ecosystems that have already occurred (Carpenter *et al.*, 1992).

FUTURE CLIMATE

Climate Models

Atmospheric general circulation models (GCMs) have been widely used to generate climate expectations for both past and future climates (e.g. Saltzman, 1990; Schneider *et al.*, 1990; Washington, 1992, and references therein). The results from GCM simulations of past climate (the past 10^5 years) suggest, on global, hemispherical, and continental scales, the range and type of changes that have occurred as a result of, for example, changes in earth–solar geometry and atmospheric composition. Predictions of future climate (the next 10^2 years) are based on the projected response to increased trace gas concentrations in the atmosphere. At the scale of the BRSWM, the models lack the ability to simulate details of regional climate (Grotch, 1988; Mearns *et al.*, 1990; Grotch and McCracken, 1991). Present computer power is inadequate to allow GCMs to be run at resolutions fine enough to provide the accuracy required for climatic and hydrological information related to aquatic ecosystems (Hostetler, 1994).

A major problem with GCMs is their inability to simulate convective precipitation (e.g. Washington, 1992; Hostetler, 1994), which is a large component of the annual precipitation in many parts of the BRSWM. Although advances have been made in *diagnostic* modelling of atmosphere–ocean phenomena such as El Niño, GCMs cannot model El Niños outside the period of data record (e.g. Cane, 1992 and references therein). Because of these problems, climate variables representing atmospheric conditions that lead to high magnitude precipitation and flood events or droughts in the BRSWM cannot be obtained from GCMs.

Hydrological Models

The BRSWM encompasses climates ranging from continental in the north, to arid desert in the southwestern USA, to tropical in southern Mexico, and is perhaps the most hydrologically diverse of all regions. This diversity is characterized by: (1) a large range of precipitation and temperature gradients; (2) the dependency of much of the region on high elevation precipitation for water supply; (3) surface–groundwater interactions associated with hydrologically closed basins; and (4) a very high degree of alteration of the natural surface water system through flow regulation and water use patterns.

Although current state of the art in both GCMs and hydrological models is quite advanced, progress is needed to fill the gap in scale between the two types of models (Hostetler, 1994). Physically based hydrological models, i.e. those in which the physics of flow, water storage and energy are accounted for mathematically, can be used to model small catchment areas that are homogeneous relative to the region as a whole. These models, which use time-series of meteorological parameters as input, can make use of output from climate models. However, the heterogeneity of precipitation, geology and land surface, compounded with the general problem that climate–hydrological interactions and processes are poorly understood in the region, provide major obstacles to aggregating small area models up to the regional scale.

Statistical models, such as time-series models, provide an alternative to physically based hydrological models. Time-series models are calibrated by using observed records and can be used to associate atmospheric circulation patterns with runoff. The calibrated models can be used to explore periods of flood or drought in the historical records (e.g. Ely *et al.*, 1993). Such investigations provide valuable insights into past climatic and hydrological variations, but time-series models cannot be used to make forecasts or extrapolations without violating the assumptions (e.g. stationarity) on which the calibrations are made.

Thus, the task of modelling hydrological responses to climate change remains a challenge. To gain an ability to project the effects of climate change on the region, we need to assess the influences of warming on precipitation (including its variability) through atmospheric modelling, and to investigate the role of vegetation feedbacks (such as evapotranspiration), soil characteristics and geology. This will require further research on development and the application of new and existing models and technology.

POTENTIAL RESPONSES OF AQUATIC ECOSYSTEMS

Approach

The problems discussed here preclude the matching of predicted climate with anticipated ecosystem changes in the BRSWM. Before we can make reasonable ecological predictions, we must know which aquatic ecosystems, or components of those ecosystems, are sensitive to climate. We present an overview of the sensitivities of BRSWM aquatic ecosystems to broad climate changes of four types (Table II): (1) overall changes in hydrological parameters, arising from enhanced or reduced precipitation with or without altered evapotranspiration, that lead to a reduction or increase in net basin supply (P−E); (2) changes in seasonality of precipitation and runoff; (3) changes in variability of precipitation and runoff; and (4) changes in temperature. Changes in runoff variability are viewed by some as potentially more disruptive of ecosystems than changes in mean conditions (Walker, 1991; Poff, 1992). Table II lists the properties that we identified as most sensitive to change for each ecosystem type, and the elements of climate, hydrology or anthropogenic stress to which they are most likely to be sensitive.

Table II. Properties of ten types of aquatic ecosystem in the BRSWM that are expected to be most sensitive to change. Third column lists the major climate, hydrology or anthropogenic variables (*) to which these properties are likely to respond. NBS = net basin supply (P-E); P/RO = precipitation and runoff. Numbers in parentheses refer to the temporal scale (yr) of P/RO variability to which the ecosystem would be most sensitive, and may apply to either the recurrence interval of extreme events or the duration of time periods over which frequency of extreme events is altered

Ecosystem type	Property	Sensitive to
Spring-fed streams	Permanence	NBS Groundwater recharge Groundwater withdrawal* P/RO seasonality
	Thermal and hydrological stability	NBS Temperature P/RO variability ($\times 10^2$ yr)
Lowland/desert streams	Flow permanence	P/RO seasonality NBS Groundwater recharge Groundwater withdrawal*
	Geomorphological structure	P/RO variability (10^2–10^3 yr)
	Riparian zone: recruitment and stability	Flow permanence Groundwater withdrawal* P/RO variability (10^1–10^2 yr)
Large rivers	Discharge	NBS (upper basin) Consumptive use* Regulation*
	Water quality	Diversion* Impoundment* Spatial variability in RO
Riparian zones or riverine wetlands	Permanence, biotic structure	Regulation* Groundwater withdrawal* P/RO variability
Lowland lakes, wetlands	Existence, permanence	NBS Groundwater withdrawal* P/RO variability (10^1–10^2 yr)
	Salinity/water quality	NBS P/RO variability (10^0–10^1 yr)
Lowland springs	Existence, permanence	NBS Groundwater recharge Groundwater withdrawal*
	Thermal stability	Temperature
Playas	Frequency of inundation, existence	NBS P/RO variability (10^1–10^2 yr)
Subalpine lakes (e.g. Great Basin)	Water balance	NBS P/RO seasonality
	Thermal stratification	Temperature P/RO seasonality
Montane lakes (e.g. Mexico)	Water balance	NBS Diversion* Consumptive use*
	Water quality	NBS Diversion* Consumptive use*
Reservoirs	Nutrient availability	P/RO seasonality P/RO variability (10^{-1}–10^0 yr)
	Habitat availability	NBS Consumptive use* P/RO seasonality

Streams, Rivers and Riparian Zones

Hydrology. The precipitation regime, particularly how precipitation translates to runoff, is paramount in its effect on stream and river ecosystems of the BRSWM. A small change in mean annual precipitation can yield large changes in surface flow from an arid or semi-arid catchment. For example, a decrease in mean annual precipitation of 10% can reduce surface runoff by 30–50% (Nemec, 1986; Dahm and Molles, 1992). For streams fed by springs, the impact of a changing precipitation regime will be strongly linked to groundwater recharge in the source areas. Lags of months to years, and longer, can occur between a change in aquifer recharge and the response of down-slope springs. Cessation of flow and conversion of perennial stream segments to intermittent reaches would be a likely by-product of diminished recharge of groundwater from an overall decrease in annual precipitation. This would be exacerbated by decreases in cool season precipitation in the northern BRSWM, as most aquifer recharge there derives from snowmelt during seasons when evapotranspiration rates are lower.

The timing and form of precipitation and runoff are influenced by temperature changes. If warming occurs, the likelihood of intense flooding from rain on snow events in the late winter or spring may increase. Such events are the cause of many of the catastrophic floods in the northern, cool deserts of the BRSWM that have strong effects on both riparian vegetation and stream biota (Baker, 1990; Cushing and Gaines, 1989). Pacific Ocean frontal storms of late winter and early spring occasionally provide heavy inputs of precipitation to the valleys and mountains of the northern BRSWM. A warmer climate could bring much of this moisture in the form of rain rather than snow, increasing the likelihood of catastrophic flooding and causing earlier removal of the snowpack, which in turn may increase the susceptibility of these ecosystems to extreme drying during the warm seasons of the year.

Timing is also critical in hot desert regions and in the seasonal rivers of Mexico. More streams of a given drainage area are dry in summer in the western deserts (Mohave, western portions of the Sonoran Desert) because they experience few summer monsoon storms. In contrast, streams that typically flow only in response to summer precipitation (Chihuahuan Desert) are less likely to have perennial segments because evapotranspiration is so high during summer. Although the southern portion of the BRSWM has more distinct wet and dry seasons, the combined effects of brief periods of intense rainfall, increased evaporation resulting from deforestation and reduced infiltration owing to heavy silt loads have led to the increased incidence of severe floods (Chacón and Múzquiz, in press). This change has occurred during this century; shifts in seasonality in the future could either alleviate or exacerbate the effect. In Sycamore Creek, an intensively studied, mid-sized stream of the northern Sonoran Desert, annual flow is dictated more by winter precipitation amounts than by summer rains, although rain falls in both seasons (Grimm and Fisher, 1992). During the five driest years of this stream's 30-year record, winter flows were slight, and accelerated drying conditions (indicated by $\geqslant$200-day periods without floods) were prevalent an average of 167 days, or 46% of the year (Grimm, 1993). Extended drying can lead to loss of habitat for aquatic organisms, slower recovery following rewetting and loss of aquatic ecosystem 'functions' such as nutrient retention and instream and riparian production (e.g. Stanley and Fisher, 1992; Stanley *et al.*, 1994).

Ecosystem response. Changes in hydrological factors, such as increased or decreased spate frequency and magnitude, changes in timing of high and low discharge events, changes in frequency of drying events or prolongation of drying, can affect the ecology of streams and rivers in numerous ways. Flash floods in hot deserts can obliterate much of the stream biota, but recovery is usually rapid (from a few weeks to 1–2 months). This high resilience is attributable to high temperatures and light (supporting high primary production) and a fauna characterized by extraordinarily rapid development (Gray and Fisher, 1981). Similarly, biotic communities of the northern BRSWM are disturbance prone but capable of rapid colonization and growth following disturbances (Cushing and Wolf, 1984; Cushing and Gaines, 1989). The stability of hyporheic (subsurface) habitats in these disturbance prone ecosystems may, in some cases, provide a refuge for many species, and in others has led to the development of a distinct and unique hyporheic faunal component (e.g. Boulton *et al.*, 1992).

Because lotic ecosystems of the BRSWM are disturbance prone, their resilient biotas may be less sensitive to increased variability than those of more constant ecosystems. But larger scale changes in fluvial systems can result from extended periods of altered precipitation and runoff variability. An arroyo-cutting and ciénega-draining episode of the late 1800s provides an example (see Hastings and Turner, 1965). When explorers first visited the Southwest, they encountered lush aquatic and riparian vegetation in extensive marshes (ciénegas) along streams and rivers. A period of erosion, beginning *ca.* 1880, drained most of these ciénegas, leaving steep-walled, channelized, and incised arroyos (Hastings and Turner, 1965). There is general agreement that climatic variation (a period of high intensity rainfall) was at least partially responsible for the arroyo-cutting era (Cooke and Reeves, 1976; Graf, 1979). Thus, changes in precipitation variability, in this case the frequency of large storms, can alter the geomorphological structure of streams. This, in turn, has profound consequences for ecosystem structure and functioning (Hendrickson and Minckley, 1984).

Riparian zones are also sensitive to precipitation and runoff variability, perhaps on a somewhat shorter time-scale. Although extreme events can prove damaging to extant forests, a period of wet weather and frequent floods also provides 'windows of recruitment' for some tree species (Baker, 1990; Stromberg *et al.*, 1991).

Consumption of water in the lower Colorado Basin is higher than that now supplied by reservoirs or rivers. This basin is thus sensitive to modifications in water gain or loss (Waggoner and Schefter, 1990). However, changes in lowland systems resulting from climate change will (except for evaporative losses) result from effects seen upstream and at higher elevation (i.e. in the upper Colorado Basin). Snowmelt represents almost 90% of annual runoff in the lower Colorado River Basin, thus 10–15% of the land area (above 2800 m) supplies three-quarters of the total hydrological flow (Schaake, 1990). At an intermediate scale, the region is subject to apparent non-equilibrium processes such as ENSO circulations (Molles *et al.*, 1992). The upper basin therefore has high stream flow variability (and is sensitive to climatic change) but the lower basin progressively integrates that variation through storage and thus greatly reduces climatic signals (Rhodes *et al.*, 1984; Gleick, 1990). Thus, upstream flow regulation and hydrological conditions, and climatic responses of upstream terrestrial ecosystems have primary control of lower Colorado basin hydro/limnological systems. In contrast, climate change occurring within the lower basin of the Colorado River should elicit very little detectable response against the background of anthropogenic manipulation.

Lowland Lakes, Playas and Wetlands

Cole (1974) suggests several aspects of desert limnology that are applicable to this region in terms of sensitivity to climate change. Since many of the systems are either permanently or seasonally closed basins, inflow and evaporation rates (usually negatively correlated) affect the water balance of lakes, which influences electrolyte concentrations and chemistry. Evaporation rates from desert lakes are high. For example, direct atmospheric losses from Pyramid and its companion pluvial relict, Walker Lake, are approximately 125 cm/year; Lake Mead (surrounded by the Mojave Desert) evaporates up to 200 cm/yr (Mifflin and Wheat, 1979; Galat *et al.*, 1981) and central Arizona reservoirs nearly 300 cm/yr (Sellers and Hill, 1974). Local precipitation inputs to desert lakes are insignificant relative to remote up-slope watershed rain and snow (Cole, 1974). Thus, the ontogeny of desert lakes, and in some cases the very existence of desert lakes, will be determined by patterns of regional and watershed climate modification.

Lakes in the Great Basin may be among the most vulnerable to climate change in the US, because precipitation and evaporation are nearly balanced (Gleick, 1990). The case of the Great Salt Lake illustrates this susceptibility very clearly at a variety of time-scales. In the wet Pleistocene, the Great Salt Lake covered 49 000 km^2, extended into three states and had an abundant freshwater fauna (Benson *et al.*, 1990). A 153-year historical record of lake level (Figure 2) demonstrates how sensitive the closed basin lakes are to shorter term climatic changes. In 1963 the lake had shrunk to only 2470 km^2, salts were concentrated to 280 g/l and the only higher organisms present were herbivorous brine shrimp and brine flies (Stephens, 1990). From 1963 to 1986 the lake level rose 6 m, and salinities dropped to 50 g/l. This allowed several predacious invertebrates to invade (see Figure 3). The predators eradicated the filter-feeding brine shrimp

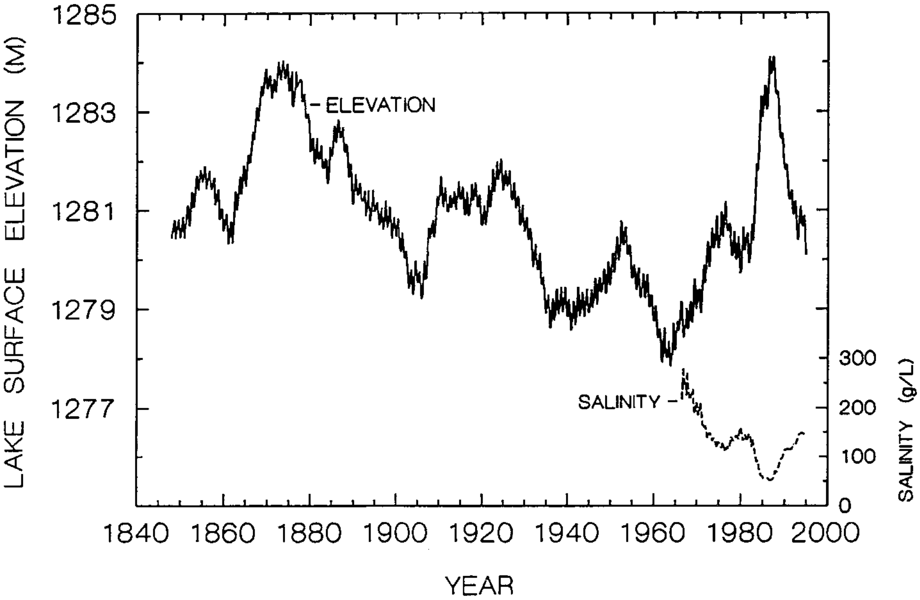

Figure 2. Changes in surface elevation (1847-1994) and salinity (1966-1994) of the Great Salt Lake, Utah, resulting from climatic changes. Note the inverse relationship between lake elevation and salinity in this terminal lake. Data provided by the Utah Geological Survey

(*Artemia franciscana*) and decreased overall herbivore biomass by more than an order of magnitude. This allowed algal levels to increase 20-fold, resulting in decreases in soluble nutrients and water clarity. Decreased light penetration reduced heating in the monimolimnion of the lake. Birds dependent on the brine shrimp in the lake became rare. Thus, climatically induced changes in runoff over a two-year period profoundly affected the food-web, chemistry and physics of the lake (Wurtsbaugh and Berry, 1990; Wurtsbaugh, 1992).

One recent modelling projection of the water and energy balances of saline Pyramid Lake under a warmer climate indicated potential changes in the timing of stratification (Hostetler and Giorgi, 1995). In one sensitivity test, the lake ceased annual turnover altogether. Like most lakes in the BRSWM, Pyramid Lake's water balance, especially inflow volume and seasonality, are largely controlled by anthropogenic watershed diversions (Galat *et al.*, 1981; Hostetler and Giorgi, 1995), confounding accurate interpretation of climatic effects.

Smaller closed basin lakes and spring pools could also be affected by future climatic change because the size, salinity and even the existence of each system is tightly coupled to runoff (Neal, 1975). A regional climatic change that decreased precipitation might eliminate many of the smaller water bodies and the aquatic communities dependent on them. Many isolated spring systems that harbour endemic fishes would be at risk (Minckley and Deacon, 1991). Conversely, a sustained increase in precipitation might increase the number and size of standing lakes. This can be beneficial for aquatic organisms, but may destroy human developments built in lake bottoms during drier times. Salinity changes would probably lead to altered community structures (Stephens. 1990), as described for the larger Great Salt Lake.

The sensitivity of playas to climate is implicit. Currently ephemeral lakes could become permanent with an increase in precipitation (Mifflin and Wheat, 1979), whereas drier and warmer conditions would lengthen the intervals between inundations and decrease the episodic durations of open water. Many species of playa invertebrates may be limited by long periods of desiccation in certain playa basins (Belk and Cole, 1975) and others by temperature extremes (Horne, 1972). These physiological constraints, coupled with changes in life history timing, may shift the geographical distribution of some species or community types in the face of

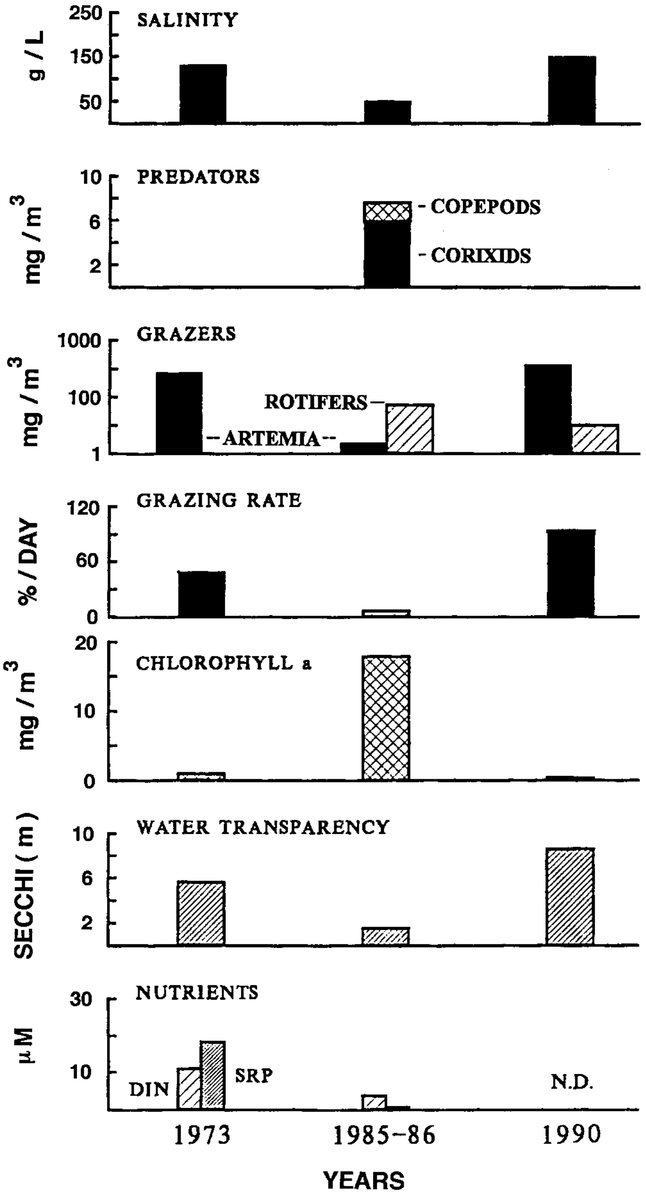

Figure 3. Changes in the Great Salt Lake ecosystem resulting from climatic changes that modified the runoff and consequently the salinity of this terminal lake. Decreasing salinity between 1973 and 1985 allowed invertebrate predators (*Trichocorixa verticalis*, *Diaptomus connexus*, *Cletocampus albuquerquensis*) to invade, which in turn initiated a trophic cascade within the lake. During the dry period that followed, salinity increased and the ecosystem reverted to its former state. Grazing rate = % of water column filtered per day by the zooplankton community; SRP = soluble reactive phosphorus; DIN = nitrate- + nitrite- + ammonium-nitrogen; N.D. = no data. Modified from Wurtsbaugh (1992)

climate change. On the other hand, the evolutionary history of the dominant playa faunal groups (eubranchiopods and ostracods) extends back more than 100 Ma (Tasch, 1980); contemporary climate change seems unlikely to threaten the taxa.

Wetlands, as complex free-standing aquatic systems or as wet/dry ecotones (*sensu* Risser, 1990), may (Franzen, 1994; Neilson, 1993) or may not (Noble, 1993) respond strongly to climate change. Natural wetlands in the desert, however, will probably be influenced, because their existence is continuously threatened by both the inherent variability of the regional climate and anthropogenic pressures. Wetlands in the intermountain region are usually subject to human management (diversion and regulation) which is driven by economic and political forces and, to a lesser degree, by climatic or hydrological patterns. This is clearly demonstrated in the history of the Stillwater Marsh–Lahontan Valley wetland complex, which has experienced high magnitude interannual variations in inflow and wetland water levels that are only partially coincident with changes in regional hydrological patterns (Yardas, 1994). Primary productivity, biodiversity, organic deposition and flux and nutrient cycling are dependent on hydrological patterns (Gosselink and Turner, 1978; Hogenbirk and Wein, 1991) and could be altered by shifts in seasonality or changes in net basin supply.

The southern portion of the BRSWM has a number of shallow endorheic basins, which are the remnants of an extensive late-Pliestocene lake system (Clements, 1963). These lakes are only moderately saline and have extensive wetlands along their perimeters. They are important wildlife habitats with large numbers of native and seasonally migrant birds. Increased water to these lakes might expand littoral wetlands, whereas a decrease in water supply could eliminate them as significant wildlife habitat.

High elevation systems, such as the numerous subalpine lakes in isolated mountain ranges of the BRSWM, have limnological characteristics that make them susceptible to climate change. Their small watersheds are not well buffered hydrologically and their inflows are limited to nearby snowmelt or small springs. Interannual variability can be very severe, and the open water season short. Any sustained and significant change in temperature and/or precipitation will modify the water balance, lake persistence and seasonal characteristics.

A regional climate change that affected net basin supply would have larger effects on small reservoir systems in the BRSWM than on large ones. For example, increased reservoir drawdown would decrease the mean annual size of each system, reducing available habitat for fishes, and perhaps decreasing oxygen levels in the more restricted hypolimnetic strata (Ploskey, 1986). Nutrient and organic matter inputs to reservoirs, like natural lakes, occur in pulses associated with extreme events or seasonal runoff; we therefore expect these systems to be sensitive to shifts in precipitation and runoff variability and seasonality. Larger reservoirs, like those of the Colorado River discussed earlier, are less likely to be sensitive to local climate change, because the characteristics of these systems represent integration of upstream and extraregional hydrological processes.

Temperature effects

Although we have proposed that hydrological factors are the most likely to effect change in aquatic ecosystems of the BRSWM (as influenced by changes in precipitation and runoff), the southernmost tropical subregion may be sensitive to changes in the thermal regime. This tropical zone normally has a very small temperature variation, both on daily and seasonal bases. For example, annual mean water column temperature in Lake Chapala is 21·7°C, but maximum seasonal temperature range during the 60-year period of record for this lake was 6°C. Organisms that have evolved under such constant conditions would be expected to be stenotherms. A strong biotic response to warming is likely in relatively constant thermal environments such as these, where large changes in temperature or temperature variability have not been experienced in ecological or recent evolutionary time. The surface temperature of Lake Pátzcuaro, Mexico has increased in comparison with past records (Chacón, 1993), and there is some evidence that spawning by native silversides (Pisces: Atherinidae), once a year-round event, is now restricted to the winter months (T. A. Chacón, personal observation).

In the mountainous and semi-arid region of the southern BRSWM, aquatic ecosystems are extremely isolated and endemism is common. There are also unique species flocks of native fishes in lakes located at different altitudes (Echelle and Echelle, 1984). Temperature changes might affect such communities both by disturbing the interspecies relationships within the flocks, and, possibly, by migration of species up or down the altitude gradient with rising or falling temperatures. Such migration, however, is less likely in this region, where few water holes are separated by vast expanses of desert.

In the northern subregion, the biotic effects of temperature change would most likely result from runs of abnormally warm weather that drive the stream temperature above thermal tolerances for those aquatic organisms adapted to cold desert and semi-arid environments. Cushing (1996) and Minshall (1978) show a relatively small variation in temperature at the source areas of spring-fed perennial reaches of a stream, but wider temperature ranges downstream. The downstream reaches of these ecosystems would be more likely to reflect warmer air temperatures and stenothermal organisms may be replaced by eurythermal species.

Changes in insolation and water temperature would also have an effect on lentic systems in the northern part of the region. Recent sensitivity experiments suggest that the duration of ice cover on dimictic lakes might be reduced and that summer temperatures would be warmer (Hostetler and Giorgi, 1995). As a result, increased insolation reaching the lake surfaces would most likely increase the annual productivity. Cold water species, particularly recreationally important salmonids, might disappear from lakes and reservoirs that warm, because many are already at their upper temperature limit during summer, and are restricted from deeper layers by anoxia (Utah Department of Health, 1982).

RECOMMENDATIONS

Aquatic ecosystems may be most effectively managed in the context of global climate change if both the more pressing anthropogenic threats and the occurrence of extreme events are considered and incorporated into management plans. Research and monitoring activities should focus on: (1) reconstruction and analysis of past climates and associated ecosystem characteristics; (2) continuation and/or initiation of long-term studies to discriminate directional change vs year to year variability; and (3) studies of ecosystems affected by human activity. When using a time-series approach, we should seek evidence of aquatic ecosystem responses or sensitivity to extremes (for example, wet or dry periods, years of especially high or low frequency of disturbance events). Such an effort would benefit from a coordinated study by hydrologists, climatologists, geomorphologists and ecologists using complementary techniques, and should focus on the identification of sensitive ecosystem components.

In this extreme and variable environment, a climate change signal may not be detectable against the background of extensive human manipulation; yet, we need a better understanding of how such manipulation has and will continue to alter the structure and function of aquatic ecosystems. To incorporate human-influenced ecosystems, we advocate a comparative ecosystem approach wherein relatively unaltered ecosystems are compared with highly manipulated ones.

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