EFFECTS OF CLIMATE CHANGE ON INLAND WATERS OF THE PACIFIC COASTAL MOUNTAINS AND WESTERN GREAT BASIN OF NORTH AMERICA

JOHN M. MELACK,1 JEFF DOZIER,2 CHARLES R. GOLDMAN,3 DAVID GREENLAND,4 ALEXANDER M. MILNER5 AND ROBERT J. NAIMAN6

1Department of Ecology, Evolution and Marine Biology, and Institute for Computational Earth System Science, University of California, Santa Barbara, CA 93106, USA
2School of Environmental Science and Management, University of California, Santa Barbara, CA 93106, USA
3Division of Environmental Studies, University of California, Davis, CA 95616, USA
4Department of Geography, University of Oregon, Eugene, OR 97403-1251, USA
5School of Geography, University of Birmingham, Birmingham B15 2TT, UK
6Center for Streamside Studies, University of Washington, Seattle, WA 98195, USA

ABSTRACT
The region designated as the Pacific Coastal Mountains and Western Great Basin extends from southern Alaska (64°N) to southern California (34°N) and ranges in altitude from sea level to 6200 m. Orographic effects combine with moisture-laden frontal systems originating in the Pacific Ocean to produce areas of very high precipitation on western slopes and dry basins of internal drainage on eastern flanks of the mountains. In the southern half of the region most of the runoff occurs during winter or spring, while in the northern part most occurs in summer, especially in glaciated basins. Analyses of long-term climatic and hydrological records, combined with palaeoclimatic reconstructions and simulations of future climates, are used as the basis for likely scenarios of climatic variations. The predicted hydrological response in northern California to a climate with doubled CO2 and higher temperatures is a decrease in the amount of precipitation falling as snow, and substantially increased runoff during winter and less in late spring and summer. One consequence of the predicted earlier runoff is higher salinity in summer and autumn in San Francisco Bay. In saline lakes, the incidence of meromixis and the associated reduction in nutrient supply and algal abundance is expected to vary significantly as runoff fluctuates. In subalpine lakes, global warming will probably lead to increased productivity. Lacustrine productivity can also be altered by changes in wind regimes, drought-enhanced forest fires and maximal or minimal snowpacks associated with atmospheric anomalies such as El Niño–Southern Oscillation (ENSO) events. Reduced stream temperature from increased contributions of glacial meltwater and decreased channel stability from changed runoff patterns and altered sediment loads has the potential to reduce the diversity of zoobenthic communities in predominately glacier-fed rivers. Climatic warming is likely to result in reduced growth and survival of sockeye salmon in freshwater, which would, in turn, increase marine mortality. Further research activities should include expanded studies at high elevations and of glacier mass balances and glacial runoff, applications of remote sensing to monitor changes, further refinement of regional climatic models to improve forecasts of future conditions and continued analyses of long-term physical, chemical and biological data to help understand responses to future climates.

INTRODUCTION
Climatic conditions affecting inland waters of the Pacific Coastal Mountains and Western Great Basin encompass an extraordinary range. Orographic effects combine with moisture-laden frontal systems originating in the Pacific Ocean to produce areas of very high precipitation on western slopes and dry basins.
of internal drainage on eastern flanks of the coastal and interior mountains. While seasonal temperature variation along the coast is moderated by the proximity of the ocean, low temperatures occur at high latitudes and altitudes within the region. In the southern half of the region most of the runoff occurs during the winter or early spring, while in the northern part most of the runoff occurs in the summer, especially in glaciated basins. Climatic anomalies, such as the El Niño–Southern Oscillation (ENSO), can produce large interannual differences in runoff. These widely varying climatic conditions make regional forecasts of likely climate change, induced by increased CO₂ concentrations, difficult.

Numerous small to medium-sized rivers and small, high elevation lakes occur throughout the region. Several large freshwater and saline lakes are also prominent, as are San Francisco Bay and Puget Sound. To the north, glaciated basins increase and are especially common in Alaska. Anthropogenic effects on the aquatic habitats of the region are considerable in the more populated southern portion but are smaller in much of the northern portion and at high elevations. Therefore, the potential effects of climatic changes on the inland waters are expected to differ between the aquatic habitats and to be modulated by human activities in parts of the region.

Our contribution is divided into four sections. First, we review the regional characteristics of current climatic and hydrological conditions. Secondly, we discuss the climatic variability documented in historical records and derived from palaeoclimatic evidence as well as scenarios of future climates based on general circulation models (GCMs). Thirdly, we present the possible responses of aquatic environments to the potential consequences of climatic change. Finally, we make recommendations for research and monitoring activities.

REGIONAL CHARACTERISTICS

The region designated as the Pacific Coastal Mountains and Western Great Basin spans 30 degrees of latitude from south-central Alaska (64°N) to southern California (34°N). Distances from the Pacific coast to the eastern boundary vary with latitude: 400 km in California, 200 km in Oregon and Washington, 300–400 km in British Columbia and up to 600 km in Alaska where the boundary becomes northern. Tectonic, volcanic and glacial activity has created a region of great relief characterized by mountain ranges and inland valleys. While the ranges nearest the coast are typically 500–2000 m, the mountains forming the eastern and northern boundary are 3000–4000 m with peaks reaching 5000–6000 m in northern British Columbia and Alaska, where Denali attains 6200 m (Hunt, 1974).

Within California, the Central Valley is bordered on the west by the Coast Ranges and on the east by the Sierra Nevada, which also forms the western edge of the Great Basin. The Klamath Mountains link the Cascades and the Coast Range in southern Oregon. Further north, the Cascades and the Coast Range are separated by the Willamette Valley and the Puget Sound Trough. The Olympic Mountains are a major feature at the northern end of the Coast Range in Washington. Insular and coastal Mountains extend through British Columbia to south-eastern Alaska where elevations exceed 4000 m in the heavily glaciated St Elias Mountains. The Chugach Mountains lie in south-central Alaska, where further inland are the Wrangell and Talkeetna Mountains and the Alaska Range. To the west lies the Aleutian Range (Hunt, 1974; Muhs et al., 1987).

Major urban areas, including Vancouver, Seattle, Portland, San Francisco, Sacramento, Fresno and the northern edge of Los Angeles, contain the majority of people in the region. Irrigated agriculture has changed the landscape in the Central Valley of California, and a mixture of grazing and agriculture continues on the coastal plains and inland valleys northwards to southern British Columbia. The mountainous terrain throughout the region supports extractive forestry and some silviculture; large tracts are designated as wilderness areas or parks.

After a general overview of the climatic and hydrological features of the whole region, we will describe several subregions in more detail. Regional temperature and rainfall patterns for the Pacific coastal region described below, are evident in Plates 2–4 in Leavesley et al., (1997). Mean July temperatures are 15–20°C.
along the California coast and throughout most of Oregon, Washington and southern British Columbia. Within the southern interior of California, July temperatures range from 20–30°C, while inland in British Columbia and throughout southern Alaska mean July temperatures are 10–15°C. Mean January temperatures in California and coastal Oregon are 5–10°C, and those in Washington and southern British Columbia and inland in northern California and Oregon are 0–5°C. Along the coast of central and northern British Columbia and southern Alaska mean January temperatures are 0 to −5°C, while interior temperatures in northern British Columbia and south-central Alaska range from −5 to −20°C.

Average annual precipitation in southern California and on the western edge of the Great Basin ranges from 150 to 600 mm, while in the Sierra Nevada and northern California it is 600–1800 mm. With the exception of the Olympic Mountains, which receive 2400–4000 mm, annual precipitation in western Oregon and western Washington is 1000–3000 mm. Annual precipitation in British Columbia and southern and south-central Alaska ranges up to 5000 mm.

The quantity, variability and timing of runoff, which may be altered if climate changes, influence many ecological processes (Poff and Ward, 1989; Naiman et al., 1992; Statzner et al., 1992). When compared with streams of the rest of the coterminous United States, three patterns of stream flow variability dominate in California, Oregon and Washington: intermittent and flashy, winter rain generated and snowmelt generated (Poff and Ward, 1989). Strong latitudinal patterns in stream flow and water temperatures are evident along the Pacific coast (Figures 1 and 2). Mean annual runoff and its variability increase with latitude. The proportion of annual discharge occurring in winter decreases from California to Alaska, and, conversely, the proportion in summer increases with latitude. Mean annual water temperature and the range of temperatures decreases with latitude. The temperature extremes reached in the southern and northern portions of the region are ecologically significant. Water temperatures near or above 25°C in Californian streams are physiologically limiting to many aquatic organisms adapted to cool conditions (Bjornn and Reiser, 1991). With winter temperatures at 0°C above a latitude of 48°N, surface, anchor and frazil ice may form and influence the survival of aquatic organisms (Oswood et al., 1991).

The Sierra Nevada, 700 km in length, is the longest continuous mountain range in the coterminus United States. The climate is characterized by warm, dry summers and cool, wet winters with strong altitudinal variation (Miller, 1955). Eleven major rivers flow west from the Sierra Nevada; the eastern side of the range is drained by many streams, all of which terminate in the Great Basin, except those diverted to the city of Los Angeles.

The Sierra Nevada generates about 25 km³ of runoff annually, and supplies most of the water used by California’s cities, agriculture, industry and hydroelectric facilities (Kahrl, 1978). Stream flow in the Sierra Nevada is generated by seasonal rainfall and snowmelt, and is modified by impoundments and diversion schemes. Basin-wide means of 1 April water equivalence for snow courses above 2500 m indicate that peak snowpack water equivalence for the high Sierra Nevada averages 750–850 mm, decreases from north to south and is lower on the east side of the crest than on the west side (California Cooperative Snow Survey, 1986). Snow courses between 1800 and 2500 m have an average peak water equivalence of about 600 mm.

Snowmelt runoff becomes more important, and midwinter rainfall-generated runoff becomes less important with increasing elevation (Cayan and Riddle, 1993). For example, in the American River basin, less than half of the annual runoff occurs from April to July in the lower two-thirds of the basin, while in catchments adjoining the Sierra Nevada crest, more than two-thirds of the annual runoff occurs during this period (Elliott et al., 1978). Overall, about half of the precipitation in the major river basins of the western slope of the Sierra Nevada becomes stream flow (Kattelmann et al., 1983).

Stream flow, both in absolute magnitude and as a proportion of precipitation, increases with elevation. In the American River Basin, stream flow data from 25 sub-basins (Armstrong and Stidd, 1967) indicate an increase in stream flow of about 30 mm per 100 m gain in elevation. Runoff efficiency increases from about 30% in the foothills to more than 80% near the crest (Elliott et al., 1978).

The flow in Sierra Nevada rivers is highly variable in time, both within and between years. Annual volumes can be 20 times greater in very wet years than in very dry years. Peak flows in the Sierra Nevada
Figure 1. (A) Mean annual runoff as a function of latitude for 151 rivers of the Pacific coast from central California to southern Alaska divided into four subregions: (●) southern coastal mountains, (○) Olympic mountains, (△) northern lowlands and islands, and (■) northern mainland mountains. (B) Proportion of mean annual discharge occurring during three winter months. (C) Proportion of mean annual discharge occurring during three summer months. (From Naiman and Anderson, 1997)
result from snowmelt, warm winter storms and summer and early autumn convective storms (Kattelmann, 1990). In rivers with headwaters at high elevation, snowmelt floods occur each spring as periods of sustained high flow, long duration and large volume. However, they rarely produce the highest instantaneous peaks. Large snowmelt floods occurred in 1906, 1938, 1952, 1969 and 1983. Midwinter rainfall on snow cover has produced all the highest flows in major Sierra Nevada rivers during this century (Kattelmann et al., 1991). When subtropical air masses move into the Sierra Nevada in summer and early autumn, sufficient moisture is available to generate extreme rainfall. These storms may generate the greatest floods in some alpine basins that are high enough to avoid midwinter rain on snow events.

Stream flow in Sierra Nevada rivers may be low during intense or extended droughts. For example, during 1977 when average snow water equivalence in early April was only 25% of the long-term mean, stream flow as a proportion of average annual flow ranged from 0.08 to 0.26. Dry periods may last for several years. From 1928 to 1937, runoff was below average in each year. The past two decades have included record droughts for one year (1977), two years (1976–1977), three years (1990–1992) and six years (1987–1992).

The Cascade Mountains extend 1100 km south to north and link the Sierra Nevada in northern California to the Coast Mountains in southern British Columbia (Nelson, 1991). The Cascades separate a mild, maritime climate with high precipitation and dense forests to the west from the colder, high elevation deserts of the Columbia–Snake River Plateau and Great Basin to the east. Mean annual temperatures in the Cascades range from 4 to 10°C, and average annual precipitation along the crest ranges from 2500 mm/yr in the north to about 1200 mm/yr in the south (Hunt, 1974). About 80% of annual precipitation (above 600 m) falls as snow from October to April, and runoff peaks during snowmelt in May and June (Rasmussen and Tangborn, 1976).

Along the Pacific coast of Canada two similar climatic regions occur in insular and coast mountains (Slaymaker, 1990). The mountains of Vancouver and Queen Charlotte islands experience mean annual precipitation above 4000 mm, almost all as rain, and regional runoff of about 3500 mm, 64% of which occurs in winter. At sea level, the mean annual temperature is 8.5°C. In the coastal mountains, mean annual precipitation (3500 mm), runoff (3150 mm, 30% of which occurs in winter) and temperature (5–8°C) are only slightly less than on the islands. Permafrost is sporadic and only at the highest elevations.

In south-central Alaska, average annual rainfall varies from 480 mm in the Kenai area to 310 mm in more northerly areas away from coastal influences. Further south along the coast, annual rainfall increases, reaching annual peaks of 5000 mm in south-east Alaska. Permafrost is restricted to south-central Alaska in
areas away from coastal influence and is discontinuous, being mainly confined to north-facing slopes. In south-central Alaska, winter flows in non-glacial streams are low (<5% of total runoff), and the principal peak is during spring snowmelt, often with a second lower peak in the autumn. Further from the maritime influence, the autumn peak is typically smaller and streams do not return to baseflow in the summer because of the prolonged snowmelt season. Non-glacial rivers in south-east Alaska have significant winter flow (10–15% of total runoff) and two peaks, one during spring snowmelt and a second larger peak during the autumn rainy season (Milner et al., 1997).

Glaciated basins are important along the northern Pacific coast of North America. In Alaska, estimates of glacial area vary from 65,800 km² (Brown, 1989) to 74,700 km² (Post and Meier, 1980). The majority of glaciers in the coterminous US are located in the Olympic Mountains (266 glaciers) and the North Cascade Mountains (742 glaciers) of Washington (total area 420 km²) and the Sierra Nevada (497 glaciers) of California (total area 55 km²).

Runoff from glaciated basins arises from both glaciers and ice-free areas (Collins, 1985), and glacial runoff continues throughout the summer months, usually reaching a peak in July (Milner and Petts, 1994). Glacial runoff in Alaska is considerable with an estimated runoff rate of 220 km³ annually, equivalent to 35% of the total runoff in Alaska, 14% of the total runoff from the coterminous states and 10% of the total runoff in the US (Mayo, 1986).

CLIMATIC VARIABILITY AND CHANGE

To evaluate plausible scenarios for changes in climate and its variability in the next century, as concentrations of greenhouse gases increase, several complementary approaches, each with strengths and weaknesses, are useful. Examination of historical records permits statistical analysis of relationships between atmospheric circulation, temperature, precipitation and runoff (Cayan and Peterson, 1989; Redmond and Koch, 1991). Moreover, trends and anomalies observed over prior decadal periods are similar to those expected as climate changes in the next century (Karl and Riebsame, 1989). However, the factors causing the observed climatic variations could differ from those related to the radiative effects of greenhouse gases. Analyses of climatic changes during the geological past indicate climatic sensitivities to radiative forcing and oceanic circulation (Broecker and Denton, 1989), but are not exact analogies to the rate and nature of current increases in greenhouse gases (Schneider et al., 1990). Large-scale models of climate, i.e. GCMs, attempt to represent mathematically the physical interactions between the atmosphere, oceans and land. Because of computational limitations and imprecise parameterizations of hydrological and meteorological processes, however, GCMs do not include important complexities. Their ability to simulate regional climates and their estimates of climatic variability at the regional level, especially, are in need of improvement.

Historical records and palaeoclimatic evidence

Instrumental climatological records for the Pacific coast of North America date back to the 1820s (Roden, 1989). The longest quasi-continuous data are from Sitka, Alaska, where Russian measurements began in 1828. Many meteorological records are available for the Pacific coast since the mid-1800s, and these data have received considerable statistical analysis (e.g. Roden, 1966; Granger, 1977a; McGuirk, 1982; Roden, 1989; Goodridge, 1991a, b).

Climatic variability at a site results from a combination of local and distant processes, the relative importance of which can vary in space and time. Hence, large-scale physical forcing need not always produce spatially coherent effects. For example, while temperature at exposed coastal sites is usually coherent over long distances, precipitation and winds in mountainous terrain are not (Roden, 1989). Therefore, when evaluating climatological trends, variations or patterns statistically or mechanistically, the spatial and temporal coherence of the data must be carefully considered.

Climatic variability along the Pacific coast of North America on an interannual scale is often associated with mid and high latitude variations in the polar jet stream, which are greatest during the winter
Variations in runoff can result from changes in temperature and precipitation. Since about 1950 in the Sierra Nevada, the proportion of total annual stream flow occurring during April–July has decreased, while the portion during the autumn and winter has increased (Aguado et al., 1992). Although climatic warming may be implicated, concomitant increases in autumn precipitation and decreases in precipitation in May–July were also recorded. Moreover, based on 50 years of historical records for two streams in the northern Sierra Nevada, Pupacko (1993) reported increased winter and early spring runoff during the period 1965–1990 compared with 1939–1964, which he attributed to small increases in temperature that enhanced the rain to snow ratio.

In rivers of the eastern slope of the Sierra Nevada, events at both extremes have been evident in recent years (Kattelmann, 1992). Five of the largest snowmelt floods since the 1920s (in terms of volume) occurred from 1978 to 1986. Five of the smallest snowmelt floods, occurred from 1987 to 1991. These events support the theories of some climatologists that extreme events are becoming more common in the western United States (Granger, 1977b; Michaelsen et al., 1987).

Furthermore, studies of past climate based on widths of tree rings have detected multiple wet and dry periods and warm and cool intervals in the Coastal Mountains and Sierra Nevada of California and in the Pacific Northwest that have persisted from years to decades to more than two centuries (Graumlich and Brubaker, 1986; Graumlich, 1987, 1993; Michaelsen et al., 1987; Haston and Michaelsen, 1994; Stine, 1994). The presence of tree stumps well below modern lake levels provides strong evidence for very arid conditions in the past (Lindström, 1990; Stine, 1994). Conversely, the period 1937–1986 was an anomalously wet period in a 1000-year reconstruction of precipitation from dendrochronological evidence (Graumlich, 1993). Furthermore, a warm period from ca. 1100 to 1375 AD in California, corresponding to widespread warmth in the north temperate latitudes when pre-industrial, low CO₂ concentrations existed, indicates the need to consider climatic forcing other than increased concentrations of greenhouse gases. Tree ring studies undertaken on the central coast of California also indicate major fluctuations in the variability of precipitation over the last 600 years (Haston and Michaelsen, 1994).

Another rich source of information about climate during the geological past are the sediments and exposed shorelines of lakes (Street and Grove, 1979; Benson and Thompson, 1987). An exceptionally long palaeolimnological record of Tule Lake in northern California documents the last three million years of the lake’s history (Bradbury, 1992). Besides indicating warmer and wetter conditions beginning about 15 000 years ago, the inference of a warm, monomictic lake experiencing a climate with low seasonality during the Pliocene may be analogous to the projected period of climate warming in the next century. A detailed analysis of deltaic deposits in combination with other sedimentary, geomorphological, tephrostratigraphic and historical evidence at Mono Lake, California, documented lake level fluctuations of 40 m over the past 3800 years (Stine, 1990). Throughout most of the last 2000 years the level of Mono Lake has been above its natural historical levels, and, perhaps more importantly, on at least two occasions, has experienced climatic conditions as dry as those during the severe drought between 1928 and 1934.

Large-scale atmospheric patterns have been linked statistically to variability in precipitation and stream flow along the Pacific coast of North America (Cayan and Roads, 1984, Cayan and Peterson, 1989; Schonher and Nicholson, 1989; Leathers et al., 1991; Redmond and Koch, 1991; Cayan and Riddle, 1993; Dettinger and Cayan, 1995). Oceanic and atmospheric interconnections relevant to the synoptic meteorology of the Pacific coast have been examined with principal component analysis and teleconnective studies that include the Southern Oscillation (SOI), Pacific–North America (PNA) and Central North Pacific (CNP) indices (Cayan and Peterson, 1989; Leathers and Palecki, 1992; Figure 3). Strongly positive and negative PNA indices are associated with warm event (low SOI values) and cold event (high SOI values) ENSOs, and with precipitation and temperature anomalies on the west coast of North American
During periods with a weak CNP index, stream flows are high in Washington and Oregon, and, conversely, stream flows are often low during times with a strong CNP index (Cayan and Peterson, 1989). The strength of the teleconnective patterns can vary. For example, the Pacific Northwest may be inside or on the southern edge of a region with lower rainfall during and after an ENSO event (Ropelewski and Halpert, 1986).

Persistent climatic anomalies during the Holocene, such as the ‘Little Ice Age’ and ‘Medieval Warm Period’ may be explained by changes in the frequency of anomalous circulation patterns. For example, the existence of shallow lakes for several decades ca. 3600 and 400 BP in the Mojave Desert may have resulted from a weakening of the subtropical high in the eastern Pacific, which led to an anomalously low pressure system and heavy precipitation along the Pacific coast of North America (Enzel et al., 1989). Potentially, analogous changes in large-scale atmospheric circulation could occur in the future, but are difficult to predict with extant models.

**GCMs**

Results from GCMs suggest that global warming, induced by a doubling of atmospheric CO$_2$ concentrations, would range from 0 to 10°C along the Pacific coast of North America, depending on the version of GCM used and the season or latitude considered (Schlesinger and Mitchell, 1987). Projections of changes in precipitation along the Pacific coast range from slight decreases during the summer in southern portions to no change, or to increases elsewhere (Schlesinger and Mitchell, 1987).

Outputs from five GCM simulations of climatic conditions in coastal Canada (50–60°N) under a doubled atmospheric concentration of CO$_2$ by 2050 all indicate warming, and most suggest increased precipitation (Slaymaker, 1990). The warmest and driest scenario predicted winter temperatures of +6°C and summer temperatures of +4.2°C with no change in precipitation. The coolest and wettest scenario calculated winter temperatures of +2.4°C and summer temperatures of +0.6°C with winter precipitation of +200 mm and summer precipitation of +100 mm.

Recent developments, which have nested limited-area models (LAMs) within GCMs, are especially useful for the Pacific coast because of the importance of complex topography and oceanic influences (Giorgi and Mearns, 1991). In a promising effort, Giorgi et al. (1993) have tested a LAM-GCM with 60 km resolution.
over the western United States for periods that included the 1982–1983 El Niño and a drought. Seasonally averaged biases for daily average temperatures ranged from $+0.81$ to $-0.61\,^\circ C$ for California and the Pacific Northwest. The seasonal precipitation biases were less than 20% of observations for all seasons in the Pacific Northwest, and, over California, precipitation was underestimated by 10–30% except in summer, when it was overestimated by 50%. Snow depth was most accurately predicted for the Pacific Northwest. Further effort with a LAM nested in a GCM has projected climatic changes for the US after CO$_2$ doubling as another step in testing the methodology (Giorgi et al., 1994). Although the simulations forecast scenarios such as an increase in winter precipitation along the Pacific coast, Giorgi et al. (1994) caution against using such scenarios in assessments of the effects of potential climate change.

EFFECTS OF CLIMATE CHANGE ON AQUATIC ECOSYSTEMS

Potential responses of aquatic ecosystems to climatic change have been considered in general terms in several recent reviews (e.g. Carpenter et al., 1992; Firth and Fisher, 1992). Our approach is to emphasize results specifically pertinent to the Pacific Coastal Mountains and Western Great Basin. We have included results from mechanistic and empirical models, analyses of long-term data sets and discussion of qualitative hypotheses. We consider rivers and estuaries, saline and montane lakes, glaciated basins and riparian zones and salmon ecology.

Rivers and estuaries

In principle, hydrological models of runoff could be coupled with climatic information generated from GCMs to evaluate the potential effects of climate change on river discharge. In practice, incompatibilities of space and, to some extent, time between the hydrological and atmospheric models complicate such a coupling (Miller and Russell, 1992; Hostetler, 1994). Moreover, some parameterizations and step jumps of CO$_2$ levels used in the models are simplifications. Hence, hydrological results derived from the output of GCMs should not be judged as predictions. With these caveats in mind, Lettenmaier and Gan (1990) examined the hydrological sensitivities of four medium-sized montane catchments in the Sacramento and San Joaquin river basins to scenarios for long-term warming derived from three GCMs.

The four catchments [McCloud, Thrones, American (North Fork) and Merced, Figure 4] considered by Lettenmaier and Gan (1990) currently experience a mediterranean climate with almost all the precipitation occurring between November and April and with snow predominating at the higher elevations. Runoff is derived mainly from snowmelt in spring and summer. Hydrological conditions were simulated by coupling the snowmelt and soil moisture models of the US National Weather Service River Forecasting System; calibration and verification of the coupled models were performed for different periods using historical data. Steady-state climate scenarios after a CO$_2$ doubling were obtained from three GCMs [Geophysical Fluid Dynamics Laboratory (GFDL), Goddard Institute of Space Science (GISS) and Oregon State University (OSU)], and simulated changes in temperature and precipitation were used to drive the hydrological models. Other climatic variables such as relative humidity and wind were held constant because of the difficulty in obtaining consistent and reliable values from the GCMs. Moreover, interactions between hydrological responses and potential changes in vegetation of the catchments caused by climatic changes were not considered.

All three GCMs simulated increases in temperatures that averaged between 2 and $5\,^\circ C$. Although increases and decreases in precipitation were forecast by the GCMs, both the GFDL and GISS models generally simulated augmented precipitation in the autumn and winter. The primary hydrological effect of the climate having higher temperatures after doubled CO$_2$ was a decrease in the amount of precipitation falling as snow and less snow available to generate runoff in spring and summer. In fact, the temperature increases simulated by the GFDL and GISS models were of sufficient magnitude to eliminate almost completely water storage as snow in all the catchments except the Merced, which has the highest average elevation. As a consequence, runoff increased substantially during winter and decreased in late spring and summer (Figure 5). Site-specific...
differences stem from differences in elevation and the resulting proportions of rain and snow. Further consequences of simulated climatic warming were large increases in flood maxima and the occurrence of many large floods in winter instead of spring. These shifts in the seasonal distribution and variability of runoff have major implications for the management of water resources (Gleick, 1987, 1989; Lettenmaier and Sheer, 1989; Vankatwijk et al., 1993), for transport of solutes and particles and for the ecology of aquatic biota (Regier and Meisner, 1990).

At the mouth of the Sacramento–San Joaquin River system lies San Francisco Bay, one of the largest estuaries in western North America. The spatial and temporal variability of salinity in the Bay is fundamental to the physics, chemistry and ecology of the estuarine ecosystem (Nichols et al., 1986) and affects all levels of the food-web, from phytoplankton to predators (Jassby et al., 1995). Because the main control on salinity fluctuations is the volume of freshwater flowing into the Bay (Peterson et al., 1989), the earlier spring runoff expected by the climate warming scenarios examined by Lettenmaier and Gan (1990) are likely to produce higher summer and autumn salinity in the Bay.

An alternative approach to assess how changes in climate might affect the Bay’s salinity was applied by Cayan and Peterson (1993). They used about 60 years of historical records to investigate how extreme categories of spring climates (i.e. cool and wet, warm and wet, cool and dry, and warm and dry), produced by distinct atmospheric circulation patterns, influence the Bay’s salinity. Anomalously warm and/or dry springs tended to cause earlier snowmelt with less runoff in summer and higher salinities in the autumn. Furthermore, diversions for human uses tended to reduce spring inflows to the Bay and to do so disproportionately during drier periods.
Figure 5. Monthly mean stream flow for baseline condition and with three GCM forecasts (A1, GFDL; A2, GISS; A3, OSU) of climate change after doubling of CO₂ concentration. (From Lettenmaier and Gan, 1990)
Saline lakes

Within the endorheic catchments of the Western Great Basin occur several large saline lakes (e.g. Mono, Walker, Pyramid and Abert) which have undergone major changes in size and salinity as the regional climate has varied (Benson and Thompson, 1987; Stine, 1990). During the last few decades, diversion of inflows for human uses have caused lake levels to decline and salinities to increase in several of these lakes. The observed and anticipated ecological effects of the increasing salinities in Mono and Pyramid lakes have resulted in many long-term, experimental and modelling studies that can be used to infer potential responses to climatically induced changes in size and salinity (Patten et al., 1987; Galat et al., 1988).

Aquatic organisms living in saline waters expend a greater portion of their energy on osmotic regulation and less on growth and reproduction as salinity increases. For example, salinity bioassays on algal (Melack et al., 1985; Herbst and Castenholz, 1994) and invertebrate species (Herbst et al., 1993) from Mono Lake showed declining productivity with increasing salinity. However, results from physiological experiments do not translate necessarily to fully natural conditions. In fact, a model of plankton dynamics in Mono Lake, which incorporated nitrogen cycling, predicted lower reductions in productivity at higher salinities than the laboratory experiments (Jellison et al., 1993a).

Abrupt increases in lake level have also occurred in Mono and Pyramid lakes because of exceptional runoff associated with ENSO events such as those observed in the 1980s (Galat et al., 1990; Jellison and Melack, 1993a). One consequence of the large volume of freshwater inflow was the lakes becoming meromictic. Meromixis is persistent chemical stratification with incomplete vertical mixing over the course of a year. In Mono Lake, meromixis persisted from 1983 to 1988 and was characterized by a marked decrease in vertical mixing (Jellison and Melack, 1993a) and nutrient transport across the pycnocline (Jellison et al., 1993b) which resulted in diminished algal productivity (Jellison and Melack, 1993b).

To assess the incidence of meromixis during a period of declining lake levels punctuated with occasional ENSO events, Romero and Melack (1996) applied a one-dimensional vertical mixing model to Mono Lake using 50 years of historical stream flow and precipitation data. They assumed that the historical records, which included strong and weak ENSO events and 50 years of stream diversions, would simulate the expected long-term reduction in regional precipitation. A greater incidence of meromixis was predicted to occur at low lake levels because of greater dilution of the mixolimnion per unit freshwater input and higher initial salinities of the lake. Furthermore, a more variable interannual hydrology increased the likelihood of meromixis.

The reduction in nutrient supply to the euphotic zone during meromixis will lead to changes in algal abundance, composition and productivity. For example, meromixis and even temporary winter stratification in Pyramid Lake led to nitrogen limitation and to nitrogen-fixing cyanobacterial blooms (Galat et al., 1990). Following the onset of meromixis in Mono Lake, algal biomass in the spring and autumn and annual productivity were less than during periods with complete winter mixing (Jellison and Melack, 1993b). In contrast, annual production was very high the year meromixis ended. Hence, predictions of the regional climate having a more strongly seasonal stream flow with increased peak runoff, earlier snowmelt and lower baseflows (Cooley, 1990; Lettenmaier and Gan, 1990; Pupacko, 1993) will probably lead to greater variance in planktonic dynamics in saline lakes.

Montane lakes

Changes in snowmelt in response to altered precipitation and energy fluxes are likely to modify the timing and quantity of hydrological and chemical fluxes in montane catchments (Williams et al., 1996). The potential consequences to the montane lakes and streams may be altered flushing rates and residence times, stratification and heat content and inputs of nutrients and other solutes, including those causing acidification. Time-series spanning two decades and results from simulations available for montane lakes in California offer the possibility of assessing the magnitude of such responses to changes in snowmelt.
Emerald Lake, a representative high elevation lake in the southern Sierra Nevada (Melack and Stoddard, 1991), has experienced extreme variations in snowfall during the past decade (Kattelmann and Elder, 1991; Melack et al., 1993). The El Niño of 1982–1983 was the strongest of the twentieth century and produced extraordinary precipitation in California and elsewhere (Quiroz, 1983). The subsequent period included a prolonged, severe drought and two additional years with very large snowfall.

To assess the responses of stream chemical composition to an increased rate of snowmelt, as expected from global warming, Wolford and Bales (1996) have applied a mechanistic hydrological and geochemical model to the Emerald Lake catchment. Inputs from two contrasting years, one with high and one with low snowfall, were used to drive the model under the observed conditions and with snowmelt rates increased by 30%. During the period of rapid snowmelt, modelled concentrations of calcium and acid-neutralizing capacity (ANC) were lower at the higher snowmelt rate. Conversely, the higher rate of snowmelt caused the snow to disappear sooner, which led to very low discharge in late summer and much higher concentrations of solutes. When a 30% higher rate of snowmelt was combined with a doubled wet atmospheric deposition of solutes, ANC was depressed to near or below zero. In the exceptionally dilute waters of the Sierra Nevada, these changes in solute concentrations may influence the aquatic biota, as was demonstrated experimentally in streams and lakes of the region (Barmuta et al., 1987; Kratz et al., 1993).

Temperature profiles measured regularly for two decades in Castle Lake, California, a small subalpine lake, have revealed large interannual differences in heat content associated with the amount of winter snowfall (Strub et al., 1985). In all years with anomalously large heat content, the snowfall was lower than average; while in all years (except 1973) with anomalously small heat contents, snowfall was higher than average. ENSO events produced both anomalies, but some anomalous years were without ENSOs. Hence, simple interpretations of effects from ENSO events would not be appropriate.

Ecological processes in montane lakes such as Castle Lake may be strongly influenced by climatic conditions, and, therefore, be sensitive to changes in climate caused by global warming. For example, during the extraordinary El Niño of 1983, Castle Lake remained frozen until early July and summer primary productivity was only 25% of the long-term average (Strub et al., 1985). In years with incomplete vertical mixing, productivity is often less than in years with spring holomixis (Goldman and de Amezaga, 1984). A 27-year record of summer primary productivity had no long-term trend, but considerable interannual variability, with extreme years often occurring when ENSOs occurred (Jassby and Goldman, 1992). Further statistical analysis of interactions between the early summer productivity and climate revealed negative associations with the time of ice-out and total precipitation preceding the spring bloom (Goldman et al., 1989; Jassby et al., 1990). The time of ice-out sets the length of the growing season, and total precipitation affects flushing rates.

Additional evaluation of the potential effects of global warming on primary productivity in montane lakes is possible by linking GCM projections of climate change with a model of lacustrine productivity. Byron and Goldman (1990) attempted such an approach by using almost three decades of limnological data from Castle Lake to develop a regression model that related algal productivity to regional temperature and precipitation. When used in combination with GCM calculations of temperature and precipitation under doubled CO₂ concentrations, their model predicted increased algal productivity. These increases were driven by the GCM-projected higher temperatures, which were linked to earlier melt and a longer growing season. Because the GCMs calculated January–May precipitation as being similar to historical records, no effect of doubled CO₂ on runoff was observed; this result deserves additional study using newer, regional predictions of climate change.

In larger lakes, longer residence times and larger volumes buffer some short-term climatic variability that affects smaller lakes such as Castle and Emerald lakes. However, even in Lake Tahoe, climate-related factors are apparent in the three decades of limnological data available. Through a careful statistical analysis, Goldman et al. (1989) demonstrated that the May peak in primary productivity was associated with the maximum depth of spring mixing. The depth of mixing reflected the intensity of storms in March. Hence,
projections of climate change would need to face the significant challenge of predicting wind regimes to allow forecasts of effects on some lakes.

Atmospheric deposition of nutrients can influence algal abundance and productivity in oligotrophic lakes (Jassby et al., 1994), and climatic conditions can be linked to atmospheric deposition in several ways (Lesack and Melack, 1991). Large forest fires can result occasionally in considerable nutrient inputs to lakes with a stimulating effect on productivity (e.g. Goldman et al., 1990). Hence, the potential influence of climate change on the incidence of fires should be evaluated.

**Glaciated basins**

A common hypothesis is that global warming will cause mid-latitude glaciers to recede as a result of increased melting and, consequently, sea levels will rise (Roots, 1989). However, this may be a simplified hypothesis, and the effect may vary according to the geographical area and whether the glacier’s terminus is on land or at tide water (Oswood et al., 1992). Evidence from the European Alps indicates that the twentieth century has been characterized by a general retreat of alpine valley glaciers (Groves, 1988) with a consequent overall reduction in glacial runoff (Collins, 1985). However, this widespread retreat of glaciers in the European Alps appeared to be generally arrested in the mid 1960s, and, subsequently, the termini of many glaciers have slowly re-advanced, although overall increases in area have been small (Kasser, 1983). Loss of mass has been shown for glaciers in the Cascade Mountains of Washington (Krimmel, 1989).

In Alaska, many tide water glaciers along the south-east and south-central coast have shown a rapid retreat within the last century, but this phenomenon is considered to be related more directly to local fjord topography than to climate-induced effects (Powell, 1990). For Alaskan glaciers with their termini on land, records for the period of the mid-1970s to the late 1980s would appear to indicate an increase in mass balance for the Wolverine Glacier (maritime) in south-central Alaska and the Gulkana Glacier (continental) in the Alaska Range (Mayo and Trabant, 1986; Mayo and March, 1990). However, when examining the 30-year record for these glaciers, it is apparent that there is an overall net negative balance for the period 1966–1994 (Hodge, personal communication).

The relationship between glacier mass balance and glacial runoff is complex. Glacier recession will initially lead to runoff additional to that produced if the glacier was in a steady state, but sustained deglaciation will result in diminished flows (Collins, 1987). Unfortunately, runoff data for the Wolverine and Gulkana glaciers are not complete during the years of record for the glacier mass balances. During positive mass balances in the late 1970s, total runoff appeared to increase, but runoff patterns in relation to negative mass balances are not readily apparent (Hodge, personal communication). Clearly, there is a lag between alterations in runoff and changes in glacier mass balance.

Other factors, mediated by climatic variations, may influence the relationship between runoff and glacier mass. Increased snow accumulation from winter precipitation may increase the time before the underlying ice is exposed to radiation, and thus may retard the onset of ice melt and, since snow has a higher albedo than ice, the amount of melting under direct radiation will be reduced (Collins, 1985, 1987). A matter of some debate is the likely role of cloud cover in climate change. Increased cloud cover would reduce the amount of radiation reaching the ice surface, potentially reducing ice melt. Associated with increased cloud cover could be increased precipitation, which would elevate the contribution of non-glacial sources to runoff.

**Glacier-fed rivers**

The ecology of glacier-fed rivers has been relatively unstudied compared with rivers originating from other sources. Milner and Petts (1994) proposed a qualitative model to predict the gradient of zoobenthic communities in rivers downstream of glacier margins as determined by two principal variables, water temperature and channel stability. Water temperature conveys deterministic trends to the typical pattern of invertebrate communities in glacial rivers, and determines the point at which certain taxa may colonize. However, even if temperatures are suitable, channel instability may delay colonization and allow some of the cold-tolerant taxa to remain dominant in the community. Chironomid larvae of the genus Diamesa are
typically the sole taxa present when $T_{\text{max}} < 2^\circ \text{C}$, and are joined by other Diamesinae, Orthocladiinae and Simulidae when $T_{\text{max}}$ is $2–4^\circ \text{C}$. *Diamesa* larvae typically possess long posterior pro-legs with strong claws that enable them to grip the substrata in unstable channels. Increased glacial runoff may have a significant effect on flow, temperature and sediment regimes in glaciated basins. Reduced stream temperature from increased contributions of glacial meltwater and decreased channel stability from changed runoff patterns and altered sediment loads, will, potentially, reduce the diversity of zoobenthic communities in glacier-fed rivers and cause an increase in the relative abundance of a number of key taxa, most notably *Diamesa* spp.

Oswood *et al.* (1992) considered the biogeographical implications for freshwater invertebrates of a less rigorous thermal environment at higher latitudes. Increased water temperature and decreased permafrost in areas south of the Alaska Range allow for potential redistributions of benthic invertebrate communities with the possible arrival of new predators (e.g. Megaloptera) and the loss of some cold water stenotherms at their southerly ranges. The altitudinal range of invertebrates in mountain streams may also change with the extension of some species to higher elevations and the reduction in the amount of habitat for cold water stenotherm taxa.

**Riparian zones**

Biological communities at the boundary between terrestrial and freshwater ecosystems are particularly sensitive to climate change. Examples include riparian forests, marginal wetlands, littoral zones in lakes, floodplain lakes and forests, and areas with significant groundwater–surface water exchange (Naiman *et al.*, 1988). For example, in response to climate change, it is expected that there will be changes in the ratios of the number of vegetative patch types and their areas.

Riparian zones associated with rivers in the Pacific Coastal Mountains and Western Great Basin are likely candidates for alteration as climate changes. For example, in the Queets River, Washington, and other coastal rivers, variability in sediment delivery, discharge and benthic shear stress determine the structure, composition and spatial distribution of riparian vegetation (Fetherston *et al.*, 1995). Climatically induced changes in the hydrological regime are expected to have substantial consequences for riparian forests, in terms of their structure, biogeochemical processes and resiliency (Naiman *et al.*, 1993). Much of the possible variability is apparent in the species, and their life history strategies in the temperate coastal rainforest (Naiman and Anderson, 1997). Rivers with high discharge favour willow, sexually reproducing black cottonwood and many exotic species (DeFerrari and Naiman, 1994). In contrast, rivers with little variability favour more upland species such as western hemlock, sitka spruce and Douglas fir, asexually reproducing cottonwood and less exotic species.

**Salmon ecology**

Salmon, a major natural resource in the Pacific Northwest respond to climate-induced changes in temperature and runoff (Neitzel *et al.*, 1991; Levy, 1992). However, the potential responses of each salmonid species and subspecies may vary owing to different life cycle adaptations to environmental conditions in its natal river system. Furthermore, changes in both inland waters and the Pacific Ocean must be considered for these anadromous fish.

Neitzel *et al.* (1991) evaluated the potential effects of changes in hydrographs, total annual discharge, water temperature and texture of the stream bed on salmonid reproductive cycles resulting from a hypsithermal-type warmer, drier climate in the Columbia River Basin. Spring and summer chinook responded negatively to the hypsithermal-type climate because of changes in the timing and size of spring runoff. Autumn chinook and coho are affected by temperature, discharge and the timing of snowmelt; hence, positive responses were indicated in rivers on the west side of the Cascades while negative effects appeared likely on the east side. In contrast to other species, sockeye salmon live in lakes during part of their life cycle; the warmer summer temperatures in lakes and lower spring flows expected after climatic warming would probably cause negative effects on the sockeye salmon the Columbia River Basin. Alterations in the regional

allocation of water resources to hydroelectric generating facilities and irrigation may well compound the
direct effects of climate change on the salmon.

Changes to the climates of British Columbia and the north-east Pacific may influence the production of
Fraser River sockeye salmon (*Oncorhynchus nerka*), the most valuable salmon resource in British Columbia. These salmon are especially susceptible to climatic warming because they are at the southern range of sockeye in North America and because they make long migrations in near-surface waters of the Pacific Ocean. Bioenergetic models (Hinch *et al*., 1994) and qualitative analyses (Henderson *et al*., 1992; Levy, 1992) have been applied to assess the probable consequences of climate warming on production of sockeye salmon.

Henderson *et al*. (1992) examined the probable effects of atmospheric warming on the Adams River stock, a large and commercially important population in the Fraser River Basin, using a 2.5°C summer and 4.0°C winter increase in temperature derived from GCMs run for western Canada. Anadromous adult salmon return to the Adams River to spawn in late summer and early autumn, the fertilized eggs incubate in river gravels and alevins hatch and emerge in spring. The young sockeye enter Shuswap Lake, where they feed until the following spring. Then, they move into the Pacific Ocean, where they remain for two years before returning to their natal spawning ground as four-year-olds.

The warmer atmospheric temperatures predicted to occur with doubling of atmospheric CO₂ concentrations were surmised to influence the ecological conditions in Shuswap Lake and the river in several ways. Greater input of nutrients during the winter isothermal period instead of during the spring, and a longer period of thermal stratification, were deemed likely to lead to lower planktonic productivity, and smaller juvenile sockeye. Based on the work of Brett *et al*. (1969), which determined the optimal temperatures for juvenile sockeye growth as a function of food supply, and an examination of the vertical distribution of the fish and their zooplankton prey, Henderson *et al*. (1992) concluded that climatic warming would result in reduced growth and survival of sockeye salmon in freshwater, which would, in turn, lead to a decrease in smolt to adult survival (Henderson and Cass, 1991). Moreover, climatic warming may change aspects other than temperature in the river system utilized by the salmon. For example, if flow in the Fraser River is diminished, as is anticipated, adult fish would be hindered in their spawning runs and some spawning gravels could desiccate.

During the time the Fraser River sockeye spend in the ocean almost all their growth occurs and the surplus energy reserves needed for their migration and spawning are acquired. GCMs forecast increased sea surface temperatures (SST) and weaker north–south pressure gradients over the north-east Pacific Ocean, which could weaken oceanic upwelling and reduce secondary productivity (Hsieh and Boer, 1992). In turn, warmer, SSTs and less zooplankton would probably result in smaller adult sockeye with fewer and smaller eggs and less energy reserves (Hinch *et al*., 1994, 1995). Hence, during both the freshwater and marine stages of their life history, sockeye salmon are likely to be adversely affected by climatic warming.

A recent study of lakes on the Alaskan Peninsula examined sockeye salmon returns from spawning adults to Lake Becharof, via the Egegik River, and to Lake Ugashik (Mathiesen *et al*., 1997). An earlier study reported that the primary productivity of Lake Becharof tended to be nutrient and, probably, light limited (Goldman, 1960). In attempting to account for the increased escapement beginning in the 1970s, Mathiesen *et al*. (1997) found that the surface temperatures at the outflows of the lakes had increased from 7.6 to 8.8°C for Lake Becharof from 1962 to 1989, and from 8.8 to 9.2°C in the smaller Ugashik Lake. Both lakes, probably because of their proximity to the sea, had shorter periods of winter ice cover than the much larger Lake Iliamna or Naknek Lake, which are situated north and inland. The decaying carcasses from the larger return of adults from the sea also provided fertilizing nutrients to the nursery lakes, helping to sustain the food-web during the longer growing season.

In south-central Alaska, several major systems of lakes support large runs of sockeye salmon and include the Kenai, Tustamena and Skilak lakes, all glacially influenced. Climate-induced increases in glacial runoff into these lakes in summer could cause concomitant increases in turbidity and reductions in primary productivity. The offsetting effects of a shorter period of ice cover and warmer water temperatures could enhance zooplankton and salmon fry growth.
With increasing latitude, overwintering mortality becomes a significant factor in the production of salmonids. Consequently, a reduction in the length of ice cover in streams may enhance overwintering survival. Conversely, increased winter flows and spring peaks may reduce salmonid egg to fry survival, particularly if the cumulative effects of altered land use are considered, e.g. increased erosion and runoff. Higher spring peaks in flow and warmer water temperatures may cause earlier emergence of fry and migration of pink and chum salmon fry to estuaries at a time when their food sources have not developed adequately. Lower summer flow may reduce the amount of suitable spawning and rearing habitat.

**RECOMMENDATIONS FOR RESEARCH**

Further research activities should include expanded studies at high elevations and of mass balances of glaciers, applications of remote sensing to monitor changes, further refinement of regional climatic models to improve forecasts of future conditions and continued analyses of long-term physical, chemical and biological data to help understand responses to future climates.

The selection of appropriate scales of measurement can be difficult because of discordant scales amongst atmospheric, hydrological and ecological systems (O’Neill, 1988; Hostetler, 1994). Furthermore, detection of gradual changes requires consistent monitoring for long periods at a range of spatial scales. One alternative to comprehensive, and hence expensive, monitoring programme is to focus on unusual circumstances that can indicate how a system responds to perturbations. Actual experimental treatments can do just that, but, in many situations, the large scale of the system precludes replicated, experimental designs.

Along the Pacific coast of North America, high elevation environments, whilst a conspicuous feature and one susceptible to climatic changes, have received insufficient attention and, in general, lack long-term data. Similarly, while glaciers are abundant in the northern portion of the region, more studies of mass balance and analyses of glacial runoff are needed to assess glacial responses to varying climate. Moreover, maintenance of existing stations gauging the discharge of rivers throughout the region is crucial.

Remote sensing has great potential for augmenting ground-based studies in the analysis of regional aspects of hydrological and ecological conditions (e.g. Sellers, 1995). Relevant variables amenable to remote sensing include snow covered area, water vapour and fluxes, cloud cover, radiation and land cover. A combination of optical and microwave sensors carried on several satellites, improved algorithms for calculating relevant variables and electronic communication networks offer many opportunities for merging of measurements and modelling.

Increased coupling of regional climate models with hydrological models operated at the scale of catchments or lakes (e.g. Hostetler and Giorgi, 1993) would provide valuable information for subsequent ecological studies. One challenge to such efforts is the inclusion of wind regimes, which are very difficult to simulate, especially in mountainous terrain. Furthermore, because of the importance of ENSO events along the Pacific coast, special attention should be given to modelling (e.g. Meehl and Branstator, 1992) and palaeoclimatic research (e.g. Enfield, 1992) that considers the robustness of ENSOs to major changes in atmospheric boundary conditions. A related issue, in need of improved GCM modelling, is the extent to which climatic variability will change as concentrations of greenhouse gases increase (e.g. Rind et al., 1989).

Hydrological models also require improvements to increase their utility for assessing the effects of climatic changes (Leavesley, 1994). Besides conceptual advances and better parameter estimation techniques, innovative approaches to generate climate scenarios (e.g. Dettinger and Cayan, 1992) are needed. Furthermore, because of interactions between vegetation and runoff (e.g. Kattelmann, 1991), hydrological models should be linked with ecological models (e.g. Neilson and Marks, 1994).

While many usual environmental measurements are appropriate and necessary to evaluate ecological responses to climatic changes, several are worthy of special mention based on their pertinence to the Pacific coastal region. Fire is a common occurrence in the region, and optical and nutritional conditions in lakes and streams can be influenced by burning of vegetation in their catchments. Moreover, because the frequency of fire is highly dependent on climatic conditions, both measurements and modelling should include the role of...
fire. Snowmelt and associated ice cover play dominant roles in hydrological and hydrochemical conditions in the high elevation streams and lakes of the region, and are particularly sensitive to climatic perturbations. Hence, experimental and monitoring programmes should target the annual extent of ice cover on lakes and the snowmelt period. To evaluate the probable consequences of climatic warming for salmon requires examination of the responses of all life history stages to the cumulative effects of likely environmental changes in the lakes, rivers and oceans inhabited by the fish. Overall, these activities will require careful coupling of reliable limnological and climatic data and should provide valuable insights into the complex results of possible future climatic change.

ACKNOWLEDGEMENTS

We thank R. Kattelmann for valuable material on stream flow in the Sierra Nevada. Preparation of the manuscript benefited from comments by two anonymous reviewers and was supported in part by NASA grant NTW-2602. Permission to use figures 1 and 2 was granted by Island Press, Washington, DC.

REFERENCES


