

GLOBAL CHANGE AND FRESHWATER ECOSYSTEMS

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INTRODUCTION

The biosphere contains only 0.014% of Earth's water, distributed among lakes (0.008%), soils (0.005%), and the atmosphere, rivers, and biota (0.001%) (79). An additional 2.58% of Earth's water is fresh, occurring as ice (1.97%) or groundwater (0.61%). The remainder of Earth's water is saline. Climate affects key fluxes (evaporation, water vapor transport, and precipitation) that determine the amount and distribution of freshwater (79). The availability of freshwater to both ecosystems and humans is therefore sensitive to changes in climate.

The small amount of water found in the biosphere has large significance for ecosystems and society. The availability of water influences the distributions of major biome types and potential agricultural productivity (35). Humans depend directly on freshwater for drinking, irrigation, industry, transportation, recreation, and fisheries. Expanding human populations and changes in global climate will exacerbate already severe stress to freshwater resources in some regions (1, 79, 108, 163, 172). In others, increased availability of water will potentially mitigate stress (1, 15, 163, 172).

This review addresses the potential effects of global climate change on lake and stream ecosystems. Concern for brevity severely constrained the topics covered. Sustained shifts in global climate will have enormous effects on distributions and interactions of species (38, 71). We limit this review to

fishes, which interact strongly with lower trophic levels (18, 122), illustrate key considerations common to other aquatic organisms, and are significant to the public. Although wetlands interact intimately with streams and lakes (169), our consideration is limited to their interactions with atmospheric chemistry.

The major consequences of global change for freshwater ecosystems depend on the temporal and spatial scales at which effects are assessed. We have organized this review around two broad scales of change. Transitional scales pertain to landscape-level shifts in location, morphometry, and persistence of lakes and streams and their biotas over decades to centuries. Perturbational scales pertain to events with return times of years to decades that affect entire stream or lake ecosystems, such as floods, droughts, or fish recruitment events. We then turn to ecosystem metabolism as an integrated response to climate, and to feedbacks between freshwaters and regional climate; we close the review with salient uncertainties that should influence future research priorities.

FRESHWATERS IN TRANSITION

Future Distributions of Freshwaters

Over the past 25,000 years, freshwater ecosystems have undergone massive changes in spatial extent correlated with trends in regional climate (150). Future climate change is likely to produce comparable changes in the supply and distribution of freshwater.

Forecasts of future precipitation and evaporation are uncertain, but the consensus is that greenhouse warming will increase both (139). Some areas of the Earth will become wetter and others drier, thereby shifting the global distribution of streams, lakes, and wetlands (163). Predictions of variability are more uncertain than predictions of means (139). A recent analysis indicates that greenhouse warming may decrease variability of temperature and the diurnal range, while increasing the variability of precipitation (133).

The difficulty of forecasting future distributions of freshwaters is exacerbated by the effect of transpiration on runoff (64, 135, 170). Climate change is likely to alter terrestrial vegetation, soils, and soil moisture, which affect evapotranspiration (29, 35, 113).

Numerous hydrologic studies predict changes in runoff over the next century if global warming of 2–4°C occurs (Table 1). These regional studies of large basins apply water balance models (155) driven by precipitation, soil moisture, and potential evapotranspiration. Generalizations that emerge are: (i) the precipitation-runoff relationship is nonlinear (170); (ii) under reduced precipitation scenarios (predicted for continental interiors—171), reductions

in streamflow are likely, particularly in western US basins (Table 1; see also 172); (iii) arid basins are more sensitive to precipitation changes than are humid basins (Table 1; see also 69, 170); (iv) seasonal shifts in streamflow distributions are probably more significant than changes in total annual runoff, particularly in cold or mountainous regions where winter precipitation now occurs as snow (Table 1; see also Ref. 81).

In arid regions such as the North American Great Basin, drier conditions may decrease water supply rates below current human demand (44). Lakes and wetlands are expected to contract in area. Projected water quality changes are negative (172).

In currently moist regions such as the Laurentian Great Lakes, drying will decrease stream flows, lake levels, wetland areas, and water supplies (24, 132). In heavily populated areas, the magnitude of change is uncertain because effects on water demand for irrigation, energy, and cooling are unknown (23). Drier conditions may affect transportation in regions that now have abundant water. In the Great Lakes, shippers will enjoy a longer ice-free season but will encounter lower lake levels (87).

Certain regions may become wetter as a result of global climate change (140). Increased stream flow, more frequent floods, and expansion of lakes and wetlands are likely (15). Reduced snow cover will reduce the need to salt roads, and water quality will benefit (15).

Fluvial Geomorphology

Changes in river channel form will be a consequence of global warming and associated precipitation changes. Erosion and sediment transport are linked to climate (68, 173), with highest rates in regions having the most variable precipitation and runoff (2, 54). Holocene arid phases of centuries duration were characterized by rare, high-magnitude flash floods, while floods in humid phases were more frequent but less intense (76). High magnitude floods cause channel widening, which is exacerbated by sparse riparian vegetation characteristic of drought phases. Periods of increased precipitation permit reestablishment of vegetation with attendant channel narrowing and flood flow moderation (89). Arid and semiarid regions experience, in comparison to humid regions, amplified runoff response to precipitation change (28, 170), higher streamflow variability (118), and more severe flash floods (2, 48). These facts lead several authors to suggest that these systems might provide early warnings of global change (28, 52, 118).

In forest streams, wood is an important geomorphic agent with a long residence time (61). Large woody debris in streams influences channel morphology (55, 70, 159), habitat, and stream ecosystem processes (7, 160) but can be removed by debris flows (4, 151). Frequency of debris torrents, landslides, and earthflows, which are triggered by extreme rainstorms, will no

Table 1 Results of hydrologic modeling and water balance studies predicting regional impacts of climate warming on runoff. Scenarios are: 2°C temperature increase (unless otherwise indicated) and -20% to +20% change in precipitation. Runoff values are expressed as per cent change and are annual averages unless otherwise indicated. Where 2 values are listed, they represent minimum and maximum estimates.

| Location and Characteristics | Per cent change in precipitation | | | | | Comments | Reference |
|------------------------------|----------------------------------|------|------|-----|------|--|-----------|
| | -20 | -10 | 0 | +10 | +20 | | |
| Western USA (7 basins) | -40 | | | | | | 1 |
| | -76 | | | | | | |
| Arid basin | -50 | | +50 | | | 1°C temperature increase | 2 |
| Humid basin | -25 | | +25 | | | | |
| Colorado River Basin | -40 | | -18 | | | | 3 |
| Sacramento River | -42 | -32 | -22 | -12 | -1 | Summer runoff | |
| | -24 | -9 | +8 | +25 | +44 | Winter runoff | 4 |
| Great Basin (4 basins) | -33 | -17 | | | | Col 1 is -25% precipitation | 5 |
| | -51 | -28 | | | | | |
| Delaware River | -51 | -32 | -14 | +8 | +31 | Seasonal runoff change, especially in cold northern portion of basin | 6 |
| Greece-(3 basins) | -27 | -15 | 0 | +12 | +25 | Seasonal runoff change, especially mountainous basins; humid basin less sensitive. | 7 |
| | -31 | -17 | -3 | +13 | +27 | | |
| Saskatchewan River | -36 | -21 | 0 | -3 | +27 | Semi-arid sub-basins most sensitive (highest extremes) | 8 |
| | -100 | -100 | -100 | +63 | +286 | | |

References: 1- Stockton & Boggess 1979; 2- Nemeec & Schaake 1982; 3- Revelle & Waggoner 1983; 4- Gleick 1987; 5- Flaschka et al. 1987; 6- McCabe and Ayers 1989; 7- Mimmikou et al. 1991; 8- Cohen 1991.)

doubt change as precipitation variability and timing change. Altered regimes of drought and moisture may also increase the incidence of fire in forest, scrub, and grassland (113), thereby changing the rate, input regime, and role of wood in streams (103).

Inputs from Terrestrial to Freshwater Ecosystems

The zone of intense biogeochemical activity at the land-water interface will expand and contract with fluctuations in the water supply (169). This interface is especially important in streams, temporary ponds, and small lakes because of their large perimeter-to-volume ratio. Stream ecologists have paid close attention to the influence of terrestrial vegetation on freshwaters (43, 63). Utility of terrestrial leaf litter to detritivores varies greatly among species (115) and in the combination of species within individual leaf packs (5, 152). Change in climate will likely alter the total biomass, productivity, and species composition of the riparian community and, in turn, the supply of organic matter and nutrients to freshwaters (99).

Climate change may alter the composition of riparian vegetation (99). Past vegetation changes that had substantial effects on stream ecosystems include the demise of American chestnut (143) and the spread of exotic saltcedar (*Tamarisk* spp.) through the Colorado basin (147). Transplant experiments indicate that aquatic consumers prefer detritus derived from local plants (91, 102). As high CO₂ levels cause N content of leaves to decline, grazing by terrestrial insects may decline (36), increasing the proportion of leaf production that enters streams and slowing in-stream decomposition (99). Such changes in the riparian zone will likely force marked alterations in aquatic communities and the nature and rates of ecosystem processes. While there is little question that adjustment of the aquatic sector can keep pace with riparian dynamics, consequences of vegetation shifts may also be translated far downstream through transport, altering longitudinal patterns described by the River Continuum Concept (162).

Distribution of Freshwater Fishes

Temperature tolerances often govern both the local and biogeographic distribution limits of freshwater fishes, which are generally grouped as coldwater (e.g. Salmonidae), coolwater (e.g. Percidae) or warmwater (e.g. Centrarchidae and Cyprinidae) forms (84). Thermal limits will be altered by global warming. Distributions of aquatic species will change as some species invade more high latitude habitats or disappear from the low latitude limits of their distribution (66, 142).

Small, shallow habitats (ponds, headwater streams, marshes, and small lakes) will first express effects of reduced precipitation (83). Consequences for aquatic organisms are obvious. Of greatest immediate concern are the

severely limited desert pool and stream habitats now occupied by threatened and endangered fishes (90, 100). Similarly, the spawning habits of many species require small and shallow habitats as refuge and nursery for both gametes and early life history stages. Prospects for successful relocation of spawning activities exist but may be thwarted by the strong imprinting and homing behavior known for many species.

Warming will alter the stream habitat of coldwater fishes such as trout, charr, and salmon (94). Projected increases in air temperature will be transferred, with local modification, to groundwaters, resulting in elevated temperatures and reduced oxygen concentrations. At low latitudes and altitudes these changes may have immediate adverse effects on eggs and larvae, which are usually deposited at sites of groundwater discharge. They may also reduce suitable habitat during summer months. Conversely, the winter stressors of osmoregulation at extremely low temperatures and physical damage by ice will be diminished. At higher latitudes and altitudes, elevated groundwater temperatures will increase the duration and extent of optimal temperatures; all life history stages benefit accordingly (94).

Many major river systems have an east-west drainage pattern. Lacking the opportunity to move north within the river courses, many freshwater fishes will not have access to a thermal refuge. Some genetic adaptation is possible but the rates of mutation are low and the prospect for development of tolerant strains is an inverse function of the rate of warming (90). Strong selection pressure and low capacity for adaptation may lead to local extinctions for some species (125).

Warming of freshwater habitats at higher latitudes is more likely to open them to invasion. Shuter & Post (142) examined life histories and energy requirements for a variety of temperate, North American fishes. All aspects of the life history were accelerated by global warming. The constraint of size-dependent winter starvation would be relaxed and permit many species to expand their distributions.

By coupling output from physical models of thermal structure for the Great Lakes with a fish bioenergetics model (74), Magnuson et al (85) analyzed potential responses for guilds of coldwater, coolwater, and warmwater fishes. Results included greater total annual growth due to increases in duration of the growing season and volume of habitat offering preferred temperatures (60). Higher water temperatures and increased metabolic costs would lead to growth declines if prey production was insufficient.

An insightful analysis of prospective invasion of the Great Lakes was offered by Mandrak (86). After glaciation, the Great Lakes were colonized by at least 122 fish species from the Mississippi and Atlantic refugia. Fishes now present in those drainages but not recorded in the Great Lakes were

evaluated as candidates for future invasion on the basis of habitat requirements (trophic interactions, reproductive biology, thermal niche). Of the 58 species considered, 27 (mostly Cyprinidae and Centrarchidae) were deemed likely to invade Great Lakes habitats if global warming released the temperature constraints to the limits of their northerly distribution.

Mandrak's (86) large-scale analysis raises issues pertinent at the local scale of other lakes. Omnivorous warmwater fishes that have short life spans are most likely to invade and flourish in habitats where impoundment, water quality degradation, and fishery exploitation have disturbed the environment (82, 83). Few lakes and streams have been spared these anthropogenic effects. As a result, few fish communities may be resistant to colonization as thermal barriers to migration are removed (93). Autecological constraints, the regional pool of potential invaders, and local community composition must be considered to assess prospects for invasion (156).

Fish species diversity, biological production rates, and fisheries yields are inversely related to latitude (22, 128). The majority of freshwater fish species occupy low-to-middle latitude environments. Most of the world's lakes are of glacial origin and occupy higher latitudes. Global warming makes the thousands of glacial lakes of North America, Europe, and Asia more open to colonization and thermal enhancement of production. In total, the volume of habitat available to fishes is likely to increase. Destabilization of current communities may occur as glacial relicts and coldwater species are displaced (138), but compensatory replacement will likely proceed as invasions by coolwater and warmwater species occur. As a result, the overall diversity and productivity of fishes in north temperate lakes will probably increase. Principles expressed in the thermal ecology of fishes likely extend to other aquatic fauna. Freshwater communities will reflect changes in autecological constraints and the ecological ramifications of changing food webs (38, 71).

RHYTHMS OF PERTURBATION

Analysts of climate change expect the frequency of surprises to increase (139). Surprises include floods, droughts, and thermal extremes that cause abrupt change in ecosystem process rates or populations of key species. Such changes have substantial ecological significance because rhythms of temporal variability in streams and lakes are entrained by cycles of hydrology and recruitment of keystone species (17, 52). Such cycles typically have periods of one to many years, measured at the spatial scale of a particular stream or lake ecosystem. Here we consider the consequences of changing perturbation cycles for riparian and floodplain ecosystems, hydrologic disturbances of streams, water renewal in lakes, and fish recruitment.

Perturbations of Riparian Zones and Floodplains

The riparian zone undergoes a cycle of establishment and destruction owing to patterns of hydrologic disturbance and recruitment characteristics of riparian trees (3, 31, 49). Rare catastrophic events such as mass wasting of hillslopes remove soil, debris, and vegetation from affected areas and expose bedrock surfaces. These events affect only a small fraction of the watershed but may influence up to 10% of the channel network as material enters and dams recipient streams (151). The geomorphic effect of slumps and earthflows can persist for thousands of years (34); however, biota of recipient streams may recover to predisturbance levels in 1–2 years (77). Rate of recovery of riparian vegetation is between these extremes.

In arid regions, riparian vegetation is very sensitive to the availability of water, which in turn depends upon amount and distribution of precipitation. Conversion of chaparral to grass in a small Arizona watershed increased water yield and converted a previously intermittent stream to permanent flow, increasing density and extent of riparian vegetation (65). Similar oscillations may occur in unmanipulated desert streams in response to climate change (52). Recovery of in-stream processes after flood or drought is rapid (40); however, the riparian zone is likely to respond more slowly. Because of the strong interaction of aquatic and riparian components (even in aridland streams where riparian vegetation is sparse), it is unlikely that either phase approaches equilibrium given that return times for effective disturbance events differ markedly and disturbance-recovery cycles are always out of phase.

The floodplain is the zone of maximum interaction between a river and its valley (20); the floodplain depends upon regular inundation to supply nutrients and organic matter supply and to provide a breeding ground for fishes and their food organisms. Especially during initial stages, inundation influences river water chemistry (168). Inundation extent and duration are sensitive to climate, so changes in precipitation and runoff amount and timing will influence floodplain-river interactions. The inundation both provides waters and stresses riparian plants, and it controls colonization by exotics (11). Thus climate change has a substantial potential for altering riparian vegetation in this and similar drainages.

In the Mississippi River, floods of less than annual return frequency may be significant disturbances which influence, through erosion and sedimentation, the distribution of macrophytes and primary production (145). The influence of floodplains in this system extends far downstream. Similarly, dependence upon allochthonous inputs increases longitudinally with river size in the blackwater Ogeechee River of Georgia owing to lateral floodplain contributions (98), counter to predictions of the river continuum concept (162). Floodplain contribution to the stream's energy budget is linked to

seasonal flooding, which provides a bimodal pulse of organic matter to stream consumers (80, 97).

Hydrologic Disturbance of Streams

The most obvious and immediate effects of global climate change on stream ecosystems involve changes in hydrologic patterns. Complex relationships link climate to runoff (163). Changes in total precipitation, extreme rainfall events, and seasonality will affect the amount, timing, and variability of flow. Changes in total amount or timing of runoff may result in increased or decreased intermittency (118, 165), while altered amount, variability, and extremes of runoff may affect timing, frequency and severity of flash flooding (47). Such changes in magnitude and temporal distribution of extreme events may disrupt ecosystems more than changes in mean conditions (52, 118, 164). Extreme events comprise the disturbance regime of lotic ecosystems and are mediated by catchment geology, soil chemistry, and vegetation (101, 118, 165).

The role of disturbance in lotic communities and ecosystems is currently a major focus of research (111, 114, 119, 124, 131, 175). Despite the attention it has received, there is no consensus as to the importance of disturbance in determining structure and functioning (but see 131), although a strong case can be made for expecting regional variation (39, 119, 120). Poff (118) suggests that in a warmer, drier climate many perennial streams fed by runoff might become intermittent because of their high flow variability, while groundwater-fed streams would be buffered against such changes. Streams fed by snowmelt, which have highly predictable flood and flow regimes, might become less predictable with winter warming (increased rain-on-snow events). Increasing aridity may render flows of many more streams unpredictable (52). The non-linear runoff response of arid regions may be caused by development of a hydrophobic layer on soils during dry periods, which increases the likelihood of overland flow (28).

Altered seasonality of both rainfall and spates is a likely consequence of global warming that would alter temporal variation in controls of ecosystem processes (50, 52). Post-flood succession (i.e. disturbance control) occurs during approximately 30 days following spates in desert streams (40); thereafter biotic controls predominate. Comparison of years that differ in flood timing but that have similar total annual runoff revealed dramatic shifts in the balance of disturbance controlled vs biotically controlled states (50). Similar inferences could be made for many other streams in which disturbance and biotic controls alternate (see 37, 58, 59, 121, 123).

As streams dry, mobile organisms are concentrated and biotic interactions surely intensify (148, 153). These interactions or physiological stresses may

differentially affect species or size classes of organisms (e.g. 130). Competitive interactions are normally important only in summer in a California stream, but they persisted year round during a drought year when caddisfly densities were not reduced by the usual high winter flows (37). Year-to-year variation in competition was attributed in another study to variation in timing and intensity of winter floods (58).

Reduced flows can concentrate pollutants (9, 78, 157). For this reason, assessment of the likelihood of extreme low flows in streams influenced by pollutant discharges is a high priority (see also 45, 99). Chessman & Robinson (21), for example, reported poor water quality associated with record low flows. These water quality changes included reduced oxygen concentration, a likely consequence of reduced or intermittent flow even in unimpacted streams (149).

During floods, the hydrologic linkage between streams and hyporheic or groundwater zones is accentuated (88). As surface flow declines during drying, the hyporheic zone assumes more importance in its effects on surface water chemistry and biota (149), including input of low-oxygen and high-nutrient water (161). Loss of hydrologic connection between these subsystems (149), however, can result in significant stresses to biota in underground habitats.

Water Renewal and Chemical Inputs to Lakes

Allochthonous inputs to lakes depend on the timing, frequency, and magnitude of runoff events (72, 163). These effects are amplified where human activities have disturbed soils or vegetation (108). Increases in precipitation and its variability would increase nutrient inputs to lakes, contributing to eutrophication (127, 163).

Conversely, increases in water renewal rate can decrease concentrations of nutrients and contaminants derived from point sources or sediments (62, 127, 136). The water renewal rate scales the rate of ecosystem response to chemical inputs (127). In lakes of western Ontario during 1969–1989, decreased precipitation and increased evaporation decreased the water renewal rate, increasing concentrations of chemicals in both lakes and streams (138). Increased nutrient concentrations lead to increases in primary production and reductions in hypolimnetic oxygen, potentially endangering some fish stocks (138). In softwater lakes susceptible to acidification by acid deposition, drought can cause both pH and acid neutralizing capacity to decline (166). Drought reduces groundwater inputs rich in acid neutralizing chemicals (166). Concentrations of contaminants such as organochlorine compounds and heavy metals can also be expected to increase as the water renewal rate declines, possibly increasing accumulation in the aquatic food chain and ingestion of the chemicals by wildlife and humans (126, 154). Theory predicts that all of

these trends would be reversed in lakes that undergo increases in water renewal rate (127). Fluctuations in water renewal rate caused by global change therefore translate into fluctuations in primary production and cycling of nutrients and contaminants.

Variability in Fish Recruitment

If climate becomes more variable (139), local populations will more often experience extreme events such as those that produce lethal conditions for short periods of time. Depletion of adult stocks by short-lived stress can ramify throughout the trophic network for extended periods. Most vulnerable are the populations of coldwater fishes in habitats near the low-latitude limits of their range. For example, a summerkill of the pelagic, planktivorous lake herring (*Coregonus artedii*) in Lake Mendota, Wisconsin, occurred during a period of high temperatures and low wind velocities. As a result, total predation on zooplankton was reduced by nearly 50%, large *Daphnia* increased, and intensified grazing by *Daphnia* caused substantial reduction in phytoplankton (72). Analogous examples can be drawn from river systems where effects of variable temperatures and flows affect the fishes and alter the network of interactions regulating both herbivores and the filamentous algae they consume (121, 123). Similarly, the synchrony of predator and prey life histories in reservoirs is affected by rates of warming (30).

The relative strengths of year classes in many fishes correlate with weather conditions during the spawning and early life history stages (158). Relatively modest changes in the weather can dramatically increase variability in recruitment (27). A cascade of food web effects can follow from the removal or enhancement of fishes whose effects as predators cause variability in the trophic structure, productivity, and water quality of lakes (17–19, 30, 53).

One of the immediate interactions between the public and the effects of global change will occur in recreational and commercial fisheries. Fish populations are notoriously variable, and fisheries yields are often heavily dependent on the occasional strong year class (117). Because survival during early life history stages is a key to recruitment success (158, 174), the increased variability in critical habitat will increase variability in the success of individual cohorts. The social and economic effects will be immediately apparent and, if history is a guide, the subject of policy to remedy the wrongs of nature (46).

ECOSYSTEM METABOLISM

Stream Metabolism

Temperature directly affects rate of photosynthesis and respiration in streams, but it does so differentially: as temperature rises, respiration tends to increase

faster than primary production, and the P/R ratio falls (16), assuming ample organic substrates are present. Other factors being equal, a drop in P/R renders streams more of a sink than a source for organic matter and will decrease export downstream (16).

In addition to production and respiration, stream ecosystem metabolism depends on import, export, and intrasystem storage pools of organic matter (43). Litter input from the riparian zone may change in quantity and quality as temperature rises (99). Dissolved organic carbon entering streams via interflow may decrease as soil respiration rises (99). Rate of decomposition of organic matter in situ may change as well if shredder (leaf-consuming) macroinvertebrate populations are enhanced, or it may decline as a result of increased temperature. Changes in inputs of wood affect the capacity of streams to retain leaves and fine particulate organic matter, altering respiration associated with organic substrates (67, 144).

Floods affect primary production in some streams (6, 41) and may flush significant amounts of detritus downstream (57). In some cases, floods remove entire ecosystem components. Grimm & Fisher (51) showed that the hyporheic zone can be an important contributor to ecosystem respiration, reducing the P/R ratio in proportion to hyporheic volume. Storm events can alter hyporheic volume by export of sand and shift the P/R ratio upward (39, 42). In this manner, altered hydrology due to changing climate can convert a system that is largely a processor of organic matter ($P/R < 1$) to one that is primarily an exporter ($P/R > 1$).

Heterotrophic streams of coniferous forests are equally sensitive to the hydrologic regime and are far less efficient during wet than dry years (26). Spiralling distance, an index of processing efficiency (109), also increases with discharge. This affects spiralling not only of organic matter (104, 110) but also of inorganic substances, because organic substrates are especially active in nutrient retention (106).

Lake Productivity

In temperate lakes, global warming is expected to increase the heat content and the durations of the ice-free and stratified seasons (92). Analyses across a latitude gradient from the equator to 75° N showed that primary production was directly related to mean air temperature and length of the growing season (14). Trophic transfer efficiencies across the same gradient suggest that secondary and tertiary production are also related inversely to latitude (14). The seasonal variability of primary production increased with latitude across a similar gradient (95). An empirical analysis of responses of aquatic systems to temperature change suggested that global warming would lead to a general increase in lake productivity at all trophic levels (128). Increased production will exacerbate hypolimnetic oxygen depletion in productive lakes (8).

Changes in cloud cover are among the critical uncertainties in projections of future climate (33). Increased frequency of cloudy days has significant implications for deep-dwelling phytoplankton that account for substantial primary production in oligotrophic and mesotrophic lakes during summer stratification (105, 146). Deep algal layers exploit high rates of nutrient supply by eddy diffusion from the hypolimnion, but these algae can be limited by grazers, low temperatures, or low light (146). If global warming reduces vertical mixing (92), the metalimnion will become a more important habitat for phytoplankton. Increased cloud cover may reduce surface irradiance to the point that algae cannot maintain a positive carbon balance in deep, nutrient rich water. If photosynthesis were restricted to nutrient poor surface waters, primary production would decrease by factors of two to three (105, 146).

FEEDBACKS

Greenhouse Gases

Wetlands contribute 22% of the annual methane flux to the atmosphere (56). These ecosystems, which achieve their greatest extent in polar and tropical belts (56), are active sites because of waterlogged soils and anoxia (required for the anaerobic process of methanogenesis). Most of the methane production by wetlands occurs above 40°N latitude (137), where global warming may be greatest (140). Rates of methanogenesis are directly related to temperature (56). Increased temperature will thaw permafrost, which may promote both areal expansion of wetlands and drying of extant ones (134). The balance of these processes will determine whether the northern wetland contribution to increasing atmospheric methane increases or decreases.

Extensive wetlands are connected to large tropical rivers through seasonal cycles of flood and drought (167). Substantial methane derives from these systems (32, 137). Disruptions of the hydrologic cycle could profoundly influence seasonal patterns of inundation and thereby affect methanogenesis in tropical and subtropical wetlands (25, 99).

Carbon Storage

One of the largest uncertainties in global climate feedbacks concerns alteration of carbon storage. Thawing of permafrost in polar regions could have significant effects on carbon storage (137). Aquatic systems are particularly important in fluxes of peat-derived carbon (116), which is oxidized in aquatic ecosystems (75) and exported from arctic rivers (112).

Regional Climate

Large freshwater ecosystems moderate regional climates through effects on the hydrologic cycle and on ocean circulation. Water evaporated from

extensive tropical wetlands falls as rain over a much wider area (e.g. all of South America plus the southwestern Atlantic Ocean for Amazon basin evaporation; 96); drying or expansion of these areas will thus influence climate over large regions. Changes in discharge from the world's large rivers may alter ocean circulation and thus influence world climate (12, 13). Melack (96) summarized paleoceanographic evidence for a major climatic impact on North Atlantic regions of cool, glacial meltwater discharged by the Mississippi River into the Gulf of Mexico. North-flowing rivers like the MacKenzie can move enough heat into arctic regions to moderate regional climate (137). Glacier melting due to global warming, in addition to having catastrophic effects on stream ecosystems (112), may also contribute to changes in oceanic circulation and thus climate.

Anthropogenic Effects

Abundant freshwaters attract human settlement, activating feedbacks that alter ecosystems and regional climate. In most developed nations, extensive draining and filling of wetlands (108) has implications for trace gas budgets. In North America, trapping reduced beaver populations to near extinction, which affected the extent of waterlogged, anoxic soils over vast regions and potentially altered global methane flux (107). Simplification of river channels has reduced extent of floodplains and associated wetlands (10, 141) with unknown consequences for trace gas flux. Abuses of water supply create the need for water development, water treatment, desalinization, fertilizer use, health care, flow diversion, and ecosystem restoration, all of which require combustion of fossil fuels and release of greenhouse gases.

We can expect humans to redistribute freshwater as an adaptive response to global climate change (1, 137). The direct effects on aquatic resources and indirect effects on climate of such policies are largely unknown.

PRIORITIES

Freshwaters have been neglected in research planning for global change (1). Yet, freshwaters are critical for sustainability of ecosystems and society and are tightly coupled to climate and land use (38, 73). Although much of the literature of aquatic ecology is relevant to global change, little work has focused explicitly on the consequences of global change for freshwater ecosystems. It is time to correct these oversights. We will be surprised and disappointed if this review is not outdated in a few years.

Aquatic ecologists and global climatologists need to adjust their research to a common scale. Aquatic ecologists must reinvigorate research at landscape and watershed scales, breaching the walls that divide hydrology, wetland ecology, stream ecology, and limnology. We need mesoscale climate models

(139) capable of translating global climate scenarios to ecosystem scales and accommodating the effects of freshwaters on climate. Models that account for effects of precipitation, plant responses to CO₂, vegetation change, and soil change on runoff are also needed.

To date, the most severe stresses on freshwater ecosystems have come from watershed modifications and use and contamination of aquatic resources by humans. Climate change adds to and interacts with substantial ongoing anthropogenic changes in ecosystems. It is impossible to study the effects of climate change in isolation from the effects of land use change and direct human use of freshwater resources. Humans are an interactive component of aquatic ecosystems, responding to changes in freshwater resources and thereby causing further change. That powerful feedback must be incorporated in our views of ecosystem dynamics.

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