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State of the World's Freshwater Ecosystems: Physical, Chemical, and Biological Changes

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aquatic invasive species, climate change, ecosystem services, freshwater biogeochemistry, land-use change, natural capital

Abstract

Surface freshwaters—lakes, reservoirs, and rivers—are among the most extensively altered ecosystems on Earth. Transformations include changes in the morphology of rivers and lakes, hydrology, biogeochemistry of nutrients and toxic substances, ecosystem metabolism and the storage of carbon (C), loss of native species, expansion of invasive species, and disease emergence. Drivers are climate change, hydrologic flow modification, land-use change, chemical inputs, aquatic invasive species, and harvest. Drivers and responses interact, and their relationships must be disentangled to understand the causes and consequences of change as well as the correctives for adverse change in any given watershed. Beyond its importance in terms of drinking water, freshwater supports human well-being in many ways related to food and fiber production, hydration of other ecosystems used by humans, dilution and degradation of pollutants, and cultural values. A natural capital framework can be used to assess freshwater ecosystem services, competing uses for freshwaters, and the processes that underpin the long-term maintenance of freshwaters. Upper limits for human consumption of freshwaters have been proposed, and consumptive use may approach these limits by the mid-century.

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INTRODUCTION

An essential resource for human life, freshwater has no substitutes. Freshwater is also essential for many natural systems that support human well-being. Expanding human activity has extensively altered the planet's freshwaters, with modifications impacting the physical, chemical, and biological features of aquatic systems. In this review, we first describe freshwaters with a focus on lakes, reservoirs, and rivers. We then address the major drivers of change and the responses in terms of freshwaters to these drivers. These changes have many implications for human well-being that we discuss in a natural capital framework. We also consider the idea that human well-being can be maintained only if human uses of freshwater stay within certain boundaries. Most freshwaters have been altered in multiple ways, and changes in any particular freshwater system usually have multiple causes. These interactions are noted throughout the paper.

This review emphasizes large-scale physical, chemical, and biological changes in freshwaters and their associated drivers, including human factors that affect freshwaters, but does not address institutional aspects of water management. Water management is a vast subject embracing such diverse topics as water markets (1), political conflict over water (2), connections between water and social development (3), and social aspects of drought (4). This review focuses on the natural science aspects of freshwater resources while recognizing that a comprehensive approach to sustaining freshwater resources will go beyond this scope to address aspects of engineering and policy as well (5).

EARTH'S SURFACE FRESHWATERS

All freely available water (liquid, solid, or gas) in the atmosphere, on Earth's surface, and in Earth's crust to a depth of 2 km, a water volume of approximately 1.386×10^6 km^3, compose the hydrosphere (6). Only 2.5% of this water is freshwater, of which 68.7% is perennially frozen and 29.9% is groundwater. Only 0.26% of liquid freshwater on Earth is in lakes, reservoirs, and rivers, which are the focus of this article. We do not consider freshwater wetland habitats and consider groundwater only with respect to its interactions with surface freshwater. For recent reviews on groundwater and wetlands, see References 7 and 8, respectively.

Surface freshwaters are in rapid flux compared with other pools of liquid water on Earth. The turnover time is approximately 160 years for lake and reservoir water and 16 days for rivers (9), compared with 1,500 years for groundwater and 2,500 years for the oceans (6). Globally, lakes cover approximately 2.7×10^6 km^2 with a volume of approximately 175×10^3 km^3. The role of small lakes and impoundments has been poorly recognized and could add to these area and volume estimates (10, 11).

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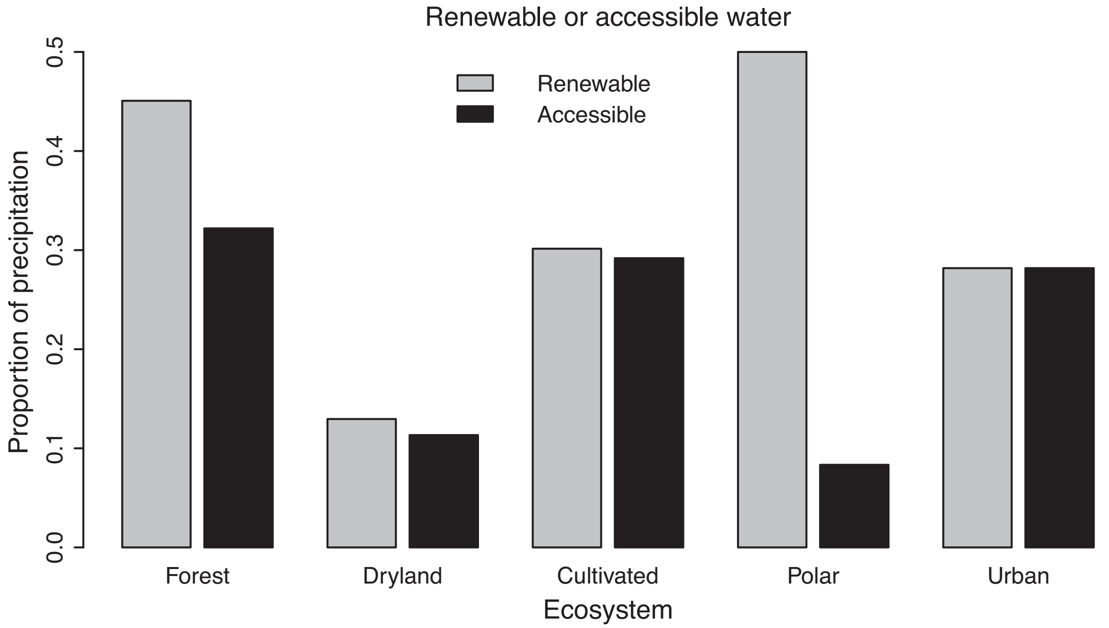

Figure 1

Renewable and accessible freshwater as a proportion of precipitation for selected ecosystem types (Reference 16, chapter 7, table 7.2).

Water withdrawals by humans are used for agriculture (76% or 3.81×10^3 km^3 year^{-1}), in various industries (15% or 0.77×10^3 km^3 year^{-1}), and within domestic households (9% or 0.38×10^3 km^3 year^{-1}) (9). However, most of the water withdrawn for agriculture is consumed (transferred to the atmosphere as water vapor), whereas most of the water withdrawn for industrial and domestic use is returned to surface flows.

Surface freshwaters supply approximately three-quarters of the water withdrawn for human use. Ecosystems differ in their capacities to generate renewable water [i.e., water that is not lost immediately to evapotranspiration (ET)] and accessible water that is available for human use (**Figure 1**). Forests receive roughly half of the global precipitation over land and contribute approximately half of the global renewable freshwater. Drylands are larger in area than are forests and receive appoximately the same annual volume of precipitation, but they generate far less runoff.

WHY ARE FRESHWATERS CHANGING?

Freshwaters are always in flux, but current changes are novel and exceptionally large. Major drivers of change are climate, human alteration of water flows, land-use and cover alterations, chemical inputs, aquatic invasive species, and human harvest including aquaculture (**Figure 2**).

Climate Change

Climate change directly affects freshwaters as a result of increased temperatures, greater variability of precipitation among locations and over time, and rising sea levels. Several observed climate trends are significant for freshwaters: increased precipitation over land north of 30°N since 1901, decreased precipitation over land between 10°S and 30°N after the 1970s, and increasing intensity of precipitation in some regions and droughts in others (12). In turn,

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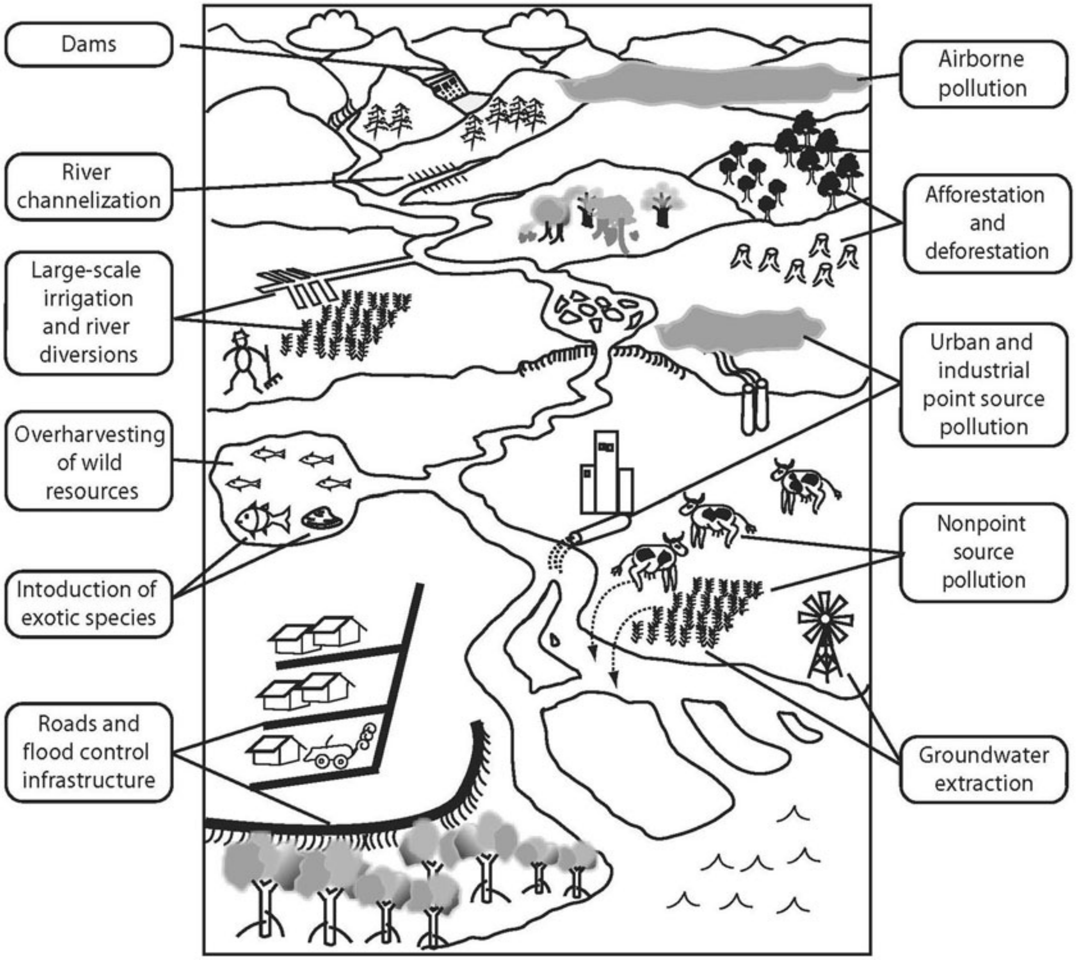

Figure 2

Many interacting drivers, and interacting responses, affect the condition of freshwaters on any particular landscape. Reprinted from Carpenter & Biggs (5) and used by kind permission from Springer Science+Business Media B.V.

changing precipitation and temperature are associated with decreased extent of glaciers and duration of ice cover and snowpack; increased thawing of permafrost; and regional changes in ET, lake levels, and streamflow (12). Modeled future trends relevant to freshwaters are warming temperatures, more variable precipitation, and rising sea level (12).

Warmer water temperatures decrease the amount of oxygen that can be dissolved in surface waters and thereby decrease the availability of oxygen for respiration by organisms and processing of organic matter and pollutants. Warming also decreases thermal niche and habitat availability for aquatic organisms that require cold water, such as galaxid or salmonid fishes (13, 14). At higher latitudes and elevations, warming decreases the duration of the ice season and melts glaciers and permafrost, thereby changing the seasonality, magnitude, and sources of hydrologic flows. Greater variability of precipitation, over time and among locations, adds to the variability of hydrologic inputs to lakes and streams.

Rising sea levels increase the extent of saltwater penetration into tidal rivers. The effects

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of rising sea levels on lowland rivers are exacerbated by decreased buildup of sediment due to siltation in impoundments upstream and decreased runoff due to irrigation (15).

Hydrologic Change

Freshwater is distributed unevenly in space and time. To counter this heterogeneity, water resource development and management activities attempt to make water accessible for all human needs at all times. The tendency to store or divert water when it is present in excess or procure it when it is lacking is global in scope and is accomplished by irrigation, drainage, groundwater pumping, impoundment, levee construction, and interbasin transfer. Because of these manipulations and climate change, the world's hydrologic cycle is changing with notable, widespread alterations in the hydrologic regimes of the world's freshwater ecosystems (16).

Water scarcity is the single largest global challenge facing water resource management. Over large continental areas, human demand for freshwater approaches or exceeds current supply, and approximately 2.4 billion people live in water-stressed environments (9). Provisioning of water to water-stressed regions for human needs is routinely done at the expense of ecosystems, both aquatic and terrestrial (16–18). Conventional responses to water scarcity are withdrawals of deep groundwater and surface water storage. In many regions in North Africa, the Middle East, South and Central Asia, western North America, and Australia, groundwater withdrawals exceed recharge, so groundwater pools are declining (7) and groundwater-dependent ecosystems are threatened (19).

Surface water storage in ponds and reservoirs is the most common strategy for ensuring a reliable water supply, especially because dam building can also provide other economic benefits such as electricity generation and flood control (20). Although reservoirs may provide a reliable source of water to meet human demand, they have transformative effects on rivers, including fragmentation, flow regime modification, enhanced evaporative loss, and increased water residence times, in addition to wide-ranging consequences impacting aquatic communities. Dam construction has shifted from developed to developing regions, especially China, India, and South America in the past 20 years (21). Thus hydrologic changes to rivers are continuing to increase both in spatial extent and degree of alteration. Our current understanding of the effects of dams on freshwater environments is strongly biased toward the impacts of large structures, yet small dams (less than 15 m) outnumber large dams by perhaps tenfold. The number of small ponds and impoundments has increased over the past two decades, particularly in arid regions. Over the past 50 years, increases have been 60% in India (10) and 900% in some areas of Africa (22). This trend will likely continue, and the poorly appreciated but significant roles of these diminutive but numerous systems will also expand (10).

Transfer of water among different drainage basins is often expensive, yet it is common in places where water can be moved from snowy mountainous areas to low-lying arid regions (23). Large metropolitan areas in the western United States (e.g., Los Angeles, California, and Phoenix, Arizona) rely on such transfers, delivering water from the Sierra Nevada and Rocky Mountains via an extensive series of canals and aqueducts. More elaborate plans have been proposed, ranging from towing icebergs to large-scale desalinization operations (24). Such unconventional strategies will likely continue and expand over the next several decades, and they will affect freshwater environments in ways that are only beginning to be recognized and quantified.

Land-Use Change

Land-use change, the conversion of natural lands to human use or the alteration of management practices on human-dominated lands, is a major driver of ecosystem change (25). Land-use change affects freshwater flows by changing the fates of precipitation among ET, runoff, and groundwater recharge. Conversion of natural

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ecosystems to cropland or urban uses generally increases runoff as well as flood frequency and intensity, and it decreases ET and groundwater recharge (16). Invasion by terrestrial plant species (such as *Tamarix* in the western United States) with high ET rates has the opposite effect of decreasing runoff to surface waters (26).

Agricultural land use for pasture or cropland occupies 37% of terrestrial land area (27). Among human activities, agriculture uses the greatest amount of freshwater (28), emits the highest levels of greenhouse gases into the atmosphere (29–31), and contributes the most to soil erosion and runoff of nutrients to freshwaters (32, 33). Agriculture accounts for 52% and 84% of global human emissions of the greenhouse gases CH_4 and N_2O, respectively (31). Intensive agriculture employs high fossil fuel inputs and reduces soil storage of carbon (C), although the C balance of agriculture varies considerably among tillage practices (30, 31, 34). Croplands, high-density livestock operations, and urban lands add silt, nutrients, and toxic pollutants to surface waters (32).

Substantial expansion of agricultural production and water use will be needed in coming decades to meet the demand for food and perhaps biofuels (28, 35). Alternative agricultural practices have different implications for intensification or extensification of land use, magnitude of water use, nutrient emission, and greenhouse gas emission (31, 34, 36, 37). Future trends in agricultural production will affect freshwater sources directly through water withdrawals, nutrient emissions, and effects on riparian ecosystems as well as indirectly through climate change.

Although much smaller in extent than agriculture, Earth's urban areas are growing rapidly. Food and fiber production that supports urban populations requires substantial flows of water (38). Although groundwater accounts for only one-quarter of the world's water withdrawals, it makes up approximately half the world's potable water and provides drinking water for many of the world's cities (7).

Changing Chemical Inputs

The history of pollution of freshwater is perhaps as long as that of water resource development. Both are consequences of human population expansion. Hydrology and biogeochemistry interact in many ways (39), and water management and water quality impacts show strong spatial correlation (40). The increase in chemical inputs to freshwaters is a result of diffuse inputs from landscapes dominated by human use (agricultural and urban areas) and atmospheric sources as well as from direct discharges of waste waters from sources such as mining, industry, or municipal sewage. The diverse array of anthropogenic chemicals added to freshwaters includes organic compounds, heavy metals, acids, and alkalis, some of which are toxic to aquatic organisms or humans.

The role of agriculture in providing diffuse (nonpoint-source) inputs of nutrients (nitrogen, N, and phosphorus, P) and other chemicals to aquatic systems is well established (32). Urban areas are also becoming significant sources of chemicals to freshwater environments. Limited investment in water supply and treatment infrastructure and rapid urban population growth—particularly in developing countries—interact to create water-quantity and -quality problems (41). When present, wastewater treatment mitigates nutrient- and organic-matter loading to freshwaters. Treatment of point-source effluents is far more common in economically developed nations, as less than 20% of the population was connected to sewer systems in Africa and southern Asia in 2000 (16). Even in Europe, estimates of the percent of the population connected to wastewater treatment facilities range from 35% to 80% among different countries (42). Furthermore, much of the water infrastructure in developed countries such as the United States is now aged and prone to leakage and failure (43). Urban areas also contribute surface runoff enriched in metals or organic compounds as well as atmospheric inputs of automobile and industrial emissions that can eventually move into aquatic systems. Southeast Asia, a region of rapid economic development with limited environmental regulations, is now a major source of these pollutants.

Aquatic Invasive Species

Humans intentionally and accidentally transport vast numbers of live organisms outside of their native range. Only a fraction of introduced species establish self-sustaining populations, and a fraction of those become a nuisance, spread, and cause harm (44). Nevertheless, species invasion is now recognized as an important driver of global environmental change (45, 46), and freshwater ecosystems are especially vulnerable to species invasion and its effects (47).

The scope of biological invasions in freshwater ecosystems is enormous. Biomass and species diversity of many freshwater ecosystems (e.g., the Laurentian Great Lakes) and even entire faunas (Mediterranean fishes) are currently dominated by nonnative species (48, 49). There are >180 nonnative species in the Laurentian Great Lakes, and the rate of new invasions is accelerating (48). The Nonindigenous Aquatic Species Database (Biological Resources Division, U.S. Geological Survey, **http://nas.er.usgs.gov/**) reports 1,147 freshwater-introduced species (and 77 additional species inhabiting brackish water) in the United States. Approximately 40% of these are native to the United States but now occur beyond their native range. Although many aquatic invasive species were accidentally introduced, others have been introduced deliberately—stocked for aquaculture, pest control, aesthetic reasons, and recreational fisheries.

Aquatic invasive species have altered the physical, chemical, and ecological conditions of freshwater ecosystems, and they are one of the two most important factors threatening aquatic ecosystems and biodiversity (50). Ross (51) reported that in 77% of cases the introduction of nonnative fish corresponded with the reduction or elimination of native fishes. Introductions of predatory sport fishes are the major threat to endemic fishes in the western United States (52). Introducing the Nile perch to Lake Victoria caused the extinction of perhaps hundreds of native haplochromine cichlids (53). Invasive species were a central factor in the food-web disruption of the Laurentian Great Lakes (see The Laurentian Great Lakes, sidebar below). Introduction of opossum shrimp (*Mysis relicta*) to Flathead Lake, Montana, disrupted the food web and affected the plankton, fish, bear, and eagle communities (54). Invasion by zebra mussels is accelerating extinction rates of native Unionid mussels (55). The spread of nonnative freshwater species is a key contributor to the ongoing biotic homogenization of freshwater ecosystems occurring at the global level (56).

The implications of aquatic invasive species for ecosystem services are not well known.

THE LAURENTIAN GREAT LAKES

The history of the Laurentian Great Lakes is that of a progression of successive anthropogenic impacts spanning nearly two centuries. The nineteenth century saw the wholesale loss of forests, lake-shoreline alteration, wetland destruction, and dam building on tributaries. It was also a period of intense fishery exploitation. By the mid-1800s, fisheries had already overexploited the fish populations, and declines and collapses of fish stocks continued into the mid-twentieth century. Invasive sea lamprey invasion further decimated fisheries from the 1940s onward. Concern over cultural eutrophication as well as the bioaccumulation of toxic substances peaked in the 1960s and 1970s. Zebra mussel invasion in the 1980s focused attention on the multitude of nonnative species (>180 species) in the Laurentian Great Lakes, both intentional and accidental in origin. More recent concerns include changing lake levels and the system-wide effects of climate change (158).

Over this period, some impacts have abated. Nutrient loading and levels of some contaminants have declined, and sea lamprey populations have been successfully controlled. Nevertheless, the ecosystems have been fundamentally transformed. Much of the native biota has been lost, including a suite of endemic deepwater coregonids. These have been replaced by a suite of nonnative fishes such as rainbow smelt, alewife, and stocked Pacific salmonids. Food webs composed of nonnative species now support valuable recreational fisheries and pose some management challenges owing to competing human goals for these ecosystems.

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Awareness of the need for valuation studies is growing (57). Examples of economic impacts include water hyacinth effects on navigation in Lake Victoria and other tropical African lakes (58), zebra mussel fouling of water systems (59), and *Tamarix* reduction of riparian water availability in the southwestern United States (26). Annual economic damages from each of the above examples are in the US$$10^7$ to 10^8 range.

Perhaps the most troubling feature of aquatic invasive species is their irreversibility once established. In contrast with chemical pollutants, which can diminish over time, invasive species often exhibit accelerated rates of spread following initial establishment. Preventing the introduction of new species and containing existing species are central to managing their impacts, and some progress has been made in regulating key vectors such as ballast water and recreational boaters (60). Quantifying the economic impacts and consequences for ecosystem services is a critical step to improve management (57).

Harvest

Fish production is a valuable provisioning ecosystem service generated by freshwater ecosystems. Aquatic resources, particularly fish and invertebrates, but also birds, reptiles, and amphibians, are harvested for local subsistence, commercial use, recreational use, or pet trade. Recent concern about the "global fisheries crisis" has focused almost exclusively on marine ecosystems, although the impacts of recreational fishing and overfishing of inland waters have garnered increased attention (61, 62).

Declining fish stocks and increasing demand for fish have led to sharp increases in aquaculture production in recent decades (63). Freshwater ecosystems constitute nearly half of the global aquaculture production, estimated at 68 million metric tons (64). This inland aquaculture boom has led to increases in the harvesting of wild fish for feed, water pollution, altered hydrologic flows, and the accidental release of nonnative species (63).

The annual commercial and subsistence fish harvest from inland waters, excluding aquaculture and recreational fishing, has increased approximately fourfold since 1950 and is currently estimated at 10 million metric tons (64), with Asia (65%) and Africa (24%) dominating (62). In contrast, annual harvests from marine fisheries are approximately 80 million metric tons (64). Fisheries that target high-value species provide many examples of harvesting that have caused sharp reductions in catch, abundance, and body size [e.g., Nile perch in Lake Victoria, lake trout in the Laurentian Great Lakes (62)]. For multispecies fisheries, more common in tropical waters, the limited data suggest that intensive harvesting has often led to depletion of large body-sized fishes, causing a shift toward the harvesting of smaller species and younger fish (62, 65).

In contrast with commercial fisheries, inland recreational fisheries are poorly tracked, although there is growing interest in their potential effects on aquatic resources (66). Recreational fishing is a multibillion-dollar industry, with diverse subsectors and rapid growth driven by affluent anglers in rich countries. Post et al. (61) documented the widespread decline of recreational fisheries adjacent to population centers in Canada, demonstrating that recreational fisheries often show depensatory dynamics and that recreational fishing can collapse freshwater fisheries. Fishery declines are often masked and exacerbated by fish stocking (67). These recent findings challenge the conventional belief that recreational fisheries tend to be self-regulating and less vulnerable to collapse than commercial fisheries.

An assessment of inland fisheries by the Food and Agriculture Organization (68) concluded that many inland fisheries were overfished and degraded by pollution and habitat loss. Fisheries often target large and high-value apex predators that have life-history traits that make them especially vulnerable to overexploitation. Following overexploitation, target species are often replaced by smaller, faster-growing, or less desirable species, which subsequently become the new target

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of fisheries. In addition to impacting target species directly, fishery overharvest can produce ecosystem-level effects. Fishes can play an important role in regulating ecosystem processes via nutrient excretion, bioturbation, and mass migration (69). The decline of apex predators produces trophic cascades that can extend to the base of the food web (70).

The harvest of wild freshwater fishes and aquaculture make up an essential and rapidly growing source of protein for the world's populations (63). This situation necessitates balancing current demand with the protection of freshwater ecosystems to preserve future harvest potential and other ecosystem services. Degraded fisheries are often difficult to rebuild, and the available management tools (stocking of hatchery fish) can exacerbate the problem. Recreational and subsistence harvests are widely distributed on the landscape, not well quantified, and difficult to regulate. Perhaps most importantly, overharvest often acts synergistically with other human impacts.

HOW ARE FRESHWATERS CHANGING?

Multiple aspects of freshwaters are affected by the drivers described above, and frequently, there are complex interactions among the resulting responses. We focus here on changes in physical features, biogeochemistry, ecosystem metabolism, biotic transformations, and disease.

Physical Transformations

Dam construction is perhaps the most conspicuous anthropogenic modifier of riverine systems and their hydrology. Natural flow regimes and hydrologic connectivity of approximately 60% of the world's large river basins are now affected by dams (20). Dams often stabilize discharge patterns by reducing the magnitude and duration of high flows and by supplementing low flows (71). The net global effect of impoundments has been to reduce the average annual discharge to the ocean as a result of storage, evaporation, and withdrawal, leading in some cases to complete desiccation of the aquatic ecosystem (72). Other water management practices such as levee building and ditching generally increase baseflow and flood magnitudes by rapidly routing water to channels and confining flow to these conduits (73, 74), whereas interbasin transfers increase flows in one region at the expense of discharge in another.

The hydrology of many freshwater systems is profoundly affected by agriculture. Over the past three centuries, the expansion of pasture and nonirrigated croplands has increased streamflow approximately tenfold by reducing ET. Conversely, the expansion of irrigation-based farming is associated with declining streamflow (75). At the global scale, the combined effects of agricultural water withdrawals and reservoirs have been estimated at a modest 3.5% reduction in the long-term average riverine discharge to the ocean. However, among regions, this decline varies substantially, from no measurable change (e.g., in parts of Southeast Asia) to an average annual discharge decrease of 35% or more (representing 16% of the global land area excluding Greenland and Antarctica) (76).

Finally, the hydrologic consequences of land use and reservoir construction manifest within the context of changing climate conditions. Analyses of long-term discharge records have linked regional climate dynamics to a variety of river-flow trends, including both increased and decreased annual discharge and shifts in seasonal flow magnitudes (12). Climate-driven hydrologic changes have also been accompanied by temperature warming and decreased ice duration (77). Warming is most rapid in the mid- and high latitudes of the Northern Hemisphere, and surface temperatures in several lakes are increasing faster than regional air temperatures (78). Surprisingly, some of the best examples of lake warming are provided by the world's largest lakes—Superior (79), Tanganyika (80), and Baikal (81)—a puzzling trend because these very large masses of water would be expected to warm slowly. Warming trends and previous ice-out dates (and in some cases, ice-free winters) increase the stability of thermal stratification, thus limiting the upwelling of nutrient-rich waters and primary productivity (80) and modifying planktonic population and community dynamics (81, 82).

FRESHWATER CONSERVATION PRIORITIES

Certain species groups and ecosystem types are particularly sensitive or vulnerable to anthropogenic impacts and, thus, are particularly threatened. Below we highlight several examples:

Diadromous fishes: Diadromous fishes migrate between freshwater and marine systems to complete their life cycle. A recent assessment described dramatic and widespread declines in the diadromous fish stocks of the North Atlantic (159). Thirty-two of the 35 stocks showed overall declines, and 68% (24/35) of the stocks showed abundance declines of 90% or more. All species underwent population extirpations. A suite of threats—dams, alteration of flow regimes, overfishing, invasives, pollution, and climate change—are responsible for the declines (159).

Megafishes: A large number of the world's largest freshwater fishes, the megafishes, are threatened with extinction (**http://megafishes.org/**). These species often inhabit large river ecosystems, are highly migratory, and inhabit large geographic ranges—characteristics that make them particularly vulnerable to overharvest, habitat destruction, pollution, dams, and altered flow regimes. These impacts all threaten the extinction of these species. Accordingly, the plight of the megafishes also serves as an indicator of the threats faced by many of the world's large river ecosystems.

Floodplains: Floodplains are among the most dynamic, productive, and diverse ecosystems on Earth. In developed regions, most rivers have been channeled and leveed, floodplains have been converted for agricultural and urban use, and natural flow regimes have been altered through river regulation. This combination has led to widespread elimination of floodplain function and the associated floodplain aquatic ecosystems, both of which are defined by lateral connectivity with the river. Though floodplains cover ~1.5% of land surface, they provide >25% of all terrestrial ecosystem services including nutrient removal, flood regulation, water supply, and fishery production. The tremendous value of these ecosystem services highlights the need to protect and restore floodplain ecosystems. Yet, floodplains ecosystems are being lost at a rapid rate, particularly in Asia and parts of the developing world (86).

Changes to the physical structure and geomorphic processes of freshwater environments are closely linked to hydrologic modifications, and they similarly vary within and among regions. For example, riverine transport of sediment has both increased (owing to human land use, particularly agriculture) and decreased (owing to retention by reservoirs) (83). Changes in flow and sediment regimes cause a variety of channel form adjustments (e.g., incision, bed armoring, siltation, bank failures), which, in turn, often trigger management responses intended to stabilize channels (e.g., hardening of stream banks by addition of large boulders). Anthropogenic modifications can occur in lakes as well: Littoral habitats are modified by shoreline structures; armoring of banks; and removal of riparian vegetation, coarse woody habitat, and aquatic plants. Such alterations generally decrease fish abundance, biomass, and diversity (84).

Other manipulations of river channels include dredging and installation of hydraulic devices to maintain navigation channels and boat access, channel redesigns (e.g., ditching, channel relocation), and wood removal associated with deforestation and/or human development (85). The most extreme form of modification involves elimination of specific habitats (e.g., disconnection of floodplains via levee construction) or of the entire ecosystem, and such alterations are common. Floodplains, which are heavily used by humans because of abundant ecosystem services (see the Freshwater Conservation Priorities sidebar), are frequently modified. Floodplain loss can be extensive; for example, as much as 90% of floodplain habitats have been eliminated from European rivers (86).

Expansion of urban areas is associated with engineered adjustments in channel form, followed by conversion to canals or ditches (87), and ultimately burial (88). Headwater streams in the United States have been buried under overburden materials from mountaintop mining (89). Such physical changes have substantial consequences for structure and, more broadly, biodiversity of aquatic communities.

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Biogeochemistry and Nutrients

The capacity of freshwater ecosystems to transform or retain added solutes is a function of inputs, hydrology, and biogeochemical processing. As noted above, inputs and hydrology are changing. Biogeochemical processing rates are also subject to change as a result of altered temperature regimes, chemical composition, and biota. A shift in any one driver is unlikely to affect just one chemical constituent alone, and similarly, a change in one individual chemical typically reflects multiple and often interacting causes that vary geographically. Modification of any one chemical can trigger a cascade of responses in other chemicals. Here we provide select examples of ongoing, large-scale changes in the biogeochemistry of freshwater systems.

Freshwaters exhibit geographically extensive changes in concentrations of key nutrients (N and P), inorganic and organic C, sulfate (SO_4), total dissolved salts, and micropollutants. Nutrient-enriched runoff from agriculture and urban land is a major cause of eutrophication, i.e., the overenrichment of aquatic ecosystems with nutrients or organic matter, leading to harmful blooms of algae, deoxygenation, loss of economically valuable species, and human health problems (32, 90). Seitzinger et al. (91) estimated that global riverine loads of N and P increased by approximately 30% between 1970 and 2000. Although riverine loads increased on all continents, the greatest increases and largest total loads occured in southern Asia. Whereas riverine fluxes of inorganic P declined in North America and Europe over this 30-year period, they increased in Africa, South America, Oceania, and South Asia (91). Organic C pools and fluxes are also changing, as soil disruption, altered plant cover, use of organic fertilizers, and effluent discharges are influencing organic C quantity and quality in aquatic systems (92).

Chemicals transferred to aquatic environments via the atmosphere affect large regions and include SO_4, nitrate (NO_3), and contaminants such as mercury. SO_4 emissions from coal burning and industrial activities date from the start of the Industrial Revolution, and aquatic consequences became apparent during the 1960s and 1970s (93). Policies that curtailed emissions in Europe and North America prompted a decline in SO_4 concentrations and the recovery of pH in many lakes and rivers (94, 95). However, both biotic and chemical recovery has been delayed or incomplete in some affected regions (96, 97). Three additional chapters to the acid rain story are now emerging. First, long-term inputs of acid and SO_4-rich precipitation has triggered a cascade of other chemical trends in many acid-sensitive freshwaters that are now becoming apparent. These include declines in base cations (98) and increases in dissolved organic carbon (DOC) (99). Second, rather than diminishing as a global problem, acid rain and acidification have moved from North America and Europe to other continents. Acid rain is now a notable environmental issue in China (100) and will likely emerge in other developing industrial areas. Third, even though SO_4 emissions have decreased in some parts of the world, emissions of oxidized nitrogen (NO_x), mercury, and other pollutants from fossil fuel combustion have not. Inputs of these constituents are increasing globally, especially

Large lakes: The 189 largest lakes (>500 km^2 each) contain ~68% of the planet's liquid surface freshwater (158). Large lakes are of tremendous importance to humans. They are magnets for human settlements and provide a wide range of services: transportation, fishing, power generation, waste disposal, irrigation, and domestic and industrial water supplies. Consequently, the world's large lakes have been disproportionately altered by human activity. Many are ancient and support large numbers of endemic species. The Great African Rift lakes (Victoria, Tanganyika, Malawi) are heavily impacted by rapid human population growth, deforestation, soil erosion, and overfishing. Invasion of water hyacinth and Nile perch in Lake Victoria have had major effects including the widespread decline of native fishes. In contrast, the world's oldest lake (25 million years old), Lake Baikal is remote, and although it has been affected by industrial and domestic pollution and overfishing, its water quality remains high, and none of the 1,500–2,000 endemic species have been lost (158).

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in southeast Asia, and are producing a range of ecological and, in the case of mercury, human health effects (101).

Mercury is just one example of a growing number of micropollutants that are becoming more concentrated and more widely distributed in freshwater environments. Products from industrial, farming, and mining activities entering surface waters range from heavy metals to organic compounds such as polychlorinated biphenyls and polycyclic aromatic hydrocarbons, and they can contribute to biological consequences such as direct toxicity, mutagenesis, developmental disruption, and reduced primary production in aquatic environments (102, 103). A few toxins, such as hydrocarbons and methyl mercury, are magnified in concentration as they move through food chains and therefore are most harmful to top predators including humans. Pesticides from agriculture, including genetically engineered insecticides (104), can change freshwater invertebrate communities. Pharmaceuticals and personal-care products are found in surface waters at concentrations that may affect freshwater organisms (105, 106), whereas health risks to humans are plausible but poorly understood (107).

Many freshwaters are becoming increasingly saline, particularly in urban and dryland settings. Multiple processes are involved in salinization of freshwaters, including point-source discharge of treated effluents, irrigation, marine saltwater intrusion due to overpumping of coastal aquifers, sea-level rise, and, in some cold climate regions, road salting (108), but irrigation and water abstraction in water-stressed environments is the most widespread cause (72). Chloride and sodium can interact with other chemical constituents, and salinization has been associated with increased base cation concentrations in lakes (109), altered DOC flushing from soils, and interactions with other metal contaminants (110). Chloride concentrations often surpass chronic and acute toxicity levels (108); thus, they represent a major stressor of resident biota.

Rates of biogeochemical processes are often modeled as a function of temperature and concentrations of substrates. The total amount of chemical processing is, in turn, dictated by the time available for these processes to occur. As discussed in sections above, all these factors are undergoing anthropogenic modification. Residence times have been alternatively expedited or delayed, temperatures are often increasing, and concentrations of some reactants are declining while those of many more are increasing.

Examples of shifting biogeochemical rates in freshwaters are accruing in the literature. Because they increase residence time, reservoirs substantially influence sediment as well as C, N, P, and silicon (Si) fluxes from continents to oceans (83, 91). Increased nutrient inputs promote primary production and ecosystem respiration, and they reduce the efficiency of nutrient uptake because biological demand is saturated (111). Shifting ratios of C, N, and P favor different biogeochemical transformations as well as the species composition of aquatic communities (112).

Ecosystem Metabolism and Carbon Balance

Although freshwaters cover only a small percentage of Earth's land surface, they play a disproportionately large role in the C cycle because net C fluxes per unit area are greater for freshwater systems than for the surrounding land (113). Freshwater systems tend to have high rates of carbon dioxide (CO_2) and methane (CH_4) emissions to the atmosphere. Whereas freshwater CH_4 emissions offset approximately 25% of the continental sink for organic C (114), lakes and reservoirs contribute to the C sink through C storage in stable, long-lasting sediments.

Current land storage of organic C is estimated to be approximately 1,500 Pg in soils and 560 Pg in biomass (115, 116). Over the Holocene, lake sediments accumulated approximately 420–820 Pg C (113). The current storage rate in freshwater ecosystems is at least 0.23 Pg C year^{-1} (113). By comparison, during the 1980s–1990s, land-use change is thought to

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have released 0.3–3 Pg C $year^{-1}$ to the atmosphere, whereas terrestrial ecosystems stored between 0 and 5 Pg C $year^{-1}$ (16). Organic C in lake sediments is preserved for a considerably longer duration (tens of thousands or more years) than organic C in terrestrial ecosystems (decades to centuries).

Intensive metabolism or storage of organic C in freshwaters may also be significant for regional C budgets. In the Northern Highland Lake District of Wisconsin, a region of ~7,000 km^2, freshwater wetlands and lakes cover only 20% and 13% of the land area, respectively, but account for >90% of the stored organic C (117). In Amazonia, upland forests appear to be accreting organic C, but for the region as a whole, the C budget is roughly balanced owing to large CO_2 emissions from wetlands and rivers (118).

Changing climate and land use are likely to affect processing and storage of organic C in freshwaters. Building of reservoirs for irrigation, flood control, or hydropower increases sedimentation and C storage while producing energy, thereby offseting greenhouse gas emissions (119). However, reservoirs also emit greenhouse gases to the atmosphere at rates that can offset the benefits of reservoirs (120). Sediment organic C burial rates by reservoirs range from 150 to 17,000 g C m^{-2} $year^{-1}$, far greater than sedimentation rates in natural lakes and oceans (121). Globally, impoundments bury approximately four times as much organic C as the world's oceans (121). Warming temperatures increase aquatic ecosystem respiration (122, 123) and are likely to decrease rates of organic C storage while increasing rates of CO_2 and CH_4 emission to the atmosphere.

Biotic Transformations

Although freshwater composes less than 1% of the planet's surface, the 126,000 known freshwater animal species make up approximately 10% of described animal species and one-third of global vertebrate diversity (124). Freshwaters support ~15,000 fish species (45% of the global total)—a disproportionate concentration of global fish diversity (**http://www.iucn.org/what/tpas/biodiversity/**). A number of other measures indicate that freshwater ecosystems support a disproportionately high level of species diversity relative to their area. Rates of endemism can be high for freshwaters, especially for ancient and physically isolated ecosystems (125). High levels of endemism increase species vulnerability to extinction. Aquatic biodiversity remains poorly described, even for better-known groups such as vertebrates. For example, each year, approximately 200 new fish species are described (126).

Aquatic biota are subject to a wide range of interacting threats. Direct alteration of aquatic ecosystems as well as their low-lying and integrative position within catchments makes aquatic biota sensitive to altered land-use practices. Sediment and nutrient loading from nonpoint-source pollution, invasive species, and altered flow regimes due to impoundment operations were the leading threats to imperiled freshwater taxa in North America (127).

Some of the most detailed data regarding species imperilment is for North America and the United States. Freshwater taxa have a higher rate of imperilment than do terrestrial or marine taxa (128), and the taxonomic groups with the greatest proportion of at-risk species are all freshwater. The list is topped by freshwater mussels (69% at risk or extinct), crayfishes (51%), stoneflies (43%), freshwater fishes (37%), and amphibians (36%). High-profile terrestrial taxonomic groups have lower rates of imperilment (birds 14%, mammals 16%) (129). High rates of imperilment for North American freshwater fishes have been recently corroborated by an American Fisheries Society assessment (39% imperiled: 230 vulnerable, 190 threatened, 280 endangered, and 61 extinct or extirpated) (130).

The Red Lists for freshwater species by the Internation Union for Conservation of Nature (IUCN) parallel imperilment trends for the United States, although the IUCN assesses fewer taxa. The 2009 IUCN Red List notes 1,147 freshwater fishes (37% of species

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assessed) and 1,369 species of freshwater invertebrates (131). Listed invertebrates are dominated by the handful of assessed and relatively well-studied invertebrate taxa: mollusks, crayfishes, and odonates. For these groups, approximately 8% of species are classified as imperiled, and 73% of listed invertebrate species are from North America, Europe, Australia, and New Zealand, reflecting the greater amount of recorded biological data in these countries. The majority of groups have not been assessed, but if overall rates are comparable with those for assessed groups, then 12,000 freshwater invertebrate species may be extinct or imperiled (131). High rates of imperilment are documented for other freshwater taxa such as amphibians, freshwater-reliant reptiles, and waterbirds (16). The Living Planet Index developed by the World Wildlife Fund (**http://www.wwf.panda.org**) provides a composite measure of trends in biota. The Freshwater Living Planet Index, based on trends for 1,463 freshwater vertebrate populations (458 species), declined by 35% since 1970—more rapidly than either terrestrial or marine indices.

Human activities have caused species extinction rates that far exceed background rates. Current and projected extinction rates for freshwater faunal groups in North America are five times those of terrestrial taxa and are on par with species extinction rates for tropical rainforests. Freshwater extinction rates were estimated to be 1,000 times greater than background rates (128). Researchers have documented 123 North American freshwater taxa as extinct (128), including approximately 60 mussel species (131). Global extinctions are difficult to tally, but range from 95 to 290 fish species (132).

A species-by-species view of the status of freshwater biological resources may not be optimal for considering freshwater biota, particularly for invertebrates, which are highly diverse and not well-known (131). There has been growing interest in classifying and assessing freshwater communities and ecoregions at broad geographic scales. Efforts to assess the status of wetland plant communities or associations (classification based on the U.S. National Vegetation Classification System) in North America indicated high rates of imperilment: Of the 1,560 wetland plant communities, 60% are considered at risk, 12% critically imperiled, 24% imperiled, and 25% vulnerable (**http://www.natureserve.org/servlet/NatureServe?init = Ecol**). Freshwater ecoregions provide a starting point for assessing and prioritizing conservation efforts (132a). Rather than focus on the status of individual species, conservation efforts may be more effectively focused on unique community and ecosystem types as well as on hot spots of species diversity and endemism such as ancient rivers, floodplains, groundwater ecosystems, and large or ancient lakes (see Freshwater Conservation Priorities, sidebar above).

Species extinctions are generally due to the extirpation of many individual populations (133). Rates of population extirpation of freshwater taxa are not well-known. Using historical data for rivers in Mexico, Mercado-Silva et al. (134) reported native-species loss rates of 10%–30% per decade and a concomitant 10%–20% increase per decade in nonnative species. Numerous other studies report similar trends of extirpation of native species and increasing incidence of nonnative species (135). This is a classic example of biotic homogenization, whereby many species are declining as a result of human activity and are being replaced by a small number of tolerant and expanding species. The consequence is that biotic communities become increasingly similar over time. Three key processes—habitat alternation, invasions, and extinctions—interact in ways that tend to further biotic homogenization (56).

Species replacement can alter ecosystem processes (136). A variety of mechanisms are involved, including alterations in habitat structure and in species abundances resulting from changes in predation and competition. There are numerous examples of how loss or gain of species impacts ecosystems. For example, declines of a migratory tropical fish decreased downstream transport of organic C and increased primary production and respiration

(137). McIntyre et al. (138) found that nutrient cycling rates and N:P ratios were highly sensitive to changes in the fish community. Consumer-driven changes in nutrient availability and N:P can have strong impacts on autotrophic productivity and species composition (69). Changes to the top predators in lakes have altered primary production, ecosystem respiration, the direction and magnitude of CO_2 exchange with the atmosphere, and sedimentation rates (139).

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Disease Emergence and Transmission

Water availability is a major determinant of human health, particularly in regions of limited economic development (9). Risk of waterborne diseases increases when encounters between aquatic vectors and humans are high, as occur when water is scarce and people aggregate around limited water points or when water is abundant and aquatic vector populations (such as mosquitoes) are widespread (140). Waterborne diseases are closely associated with absent or compromised waste-management infrastructure and water pollution (141). Contamination of domestic water supplies with human or animal feces increases the risk of cholera, other diarrheal diseases, and a range of parasitic infections. Ironically, construction of impoundments also increases the risk of diseases such as schistosomiasis (bilharzia) and malaria by creating or expanding the habitat for aquatic disease vectors such as snails and mosquitoes (142). Deforestation; land-use change; and the development of dams, canals, and irrigation systems are associated with increases in the habitat available for parasites and vectors and with human morbidity and mortality related to emergent parasitic diseases (143). Biodiversity loss frequently increases the incidence of human and wild-organism diseases (144).

Whereas relationships between water and human diseases are well studied, the dynamics and ecological significance of diseases of aquatic organisms have only recently begun to garner significant attention. Diseases play an important role in aquaculture and fish production and are a factor in the global decline in amphibians. Vertebrate models dominate the literature, although examples are also known for disease impacts on aquatic invertebrates (145).

As with species invasions, disease spread involves transport, establishment, and expansion of pathogens and vectors in new habitats. In the case of fish, introduction of nonnative species has been a major pathway for disease spread. For example, in European freshwaters, aquaculture has been associated with the introduction and translocation of 94 known pathogens from 13 different taxonomic groups (146). Reports of antibiotic-resistant bacteria in and around aquaculture facilities are increasing (147). Pathogenicity, host susceptibility, and disease spread can be affected by the trophic status of an infected water body; although specific mechanisms vary, nutrient enrichment is a common attribute of disease outbreaks across a range of freshwater systems and taxonomic groups (145). Eutrophication often increases infection risk by acting in concert with other environmental stressors such as agrochemicals (148) that weaken host resistance.

FRESHWATER CHANGE AND HUMAN WELL-BEING

Ecosystem services are the benefits that humans derive from nature (16). Ecosystem services from freshwater include flows that are withdrawn (e.g., for irrigation or municipal use) and in situ flows (e.g., for hydropower or transportation) (149). In addition to water flows, freshwaters also provide fish, waterfowl, edible plants such as wild rice, and other natural products for human use. Freshwaters are associated with several processes that regulate the condition of ecosystems or the capacity of ecosystems to provide services (16). Floods can be moderated or intensified, depending on the physical configuration of landscapes and the capacity of the land to hold water. Nutrient flows can be regulated by the capacity of riparian ecosystems to retain sediment and nutrients. Disease can be regulated by ecosystem processes, such as the association of cholera

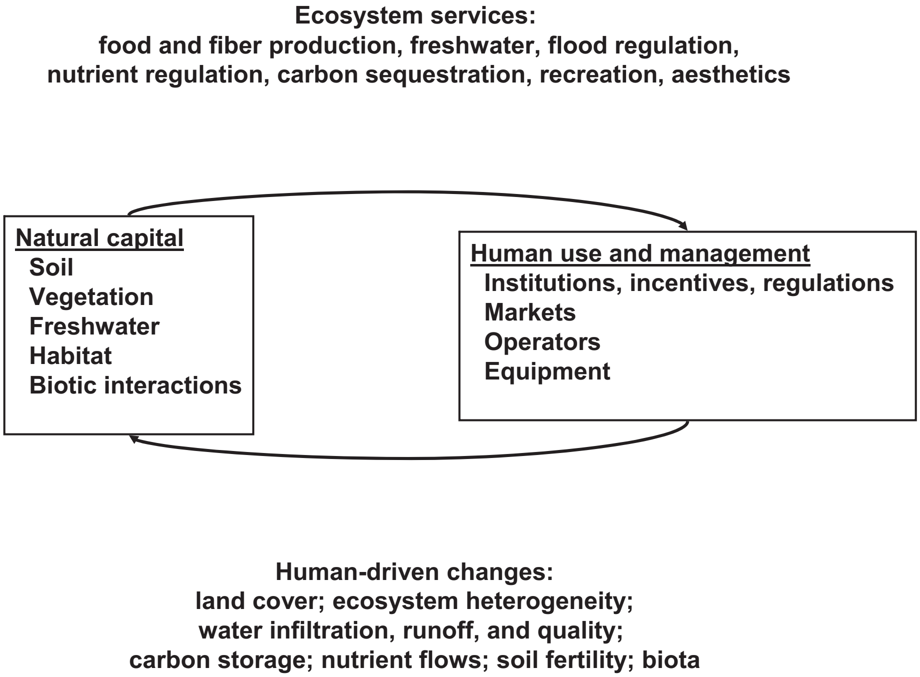

Figure 3

Freshwater ecosystem services are derived from natural capital as well as the human-use and management practices of a region.

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outbreaks with phytoplankton blooms (150). Finally, freshwater ecosystems provide cultural benefits in terms of education, enjoyment of nature, recreation, or spiritual values.

Freshwater ecosystem services interact with other ecosystem services through the dynamics of natural capital (**Figure 3**). Natural capital is the capacity of a particular place or region to provide ecosystem services in both the present and the future. Natural capital includes, e.g., the region's soils, vegetation, freshwater, habitat, as well as biota and their interactions. The dynamics of natural capital depend on external factors such as climate, internal physical and biotic processes, and human actions. Human use and management affect not only the current status and future trends of natural capital, but also the ecosystem services derived from it. Depending on human use and management, a region's natural capital can be configured quite differently and yield distinct sets of ecosystem services. Efforts to maximize food and fiber production often degrade water quality, groundwater recharge, and the capacity of landscapes to moderate floods (16).

Up to one-third of Earth's human population is affected by water scarcity and the attendant problems associated with food production, human health, and diversion of labor simply to meet water needs (16). Nations affected by water shortage may choose to purchase water-intensive commodities on the global market. The resulting trade in virtual water may lead to significant efficiencies in water use (**Figure 4**). However, dependency on the virtual water trade may decrease global flexibility to respond to severe famines caused by drought or crop failures (151).

ARE THERE LIMITS?

Access to adequate water is recognized by the United Nations as a basic human right (152). South Africa has legalized water priorities for

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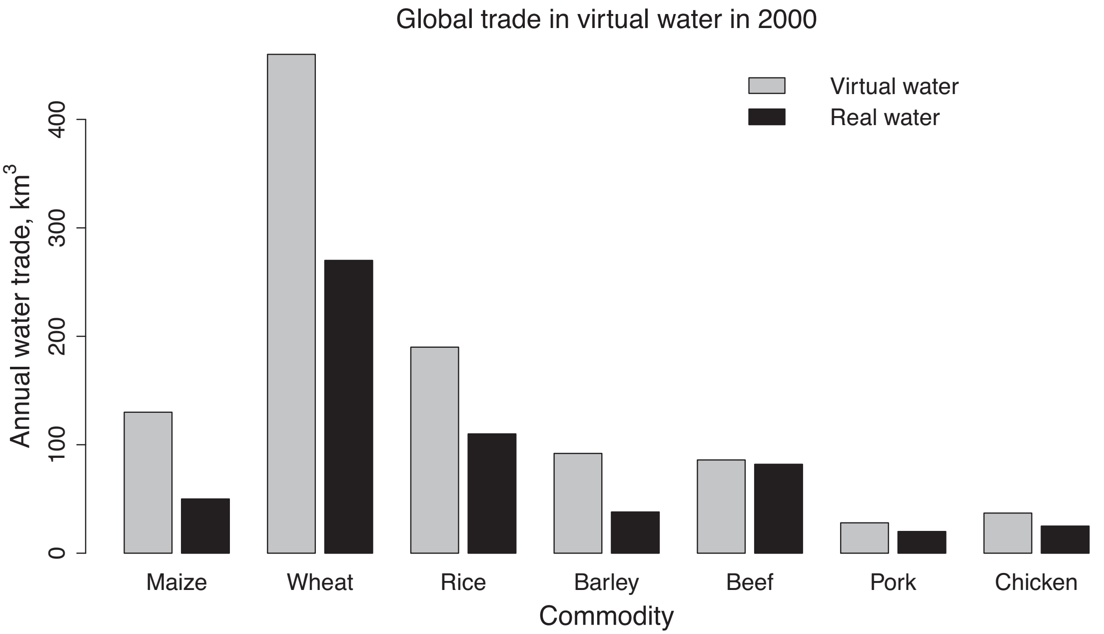

Figure 4

Global trade in virtual water in 2000 (Reference 16, chapter 7, table 7.8). Virtual water is the water that would have been used by the importing country to produce the commodity. Real water is the water that was in fact used by the exporting country to produce the commodity.

human and ecosystem needs by establishing a "reserve" that provides an allocation of 25 liters per person per day to meet basic human needs (5). The ecological reserve is defined as the water necessary to maintain ecosystems needed to ensure sustainable development. Concepts of peak renewable water (flow constraints limit water availability), peak nonrenewable water (extraction rates exceed recharge rates of groundwater systems), and peak ecological water (aggregate loss of natural capital from water extraction exceeds the total value from human use of water) clarify trade-offs in water-allocation decisions (153).

Pollution and water flows are closely coupled given that concentrations of a pollutant equal its mass divided by the water volume. In economic terms, pollution decreases the supply of clean water and adds to the costs of water use. Thus many countries have established upper limits for pollution of freshwater by N, P, or toxic materials. These upper limits are based on expectations of water flows sufficient to dilute pollutants to acceptable concentrations. Policy instruments for the management of water supply must also take account of changing climate, land use, and chemical inputs to freshwaters.

Are there natural upper limits for human use of freshwater resources? Between 5% and 25% of global freshwater extraction exceeds the renewable supply, although there is great variability among regions (16). Sustainable water withdrawals computed for the driest 10% of years are substantially lower than those computed for the average year (25). Thus planning for average conditions is of little use in drought-prone regions.

Because freshwater is heterogeneously distributed and expensive to transport, it is difficult to establish an upper limit for human consumptive use of freshwater at the global scale. If overconsumption of water is widespread, however, it will be difficult to meet needs by moving water from place to place. Thus a global pattern of overconsumption would raise concern about exceeding global limits. Any upper limit for water consumption, regional or global, must allow for environmental flows to maintain natural capital that supports essential ecosystem services. A safe upper limit for human consumptive use of freshwater worldwide was suggested to be 4,000–6,000 km^3 $year^{-1}$ (154). Current consumptive water use of approximately 2,600 km^3 $year^{-1}$ is within this boundary. However, global requirements for water to meet food and biofuel demand may bring consumptive use close to the proposed upper limits by mid-century (155, 156).

SUMMARY POINTS

1. Freshwaters, along with land transformed for agriculture use, are the most extensively and rapidly altered ecosystems on the planet. Responses by freshwater systems are also broad in scope, encompassing changes in physical structure, chemistry, ecosystem processes, biotic characteristics, and diseases.
2. Major drivers of change include climate, hydrologic modification, land use, chemical inputs, invasive species, and harvest. All drivers play a role, but some have already had substantial effects on freshwaters (e.g., changing hydrology, channel form, land use, chemical inputs, species introductions, harvest), whereas the impacts of others have not yet reached their peak impact.
3. The projections of long-term directional climate change suggest massive effects on freshwaters within a few decades. Because temperature and precipitation patterns affect freshwater flows, rates of nutrient cycling and toxin breakdown, as well as thermal niches of organisms, the effects of future climate change could impact all aspects of freshwaters.
4. The drivers of change and the responses of freshwaters interact. For example, variation in storm intensity affects stream channel form, inputs of nonpoint pollutants, habitat, and transport of invasive species and diseases. Deforestation, urbanization, and infrastructure development often lead to increases in the host vectors of human parasites, resulting in increased disease rates. Reservoirs, in addition to their hydrologic and biogeochemical effects, facilitate the spread of nonnative species and are associated with spread of diseases such as schistosomiasis (bilharzia).
5. Human impacts on freshwater ecosystems sometimes follow a predictable sequence. Overharvest often precedes other anthropogenic effects on aquatic ecosystems, producing declines in populations of the most valuable fishes. These changes have often been followed by increases in pollution, invasive species, and habitat destruction. This suite of stressors inhibits the future recovery of many degraded fisheries, such that in the absence of harvest, many major fisheries may never return to their previous abundance.

FUTURE ISSUES

1. Substantial uncertainties remain about the effects changing climate and land use have on surface and groundwater flows, water quality, and aquatic biota.
2. Agricultural policies and practices will have powerful effects on surface and groundwater flows, flood frequency and spatial pattern, water quality, human and wild-organism diseases, and living aquatic resources.

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3. Basic research is needed to determine the factors that control transport, the establishment and expansion of invasive species, and aquatic diseases related to humans and wild organisms.
4. Effective policies, practices, and technologies must be invented and implemented to contain the spread of, or extirpate, harmful freshwater diseases and invasive species.
5. There is a critical need for research to develop a basic understanding, technologies, policy instruments, and institutions that can maintain the flow of freshwater ecosystem services without degrading the natural capital that creates these services. This research will go beyond the natural science disciplines we draw from here and embrace engineering and policy sciences as well.
6. Appropriate policy instruments, economic incentives, and technologies are needed to constrain pollution by N, P, and other chemicals within boundaries for acceptable water quality.

DISCLOSURE STATEMENT

The authors are not aware of any biases or conflicts of interest that might be perceived as affecting the objectivity of this review.

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