Sustaining Ecosystem Services in Human-Dominated Watersheds: Biohydrology and Ecosystem Processes in the South Platte River Basin

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ABSTRACT / Sustaining ecosystem services important to humans while providing a dependable water supply for agriculture and urban needs is a major challenge faced by managers of human-dominated watersheds. Modification of natural flow regimes alters the abundance and composition of native plant and animal communities, affecting ecosystem services such as water storage and nutrient cycling that depend on particular species or functional groups. Because complete restoration of natural hydrology is generally not an option in human-dominated watersheds, there is a need to determine which specific flow manipulations are necessary to restore species-dependent ecosystem services in particular systems. Here we propose a framework for predicting ecological consequences of flow manipulations that is based on the role of hydrology in linking population, community, and ecosystem processes. We use a case-study approach to examine how interactions among the flow regime and species' functional traits help organize local biotic communities and generate alternate states of ecosystem functioning. Results indicate the importance of integrating hydrology and biology to predict ecological consequences of flow regime manipulations and the need to apply general flow-restoration principles on a case-by-case basis.

A new paradigm in watershed management focuses on the role of natural flow variation in generating and maintaining the ecological integrity of river–floodplain ecosystems (Sparks 1995, Barinaga 1996, Richter and others 1997, Poff and others 1997). In this view, restoration of natural hydrology is the key to recovering biodiversity and ecosystem processes in degraded watersheds. However, in most human-dominated watersheds hydrologic regimes have been modified substantially to supply water for multiple human uses, and complete restoration of natural hydrology is generally not an option. Moreover, because future states of ecological systems are highly dependent on existing conditions (Botkin 1990), flow restoration can have unanticipated consequences if current physical and biotic constraints, such as changed channels, established nonnative species, and altered soil chemistry, are not taken into account (Frissell and Bayles 1996). Therefore, restoration will require methods that can be adjusted for specific systems to predict what changes to the human-modified flow regime will restore local plant and animal communities and the ecosystem processes they perform (Schulze and Mooney 1993, Grimm 1995, Mooney and others 1996, Chapin and others 1997).

Here we present a framework for predicting ecological consequences of flow manipulations that is based on the role of hydrology in linking population, community, and ecosystem processes. Our purpose is to provide a conceptual tool to guide research and management concerned with the restoration of degraded watersheds. As human populations increase and water supplies diminish, there will be increased urgency to recover and sustain ecosystem services in human-dominated watersheds, including the storage and delivery of clean water (Ehrlich and Ehrlich 1992, Postel 1992, National Research Council 1992, Naiman and others 1995, Postel and Carpenter 1997). Restoration will depend on mechanistic understanding of how hydrology interacts with biological processes to control species composition and ecosystem functions. We illustrate this by applying our framework to a case study of the South Platte River Basin, a heavily modified watershed of the North American Great Plains.

KEY WORDS: Biohydrology; Aquatic ecosystems; Community assembly; Ecological integrity; Watershed restoration; Ecosystem services

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Conceptual Framework

Hydrology, Biodiversity and Ecosystem Processes

Our framework focuses on how hydrology integrates population, community, and ecosystem processes in river-floodplain ecosystems (Figure 1). At the popula-

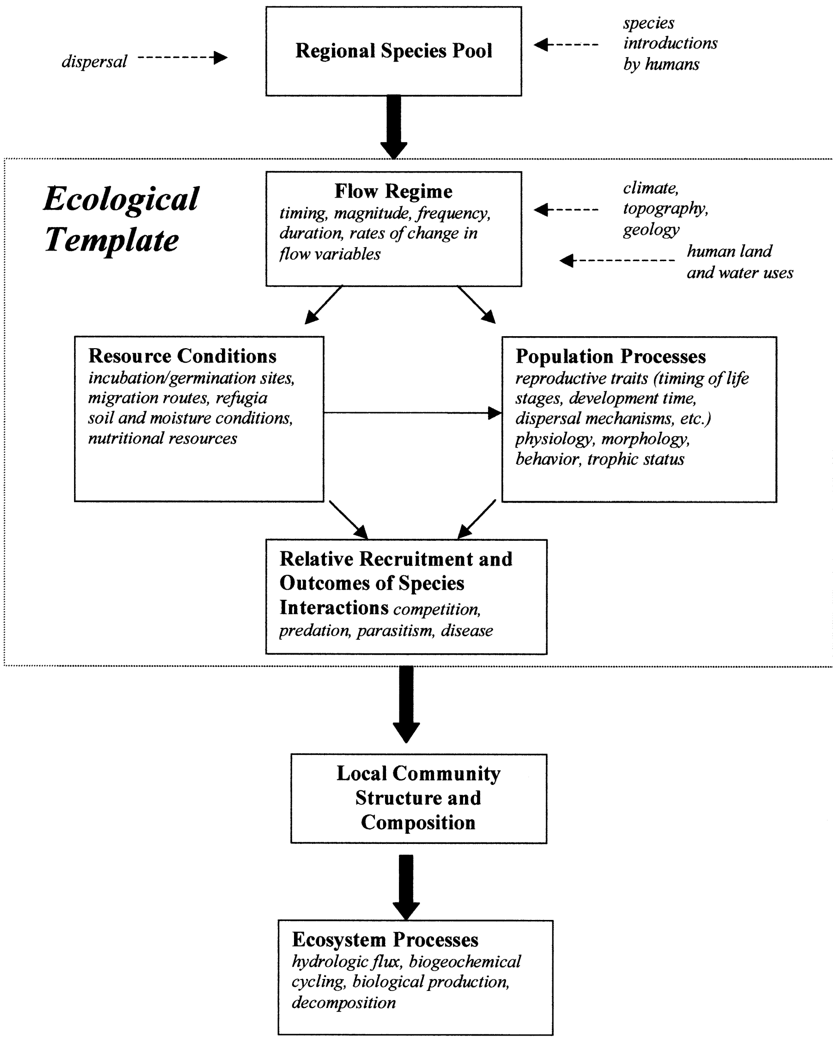

Figure 1. Conceptual framework of the role of hydrology in the development of biotic communities and ecosystem functions in river-floodplain ecosystems (see Poff and Ward 1989, Tonn 1990, Poff and Allan 1995, Richter and others 1997, Poff 1997, Poff and others 1997).

tion level, the flow regime controls resource levels that regulate species growth and survival and demographic processes such as spawning and seed germination (Poff and others 1997). As a result of species differences in response to flow variables and flow-related resource conditions, different species are favored at different times as flow conditions vary. In this way, the flow regime regulates species' relative abundances, outcomes of species' interactions, and invasion into the local community, resulting in the development of alternate community states under different flow regimes (Strange and Foin 1999). In turn, flow-driven changes in community structure and composition affect rates of ecosystem processes, such as primary productivity, nutrient cycling, and water storage, which depend on particular keystone species or functional groups (Schulze and Mooney 1993, Grimm 1995, Power 1995, Mooney and others 1996, Chapin and others 1997). As changes in species composition alter ecosystem processes, freshwater services important to humans are also disrupted (Postel and Carpenter 1997) (Table 1).

For example, water development in the southwestern United States has led to significant groundwater declines, resulting in invasion of deep-rooted riparian plants, such as species of the genus *Tamarix* (saltcedar), which show greater tolerance for increased groundwater depths than native species (Graf 1982, Stromberg and others 1996). Because *Tamarix* show high rates of evapotranspiration, *Tamarix* invasion reduces surface water supplies and rates of water flow, increases sedimentation, and alters channel structure (Graf 1978, Blackburn and others 1982). Not only does this impair the delivery of water for human needs, but also soil moisture levels can become unsuitable for native vegetation. This can lead to additional species losses and further alteration of ecosystem functioning.

Table 1. Ecosystem processes and resulting services provided by river-floodplain ecosystems

Ecosystem processes	Human services
Hydrologic Flux	Water storage and delivery for industrial, domestic, and agricultural uses Pollution dilution Hydropower regeneration Regulation of runoff and flood control Sediment transport Groundwater inputs to instream flow Dispersal of seeds, eggs, and larvae of biota
Biogeochemical Cycling	Sediment storage and release Storage and recycling of nutrients Storage and recycling of organic matter Contaminant absorption and detoxification
Biological Production	Creation and maintenance of habitat Fish and wildlife production Soil formation and fertilization Invertebrate fauna Riparian vegetation
Decomposition	Processing of organic matter Processing of human wastes

After Naiman and others (1995), Prugh (1995), Lemly (1997), Postel and Carpenter (1997).

Flow Regime and Invasion Dynamics

Similar frameworks focus on the ''habitat templet'' (Southwood 1977, 1988) that constrains or ''filters'' the dispersal of species from a regional species pool according to their responses to local physical conditions (Poff and Ward 1989, 1990, Tonn 1990, Townsend and Hildrew 1994, Poff and Allan 1995, Poff 1997). Our framework also emphasizes the role of the physical regime in varying outcomes of species interactions and therefore the ability of potential colonizers to successfully invade and persist in a local community (Strange and Foin 1999). In the case of riverine ecosystems, several studies show that if interacting species respond differently to flow variables, changes in the flow regime can reverse the ratio of invader to resident species, altering competitive outcomes and predator–prey dynamics, and leading to changes in community structure (Minckley and Meffe 1987, Strange and others 1992, Wootton and others 1996). In streams of the American southwest, natural flooding in unregulated streams promotes coexistence of native fishes and an introduced predatory fish by periodically reducing the introduced species, which is poorly adapted to floods (Meffe 1984, 1985). In streams where floods are eliminated by upstream dams, the introduced predator is able to invade and persist in the local community and typically eliminates the native species within a few years. Thus, the flow regime can alter and even reverse outcomes of species interactions and invasion into a local community (Strange and Foin 1999).

Case Study: The South Platte River Basin

In the following sections, we apply this view of the role of hydrology in river–floodplain ecosystems to an analysis of the South Platte River Basin. We use our framework to integrate existing hydrological and biological information and to analyze effects of altered hydrology on population, community, and ecosystem processes. First, we outline what is known about the natural hydrology of the South Platte River and changes due to land and water development. Then we discuss flow-related changes in the biota and associated ecosystem processes.

Natural Hydrology

The South Platte River has its headwaters in the central Rocky Mountains, descends through a transition zone, and flows across the Great Plains of northeastern Colorado about 725 km to join the North Platte River in Nebraska (Dennehy and others 1993) (Figure 2). The basin has a continental-type climate, with cold winters and hot summers. Precipitation is mostly in the form of mountain snowmelt in spring and sudden, unpredictable thunderstorms in summer along the plains. Annual precipitation ranges from 100 cm in the mountains to less than 40 cm in the plains (Dennehy and others 1993). There are few records of presettlement hydrology of the South Platte River, but journals of early explorers (e.g., the Long expedition of 1820 and the Frémont expeditions of 1842 and 1843) provide insight into key features of the highly variable natural regime (see Jordan 1891, Jackson and Spence 1970, Eschner and others 1983, Kircher and Karlinger 1983, Fausch and Bestgen 1997).

Annual and seasonal variation. Large year-to-year variation in precipitation and distinct seasonality characterized the natural hydrograph of the South Platte River mainstem. Under natural conditions, flows peaked in May and June from mountain snowmelt runoff, receded by July, and then remained at low levels from August through April. The magnitude of spring runoff varied from year to year depending on climatic events that determine annual snowfall (Covich and others 1997). In some years, late summer baseflow in some mainstem reaches was punctuated by floods from tributaries due to summer thunderstorms (see below).

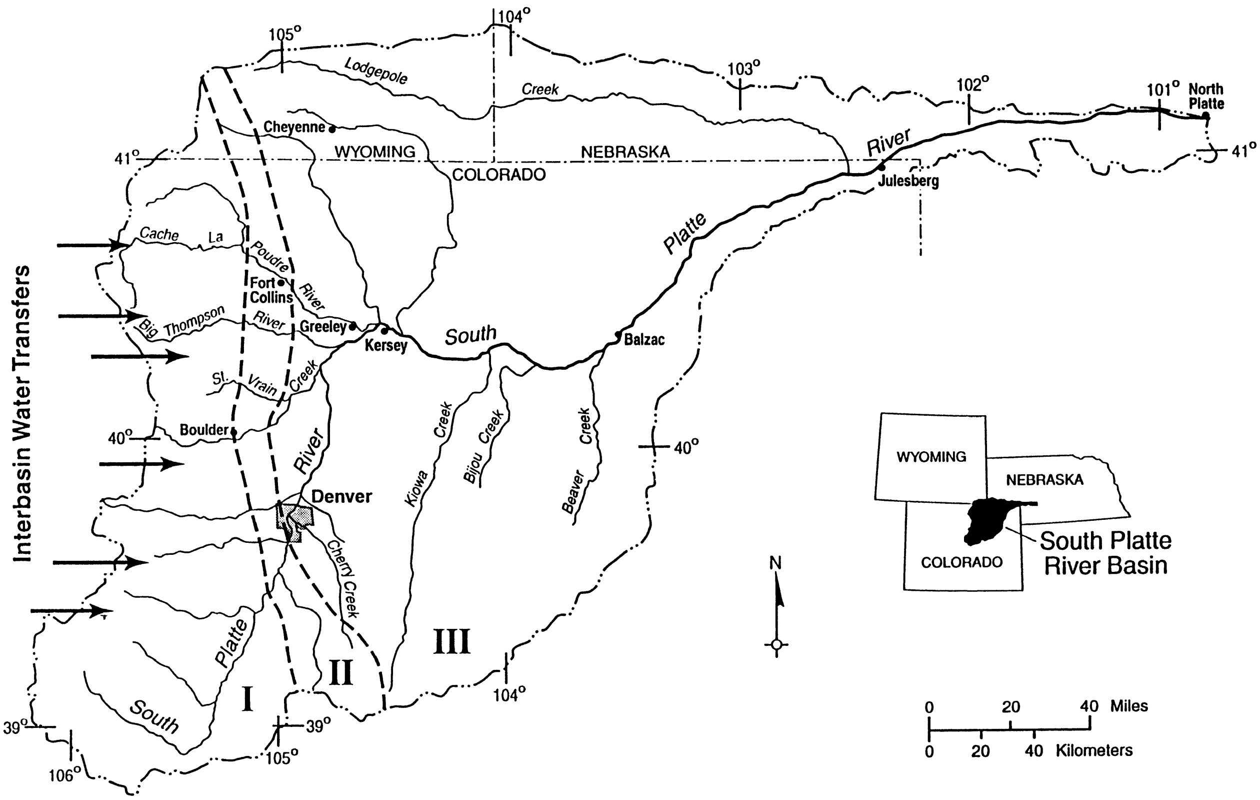

Figure 2. Map of the South Platte River Basin (after Propst 1982, Dennehy and others 1993).

Intermittency: Mainstem vs plains tributaries. Along the mainstem of the historic South Platte River, dewatered reaches were probably uncommon because of the large drainage area, numerous tributaries, and groundwater influx during low flows (Eschner and others 1983). Under historical conditions, many mainstem reaches had perennial flow and some reaches were probably intermittent with unconnected pools, but it is believed to be unlikely that the river was ever completely dry. Of 100 references by surveyors from 1858 to 1881, none refer to a dry riverbed (Johnson 1994).

In contrast, flows in plains tributaries (e.g., Kiowa Creek, Bijou Creek, Beaver Creek, Lodgepole Creek) are typically intermittent because in most years precipitation is insufficient to recharge the aquifer and maintain continuous base flow (Dennehy and others 1993). Most precipitation on the plains occurs from April to September due to spring rains and localized summer thunderstorms. As a consequence, summer flows in plains streams are highly variable (Fausch and Bramblett 1991). Spring and summer storms can produce large floods that attenuate rapidly. For example, in 1965 a storm in Bijou Creek produced 13,197 m^3/sec, resulting in mainstem flows of 3483 m^3/sec at Balzac and 1065 m^3/sec at Julesburg (Matthai 1969). Bijou Creek flows, which average less than 1 m^3/sec annually, were so great that when they reached the South Platte mainstem they moved both upstream and downstream and onto the floodplain.

Channel morphology. High spring flows and abundant fine sediments of the historic river maintained a wide, shallow, and braided channel, with numerous, shifting sandbars and unvegetated alluvial islands (Nadler and Schumm 1981). Under natural conditions, large annual flood events could completely rework the channel over a period of several years (Friedman and others 1997). Floods promoted germination of native riparian plants, which initiated a period of channel narrowing. Vegetation establishment encouraged deposition of fine sediments and reduced erosion, stabilizing the channel at a narrower width. However, the channel began widening again with the next major flood.

Land and Water Development

Water development began in the South Platte River in the 1840s with hand-dug irrigation ditches followed by construction of large irrigation canals between 1860 and 1885 (Eschner and others 1983). By the early 1880s summer flows were overappropriated, and from 1885 to 1930 dozens of off-channel reservoirs were built to store spring snowmelt runoff to meet irrigation needs. Beginning in 1930, groundwater pumping and diversions of water from river basins of the western slope of the Rocky Mountains were used to augment declining supply.

Today, nearly 2.5 million people live in the basin, mostly along the foothills between Denver and Fort Collins (Dennehy and others 1993). The river now resembles an elaborate plumbing system more than a natural river, with 15 interbasin diversions that add water from West Slope basins, and about 500 irrigation ditches and 1000 reservoirs that remove water for urban and agricultural needs (Milliken 1988, Dennehy and others 1993). Nearly 25% of South Platte flow is now imported from West Slope rivers (Dennehy and others 1993). Groundwater pumping has increased in importance as population growth has accelerated. For example, the Denver Basin aquifer system has become an important water source for metropolitan Denver and rural communities in east-central Colorado. Over the past 20 years, water levels in one of the system's four major aquifers, the Arapahoe aquifer, have dropped 700–800 ft in parts of the southern metropolitan area, and in some cases domestic wells have run dry (Romero and Bainbridge 1989, Colorado Division of Water Resources 1996). The Denver-area population is expected to climb by 1 million over the next two decades, and groundwater supply is an increasing concern (Long 1996).

South Platte River water is used extensively for industrial and domestic needs in the Denver area and for agriculture and livestock production downstream on the plains. Although about 70% of current offstream water use is for irrigated agriculture, in recent years there has been a gradual reallocation of water away from agriculture as water costs and urban demands have increased (Smith and others 1996). It is estimated that 90,000 acres of farmland and ranchland is lost to development in Colorado each year (Long 1996). From 1989 to 1991 the value of water traded in Colorado doubled, indicating the importance of water reallocation to support increased human development (Postel 1992).

Altered Hydrology and Channel Structure

No flow records predate the rise in water development in the South Platte River Basin beginning in the 1840s, making impossible a complete analysis of how the natural hydrograph has been altered. However, records for different locations and time periods reveal significant changes in spatial and temporal patterns of flow, particularly over the past century.

Spatial variation in streamflow. Although large interannual variation in streamflow still occurs in the South Platte River, hydrologic characteristics vary distinctly according to stream reach due to differences in land and water use in urban and agricultural areas (Dennehy and others 1993). Upstream from Denver, the river is regulated by water-supply reservoirs. Most of the river's flow is diverted via pipelines for industrial and domestic use, and returns to the river via wastewater treatment plants. For nearly 100 km downstream from Denver, river flow is almost entirely wastewater effluent except during spring runoff. In downstream agricultural areas, river water is removed by irrigation ditches and added by irrigation return flows, making the South Platte mostly a ''recycled river'' along the eastern plains. Groundwater return flows from irrigation and canal and reservoir seepage comprise most of the river's flow (Dennehy and others 1993, McMahon and others 1995, Litke 1996, Smith and others 1996). Nearly 60% of the water withdrawn for agriculture is returned to the river, along with significant amounts of added nutrients and chemicals from fields and feedlots (Dennehy and others 1993). Excess irrigation water returns to the river as runoff or seeps into the ground and slowly returns to the river over months or even years. As early as the 1920s, irrigation return flows substantially increased summer base flows above historic levels (Parshall 1922), and the river changed from a losing to a gaining stream (Minges 1983, Ruddy 1984).

Hydrologic differences in urban and agricultural areas are illustrated by three sites on the South Platte River between Denver and the Nebraska border (Figure 3). At Denver, natural spring peak flows have been reduced due to upstream reservoir storage. In contrast, at Kersey three major tributaries with mountain headwaters (St. Vrain Creek and the Cache La Poudre and Big Thompson rivers) contribute substantial snowmelt runoff to the river in spring. In addition, peak flows and annual mean flows at Kersey have generally increased in magnitude over the past century due to augmentation by interbasin transfers (Johnson 1994, Dennehy and others 1993). Here base flows are also higher than historic levels throughout fall and winter due to irrigation return flows. As water flows downstream towards Julesburg, river flows decline substantially. Plains tributaries contribute little flow below Kersey, and therefore the effects of irrigation diversions and return flows are more pronounced in the lower South Platte River. The process of diversion of river flow to zero followed by groundwater replenishment results in spatially discontinuous flow along many downstream reaches (Dennehy and others 1993).

Daily flow variation. Representative hydrographs for the same three locations suggest that extreme variations in daily flows now also occur during summer months

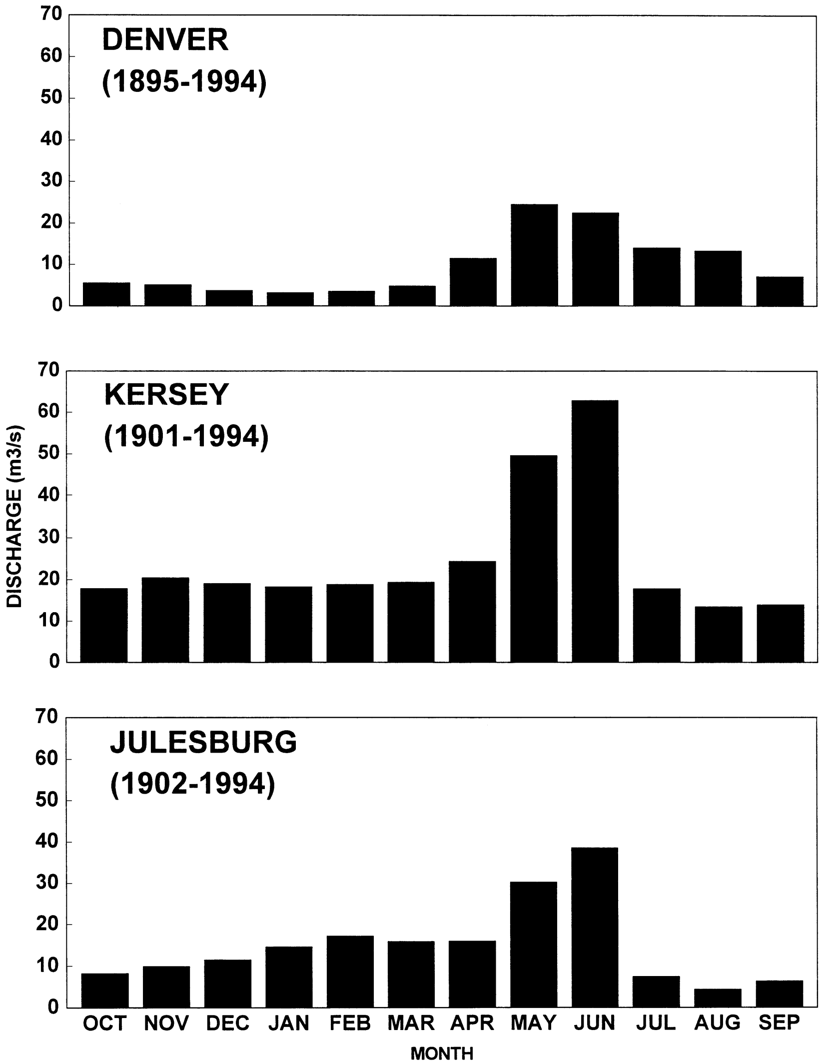

Figure 3. Monthly streamflows averaged over the periods of record for USGS gaging stations on the South Platte River at Denver (drainage area = 10,000 km^2), Kersey (drainage area = 24,864 km^2), and Julesburg (drainage area = 60,070 km^2).

due to human uses of water (Figure 4). Daily fluctuations in summer streamflows in the Denver area are largely due to variation in rates of lawn watering. In downstream agricultural areas, daily fluctuations in flows are even more pronounced. During the irrigation season the river's flows can fluctuate over two orders of magnitude within a few days. In most years, drawdown of spring peaks is apparent before spring runoff, beginning in May in agricultural areas near Kersey and Julesburg (Figure 4). In early June, runoff typically peaks at over 100 m^3/sec, and then diversions reduce flows to less than 5 m^3/sec by early July. From July on, there are extreme daily fluctuations, especially near Kersey, because water is continually removed by diversions and added from both irrigation return flows and wastewater treatment plant discharges to tributaries.

Modern channel characteristics. Under natural conditions, the channel bed was largely shifting sand that scoured and filled rapidly during snowmelt runoff, forming numerous sandbars and islands (Nadler and Schumm 1981). Today the natural river channel through Denver is highly modified by channelization and other structural modifications. Here the modern river is mostly a single channel, with substrata ranging from cobble and gravel just below Chatfield Dam to sand in the Denver area (Dennehy and others 1995). Particle size increases downstream from urban to agricultural lands. In agricultural areas of the lower South Platte, fine-grained sediments are continually removed through irrigation, leaving larger, sand-sized particles in the main channel (Dennehy and others 1995).

Downstream through the eastern plains to Nebraska, flow diversions and a period of drought during the 1930s combined to allow vegetation encroachment of the channel and expansion of riparian woodland (Johnson 1994, Friedman and others 1997). Vegetation

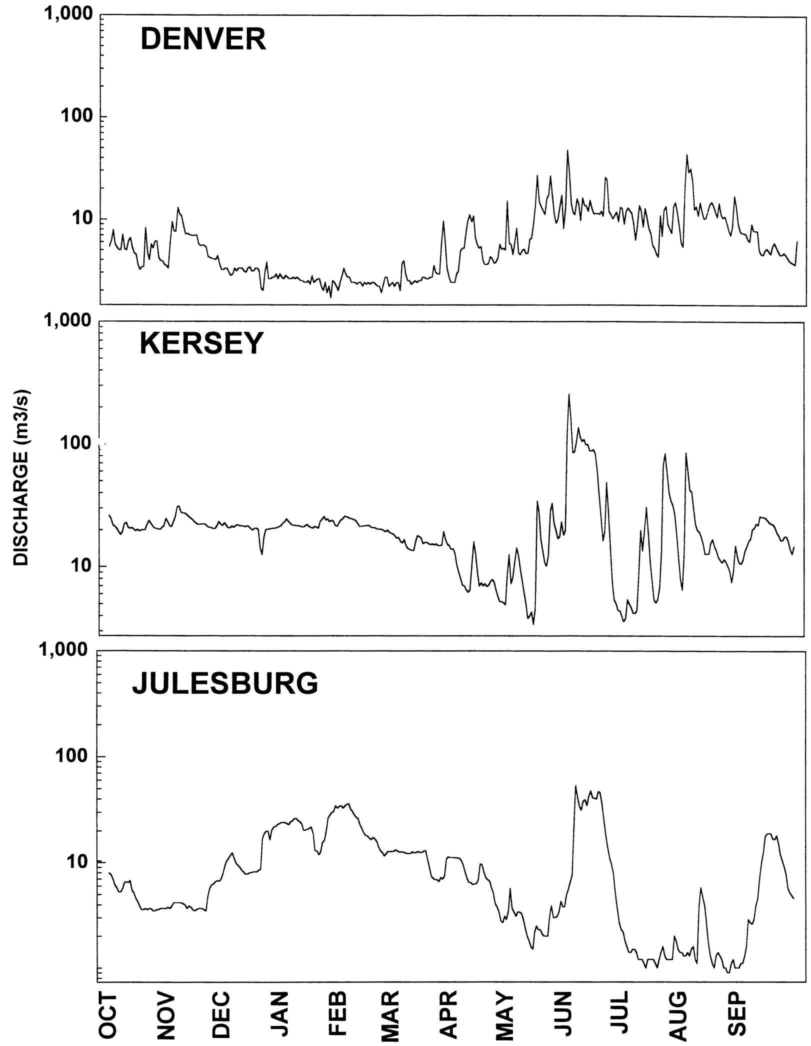

Figure 4. Daily discharges for the 1991 water year (logarithmic scale) for USGS gaging stations on the South Platte River at Denver, Kersey, and Julesburg (drainage areas as in Figure 3 legend).

within the channel stabilized shifting sandbars. As a result of sediment retention by vegetated sandbars, the wide, braided channels of the historic river were converted to a single, narrow, meandering main channel with numerous secondary channels (Nadler and Schumm 1981). Channel width declined by an estimated 15% (Friedman and others 1997). In recent years, expansion of riparian woodland and channel narrowing have ceased, and along some reaches channel width has increased again as channel and woodland area have stabilized in response to stabilization in flow use (Johnson 1994, Friedman and others 1997).

Hydrology and Riparian Vegetation

Life history differences of native and nonnative vegetation. Early successional native trees of the South Platte River Basin, such as plains cottonwood (*Populus deltoides*) and other members of the Salicaceae family (cottonwoods and willows), require a bare, moist substrate for germination, followed by a period free from disturbance for seedling establishment (Johnson 1994, Shafroth and others 1995, Friedman and others 1997). Seeds are released during spring runoff and germinate as flows recede and expose newly scoured surfaces. Seeds only remain viable for a few weeks in June, and recruitment is greatest if flows recede by mid-June (Johnson 1994). Young seedlings need the continuously moist substrate provided by receding floods until root growth is deep enough to survive natural declines in the water table during summer. Seedlings are also intolerant of shade and fail to establish under an existing stand of trees or herbs.

Unlike cottonwood, the introduced Russian olive (*Elaeagnus angustifolia* L.) is shade-tolerant and therefore can establish under an existing canopy. Russian olive seeds are released throughout the summer and germinate under a wide range of moisture and light conditions (Knopf and Olson 1984, Olson and Knopf

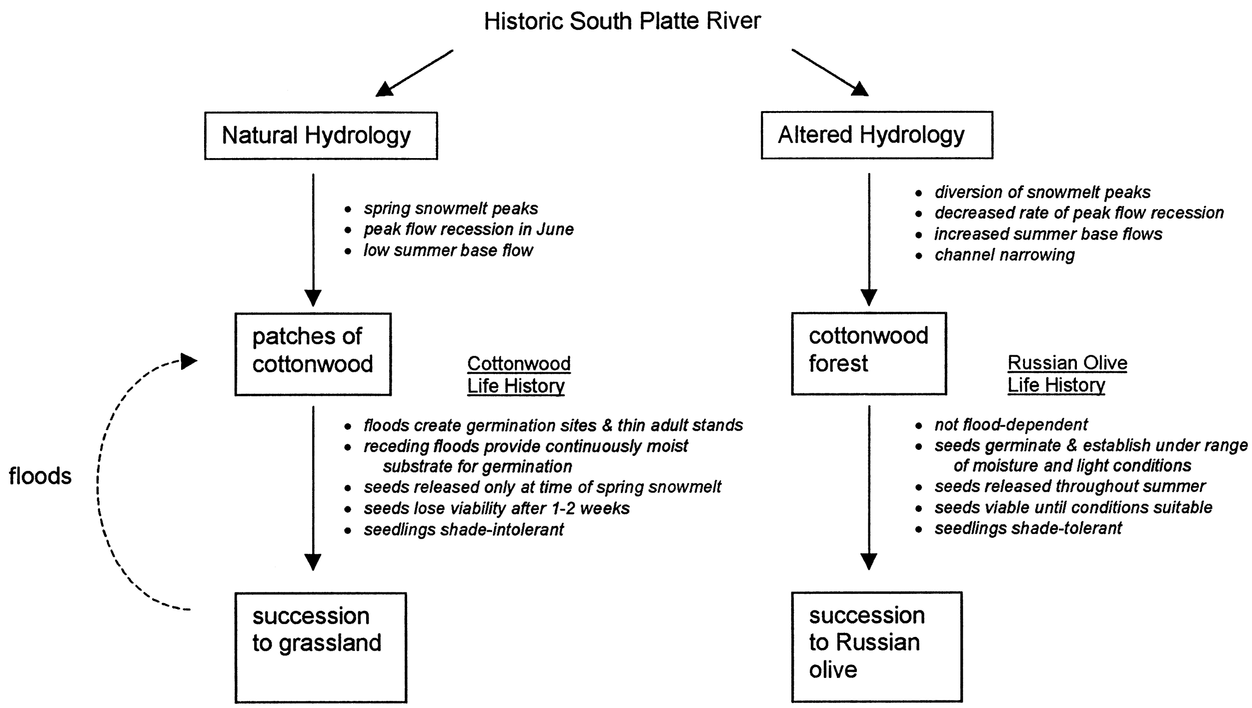

Figure 5. The flow regime and alternate pathways of vegetation succession in the riparian zone of the lower South Platte River (Friedman and others 1997).

1986, Shafroth and others 1995, Friedman and others 1997). In addition, seeds remain viable until conditions are suitable, sometimes for many months (Shafroth and others 1995).

Hydrology and alternate pathways of vegetation succession. As a result of life history differences in response to flow conditions of cottonwood and the introduced Russian olive, different successional pathways have occurred in the riparian zone of the lower South Platte River under natural and human-modified flow regimes (Figure 5). Under natural conditions, cottonwood recruitment was high following a major flood in spring, but unless large floods in subsequent years cleared more substrate for new pulses of recruitment, cottonwood stands aged and thinned and succession to grassland occurred (Friedman and others 1997). Explorer journals of the 1800s (e.g., Jackson and Spence 1970) describe the distribution of cottonwood in widely scattered stands of different ages, indicating variation in cottonwood recruitment corresponding to natural variation in precipitation, streamflow, and soil moisture.

Introduction of nonnative riparian plant species adapted to the altered flow conditions of the modern river, combined with loss of conditions favorable to cottonwood, resulted in a fundamental shift to a new successional pathway (Knopf and Scott 1990, Snyder and Miller 1991, Friedman and others 1997). In 1935, a major flood cleared substrate for a large pulse of cottonwood recruitment. Subsequent years of drought and reductions in flows due to water development favored cottonwood establishment within the channel and throughout the riparian zone, leading to a period of channel narrowing and expansion of cottonwood forest. Since the 1930s, cottonwood stands have gradually been invaded by shade-tolerant exotics such as Russian olive that are favored by management changes in the timing, magnitude, and duration of peak flows and elevated summer base flows due to irrigation return flows, and a new successional pathway has been established.

Riparian Vegetation and Ecosystem Processes

The composition of riparian vegetation helps determine rates of erosion, siltation, and nutrient inputs to streams, controlling water quality and aquatic production (Allan 1995, Naiman and Décamps 1997). The type and quantity of vegetation cover also influences the quantity and distribution of water in the river and floodplain. In addition, riparian vegetation provides habitat for numerous terrestrial species. Along the South Platte River, loss of native riparian vegetation has led to alteration of a number of such critical ecosystem processes, as described below.

Production of avian habitat and nutritional resources. Changes in riparian vegetation due to hydrologic alterations have resulted in significant changes in habitat and nutritional resources for other riparian species, particularly birds (Knopf and Olson 1984, Knopf and Scott 1990, Knopf 1986, 1996). Along the lower South Platte River, a large bird community developed in the cottonwood-dominated riparian zone of the modern river. However, many of these species are nonnatives, and in many areas endemic species are in decline. Nearly 90% of the 82 breeding bird species currently present were not in the region at the turn of the century (Knopf 1986). This increase is thought to be due to expanded cottonwood forest that allowed an influx of East and West Coast bird species, particularly habitat generalists of forest edges. The changed vegetation led to the loss of at least four native bird species through hybridization with nonnative congeners. As one scientist observed, ''We have changed the landscape so much on the Platte that we've changed the direction of evolution'' (F. Knopf, National Biological Service, Ft. Collins, Colorado, quoted in the *Denver Post,* 23 July, 1996).

The current lack of cottonwood regeneration is a concern because of loss of habitat for the existing native and nonnative riparian avifauna. However, interruption of the natural successional pathway from cottonwood to grassland as a result of water development is also eliminating habitat for many grassland-dependent native species (Knopf and Samson 1997). Bird species diversity and abundance is less in Russian olive stands than in native vegetation because Russian olive provides little insect food and poor habitat for cavity-nesting birds (Knopf and Olson 1984). It is estimated that continued succession to Russian olive in place of grassland will result in loss of nearly a third of native bird species (F. Knopf, National Biological Service, Ft. Collins, Colorado, personal communication).

Regulation of water and soil salinity. High return flows from excess irrigation combined with loss of native riparian vegetation to cropland concentrates salts in riparian soils and river water (National Research Council 1996). At present, most of the agricultural soils in the South Platte River Basin are only slightly saline (Dennehy and others 1993). However, the salinity concentration of river water along the lower South Platte is five times that of the Denver area because of repeated recycling of return flows (Dennehy and others 1993). High salinity of river water is stressful for some aquatic species, and excess salts in agricultural soils can reduce crop yields and impede restoration of native vegetation intolerant of high salinity.

Nutrient cycling and water quality. Riparian plants and microbes help purify water by absorbing and transforming nutrients that are essential for plant growth but cause water-quality problems when in excess supply (Karr and Schlosser 1978, Allan 1995, Naiman and Décamps 1997). Water quality is also regulated by ecological processes that occur as water moves between the surface and hyporheic zone, or area of subsurface flow (Stanford and Ward 1988, 1993, Triska and others 1989).

In the South Platte River Basin, agriculture currently contributes 132,000 tons of nitrogen and 14,000 tons of phosphorus annually, and manure from feedlots contributes another 94,000 tons of nitrogen and 26,000 tons of phosphorus (Litke 1996). Nutrients from wastewater treatment plants are less (7000 tons of nitrogen, 1200 tons of phosphorus), but these nutrients are discharged directly into the river and therefore can pose a greater water-quality problem in urban areas (Litke 1996).

Nutrient enrichment of river water can contribute to algal blooms and die-offs and to decomposition and depletion of dissolved oxygen, reducing water quality and creating unfavorable conditions for other aquatic life (Cole and others 1993, Mueller and Helsel 1996). A recent study by the United States Geological Survey found that the South Platte River had the highest contamination by ammonia and nitrate and the second highest levels of phosphorus among 20 major US rivers (Mueller and others 1995). Dissolved phosphorus concentrations range from 0.37 to 1.40 mg/liter at Denver and from 0.15 to 0.30 mg/l at Balzac on the eastern plains, often exceeding the EPA limit of 0.10 mg/l for control of eutrophication (Litke 1996). Dissolved ammonium concentrations are largest downstream from Denver's wastewater treatment plants, reaching a high of 4.6 mg/l in winter at Henderson (Litke 1996). At Henderson, un-ionized ammonia concentrations (calculated on the basis of pH, water temperature, and dissolved ammonium) sometimes exceed the state standard 0.10 mg/l (Litke 1996). Along these reaches, dissolved oxygen standards can fall below standards for aquatic life during low flow periods (McMahon and others 1995). Recent improvements in wastewater treatment have reduced the proportion of nitrogen present as ammonia, but the nitrate proportion has increased because nitrification is used in the treatment process, leaving total nitrogen unchanged (Dennehy and others 1995). As a result, nitrogen levels below wastewater treatment plants can still pose water quality concerns.

Dissolved ammonium concentrations gradually decrease below the Denver metropolitan area due to biotic uptake and conversion to nitrate by bacteria (Litke 1996). Below Henderson the effluent-dominated water is replaced by groundwater, and the river from Kersey downstream is dominated by nonpoint sources of nutrient enrichment, especially nitrate from runoff of excess fertilizer and manure application that discharges back to the river in groundwater (Dennehy and others 1995, McMahon and others 1995, Litke 1996).

Native soil bacteria of the South Platte basin remove 15–30% of nitrate from groundwater before it discharges back into the river, helping to reduce nitrate in surface water supplies (McMahon 1995). However, recent groundwater monitoring by the Colorado Department of Public Health and Environment indicated that nitrate levels in 35% of domestic wells between Denver and Julesburg exceed the EPA standard for drinking water (Colorado Department of Health 1995). Nitrate is a form of nitrogen that can interfere with the oxygen supply in the bloodstream of infants, causing methemoglobinemia or ''blue baby'' syndrome (Nash 1993).

Loss or replacement of native riparian vegetation due to flow alterations can reduce uptake of excess nutrients in surface runoff, increasing nutrient levels in river water and altering the species composition and abundance of aquatic biota. In the South Platte River, a recent study found that nutrient-enriched reaches in heavily developed areas show higher algal abundance and lower density and diversity of benthic invertebrates than relatively undisturbed sites (Tate and Heiny 1995). For example, the South Platte River at Henderson, which is influenced by significant wastewater treatment plant discharges, was found to have high algal abundance and relatively low density and diversity of invertebrates ($3290/m^2$ from 12 taxa). In contrast, a forested site above Denver showed lower algal abundance and significantly higher invertebrate density and diversity ($10{,}600/m^2$ from 25 taxa).

Light and water temperature. Riparian canopy cover regulates stream metabolism by supplying organic detritus and controlling light intensity and water temperature (Allan 1995, Naiman and Décamps 1997). In relatively undisturbed riverine ecosystems of the Great Plains, riparian forests limit primary production by shading, whereas low summer flows and low available nitrogen and phosphorus limit primary production along grassland-dominated reaches (Tate 1990, Brown and Matthews 1995). In modified riverine systems, reduction of riparian canopy increases light and water temperatures, leading to development of thick mats of filamentous green algae due to excess primary production, and altering the balance between production and respiration. Nutrient loading and increased summer base flows may have similar effects along prairie reaches of modified rivers, but such relationships have not been studied.

Hydrology and the South Platte Fish Fauna

Life history strategies of South Platte fishes. Life history responses to flow conditions of fishes of the South Platte River Basin are poorly understood (Nesler and others 1997). However, it is known that native fishes show numerous adaptations to the natural flow regime, including reproductive strategies that help protect eggs and larvae from high spring flows and shifting substrates (Fausch and Bestgen 1997). Under natural flow conditions, one strategy is to deposit eggs in the water column during peak flows in May and June (e.g., plains minnow, *Hybognathus placitus*) (Lehtinen and Layzer 1988, Taylor and Miller 1990), where they absorb water, increase two to three times their original size, and become semibuoyant. High flows then carry the eggs downstream, where they can develop away from the shifting streambed. Eggs develop and hatch relatively quickly, limiting exposure to harsh conditions associated with spring flooding. Another strategy is to spawn as high flows recede, attaching adhesive eggs to solid surfaces above the unstable stream bed (e.g., red shiner, *Cyprinella lutrensis*) (Gale 1986). Most fish species in plains streams spawn repeatedly from spring to late fall, increasing chances that eggs and larvae from at least one cohort will encounter favorable flow conditions (Fausch and Bestgen 1997). Among the most flexible is the red shiner, which can increase production of eggs when flows are favorable or retain eggs when conditions are poor such as during droughts or floods.

Altered hydrology and fish community composition. Although effects of altered hydrology on the South Platte fish fauna have not been studied, results of other studies (Fausch and Bestgen 1997, Poff and others 1997) suggest several hydrologic changes that are likely to be important: (1) dewatering of downstream reaches due to diversions, (2) fragmentation of habitat, (3) higher flows that persist throughout summer due to irrigation return flows, (4) increased daily flow fluctuations, (5) excess nutrients in river water due to increased wastewater discharges coupled with reduced dilution capacity, and (6) increased salinity and other changes in water quality due to repeated reuse of return flows.

Such conditions can affect different species in different ways depending on species' traits, such as (1) time of spawning and rate of larval development in relation to periods of rapid flow fluctuation that include stream dewatering (Bain and others 1988), (2) vulnerability of early life stages to high flow velocities (Schlosser 1985, 1990, Harvey 1987), (3) buoyant eggs that can be displaced into unfavorable habitat under prolonged high summer flows (Robertson 1997), (4) juvenile or adult dispersal that is disrupted by loss of floodplain connectivity (Welcomme 1979) or by discontinuous flow and habitat fragmentation due to dams and diversions (Ward and Stanford 1979, Fausch and Bestgen 1997), (5) reduction in habitat types needed for different life stages due to loss of flows that move bed and bank sediments and modify in-channel and floodplain habitats (Leopold and others 1964, Hill and others 1991, Ligon and others 1995), and (6) physiological tolerances to water-quality changes.

It is difficult to determine possible changes to the South Platte fish fauna due to hydrologic changes because neither historical nor current abundances are well-known (Fausch and Bestgen 1997). However, comparison of studies in the 1960s and 1970s (Li 1968, Propst 1982, Propst and Carlson 1986) with recent studies by the Colorado Division of Wildlife (Nesler and others 1997) indicates that six fish species native to the South Platte River Basin are in decline and are under consideration for state listing as threatened or endangered. At the same time, the percentage of nonnative fishes has increased. Of the approximately 50 fish species that now occur in the South Platte River Basin in Colorado, at least 18 are nonnatives (Propst and Carlson 1986, Fausch and Bestgen 1997).

It is thought that the severe physical conditions of the historic South Platte River restricted potential fish invaders (Fausch and Bestgen 1997). Nonnative species stocked for sportfishing have generally failed to persist, apparently being unable to withstand the extreme physical conditions. However, as the natural flow regime is altered, the potential for successful invasions increases if conditions become unsuitable for native species or favor nonnatives that may be better adapted to changed conditions. Although most nonnative species are not currently reproducing in rivers, they are present in the basin and ready to invade if conditions permit. For example, northern pike (*Esox lucius*), originally stocked in a reservoir in the adjacent Arkansas River Basin to the south, have colonized a 13-km reach of a plains tributary upstream and nearly eliminated Arkansas darter (*Etheostoma cragini*) and several other native fishes (T. Labbe and K. Fausch, Colorado State University, unpublished observations). Thus, native fish assemblages may become more susceptible to invasion by exotic species as flow regimes continue to be modified, posing potential problems due to competition, predation, or hybridization.

Fish Fauna and Ecosystem Processes

The major functional roles of Great Plains fishes are thought to be: (1) as predators on smaller fishes and invertebrates, (2) as algivores affecting the abundance and diversity of algae and rates of primary production, (3) as translocators of nutrients and algae by fecal production, and (4) as food for terrestrial predators that transport nutrients from the river back onto land (Brown and Matthews 1995). As a result of the functional roles of different species, changes in fish species composition can have significant consequences for ecosystem processes. For example, loss of top predators can lead to increased abundance of filamentous green algae, reducing water quality (Power 1990). Lake studies have shown that changes in fish community composition can affect nutrient recycling rates, shifting the limiting nutrient between nitrogen and phosphorus, thereby altering aquatic plant species composition (Carpenter 1988, 1992, Scheffer 1991, Scheffer and others 1993). In large Pacific Coast rivers, human stabilization of the flow regime has reduced the abundance of predator-susceptible invertebrate herbivores and increased predator-resistant species, diverting energy away from predatory fish of interest to sport anglers (e.g., steelhead, *Oncorhynchus mykiss*) (Power and others 1996, Wootton and others 1996). In general, as the structure and composition of fish communities changes in response to flow alterations, changes in ecosystem processes, including primary production and nutrient cycling, can be expected to affect water quality and other ecosystem services important to humans.

A Strategy for Ecosystem Management and Restoration

Our framework is designed to focus attention on interactions among hydrology and biological processes, providing a mechanistic basis for watershed management. When applied to information for a specific system, the framework can help managers trace connections among flow conditions, population and community processes, and ecosystem functioning. This can improve predictions of ecological consequences of specific human activities and help managers plan flow manipulations to increase biodiversity and ecosystem services in degraded watersheds. In this way, managers can define management options for the ecosystem as a whole, including what species composition and levels of ecosystem function are possible and sustainable given local physical and biotic constraints and social values (Figure 6).

Although these principles have not been widely applied, the role of hydrology in generating biodiversity is receiving increasing attention, and there are some recent examples of hydrologically based management strategies. In impounded wetlands, coordinated management of vegetation and wildlife has involved varying water manipulations within and among years based on effects on different species of factors such as timing,

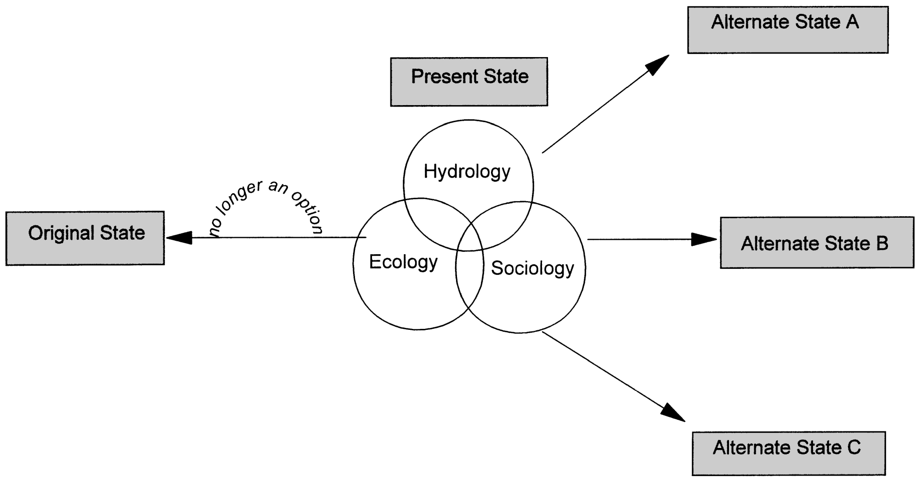

Figure 6. A conceptual view of management alternatives resulting from interactions among hydrologic, ecological, and social processes in human-dominated watersheds.

depth, duration, and extent of flooding (Fredrickson 1997, Fredrickson and Laubhan 1994, Laubhan and Fredrickson 1993, Fredrickson and Taylor 1982). This has made possible multispecies management and ongoing protection of species diversity.

In the case of the South Platte River Basin, although population-level effects of hydrology are well known for many riparian plant species, responses to flow conditions are poorly understood for most other groups, including South Platte fishes. Studies of biological responses to hydrology are needed for such lesser-known species. Such studies must be conducted at temporal and spatial scales appropriate for different species. As our case study indicates, flow regime changes occurring over decades are likely to be most important for tree species and the birds they support, while changes in annual, seasonal, or daily flow patterns may be more critical for short-lived species such as invertebrates and many fishes.

In analyzing specific river–floodplain systems, it will also be important to consider how existing geomorphic constraints will interact with hydrologic changes to influence species responses to particular flow manipulations (Ligon and others 1995, Power and others 1996). For example, along meandering channels of the Great Plains reduction in peak flows is known to slow cottonwood regeneration, whereas along braided channels flow reduction initiates a period of channel narrowing that temporarily increases regeneration (Friedman and others 1997).

It will also be necessary to anticipate how flow regime changes may reverse competitive outcomes or destabilize predator–prey dynamics, particularly in cases where species introductions are a factor (Strange and others 1992, Power and others 1996, Strange and Foin 1999). Predicting such effects will depend on knowing how interacting species differ in response to key flow variables. This will help managers avoid flow manipulations that can allow an invading species to increase and displace or even eliminate native species through competition, hybridization, or alteration of food web dynamics.

Analysis of specific systems will also help improve understanding of how flow-driven changes in community structure and composition affect ecosystem functioning (Angermeier and Schlosser 1995, Postel and Carpenter 1997). Previous work has stressed the need to integrate population and ecosystem studies to define critical relationships among species' functional traits and ecosystem processes (Vitousek 1990). It will also be important to understand how particular biotic communities influence ecosystem functioning, including potential differences in the functional importance of native and nonnative assemblages.

Conclusions

Like other human-dominated watersheds, the South Platte River Basin has been completely redefined by human land and water uses, and there is increasing concern that substantial changes will be required to ensure sustainability of essential ecosystem services (Woodring 1993, Covich and others 1995). Because restoration of natural hydrology and a return to original conditions is no longer an option, managers need improved methods for predicting what species composition and levels of ecosystem function are possible and sustainable based on existing local constraints. The framework we propose focuses on the ecological mechanisms by which hydrology integrates population and community processes to control ecosystem functioning and transitions among alternate ecosystem states. When applied to a specific river–floodplain system, the framework can help managers integrate existing information to predict flow-dependent biodiversity changes that may alter or restore a system's functional integrity and the supply of ecosystem services.

Management and restoration of human-dominated watersheds will take on increasing importance as human populations and demands for freshwater services increase (Postel and Carpenter 1997). Sustainability will depend on whether changes to existing hydrologic regimes can restore and maintain critical relationships among riparian and aquatic species and the ecosystem processes they perform (National Research Council 1992, Naiman and others 1995, Christensen and others 1996). Our results suggest that if restoration programs are to be successful, managers will need to anticipate effects of different flow manipulations on interactions among population, community, and ecosystem processes. Without an understanding of how hydrology and biotic processes interact to sustain ecosystem functioning and the provision of ecosystem services, it will be difficult to place either an ecological or social value on alternative water management scenarios. The framework we present is a tool to guide the integration and analysis of information for specific systems as a first step in developing such understanding.

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Literature Cited

Allan, J. D. 1995. Stream ecology, structure and function of running waters. Chapman & Hall, London, England.

Angermeier, P. L., and I. J. Schlosser. 1995. Conserving aquatic biodiversity: Beyond species and populations. *American Fisheries Society Symposium* 17:402–414.

Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. *Ecology* 69:382–392.

Barinaga, M. 1996. A recipe for river recovery? *Science* 273:1648–1650.

Blackburn, W. H., R. W. Knight, and J. L. Schuster. 1982. Saltcedar influence on sedimentation in the Brazos River. *Journal of Soil and Water Conservation* 37:298–301.

Botkin, D. 1990. Discordant harmonies. Oxford University Press, New York.

Brown, A. V., and W. J. Matthews. 1995. Stream ecosystems of the central United States. Pages 89–116 *in* C. E. Cushing, K. W. Commins, and G. W. Minshall (eds.), River and stream ecosystems. Elsevier, Amsterdam.

Carpenter, S. R. (ed.). 1988. Complex interactions in lake communities. Springer-Verlag, New York.

Carpenter, S. R. 1992. Destabilization of planktonic ecosystems and blooms of blue-green algae. Pages 461–481 *in* J. F. Kitchell (ed.), Food web management: A case study of Lake Mendota. Springer-Verlag, New York.

Chapin, F. S., and others. 1997. Biotic control over the functioning of ecosystems. *Science* 277:500–504.

Christensen, N. L., and others. 1996. The report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* 6:665–691.

Cole, J. J., B. L. Peierls, N. F. Caraco, and M. L. Pace. 1993. Nitrogen loading of rivers as a human-driven process. Pages 141–157 *in* M. J. McDonnell and S. T. A. Pickett (eds.), Humans as components of ecosystems. Springer-Verlag, New York.

Colorado Department of Health. 1995. Ground water monitoring in the South Platte Valley. South Platte Monitoring Fact Sheet #10, March 1995.

Colorado Division of Water Resources. 1996. Water levels in the Denver Basin bedrock aquifers. Office of the State Engineer, Colorado Division of Water Resources.

Covich, A. P., W. H. Clements, K. D. Fausch, J. D. Stednick, J. Wilkins-Wells, and S. R. Abt. 1995. Ecological integrity and western water management: A Colorado perspective. Water in the Balance No. 3, Colorado Water Resources Research Institute, Colorado State University, Fort Collins, Colorado.

Covich, A. P., S. C. Fritz, P. J. Lamb, R. D. Marzolf, W. J. Matthews, K. A. Poiani, E. E. Prepas, M. B. Richman, and T. C. Winter. 1997. Potential effects of climate change on aquatic ecosystems of the Great Plains of North America. *Hydrological Processes* 11:993–1021.

Dennehy, K. F., D. W. Litke, C. M. Tate, and J. S. Heiny. 1993. South Platte River Basin—Colorado, Nebraska, and Wyoming. *Water Resources Bulletin* 29:647–683.

Dennehy, K. R., D. W. Litke, P. B. McMahon, J. S. Heiny, and C. M. Tate. 1995. Water-quality assessment of the South Platte River Basin, Colorado, Nebraska, and Wyoming—analysis of available nutrient, suspended-sediment, and pesticide data, water years 1980–92. United States Geological Survey Water-Resources Investigation Report 94-4095.

Ehrlich, P. R., and A. H. Ehrlich. 1992. The value of biodiversity. *Ambio* 21:219–226.

Eschner, T. R., R. F. Hadley, and K. D. Crowley. 1983. Hydrologic and morphologic changes in channels of the Platte River Basin in Colorado, Wyoming, and Nebraska: a historical perspective. United States Geological Survey Professional Paper 1277-A.

Fausch, K. F., and K. Bestgen. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pages 131–166 *in* F. L. Knopf and F. B. Samson (eds.), Ecology of Great Plains vertebrates and their habitats. Springer-Verlag, New York.

Fausch, K. D., and R. G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. *Copeia* 1991:659–674.

Fredrickson, L. H. 1997. Managing forested wetlands. Pages 147–177 *in* M. S. Boyce and A. Haney (eds.), Ecosystem management, applications for sustainable forest and wildlife resources. Yale University Press, New Haven.

Fredrickson, L. H., and M. K. Laubhan. 1994. Managing wetlands for wildlife. Pages 623–647 *in* T. A. Bookhout (ed.), Research and management techniques for wildlife and habitats, 5th ed. The Wildlife Society, Bethesda, Maryland.

Fredrickson, L. H., and T. S. Taylor. 1982. Management of seasonally flooded impoundments for wildlife. Resource Publication 148, U S Fish and Wildlife Service, Washington, DC.

Friedman, J. M., M. L. Scott, and G. T. Auble. 1997. Water management and cottonwood forest dynamics along prairie streams. Pages 48–71 *in* F. L. Knopf and F. B. Samson (eds.), Ecology of Great Plains vertebrates and their habitats. Springer-Verlag, New York.

Frissell, C. A., and D. Bayles. 1996. Ecosystem management and the conservation of aquatic biodiversity and ecological integrity. *Water Resources Bulletin* 32:229–240.

Gale, W. F. 1986. Indeterminate fecundity and spawning behavior of captive red shiners—fractional, crevice Spawners. *Transactions of the American Fisheries Society* 115:429–437.

Graf, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. *Geological Society of America Bulletin* 89:1491–1501.

Graf, W. L. 1982. Tamarisk and river-channel management. *Environmental Management* 6:283–296.

Grimm, N. B. 1995. Why link species and ecosystems? A perspective from ecosystem ecology. Pages 5–15 *in* C. G. Jones and J. H. Lawton (eds.), Linking species and ecosystems. Chapman & Hall, New York.

Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* 116:851–855.

Hill, M. T., W. S. Platts, and R. L. Beschta. 1991. Ecological and geomorphological concepts for instream and out-of-channel flow requirements. *Rivers* 2:198–210.

Jackson, D., and M. L. Spence (eds.). 1970. The expeditions of John Charles Frémont, Volume 1. University of Illinois Press, Urbana.

Johnson, W. C. 1994. Woodland expansion in the Platte River, Nebraska: Patterns and causes. *Ecological Monographs* 64:45–84.

Jordan, D. S. 1891. Report on explorations in Colorado and Utah during the summer 1889, with an account of fishes found in each of the river basins examined. *United States Fisheries Commission Bulletin* 9:1–40.

Karr, J. R., and I. J. Schlosser. 1978. Water resources and the land-water interface. *Science* 201:229–234.

Kircher, J. E., and M. R. Karlinger. 1983. Effects of water development on surface-water hydrology, Platte River Basin in Colorado, Wyoming, and Nebraska upstream from Duncan, Nebraska. Hydrologic and Geomorphic Studies of the Platte River Basin. United States Geological Survey Professional Paper 1277-B.

Knopf, F. L. 1986. Changing landscapes and the cosmopolitanism of the eastern Colorado avifauna. *Wildlife Society Bulletin* 14:132–142.

Knopf, F. L. 1996. Prairie legacies—birds. Pages 135–149 *in* F. B. Samson and F. L. Knopf (eds.), Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Covelo, California.

Knopf, F. L., and T. E. Olson. 1984. Naturalization of Russian-olive: Implications to Rocky Mountain wildlife. *Wildlife Society Bulletin* 12:289–298.

Knopf, F. L., and F. B. Samson. 1997. Conservation of grassland vertebrates. Pages 273–289 *in* F. L. Knopf and F. B. Samson (eds.), Ecology of Great Plains vertebrates and their habitats. Springer-Verlag, New York.

Knopf, F. L., and M. L. Scott. 1990. Altered flows and created Landscapes in the Platte River headwaters, 1840–1990. Pages 47–70 *in* J. M. Sweeney (ed.), Management of dynamic ecosystems. North Central Section, The Wildlife Society, West Lafayette, Indiana.

Laubhan, M. K., and L. H. Fredrickson. 1993. Integrated wetland management: Concepts and opportunities. *Transactions of the North American Wildlife and Natural Resources Conference* 58:323–334.

Lehtinen, S. F., and J. B. Layzer. 1988. Reproductive cycle of the plains minnow, *Hybognathus placitus* (Cyprinidae), in the Cimarron River, Oklahoma. *Southwest Naturalist* 33:27–33.

Lemly, A. D. 1997. Risk assessment as an environmental management tool: Considerations for freshwater wetlands. *Environmental Management* 21:343–358.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W. H. Freeman & Sons, San Francisco.

Li, H. 1968. Fishes of the South Platte River basin. Unpublished MS thesis. Colorado State University, Fort Collins, Colorado.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. *BioScience* 45:183–192.

Litke, D. W. 1996. Sources and loads of nutrients in the South Platte River, Colorado and Nebraska, 1994–95. United States Geological Survey Water-Resources Investigation Report 96-4029.

Long, M. E. 1996. Colorado's Front Range. *National Geographic* November 1996.

Matthai, H. F. 1969. Floods of June 1965 in South Platte River Basin, Colorado. United States Geological Survey Water-Supply Paper 1850-B.

McMahon, P. B. 1995. Some bacteria are beneficial! United States Geological Survey, Colorado Fact Sheet, FS-102-95.

McMahon, P. B., K. J. Lull, K. F. Dennehy, and J. A. Collins. 1995. Quantity and quality of ground-water discharge to the

South Platte River, Denver to Fort Lupton, Colorado, August 1992 through July 1993. United States Geological Survey Water-Resources Investigation Report 95-4031.

Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator and prey fish species. *Ecology* 65:1525–1534.

Meffe, G. K. 1985. Predation and species replacement in American southwestern fishes: A case study. *Southwestern Naturalist* 30:173–187.

Milliken, J. G. 1988. Water management issues in the Denver, Colorado urban area. Pages 333–376 *in* M. T. El-Ashry and D. C. Gibbons (eds.), Water and arid lands of the western United States. Cambridge University Press, Cambridge, UK.

Minges, D. R. 1983. Selected hydrologic characteristics of the South Platte River in the vicinity of the proposed Narrows Reservoir near Fort Morgan, Colorado. United States Geological Survey Water-Resources Investigation Report 82-4071.

Minckley, W. L., and G. K. Meffe. 1987. Differential selection by flooding in stream-fish communities of the arid American southwest. Pages 93–104 *in* W. J. Matthews and D. C. Heins (eds.), Community and evolutionary ecology of North American stream fishes, University of Oklahoma Press, Norman, Oklahoma.

Mooney, H. A., J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulze. 1996. Functional Roles of biodiversity: A global perspective. John Wiley, Chichester, England.

Mueller, D. K., and D. R. Helsel. 1996. Nutrients in the nation's waters—too much of a good thing? United States Geological Survey Circular 1136.

Mueller, D. K., P. A. Hamilton, D. R. Helsel, K. J. Hitt, and B. C. Ruddy. 1995. Nutrients in ground water and surface water of the United States—an analysis of data through 1992. U.S. Geological Survey Water-Resources Investigations Report 95-4031.

Nadler, C. T., and S. A. Schumm. 1981. Metamorphosis of the South Platte and Arkansas Rivers, eastern Colorado. *Physical Geography* 2:95–115.

Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28:621–658.

Naiman, R. J., J. J. Magnuson, D. M. McKnight, and J. A. Stanford. 1995. The freshwater imperative: A research agenda. Island Press, Washington, DC.

Nash, L. 1993. Water quality and health. Pages 25–39 *in* P. H. Gleick (ed.), Water in crisis: A guide to the world's freshwater resources. Oxford University Press, New York.

National Research Council. 1992. Restoration of aquatic systems: Science, technology, and public policy. National Academy Press, Washington, DC.

National Research Council. 1996. A new era for irrigation. National Academy Press, Washington, DC.

Nesler, T. P., R. VanBuren, J. A. Stafford, and M. Jones. 1997. Inventory and status of South Platte River native fishes in Colorado. Final Report, June 1997, Colorado Division of Wildlife, Fort Collins, Colorado.

Olson, T. E., and F. L. Knopf. 1986. Naturalization of Russian-olive in the western U.S. *Journal of Applied Forestry* 1:65–69.

Parshall, R. 1922. Return of seepage water to the lower South Platte River in Colorado. Bulletin 279, Agricultural Experiment Station, Colorado Agricultural College, Fort Collins, Colorado.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391–409.

Poff, N. L., and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology* 76:606–627.

Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805–1818.

Poff, N. L., and J. V. Ward. 1990. The physical habitat template of lotic systems: recovery in the context of historical pattern of spatio-temporal heterogeneity. *Environmental Management* 14:629–646.

Poff, N. L., and others. 1997. The natural flow regime: A paradigm for river conservation and restoration. *BioScience* 47:769–784.

Postel, S. 1992. Last oasis: Facing water scarcity. W. W. Norton & Company, New York.

Postel, S., and S. Carpenter. 1997. Freshwater ecosystem services. Pages 195–214 *in* G. C. Dailey (ed.), Nature's services. Island Press, Washington, DC.

Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:811–814.

Power, M. E. 1995. Floods, food chains, and ecosystem processes in rivers. Pages 52–61 *in* C. J. Jones and J. H. Lawton (eds.), Linking species and ecosystems. Chapman & Hall, New York.

Power, M. E., W. E. Dietrich, and J. C. Finlay. 1996. Dams and downstream aquatic biodiversity: Potential food web consequences of hydrologic and geomorphic change. *Environmental Management* 20:887–895.

Propst, D. L. 1982. Warmwater fishes of the Platte River basin, Colorado: Distribution, ecology, and community dynamics. Unpublished PhD, dissertation. Colorado State University, Fort Collins, Colorado.

Propst, D. L., and C. A. Carlson. 1986. The distribution and status of warmwater fishes in the Platte River Drainage, Colorado. *Southwestern Naturalist* 31:149–167.

Prugh, T. 1995. Natural capital and human economic survival. ISEE Press, International Society of Ecological Economics, Solomons, Maryland.

Richter, B. D., J. V. Baumgartner, R. Wigington, and D. P. Braun. 1997. How much water does a river need? *Freshwater Biology* 37:231–249.

Robertson, L. 1997. Water operations on the Pecos River, New Mexico and the Pecos bluntnose shiner, a federally-listed minnow. United States Conference on Irrigation and Drainage Symposium.

Romero, J. G., and H. C. Bainbridge. 1989. Water levels in the bedrock aquifers of the Denver Basin, Colorado 1989. Office of the State Engineer, Division of Water Resources.

Ruddy, B. C. 1984. Streamflow gain-and-loss and suspended sediment characteristics of the South Platte River and three canals near Fort Morgan, Colorado. United States Geological Survey Water-Resources Investigation Report 84-4220.

Scheffer, M. 1991. Fish and nutrients interplay determines algal biomass: a minimal model. *Oikos* 62:271–282.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8:275–279.

Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* 66:1484–1490.

Schlosser, I. J. 1990. Environmental variation, life history attributes, and community structure in stream fishes: Implications for environmental assessment. *Environmental Management* 14:621–628.

Schulze, E.-D., and H. A. Mooney (eds.). 1993. Biodiversity and ecosystem function. Springer-Verlag, Berlin.

Shafroth, P. B., G. T. Auble, and M. L. Scott. 1995. Germination and establishment of native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). *Conservation Biology* 9:1169–1175.

Smith, D. H., K. Klein, R. Bartholomay, I. Broner, E. G. Cardon, and W. M. Frasier. 1996. Irrigation water conservation: opportunities and limitations in Colorado. Completion Report No. 190, Colorado Water Resources Research Institute, Fort Collins, Colorado.

Snyder, W. D., and G. C. Miller. 1991. Changes in plains cottonwoods along the Arkansas and South Platte Rivers—Eastern Colorado. *Prairie Naturalist* 23:165–176.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46:337–365.

Southwood, T. R. E. 1988. Tactics, strategies and templets. *Oikos* 52:3–18.

Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. *BioScience* 45:168–182.

Stanford, J. A., and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. *Nature* 335:64–66.

Stanford, J. A., and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. *Journal of the North American Benthological Society* 12:48–60.

Strange, E. M., and T. C. Foin. 1999. Interaction of physical and biological processes in the assembly of stream fish communities. *In* E. Weiher and P. Keddy (eds.), The search for assembly rules in ecological communities. Cambridge University Press (in press).

Strange, E. M., P. B. Moyle, and T. C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. *Environmental Biology of Fishes* 36:1–15.

Stromberg, J. C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecological Applications* 61: 113–131.

Tate, C. M. 1990. Patterns and controls of nitrogen in tallgrass prairie streams. *Ecology* 71:2007–2018.

Tate, C. M., and J. S. Heiny. 1995. The ordination of benthic invertebrate communities in the South Platte River Basin in relation to environmental factors. *Freshwater Biology* 33:439–454.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, G. W. Zellweger, and K. E. Bencala. 1989. Retention and transport of nutrients in a third-order stream in northwestern California: Hyporheic processes. *Ecology* 70:1893–1905.

Taylor, C. M., and R. J. Miller. 1990. Reproductive ecology and population structure of the plains minnow, *Hybognathus placitus* (Pisces: Cyprinidae), in central Oklahoma. *American Midland Naturalist* 123:32–39.

Tonn, W. M. 1990. Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society* 119:337–352.

Townsend, C. R., and A. G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* 31:265–276.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.

Ward, J. V., and J. A. Stanford. 1979. The ecology of regulated streams. Plenum Press, New York.

Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers. Longman Press, New York.

Woodring, R. C. (ed.). 1993. Defining ecological and sociological integrity for the South Platte River Basin. Proceedings of the 1992 South Platte Conference, 27–28 October, 1992. Information Series No. 72, Colorado Water Resources Research Institute, Colorado State University, Fort Collins, Colorado.

Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558–1561.