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Source: *BioScience*, Vol. 47, No. 11 (Dec., 1997), pp. 769-784
Published by: Oxford University Press on behalf of the American Institute of Biological Sciences
Stable URL: https://www.jstor.org/stable/1313099
Accessed: 26-08-2019 01:16 UTC

The Natural Flow Regime

A paradigm for river conservation and restoration

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Humans have long been fascinated by the dynamism of free-flowing waters. Yet we have expended great effort to tame rivers for transportation, water supply, flood control, agriculture, and power generation. It is now recognized that harnessing of streams and rivers comes at great cost: Many rivers no longer support socially valued native species or sustain healthy ecosystems that provide important goods and services (Naiman et al. 1995, NRC 1992).

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The ecological integrity of river ecosystems depends on their natural dynamic character

The extensive ecological degradation and loss of biological diversity resulting from river exploitation is eliciting widespread concern for conservation and restoration of healthy river ecosystems among scientists and the lay public alike (Allan and Flecker 1993, Hughes and Noss 1992, Karr et al. 1985, TNC 1996, Williams et al. 1996). Extirpation of species, closures of fisheries, groundwater depletion, declines in water quality and availability, and more frequent and intense flooding are increasingly recognized as consequences of current river management and development policies (Abramovitz 1996, Collier et al. 1996, Naiman et al. 1995). The broad social support in the United States for the Endangered Species Act, the recognition of the intrinsic value of noncommercial native species, and the proliferation of watershed councils and riverwatch teams are evidence of society's interest in maintaining the ecological integrity and self-sustaining productivity of free-flowing river systems.

Society's ability to maintain and restore the integrity of river ecosystems requires that conservation and management actions be firmly grounded in scientific understanding. However, current management approaches often fail to recognize the fundamental scientific principle that the integrity of flowing water systems depends largely on their natural dynamic character; as a result, these methods frequently prevent successful river conservation or restoration. Streamflow quantity and timing are critical components of water supply, water quality, and the ecological integrity of river systems. Indeed, streamflow, which is strongly correlated with many critical physicochemical characteristics of rivers, such as water temperature, channel geomorphology, and habitat diversity, can be considered a "master variable" that limits the distribution and abundance of riverine species (Power et al. 1995, Resh et al. 1988) and regulates the ecological integrity of flowing water systems (Figure 1). Until recently, however, the importance of natural streamflow variability in maintaining healthy aquatic ecosystems has been virtually ignored in a management context.

Historically, the "protection" of river ecosystems has been limited in scope, emphasizing water quality and only one aspect of water quantity: minimum flow. Water resources management has also suffered from the often incongruent perspectives and fragmented responsibility of agencies (for example, the US Army Corps of Engineers and Bureau of Reclamation are responsible for water supply and flood control, the US Environmental Protection Agency and state environmental agencies for water quality, and the US Fish &

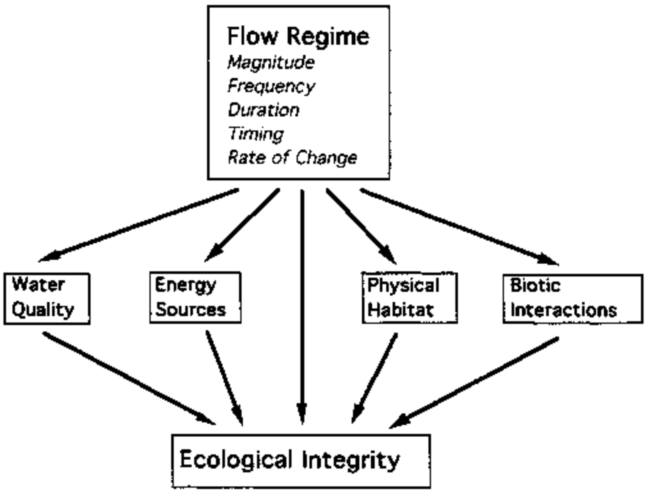

Figure 1. Flow regime is of central importance in sustaining the ecological integrity of flowing water systems. The five components of the flow regime—magnitude, frequency, duration, timing, and rate of change—influence integrity both directly and indirectly, through their effects on other primary regulators of integrity. Modification of flow thus has cascading effects on the ecological integrity of rivers. After Karr 1991.

Wildlife Service for water-dependent species of sporting, commercial, or conservation value), making it difficult, if not impossible, to manage the entire river ecosystem (Karr 1991). However, environmental dynamism is now recognized as central to sustaining and conserving native species diversity and ecological integrity in rivers and other ecosystems (Holling and Meffe 1996, Hughes 1994, Pickett et al. 1992, Stanford et al. 1996), and coordinated actions are therefore necessary to protect and restore a river's natural flow variability.

In this article, we synthesize existing scientific knowledge to argue that the natural flow regime plays a critical role in sustaining native biodiversity and ecosystem integrity in rivers. Decades of observation of the effects of human alteration of natural flow regimes have resulted in a well-grounded scientific perspective on why altering hydrologic variability in rivers is ecologically harmful (e.g., Arthington et al. 1991, Castleberry et al. 1996, Hill et al. 1991, Johnson et al. 1976, Richter et al. 1997, Sparks 1995, Stanford et al. 1996, Toth 1995, Tyus 1990). Current pressing demands on water use and the continuing alteration of watersheds require scientists to help develop management protocols that can accommodate economic uses while protecting ecosystem functions. For humans to continue to rely on river ecosystems for sustainable food production, power production, waste assimilation, and flood control, a new, holistic, ecological perspective on water management is needed to guide society's interactions with rivers.

The natural flow regime

The natural flow of a river varies on time scales of hours, days, seasons, years, and longer. Many years of observation from a streamflow gauge are generally needed to describe the characteristic pattern of a river's flow quantity, timing, and variability—that is, its natural flow regime. Components of a natural flow regime can be characterized using various time series (e.g., Fourier and wavelet) and probability analyses of, for example, extremely high or low flows, or of the entire range of flows expressed as average daily discharge (Dunne and Leopold 1978). In watersheds lacking long-term streamflow data, analyses can be extended statistically from gauged streams in the same geographic area. The frequency of large-magnitude floods can be estimated by paleohydrologic studies of debris left by floods and by studies of historical damage to living trees (Hupp and Osterkamp 1985, Knox 1972). These historical techniques can be used to extend existing hydrologic records or to provide estimates of flood flows for ungauged sites.

River flow regimes show regional patterns that are determined largely by river size and by geographic variation in climate, geology, topography, and vegetative cover. For example, some streams in regions with little seasonality in precipitation exhibit relatively stable hydrographs due to high groundwater inputs (Figure 2a), whereas other streams can fluctuate greatly at virtually any time of year (Figure 2b). In regions with seasonal precipitation, some streams are dominated by snowmelt, resulting in pronounced, predictable runoff patterns (Figure 2c), and others lack snow accumulation and exhibit more variable runoff patterns during the rainy season, with peaks occurring after each substantial storm event (Figure 2d).

Five critical components of the flow regime regulate ecological processes in river ecosystems: the magnitude, frequency, duration, timing, and rate of change of hydrologic conditions (Poff and Ward 1989, Richter et al. 1996, Walker et al. 1995). These components can be used to characterize the entire range of flows and specific hydrologic phenomena, such as floods or low flows, that are critical to the integrity of river ecosystems. Furthermore, by defining flow regimes in these terms, the ecological consequences of particular human activities that modify one or more components of the flow regime can be considered explicitly.

- The *magnitude* of discharge[1] at any given time interval is simply the amount of water moving past a fixed location per unit time. Magnitude can refer either to absolute or to relative discharge (e.g., the amount of water that inundates a floodplain). Maximum and minimum magnitudes of flow vary with climate and watershed size both within and among river systems.
- The *frequency* of occurrence refers to how often a flow above a given magnitude recurs over some specified time interval. Frequency of occurrence is inversely related to flow magnitude. For example, a 100-year flood is equaled or exceeded on average once every 100 years (i.e., a chance of 0.01 of occurring in any given year). The average (median)

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[1] Discharge (also known as streamflow, flow, or flow rate) is always expressed in dimensions of volume per time. However, a great variety of units are used to describe flow, depending on custom and purpose of characterization: Flows can be expressed in near-instantaneous terms (e.g., ft^3/s and m^3/s) or over long time intervals (e.g., acre-ft/yr).

flow is determined from a data series of discharges defined over a specific time interval, and it has a frequency of occurrence of 0.5 (a 50% probability).

- The *duration* is the period of time associated with a specific flow condition. Duration can be defined relative to a particular flow event (e.g., a floodplain may be inundated for a specific number of days by a ten-year flood), or it can be a defined as a composite expressed over a specified time period (e.g., the number of days in a year when flow exceeds some value).
- The *timing*, or *predictability*, of flows of defined magnitude refers to the regularity with which they occur. This regularity can be defined formally or informally and with reference to different time scales (Poff 1996). For example, annual peak flows may occur with low seasonal predictability (Figure 2b) or with high seasonal predictability (Figure 2c).
- The *rate of change*, or *flashiness*, refers to how quickly flow changes from one magnitude to another. At the extremes, "flashy" streams have rapid rates of change (Figure 2b), whereas "stable" streams have slow rates of change (Figure 2a).

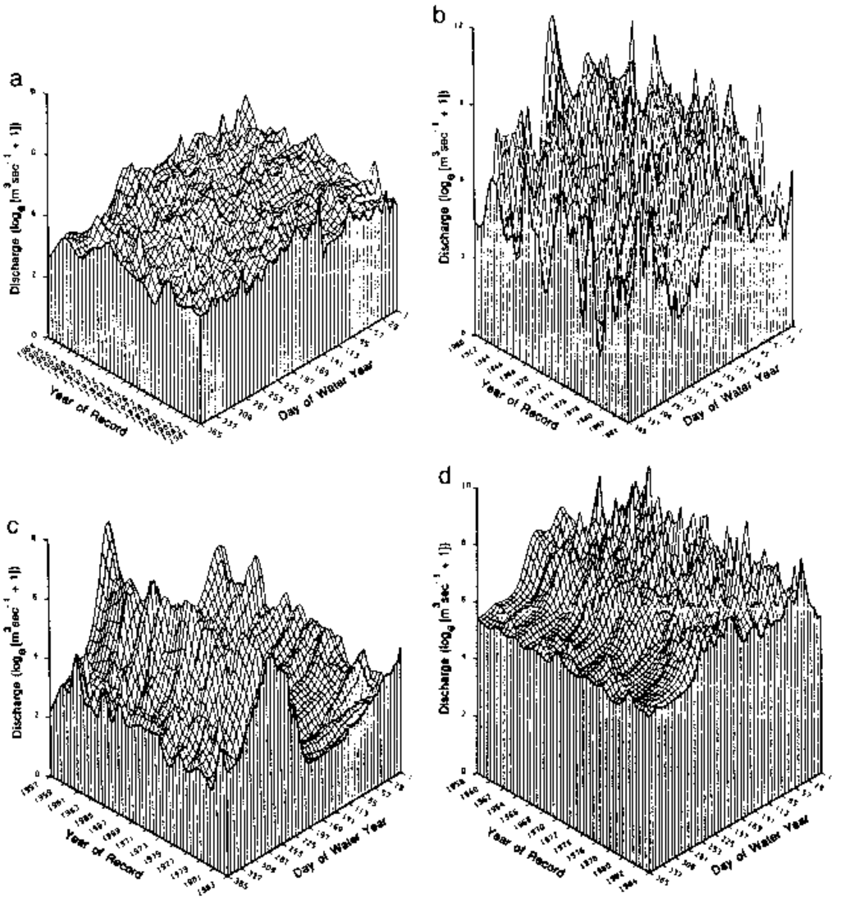


Figure 2. Flow histories based on long-term, daily mean discharge records. These histories show within- and among-year variation for (a) Augusta Creek, MI, (b) Satilla River, GA, (c) upper Colorado River, CO, and (d) South Fork of the McKenzie River, OR. Each water year begins on October 1 and ends on September 30. Adapted from Poff and Ward 1990.

Hydrologic processes and the flow regime. All river flow derives ultimately from precipitation, but in any given time and place a river's flow is derived from some combination of surface water, soil water, and groundwater. Climate, geology, topography, soils, and vegetation help to determine both the supply of water and the pathways by which precipitation reaches the channel. The water movement pathways depicted in Figure 3a illustrate why rivers in different settings have different flow regimes and why flow is variable in virtually all rivers. Collectively, overland and shallow subsurface flow pathways create hydrograph peaks, which are the river's response to storm events. By contrast, deeper groundwater pathways are responsible for baseflow, the form of delivery during periods of little rainfall.

Variability in intensity, timing, and duration of precipitation (as rain or as snow) and in the effects of terrain, soil texture, and plant evapotranspiration on the hydrologic cycle combine to create local and regional flow patterns. For example, high flows due to rainstorms may occur over periods of hours (for permeable soils) or even minutes (for impermeable soils), whereas snow will melt over a period of days or weeks, which slowly builds the peak snowmelt flood. As one proceeds downstream within a watershed, river flow reflects the sum of flow generation and routing processes operating in multiple small tributary watersheds. The travel time of flow down the river system, combined with nonsynchronous tributary inputs and larger downstream channel and floodplain storage capacities, act to attenuate and to dampen flow peaks. Consequently, annual hydrographs in large streams typically show peaks created by widespread storms or snowmelt events and broad seasonal influences that affect many tributaries together (Dunne and Leopold 1978).

The natural flow regime organizes and defines river ecosystems. In rivers, the physical structure of the environment and, thus, of the habitat, is defined largely by physical processes, especially the movement of water and sediment within the channel and between the channel and floodplain. To understand the biodiversity, production, and sustainability of river ecosystems, it is necessary to appreciate the central organizing role played by a dynamically varying physical environment.

The physical habitat of a river includes sediment size and heterogeneity, channel and floodplain morphology, and other geomorphic features. These features form as the available sediment, woody debris, and other transportable materials are moved and deposited by flow. Thus, habitat conditions associated with channels and floodplains vary among

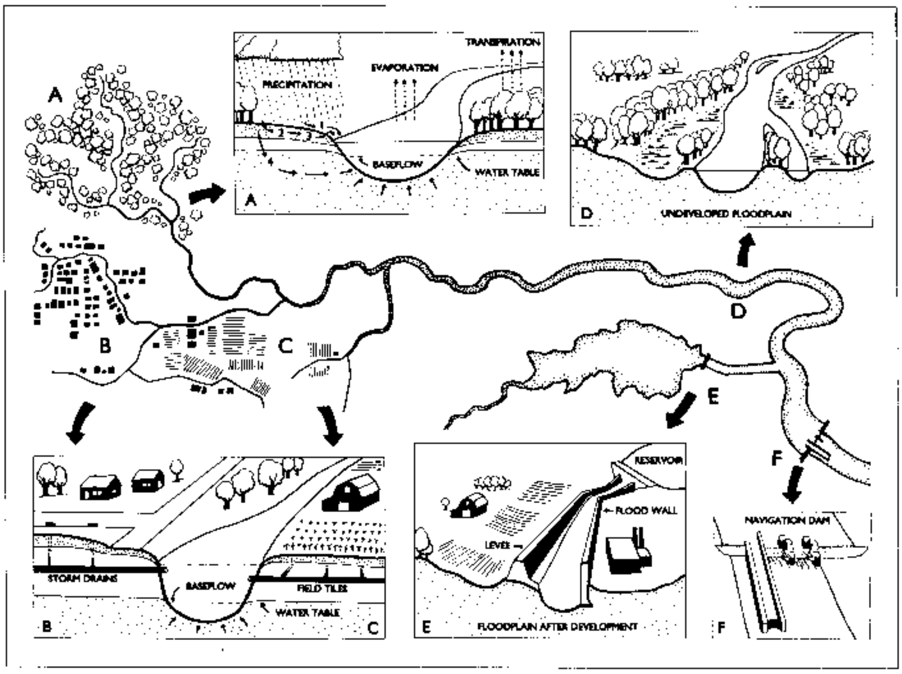


Figure 3. Stream valley cross-sections at various locations in a watershed illustrate basic principles about natural pathways of water moving downhill and human influences on hydrology. Runoff, which occurs when precipitation exceeds losses due to evaporation and plant transpiration, can be divided into four components (a): overland flow (1) occurs when precipitation exceeds the infiltration capacity of the soil; shallow subsurface stormflow (2) represents water that infiltrates the soil but is routed relatively quickly to the stream channel; saturated overland flow (3) occurs where the water table is close to the surface, such as adjacent to the stream channel, upstream of first-order tributaries, and in soils saturated by prior precipitation; and groundwater flow (4) represents relatively deep and slow pathways of water movement and provides water to the stream channel even during periods of little or no precipitation. Collectively, overland and shallow subsurface flow pathways create the peaks in the hydrograph that are a river's response to storm events, whereas deeper groundwater pathways are responsible for baseflow. Urbanized (b) and agricultural (c) land uses increase surface flow by increasing the extent of impermeable surfaces, reducing vegetation cover, and installing drainage systems. Relative to the unaltered state, channels often are scoured to greater depth by unnaturally high flood crests and water tables are lowered, causing baseflow to drop. Side-channels, wetlands, and episodically flooded lowlands comprise the diverse floodplain habitats of unmodified river ecosystems (d). Levees or flood walls (e) constructed along the banks retain flood waters in the main channel and lead to a loss of floodplain habitat diversity and function. Dams impede the downstream movement of water and can greatly modify a river's flow regime, depending on whether they are operated for storage (e) or as "run-of-river," such as for navigation (f).

rivers in accordance with both flow characteristics and the type and the availability of transportable materials.

Within a river, different habitat features are created and maintained by a wide range of flows. For example, many channel and floodplain features, such as river bars and riffle–pool sequences, are formed and maintained by dominant, or bankfull, discharges. These discharges are flows that can move significant quantities of bed or bank sediment and that occur frequently enough (e.g., every several years) to continually modify the channel (Wolman and Miller 1960). In many streams and rivers with a small range of flood flows, bankfull flow can build and maintain the active floodplain through stream migration (Leopold et al. 1964). However, the concept of a dominant discharge may not be applicable in all flow regimes (Wolman and Gerson 1978). Furthermore, in some flow regimes, the flows that build the channel may differ from those that build the floodplain. For example, in rivers with a wide range of flood flows, floodplains may exhibit major bar deposits, such as berms of boulders along the channel, or other features that are left by infrequent high-magnitude floods (e.g., Miller 1990).

Over periods of years to decades, a single river can consistently provide ephemeral, seasonal, and persistent types of habitat that range from free-flowing, to standing, to no water. This predictable diversity of in-channel and floodplain habitat types has promoted the evolution of species that exploit the habitat mosaic created and maintained by hydrologic variability. For many riverine species, completion of the life cycle requires an array of different habitat types, whose availability over time is regulated by the flow regime (e.g., Greenberg et al. 1996, Reeves et al. 1996, Sparks 1995). Indeed, adaptation to this environmental dynamism allows aquatic and floodplain species to persist in the face of seemingly harsh conditions, such as floods and droughts, that regularly destroy and re-create habitat elements.

From an evolutionary perspective, the pattern of spatial and temporal habitat dynamics influences the relative success of a species in a particular environmental setting. This habitat template (Southwood 1977), which is dictated largely by flow regime, creates both subtle and profound differences in the natural histories of species in different segments of their ranges. It also influences species distribution and abundance, as well as ecosystem function (Poff and Allan 1995, Schlosser 1990, Sparks 1992, Stanford et al. 1996). Human alteration of flow regime changes the established pattern of natural hydrologic variation and disturbance, thereby altering habitat dynamics and creating new conditions to which the native biota may be poorly adapted.

Human alteration of flow regimes

Human modification of natural hydrologic processes disrupts the dynamic equilibrium between the movement of water and the movement of sediment that exists in free-flowing rivers (Dunne and Leopold 1978). This disruption alters both gross- and fine-scale geomorphic features that constitute habitat for aquatic and riparian species (Table 1). After

Table 1. Physical responses to altered flow regimes.

Source(s) of alteration	Hydrologic change(s)	Geomorphic response(s)	Reference(s)
Dam	Capture sediment moving downstream	Downstream channel erosion and tributary headcutting	Chien 1985, Petts 1984, 1985, Williams and Wolman 1984
		Bed armoring (coarsening)	Chien 1985
Dam, diversion	Reduce magnitude and frequency of high flows	Deposition of fines in gravel	Sear 1995, Stevens et al. 1995
		Channel stabilization and narrowing	Johnson 1994, Williams and Wolman 1984
		Reduced formation of point bars, secondary channels, oxbows, and changes in channel planform	Chien 1985, Copp 1989, Fenner et al. 1985
Urbanization, tiling, drainage	Increase magnitude and frequency of high flows	Bank erosion and channel widening	Hammer 1972
		Downward incision and floodplain disconnection	Prestegaard 1988
	Reduced infiltration into soil	Reduced baseflows	Leopold 1968
Levees and channelization	Reduce overbank flows	Channel restriction causing downcutting	Daniels 1960, Prestegaard et al. 1994
		Floodplain deposition and erosion prevented	Sparks 1992
		Reduced channel migration and formation of secondary channels	Shankman and Drake 1990
Groundwater pumping	Lowered water table levels	Streambank erosion and channel downcutting after loss of vegetation stability	Kondolf and Curry 1986

such a disruption, it may take centuries for a new dynamic equilibrium to be attained by channel and floodplain adjustments to the new flow regime (Petts 1985); in some cases, a new equilibrium is never attained, and the channel remains in a state of continuous recovery from the most recent flood event (Wolman and Gerson 1978). These channel and floodplain adjustments are sometimes overlooked because they can be confounded with long-term responses of the channel to changing climates (e.g., Knox 1972). Recognition of human-caused physical changes and associated biological consequences may require many years, and physical restoration of the river ecosystem may call for dramatic action (see box on the Grand Canyon flood, page 774).

Dams, which are the most obvious direct modifiers of river flow, capture both low and high flows for flood control, electrical power generation, irrigation and municipal water needs, maintenance of recreational reservoir levels, and navigation. More than 85% of the inland waterways within the continental United States are now artificially controlled (NRC 1992), including nearly 1 million km of rivers that are affected by dams (Echeverria et al. 1989). Dams capture all but the finest sediments moving down a river, with many severe downstream consequences. For example, sediment-depleted water released from dams can erode finer sediments from the receiving channel. The coarsening of the streambed can, in turn, reduce habitat availability for the many aquatic species living in or using interstitial spaces. In addition, channels may erode, or downcut, triggering rejuvenation of tributaries, which themselves begin eroding and migrating headward (Chien 1985, Petts 1984). Fine sediments that are contributed by tributaries downstream of a dam may be deposited between the coarse particles of the streambed (e.g., Sear 1995). In the absence of high flushing flows, species with life stages that are sensitive to sedimentation, such as the eggs and larvae of many invertebrates and fish, can suffer high mortality rates.

For many rivers, it is land-use activities, including timber harvest, livestock grazing, agriculture, and urbanization, rather than dams, that are the primary causes of altered flow regimes. For example, logging and the associated building of roads have contributed greatly to degradation of salmon streams in the Pacific Northwest, mainly through effects on runoff and sediment delivery (NRC 1996). Converting forest or prairie lands to agricultural lands generally decreases soil infiltration and results in increased overland flow, channel incision, floodplain isolation, and headward erosion of stream channels (Prestegaard 1988). Many agricultural areas were drained by the construction of ditches or tile-and-drain systems, with the result that many channels have become entrenched (Brookes 1988).

These land-use practices, combined with extensive draining of wetlands or overgrazing, reduce retention of water in watersheds and,

A controlled flood in the Grand Canyon

Since the Glen Canyon dam first began to store water in 1963, creating Lake Powell, some 430 km (270 miles) of the Colorado River, including Grand Canyon National Park, have been virtually bereft of seasonal floods. Before 1963, melting snow in the upper basin produced an average peak discharge exceeding 2400 m^3/s; after the dam was constructed, releases were generally maintained at less than 500 m^3/s. The building of the dam also trapped more than 95% of the sediment moving down the Colorado River in Lake Powell (Collier et al. 1996).

This dramatic change in flow regime produced drastic alterations in the dynamic nature of the historically sediment-laden Colorado River. The annual cycle of scour and fill had maintained large sandbars along the river banks, prevented encroachment of vegetation onto these bars, and limited bouldery debris deposits from constricting the river at the mouths of tributaries (Collier et al. 1997). When flows were reduced, the limited amount of sand accumulated in the channel rather than in bars farther up the river banks, and shallow low-velocity habitat in eddies used by juvenile fishes declined. Flow regulation allowed for increased cover of wetland and riparian vegetation, which expanded into sites that were regularly scoured by floods in the constrained fluvial canyon of the Colorado River; however, much of the woody vegetation that established after the dam's construction is composed of an exotic tree, salt cedar (*Tamarix* sp.; Stevens et al. 1995). Restoration of flood flows clearly would help to steer the aquatic and riparian ecosystem toward its former state and decrease the area of wetland and riparian vegetation, but precisely how the system would respond to an artificial flood could not be predicted.

In an example of adaptive management (i.e., a planned experiment to guide further actions), a controlled, seven-day flood of 1274 m^3/s was released through the Glen Canyon dam in late March 1996. This flow, roughly 35% of the pre-dam average for a spring flood (and far less than some large historical floods), was the maximum flow that could pass through the power plant turbines plus four steel drainpipes, and it cost approximately $2 million in lost hydropower revenues (Collier et al. 1997). The immediate result was significant beach building: Over 53% of the beaches increased in size, and just 10% decreased in size. Full documentation of the effects will continue to be monitored by measuring channel cross-sections and studying riparian vegetation and fish populations.

instead, route it quickly downstream, increasing the size and frequency of floods and reducing baseflow levels during dry periods (Figure 3b; Leopold 1968). Over time, these practices degrade in-channel habitat for aquatic species. They may also isolate the floodplain from overbank flows, thereby degrading habitat for riparian species. Similarly, urbanization and suburbanization associated with human population expansion across the landscape create impermeable surfaces that direct water away from subsurface pathways to overland flow (and often into storm drains). Consequently, floods increase in frequency and intensity (Beven 1986), banks erode, and channels widen (Hammer 1972), and baseflow declines during dry periods (Figure 3c).

Whereas dams and diversions affect rivers of virtually all sizes, and land-use impacts are particularly evident in headwaters, lowland rivers are greatly influenced by efforts to sever channel–floodplain linkages. Flood control projects have shortened, narrowed, straightened, and leveed many river systems and cut the main channels off from their floodplains (NRC 1992). For example, channelization of the Kissimmee River above Lake Okeechobee, Florida, by the US Army Corps of Engineers transformed a historical 166 km meandering river with a 1.5 to 3 km wide floodplain into a 90 km long canal flowing through a series of five impoundments, resulting in great loss of river channel habitat and adjacent floodplain wetlands (Toth 1995). Because levees are designed to prevent increases in the width of flow, rivers respond by cutting deeper channels, reaching higher velocities, or both.

Channelization and wetland drainage can actually increase the magnitude of extreme floods, because reduction in upstream storage capacity results in accelerated water delivery downstream. Much of the damage caused by the extensive flooding along the Mississippi River in 1993 resulted from levee failure as the river reestablished historic connections to the floodplain. Thus, although elaborate storage dam and levee systems can "reclaim" the floodplain for agriculture and human settlement in most years, the occasional but inevitable large floods will impose increasingly high disaster costs to society (Faber 1996). The severing of floodplains from rivers also stops the processes of sediment erosion and deposition that regulate the topographic diversity of floodplains. This diversity is essential for maintaining species diversity on floodplains, where relatively small differences in land elevation result in large differences in annual inundation and soil moisture regimes, which regulate plant distribution and abundance (Sparks 1992).

Ecological functions of the natural flow regime

Naturally variable flows create and maintain the dynamics of in-channel and floodplain conditions and habitats that are essential to aquatic and riparian species, as shown schematically in Figure 4. For purposes of illustration, we treat the components of a flow regime individually, although in reality they interact in complex ways to regulate geomorphic and ecological processes. In describing the ecological functions associated with the components of a flow regime, we pay particular attention to high- and low-flow events, because they often serve as ecological "bottlenecks" that present critical stresses and opportunities for a wide array of riverine species (Poff and Ward 1989).

The magnitude and frequency of high and low flows regulate numerous ecological processes. Frequent, moderately high flows effectively transport sediment through the channel (Leopold et al. 1964). This sediment movement, combined with the force of moving water, exports organic resources, such as detritus and attached algae, rejuvenating the biological community and allowing many species with fast life cycles and good colonizing ability to reestablish (Fisher 1983). Consequently, the composition and relative abundance of species that are present in a stream or river often reflect the frequency and intensity of high flows (Meffe and Minckley 1987, Schlosser 1985).

High flows provide further ecological benefits by maintaining ecosystem productivity and diversity. For example, high flows remove and transport fine sediments that would otherwise fill the interstitial spaces in productive gravel habitats (Beschta and Jackson 1979). Floods import woody debris into the channel (Keller and Swanson 1979), where it creates new, high-quality habitat (Figure 4; Moore and Gregory 1988, Wallace and Benke 1984). By connecting the channel to the floodplain, high overbank flows also maintain broader productivity and diversity. Floodplain wetlands provide important nursery grounds for fish and export organic matter and organisms back into the main channel (Junk et al. 1989, Sparks 1995, Welcomme 1992). The scouring of floodplain soils rejuvenates habitat for plant species that germinate only on barren, wetted surfaces that are free of competition (Scott et al. 1996) or that require access to shallow water tables (Stromberg et al. 1997). Flood-resistant, disturbance-adapted riparian communities are maintained by flooding along river corridors, even in river sections that have steep banks and lack floodplains (Hupp and Osterkamp 1985).

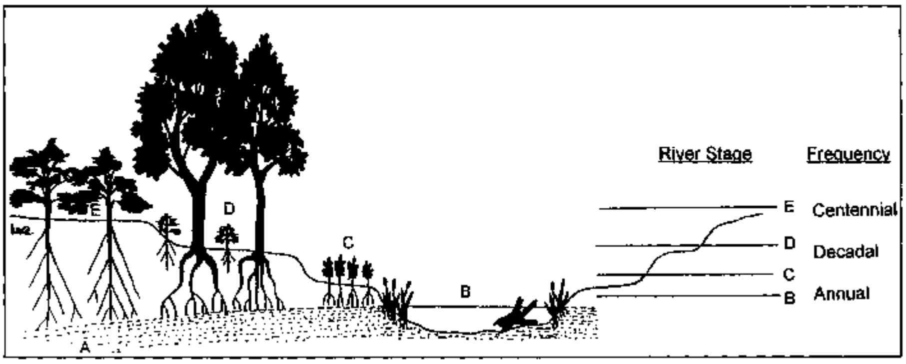


Figure 4. Geomorphic and ecological functions provided by different levels of flow. Water tables that sustain riparian vegetation and that delineate in-channel baseflow habitat are maintained by groundwater inflow and flood recharge (A). Floods of varying size and timing are needed to maintain a diversity of riparian plant species and aquatic habitat. Small floods occur frequently and transport fine sediments, maintaining high benthic productivity and creating spawning habitat for fishes (B). Intermediate-size floods inundate low-lying floodplains and deposit entrained sediment, allowing for the establishment of pioneer species (C). These floods also import accumulated organic material into the channel and help to maintain the characteristic form of the active stream channel. Larger floods that recur on the order of decades inundate the aggraded floodplain terraces, where later successional species establish (D). Rare, large floods can uproot mature riparian trees and deposit them in the channel, creating high-quality habitat for many aquatic species (E).

Flows of low magnitude also provide ecological benefits. Periods of low flow may present recruitment opportunities for riparian plant species in regions where floodplains are frequently inundated (Wharton et al. 1981). Streams that dry temporarily, generally in arid regions, have aquatic (Williams and Hynes 1977) and riparian (Nilsen et al. 1984) species with special behavioral or physiological adaptations that suit them to these harsh conditions.

The duration of a specific flow condition often determines its ecological significance. For example, differences in tolerance to prolonged flooding in riparian plants (Chapman et al. 1982) and to prolonged low flow in aquatic invertebrates (Williams and Hynes 1977) and fishes (Closs and Lake 1996) allow these species to persist in locations from which they might otherwise be displaced by dominant, but less tolerant, species.

The timing, or predictability, of flow events is critical ecologically because the life cycles of many aquatic and riparian species are timed to either avoid or exploit flows of variable magnitudes. For example, the natural timing of high or low streamflows provides environmental cues for initiating life cycle transitions in fish, such as spawning (Montgomery et al. 1983, Nesler et al. 1988), egg hatching (Næsje et al. 1995), rearing (Seegrist and Gard 1978), movement onto the floodplain for feeding or reproduction (Junk et al. 1989, Sparks 1995, Welcomme 1992), or migration upstream or downstream (Trépanier et al. 1996). Natural seasonal variation in flow conditions can prevent the successful establishment of nonnative species with flow-dependent spawning and egg incubation requirements, such as striped bass (*Morone saxatilis*; Turner and Chadwick 1972) and brown trout (*Salmo trutta*; Moyle and Light 1996, Strange et al. 1992).

Seasonal access to floodplain wetlands is essential for the survival of certain river fishes, and such access can directly link high wetland productivity with fish production in the stream channel (Copp 1989, Welcomme 1979). Studies of the effects on stream fishes of both extensive and limited floodplain inundation (Finger and Stewart 1987, Ross and Baker 1983) indicate that some fishes are adapted to exploiting floodplain habitats, and these species decline in abundance when floodplain use is restricted. Models indicate that catch rates and biomass of fish are influenced by both maximum and minimum wetland area (Power et al. 1995, Welcomme and Hagborg 1977), and empirical work shows that the area of floodplain water bodies during nonflood periods influences the species richness of those wetland habitats (Halyk and Balon 1983). The timing of floodplain inundation is important for some fish because migratory and reproductive behaviors must coincide with access to and avail-

Table 2. Ecological responses to alterations in components of natural flow regime.[a]

Flow component	Specific alteration	Ecological response	Reference(s)
Magnitude and frequency	Increased variation	Wash-out and/or stranding	Cushman 1985, Petts 1984
		Loss of sensitive species	Gehrke et al. 1995, Kingsolving and Bain 1993, Travnichek et al. 1995
		Increased algal scour and wash-out of organic matter	Petts 1984
		Life cycle disruption	Scheidegger and Bain 1995
		Altered energy flow	Valentin et al. 1995
	Flow stabilization	Invasion or establishment of exotic species, leading to:	
		Local extinction	Kupferberg 1996, Meffe 1984
		Threat to native commercial species	Stanford et al. 1996
		Altered communities	Busch and Smith 1995, Moyle 1986, Ward and Stanford 1979
		Reduced water and nutrients to floodplain plant species, causing:	
		Seedling desiccation	Duncan 1993
		Ineffective seed dispersal	Nilsson 1982
		Loss of scoured habitat patches and secondary channels needed for plant establishment	Fenner et al. 1985, Rood et al. 1995, Scott et al. 1997, Shankman and Drake 1990
		Encroachment of vegetation into channels	Johnson 1994, Nilsson 1982
Timing	Loss of seasonal flow peaks	Disrupt cues for fish:	
		Spawning	Fausch and Bestgen 1997, Montgomery et al. 1993, Nesler et al. 1988
		Egg hatching	Næsje et al. 1995
		Migration	Williams 1996
		Loss of fish access to wetlands or backwaters	Junk et al. 1989, Sparks 1995
		Modification of aquatic food web structure	Power 1992, Wootton et al. 1996
		Reduction or elimination of riparian plant recruitment	Fenner et al. 1985
		Invasion of exotic riparian species	Horton 1977
		Reduced plant growth rates	Reily and Johnson 1982
Duration	Prolonged low flows	Concentration of aquatic organisms	Cushman 1985, Petts 1984
		Reduction or elimination of plant cover	Taylor 1982
		Diminished plant species diversity	Taylor 1982
		Desertification of riparian species composition	Busch and Smith 1995, Stromberg et al. 1996
		Physiological stress leading to reduced plant growth rate, morphological change, or mortality	Kondolf and Curry 1986, Perkins et al. 1984, Reily and Johnson 1982, Rood et al. 1995, Stromberg et al. 1992
	Prolonged baseflow "spikes"	Downstream loss of floating eggs	Robertson 1997
	Altered inundation duration	Altered plant cover types	Auble et al. 1994
	Prolonged inundation	Change in vegetation functional type	Bren 1992, Connor et al. 1981
		Tree mortality	Harms et al. 1980
		Loss of riffle habitat for aquatic species	Bogan 1993
Rate of change	Rapid changes in river stage	Wash-out and stranding of aquatic species	Cushman 1985, Petts 1984
	Accelerated flood recession	Failure of seedling establishment	Rood et al. 1995

[a] Only representative studies are listed here. Additional references are located on the Web at http://lamar.colostate.edu/~poff/natflow.html.

ability of floodplain habitats (Welcomme 1979). The match of reproductive period and wetland access also explains some of the yearly variation in stream fish community composition (Finger and Stewart 1987).

Many riparian plants also have life cycles that are adapted to the seasonal timing components of natural flow regimes through their "emergence phenologies"—the seasonal sequence of flowering, seed dispersal, germination, and seedling growth. The interaction of emergence phenologies with temporally varying environmental stress from flooding or drought helps to maintain high species diversity in, for example, southern floodplain forests (Streng et al. 1989). Productivity of riparian forests is also influenced by flow timing and can increase when short-duration flooding occurs in the growing season (Mitsch and Rust 1984, Molles et al. 1995).

The rate of change, or flashiness, in flow conditions can influence species persistence and coexistence. In many streams and rivers, particularly in arid areas, flow can change dramatically over a period of hours due to heavy storms. Non-native fishes generally lack the behavioral adaptations to avoid being displaced downstream by sudden floods (Minckley and Deacon 1991). In a dramatic example of how floods can benefit native species, Meffe (1984) documented that a native fish, the Gila topminnow (*Poeciliopsis occidentalis*), was locally extirpated by the introduced predatory mosquitofish (*Gambusia affinis*) in locations where natural flash floods were regulated by upstream dams, but the native species persisted in naturally flashy streams.

Rapid flow increases in streams of the central and southwestern United States often serve as spawning cues for native minnow species, whose rapidly developing eggs are either broadcast into the water column or attached to submerged structures as floodwaters recede (Fausch and Bestgen 1997, Robertson in press). More gradual, seasonal rates of change in flow conditions also regulate the persistence of many aquatic and riparian species. Cottonwoods (*Populus* spp.), for example, are disturbance species that establish after winter–spring flood flows, during a narrow "window of opportunity" when competition-free alluvial substrates and wet soils are available for germination. A certain rate of floodwater recession is critical to seedling germination because seedling roots must remain connected to a receding water table as they grow downward (Rood and Mahoney 1990).

Ecological responses to altered flow regimes

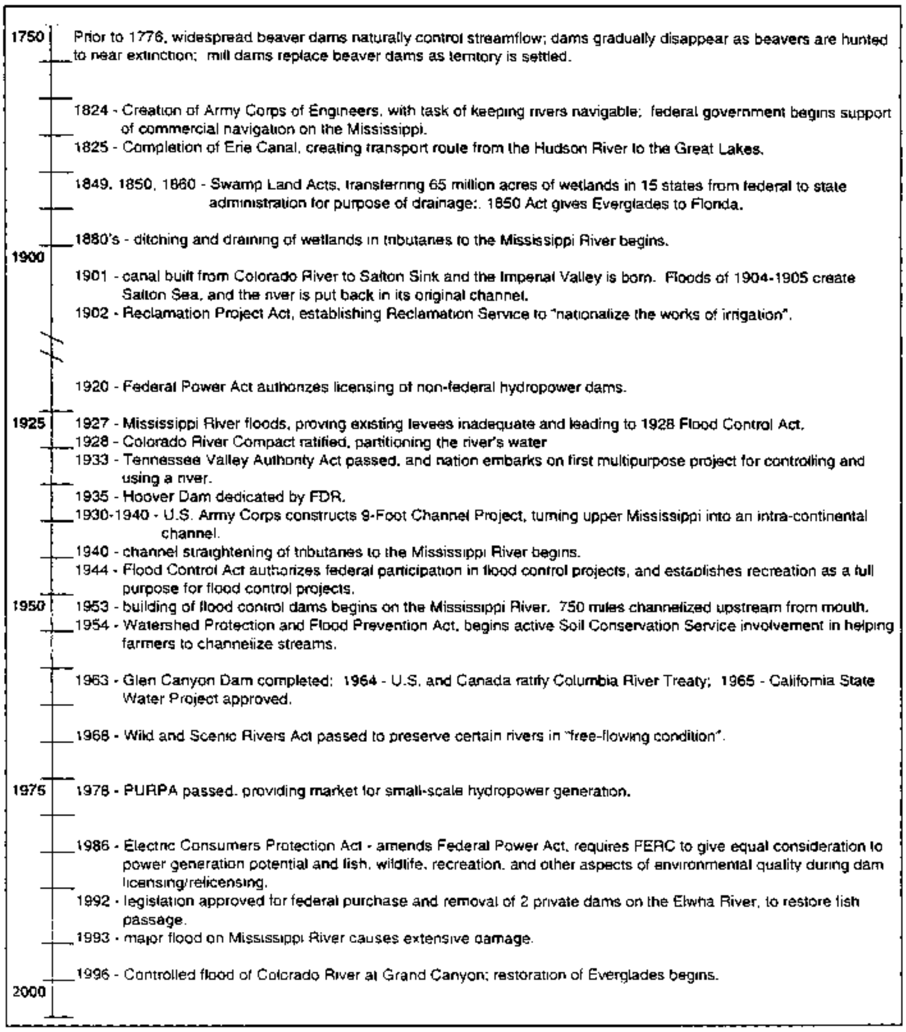
Modification of the natural flow regime dramatically affects both aquatic and riparian species in streams and rivers worldwide. Ecological responses to altered flow regimes in a specific stream or river depend on how the components of flow have changed relative to the natural flow regime for that particular stream or river (Poff and Ward 1990) and how specific geomorphic and ecological processes will respond to this relative change. As a result of variation in flow regime within and among rivers (Figure 2), the same human activity in different locations may cause different degrees of change relative to unaltered conditions and, therefore, have different ecological consequences.

Flow alteration commonly changes the magnitude and frequency of high and low flows, often reducing variability but sometimes enhancing the range. For example, the extreme daily variations below peaking power hydroelectric dams have no natural analogue in freshwater systems and represent, in an evolutionary sense, an extremely harsh environment of frequent, unpredictable flow disturbance. Many aquatic populations living in these environments suffer high mortality from physiological stress, from wash-out during high flows, and from stranding during rapid dewatering (Cushman 1985, Petts 1984). Especially in shallow shoreline habitats, frequent atmospheric exposure for even brief periods can result in massive mortality of bottom-dwelling organisms and subsequent severe reductions in biological productivity (Weisberg et al. 1990). Moreover, the rearing and refuge functions of shallow shoreline or backwater areas, where many small fish species and the young of large species are found (Greenberg et al. 1996, Moore and Gregory 1988), are severely impaired by frequent flow fluctuations (Bain et al. 1988, Stanford 1994). In these artificially fluctuating environments, specialized stream or river species are typically replaced by generalist species that tolerate frequent and large variations in flow. Furthermore, life cycles of many species are often disrupted and energy flow through the ecosystem is greatly modified (Table 2). Short-term flow modifications clearly lead to a reduction in both the natural diversity and abundance of many native fish and invertebrates.

At the opposite hydrologic extreme, flow stabilization below certain types of dams, such as water supply reservoirs, results in artificially constant environments that lack natural extremes. Although production of a few species may increase greatly, it is usually at the expense of other native species and of systemwide species diversity (Ward and Stanford 1979). Many lake fish species have successfully invaded (or been intentionally established in) flow-stabilized river environments (Moyle 1986, Moyle and Light 1996). Often top predators, these introduced fish can devastate native river fish and threaten commercially valuable stocks (Stanford et al. 1996). In the southwestern United States, virtually the entire native river fish fauna is listed as threatened under the Endangered Species Act, largely as a consequence of water withdrawal, flow stabilization, and exotic species proliferation. The last remaining strongholds of native river fishes are all in dynamic, free-flowing rivers, where exotic fishes are periodically reduced by natural flash floods (Minckley and Deacon 1991, Minckley and Meffe 1987).

Flow stabilization also reduces the magnitude and frequency of overbank flows, affecting riparian plant species and communities. In rivers with constrained canyon reaches or multiple shallow channels, loss of high flows results in increased cover of plant species that would otherwise be removed by flood scour (Ligon et al. 1995, Williams and Wolman 1984). Moreover, due to other related effects of flow regulation, including increased water salinity, non-native vegetation often dominates, such as the salt cedar (*Tamarix* sp.) in the semiarid western United States (Busch and Smith 1995). In alluvial valleys, the loss of overbank flows can greatly modify riparian communities by causing plant desiccation, reduced growth, competitive exclusion, ineffective seed dispersal, or failure of seedling establishment (Table 2).

The elimination of flooding may also affect animal species that depend on terrestrial habitats. For example, in the flow-stabilized Platte River of the United States Great Plains, the channel has narrowed dramatically (up to 85%) over a period of decades (Johnson 1994). This narrowing has been facilitated by vegetative colonization of sandbars that formerly provided nesting habitat for the threatened piping plover (*Charadius melodius*) and endangered least tern (*Sterna antillarum*; Sidle et al. 1992). Sandhill cranes (*Grus canadensis*), which made the Platte River famous, have abandoned river segments that have narrowed the most (Krapu et al. 1984).



Prior to 1776, widespread beaver dams naturally control streamflow; dams gradually disappear as beavers are hunted to near extinction; mill dams replace beaver dams as territory is settled.
1824 - Creation of Army Corps of Engineers, with task of keeping rivers navigable; federal government begins support of commercial navigation on the Mississippi.
1825 - Completion of Erie Canal, creating transport route from the Hudson River to the Great Lakes.
1849, 1850, 1860 - Swamp Land Acts, transferring 65 million acres of wetlands in 15 states from federal to state administration for purpose of drainage:. 1850 Act gives Everglades to Florida.
1880's - ditching and draining of wetlands in tributaries to the Mississippi River begins.
1901 - canal built from Colorado River to Salton Sink and the Imperial Valley is born. Floods of 1904-1905 create Salton Sea, and the river is put back in its original channel.
1902 - Reclamation Project Act, establishing Reclamation Service to "nationalize the works of irrigation".
1920 - Federal Power Act authorizes licensing of non-federal hydropower dams.
1927 - Mississippi River floods, proving existing levees inadequate and leading to 1928 Flood Control Act.
1928 - Colorado River Compact ratified, partitioning the river's water
1933 - Tennessee Valley Authority Act passed, and nation embarks on first multipurpose project for controlling and using a river.
1935 - Hoover Dam dedicated by FDR.
1930-1940 - U.S. Army Corps constructs 9-Foot Channel Project, turning upper Mississippi into an intra-continental channel.
1940 - channel straightening of tributaries to the Mississippi River begins.
1944 - Flood Control Act authorizes federal participation in flood control projects, and establishes recreation as a full purpose for flood control projects.
1953 - building of flood control dams begins on the Mississippi River. 750 miles channelized upstream from mouth.
1954 - Watershed Protection and Flood Prevention Act, begins active Soil Conservation Service involvement in helping farmers to channelize streams.
1963 - Glen Canyon Dam completed; 1964 - U.S. and Canada ratify Columbia River Treaty; 1965 - California State Water Project approved.
1968 - Wild and Scenic Rivers Act passed to preserve certain rivers in "free-flowing condition".
1978 - PURPA passed, providing market for small-scale hydropower generation.
1986 - Electric Consumers Protection Act - amends Federal Power Act, requires FERC to give equal consideration to power generation potential and fish, wildlife, recreation, and other aspects of environmental quality during dam licensing/relicensing.
1992 - legislation approved for federal purchase and removal of 2 private dams on the Elwha River, to restore fish passage.
1993 - major flood on Mississippi River causes extensive damage.
1996 - Controlled flood of Colorado River at Grand Canyon; restoration of Everglades begins.

Figure 5. A brief history of flow alteration in the United States.

Changes in the duration of flow conditions also have significant biological consequences. Riparian plant species respond dramatically to channel dewatering, which occurs frequently in arid regions due to surface water diversion and groundwater pumping. These biological and ecological responses range from altered leaf morphology to total loss of riparian vegetation cover (Table 2). Changes in duration of inundation, independent of changes in annual volume of flow, can alter the abundance of plant cover types (Auble et al. 1994). For example, increased duration of inundation has contributed to the conversion of grassland to forest along a regulated Australian river (Bren 1992). For aquatic species, prolonged flows of particular levels can also be damaging. In the regulated Pecos River of New Mexico, artificially prolonged high summer flows for irrigation displace the floating eggs of the threatened Pecos bluntnose shiner (*Notropis sinius pecosensis*) into unfavorable habitat, where none survive (Robertson in press).

Modification of natural flow timing, or predictability, can affect aquatic organisms both directly and indirectly. For example, some native fishes in Norway use seasonal flow peaks as a cue for egg hatching, and river regulation that eliminates these peaks can directly reduce local population sizes of these species (Næsje et al. 1995). Furthermore, entire food webs, not just single species, may be modified by altered flow timing. In regulated rivers of northern California, the seasonal shifting of scouring flows from winter to summer indirectly reduces the growth rate of juvenile steelhead trout (*Oncorhyncus mykiss*) by increasing the relative abundance of predator-resistant invertebrates that divert energy away from the food chain leading to trout (Wootton et al. 1996). In unregulated rivers, high winter flows reduce these predator-resistant insects and favor species that are more palatable to fish.

Riparian plant species are also strongly affected by altered flow timing (Table 2). A shift in timing of peak flows from spring to summer, as often occurs when reservoirs are managed to supply irrigation water, has prevented reestablishment of the Fremont cottonwood (*Populus fremontii*), the dominant plant species in Arizona, because flow peaks now occur after, rather than before, its germination period (Fenner et al. 1985). Non-native plant species with less specific germination requirements may benefit from changes in flood timing. For example, salt cedar's (*Tamarix* sp.) long seed dispersal period allows it to establish after floods occurring any time during the growing season, contributing to its abundance on floodplains of the western United States (Horton 1977).

Altering the rate of change in flow can negatively affect both aquatic and riparian species. As mentioned above, loss of natural flashiness threatens most of the native fish fauna of the American Southwest (Minckley and Deacon 1991), and artificially increased rates of change caused by peaking power hydroelectric dams on historically less flashy rivers creates numerous ecological problems (Table 2; Petts 1984). A modified rate of change can devastate riparian species, such as cottonwoods, whose successful seedling growth depends on the rate of groundwater recession following floodplain inundation. In the St. Mary River in Alberta, Canada, for example, rapid drawdowns of river stage during spring have prevented the recruitment of young trees (Rood and Mahoney 1990). Such effects can be reversed, however. Restoration of the spring flood and its natural, slow recession in the Truckee River in California has allowed the successful establishment of a new generation of cotton-

Table 3. Recent projects in which restoration of some component(s) of natural flow regimes has occurred or been proposed for specific ecological benefits.

Location	Flow component(s)	Ecological purpose(s)	Reference
Trinity River, CA	Mimic timing and magnitude of peak flow	Rejuvenate in-channel gravel habitats; restore early riparian succession; provide migration flows for juvenile salmon	Barinaga 1996[a]
Truckee River, CA	Mimic timing, magnitude, and duration of peak flow, and its rate of change during recession	Restore riparian trees, especially cottonwoods	Klotz and Swanson 1997
Owens River, CA	Increase base flows; partially restore overbank flows	Restore riparian vegetation and habitat for native fishes and non-native brown trout	Hill and Platts in press
Rush Creek, CA (and other tributaries to Mono Lake)	Increase minimum flows	Restore riparian vegetation and habitat for waterfowl and non-native fishes	LADWP 1995
Oldman River and tributaries, southern Alberta, Canada	Increase summer flows; reduce rates of postflood stage decline; mimic natural flows in wet years	Restore riparian vegetation (cottonwoods) and cold-water (trout) fisheries	Rood et al. 1995
Green River, UT	Mimic timing and duration of peak flow and duration and timing of nonpeak flows; reduce rapid baseflow fluctuations from hydropower generation	Recovery of endangered fish species; enhance other native fishes	Stanford 1994
San Juan River, UT/NM	Mimic magnitude, timing, and duration of peak flow; restore low winter baseflows	Recovery of endangered fish species	—[b]
Gunnison River, CO	Mimic magnitude, timing, and duration of peak flow; mimic duration and timing of nonpeak flows	Recovery of endangered fish species	—[b]
Rio Grande River, NM	Mimic timing and duration of floodplain inundation	Ecosystem processes (e.g., nitrogen flux, microbial activity, litter decomposition)	Molles et al. 1995
Pecos River, NM	Regulate duration and magnitude of summer irrigation releases to mimic spawning flow "spikes"; maintain minimum flows	Determine spawning and habitat needs for threatened fish species	Robertson 1997
Colorado River, AZ	Mimic magnitude and timing	Restore habitat for endangered fish species and scour riparian zone	Collier et al. 1997
Bill Williams River, AZ (proposed)	Mimic natural flood peak timing and duration	Promote establishment of native trees	USCOE 1996
Pemigewasset River, NH	Reduce frequency (i.e., to no more than natural frequency) of high flows during summer low-flow season; reduce rate of change between low and high flows during hydropower cycles	Enhance native Atlantic salmon recovery	FERC 1995
Roanoke River, VA	Restore more natural patterning of monthly flows in spring; reduce rate of change between low and high flows during hydropower cycles	Increased reproduction of striped bass	Rulifson and Manooch 1993
Kissimmee River, FL	Mimic magnitude, duration, rate of change, and timing of high- and low-flow periods	Restore floodplain inundation to recover wetland functions; reestablish in-channel habitats for fish and other aquatic species	Toth 1995

[a] J. Polos, 1997, personal communication. US Fish & Wildlife Service, Arcata, CA.

[b] F. Pfeifer, 1997, personal communication. US Fish & Wildlife Service, Grand Junction, CO.

wood trees (Klotz and Swanson 1997).

Recent approaches to streamflow management

Methods to estimate environmental flow requirements for rivers focus primarily on one or a few species that live in the wetted river channel. Most of these methods have the narrow intent of establishing minimum allowable flows. The simplest make use of easily analyzed flow data, of assumptions about the regional similarity of rivers, and of professional opinions of the minimal flow needs for certain fish species (e.g., Larson 1981).

A more sophisticated assessment of how changes in river flow affect aquatic habitat is provided by the Instream Flow Incremental Methodology (IFIM; Bovee and Milhous

1978). IFIM combines two models, a biological one that describes the physical habitat preferences of fishes (and occasionally macroinvertebrates) in terms of depth, velocity, and substrate, and a hydraulic one that estimates how the availability of habitat for fish varies with discharge. IFIM has been widely used as an organizational framework for formulating and evaluating alternative water management options related to production of one or a few fish species (Stalnaker et al. 1995).

As a predictive tool for ecological management, the IFIM modeling approach has been criticized both in terms of the statistical validity of its physical habitat characterizations (Williams 1996) and the limited realism of its biological assumptions (Castleberry et al. 1996). Field tests of its predictions have yielded mixed results (Morehardt 1986). Although this approach continues to evolve, both by adding biological realism (Van Winkle et al. 1993) and by expanding the range of habitats modeled (Stalnaker et al. 1995), in practice it is often used only to establish minimum flows for "important" (i.e., game or imperiled) fish species. But current understanding of river ecology clearly indicates that fish and other aquatic organisms require habitat features that cannot be maintained by minimum flows alone (see Stalnaker 1990). A range of flows is necessary to scour and revitalize gravel beds, to import wood and organic matter from the floodplain, and to provide access to productive riparian wetlands (Figure 4). Interannual variation in these flow peaks is also critical for maintaining channel and riparian dynamics. For example, imposition of only a fixed high-flow level each year would simply result in the equilibration of in-channel and floodplain habitats to these constant peak flows.

Moreover, a focus on one or a few species and on minimum flows fails to recognize that what is "good" for the ecosystem may not consistently benefit individual species, and that what is good for individual species may not be of benefit to the ecosystem. Long-term studies of naturally variable systems show that some species do best in wet years, that other species do best in dry years, and that overall biological diversity and ecosystem function benefit from these variations in species success (Tilman et al. 1994). Indeed, experience in river restoration clearly shows the impossibility of simultaneously engineering optimal conditions for all species (Sparks 1992, 1995, Toth 1995). A holistic view that attempts to restore natural variability in ecological processes and species success (and that acknowledges the tremendous uncertainty that is inherent in attempting to mechanistically model all species in the ecosystem) is necessary for ecosystem management and restoration (Franklin 1993).

Managing toward a natural flow regime

The first step toward better incorporating flow regime into the management of river ecosystems is to recognize that extensive human alteration of river flow has resulted in widespread geomorphic and ecological changes in these ecosystems. The history of river use is also a history of flow alteration (Figure 5). The early establishment of the US Army Corps of Engineers is testimony to the importance that the nation gave to developing navigable water routes and to controlling recurrent large floods. However, growing understanding of the ecological impacts of flow alteration has led to a shift toward an appreciation of the merits of free-flowing rivers. For example, the Wild and Scenic Rivers Act of 1968 recognized that the flow of certain rivers should be protected as a national resource, and the recent blossoming of natural flow restoration projects (Table 3) may herald the beginning of efforts to undo some of the damage of past flow alterations. The next century holds promise as an era for renegotiating human relationships with rivers, in which lessons from past experience are used to direct wise and informed action in the future.

A large body of evidence has shown that the natural flow regime of virtually all rivers is inherently variable, and that this variability is critical to ecosystem function and native biodiversity. As we have already discussed, rivers with highly altered and regulated flows lose their ability to support natural processes and native species. Thus, to protect pristine or nearly pristine systems, it is necessary to preserve the natural hydrologic cycle by safeguarding against upstream river development and damaging land uses that modify runoff and sediment supply in the watershed.

Most rivers are highly modified, of course, and so the greatest challenges lie in managing and restoring rivers that are also used to satisfy human needs. Can reestablishing the natural flow regime serve as a useful management and restoration goal? We believe that it can, although to varying degrees, depending on the present extent of human intervention and flow alteration affecting a particular river. Recognizing the natural variability of river flow and explicitly incorporating the five components of the natural flow regime (i.e., magnitude, frequency, duration, timing, and rate of change) into a broader framework for ecosystem management would constitute a major advance over most present management, which focuses on minimum flows and on just a few species. Such recognition would also contribute to the developing science of stream restoration in heavily altered watersheds, where, all too often, physical channel features (e.g., bars and woody debris) are re-created without regard to restoring the flow regime that will help to maintain these re-created features.

Just as rivers have been incrementally modified, they can be incrementally restored, with resulting improvements to many physical and biological processes. A list of recent efforts to restore various components of a natural flow regime (that is, to "naturalize" river flow) demonstrates the scope for success (Table 3). Many of the projects summarized in Table 3 represent only partial steps toward full flow restoration, but they have had demonstrable ecological benefits. For example, high flood flows followed by mimicked natural rates of flow decline in the Oldman River of Alberta, Canada, resulted in a massive cottonwood recruitment that extended for more than 500 km downstream from the Oldman Dam. Dampening of the unnatural flow fluctuations caused by hydroelectric generation on the Roanoke River in

Virginia has increased juvenile abundances of native striped bass. Mimicking short-duration flow spikes that are historically caused by summer thunderstorms in the regulated Pecos River of New Mexico has benefited the reproductive success of the Pecos bluntnose shiner.

We also recognize that there are scientific limits to how precisely the natural flow regime for a particular river can be defined. It is possible to have only an approximate knowledge of the historic condition of a river, both because some human activities may have preceded the installation of flow gauges, and because climate conditions may have changed over the past century or more. Furthermore, in many rivers, year-to-year differences in the timing and quantity of flow result in substantial variability around any average flow condition. Accordingly, managing for the "average" condition can be misguided. For example, in human-altered rivers that are managed for incremental improvements, restoring a flow pattern that is simply proportional to the natural hydrograph in years with little runoff may provide few if any ecological benefits, because many geomorphic and ecological processes show nonlinear responses to flow. Clearly, half of the peak discharge will not move half of the sediment, half of a migration-motivational flow will not motivate half of the fish, and half of an overbank flow will not inundate half of the floodplain. In such rivers, more ecological benefits would accrue from capitalizing on the natural between-year variability in flow. For example, in years with above-average flow, "surplus" water could be used to exceed flow thresholds that drive critical geomorphic and ecological processes.

If full flow restoration is impossible, mimicking certain geomorphic processes may provide some ecological benefits. Well-timed irrigation could stimulate recruitment of valued riparian trees such as cottonwoods (Friedman et al. 1995). Strategically clearing vegetation from river banks could provide new sources of gravel for sediment-starved regulated rivers with reduced peak flows (e.g., Ligon et al. 1995). In all situations, managers will be required to make judgments about specific restoration goals and to work with appropriate components of the natural flow regime to achieve those goals. Recognition of the natural flow variability and careful identification of key processes that are linked to various components of the flow regime are critical to making these judgments.

Setting specific goals to restore a more natural regime in rivers with altered flows (or, equally important, to preserve unaltered flows in pristine rivers) should ideally be a cooperative process involving river scientists, resource managers, and appropriate stakeholders. The details of this process will vary depending on the specific objectives for the river in question, the degree to which its flow regime and other environmental variables (e.g., thermal regime, sediment supply) have been altered, and the social and economic constraints that are in play. Establishing specific criteria for flow restoration will be challenging because our understanding of the interactions of individual flow components with geomorphic and ecological processes is incomplete. However, quantitative, river-specific standards can, in principle, be developed based on the reconstruction of the natural flow regime (e.g., Richter et al. 1997). Restoration actions based on such guidelines should be viewed as experiments to be monitored and evaluated—that is, adaptive management—to provide critical new knowledge for creative management of natural ecosystem variability (Table 3).

To manage rivers from this new perspective, some policy changes are needed. The narrow regulatory focus on minimum flows and single species impedes enlightened river management and restoration, as do the often conflicting mandates of the many agencies and organizations that are involved in the process. Revisions of laws and regulations, and redefinition of societal goals and policies, are essential to enable managers to use the best science to develop appropriate management programs.

Using science to guide ecosystem management requires that basic and applied research address difficult questions in complex, real-world settings, in which experimental controls and statistical replication are often impossible. Too little attention and too few resources have been devoted to clarifying how restoring specific components of the flow regime will benefit the entire ecosystem. Nevertheless, it is clear that, whenever possible, the natural river system should be allowed to repair and maintain itself. This approach is likely to be the most successful and the least expensive way to restore and maintain the ecological integrity of flow-altered rivers (Stanford et al. 1996). Although the most effective mix of human-aided and natural recovery methods will vary with the river, we believe that existing knowledge makes a strong case that restoring natural flows should be a cornerstone of our management approach to river ecosystems.

Acknowledgments

We thank the following people for reading and commenting on earlier versions of this paper: Jack Schmidt, Lou Toth, Mike Scott, David Wegner, Gary Meffe, Mary Power, Kurt Fausch, Jack Stanford, Bob Naiman, Don Duff, John Epifanio, Lori Robertson, Jeff Baumgartner, Tim Randle, David Harpman, Mike Armbruster, and Thomas Payne. Members of the Hydropower Reform Coalition also offered constructive comments. Excellent final reviews were provided by Greg Auble, Carter Johnson, an anonymous reviewer, and the editor of *BioScience*. Robin Abell contributed to the development of the timeline in Figure 5, and graphics assistance was provided by Teresa Peterson (Figure 3), Matthew Chew (Figure 4) and Robin Abell and Jackie Howard (Figure 5). We also thank the national offices of Trout Unlimited and American Rivers for encouraging the expression of the ideas presented here. We especially thank the George Gund Foundation for providing a grant to hold a one-day workshop, and The Nature Conservancy for providing logistical support for several of the authors prior to the workshop.

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