Ecological Applications, 11(3), 2001, pp. 701–710
© 2001 by the Ecological Society of America

PLANNED FLOODING AND COLORADO RIVER RIPARIAN TRADE-OFFS DOWNSTREAM FROM GLEN CANYON DAM, ARIZONA

LAWRENCE E. STEVENS,[1] TINA J. AYERS,[2] JEFFERY B. BENNETT,[3] KERRY CHRISTENSEN,[4] MICHAEL J. C. KEARSLEY,[2] VICKY J. MERETSKY,[5] ARTHUR M. PHILLIPS III,[6] RODERIC A. PARNELL,[3] JOHN SPENCE,[7] MARK K. SOGGE,[8] ABRAHAM E. SPRINGER,[3] AND DAVID L. WEGNER[9]

[1]*P.O. Box 1315, Flagstaff, Arizona 86002 USA*
[2]*Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA*
[3]*Geology Department, Northern Arizona University, Flagstaff, Arizona 86011 USA*
[4]*Hualapai Department of Natural Resources, P.O. Box 300, Peach Springs, Arizona 86434 USA*
[5]*School of Public and Environmental Affairs, Indiana University, Bloomington, Indiana 47405 USA*
[6]*P.O. Box 201, Flagstaff, Arizona 86002 USA*
[7]*Glen Canyon National Recreation Area, Page, Arizona 86040 USA*
[8]*U.S. Geological Survey Forest and Rangeland Ecosystem Science Center, Colorado Plateau Field Station, Northern Arizona University, Flagstaff, Arizona 86011-5614 USA*
[9]*Ecosystem Management International, Inc., 2609 Columbine Avenue, Durango, Colorado 81301 USA*

Abstract. Regulated river restoration through planned flooding involves trade-offs between aquatic and terrestrial components, between relict pre-dam and novel post-dam resources and processes, and between management of individual resources and ecosystem characteristics. We review the terrestrial (wetland and riparian) impacts of a 1274 m^3/s test flood conducted by the U.S. Bureau of Reclamation in March/April 1996, which was designed to improve understanding of sediment transport and management downstream from Glen Canyon Dam in the Colorado River ecosystem. The test flood successfully restored sandbars throughout the river corridor and was timed to prevent direct impacts to species of concern. A total of 1275 endangered Kanab ambersnail (*Oxyloma haydeni kanabensis*) were translocated above the flood zone at Vaseys Paradise spring, and an estimated 10.7% of the total snail habitat and 7.7% of the total snail population were lost to the flood. The test flood scoured channel margin wetlands, including potential foraging habitats of endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*). It also buried ground-covering riparian vegetation under >1 m of fine sand but only slightly altered woody sandbar vegetation and some return-current channel marshes. Pre-flood control efforts and appropriate flood timing limited recruitment of four common nonnative perennial plant species. Slight impacts on ethnobotanical resources were detected >430 km downstream, but those plant assemblages recovered rapidly. Careful design of planned flood hydrograph shape and seasonal timing is required to mitigate terrestrial impacts during efforts to restore essential fluvial geomorphic and aquatic habitats in regulated river ecosystems.

Key words: *Colorado River; endangered species; Glen Canyon Dam; Grand Canyon; Kanab ambersnail* (Oxyloma haydeni kanabensis)*; planned flooding; regulated river; restoration; riparian ecology; river ecosystem; saltcedar* (Tamarix ramosissima)*; Southwestern Willow Flycatcher* (Empidonax traillii extimus).

INTRODUCTION

Flooding is an important natural phenomenon on most rivers, reorganizing and resetting the physical and ecological development of aquatic and riparian habitats (Junk et al. 1989, Gregory et al. 1991). Flow regulation that reduces flood frequency may increase the stability of downstream aquatic and riparian ecosystem domains (Risser and Harris 1989, Sedell et al. 1989, Johnson et al. 1995). Reduction in disturbance intensity in naturally highly disturbed ecosystems is predicted to increase biodiversity (Connell 1978, Huston 1979). This prediction is supported in some large, regulated river ecosystems, which have developed substantial new riparian vegetation and larger, more stable faunal populations following impoundment (e.g., Johnson et al. 1976, Rickard et al. 1982, Anderson and Ohmart 1988, Johnson 1991, Johnson 1994). As human-dominated ecosystems, most if not all large regulated rivers support both relict (pre-dam) and novel (post-dam) aquatic and terrestrial resources and processes. These components, as well as the economic benefits associated with flow regulation, are variously valued by society,

Manuscript received 22 April 1998; accepted 10 March 2000; final version received 10 April 2000. For reprints of this Invited Feature, see footnote 1, p. 633.

intensifying the debate on management priorities (Johnson and Carothers 1982, Stevens and Wegner 1995, Schmidt et al. 1998). Planned or unplanned management activities that restore natural flow dynamics of regulated rivers may differentially affect relict and novel components, aquatic and terrestrial components, and individual components and ecosystem characteristics. Careful consideration of the shape and seasonal timing of the hydrograph is essential for optimizing planned flood effects on the wide array of resources and processes of concern in regulated river ecosystems. Here we report on the impacts of the 1996 test flood from Glen Canyon Dam on riparian resources, and discuss the trade-offs associated with planned flooding.

Recently proposed river ecosystem management strategies have focused on simulation of natural hydrographs, particularly restoration of flooding (Naiman et al. 1995, Sparks 1995, Stanford et al. 1996, Poff et al. 1997); however, significant conceptual and practical issues limit potential restoration of large regulated rivers (Ward and Stanford 1983, Gore and Shields 1995, Johnson et al. 1995; Knutson and Klaas 1997). Reduced flood frequency is only one facet of environmental change downstream from large dams; changes in sediment transport, water quality (especially thermal and nutrient dynamics), and the introduction of nonnative species (e.g., plants, aquatic invertebrates, fish, and fish parasites) may exert more lasting impacts than does flood suppression (e.g., Miller et al. 1983, Minckley 1991, Brouder and Hoffnagle 1997). Also, flood frequency and magnitude can only be substantially manipulated where human population density and land use intensity are low (e.g., Izenberg et al. 1996). Therefore, planned flooding is unlikely to be an ecological panacea for the restoration of large, regulated rivers, and may negatively affect some valued novel and economic components of such ecosystems.

Prediction of flow regime impacts on aquatic and floodplain biota recently has been advanced through the development of hydrologically based models (e.g., Auble et al. 1994, Blinn et al. 1995, Power et al. 1995). For example, post-dam lower riparian zone vegetation has been shown to develop in response to comparatively subtle gradients of inundation frequency, scour disturbance, soil texture, and channel geomorphology (Day et al. 1988, Hupp 1988, Stevens et al. 1995), but few restoration experiments using planned flooding have been attempted on large river ecosystems (but see Molles et al. 1995).

Regulated river floodplains are typically subject to a wide array of land management strategies, including intensive agricultural and industrial development; however, the regulated river floodplains or reservoir shorelines of >30 large national parks in the United States are managed to maintain or restore their ecological integrity (Jackson et al. 1992). The National Park Service management strategy revolves around conservation and restoration of natural and cultural resources to benefit future generations, although the highly altered condition of many regulated rivers makes restoration a challenging goal.

The Colorado River is one of the most thoroughly regulated rivers in the United States (Ohmart et al. 1988, Hirsch et al. 1990). Glen Canyon Dam is its second largest dam, and is managed by the U.S. Bureau of Reclamation under the federally designated Adaptive Management Work Group, a committee of diverse stakeholder representatives which makes recommendations to the Secretary of the Interior regarding dam management. The Secretary bases dam management decisions on the Colorado River Storage Project Act of 1956, the Grand Canyon Protection Act of 1992, the 1995 Glen Canyon Dam Environmental Impact Statement (GCDEIS, U.S. Bureau of Reclamation 1995), and the 1996 Record of Decision (ROD) in an effort to balance hydropower production with environmental concerns for downstream resources. The GCDEIS and ROD emphasize an adaptive management strategy involving the iterative incorporation of new information to improve ecosystem management (Walters and Holling 1990). Low fluctuating flows and limited daily fluctuations were implemented in 1991 and are authorized by the ROD to increase residence time and storage of tributary-derived sediments. Occasional planned floods are recommended to rejuvenate sandbars and aquatic habitats.

To test the effectiveness of the ROD flow management strategy, the U.S. Bureau of Reclamation conducted a seven-day, constant 1274 m^3/s experimental flood from 26 March through 2 April 1996 from Glen Canyon Dam, affecting Lake Powell reservoir, all of Glen and Grand canyons, and upper Lake Mead. This test flood successfully restored sandbars throughout the Colorado River corridor (Hazel et al. 1999, Schmidt 1999). Federal, state, and tribal cooperating agencies identified five test-flood objectives related to flow and sediment management, and three objectives specifically related to terrestrial (wetland and riparian) biological resources, including: (1) maintenance of open sandbars for camping, (2) providing water to pre-dam upper riparian zone vegetation, and (3) meeting these objectives without significant adverse impacts to endangered species. The eight objectives differ somewhat from those described in the GCDEIS and the ROD, which emphasize the use of high flows to ". . . rebuild high elevation sand bars, deposit nutrients, restore backwater channels, and provide some of the dynamics of a natural system" (U.S. Bureau of Reclamation 1995: 14). For example, wetland and riparian vegetation assemblages are identified in the GCDEIS as important wildlife habitat and ethnobotanical resources, rather than as nuisance cover on sandbars.

In this report we summarize the impacts of the test flood on terrestrial biological components and pro-

cesses in relation to the above objectives. Specifically, we address planned flood impacts on riparian soils, wetland and sandbar vegetation, ethnobotanical resources, and terrestrial species of concern. We discuss resource management trade-offs in relation to aquatic and terrestrial, relict and novel, and single species and ecosystem-scale resources and processes in this large, regulated, desert river ecosystem.

Study Area

Glen Canyon Dam was completed in 1963 and it impounds the 33-km^3 Lake Powell reservoir. The river flows 472 km between the dam and Lake Mead, including the remaining 26 km of lower Glen Canyon and all of Grand Canyon. The dam lies 26 km upstream from Lees Ferry (river kilometer [Rkm] 0), from which distances along the river are measured, and controls most of the river's flow into Lake Mead (see Fig. 1 of Patten et al. [2001] in this feature). This portion of the river drops in elevation from 975 m to 370 m. It is constrained by bedrock and talus slopes, and is surrounded by the 2100 m to 2800 m high Colorado Plateau. The river flows through 13 bedrock-controlled reaches that vary in characteristic width and depth (Schmidt and Graf 1990, Stevens et al. 1997*c*). The climate is continental and arid, with mean total annual precipitation varying from 150 to 280 mm/yr (Sellers et al. 1985). Vegetation in these reaches includes xeric Mohave desertscrub in upland settings, and desert riparian and strandline assemblages along the river (Warren et al. 1982). Other aspects of the geomorphology and ecology of this large desert river ecosystem are described by Howard and Dolan (1981), Johnson (1991), O'Conner et al. (1994), Stevens et al. (1995, 1997*a*, *c*), and Bowers et al. (1997).

Impoundment by Glen Canyon Dam reduced sediment transport, the mean and variability of temperature in the river, and flood frequency (Howard and Dolan 1981, Stevens et al. 1997*c*). Virtually no suspended inorganic sediments pass through the dam, but the suspended load increases over distance downstream as the Paria River (Rkm 1), the Little Colorado River (LCR; Rkm 98), and other tributaries contribute sediment. Erosion of sandbars has occurred during post-dam time (Howard and Dolan 1981, Schmidt and Graf 1990, Hazel et al. 1999). Cold hypolimnetic releases and introduction of 20 nonnative fish has led to the virtual or complete extirpation of four of the eight native fish species in this portion of the river (Minckley 1991, Valdez and Ryel 1997; L. Stevens, *unpublished data*).

Flood control allowed profuse stands of riparian vegetation to colonize river shorelines, especially in the wider reaches of the river (Turner and Karpiscak 1980, Johnson 1991). Local vegetation zonation and system-wide, reach-based and local/microsite spatial scale differences influence vegetation cover and composition (Johnson 1991). In particular, highly productive marshes develop in return-current channels (RCCs), which are slough-like habitats that form in association with reattachment sandbars (Schmidt and Graf 1990, Stevens et al. 1995). Novel post-dam vegetation directly or indirectly supports expanding terrestrial animal populations, including: endangered Kanab ambersnail (KAS; Succineidae: *Oxyloma haydeni kanabensis*; Stevens et al. 1997*b*); Peregrine Falcon (*Falco peregrinus anatum*; Brown et al. 1992); summer breeding and winter waterfowl (Stevens et al. 1997*a*); and abundant Neotropical migrant songbirds, including endangered Southwestern Willow Flycatcher (SWWF; *Empidonax trailii extimus*; Brown 1988, Brown and Trosset 1989, Stevens et al. 1996, Sogge et al. 1997). In addition, federally listed wintering Bald Eagles (*Haliaeetus leucocephalus*; Brown et al. 1989) use the riparian habitats for resting and foraging. As in many highly managed ecosystems, these endangered species are assumed to be surrogate indicators of ecosystem health. In addition to these ecological concerns, several Native American tribes and the National Park Service value the numerous archeological, historical, and other culturally significant sites and biota along the river, and the river corridor is intensively used by recreational river runners (Myers et al. 1999).

Synopsis of Terrestrial Biological Impacts

In the following sections we describe or review flood-induced changes in soils, nutrient dynamics, vegetation, habitats, and populations of special concern that were measured prior to, immediately after, and up to two growing seasons after the test flood (Table 1).

Riparian soils

Unlike large pre-dam floods, which generally scoured lower riparian zone vegetation, the test flood buried much of the pre-existing riparian vegetation under ≤2 m of evenly sorted fine sand throughout the river corridor (Schmidt 1999). Sedimentological studies have focused primarily on sand distribution, and largely ignored the deposition of silt and clay. These finer sediment fractions are important determinants of potential vegetation development along the Colorado River (Stevens 1989, Stevens et al. 1995). The test flood deposited uniform fine sand on many sandbar surfaces (Kearsley and Ayers 1999). For example, ≤1.5 m of fine sand was deposited at a large bar at Rkm 89R (R and L following Rkm numeral designations refer to river right or river left facing downstream). Sand deposition occurred where flow velocities were >0.2 m/s, while 0.1 m of silt was deposited where velocity was <0.2 m/s (Parnell et al. 1997). Most large return-current channels prior to the test flood were floored with silt and clay deposits. The RCC at Rkm 89R was not scoured by the test flood, despite velocities of up to 0.9 m/s; rather, it aggraded with new sand (Parnell et al. 1997), a pattern observed at many large RCCs.

TABLE 1. Impacts of the 1996 test flow on terrestrial biota in three land management divisions of the Colorado River corridor downstream from Glen Canyon Dam, Arizona, USA.

Resource	Management division		
	Glen Canyon National Recreation Area	Grand Canyon National Park	Hualapai Indian Reservation
Soil nutrients	none to +	none to +	none to +
Vegetation			
Wetland	none to −	none to −	none to −
Perennial bar/channel margin	none	none	none
Upper riparian zone	none	none	none
Nonnative species colonization	none	none to slight +	none to slight +
Kanab ambersnail†	NA	−	NA
Niobrara ambersnail	none	NA	NA
Northern leopard frog	none	NA	NA
Avifauna			
Waterfowl	none	none	none
Bald Eagle†	none	none	none
Peregrine Falcon†	none	none	none
Belted Kingfisher	none	none	none
Southwestern Willow Flycatcher†	none	none to −	?

† Federally endangered species at the time of the test flood.

Debris fan–eddy complexes are characteristic geomorphic units in this canyon-bound river (Schmidt and Graf 1990) and their geomorphology may influence local and reach-based nutrient dynamics in this eddy-dominated river ecosystem through groundwater flow patterns in sandbars. The transport rate of water and associated nutrients through the Rkm 89R reattachment bar was examined through measurement of hydraulic conductivity of the aquifer materials (Springer et al. 1999). The new sediments deposited on the bar compressed the underlying sediments, greatly reducing the hydraulic conductivity, and therefore the velocity of groundwater and nutrient transport through the bar.

Parnell et al. (1999) demonstrated that the decomposition of buried wetland, grass, and herbaceous vegetation resulted in a 2-yr increase in soil nutrient availability. They placed 44 wells (1.5, 3, and 6 m deep) in large reattachment bars at Rkm −10.5L, 89R, and 312L. Field nutrient analyses included nitrate, nitrite, ammonium, and dissolved oxygen (DO), and laboratory analyses included nonpurgeable organic carbon (NPOC) and orthophosphate. Groundwater NPOC and ammonium increased by 85–278% and 79–617%, respectively after the flood, and remained elevated for more than one year afterwards, decreasing in mid-1997. Groundwater DO concentrations decreased at two of the sites, reflecting increased microbial decomposition of buried vegetation. These data indicate linkage between groundwater and surface-water nitrogen concentrations. In contrast, groundwater and surface-water orthophosphate concentrations appeared little affected by the test flood, but may be influenced by large, rapid changes in discharge.

Wetland and riparian vegetation

Sandbar and channel margin riparian vegetation in this system is novel, post-dam habitat, with high biodiversity and productivity (Johnson 1991, Stevens et al. 1995). Fluvial marshes along the post-dam Colorado River exist on silt/clay-enriched fine sand deposits in low-lying, low velocity settings (Stevens et al. 1995). Pre- and post-flood mapping of wetland vegetation by Kearsley and Ayers (1999) indicate little overall impact of the test flood on five of nine previously established RCC marshes. This may be attributable to low velocity or erosion-resistant soils. For example, Parnell et al. (1999) reported that current velocities of 0.9 m/s were not sufficient to scour the RCC floor at the Rkm 89R RCC. At the Rkm 69L and 312L sites, high densities of cattail (*Typha* spp.) and common reed (*Phragmites australis*) stems may have further reduced current velocity and limited scour. Large RCC marshes are relatively rare, and numerous small patches of channel margin marsh vegetation that had developed during interim flows (low fluctuating flows) from 1991 through 1995 were scoured throughout the river corridor (L. Stevens, *unpublished data*). Density of small marsh patches decreased by 20% to 40% among the 11 reaches analyzed, as a result of the test flood, and more scour was observed in narrow reaches.

Sandbar vegetation was altered by the test flood, but impacts varied between ground-covering and woody species. Aggradation of 1–2 m of fine sand on sandbar surfaces buried highly productive, ground-covering grass and herbaceous assemblages (Stevens et al. 1996, Kearsley and Ayers 1999). In contrast, pre-established woody perennial species, such as saltcedar (*Tamarix ramosissima*), coyote willow (*Salix exigua*), and seep-willow (*Baccharis* spp.), grew up through the new sand deposits, with little apparent mortality. Although the process was not studied, profuse regrowth and rapid recovery of perennial cover may have been influenced by increased soil nutrient availability (Parnell et al. 1999). Kearsley and Ayers (1999) documented a re-

duction in the sandbar seed bank by germinating seeds from three surficial soil samples/vegetation polygon. Soil samples from below the flood stage showed an 80% reduction in seedling density and species richness following the flood, while samples from above the flood stage revealed little overall pre- vs. post-flood difference.

The test flood was specifically scheduled to avoid dispersal and germination of nonnative plant species, including saltcedar (*Tamarix ramosissima*) and ravenna grass (*Saccharum ravennae*). Saltcedar is a wind- and flood-dispersed invading species in this river system (Stevens and Waring 1985); however, its seeds are short-lived and do not persist over winter (Stevens 1987). The test flood was timed to allow at least several weeks for the reworked sandbar surfaces to desiccate before saltcedar seed release, and thereby prevent a wave of germination by this weedy tree species. Although this scheduling strategy was successful, subsequent high steady flows in 1996 and 1997 permitted some additional saltcedar establishment on low-lying sandbar surfaces (L. Stevens, *personal observation*).

Ravenna grass is a tall, European bunchgrass that was introduced by the National Park Service as an ornamental species at Wahweap Marina on Lake Powell. The invasion of that species, as well as giant-reed (*Arundo donax*) and Russian olive (*Eleagnus angustifolia*), into the river ecosystem was recognized in 1991 by Stevens and Ayers (*in press*). In 1993, as discussions of planned flooding began, L. Stevens and T. Ayers initiated a nonnative plant control program. Volunteers mechanically removed 10^4 ravenna grass plants, and numerous individuals of Russian olive and giant-reed. As a result of that effort, those species have not proliferated, and an ongoing National Park Service monitoring and control program has effectively prevented further expansion (L. Stevens, *personal observation*). Nonnative *Lepidium latifolium* (Brassicaceae), *Eragrostis curvula* (Poaceae), and camelthorn (Fabaceae: *Alhagi camelorum*) distributions were not obviously affected by the test flood (Kearsley and Ayers 1999), but established plants may have derived benefits from the flood-related soil nutrient pulse (Parnell et al. 1999).

Pre-dam vegetation was identified by stakeholders as a resource that could benefit from the test flood. This vegetation zone characterized the pre-dam river ecosystem, and may be in a state of long-term decline because of failing recruitment (Turner and Karpiscak 1980). However, exhaustive stem growth and dendrochronological studies by Anderson and Ruffner (1988) failed to document increased growth under flows of >2700 m³/s in 1983 and flows >1274 m³/s in 1984–1986. This stakeholder objective was not studied during the test flood because the test-flood stage and duration were shorter than those of the 1983–1986 floods.

Hualapai Tribal researchers reported that although the flood-related increases in grain size were detectable for >430 km downstream from the dam (>20 km onto upper Lake Mead), overall flood impacts on riparian vegetation were nominal (Balsom 1999). They documented reduced richness of native and nonnative plant species at two of four large study sites, but equivalent cover prior to and after the flood at the two downstream sites, and rapid recovery of the affected sites during 1996 and 1997.

Species of special concern

Kanab ambersnail.—Known populations of this endangered snail occur only at a few springs in the Southwest, one of which is Vaseys Paradise (VP) at Colorado River Rkm 51R (Stevens et al. 1997*b*). That KAS population occurs primarily on two host-plant species: native scarlet monkeyflower (*Mimulus cardinalis*) and nonnative watercress (*Nasturtium officinale*). The cover of KAS host-plant species increased downslope from the 3540 m³/s stage elevation at VP following dam construction (Turner and Karpiscak 1980), and is now ~40% greater than in pre-dam time (Stevens et al. 1997*b*). The Kanab Ambersnail Interagency Monitoring Group (KAIMG) documented test-flood impacts on this snail population (KAIMG 1997; Meretsky et al. 2000). Topographic surveys at VP revealed that 119.4 m (13.4%) of the total 0.09 ha of KAS habitat existed downslope of the 1274 m³/s stage, including 51.3 m of monkeyflower and 39.2 m of watercress. The flood scoured 10.7% of the total primary KAS habitat, leaving only 14.3 m of monkeyflower and 14.1 m of watercress of low quality cover in the flood zone. Habitat recovery required two full growing seasons to return to pre-flood levels, but slow recolonization rates on scoured, steeply angled bedrock surfaces resulted in reduced KAS habitat quality in the flood zone through 1999.

The KAIMG team sampled 180 20-cm diameter plots before the flood and estimated that ~2115 snails, 19.4% of the total KAS population, existed below the 1274 m³/s stage (KAIMG 1997). A total of 1275 KAS were marked and moved above the 1274(+0.5) m³/s stage prior to the flood, and the remaining 840 snails (7.7% of the total population) were lost to the test flood. KAS recolonization began immediately, and by mid-April, 1996, the KAIMG estimated that 400 KAS existed downslope from the peak flood stage, based on analysis of 96 20-cm diameter plots or full patch counts. Subsequent monthly surveys revealed that the population remained lower than 1995 levels until midsummer, 1997.

Southwestern Willow Flycatcher.—This endangered Neotropical migrant passerine historically nested at Lees Ferry, and in post-dam time nests in wide reaches of the Colorado River in Grand Canyon, including upper Lake Mead (Brown 1988, Sogge et al. 1997; K. Christensen, *personal communication*). Over the past

two decades of study, SWWF in upper Grand Canyon have preferentially nested in dense groves of nonnative saltcedar, which occasionally have a scattered overstory of taller trees, and all nest sites are near fluvial marshes. The riparian corridor from Rkm 62.8 to 115 has been designated as critical SWWF habitat (U.S. Fish and Wildlife Service 1993, 1997). A 1996 U.S. Fish and Wildlife Service Biological Opinion on the test flood defined several measures to mitigate impacts on SWWF in Grand Canyon. Stevens et al. (1996) studied habitat changes at the four historical nest sites in upper Grand Canyon. Fluvial marshes at these sites were dominated by common reed, horsetail (*Equisetum* spp.), and cattail. SWWF research activities included verifying stage-to-discharge relations, quantifying flow depth and velocity at nest sites, describing litter/understory characteristics of territories, and determination of nest site and foraging habitat structure, and nesting success.

Measured peak flood stage at SWWF nest sites lay within 0.4 m of predicted elevations (Stevens et al. 1996). Nest stand vegetation impacts were nominal: two stands were slightly scoured, and three sites sustained a slight reduction in groundcover and/or branch abundance at <0.6 m above the ground; however, no reduction in branch abundance or alteration of stand composition occurred, and high flows did not reach any historical nest trees. Impacts on marsh foraging habitats were more severe, with decreases in area of 1% to >72%. Two of the four marshes regained vegetated area during the summer of 1996, while the other two marshes had not recovered by the end of the 1997 growing season.

The SWWF is one of the most endangered vertebrates in Grand Canyon, with <3 nesting pair per year through the 1990s. Sogge et al. (1997) reported three singing SWWF, but only one successfully breeding pair along the Colorado River in upper Grand Canyon in 1996. That pair apparently fledged two young. SWWF nesting success in this system is limited by Brown-headed Cowbird (*Molothrus ater*) brood parasitism (Brown 1994, Sogge et al. 1997). In 1997 and 1998 SWWF failed to nest successfully in upper Grand Canyon because of cowbird brood parasitism and nest loss, respectively (M. Sogge and J. Spence, *unpublished data*). Nesting SWWF in lower Grand Canyon (Rkm 425–433) apparently were not affected by the test flood.

Other species of concern.—Several other rare taxa were monitored during the test flood. A single population of northern leopard frog (*Rana pipiens*) exists at a riverside spring at Rkm 15L (Drost and Sogge 1995). Although most of its habitat was inundated by the test flood, the frog population persisted apparently without major impact (J. Spence, *unpublished data*). The exceptionally warm winter of 1995–1996 may have allowed the frog population to be active prior at the onset of higher flows. Also, one of two known populations of Niobrara ambersnail (*Oxyloma h. haydeni*) in Arizona occurs at that spring and likewise survived the test flood; however, no population estimates were made.

The seasonal timing of the test flood was designed to prevent major impacts to other avian species. Then endangered (now threatened) Bald Eagle concentrate in upper Grand Canyon during February and early March, to feed on nonnative spawning rainbow trout (*Oncorhynchus mykiss*; Brown et al. 1989). Grand Canyon Bald Eagle foraging is reduced during high flows (Brown et al. 1998). By staging the test flood one month after the peak eagle concentration period, no impacts were anticipated or observed on this threatened species, save those induced by human disturbance (Brown and Stevens 1997). Migrant passerine bird densities in Glen Canyon National Recreation Area declined after the test flood (J. Spence, *unpublished data*), but distinguishing migration from flood-related impacts was not possible. Neotropical migrant passerine bird populations and then endangered Peregrine Falcon typically do not commence nesting until early to mid-April and were not expected to be influenced by the test flood (Brown et al. 1992). Belted Kingfisher and Osprey are Arizona species of concern, and are most abundant during April (Stevens et al. 1997*a*), but no test-flood impacts were detected. As with nonnative plant dispersal, appropriate hydrograph scheduling may have reduced undesirable impacts on many terrestrial biological resources.

Discussion and Management Implications

The 1996 test flood was successful as a sediment management exercise (Schmidt 1999, Schmidt et al. 2001) and as an experiment in large-scale ecosystem management; however, adoption of planned flooding as a management strategy is likely to have both short-term and long-term impacts on riparian components and processes. Planned flooding is not a panacea for adaptive management of the Colorado River ecosystem; rather, it illuminates at least three trade-off dilemmas, one practical and two related to issues of societal valuation.

First, from a practical standpoint, management of some valued aquatic and sediment-related resources and processes may directly conflict with that of other aquatic and riparian resources and processes (Table 1). The test flood substantially rejuvenated many sandbars, and briefly doubled backwater (fish nursery) habitat area; however, aggradation and erosion subsequently reduced backwater area to below pre-treatment levels by September 1996 (Brouder et al. 1999, Schmidt et al. 2001), and the flood hydrograph shape needed for longer term rejuvenation of backwater habitats remains unknown. The test flood also reduced shoreline habitats of endangered wetland and riparian snail and avifauna species; however, these impacts were relatively minor.

TABLE 2. Distribution, impacts of flow regulation, and predicted long-term consequences of the ROD flow regime, including 1274 m^3/s planned floods, on wetland and riparian habitats, biota, and assemblages in the Colorado River ecosystem downstream from Glen Canyon Dam.

Species or assemblage	Range in river corridor (km)	Flow regulation effects	ROD consequences
Fluvial marshes	Throughout	Increased cover	Some reduction
Sandbar vegetation	Throughout	Increased cover	Some reduction
Pre-dam upper riparian zone	Throughout	Possible long-term decline	Reduced recruitment without flows >3000 m^3/s
Kanab ambersnail†	51R	~40% habitat increase	Reduction of post-dam habitat, population; no likely population threat
Niobrara ambersnail	−15L	Expanded?	Slight threat to habitat and population
Northern leopard frog	−15L	Declining	Slight threat to habitat and population
Zebra-tailed lizard	364L	Extirpated	No recovery planned
Bald Eagle†	Dam to Rkm 98	Increased food supply	Potential slight negative effect on winter foraging
Peregrine Falcon†	Throughout	Increased food supply	No effect
Osprey	Throughout	Increased food supply	No effect
Belted Kingfisher	Throughout	No direct effect	No effect
Other waterbirds	Throughout	Increased populations	Indirect negative effect, loss of fluvial marshes
Southwestern Willow Flycatcher†	Rkm 81–472	Increased habitat	No impact on nest stands; reduction of marsh foraging habitat, loss from upper Grand Canyon
Colorado river otter	Throughout	Extirpated?	No recovery planned
Muskrat	Middle and lower GC	Declining	No recovery planned

Note: ROD, record of decision; GC, Grand Canyon; R and L following river kilometer values indicate river right or left facing downstream.

† Federally listed endangered species at the time of the test flood.

A little-recognized positive result of the test flood was that it was accomplished with few negative impacts to resources of concern, such as endangered species, ethnobiological resources, the aquatic food base, and the trout fishery (Balsom 1999, Blinn et al. 1999, McKinney et al. 1999). Despite this success, the trade-offs between aquatic and terrestrial biological resources and processes remain central to discussions of future planned floods.

Second, management of relict (pre-dam) resources and processes is complicated by the developing refugial nature of the post-dam river ecosystem (Johnson and Carothers 1982, Schmidt et al. 1998). In contrast to the widespread loss of riparian habitat throughout the Southwest (Dahl 1990), diverse and biologically productive habitat developed as an unanticipated consequence of flow regulation downstream from Glen Canyon Dam (Johnson 1991). Flow regulation transformed this naturally flood-scoured and low productivity ecosystem into one that now supports substantial native biodiversity, conferring considerable regional conservation importance on the regulated Colorado River (Table 2). However, populations of at least nine vertebrate species have been extirpated or have precipitously declined in the riparian corridor in post-dam time. Present management strategies emphasize preservation of relict components when legally mandated (e.g., for endangered species and cultural resources), but the management objectives for many other ecologically important components (e.g., sandbars, wetlands, Grand Canyon trout, rare but not legally protected fauna, such as Niobrara ambersnail and northern leopard frog) and processes (e.g., riparian plant succession) remain nebulous. A more regional perspective on biodiversity issues may improve the management of sensitive species and their habitats in this system.

The third dilemma involves conflicts between management of individual species and overall ecosystem characteristics (Simberloff 1998). The Colorado River ecosystem is a "bottom-up" ecological house built on sand, one strongly influenced by sediment transport processes that provide the surfaces on which aquatic and terrestrial wildlife habitats develop (Stevens et al. 1995). Therefore, rejuvenation of key ecosystem processes, such as flooding, is required for habitat maintenance. More frequent, higher magnitude, shorter duration floods are being considered to prolong sand residence time by storing sand at higher elevations in channel margins and by more rapidly coarsening the bed (e.g., Rubin et al. 1998, Schmidt 1999). Also, the test flood demonstrated that flows >1274 m^3/s are required for substantial rejuvenation of native fish nursery habitats, such as RCCs. However, test flood impacts on sensitive terrestrial species and their habitats last

for more than two years, and some nonrenewable resources may be permanently reduced with increased flood disturbance intensity. As a long-term management strategy, more frequent high flows are likely to restrict plant colonization at low stage zones, and increase scour during planned floods (Stevens et al. 1995), thereby reducing the overall availability of riparian wildlife habitat.

Although the Colorado River in Grand Canyon flows through a World Heritage Park, where wilderness conditions are usually expected, it also is a strongly human-dominated ecosystem with well-defined socioeconomic values associated with hydroelectric power generation and recreation. As the first planned high flow, the 1996 test flood provides not only a baseline for planning future flood frequency and hydrograph shape, but also an opportunity to improve strategic planning for protection of individual nonrenewable biological and ethnobiological resources, as well as larger ecosystem characteristics. Clearly defined management goals based on public discussion of values, increased flexibility in flow planning, sound scientific information, and well-defined, well-supported administrative strategies are needed to resolve conflicts over existing and potential future resource conditions in this large regulated river ecosystem.

Acknowledgments

We thank the Bureau of Reclamation's Glen Canyon Environmental Studies Program staff, Applied Technology Associates, Inc., the Arizona Game and Fish Department, the U.S. Fish and Wildlife Service (especially D. Bills), the Hualapai Tribe, the National Park Service, Northern Arizona University, and O.A.R.S., Inc. for administrative and logistical support. Staff from those agencies and many volunteers contributed many hours of data collection and are thanked for their dedication and enthusiasm. The Grand Canyon Monitoring and Research Center supported manuscript preparation. We also thank R. R. Johnson, W. C. Johnson and D. T. Patten for useful comments on earlier versions of the manuscript.

Literature Cited

Anderson, B. W., and R. D. Ohmart. 1988. Structure of the winter duck community on the lower Colorado River: patterns and processes. Pages 191–236 *in* M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, Minnesota, USA.

Anderson, L. S., and G. A. Ruffner. 1988. Effects of the post-Glen Canyon Dam flow regime on the old high water zone plant community along the Colorado River in Grand Canyon. National Technical Information Service PB88-183504/AS.

Auble, G. T., J. M. Friedman, and M. L. Scott. 1994. Relating riparian vegetation to present and future streamflows. Ecological Applications **4**:544–554.

Balsom, J. R. 1999. Cultural resources and the Glen Canyon Dam–Colorado River experimental flow of 1966. Pages 183–194 *in* C. van Riper III and M. A. Stuart, editors. Proceedings of the Fourth Biennial Conference of Research on the Colorado Plateau. U.S. Geological Survey/FRESC Report Series USGSFRESC/COPL/1999/16.

Blinn, D. W., J. P. Shannon, L. E. Stevens, and J. P. Carder. 1995. Consequences of fluctuating discharge for lotic communities. Journal of the North American Benthological Society **14**:233–248.

Blinn, D. W., J. P. Shannon, K. P. Wilson, C. O'Brien, and P. L. Benenati. 1999. Response of benthos and organic drift to a controlled flood. American Geophysical Union Geophysical Monograph **110**:259–272.

Bowers, J. E., R. H. Webb, and E. A. Pierson. 1997. Succession of desert plants on debris flow terraces, Grand Canyon, Arizona, U.S.A. Journal of Arid Environments **36**:67–86.

Brouder, M. J., and T. L. Hoffnagle. 1997. Distribution and prevalence of the Asian fish tapeworm, *Bothriocephalus acheilognathi*, in the Colorado River and tributaries, Grand Canyon, Arizona, including two new host records. Journal of the Helminthological Society of Washington **64**:219–226.

Brouder, M. J., D. W. Speas, and T. L. Hoffnagle. 1999. Changes in number, sediment composition, and benthic invertebrates of backwaters. American Geophysical Union Geophysical Monograph **110**:241–248.

Brown, B. T. 1988. Breeding ecology of a willow flycatcher population in Grand Canyon, Arizona. Western Birds **19**: 25–33.

Brown, B. T. 1994. Rates of brood parasitism by Brown-headed Cowbirds on riparian passerines in Arizona. Journal of Field Ornithology **65**:160–168.

Brown, B. T., R. Mesta, L. E. Stevens, and J. Weisheit. 1989. Changes in winter distribution of Bald Eagles along the Colorado River in Grand Canyon, Arizona. Journal of Raptor Research **23**:110–113.

Brown, B. T., G. S. Mills, R. L. Glinski, and S. W. Hoffman. 1992. Density of nesting Peregrine Falcons in Grand Canyon National Park, Arizona. The Southwestern Naturalist **37**:188–193.

Brown, B. T., and L. E. Stevens. 1997. Winter Bald Eagle distribution is inversely correlated with human activity along the Colorado River, Arizona. Journal of Raptor Research **31**:7–10.

Brown, B. T., L. E. Stevens, and T. A. Yates. 1998. Influences of fluctuating river flows on Bald Eagle foraging behavior. The Condor **100**:745–748.

Brown, B. T., and M. W. Trosset. 1989. Nesting-habitat relationships of riparian birds along the Colorado River in Grand Canyon, Arizona. The Southwestern Naturalist **34**: 260–270.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302–1310.

Dahl, T. E. 1990. Wetland losses in the United States 1780's to 1980's. U.S. Department of the Interior Fish and Wildlife Service, Washington, D.C., USA.

Day, R. T., P. A. Keddy, J. McNeill, and T. Carleton. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. Ecology **69**:1044–1054.

Drost, C. A., and M. K. Sogge. 1995. Preliminary survey of leopard frogs in Glen Canyon National Recreation Area. Pages 239–254 *in* C. van Riper III, editor. Proceedings of the Second Biennial Conference on Research in Colorado Plateau National Parks. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-95-11.

Gore, J. A., and F. D. Shields, Jr. 1995. Can large rivers be restored? BioScience **45**:142–152.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540–551.

Hazel, J. E., Jr., M. Kaplinski, R. Parnell, M. Manone, and A. Dale. 1999. Sediment storage responses to controlled flooding, Colorado River in Grand Canyon. American Geophysical Union Geophysical Monograph **110**:161–184.

Hirsch, R. M., J. F. Walker, J. C. Day, and R. Kollio. 1990. The influence of man on hydrologic systems. Pages 329–

359 *in* M. G. Wolman and H. C. Riggs, editors. Surface water hydrology. Geologic Society of America Decade of North American Geology **0-1**.

Howard, A., and R. Dolan. 1981. Geomorphology of the Colorado River in Grand Canyon. Journal of Geology **89**: 269–298.

Hupp, C. R. 1988. Plant ecological aspects of flood geomorphology and paleoflood history. Pages 335–357 *in* V. R. Baker, editor. Flood Geomorphology. John Wiley and Sons, New York, New York, USA.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist **113**:81–101.

Izenberg, N. R., R. E. Arvidson, R. A. Brackett, S. S. Saatchi, G. R. Osburn, and J. Dohrenwald. 1996. Erosional and depositional patterns associated with the 1993 Missouri River floods inferred from SIR-C and TOPSAR radar data. Journal of Geophysical Research **101**:149–167.

Jackson, W. L., S. L. Ponce, and L. E. Stevens. 1992. Issues surrounding the coexistence of National Parks and regulated rivers. Symposium of the Fourth World Congress of National Parks, Caracas, Venezuela.

Johnson, B. L., W. B. Richardson, and T. J. Naimo. 1995. Past, present, and future concepts in large river ecology: how rivers function and how human activities influence river processes. BioScience **45**:134–141.

Johnson, R. R. 1991. Historic changes in vegetation along the Colorado River in the Grand Canyon. Pages 178–206 *in* G. R. Marzolf, editor. Colorado River ecology and dam management. National Academy Press, Washington, D.C., USA.

Johnson, R. R., and S. W. Carothers. 1982. External threats: the dilemma of resource management on the Colorado River in Grand Canyon National Park, USA. Environmental Management **11**:99–107.

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

Johnson, W. C., R. L. Burgess, and W. R. Keammerer. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecological Monographs **46**:59–84.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publications of Fisheries and Aquatic Sciences **106**:110–127.

Kanab Ambersnail Interagency Monitoring Group (KAIMG). 1997. The impacts of an experimental flood from Glen Canyon Dam on the endangered Kanab ambersnail at Vaseys Paradise, Grand Canyon, Arizona. Grand Canyon Monitoring and Research Center report, Flagstaff, Arizona, USA.

Kearsley, M. J. C., and T. J. Ayers. 1999. Riparian vegetation responses: snatching defeat from the jaws of victory and vice versa. American Geophysical Union Geophysical Monograph **110**:309–327.

Knutson, M. G., and E. E. Klaas. 1997. Declines in abundance and species richness of birds following a major flood in the upper Mississippi River. The Condor **114**:367–381.

McKinney, T., R. S. Rogers, A. D. Ayers, and W. R. Persons. 1999. Lotic community responses in the Lees Ferry reach. American Geophysical Union Geophysical Monograph **110**:249–258.

Meretsky, V. J., D. L. Wegner, and L. E. Stevens. 2000. Balancing endangered species and ecosystems: a case study of adaptive management in Grand Canyon. Environmental Management **25**:579–586.

Miller, J. B., D. L. Wegner, and D. R. Bruemmer. 1983. Salinity and phosphorus routing through the Colorado River/reservoir system. Pages 19–41 *in* V. D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science, Ann Arbor, Michigan, USA.

Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary? Pages 124–177 *in* G. R. Marzolf, editor. Colorado River Ecology and Dam Management. National Academy Press, Washington, D.C., USA.

Molles, M. C., Jr., C. S. Crawford, and L. M. Ellis. 1995. Effects of an experimental flood on litter dynamics in the middle Rio Grande riparian ecosystem. Regulated Rivers Research and Management **11**:275–281.

Myers, T., C. Becker, and L. E. Stevens. 1999. Fateful journey: injury and death on the Colorado River in Grand Canyon. Red Lake Books, Flagstaff, Arizona, USA.

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

O'Conner, J. E., L. L. Ely, E. E. Wohl, L. E. Stevens, T. S. Melis, V. S. Kale, and V. R. Baker. 1994. A 4500-year record of large floods on the Colorado River in the Grand Canyon, Arizona. Journal of Geology **102**:1–9.

Ohmart, R. D., B. W. Anderson, and W. C. Hunter. 1988. The ecology of the lower Colorado River from Davis Dam to the Mexico–United States boundary: a community profile. U.S. Fish and Wildlife Service Biological Report **85**(7.19).

Parnell, R. A., Jr., J. B. Bennett, and L. E. Stevens. 1999. Mineralization of riparian vegetation buried by the 1996 controlled flood. American Geophysical Union Geophysical Monograph **110**:225–249.

Parnell, R. A., A. E. Springer, and L. E. Stevens. 1997. Flood-induced backwater rejuvenation along the Colorado River in Grand Canyon, Arizona: 1996 final report. Grand Canyon Monitoring and Research Center report, Flagstaff, Arizona, USA.

Patten, D. T., D. A. Harpman, M. I. Voita, and T. J. Randle. 2001. A managed flood on the Colorado River: background, objectives, design, and implementation. Ecological Applications **11**:635–643.

Poff, N. L., K. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience **47**:769–784.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton. 1995. Hydraulic food-chain models: an approach to the study of food-web dynamics in large rivers. BioScience **45**:159–167.

Rickard, W. H., W. C. Hanson, and R. Fitzner. 1982. The non-fisheries biological resources of the Hanford Reach of the Columbia River. Northwest Science **56**:62–72.

Risser, R. J., and R. R. Harris. 1989. Mitigation for impacts to riparian vegetation on western montane streams. Pages 235–250 *in* J. A. Gore and G. E. Petts, editors. Alternatives in regulated river management. CRC, Boca Raton, Florida, USA.

Rubin, D. M., J. M. Nelson, and D. J. Topping. 1998. Relation of inversely graded deposits to suspended-sediment grain-size evolution during the 1996 flood experiment in Grand Canyon. Geology **26**:99–102.

Schmidt, J. C. 1999. Summary and synthesis of geomorphic studies conducted during the 1996 controlled flood in Grand Canyon. American Geophysical Union Geophysical Monograph **110**:329–342.

Schmidt, J. C., and J. B. Graf. 1990. Aggradation and degradation of alluvial-sand deposits, 1965 to 1986, Colorado River, Grand Canyon National Park, Arizona. U.S. Geological Survey Professional Paper **1493**.

Schmidt, J. C., R. A. Parnell, P. E. Grams, J. E. Hazel, M. A. Kaplinski, L. E. Stevens, and T. L. Hoffnagle. 2001. The 1996 controlled flood in Grand Canyon: flow, sediment transport, and geomorphic change. Ecological Applications **11**:657–671.

Schmidt, J. C., R. H. Webb, R. A. Valdez, G. R. Marzolf, and L. E. Stevens. 1998. Science and values in river restoration in the Grand Canyon. BioScience **48**:735–747.

Sedell, J. R., J. E. Richey, and F. J. Swanson. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers. Canadian Special Publications in Fisheries Aquatic Science **106**:49–55.

Sellers, W. D., R. H. Hill, and M. Sanderson-Rae. 1985. Arizona climate: the first hundred years. University of Arizona Press, Tucson, Arizona, USA.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? Biological Conservation **83**:247–257.

Sogge, M. K., T. J. Tibbitts, and J. R. Petterson. 1997. Status and breeding ecology of the Southwestern Willow Flycatcher in the Grand Canyon. Western Birds **28**:142–157.

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

Spence, J. R., and C. A. Pinnock. 1996. Survey of terrestrial avifauna in Glen Canyon and potential effects of the 1996 controlled flood. Bureau of Reclamation Glen Canyon Environmental Studies Program report, Flagstaff, Arizona, USA.

Springer, A. E., W. D. Petroutson, and B. A. Semmens. 1999. Spatial and temporal variability of hydraulic conductivity in an active reattachment bars of the Colorado River, Grand Canyon. Ground Water **37**:338–344.

Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. Regulated Rivers Research and Management **12**:391–413.

Stevens, L. E. 1987. The status of ecological research on tamarisk (Tamaricaceae: *Tamarix ramosissima*) in Arizona. Pages 99–105 *in* M. R. Kunzman, R. R. Johnson, and P. S. Bennett, editors. Tamarisk control in Southwestern United States. Special Report Number 9, Cooperative National Park Service Resources Studies Unit, Tucson, Arizona, USA.

Stevens, L. E. 1989. Mechanisms of riparian plant community organization and succession in the Grand Canyon, Arizona. Northern Arizona University. Dissertation. Flagstaff, Arizona, USA.

Stevens, L. E., and T. J. Ayers. *In press.* The biodiversity and distribution of alien vascular plants and animals in the Grand Canyon region. *In* B. Tellman, editor. Non-native species in the Sonoran Desert. University of Arizona Press, Tucson, Arizona, USA.

Stevens, L. E., K. A. Buck, B. T. Brown, and N. C. Kline. 1997*a*. Dam and geomorphological influences on Colorado River waterbird distribution, Grand Canyon, Arizona, USA. Regulated Rivers Research and Management **13**:151–169.

Stevens, L. E., V. J. Meretsky, J. R. Petterson, J. C. Nagy, and F. R. Protiva. 1996. Impacts of a beach/habitat building flow from Glen Canyon Dam on endangered southwestern willow flycatcher in Grand Canyon, Arizona: final report. Glen Canyon Environmental Studies Program, Flagstaff, Arizona, USA.

Stevens, L. E., F. R. Protiva, D. M. Kubly, V. J. Meretsky, and J. R. Petterson. 1997*b*. The ecology of Kanab ambersnail (Succineidae: *Oxyloma haydeni kanabensis*, Pilsbry 1948) at Vaseys Paradise, Grand Canyon, Arizona. Grand Canyon Monitoring and Research Center report, Flagstaff, Arizona, USA.

Stevens, L. E., J. C. Schmidt, T. J. Ayers, and B. T. Brown. 1995. Flow regulation, geomorphology, and Colorado River marsh development in the Grand Canyon, Arizona. Ecological Applications **5**:1025–1039.

Stevens, L. E., J. P. Shannon, and D. W. Blinn. 1997*c*. Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary and geomorphological influences. Regulated Rivers Research and Management **13**:129–149.

Stevens, L. E., and G. L. Waring. 1985. Effects of prolonged flooding on riparian vegetation in Grand Canyon. Pages 81–86 *in* R. R. Johnson, C. D. Ziebell, D. F. Patten, P. F. Ffolliott, and R. H. Hamre, editors. Riparian ecosystems and their management: reconciling conflicting uses. U.S. Forest Service General Technical Report RM-120, Fort Collins, Colorado, USA.

Stevens, L. E., and D. L. Wegner. 1995. Changes on the Colorado River: operating Glen Canyon Dam for environmental criteria. Pages 65–74 *in* R. J. Kirschner, editor. Proceedings of a national symposium on using ecological restoration to meet Clean Water Act goals. Northeastern Illinois Planning Commission, Chicago, Illinois, USA.

Turner, R. M., and M. M. Karpiscak. 1980. Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. U.S. Geological Survey Professional Paper **1132**.

U.S. Bureau of Reclamation. 1995. Operation of Glen Canyon Dam final environmental impact statement summary. U.S. Bureau of Reclamation, Salt Lake City, Utah, USA.

U.S. Fish and Wildlife Service. 1993. Proposed rule to list the Southwestern Willow Flycatcher as endangered with critical habitat. Federal Register **58**:39495–39522.

U.S. Fish and Wildlife Service. 1997. Endangered and threatened wildlife and plants: final determination of critical habitat for the Southwestern Willow Flycatcher; correction. Federal Register **62**:44228.

Valdez, R. A., and R. J. Ryel. 1997. Life history and ecology of the humpback chub in the Colorado River in Grand Canyon, Arizona. Pages 3–31 *in* C. van Riper III and E. T. Deshler, editors. Proceedings of the Third Biennial Conference of Research on the Colorado Plateau. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-97/12.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**: 2060–2068.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T. D. Fontaine and S. M. Bartell, editors. Ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

Warren, P. L., K. L. Reichhardt, D. A. Mouat, B. T. Brown, and R. R. Johnson. 1982. Vegetation of Grand Canyon National Park. U.S. National Park Service Cooperative Studies Unit Technical Report Number 9, Tucson, Arizona, USA.