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Invited Feature

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Restoration of the Colorado River Ecosystem Using Planned Flooding[1]

Flooding is an essential process in river ecosystems, and restoration of regulated rivers using planned flooding has been widely proposed as a management strategy. However, some authors have questioned the feasibility of restoring large rivers, and planned floods are often impractical because of impacts on human life and property. The Colorado River flows through lower Glen Canyon and all of Marble and Grand Canyons. The Grand Canyon is a world-renowned park and a World Heritage Site. The river's flow is primarily controlled by Glen Canyon Dam, which was completed in 1963. This is an ideal setting in which to test the hypothesis of river ecosystem restoration through planned flooding because it is a large, arid-lands regulated river that is adaptively managed for both economic and environmental resources, particularly its wilderness-like characteristics. In addition, there is no significant human development in the river corridor.

The pre-dam Colorado River was flood-prone and seasonally warm, and it was the primary sediment conduit for the upper Colorado River basin. Completion of Glen Canyon Dam partially decoupled the river ecosystem below the dam from the basin's climate. Fine alluvial sediment is now trapped in Lake Powell Reservoir, and in the downstream river it is now principally derived from tributaries. Low suspended sediment concentration and regulated flows produced extensive benthic biomass of algae (*Cladophora glomerata*) and associated epiphytes (e.g., diatoms and *Gammarus lacustris*) and a trophy rainbow trout (*Oncorhynchus mykiss*) fishery in the upper 26 km of the river channel, while only four of eight original native fish species remain, along with 22 nonnative species. Flow regulation also allowed development of profuse, post-dam stands of marsh and sandbar vegetation which have been extensively colonized by riparian fauna, including several endangered species. Species of most concern were the Southwestern Willow Flycatcher (*Empidonax traillii extimus*) which inhabits the woody riparian stands along the river, and Kanab ambersnail (*Oxyloma haydeni kanabensis*) at Vasey's Paradise, a spring-fed mesic site adjacent to the river. The river corridor is heavily used by river runners, and has many archeological sites and traditional cultural resources (e.g., plants and salt) of the seven American Indian tribes that inhabited the region. As a result of competing concerns, the 1992 Grand Canyon Protection Act (Title XVIII of Public Law 102-575) and the Glen Canyon Dam Environmental Impact Statement [U.S. Bureau of Reclamation. 1995. Operation of Glen Canyon Dam, final Environmental Impact Statement. Bureau of Reclamation, Salt Lake City, Utah, USA] recommended constrained flows, occasional flooding, and adaptive ecosystem management to balance the demands of water delivery, hydropower production, and reservoir and downstream recreation economics against environmental resource management.

After nearly 15 years of study on the impacts of Glen Canyon Dam operations on Lake Powell and the downstream riverine ecosystem, recommendations by scientists and resource managers convinced the Bureau of Reclamation to conduct a week-long experimental flood from the dam in March/April 1996, to test and improve existing flow and sediment transport models, and to improve understanding of high-flow impacts on biological, cultural, and socioeconomic resources. The test flood was the first large-scale test of the hydrograph restoration hypothesis, that is, returning or mimicking natural flows, in an adaptive management context.

This Invited Feature presents a series of papers synthesizing the results of the test flood. These syntheses arose from a two-day Grand Canyon Monitoring and Research Center symposium on the 1996 test flood, held in Flagstaff, Arizona, in April 1997. In addition to these syntheses, many individual flood studies, conducted by more than 100 federal, state, tribal, university, and

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privately contracted researchers have been presented elsewhere in the scientific literature [Webb, R. H., J. C. Schmidt, G. R. Marzolf, and R. A. Valdez, editors. 1999. The controlled flood in Grand Canyon. American Geophysical Union Geophysical Monograph 110, Washington, DC, USA]. This Invited Feature, which begins with an introduction about planning and implementation of the flood by Patten et al., presents an overview and background, new data, reviews, and syntheses of the results of the test flood. The impacts of a possible rapid drawdown of Lake Powell were unknown, and these are discussed by Hueftle et al. The paper by Schmidt et al. addresses downstream physical processes and changes, especially sediment dynamics, a leading reason for creating the flood and a major part of the research design. Concerns about major disruptive impacts on the aquatic and terrestrial ecosystems below the dam led to comprehensive studies of these systems during the flood. Aquatic biology is covered in two papers, one by Shannon et al. on the aquatic food base, and one by Valdez et al. on fisheries. Terrestrial biology, including riparian and endangered species, is addressed by Stevens et al. Cultural and economic resources, also studied during the flood, have been reported in other journals.

Although the 1996 test flood cost millions of dollars in research and lost power revenues, in the long term, planned flooding may still be a relatively inexpensive ecosystem management tool. However, hydrograph restoration cannot solve all environmental problems associated with impacts of dams (e.g., constant cold water temperatures, sediment deficit, and habitat fragmentation). Balanced management for competing environmental and economic concerns can only arise from a clearly defined public valuation of resources and careful evaluation of ecosystem management monitoring and experiment data. The 1996 test flood is an excellent example of cooperative multidisciplinary, integrated scientific planning, implementation, and analysis of a large-scale experiment to improve adaptive management of this large, greatly altered, and highly revered river ecosystem.

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Key words: aquatic macroinvertebrates; Colorado River; controlled flood; fish; Glen Canyon Dam; Grand Canyon; Lake Mead; marshes; restoration; riparian vegetation; riverine ecosystems; sediment dynamics.

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A MANAGED FLOOD ON THE COLORADO RIVER: BACKGROUND, OBJECTIVES, DESIGN, AND IMPLEMENTATION

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Abstract. The Colorado River ecosystem in lower Glen Canyon and throughout Marble and Grand Canyons was greatly altered following closure of Glen Canyon Dam in 1963, as flood control and daily fluctuating releases from the dam caused large ecological changes. Ecosystem research was conducted from 1983 through 1990, and intensively from 1990 through 1995 when dam releases were modified both for scientific purposes and protection of the river ecosystem. High flows (e.g., beach/habitat building flows) were included in the Glen Canyon Dam Environmental Impact Statement (EIS), which identified a preferred strategy for dam operations and protection of the downstream ecosystem. Use of high flows partially fulfills recommendations of many river and riparian scientists for return of more natural flows, as part of initial efforts in river restoration. In 1996, a seven-day experimental controlled flood was conducted at Glen Canyon Dam to closely study the effects of a high flow event equivalent to those proposed for future dam management. It is an example of modification of operations of a large dam to balance economic gains with ecological protection. Limited to 1274 m^3/s, the test flood was lower than pre-dam spring floods. The experiment was conducted to (1) test the hypothesis that controlled floods can improve sediment deposition patterns and alter important ecological attributes of the river ecosystem without negatively affecting other canyon resources and (2) learn more about river processes, both biotic and abiotic, during a flood event. Along with an explanation of the planning and background of this flood experiment, this paper summarizes expected and realized changes in canyon resources studied during the flood. Responses of specific resources to the flood are synthesized in the following compendium papers.

Key words: canyon resources; Colorado River; dam operations; Glen Canyon Dam; Grand Canyon; managed flood; riparian habitat; riverine ecosystems; sediment deposition; test flood.

INTRODUCTION

In spring 1996, the Colorado River ecosystem in lower Glen Canyon and throughout Marble and Grand Canyons sustained a flood that altered many aspects of the river ecosystem (Collier et al. 1997, Webb et al. 1999). Unlike spring floods from past centuries that often reached flows of 3000 cubic meters per second (m^3/s), with flows as high as 8500 m^3/s, this flood reached only 1274 m^3/s. However, it was a unique flood in the history of the Grand Canyon because it was fully controlled. This test flood was planned for specific dates using a controlled release from Glen Canyon Dam. This short-duration high release was designed to rebuild sandbars above nonflood river levels, deposit nutrients, restore backwater channels, and provide some of the dynamics of a natural system. The goal was to test hypotheses about sediment movements and the response of aquatic and terrestrial habitats to controlled flood events.

The test flood was the culmination of many years of research and planning, and illustrated how policies for management of dams and regulated rivers have changed over the past three decades. These changes follow years of studying effects of dams on river ecosystems (Williams and Wolman 1984), and requirements for their restoration (Ward and Stanford 1979, NRC 1992, Poff et al. 1997). When Glen Canyon Dam was constructed in the early 1960s, there was little concern for the impacts of dams on either upstream or downstream river ecosystems. Since then, awareness of changes taking place below dams has greatly increased (Turner and Karpiscak 1980, Johnson 1991, 1992, Rood and Mahoney 1995). Two factors that control many aspects of the river ecosystem were altered by Glen Canyon Dam and its operations: sediment availability to the downstream ecosystem, which is reduced through entrapment in the reservoir behind the dam (Andrews 1991); and river hydrology (quantity and quality), which is altered by timing and penstock intake location of water released from the dam. Timing

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generally coincides with power and downstream water needs, rather than ecological requirements, and intake ports are usually below the reservoir thermocline. Existence of the dam as an upstream–downstream migratory barrier for aquatic organisms is also of great concern (Minckley 1991, Stanford et al. 1996), but at present, existence of Glen Canyon Dam is assumed to be a nonnegotiable alteration of canyon geomorphology.

Lack of available sediment below dams greatly alters the morphology of channel margins, bars, and eddy complexes (Schmidt and Graf 1990, Kearsley et al. 1994, Ligon et al. 1995). In many rivers, below-dam tributaries may contribute sufficient sediment to support biological systems dependent on substrates finer grained than those occurring if dam discharge scours existing sediment and leaves cobble-armored shorelines. However, below Glen Canyon Dam where there is little tributary input of sediment, especially in downstream reaches closer to the dam, there are no acceptable solutions for sediment augmentation to the river ecosystem. Suggestions of transporting sediment from upper Lake Powell to the Lees Ferry area, via a slurry pipeline, have met with little support.

When there is sufficient sediment input from tributaries (e.g., from the Paria and Little Colorado Rivers below Glen Canyon Dam) to build sand deposits within the river channel, altered hydrology then becomes the primary driving variable to change or restore the downstream ecosystem because most aspects of the river's hydrological patterns are controlled by dam operations. These include: (1) amount of annual downstream discharge if stored water is diverted from the upstream impoundment, (2) magnitude of hydrological peaks and low flows, (3) baseflow, and (4) timing and duration of peaks and low flows.

River regulation by dams or other structures created a demand to study streamflow requirements of organisms that may be affected by altered hydrological regimes. Initial streamflow studies were aimed at defining instream flow requirements of economically important commercial and sport fish species (e.g., Bartholow and Waddle 1995, Bovee 1995). These studies primarily addressed instream habitat needs and minimum flow requirements. Eventually, streamflow requirements of other river and riparian attributes, such as riparian vegetation, were also determined (Stromberg and Patten 1989, Auble et al. 1994). Satisfying hydrological requirements for all riverine attributes with managed releases from upstream dams became a balancing act for water and dam managers. Not only did ecosystem components have different requirements, there were different hydrological factors to be addressed. Riparian vegetation did not necessarily need a baseflow, but needed sufficient annual volume to maintain a shallow alluvial water table (Stromberg et al. 1996), while fish required some minimal flow in the river (Stanford et al. 1996). Occurrence and timing of high flows also was important to both (e.g., Stromberg et al. 1991, Rood and Mahoney 1995, Stanford et al. 1996), and, in many cases, timing needs of diverse biota were very similar, a consequence of long-term adaptation by river-oriented organisms to seasonal floods.

Several regulated rivers in the West have been studied to develop plans for alteration of dam operations to satisfy downstream ecological requirements. The Colorado and Columbia Rivers are primary examples, but there are many other small-river examples. Reasons for altering dam operations may differ, and can include, for example, salmon migration in the Columbia and Trinity Rivers in the Northwest; and native fish, recreation, and riparian habitat on the Colorado River. Planning and implementation of ecologically based, modified discharges from dams that were constructed for water storage and hydropower requires extensive study, sound science, agency cooperation, policy adaptation, and acceptance by the public and river users, as well as the political will to implement recommendations.

Fourteen years of data collection, specifically designed to understand the effects of Glen Canyon Dam operations on the river ecosystem (Wegner 1991), preceded the test flood and were used to help develop hypotheses that could be tested by a flood experiment. Implementation of the test flood occurred in March 1996, but the timing of this event culminated years of planning and proposal development by many groups. For planning of future controlled floods and managed dam releases on the Colorado River and other rivers, an understanding of the foundation of scientific and management decisions leading to the test flood and the associated integrated-research program described here and in the following compendium papers is useful. These papers address the impacts of the test flood on: Lake Powell reservoir limnology (Hueftle and Stevens 2001); flow, sediment transport, sandbar and fish habitat responses (Schmidt et al. 2001); aquatic food base and drift (Shannon et al. 2001); native and nonnative fish (Valdez et al. 2001); and the riparian ecosystem, including ethnobiological concerns (Stevens et al. 2001). Elsewhere, Rubin et al. (1998) described the consequences of sediment depletion during floods in Grand Canyon, and Smith (1999) identified and described the effects of an important secondary circulation process on sediment transport that occurs during flooding in this system. Balsom (1999) demonstrated flood-related deposition of sand deposits at the foot of pre-dam terraces, which may retard erosion of archeological materials, but otherwise has trivial impacts on cultural properties. Economic research was summarized by Harpman (1999), and numerous other individual studies of test-flood research were presented in Webb et al. (1999), which serve as background to the compendium papers presented in this Invited Feature.

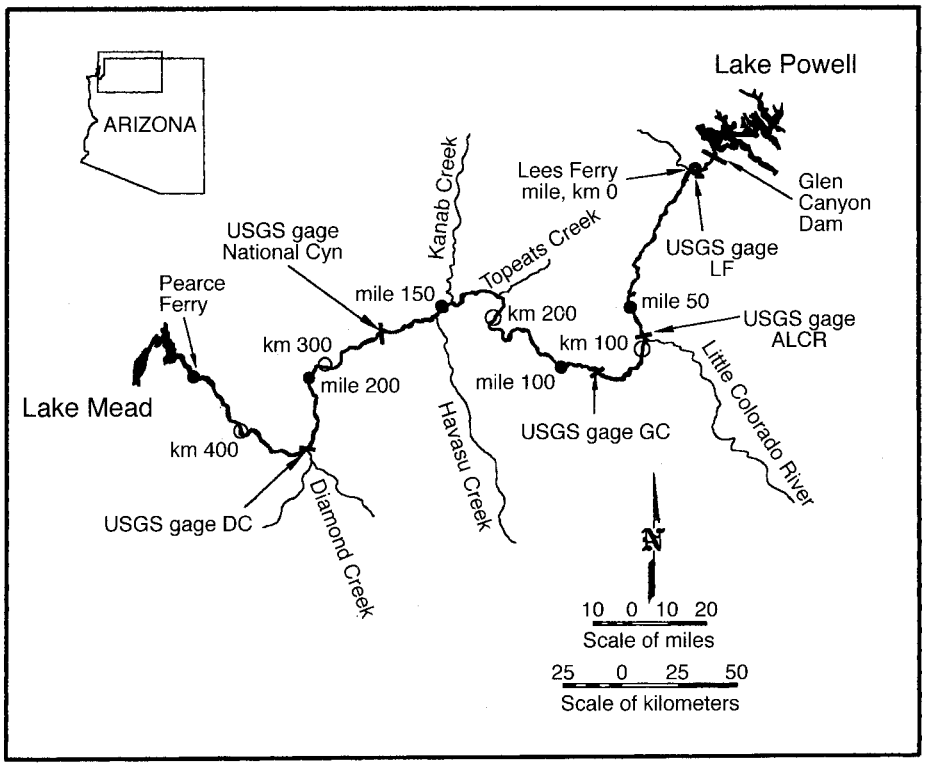

FIG. 1. Map of the Colorado River from Lake Powell to Lake Mead, Arizona. Distances along the river are measured from Lees Ferry, Arizona. Colorado River streamflow gages are monitored by the U.S. Geological Survey at the following locations: ALCR (Above Little Colorado River confluence [river km 98]); DC (Diamond Creek [river km 363]); GC (Grand Canyon near Phantom Ranch [river km 141]); and LF (Lees Ferry [river km 0]).

BACKGROUND AND SETTING

Construction of Glen Canyon Dam was completed by the U.S. Bureau of Reclamation in 1963. As the largest unit of the Colorado River Storage Project Act (1956) Glen Canyon Dam controls flow from the upper to the lower Colorado River basins (Fig. 1). Located on the Colorado River upstream from Grand Canyon National Park, this 216 m high concrete arch dam controls a drainage basin of 281 671 km^2. Eight hydroelectric generators at the dam produce up to 1288 MW of electric power. The major function of Glen Canyon Dam (and 33-km^3 Lake Powell) is water storage. The dam is specifically managed to release a minimum objective of 10.2 km^3 of water annually to the lower basin.

River resources downstream from Glen Canyon Dam through Glen, Marble, and Grand Canyons are closely interrelated and virtually all resources are associated with or dependent on water and sediment (U.S. Bureau of Reclamation 1995). In such a system, changes in a single process can affect resources throughout the entire system. For example, changes in Glen Canyon Dam operations, such as the test flood, directly affect hydropower, water supply, sediment, fish, and recreation. Vegetation, cultural resources, fish, and recreation may be affected as dam operational changes influence sediment in the river. Wildlife habitat, and threatened and endangered species can be affected through their linkages to other resources and the effects of water and sediment on those resources.

The Grand Canyon river ecosystem originally developed in a sediment-laden, seasonally and sometimes daily, fluctuating environment. Pre-dam flows ranged seasonally from spring peaks sometimes greater than 3000 m^3/s to winter lows of 28 m^3/s to 85 m^3/s. During spring snowmelt periods and summer flash floods, daily and hourly flow fluctuations occurred. While annual variability in water volume was high, a generally consistent pattern of high spring flows followed by lower summer flows provided an important environmental cue to plants and animals in the river and along its shoreline.

The construction of Glen Canyon Dam altered the natural dynamics of the Colorado River. Today, the ecological resources of Glen, Marble, and Grand Canyons depend on water releases from the dam and variable water and sediment input from tributaries. A reduced sediment supply and regulated release of reservoir water now support aquatic and terrestrial systems that did not exist before Glen Canyon Dam.

In 1982, the U.S. Bureau of Reclamation announced that, as part of its regularly scheduled replacement program, it would upgrade the generators at Glen Canyon

Dam to increase efficiency of hydroelectric power production. Environmental concerns were voiced because this potential change in dam operations could increase maximum dam releases by ~57 m^3/s to ~950 m^3/s. Consequently, Secretary of the Interior (Secretary) James Watt directed the U.S. Bureau of Reclamation to address these issues by establishing a team to study the effects of Glen Canyon Dam operations on the downstream river ecosystem. Called the Glen Canyon Environmental Studies (GCES), this group planned and managed research funded through hydropower revenues from the dam.

Glen Canyon Environmental Studies

There was no established model for designing a research program to understand full effects of dam operations on a river ecosystem. Several studies funded by the National Park Service had described how modified river flows and reduction of spring floods and sediment had altered the riparian system (Turner and Karpiscak 1980, Johnson 1991). However, subtle ecological changes resulting from dam operations such as daily changes in releases of 566 m^3/s and winter low flows of 28 m^3/s were not well understood. It was to address this paucity of information that GCES developed a research program.

Glen Canyon Environmental Studies had two phases. Phase I extended from 1982–1988, and Phase II from 1989–1996. GCES Phase I consisted of a set of studies designed to evaluate the effects of widely fluctuating releases from the dam on selected river ecosystem components. The initial effort consisted of baseline descriptive studies of ecosystem components and processes that were not integrated or coordinated. Compounding the problems of this research was a series of abnormally high inflow years. Emergency releases from the dam in June 1983 reached a peak discharge of 2755 m^3/s and flows were >1274 m^3/s for more than six weeks. This wet year was followed by more wet years from 1984–1986, affecting an ecosystem that had been scoured and was sediment starved. The 1983–1986 flood flows transported sand stored within the river channel, eroded low elevation sandbars, and aggraded high elevation sandbars in wide reaches. In many places, vegetation that had developed since dam construction was scoured, drowned, or buried, apparently reducing biological diversity. Some archeological sites also were damaged. The high elevation sandbars eroded following the return to lower flows (as they did pre-dam). A GCES Phase I evaluation of the impacts of large, unplanned, clear water floods and recovery of the river ecosystem concluded that floods in Grand Canyon have negative effects on the river ecosystem and should be avoided. Had a management group suggested mimicking natural floods in the canyon at this time, data from GCES Phase I would not have supported that recommendation.

A National Research Council (NRC 1987) review of GCES Phase I challenged the conclusions that flooding, even unplanned flooding, was harmful to the downstream ecosystem. The NRC committee recommended that, in order to fully understand the response of the ecosystem to floods or altered dam releases, future research programs should be composed of studies that were integrated, had an ecosystem orientation, and were grounded in hypothesis testing. These recommendations became guidelines for planning the GCES Phase II research program, and the test flood.

The GCES Phase II research program was designed to determine effects of dam operations under more normal, or even minimum, release years to complement the data from Phase I. Although a four to five year program had been developed, a request by the Secretary (Lujan) for the U.S. Bureau of Reclamation to prepare a Glen Canyon Dam Environmental Impact Statement (EIS) in 24 mo truncated this program.

The purpose of the EIS was to analyze alternative ways for operating Glen Canyon Dam, leading to a record of decision (ROD) that would set long-term operational guidelines.

Research flows.—The GCES Phase II integrated research program included "research flows" (Patten 1991). These represented a series of two-week "experimental flows" using different combinations of dam operational parameters: (1) magnitude of high and low discharge rates, (2) magnitude of daily fluctuations, and (3) ramping rate (the rate at which releases are increased or decreased diurnally to meet electrical load) (controlled fluctuations, $n = 9$; constant, $n = 3$; mimicking normal operational fluctuations, $n = 8$). Manipulation of operational parameters was expected to result in different, measurable effects on the downstream environment. If normal dam operations were the only pattern of operations studied over the short period, there would be little hope of gaining much information on responses of the many riverine resources to dam releases; information needed for the EIS. When research flows were approved for a 13-mo period, it set a precedent for using dam operations as a research tool.

Interim flows.—Upon completion of the research flows, the EIS had not been finalized and dam operations functioned under interim operating criteria (interim flows). These flows were designed to protect or enhance downstream resources while allowing limited flexibility for power operations. The minimum dam release was maintained higher than 1963–1990 minima to protect the aquatic food base from exposure and desiccation. The maximum release was also reduced in order to reduce sand transport thereby allowing accumulation along the riverbed. The daily fluctuation was limited so that the daily change in river stage would be nearly the same during all months; about one meter in most reaches. The down-ramp rate was set to reduce seepage-based erosion of sandbars in Glen, Marble, and

Grand Canyons and to avoid stranding of fish. The up-ramp rate was set to reduce other operation-related impacts to canyon resources, such as scour. Interim flows represented one of the first times a major dam was operated with consideration of the downstream ecosystem. These flows, along with research flows, demonstrated that under present laws and regulations (e.g., National Environmental Policy Act [NEPA] and the Colorado River Compact of 1922), a dam constructed for water storage and hydropower could be operated to balance economic gains with ecological research and protection. This also was the objective of the Glen Canyon Dam EIS, which was to examine options that, ". . . minimize, consistent with law, adverse impacts on downstream environmental and cultural resources and Native American interests . . . " (U.S. Bureau of Reclamation 1995).

Managed high flows.—Under the Glen Canyon Dam EIS the preferred alternative, or modified low fluctuating flow (MLFF) was similar to interim flows in goals and operations. It restricted maximum dam discharge, minimum discharge, ramping rates, and the daily range of discharges. MLFF also specified a number of other management actions including periodic high discharges from the dam, some within power-plant capacity and some higher. High discharges within power-plant capacity were called "habitat maintenance flows," and discharges greater than power-plant capacity were referred to as "beach/habitat-building flows." Use of high flows for management and restoration of downstream ecosystems is, along with reestablishment of other components of natural flow regimes, a keystone of many river restoration recommendations (Stanford et al. 1996, Poff et al. 1997). Decisions on timing of the various high flows were to be made by an Adaptive Management Workgroup, which would make recommendations on dam operations based on the results of long-term research and monitoring activities under the Grand Canyon Monitoring and Research Center, the replacement for Glen Canyon Environmental Studies.

Test-flood approval

NEPA compliance.—Although the final EIS was published in March 1996, an ROD could not be issued until completion of a General Accounting Office audit. Consequently, in order to run the test flood as planned in March 1996, separate National Environmental Policy Act compliance was initiated. The U.S. Bureau of Reclamation published the *Glen Canyon Dam Beach/Habitat-Building Test Flow Final Environmental Assessment and Finding of No Significant Impact* (U.S Bureau of Reclamation 1996) to provide NEPA compliance for implementing the test flood. Following the test flood, on 5 October 1996, Secretary of the Interior Bruce Babbitt issued an ROD on the future operations of Glen Canyon Dam. He announced that the facility would be operated according to the modified low fluctuating flow alternative described in the EIS.

External interest groups.—Implementation of the test flood not only required extensive scientific planning and addressing regulatory issues, but also necessitated understanding and cooperation by groups concerned with the effects of high dam discharges on their well-being or resources under their care. Aside from obvious interests such as water and power that tended to resist change in dam management policies, these interest groups included American Indian tribes with cultural concerns, white-water rafting companies, anglers and fishing guides, the Arizona Game and Fish Department, and the U.S. Fish and Wildlife Service (see *Flood experiment: Planning*). Examples of concerns were that high flows would inundate tribal deltaic agricultural lands in Lake Mead, might destroy the blue-ribbon trout fisheries below the dam, or significantly impact endangered species. When the test flood was implemented, all interest groups understood the importance of high flows to river ecosystems and supported this flood experiment.

Flood Experiment: Rationale, History, Planning, and Implementation

Rationale for the test flood

Periodic high flows occurred regularly prior to the construction of Glen Canyon Dam and are believed to be necessary to maintain integrity of the downstream river ecosystem. The test flood of 1996 was needed to test the hypotheses that the dynamic nature of fluvial landforms and aquatic and terrestrial habitats can be wholly or partially restored by short-duration dam releases substantially greater than power-plant capacity. This experiment would provide an opportunity to measure essential geomorphic and ecological processes during flood passage and recession. Data collected during the test flood would provide the information needed to test predictive models, and help to establish an operational regime to maintain, manage, and protect the riparian and aquatic resources of the Colorado River in Glen and Grand Canyons.

History

Initial discussions about creation of a controlled flood in Glen and Grand Canyons dates to the National Research Council (NRC 1987) review of GCES Phase I. NRC discussed the importance of flooding to river ecosystems and mentioned that perhaps a periodic controlled flood, with less potential for successive floods, might be a positive event for the canyon's river ecosystem under the right sediment storage conditions.

With approval from the cooperating agencies, beach/habitat-building flows were incorporated into all alternatives in the draft EIS in 1993. This initiated a planning process to test floods of greater than power-plant

magnitudes as a possible management tool for river ecosystem restoration.

Planning

After two years of planning and delays, in 1995 and early 1996, the U.S. Bureau of Reclamation and the U.S. Geological Survey developed and coordinated a detailed and integrated research program for a spring 1996 beach/habitat-building test flow. The research program was designed with a limited budget which helped facilitate a long-term goal of GCES to integrate studies by collecting data on several river ecosystem components within the same reach or area of the canyon. In this way, teams from different disciplines could assist each other, and logistic costs could be reduced.

The magnitude and duration of the test flood had been a contentious point from early planning. Most scientists thought that the greater the magnitude, the better. Early proposals were as high as 1700 m^3/s, with releases of >1400 m^3/s thought to be important for modification of sediment storage, scouring of backwaters and marshes, and possible alteration of debris fans. Information from GCES Phase I had demonstrated response of these resources to a high magnitude flood. The greater the magnitude, the greater the total amount of water needed for the experiment. After various compromises, 1274 m^3/s for one week (considered the minimum acceptable duration at that time) was accepted, and sufficient water for release during this period was planned into the annual operation plan for Glen Canyon Dam. The discharge was less than half that of the 1983 flood releases, where discharges lasted more than a week, and half to a third of the mean annual pre-dam spring flood peak.

The 1274-m^3/s level was accepted not only because of water limitations, but also because the river stage at 1274 m^3/s was considered by the U.S. Fish and Wildlife Service not likely to excessively damage the habitat and population of endangered species (i.e., Kanab ambersnail (*Oxyloma haydeni kanabensis*) and Southwestern Willow Flycatcher (*Empidonax traillii extimus*)). This demonstrates that water and power interests, as well as the Endangered Species Act of 1973, played an important role in the planning of the test flood.

The timing of the test flood was carefully considered. Although the time frame did not correspond to natural pre-dam May–June spring floods, the months of March and April were specifically selected to reduce impacts on river resources by conducting the test flood (1) prior to native fish spawning and larval dispersal periods, (2) after the period when rainbow trout spawn at Lees Ferry, (3) after concentrations of wintering Bald Eagles and waterfowl have mostly dispersed, (4) well prior to release of tamarisk (*Tamarix ramosissima*) seeds to reduce germination of this exotic plant, (5) prior to the beginning of the summer white-water boating season, and (6) prior to nesting of the endangered Southwestern Willow Flycatcher.

Description of the test flood

The test flood occurred in a year in which the dam was operated under interim operating criteria (interim flows), and modest flow fluctuations would have occurred had the test flood not been conducted (the "no action alternative" in Fig. 2). To accommodate the test flood, water volumes were redistributed from January and February to March and April (Harpman 1999). The test flood was conducted from 22 March to 8 April 1996 (Fig. 2). A four-day period of 227 m^3/s (8000 cfs) low steady flows preceded and followed the actual flood period. Releases were increased by 113 m^3/s in hourly increments (4000 cfs) until a maximum flow of 1274 m^3/s (45 000 cfs) was attained. This high release was maintained for seven days, and flow in excess of power-plant capacity was released from the river outlet works near the base of the dam (Fig. 2). To better mimic a natural receding limb of a flood, discharge was decreased hourly in steps of 42.5 m^3/s (1500 cfs), 28 m^3/s (1000 cfs), and 14 m^3/s (500 cfs), with the ramping rates reduced at 991 m^3/s (35 000 cfs), 566 m^3/s (20 000 cfs), and 227 m^3/s (8000 cfs), respectively.

Predicted effects of the test flood

The *Glen Canyon Dam Beach/Habitat-Building Test Flow Final Environmental Assessment and Finding of No Significant Impact* (U.S. Bureau of Reclamation 1996) provided NEPA compliance for the test flood, and presented a set of flood impact predictions for affected resources. These are briefly discussed along with some surprise findings from the test flood.

Water storage in Lake Powell.—Although the surface elevation of Lake Powell was expected to decrease during the test flood, its level at the end of the year was expected to be normal. During water year 1996, the total variation in the elevation of Lake Powell was ~4.7 m, which is quite typical. Lake Powell was ~0.6 m higher in February and 0.6 m lower in April than it would have been without the test flood. The elevation of Lake Powell dropped 1.1 m during the week of the test flood. These changes in lake level and the rapid withdrawal were expected to have small effects on limnology of the lake, especially the forebay region. Results of lake studies related to the test flood are presented in a compendium article by Hueftle and Stevens (2001) in this feature.

Flow and sediment.—Prior to the test flood, sediment researchers felt that sufficient sediment was available in the channel to permit development of elevated sediment deposits during the test flood, and some redistribution of sediment was also expected. However, the timing and location of flow and sediment changes could not be precisely predicted prior to the test flood, and improved modeling of these phenomena was expected

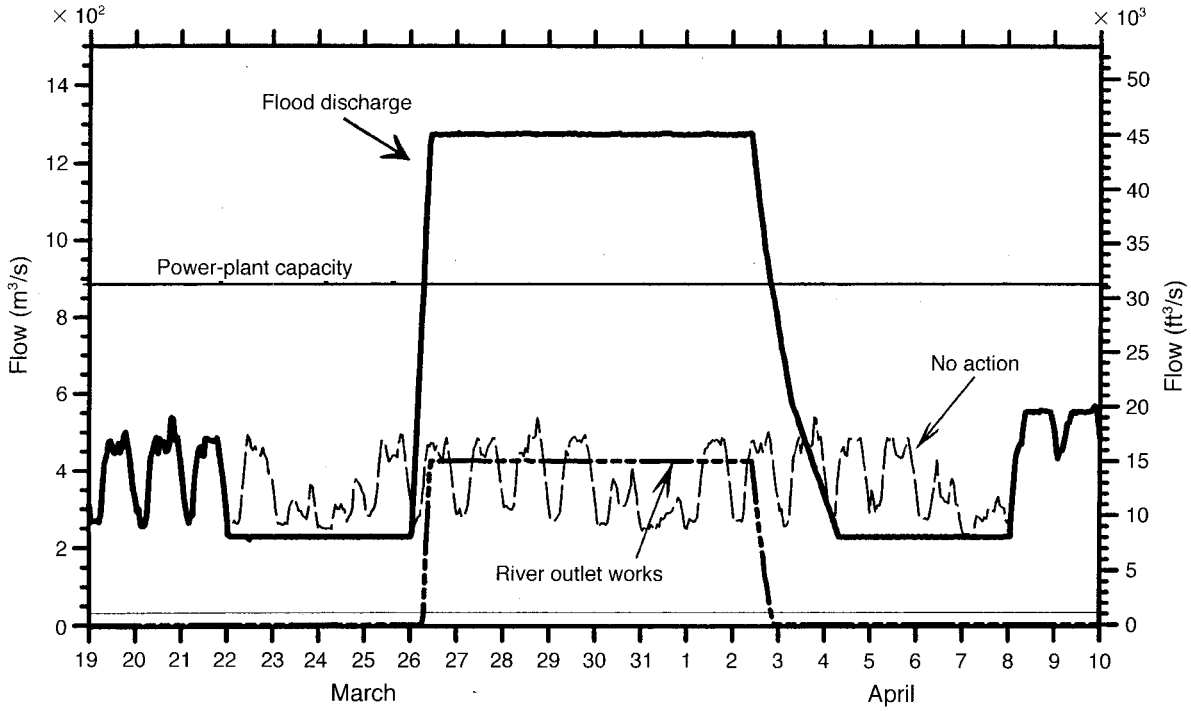

FIG. 2. The test-flood hydrograph from Glen Canyon Dam from 19 March to 10 April 1996. The graph shows the actual amount of water released (bold solid line), the "no action" alternative (thin dashed line), and the amount of water released from the river outlet works (bold dashed line). Power-plant capacity is 937 m^3/s.

as a primary scientific benefit of this experiment (Schmidt 1999; and see Schmidt et al. 2001 in this feature). Their research demonstrated that most sediment changes (i.e., scour, transport, and fill) occurred in the first few of days of the flood. On-the-ground sediment studies documented the volume of sediment changes from 33 large eddies and in several long reaches of the river corridor (Hazel et al. 1999). These sandbar response studies demonstrated a pattern of "higher, not wider" bar restoration from the test flood.

Aquatic food base and fish.—High flows were expected to scour and remove some components of the aquatic food base, particularly the abundant macrophytes that flourish in clear water below Glen Canyon Dam and above the confluence of the Little Colorado River. Impact of these changes on the native and nonnative fish populations was expected to be small. However, impact of high flows on young fish and nonnative species was not well understood, but long-term consequences were expected to be minor; and as it turned out, short-term changes were minimal as young fish used shorelines and tributary mouths as refugia from the flood. Results of aquatic food base and fish studies related to the test flood are presented in compendium articles by Shannon et al. (2001) and Valdez et al. (2001) in this feature, respectively.

Terrestrial habitat, riparian vegetation, and endangered species.—Riparian vegetation forms shoreline habitat for terrestrial species, including two endangered species, Kanab ambersnail and Southwestern Willow Flycatcher, as well as shoreline habitat and food resources for fish. High flows were expected to scour or fill low marsh areas but have little impact on woody riparian species. Sediment deposition was expected to bury or alter some riparian vegetation and habitat. Although the test flood buried ground-covering vegetation under the new sediment deposits, the magnitude of the flood was insufficient to scour perennial riparian vegetation. The endangered flycatcher was not nesting during the test flood and thus was not expected to be directly affected; however, the Kanab ambersnail habitat and population were reduced by the test flood. Results of riparian and habitat studies, and studies of the responses of endangered species related to the test flood are presented in Stevens et al. (2001) in this issue.

Cultural resources.—Most cultural resources were located above test-flood stage levels and direct impacts were not expected. However, restoration of eroded lower terraces was expected to reduce or slow the loss of cultural resources on higher terraces. Results of these and other cultural resource studies related to the test flood are presented in Balsom (1999) and in Stevens et al. (2001).

Recreation and hydropower.—Recreational use and hydropower economics are also important management considerations for this ecosystem (Harpman 1999).

Recreational potential was improved by the creation of more camping beaches (Kearsley et al. 1999, Schmidt et al. 2001). Direct recreational impacts were minimized by planning the test flood at a time when few white-water river trips occur in late March and early April (Myers et al. 1999). Economic impacts on angling, day-use rafting, and hydropower marketing were expected. During the eight days of the flood, day-use rafting was suspended and angling was largely curtailed. The income of some local businesses, which depend on anglers and day-use rafting, was slightly adversely affected; however, local expenditures by researchers, government officials, and the press more than offset those losses to the local economy.

The test flood affected hydropower economics not only during the event, but also during the remainder of water year 1996 (Harpman 1999). The test flood released 0.27 km^3 of water, and costs included $1.5 million (U.S.) for research and $2.52 million in lost revenue (3.3% of the total annual hydropower revenue), for a total cost of $4.02 million. Although it is commonly a misunderstood issue, research funds for the test flood were derived from hydropower revenue, not from the allocation of public funds from federal sources.

Conclusions

This compendium of papers describes many of the findings of the test-flood experiment, improvement of flow and sediment transport models, and updates information presented by Webb et al. (1999) and elsewhere. Eddy circulation processes under controlled conditions have helped illuminate our understanding of sediment storage and depletion mechanisms in canyon-constrained river ecosystems. Although more replication of this flow scenario is needed, the physical and biological responses of the ecosystem to a flow of this magnitude are now better understood, and new questions have arisen regarding how to use floods as management processes to improve resource conditions in Glen, Marble, and Grand Canyons.

Execution of this controlled flood, and the improved understanding of its influence on the Colorado River ecosystem, reinforce recommendations by many river and riparian scientists that restoring hydrological processes through mimicking or reestablishing natural flow regimes must be part of future river management. The test flood established an internationally recognized model for implementing future beach/habitat-building flows; however, many new questions exist around the timing and shape of future flood hydrographs. The frequency of future managed floods will be based on long-term monitoring and research programs under the Grand Canyon Adaptive Management Program. Continued cooperation among all interested parties is still needed to implement managed floods, because, as learned through this test flood, special interest groups are strongly resistant to change. Developing consensus among stakeholders on the use of scientific information and managed floods for sediment and resource management remains a primary challenge to the Adaptive Management Work Group.

Acknowledgments

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EXPERIMENTAL FLOOD EFFECTS ON THE LIMNOLOGY OF LAKE POWELL RESERVOIR, SOUTHWESTERN USA

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Abstract. In the spring of 1996, a nine-day test flood from Glen Canyon Dam involved the deepest and largest hypolimnetic withdrawals from the penstocks and the river outlet works (ROW) since 1986, interacting with ongoing hydrodynamic and stratification patterns to enhance freshening of the hypolimnion of Lake Powell reservoir and its tailwaters. Prior to the test flood, a six-year drought had produced a pronounced meromictic hypolimnion that was weakening from high inflow events in 1993 and 1995. Hypoxia, however, had continued to increase in the deepest portions of the reservoir. Over the course of the test flood, 0.893 km^3 were released from the ports located at and below the hypolimnetic chemocline. The increased discharge and mixing resulting from the test flood diminished the volume of this hypoxic and meromictic hypolimnion as far as 100 km uplake. This effect was reinforced by seasonal upwelling of hypolimnetic water at the dam and seasonal hydrologic patterns uplake. The timing and magnitude of the discharge maximized the release of the highest salinity and lowest dissolved oxygen (DO) water that typically occurs near the release structures of the dam annually. Subsequent high inflows and discharges in 1997 continued to freshen the hypolimnion.

During the flood, large aerated discharges in the tailwaters briefly increased DO to above saturation but dampened diel fluctuations in pH and DO. Downstream ion concentration levels were elevated during the test flood but resumed an enhanced freshening trend following the lower hydrograph. The results indicate that dam operations, timed with predictable limnological events, can be used to manipulate tailwater and reservoir water quality.

Key words: Colorado River; dam operations; experimental flood; Glen Canyon Dam; hydrodynamics; hypolimnion; hypoxia; Lake Powell; limnology; meromixis; multiple level withdrawal; reservoir; stratification.

INTRODUCTION

The use of dam operations as a variable to manipulate and experiment with reservoir and riverine systems is in its infancy. It is one element that differentiates reservoirs from natural lakes. In addition, reservoirs differ limnologically from natural lakes in their young age, their elongate and dendritic morphology, and because of the diversity of dam design, discharge patterns, and their typically sub-thermocline releases (Ryder 1978, Kennedy et al. 1982). These characteristics often limit the application of limnological theory derived from natural lakes to reservoirs (Kennedy et al. 1985, Thornton et al. 1990); and the great diversity of pattern and processes in reservoirs, as well as an incomplete state of knowledge, has restricted comprehensive predictive modeling of reservoir limnology. This has resulted in an individualistic management strategy for most reservoirs. The use of a large flood release from a dam allows a test of the effects on the limnology and productivity of both the upstream reservoir and the downstream river ecosystems (Ward and Stanford 1983). Thus, large reservoir discharge experiments may be used to improve the general understanding of reservoir limnology as well as refine strategies to improve reservoir management. In this paper we report on the impacts of a large experimental dam release on the limnology of Lake Powell, one of the largest reservoirs in the United States, and the Glen Canyon Dam (GCD) tailwaters downstream.

From its conception in the Colorado River Storage Project Act (1956) through 1991, GCD design and operations were motivated by hydroelectric power generation and storage allocations. With the advent of an Environmental Assessment, the Grand Canyon Protection Act (1992), and the Glen Canyon Dam Environmental Impact Statement and Record of Decision (U.S. Bureau of Reclamation 1995 and 1996, respectively), environmental concerns for the downstream ecosystems were introduced to management policy. While climate and the inflow of the Colorado and San Juan rivers primarily influence the stratification and hydrodynamics of Lake Powell, dam design and operations

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strongly influence the routing and discharge rates of various limnological strata within the reservoir and, consequently, reservoir water quality (Hart and Sherman 1996, Hueftle and Vernieu 2001). Although Colorado River ecosystem management has not been guided by concerns for Lake Powell's limnology, dam discharges have influenced the limnology of this large reservoir (Potter and Drake 1989), as well as the regulated river ecosystem downstream (Stevens et al. 1997; Valdez et al. 2001 in this feature).

Several features of dam design influence limnological development of Lake Powell. The location of the penstocks, the primary withdrawal port in GCD, has affected stratification patterns. The penstocks are located at a mid-depth bordering on the hypolimnion/epilimnion boundary, and draw from the hypolimnion almost half of the year. By isolating the hypolimnion from direct discharge, meromixis (stagnation and high chemical concentration) frequently occurs. Periods of meromixis are characterized by relatively high hypolimnetic specific conductance (a measure of salinity) and an upper boundary defined by a chemocline (chemical gradient) resistant to mixing.

Hypolimnetic stagnation and high dissolved oxygen (DO) demand can also result in hypoxia or anoxia. Anoxia and the associated reducing environment can produce hazardous compounds, such as hydrogen sulfide, which may pose hazards in-lake and downstream to both living organisms and to metal surfaces, such as the power-plant turbines. Drought conditions have resulted in several episodes of pronounced meromixis in Lake Powell since 1963, including the years preceding the test flood. Likewise, stagnation and DO demand has produced hypolimnetic hypoxia as low as 1.4 mg DO/L near the dam. Extremely low DO concentrations have not yet reached discharge elevations; a minimum of 4.5 mg DO/L has been recorded at the penstock elevation.

The river outlet works (ROW) are located deeper in the hypolimnion, almost always in the zone of meromictic stagnation. They are seldom used since they bypass power generation, but their location and operation would affect meromixis as they draw entirely from the hypolimnion except during the lowest lake stage. Data suggest that higher flow-through and ROW withdrawals may diminish the extent of hypolimnetic meromixis.

The existence and operation of Glen Canyon Dam (GCD) has significantly altered post-dam water quality in Glen and Grand Canyon (Stevens et al. 1997, Hueftle and Vernieu 2001). The presence and operation of the dam has greatly dampened seasonal variations in river flow; also, temperature, turbidity, and ionic concentration variability has been reduced to uniformly cold, clear, low nutrient waters. Post-dam discharge patterns have fluctuated greatly on a daily and weekly basis in response to power demands and are currently constrained by set ramping rates. Water quality and discharge below the dam is now dictated by reservoir water quality and the dam operations (Stanford and Ward 1986, 1991, Angradi et al. 1992). Interactions between the magnitude, duration, frequency, timing, and location of discharges from the dam influence uplake water quality, which, in turn, determines downstream water quality (Hueftle and Vernieu 2001). The effect of the unusually large and deep withdrawals of the test flood occurs in the context of seasonal limnological processes, obscuring cause-and-effect relationships. However, historical data allow comparisons of similar antecedent conditions without corresponding large discharges.

The 1996 test flood provided an opportunity to quantify these effects and elucidate the linkage between reservoir and downstream water quality. In this paper we address the following objectives: (1) describe the historical development of Lake Powell limnology; (2) determine whether the test flood's larger penstock discharges and releases from alternate structures affect Lake Powell limnology; (3) determine the extent of discharge required to produce measurable effects and how far uplake such effects are detectable; and (4) determine the impacts on downriver water quality. The large historical database (1964 through 1997), and the large size of this reservoir allow better comprehensive analysis of test-flood effects. Analysis of the limnological changes associated with a single, large discharge event may contribute to improved management of this and other large reservoirs that develop meromixis or hypoxia, in addition to improving the linkage to downstream water quality.

Methods

Study area

Glen Canyon Dam was completed in 1963, part of a series of dams resulting from the 1922 Colorado River Compact and the 1956 Colorado River Storage Act, providing for allocation and storage of water across the arid Colorado River basin. GCD is a 216.4 m high arch construction dam (Fig. 1). It provides three routes of release for the reservoir's water. Eight penstocks located 70 m below full pool elevation are the primary release structures. These can release a maximum of 940 m^3/s to the eight turbines for power generation, but are constrained to 892 m^3/s. The penstock draft tubes release below the surface of the tailwater pool, limiting aeration effects. Two alternate release structures may be used for greater discharge capacity, but both bypass power generation and their use is avoided. The ROW are located 99 m below full pool (29 m below penstock outlets) and can discharge 424–566 m^3/s. Their greater depth facilitates hypolimnetic discharge, and they have been used on seven occasions since 1963. The spillways draw from the epilimnion near the lake's surface at a depth of 16 m below full pool, although the lake

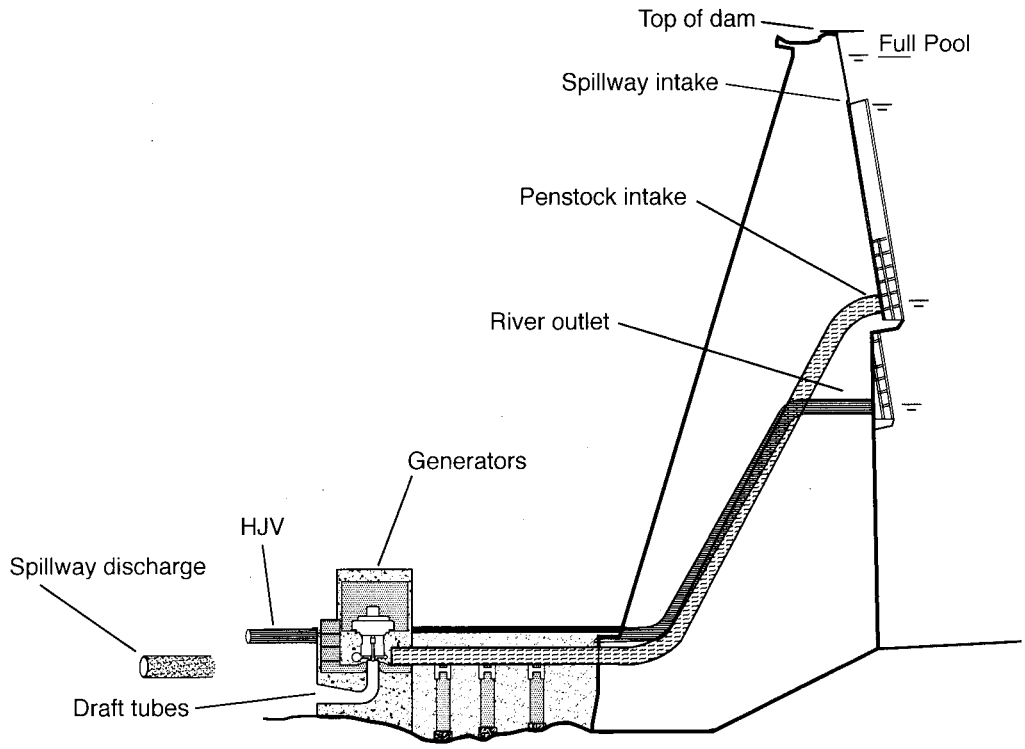

FIG. 1. Structure of Glen Canyon Dam with location and discharge capacity of outlet structures. Top of dam elevation = 1132.3 m; full pool elevation = 1127.8 m; dam base elevation = 958.6 m; spillways inlet elevation = 1111.9 m, outlet elevation = 962.3 m, maximum disharge (Q_{max}) = 5891 m^3/s; penstocks inlet elevation = 1057.65 m, outlet elevation = 947.6 m, Q_{max} = 892–940 m^3/s; river outlet works (ROW) inlet elevation = 1028.4 m, hollow jet valve (HJV) outlet elevation = 967.7 m, Q_{max}= 425–566 m^3/s.

has been below the spillways' operational levels for over half the lake's history. The spillways have a capacity of 5890 m^3/s to accommodate a 100-yr flood event, and have only been used in 1980, 1983, and 1984 (U.S. Bureau of Reclamation 1970, 1995).

Lake Powell is one of the largest U.S. reservoirs; located in southern Utah and northern Arizona, southwestern USA (Fig. 2). It first reached full pool in 1980, and has a maximum depth of 160 m, a surface area of 653 km^2, a length of 300 km, a volume of 32.1 km^3, and ~3200 km of shoreline at the full pool elevation of 1128 m above mean sea level (amsl) (U.S. Bureau of Reclamation 1970, 1995). The region has an arid continental climate: annual precipitation is 200 mm/yr and pan evaporation is 1800 mm/yr (Potter and Drake 1989).

Lake Powell is an oligotrophic lake (Potter and Drake 1989) with low nutrient levels; mean total phosphorus is 0.01–0.02 mg/L, and total Kjeldahl nitrogen is 0.16–0.2 mg/L. Results from the long-term (>30 yr) Lake Powell integrated water quality monitoring program (IWQP) identify Lake Powell as a warm meromictic reservoir; it has never completely mixed since its formation. It has a chemocline that persists near the depth of the penstock withdrawals. This meromictic hypolimnion, or monimolimnion, contains relatively stagnant water with elevated salinity (750 μS/cm to 1200 μS/cm), cold temperatures (6–9°C) and depressed DO (1.5–7 mg/L).

A previous period of meromixis at Lake Powell was disrupted by high inflows and multiple-level discharges in the 1980s during five years of exceptionally high inflows. The spillways (near the surface) and the ROW were operated on several occasions for extended periods in 1980 and from 1983 to 1986. Combined with three years of high flow-through and multiple-level withdrawals, the lake achieved a unique level of homogeneity in June 1985, with a conductance gradient 2.8 times less than the average for the lake's history. Data collection in the 1980s, however, was sporadic, with only two to five lake-wide collections per year. Trends were discerned, but relationships between dam operations and uplake processes were less clear. It was expected that analyses of the test-flood results would clarify some of the effects observed in the 1980s.

Data collection and sampling design

Historical and ongoing data from the IWQP were used, augmented with higher spatial and temporal resolution data near the dam surrounding the test flood (Fig. 2). The IWQP includes 25 long-term monitoring stations, eight that have been sampled since 1964. The

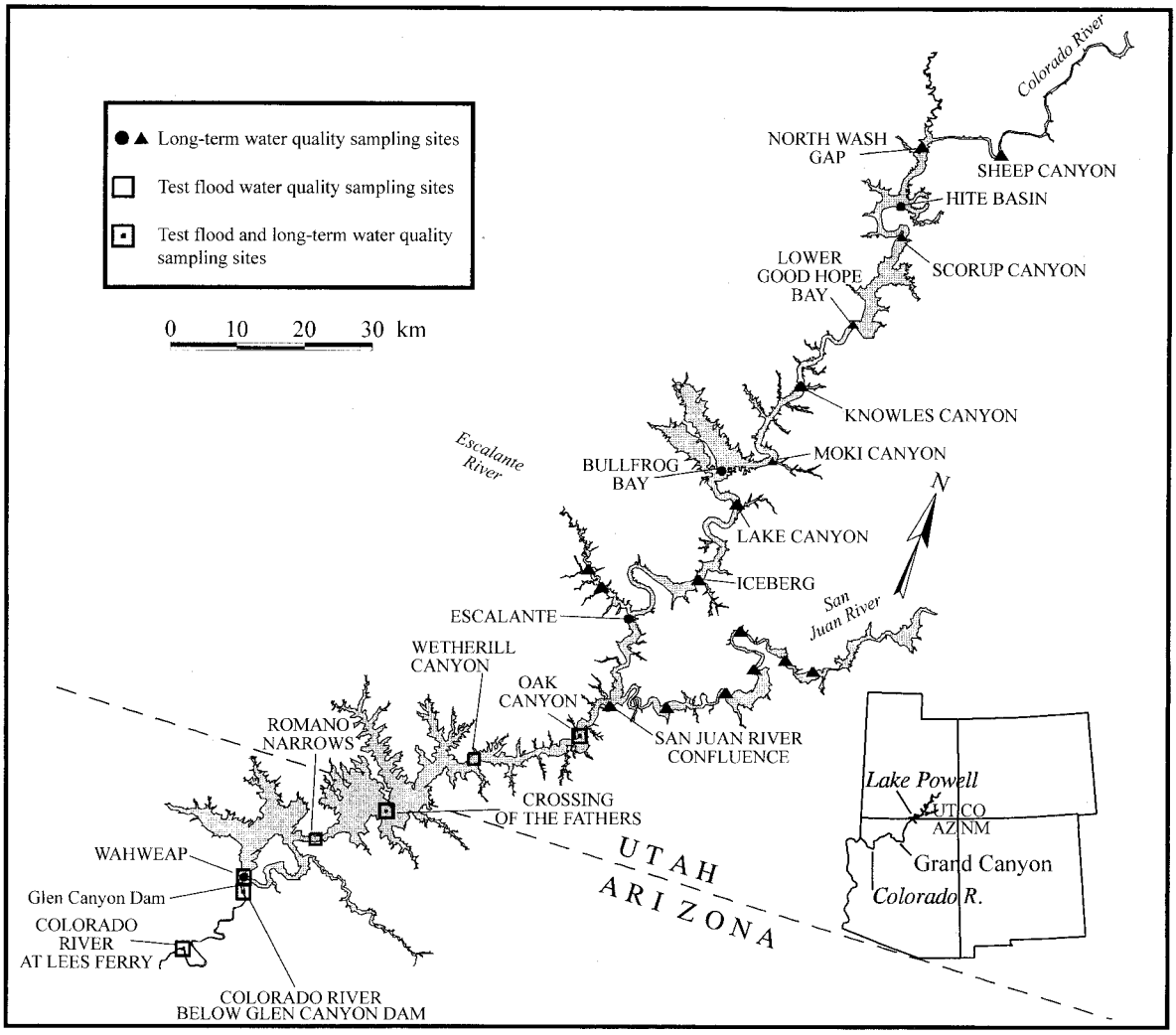

FIG. 2. Map of Lake Powell with sampling station locations, Utah and Arizona, USA.

test flood was bracketed by two full-lake quarterly IWQP sampling trips in the weeks of 1 March and 6 June 1996. These included 25 stations in the Colorado, Escalante, and San Juan river arms of Lake Powell. Using a Hydrolab Surveyor H2O multi-parameter submarine sonde (Hydrolab Corporation, Austin, Texas, USA), profiles of temperature in degrees Celsius (T), specific conductance (SC), dissolved oxygen (DO), pH, and turbidity were collected at depth intervals of 0.5 to 5 m at each station. Water chemistry samples were collected at 13 of these stations and analyzed for nutrient and major ion concentrations (APHA 1992) in the major stratigraphic layers. Secchi disk readings and biological samples of chlorophyll, phytoplankton, and zooplankton were collected at the surface. The IWQP also includes monthly sampling for all the above parameters at the Wahweap forebay station, and at the GCD and Lees Ferry tailwater stations.

The IWQP data was augmented with six additional physical profiles in the forebay immediately before, during, and after the test flood, on 22, 24, and 27 March, and 2, 3, and 5 April 1996. Synoptic channel profiling was conducted at four stations from the forebay uplake to river km 90 (Oak Canyon) on 22 and 27 March, and on 2 and 5 April; high winds, however, truncated some of these efforts. Chemical and biological samples were collected at the forebay station (2.4 km uplake from the dam) on 22 March and 5 April. An additional lake-wide collection of physical profile data was taken at 17 stations on the Colorado River arm of the reservoir to its inflow the week of 20 April 1996.

Higher resolution temporal data for the flood included three permanently deployed Hydrolab Recorders within and below the dam and at Lees Ferry, 25 km below the dam. These measured T, SC, DO, and pH at half-hour intervals. However, the high flows of the test flood rendered some of this information unusable. The Hydrolab profiles provided the finest res-

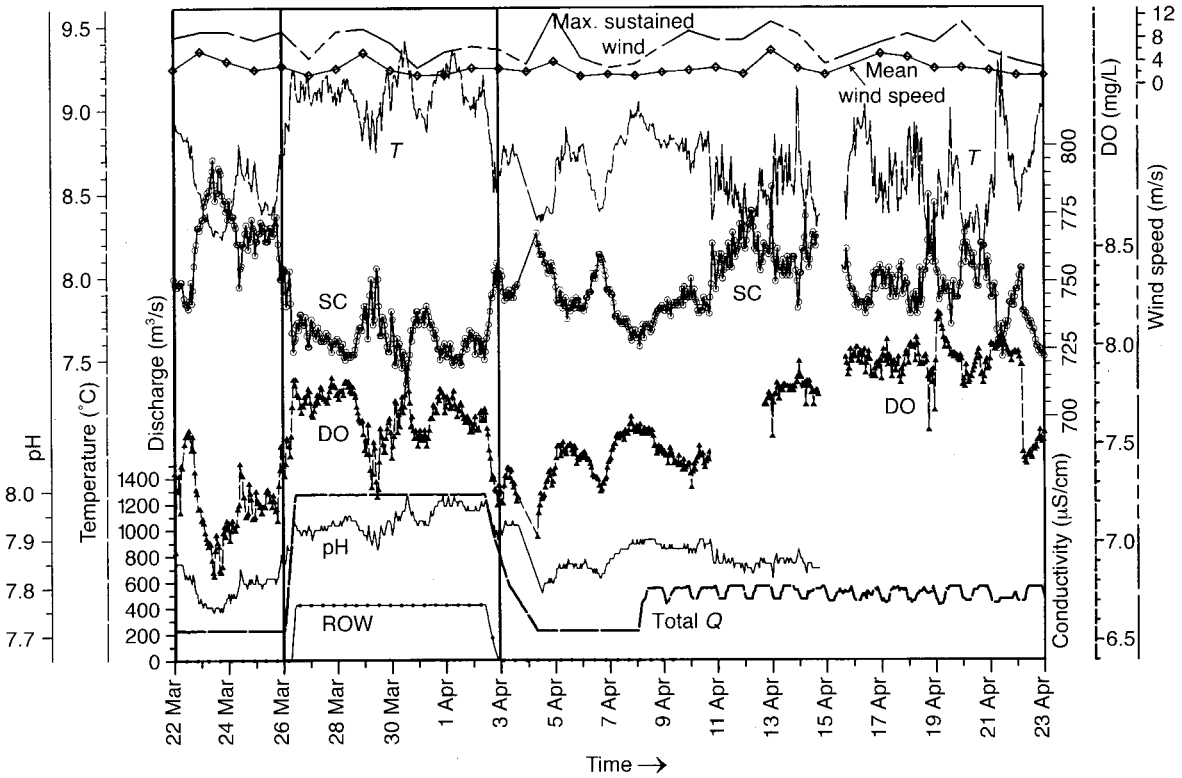

FIG. 3. Discharge (m^3/s), temperature (°C), conductivity (µS/cm), dissolved oxygen (mg/L), and wind speed (m/s) from 22 March to 23 April 1996 at the penstock draft tubes in Glen Canyon Dam, Arizona. Synchronized oscillations reflect seiche and discharge effects. Blank areas indicate instrument failure. Abbreviations are: *T*, temperature; SC, specific conductivity; DO, dissolved oxygen; ROW, river outlet works; and *Q*, discharge.

olution and the most consistent data sets, particularly at the greater depths affected by the penstock and ROW withdrawals.

All Hydrolab instruments were calibrated using standard solutions and established protocol (Hydrolab 1994) before and after each sampling period. Blanks, duplicates, and spiked samples were collected for every 10 chemical samples.

Analyses

Data were compiled, reviewed, and analyzed using SAS and Lotus software. Grapher (Golden Software 1994), and Surfer (Golden Software 1996) software were used to generate two- and three-dimensional (isopleth) graphics, respectively. Isopleths illustrating lake-wide hydrodynamic processes plot various parameters against depth (in elevation) and river channel distance uplake from Glen Canyon Dam. Long-term trend analysis was facilitated by temporal isopleths plotting various parameters against depth and time. An animation sequence of the lake-wide conductivity isopleths since 1965 is available online.[3] This demonstrates hydrodynamics, underflows, and discharges of the reservoir including profiles of the test flood.

[3] URL = ⟨http://www.gcmrc.gov/iwqp/lpanisc.htm⟩

RESULTS

Discharge hydrograph and lake elevation

Prior to the test flood, the dam had discharged at above average levels since June 1995 as a result of large inflows that spring. Flows were increased from 280–340 m^3/s to 480–537 m^3/s in June and maintained there until October 1995, and thereafter averaged 340–425 m^3/s until the test flood in 1996.

On 26 March 1996, penstock and ROW releases were increased to 850 m^3/s and 425 m^3/s, respectively (Fig. 3). A total volume of 0.893 km^3 was discharged during the test flood; 0.626 km^3 from the penstocks and 0.267 km^3 from the ROW. Following the experiment, discharges from the dam were increased to high fluctuating levels of 450–566 m^3/s for the duration of the spring to accommodate the large 1996 snowpack. Although the test flood is identified by the seven days of high releases, the experiment included eight days of low steady flows bracketing the flood, (Patten et al. 2001 in this feature) which also produced effects to lake and tailwaters.

The test flood directly affected lake elevation. Over the course of the experiment, between 22 March and 8 April, reservoir elevation had a net drop of 0.98 m. Although the reservoir dropped 1.12 m during the test

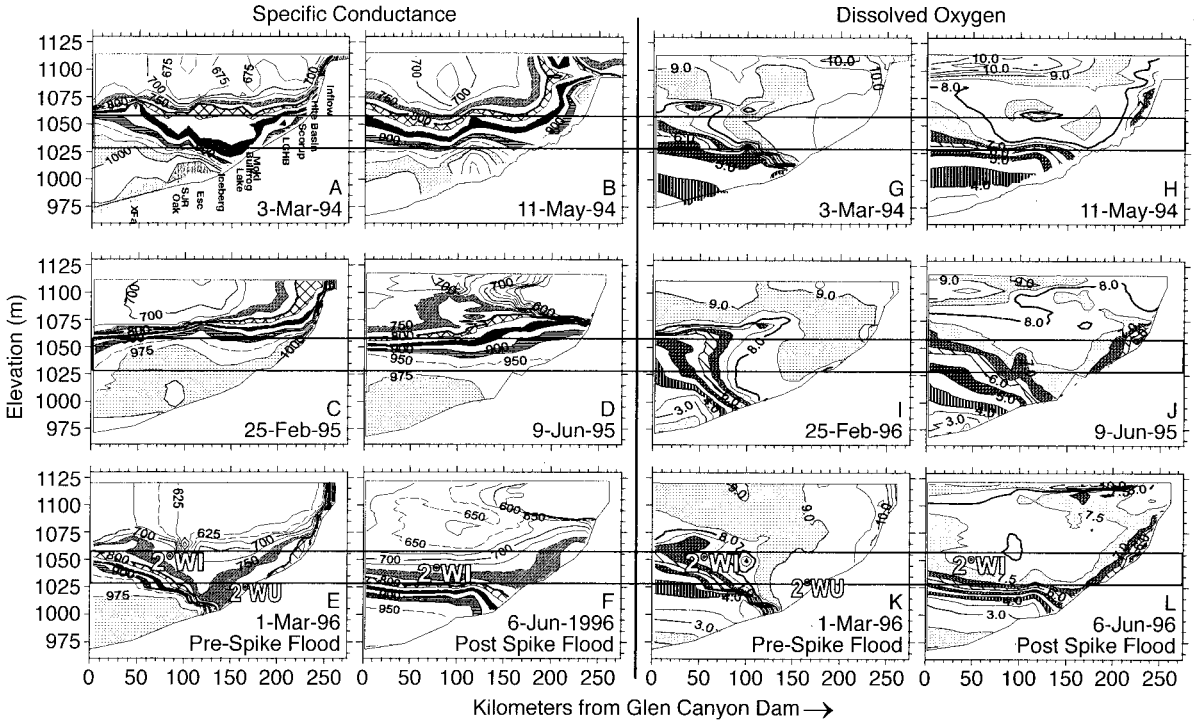

FIG. 4. Synoptic channel profiles of Lake Powell, Arizona and Utah, for conductivity (μS/cm; plots A–F) and dissolved oxygen (mg/L; plots G–L) in winter and spring from 1994 to 1996, comparing seasonal shifts in chemoclines for the test flood and two previous years. Contour interval = 25 μS/cm for SC (specific conductivity), 0.5 mg/L for DO (dissolved oxygen). Penstock, ROW (river outlet works), and sampling stations elevations are indicated on plot A. Underflows 2° WI (secondary winter interflow) and 2° WU (secondary winter underflow) are indicated on plots E, F, K, and L.

flood, the four days of 227 m^3/s discharges preceding and following the 1,274 m^3/s flood increased reservoir stage by 0.15 m. The lake elevation changes were slightly more than anticipated because of the later onset of the high spring inflows. Soon after the experiment concluded, the reservoir elevation increased substantially. The sudden drop in lake elevation required that water stored in the more eutrophic side-bays enter the mainstem (Thornton et al. 1990). The data suggests mainstem nutrient levels may have increased throughout the reservoir in June 1996, accompanied by increased chlorophyll *a* and *c* and pheophytin *a*. However, the existing IWQP includes few side-bay collections, particularly in the lower reach. Therefore, trends from side-bays are not conclusive and cannot be verified, but suggest further investigation and imply management considerations.

Stratification and hydrodynamics: antecedent conditions

The previous decade's climate and inflow patterns affected the limnological conditions prior to the test flood, and understanding these is critical to interpreting the results of the test flood on reservoir stratification and hydrodynamics. From 1987 to 1994, Lake Powell's drainage basin experienced extended drought; six of those years were among Lake Powell's lowest inflows in the reservoir's 33-yr history. This resulted in a pronounced monimolimnion with a pycnocline (density gradient) resistant to mixing. This stratification was weakened by two high inflows (fifth and sixth highest in the lake's history) in 1993 and 1995. These inflows introduced a large pool of lower SC water for winter mixing in the epilimnion.

Numerous authors, including Merritt and Johnson (1978), Johnson and Merritt (1979), Gloss et al. (1980), Gloss et al. (1981), Edinger et al. (1984), and Stanford and Ward (1986, 1991) have described Lake Powell's density currents. Normal winter hypolimnetic processes are dominated by partitioned underflows that form in the inflows and migrate advectively toward the dam (Hueftle and Vernieu 2001). The first winter underflow (1° WU) forms in the fall as a relatively warm, saline mass of dense water flows along the former riverbed toward the dam, dispersing through and thickening the monimolimnion. The secondary winter underflow (2° WU) forms in the inflow at the peak of winter, a cold, convectively mixed mass of relatively cold, oxygenated, and lower salinity water that follows the 1° WU downlake. Although its density is rarely sufficient to completely displace the hypolimnion, the 2° WU may refresh the stagnant hypolimnion if it is of sufficient

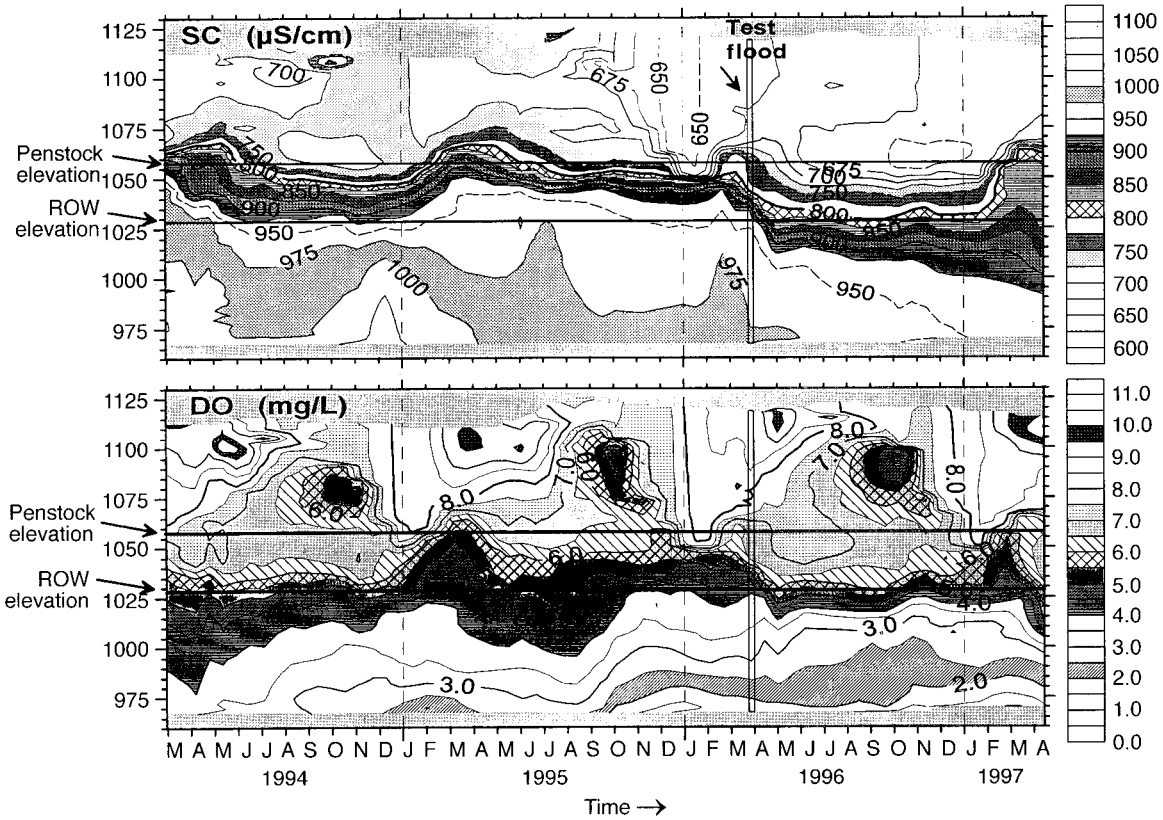

FIG. 5. Temporal isopleths of conductivity (µS/cm) and dissolved oxygen (mg/L) at the Wahweap forebay station demonstrating upwelling and chemocline migration, 1994–1997. Abbreviations are as in Fig. 3.

magnitude and density, and dam discharges are favorable. Most commonly, this 2° WU reaches the chemocline midway down the thalweg in the reservoir and becomes an interflow (2° WI), overriding or passing through the hypolimnion, depending on its relative density. It is then drawn into the penstock withdrawal zone. This 2° WI occurs regularly, and its freshening potential increases with the depth the density current achieves before diversion over the hypolimnion. Preceding the test flood, the 2° WU was in transition to a 2° WI 135 km uplake. These conditions were similar to those in 1994 (155 km) and 1995 (110 km) (Fig. 4).

A second component of the freshening 2° WU is the advective force it applies to the hypolimnion. While rarely able to penetrate the chemocline, the advective forces of the 2° WI are often sufficient to depress the hypolimnion, creating a periodic "upwelling" of the hypolimnion. As a result, the chemocline ascends the face of the dam for a period of weeks to months. This effect can be seen in the three-year forebay isopleths (Fig. 5), with the upwelling effect typically beginning in February, peaking in March, and diminishing by May. Prior to the test flood, upwelling had already peaked by mid-February and was subsiding. The upwelling effect is diminished: (1) by discharge through the dam and (2) subsidence of the upwelling as the advective forces of the 2° WI dissipate. The animation sequence as well as the synoptic channel profiles (Fig. 4) demonstrate annual winter upwelling cycles evident near the dam.

The upwelling pattern maximizes hypolimnetic discharge through the penstocks and ROW. However, the interflow pattern can confuse the interpretation of test flood impacts with seasonal hydrodynamics already underway. By late 1995, the 2° WU had shifted to a 2° WI, and its descent along the thalweg of the lake slowed as it impinged on the pycnocline and diverted horizontally downlake toward the penstocks. From the onset of the test flood, inflow hydrodynamics actively affected reservoir limnology at the penstock elevation. Therefore, distinguishing test flood effects from existing seasonal change required an examination of rates of change on water quality and the impacts from the ROW.

Effects on stratification and hydrodynamics

Test flood effects on Lake Powell were observed through shifts in chemoclines with consequent changes in strata volume, and through shifts in water quality. The synoptic channel profiles (Figs. 4 and 6) and temporal Wahweap forebay isopleths (Fig. 5) demonstrate the descending migration of the chemocline and DO

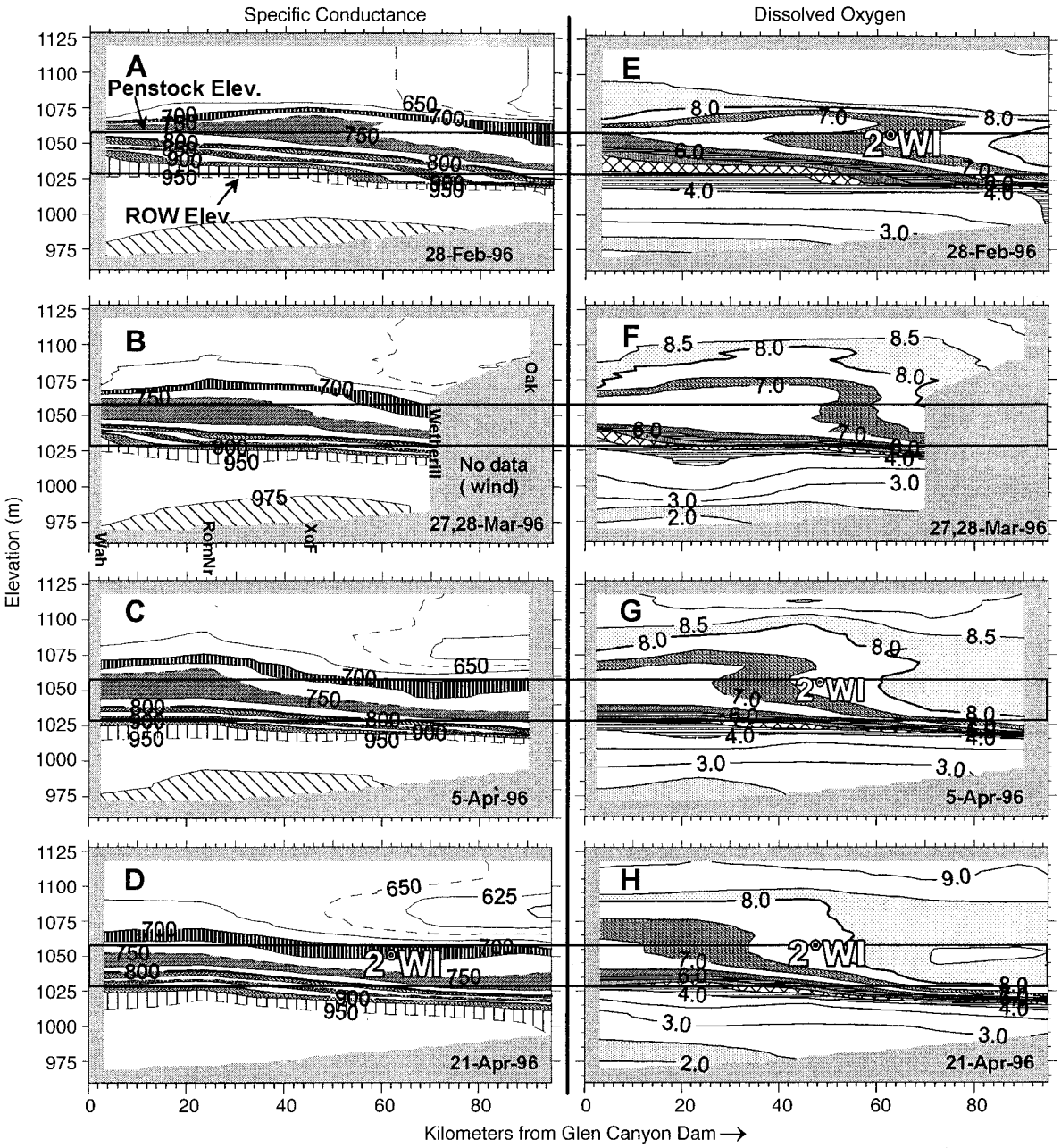

FIG. 6. Detailed synoptic channel profiles to river km 90 of Lake Powell, Arizona and Utah, showing the advancing front of the 2° WI (secondary winter interflow) through shifts in conductivity (μS/cm; plots A–D) and dissolved oxygen (mg/L; plots E–H) gradients from 28 February to 21 April 1996. Penstock and ROW (river outlet works) elevations are indicated on plot A. Sampling stations are indicated on plot B.

gradients during the test flood. Comparisons with the previous year's upwelling and subsidence patterns show the test flood effects were most pronounced at the ROW depth, where the freshening effects of the 2° WI discharge were most dramatic. Prior to the test flood, three distinctive strata were distinguished from SC and DO concentrations at the Wahweap forebay station (Figs. 4 and 6): (1) an upper convectively and wind-mixed epilimnion underlain by a distinct chemocline 7.5 m above the penstock outlets; (2) a 24-m thick 2° WI middle layer underlain by a second chemocline 13 m above the ROW; and (3) a lower 66-m thick monimolimnion. Changing the elevation and magnitude of discharge restructured these layers. As a general rule, increases in discharge result in a third power increase in kinetic energy available for mixing,

TABLE 1. Water chemistry results at the Glen Canyon Dam forebay station (Wahweap forebay station) on 22 March and 5 April 1996, before and after the test flood (respectively).

	Surface		Penstock		ROW‡	
Parameter†	22 March	5 April	22 March	5 April	22 March	5 April
Temperature (°C)	13.83	12.15	8.56	8.39	7.87	7.78
Field pH	8.18	8.12	7.78	7.76	7.6	7.58
Field SC	670	667	778	762	925	896
Turbidity (NTU)	0	0	1.2	0.9	1.2	1.1
DO (mg/L)	8.6	8.91	6.21	6.72	4.37	4.78
TDS (mg/L)	441	434	503	487	636	553
Ca (mg/L)	59.6	54.7	65.9	62.3	78.3	70.4
Mg (mg/L)	19.6	18.1	21.4	20.1	25.5	22.7
Na (mg/L)	53.8	49.7	63.8	59.1	79.9	69.2
K (mg/L)	3.37	3.21	3.22	3.63	3.94	4.08
HCO_3 (mg/L)	151	150	161	162	176	171
SO_4 (mg/L)	170	160	187	180	240	213
Cl (mg/L)	35.4	33.8	49.1	46.8	63.5	56.6
TP (mg P/L)	<0.005	<0.005	0.005	<0.005	0.006	<0.005
OP (mg P/L)	<0.005	<0.005	<0.005	<0.005	<0.005	<0.005
NH_3 (mg N/L)	0.010	<0.010	<0.010	<0.010	<0.010	<0.010
NO_{2+3} (mg N/L)	0.16	0.18	0.33	0.34	0.42	0.39
TKN (mg N/L)	0.06	0.08	0.08	0.08	0.10	0.09
Ion average	102	107	116	120	140	139
Sum of ions (mg/L)	943	913	1061	1028	1298	1165

† Parameter abbreviations: SC, specific conductance; NTU, nephelometric turbidity units; DO, dissolved oxygen; TDS, total dissolved solids; TP, total phosphorus; OP, ortho-phosphate, TKN, total Kjeldahl nitrogen.
‡ ROW = River outlet works.

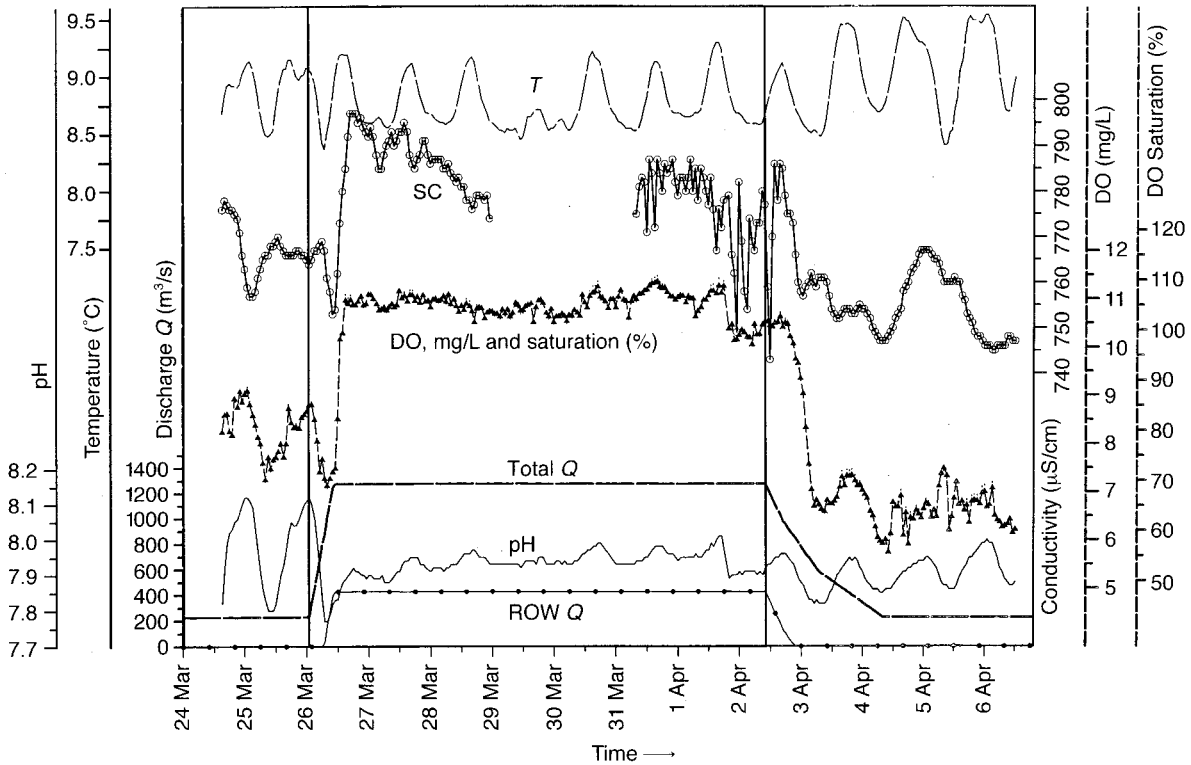

FIG. 7. Discharge (m³/s), temperature (°C), conductivity (µS/cm), dissolved oxygen (mg/L), and pH for 24 March–5 April 1996 at Lees Ferry, Arizona. Abbreviations are as in Fig. 3.

TABLE 1. Extended.

Bottom	
22 March	5 April
7.19	7.23
7.41	7.42
976	976
1.4	1.3
1.63	2.02
629	625
80.5	79.5
25.8	25.4
80.4	79.7
4.18	3.85
182	181
248	245
65.9	66.6
0.007	<0.005
<0.005	<0.005
<0.010	<0.010
0.44	0.45
0.14	0.09
144	153
1318	1309

as KE $\propto Q^3$ (Thornton et al. 1990); this extends the vertical draw of the outlets (Monismith et al. 1988). Hence, the increase from the normal penstock discharges of 390 m^3/s to bi-level discharges of 850 m^3/s and 420 m^3/s from penstocks and ROW increased mixing energy by an order of magnitude, while total discharge only increased threefold.

The addition of sub-hypolimnetic discharge intensified vertical mixing. With the onset of the bi-level high releases, the upper chemocline weakened as the penstocks drew more heavily from the epilimnion and the 2° WI. Profile data at the dam demonstrated refreshment at the penstocks as they drew from the epilimnion (Fig. 3). But below the dam at Lees Ferry, comingled penstock and ROW releases show an overall increase in ionic concentrations, reflecting the dominance of ROW hypolimnetic output (Fig. 7). The chemocline below the 2° WI and between the outlet ports weakened and descended more than 12 m to the level of the ROW at the conclusion of the flood. The 2° WI stratum was thickened 16 m as it drew from the wider wedge uplake, entraining the epilimnion and hypolimnion and weakening the associated chemoclines as it moved downlake. Isopleths indicate the withdrawal zone extended from 50 to 100 or more km uplake, even accounting for vertical uncertainty produced by localized seiche oscillations (Figs. 4 and 6). Chemical data collected near the dam before and after the test flood show consistent decreases in ionic concentrations by an average 4.4%, demonstrating the refreshment of the forebay, particularly in the upper hypolimnion (Table 1). The most pronounced shifts surrounding the test flood occurred near the ROW. This was not unexpected due to the meromictic conditions, the influx of fresher conditions provided by the 2° WI, and higher discharge. Surface and bottom samples demonstrated the least change. Calculations of the load of salt ions and DO vs. relative discharge from the ROW and penstocks illustrate the disparity in discharge vs. meromixis (Table 2). Although the ROW only accounted for a third of the flood discharge, they contained 23% higher conductance and 33% less DO than is found at the penstocks. Consequently, the introduction of discharges from the ROW had a disproportionate long-term freshening effect upon the hypolimnion compared with penstock withdrawals.

Continued dilution of the hypolimnion was apparent (Fig. 5) following the test flood through 1997. This resulted from another high inflow year and continued high releases from February to June 1997, again, commenced during the upwelling event.

Rates of change (in percentage change per day) for *T*, SC, and DO were calculated for a given point between each of the interpolated isopleths of the main channel from 28 February to 21 April. These calculations excluded the top 30 m of the lake and included the upper 100 km of the length (those zones affected by short-term seasonal influences). The results indicate the greatest changes occurred between 2–5 April immediately following the test flood (summarized in Fig. 8). The next highest rates of change were observed from 22 March to 2 April, during the test flood. These

TABLE 2. Discharge and ion load statistics for the penstocks (PS) and river outlet works (ROW).

Parameters	ROW	PS	Total for PS + ROW	Null hypothesis: no test flood†
Lake elevation (m)	1028.4	1057.65		
Dissolved oxygen (DO; metric tons)	1187	4137	5324	2062
DO discharged (%)	22.3	77.7	100.0	−61 or 2.6× less
Total dissolved solids (TDS; metric tons)	176 353	336 714	513 067	167 850
TDS discharged from each port (%)	34.4	65.6	100.0	−67 or 3.1× less
Volume discharged in test flow (km^3)	0.267	0.626	0.893	0.312
Volume discharge from each port (%)	29.9	70.1	100.0	100.0
Test release from total lake volume below port (%)	10.22	10.96	14.56	
Volume below port depth (km^3)	2.44	6.12	6.12	

† Null hypothesis values projected forecast releases of Q_{avg} = 392 m^3/s (Pattern et al. 2001) for the same period (9.21 d) as the large test flood releases.

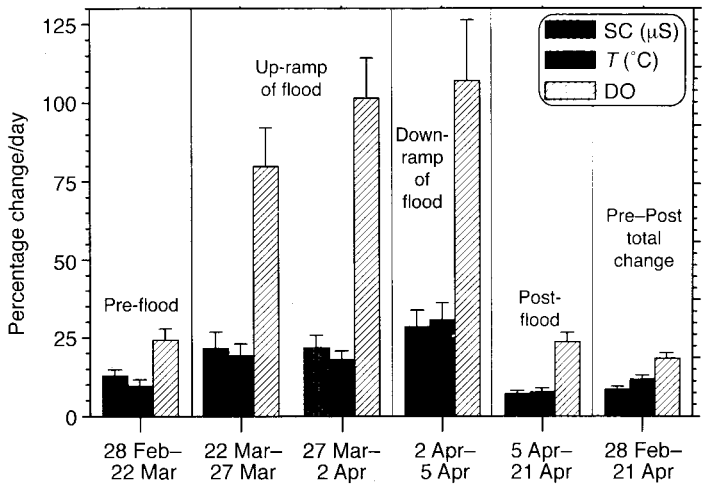

FIG. 8. Percentage change per day in Lake Powell for conductivity (SC), temperature (T), and dissolved oxygen (DO) before, during, and after the test flow from Wahweap to Good Hope Bay, Lake Powell, Arizona and Utah. Data are absolute values of percentage change per day; error bars indicate 95% confidence intervals.

results further substantiate the increased effects of the test flood over normal operations.

Withdrawal zone and tailwaters effects

During the experiment, wind and discharge conditions contributed to water quality oscillations from the Wahweap forebay station to Lees Ferry (Figs. 3 and 7). Internal seiche oscillations are frequently observed in high temporal resolution data sets during the winter at GCD. These oscillations are most evident when the reservoir's chemocline impinges on the penstock elevation, such as during the ascending and descending limbs of hypolimnetic upwelling. Isolated wind events such as those on 20 April 1996 (National Climatic Data Center 1996), initiate wind-induced internal seiche oscillations (Wetzel 1975, Cole 1994, Horne and Goldman 1994,) of T, SC, DO, and pH at the dam. As mentioned previously, changes in release rates also create rapid water quality shifts at the penstock level due to the strength and dimensions of the withdrawal plume (Hart and Sherman 1996, Hueftle and Vernieu 2001). Although at least four strong wind events (Fig. 3) occurred during the test flood and created complex interfering seiche patterns, the magnitude and timing of oscillations resulting from the test flood are clearly distinguished from wind induced seiches (Fig. 3).

The use of the hollow jet valves (the release structure for the ROW) also creates a unique signature. The valves ejected four plumes of aerated water 10 m above the tailwater pool. Combined with the draft tube discharges from the penstocks, the higher discharge was more turbulent than normal discharges. Turbidity and total suspended solids increased from 0.2 to 0.6 NTU (nephelometric turbidity units) and 2 to 19 mg/L, respectively, during the test flood (U.S. Geological Survey 1996). The effects of spray and turbulence from the hollow jet valves immediately oxygenated the tailwaters, resulting in mean DO saturation increases from 79% to 105% (Fig. 7). Typically, T, DO, and pH reflect fluctuating diurnal patterns that develop in the highly productive 25-km tailwater stretch of normally clear, lower flows (Angradi et al. 1992, Ayers and McKinney 1996). Respiration of *Cladophora glomerata* (the dominant algae) and other life-forms contribute to diel pH and DO fluctuations, while T responds to insolation. During the test flood, diurnal pH patterns were attenuated (Fig. 7), demonstrating the reduction of respiration due to increased drift (Shannon et al. 2001 in this feature) and lower light availability resulting from higher discharges, greater turbidity, and deeper water (M. Yard and D. L. Wegner, *personal communication*). Diurnal pH and DO fluctuations recovered quickly (within hours) once lower discharges recommenced, although net respiration was reduced from pre-flood levels due to the sheared biomass. Diurnal pH fluctuation levels had returned to pre-flood levels by late April 1996. During the test flows, diurnal DO patterns, though still present, were overshadowed by jet valve aeration. Conductivity reflected short-term seiche effects and higher salinity of the ROW dominated withdrawal plumes in the forebay.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Given the context of antecedent conditions, these data demonstrated significant impacts on reservoir and downstream water quality. The most influential factors were the magnitude and composition of the 2° WI; followed by the location, magnitude, timing, and duration of dam discharges, not necessarily in that order. Had the test flood not occurred during the hypolimnetic upwelling, nor the ROW been used, the penstocks alone could not have substantially flushed the hypolimnion. The ability of the penstocks to mix and entrain the hypolimnion is considerably less under normal discharge levels. Without large, carefully timed, and/or bi-level discharges, the opportunity to release mer-

omictic water may be foregone. In the reservoir, significant shifts in salinity and DO gradients were observed near the penstock and ROW elevations as far as 100 km uplake. Fresher, more oxygenated water was drawn into the middle depths of the forebay from the epilimnion and 2° WI uplake. These more dilute conditions persisted through 1997. Although of short duration, the test flood affected Lake Powell limnology in a fashion that provides insight into the dramatic shifts in water quality alluded to in the 1980s historical data set (Hueftle and Vernieu 2001).

In the tailwaters, jet valve aeration, attenuation of primary productivity, and the trace of seiches and meromictic discharge were strong signatures of the test flood, though short-lived. Shannon et al. (2001), Stevens et al. (2001), and Valdez et al. (2001), address longer term aquatic impacts on downstream resources.

These effects are important to in-lake water quality and determination of downriver water quality. Currently, large discharges are likely to occur only during periods of high lake levels and high inflows, thus, future high releases will probably occur during periods of declining meromixis. Should in-lake hypoxia or meromixis approach levels of concern, however, the test flood demonstrated a mechanism for their downstream release. Hypoxia, not always associated with meromixis, could be managed with well-timed ROW releases. Dam operations could influence the banking or release of ion concentrations, DO, *T*, and other components that were not examined here, such as biological components. Carefully timed dam releases could be used to avert problems with minimal impact to power production and water storage. For example, precise releases at peak upwelling in February or March would require less discharge volume to reduce meromixis than at other times of the year. But uplake and downstream effects must be considered prior to future actions.

This study of large and multilevel discharges from GCD has global implications for future reservoir, discharge, and downriver management opportunities, including future experimental floods, flow regimes, and other management options that are pending at Glen Canyon Dam.

Installation of a selective withdrawal system is an option outlined by the Final Environmental Impact Statement (Stanford and Ward 1996). Its purpose, via epilimnetic withdrawal, is to warm the Colorado River to encourage mainstem spawning of endangered native fish. Such action could produce unforeseen thermal, chemical, and biological changes above and below GCD. Use of hypolimnetic discharge may offset some of these impacts, and continued investigations could lead to more informed decisions.

The demonstration of the test flood effects as well as those observed during the 1980s spillway discharges alludes to impacts we could expect from the operation of a selective withdrawal system. Operational changes will have limnological impacts, and informed decisions will require a sound limnological foundation for management of water quality resources. Current knowledge of the strength, destination, and quality of winter underflows and inflows, strength of meromixis, antecedent conditions, and long-range considerations will be required for informed management in the future.

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THE 1996 CONTROLLED FLOOD IN GRAND CANYON: FLOW, SEDIMENT TRANSPORT, AND GEOMORPHIC CHANGE

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Abstract. The 1996 controlled flood released from Glen Canyon Dam into the Colorado River was a small magnitude, short duration event compared to pre-dam floods. The controlled flood was of lesser magnitude than a 1.25-yr recurrence, and only 10% of the pre-dam spring snowmelt floods during the period 1922–1962 were of lower magnitude. The flood occurred unusually early: 36–38 d prior to any previous annual flood since 1922. The stage difference between the flood's peak and the recessional baseflow was smaller than in those pre-dam years of similar magnitude or annual volume.

However, the controlled flood was large from the perspective of the post-dam flood regime. The flood had a recurrence of 5.1 yr for the period between 1963 and 1999 and a similar magnitude flood had not occurred in 10 yr. The sediment flux of the flood was small in relation to pre-dam floods, and the suspended sand concentration was within the historical variance for flows of similar magnitude.

This flood reworked fine-grained deposits that are primarily composed of sand, but the flood caused much less reworking of coarser grained deposits. Scour primarily occurred in the offshore parts of eddies, in many eddy return-current channels, and in some parts of the main channel. Return-current channels constitute important nursery habitats for the native fishery when baseflows are low, because these channels become areas of stagnant and warmer water. The number and area of these backwaters increased greatly after the flood. Fluvial marshes were extensively scoured because these habitats occur in the low elevation centers of eddies where velocities during the flood were large. Riparian shrubs that were inundated along the banks were not scoured, however, because these shrubs occur where flood velocities were very low and where deposition of suspended sediment occurred. Some physical changes persisted for several years, but other changes, such as the area of newly formed backwaters decreased quickly. Thus, the lasting effect of this flood varied among different small-scale fluvial environments.

Key words: Colorado River; ecosystem; flood; geomorphology; Glen Canyon Dam; hydrology; management.

INTRODUCTION

In many regulated rivers, scientists seek to understand the relationship between the magnitude and duration of floods and the resulting ecological disturbance. Controlled floods, such as the one that was released from Glen Canyon Dam in spring 1996, are being introduced into some regulated rivers, but there is a limited amount of water that can be allocated to these flow events. Thus, managers want to know how to efficiently provide a flood disturbance to a regulated river while using a minimum volume of water.

Large floods often cause geomorphic changes in the channel and adjacent alluvial valley (Mayer and Nash 1987, Baker et al. 1988, Bevin and Carling 1989), and these changes have the potential to alter the structure and function of associated aquatic and riparian ecosystems (Resh et al. 1988, Junk et al. 1989, Stanford et al. 1996, Poff et al. 1997). Floods may be characterized in terms of hydrology, hydraulics, sediment transport, and the magnitude and extent of aggradation and degradation. These attributes cause disturbance by hydraulic stress and erosion and deposition of substrates that constitute habitat of flora and fauna.

The purpose of this paper is to describe the hydrologic, hydraulic, and sediment transport characteristics, as well as the resulting landform changes, caused by the 1996 controlled flood on the Colorado River downstream from Glen Canyon Dam (Webb et al. 1999*b*). We compare this flow event with other floods of the Colorado River that occurred before and after completion of the dam, and we ask whether this flow was a

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For reprints of this Invited Feature, see footnote 1, p. 633.

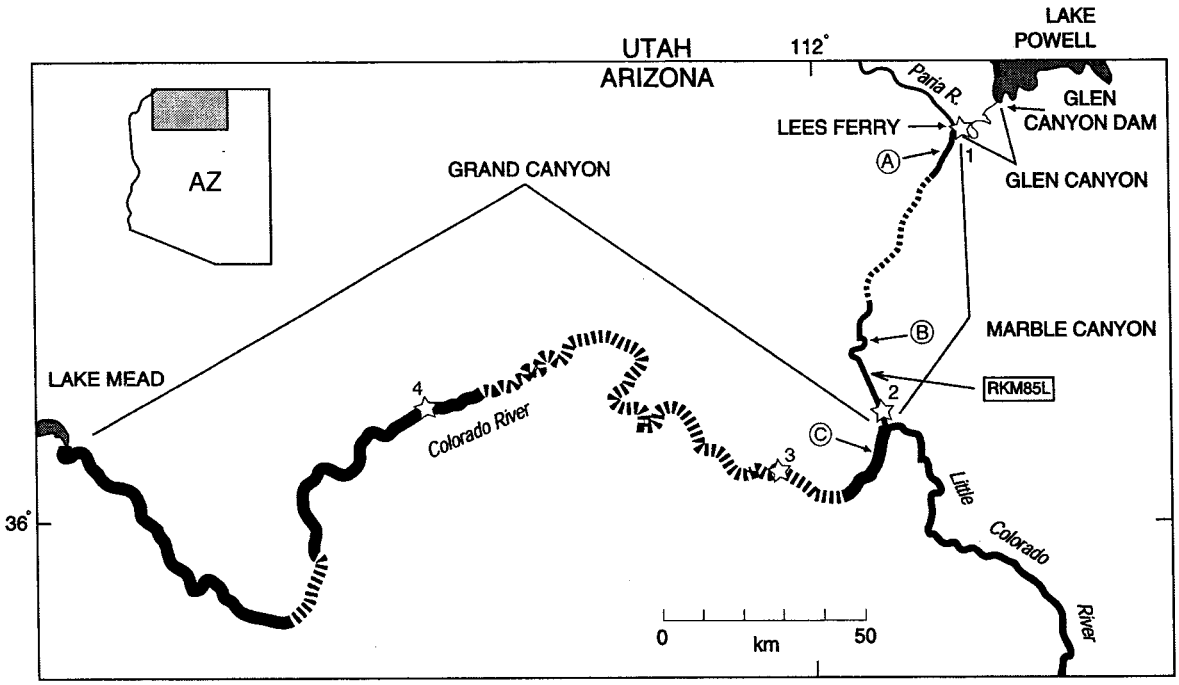


FIG. 1. The Grand Canyon region. Width of the trace of the Colorado River, Paria River, and Little Colorado River is proportional to the post-dam fine sediment load, as estimated by Topping et al. (2000). Dashed river segments are those with a narrow channel in relation to other reaches. Stars are locations of U.S. Geological Survey gaging stations. 1, Colorado River at Lees Ferry, Arizona; 2, Colorado River in Lower Marble Canyon, near Desert View, Arizona; 3, Colorado River near Grand Canyon, Arizona; and 4, Colorado River at National Canyon, near Supai, Arizona. Letters A, B, and C are locations of detailed maps shown in Fig. 2.

hydrologically and geomorphically significant disturbance. This review supplements the findings of Webb et al. (1999*b*) and includes additional data on changes in critical aquatic habitats. This review therefore provides background with which the reader can evaluate companion papers that describe ecological responses to this flow event.

EVALUATING FLOOD IMPACTS

Analysis of the landform changes caused by the 1996 controlled flood requires consideration of the characteristics of the channel and adjacent valley immediately prior to the flood, longitudinal characteristics of channel gradient and valley width, and the sequence and magnitude of previous floods. The impact of a specific flood must be evaluated within the context of that specific river/flood/floodplain environment, because the resistance to erosion of the banks and alluvial valley is determined by substrate, soil development, and vegetation (Nanson and Croke 1992), longitudinal variation in stresses exerted by the flood (Magilligan 1992), and the temporal ordering of previous floods (Yu and Wolman 1987, Kochel 1988). Some large magnitude floods have the potential to rearrange a large proportion of the alluvial valley, but similar magnitude floods in other river systems cause few changes (Magilligan et al. 1998) because the same magnitude flood will cause less change if it occurs soon after a previous large flood.

THE PHYSICAL TEMPLATE FOR THE AQUATIC AND RIPARIAN ECOSYSTEM

The large-scale template

The physical template of the Colorado River ecosystem downstream from Glen Canyon Dam has two spatial scales, and analysis of the effects of the 1996 controlled flood must be made within the context of both scales. The large-scale control on channel and floodplain processes arises from the geologic history of the southern Colorado Plateau that has determined the (1) location of the river's course, (2) relief, width, and location of canyons, (3) location of major tributaries and the characteristics of flow and sediment transport of those tributaries, (4) seasonal and spatial patterns of precipitation, and (5) elevation of geologic formations whose failure generates debris flows during intense rains. The 400 km between the dam and Lake Mead reservoir is divided into Glen, Marble, and Grand Canyons (Fig. 1), and the primary large-scale controls on channel and floodplain form are the lithology of the bedrock that occurs at river level and the size and number of debris fans that partially block the river's course (Howard and Dolan 1981, Schmidt and Graf 1990, Mel-

is 1997). The alluvial valley is wider and has a lower gradient where erodible rocks occur at river level, and talus, bouldery debris fans, or sandy alluvium are the channel's banks. Stresses exerted by a flood are typically less in these reaches. In contrast, the banks are bedrock in some reaches bounded by metamorphic rocks or limestone. The gradient is steepest and flood induced stresses are greatest in these narrow reaches. The number and size of eddies that exist during floods are greatest where debris fans are large in size and frequent in number.

Most of the river's sediment load consists of particles <0.5 mm in size (Smith et al. 1960), and the distribution of large tributaries determines the quantity of fine sediment available for transport during floods. The annual load delivered to Grand Canyon from the upper Colorado River basin, which was ~57 (± 3) × 10^6 metric tons/yr between 1949 and 1962 (Topping et al. 2000), is now deposited in Lake Powell reservoir. The flux of fine sediment is now largely determined by the distribution of sediment available for entrainment that is stored on the channel bed, in bars, or in banks, and this sediment is either relict from pre-dam conditions or is supplied from unregulated tributaries. The largest sources of sediment supply to the post-dam Colorado River are the Paria River and the Little Colorado River (LCR). Between 1949 and 1970, 3.0 (± 0.6) × 10^6 metric tons/yr of sediment entered the Colorado River from the Paria River, of which ~50% was sand, and 8.6 (± 1.7) × 10^6 metric tons/yr of sediment entered from the Little Colorado River, of which ~30% to 40% was sand (Topping et al. 2000).

Thus, the Colorado River downstream from the dam can be divided into three reaches in terms of the magnitude of the fine sediment flux (Fig. 1). The 25-km reach upstream from Lees Ferry has little tributary contribution. The Paria River is the primary supplier of fine sediment to the 100 km downstream from Lees Ferry. The Little Colorado River delivers a large load of fine sediment, and its confluence occurs 125 km downstream from the dam.

The greatly reduced sediment transport has increased water clarity, thereby converting a historically heterotrophic, allochthonous system to an autotrophic system dependent on autochthonous production (Brock et al. 1999, Marzolf et al. 1999). There is high photosynthetic productivity in Glen Canyon, where the trophic structure is supported by the green alga, *Cladophora glomerata,* and a large assemblage of ephiphytic diatoms (Blinn et al. 1995, Stevens et al. 1997). This tailwater reach is ideal for the blue-ribbon nonnative trout fishery that was introduced there. Productivity decreases greatly downstream, but water clarity is still high enough to affect behavior of the endangered humpback chub (*Gila cypha*) because of risk of predation by the abundant nonnative fishery (Valdez and Ryel 1997).

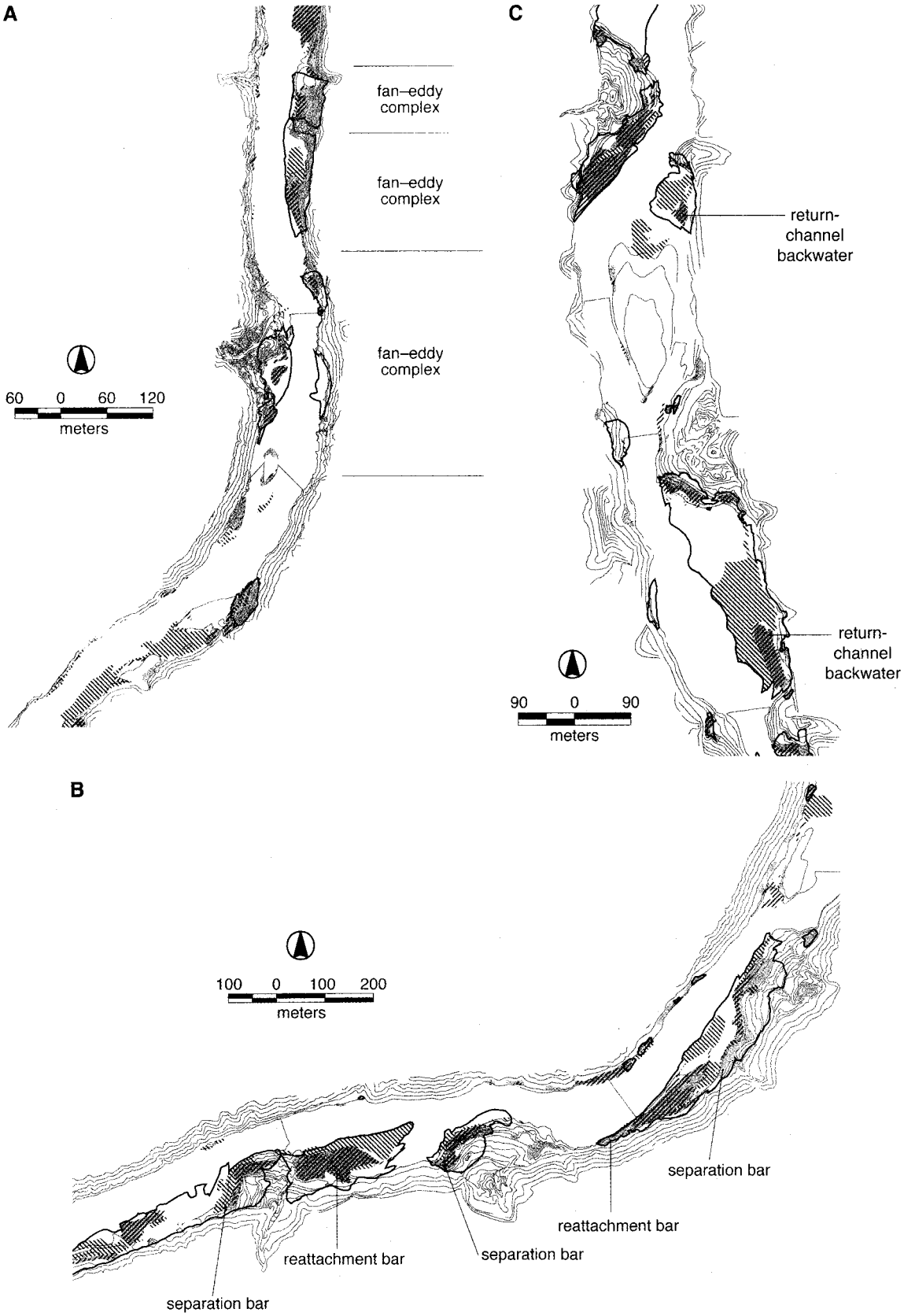
The small-scale template

At a smaller scale, the distribution of habitats and the locations of erosion and deposition during floods are determined by the hydraulic patterns created by the debris fans (Fig. 2). White-water rapids all occur where debris fans, composed of boulders too large to be transported by the river, partly block the flow. Blockage creates a reach of low-velocity, ponded flow that may extend several kilometers upstream from each fan (Kieffer 1985). Large eddies typically occur immediately downstream from rapids, and gravel bars exist further downstream. Schmidt and Rubin (1995) adopted the term fan–eddy complex for the length of the main-stem river between the ponded upstream flow and the downstream gravel bar, because the hydraulics of the intervening reach are determined by a specific debris fan.

The channel bed of the ponded flow is typically composed of sand. The banks are also composed of sand and occur as a series of distinct benches, each with a natural levee. The sand in these banks has been transported as suspended load, and the landforms are called channel-margin deposits (Schmidt and Rubin 1995). Most of these deposits have been densely colonized by native and nonnative phreatophytes since completion of the dam (Turner and Karpiscak 1980, Johnson 1991, Stevens et al. 1995).

Recirculating eddies downstream from rapids are utilized by the native and nonnative flora and fauna. These eddies are large and numerous. Schmidt et al. (1999*b*) found that the surface area of the largest eddies in 31 km of Grand Canyon is nearly 40 000 m^2 at some discharges and that the average size of eddies is between 7250 m^2 and 10 000 m^2. Circulation in these eddies is typically one-celled, with strong upstream velocity along the bank. Pockets of low, or zero, velocity exist in the lee of each debris fan and near the zone of flow reattachment, which is the downstream end of the eddy. High rates of sedimentation exist in these eddies when the main flow carries a large sediment load, because the transport capacity of eddies is much less than the main flow. Eddies change in size as discharge changes, because the velocity of the rapid and the geometry of the channel constriction and expansion change (Schmidt 1990).

The bed topography of an eddy includes a platform of shallow sand beneath the primary eddy (called a reattachment bar), a deep channel between the platform and the adjacent bank (called the primary eddy return-current channel), and a platform of sand mantling the downstream part of the debris fan (called a separation bar). Water in the deep channel between the separation and reattachment bar becomes a stagnant embayment at low discharges when the bar platform is emergent and blocks circulation from the main flow. This and other shoreline embayments are referred to as backwaters. Embayments formed in return-current channels


A
fan–eddy complex
fan–eddy complex
fan–eddy complex
60 0 60 120
meters
C
return-channel backwater
return-channel backwater
90 0 90
meters
B
100 0 100 200
meters
separation bar
reattachment bar
separation bar
reattachment bar
separation bar

over the range of discharges common to the post-dam river have been identified as the most significant backwater environments for detailed study and management (U.S. Bureau of Reclamation 1995). These areas are used extensively as nurseries by young native and nonnative fishes and as rearing and holding areas by small fishes.

By 1995, most of the large backwaters had aggraded with silt and were overgrown by marsh and bar vegetation (U.S. Bureau of Reclamation 1995), thereby shifting this geomorphic setting from a fish nursery habitat to a fluvial marsh.

This deposition pattern and shift in habitat has typically occurred within five years following each post-dam flood (Stevens et al. 1995). This shift impacts nutrient distribution and water-holding capacity in the vadose zone. Sediments rich in N, P, and organic carbon are largely restricted to return-current channels. Clays and allochthonous organic matter improve the water-holding capacity of the sediments, increase sediment cohesiveness, and are likewise restricted to return-current channels. During high flows, the river inundates the bar surface, reactivates flow in the return-current channel, and may scour the return channel of silt, clay, and organic debris. One goal of the test flood was to rejuvenate these habitats.

Dam-induced changes in hydrology and sediment supply have altered the texture of other bar and bank substrates as well, which in turn has affected riparian plant succession and productivity (Stevens 1989, Stevens et al. 1995). Typically, bars reworked by post-dam floods are coarser than higher elevation pre-dam deposits. Deposition of silt, clay, and organic materials only occurs at the time of tributary floods in low velocity environments such as backwaters, and silt and clay are not deposited across the entire reattachment bar surface (Parnell et al. 1999).

Downstream from the eddies, bars composed of gravel and cobbles occur in the main channel. These bars are composed of debris entrained from the debris fan located immediately upstream (Webb et al. 1997, Pizzuto et al. 1999). Elsewhere, gravel bars occur in Glen Canyon and the wider reaches of Grand Canyon (Schmidt et al. 1999*b*). Gravel bars in Glen Canyon are known spawning sites for rainbow trout, but the ecological role of gravel and cobble bars elsewhere has not been studied.

Characteristics of the Controlled Flood

Hydrology

The controlled flood was a small event in the context of pre-dam flows, because the flood was of short duration and small magnitude. The controlled flood consisted of a rapid rise from 227 m^3/s to a steady high discharge of 1274 m^3/s that lasted for 7 d. The flow then receded to 227 m^3/s, and this low discharge lasted for 3 d. Thereafter, normal flows resumed (Schmidt et al. 1999*a*; Patten et al. 2001 in this issue). The magnitude of the controlled flood was less than the pre-dam 1.25-yr recurrence flood of 1465 m^3/s, calculated using a log-Pearson Type III distribution for the period 1922 to 1962. Only four (10%) of the water years during the pre-dam period of stream gaging had peak discharges less than the magnitude of the controlled flood: 1931, 1934, 1954, and 1955 (Fig. 3). The test flood was larger than floods in 9 of the 40 yr (23%) of pre-dam data (1 in 4.4 yr), in terms of the total volume of water of the flood as measured by the product of mean daily discharge and number of days exceeding 1270 m^3/s (Fig. 4).

The duration of the controlled flood was short in comparison to those pre-dam years when similar magnitude floods occurred, and the magnitude and duration were low in comparison to pre-dam years when the same total annual amount of streamflow passed through Grand Canyon. The difference in magnitude between the controlled flood and baseflows during the rest of the year was less in 1996 than in those pre-dam years of similar magnitude or annual volume. For example, peak flows in 1940 and 1960 were approximately the same as in 1996, but the baseflows to which the Colorado River receded in those pre-dam years were more than 300 m^3/s less than the typical baseflows following the test flood (Fig. 5).

The test flood occurred 36 to 38 d earlier in the year than any previously measured high flow of this magnitude. The median and mean dates when mean daily discharge first exceeded 1270 m^3/s were 8 May and 10 May, respectively, for the period between 1922 and 1962. The earliest date in any year during this period when flows exceeded 1270 m^3/s was 8 April 1942.

In contrast to the pre-dam hydrology of this system, the magnitude of the controlled flood was large in relation to flows that occurred after completion of Glen Canyon Dam. The test flood was one of seven high

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FIG. 2. Patterns of erosion and deposition along the Colorado River caused by the 1996 controlled flood (A) near Lees Ferry, (B) near Point Hansborough, and (C) downstream from the Little Colorado River. Locations of these areas are shown on Fig. 1. Dark lines surround the maximum eddy bar area, as determined by historical aerial photograph analysis by Schmidt et al. (1999*b*) and H. Sondossi and J. C. Schmidt (*personal communication*). Gray shaded areas are where deposits created by the 1996 controlled flood occurred. Hatched-line areas sloping from upper right to lower left are where deposition exceeded 25 cm, and hatched-line areas sloping from upper left to lower right are where erosion exceeded 25 cm.

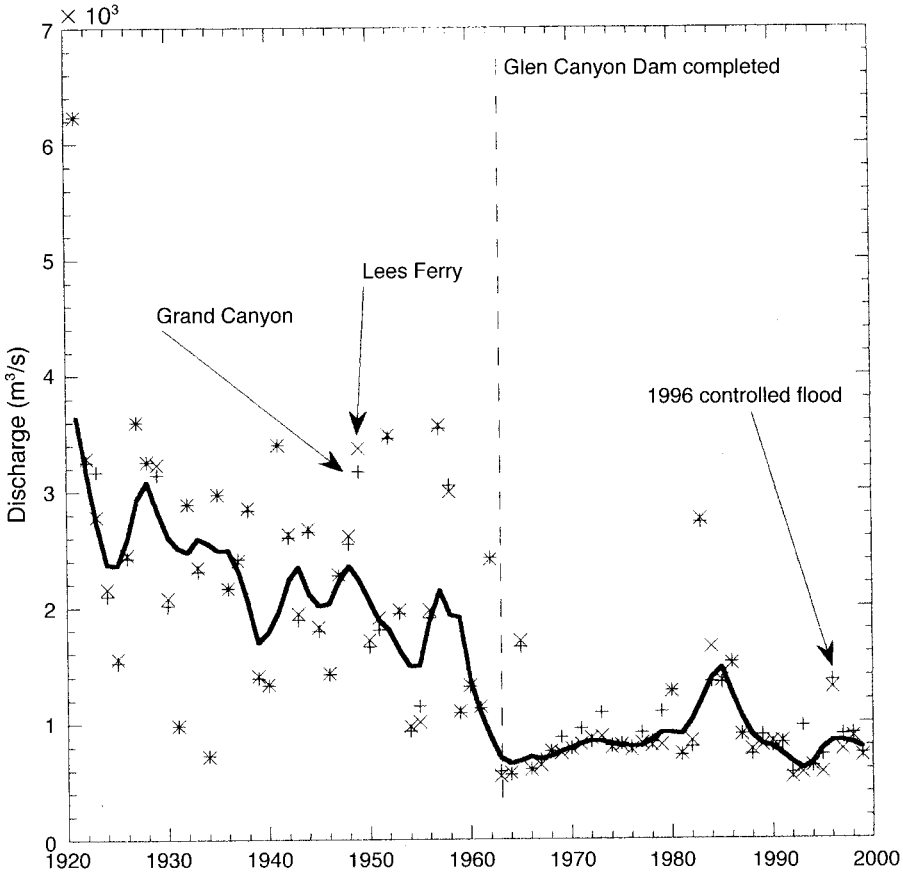

FIG. 3. Time series of annual peak discharges at the Lees Ferry and Grand Canyon gaging stations. The thin solid line is the 10-yr weighted average peak discharge.

flow events in the 36-yr history of regulated flows in this system, a 5.1-yr recurrence, and the largest flow in a decade (Fig. 3). The largest instantaneous peak discharge released from Glen Canyon Dam occurred in June 1983 and was 2724 m^3/s. Flows comparable in magnitude to the controlled flood, but of longer duration, occurred in 1965, 1980, and annually between 1984 and 1986.

Hydraulics

Flow velocity and unit stream power are related to the forces exerted on bed and bank sediments and on benthic and riparian vegetation. Thus, these are appropriate attributes of the flood with which to measure potential disturbance to the riparian and aquatic communities. Measurements during the controlled flood demonstrate the large longitudinal and cross-sectional variation in flow speed that is characteristic of confined rivers. During flood, these rivers typically have very fast main-stem velocity yet also have areas where velocity is zero or is upstream. This diverse range of hydraulic conditions creates areas where bed or bank erosion dominates, areas where sediment deposition occurs, and areas that provide refugia for aquatic organisms.

The highest velocity occurred in rapids. Webb et al. (1997) measured the mean surface speed of the left side of Lava Falls Rapid to be 6.6 m/s. Pizzuto et al. (1999) calculated the average velocity along the left bank at the same rapid to be between 0.9 and 3.9 m/s. These velocities are consistent with estimates made by Kieffer (1985) for the velocity of Crystal Rapid at 2602 m^3/s in June 1983. She estimated average speeds as large as 8.7 m/s in the fastest part of the rapid.

In contrast, velocity in the zones of flow separation and reattachment that determine the upstream and downstream ends of eddies was zero. However, the locations of these low velocity zones changed. Velocity elsewhere in eddies varied greatly, and was typically highest in the upstream return current. We measured the maximum upstream velocity in one inundated return-current channel in lower Marble Canyon to be 0.9 m/s.

Reach-average velocity was measured by recording the times at which a red fluorescent dye moved downstream past various measurement stations (Graf 1995).

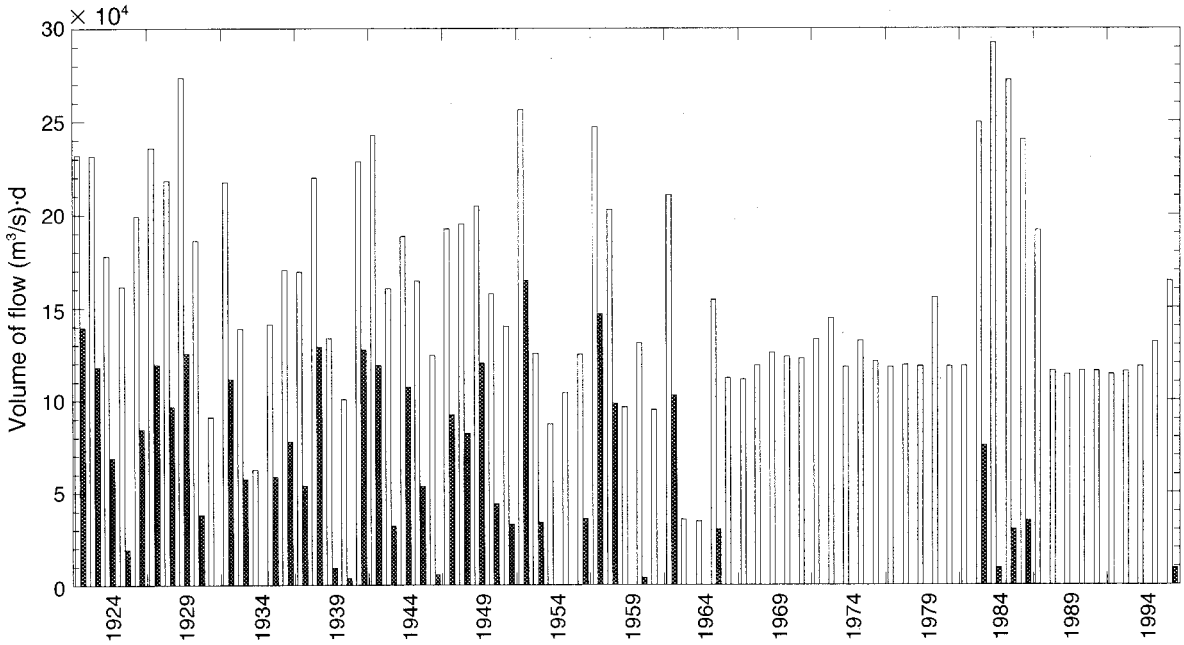

FIG. 4. Time series of the annual volume of flow and the annual volume of high flows. The annual volume of flow is measured in cubic meter per second days, in open bars, and the annual volume of high flows is measured in cubic meters per second days when mean daily discharge exceeded 1270 m^3/s, in dark bars.

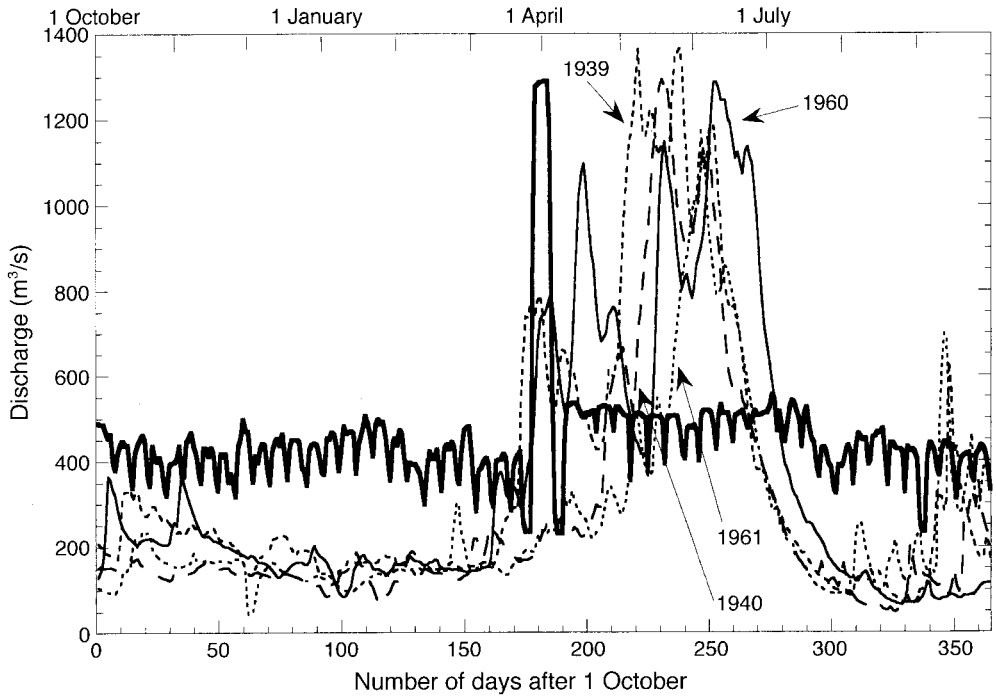

FIG. 5. Annual hydrographs for the 1996 controlled flood (thick solid line) and for four pre-dam years in which the magnitude of the annual flood was similar to that in 1996.

The average speed of the flood for the entire river length was 1.8 m/s, varying from ~1.5 to 2.1 m/s in different subreaches that were tens of kilometers in length (Konieczki et al. 1997). However, velocities varied greatly over shorter distances.

Although Magilligan (1992) proposed that geomorphically effective floods typically have unit stream power values exceeding 350 W/m^2, the great variation in flow conditions in Grand Canyon makes such arbitrary thresholds of limited value. There were areas where energy expenditure was far greater than the threshold suggested by Magilligan (1992) and other places where the expenditure was far less. Smith (1999) calculated the skin friction shear velocity and the shear velocity of the flow away from the bed to be 0.081 and 0.16 m/s, respectively, at the gaging station near National Canyon during the controlled flood. These values equal shear stresses of 6.6 and 25.6 N/m^2, respectively, and unit stream power values of 12.1 and 46.8 W/m^2, respectively. In contrast, Webb et al. (1999*a*) estimated that unit stream power ranged between 260 and 2150 W/m^2 at 10 rapids during the low discharges of 250 m^3/s that occurred immediately before and after the flood. The magnitude of these values during the event would have been much greater. Except at rapids, these values are low in relation to measurements of other rivers during large floods (Costa and O'Conner 1995).

Sediment transport during the 1996 controlled flood

The total load of sand estimated to have been transported by the Colorado River during the seven days of the controlled flood was 4.6×10^5 m^3 and 9.3×10^5 m^3 past the Lower Marble Canyon and Grand Canyon gages, respectively (Schmidt 1999). These values are very small in relation to the pre-dam annual load of the Colorado River, which was primarily transported by longer duration floods of larger magnitude flows, but these values are large in relation to post-dam flows. The total sand load transported past the Lower Marble Canyon gage during the flood was approximately equal to 70% of the average annual sand load contributed by the Paria River, and the total sand load transported past the Grand Canyon gage was approximately equal to 60% of the average annual sand load contributed by the two largest tributaries, the Paria and Little Colorado Rivers (Schmidt 1999).

The concentration of suspended sediment transported by the test flood was within the historical range of suspended sand concentrations measured during unregulated snowmelt floods of the pre-dam river at discharges similar in magnitude (Topping et al. 2000). The highest concentration of suspended sand measured at three gaging stations during the flood was ~0.11% and was measured at the Grand Canyon gage on the first day of the flood (Topping et al. 1999). The concentration of suspended sand transported past this site declined to 0.05% on the fifth day of the flood. The concentrations of suspended sand during the flood (Wiele et al. 1999) were much less than those of a 1993 Colorado River flood caused by a natural flood on the Little Colorado River, which was ~0.3%, based on one measurement made by the U.S. Geological Survey (USGS) (Topping et al. 2000). These concentrations produced conditions of sediment depletion, which created coarsening of the bed grain-size during the controlled flood and pre-dam floods. The coarsening resulted in a distinctive "coarsening upward" grain-size distribution in mainstream flood deposits (Rubin et al. 1998, Topping et al. 1999, 2000).

Landform changes

Reworking of debris fan deposits.—Reworking of debris fans may cause the geometry of downstream eddies to change and thereby cause changes in the size and extent of backwaters formed by the sandbars that occur in those eddies. Webb et al. (1999*a*) showed that the flood was of sufficient magnitude to erode the streamside face of those debris fans that had been aggraded by debris flows that were <10 yr old; little reworking occurred where debris flow deposits were older. Radio transmitters emplaced in boulders and recovery of marked boulders showed that these particles moved further downstream on the debris fans, into the deep pool immediately downstream from the rapid, and in one case, onto the cobble bar located downstream from the pool. Thus, the controlled flood not only reworked coarse debris delivered to the river from ephemeral tributaries, but also deposited cobbles and boulders in main channel pools and on cobble bars.

The greatest amount of reworking occurred at two debris fans where flows occurred less than two years before the controlled flood. Erosion of boulders from debris fans was by slab failure and by entrainment of individual particles from the bed (Pizzuto et al. 1999). Slab failures, wherein banks fail and boulders fall into the flow, provided initial motion to particles and allowed much larger particles to be moved than is predicted by traditional bed entrainment studies. Virtually all bank erosion at Lava Falls Rapid occurred during rising stage and during the first four hours of high steady discharge. This was probably the case elsewhere.

Reworking of gravel bars.—Although periphyton and aquatic macrophytes may have been scoured from gravel substrates in parts of Glen Canyon, significant bed material movement was not reported in this reach (Brock et al. 1999, Marzolf et al. 1999, McKinney et al. 1999). There were no specific studies of entrainment from gravel or cobble bars in Grand Canyon. However, Webb et al. (1999*a*) argued that the test flood was of insufficient magnitude to significantly rejuvenate cobble bars in Grand Canyon.

Scour and fill of sand in fan–eddy complexes.—Any flood has the potential to reconfigure fine-grained al-

luvial deposits and associated aquatic and riparian habitats, because the threshold of entrainment of fine-grained particles is much less than for coarser particles. This is especially the case with sandbars in large eddies, because bar configuration changes quickly when eddy flow patterns change. Scour and fill of the main channel bed may reconfigure main channel habitats, although the ecological importance of these bed configurations is unknown (Hoffnagle et al. 1999). There is a direct relationship between bed configuration and aquatic habitats in eddies, however, because of the relationship between the topography of reattachment bars and return-current channels. Scour and fill of previously vegetated areas has the potential to alter the distribution of riparian vegetation (Stevens 1989, Stevens et al. 1995).

There was a net transfer of sand from the channel bed to the banks and eddies. Hazel et al. (1999) measured net channel bed scour at 15 of 17 measurement sites upstream from the Grand Canyon gage, and Schmidt's (1999) sand budget for the controlled flood showed that sand was transferred from the bed to the banks. In some short reaches, however, bed topography was merely rearranged without net topographic change, such as near the Grand Canyon gage (Topping et al. 1999) and the National Canyon gage (Smith 1999).

Scour and fill was large in many eddy bars. Andrews et al. (1999) measured large day-to-day changes in the topography of eddy sandbars at five sites. There were areas of thick (>1 m) deposition on the first day of the controlled flood at three sites between the Lower Marble Canyon and Grand Canyon gages. However, deposition rates at these sites declined during the next six days. Andrews et al. (1999) measured large erosion events from some eddies during the last few days of the flood; they described these events as mass failures from the eddies into the channels, caused by overloading of sand in eddies.

The longitudinal differences in main-stem sediment transport rates caused longitudinal differences in eddy deposition rates and in the average extent of erosion and deposition in eddies. These differences had the potential to cause variable patterns of ecological change, because the relative extent of erosion and deposition changed downstream. Schmidt (1999) showed that eddy deposition rates were lower at two sites upstream from the Lower Marble Canyon gage than at three sites further downstream where main-stem transport rates were twice as high as at the upstream site. Sondossi and Schmidt (1999) showed that the area of significant erosion in eddies within 15 km downstream from Lees Ferry exceeded the area of significant deposition, and that the area of significant deposition exceeded the area of significant erosion elsewhere. These field observations are supported by the modeling of Wiele et al. (1999), who developed a vertically averaged two-dimensional hydraulic model to demonstrate that the size of reattachment bars depends directly on the concentration of suspended sand during each flood. Large reattachment bars are one necessary determinant of the size and persistence of backwater habitats. However, the extent of backwater habitats created by the flood also depended on the depth of excavation of the return-current channel, and changes in these two geomorphic features did not always change in a consistent way. Thus, changes in backwater habitats were measured directly.

New sand was primarily deposited within eddies and not as channel-margin deposits: between 49% and 80% of all new sand was deposited within eddies in the 31 km of channel mapped in detail by Schmidt et al. (1999*b*). Scour and fill occurred in similar places within each fan–eddy complex (Figs. 2 and 6). Most deposition occurred along the margins of the flood flow and near the zones of flow separation and reattachment; the thickness of new reattachment bars decreased upstream and downstream from this zone and most erosion occurred offshore in the deeper parts of the eddies (Hazel et al. 1999, Schmidt et al. 1999*b*).

Most of the nearshore deposition was not preceded by scour (Schmidt et al. 1999*b*). Thus, riparian vegetation on channel banks and channel margins was buried by as much as 1.5 m of sand (Parnell et al. 1999). However, riparian marsh vegetation growing on low elevation channel margins was eroded, either by scour or during failure of reattachment bars (Stevens et al. 2001 in this issue). Allochthonous organic matter consisted of vegetation produced by this process as well as organic material deposited in debris piles during earlier tributary floods. Some of this material was subsequently buried as mats of organic debris within the new flood deposits. Much of the woody phreatophytic vegetation that was merely buried survived the flood, resprouted, and recovered within the first growing season (Kearsley and Ayers 1999, Kearsley et al. 1999). However, redevelopment of fluvial marshes has been slow because of substrate grain size changes, steep bar face slopes, and reduced inundation frequency of aggraded surfaces (Stevens et al. 1995, 2001).

The sizes of fine sediment deposited by the flood coarsened with time. The percentage of silt and clay deposited with the sand was greater on the first day of the event than on following days, because silt and clay were flushed downstream during the first two days of the flood. (Rubin et al. 1998, Topping et al. 1999). Flood-deposited sediments would have had a higher silt and clay content if the flood had been of shorter duration. Thus, there is a potential to manipulate vegetation succession by controlling flood duration and the texture of deposits formed by those floods.

Persistence of flood-formed sandbars.—Readjustment of bars to moderately high flows following the controlled flood caused the area of exposed sandbars to decline rapidly. These summer flows ranged from

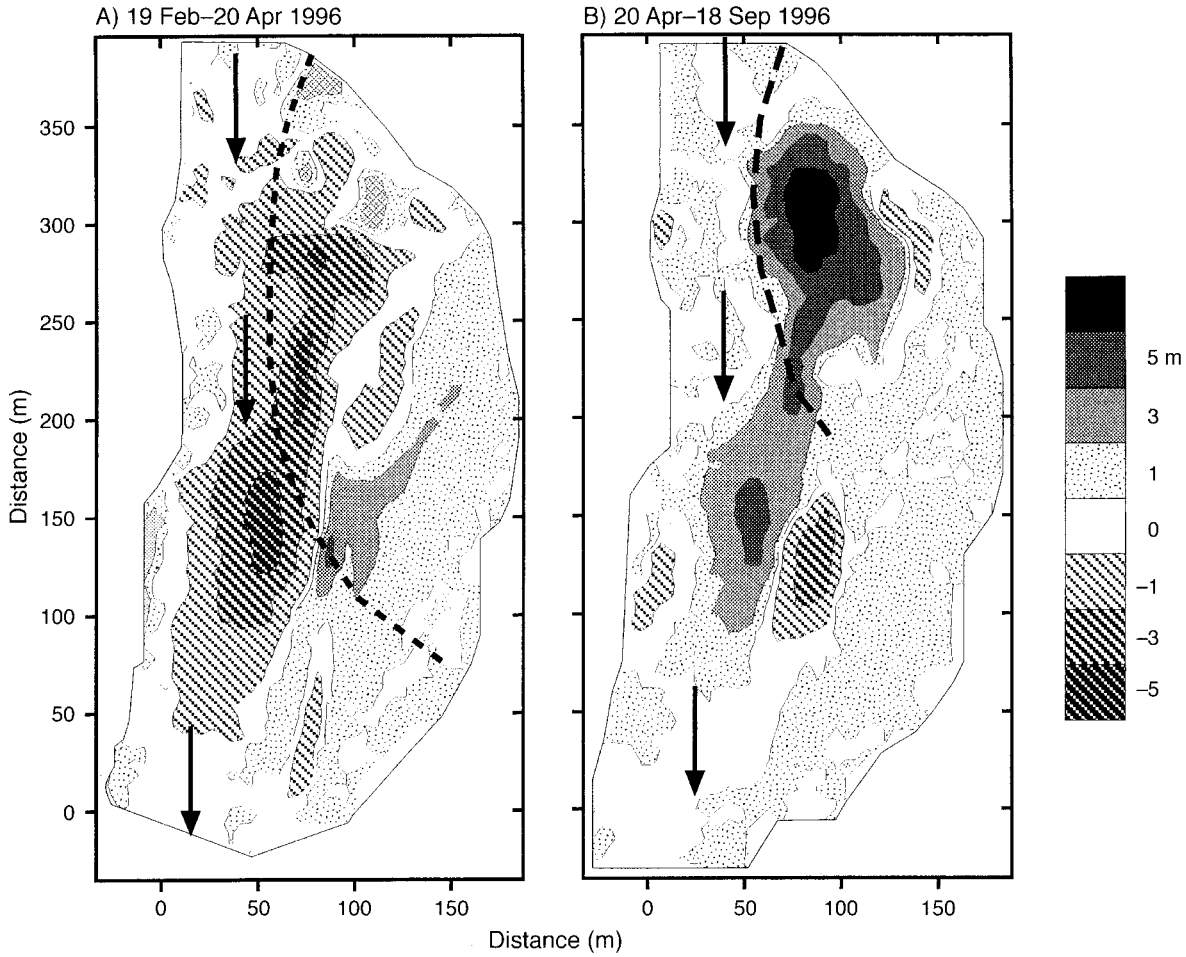

FIG. 6. Maps showing the sandbar at Rkm 85L (river left facing downstream; see Fig. 1 for location) showing zones of net erosion and deposition as a result of the controlled flood. The river flows from top to bottom; the eddy bar is on the right, and the river channel is on the left side. The dashed line represents the approximate position of the eddy fence dividing the main current (to the left) from the eddy recirculation zone (right). This pattern of erosion and deposition is typical of the response of many of the sandbars to the controlled flood, which were studied by Hazel et al. (1999). (A) Net erosion and deposition immediately following the controlled flood. (B) Subsequent net erosion and depositional patterns for the following five-month period.

421 to 523 m^3/s (Fig. 5). The general trend occurring throughout the summer was for sand deposited above the elevation of the maximum stage reached by post-flood dam releases to be eroded and transported into the subaqueous parts of the eddy and main channel (Fig. 7). For the five-month period following the flood, the high elevation parts of the bars lost 9% of their volumes each month (Hazel et al. 1999). This erosion rate decreased to between 2% and 4% per month for the next five-month period.

Terrestrial habitat rejuvenation.—The controlled flood caused physical and chemical changes which affected the terrestrial system. Burial of autochthonous and allochthonous vegetation by test flood deposits resulted in significantly increased rates of organic matter mineralization and release of dissolved, inorganic P and N and organic C into the root zones of the bars (Parnell et al. 1999). This pulse of nutrients, in unknown combination with increased water availability produced by extended periods of relatively high river stage following the flood, may have had a positive impact on terrestrial productivity (Stevens 1989, Stevens et al. 2001).

Backwater habitat rejuvenation.—We analyzed backwater distribution from Glen Canyon Dam to Lake Mead using aerial videography collected during steady research flows of 227 m^3/s on 24 March, 7 April, and 2 September 1996, and on 1 September 1997, considerably extending the work of Brouder et al. (1999). We used Map Image Processing Software (MIPS; MicroImages 1995) to view and locate each backwater, assign it a specific site name, digitize and determine its area, and describe its geomorphic setting. The area of each backwater was measured three times. Ground

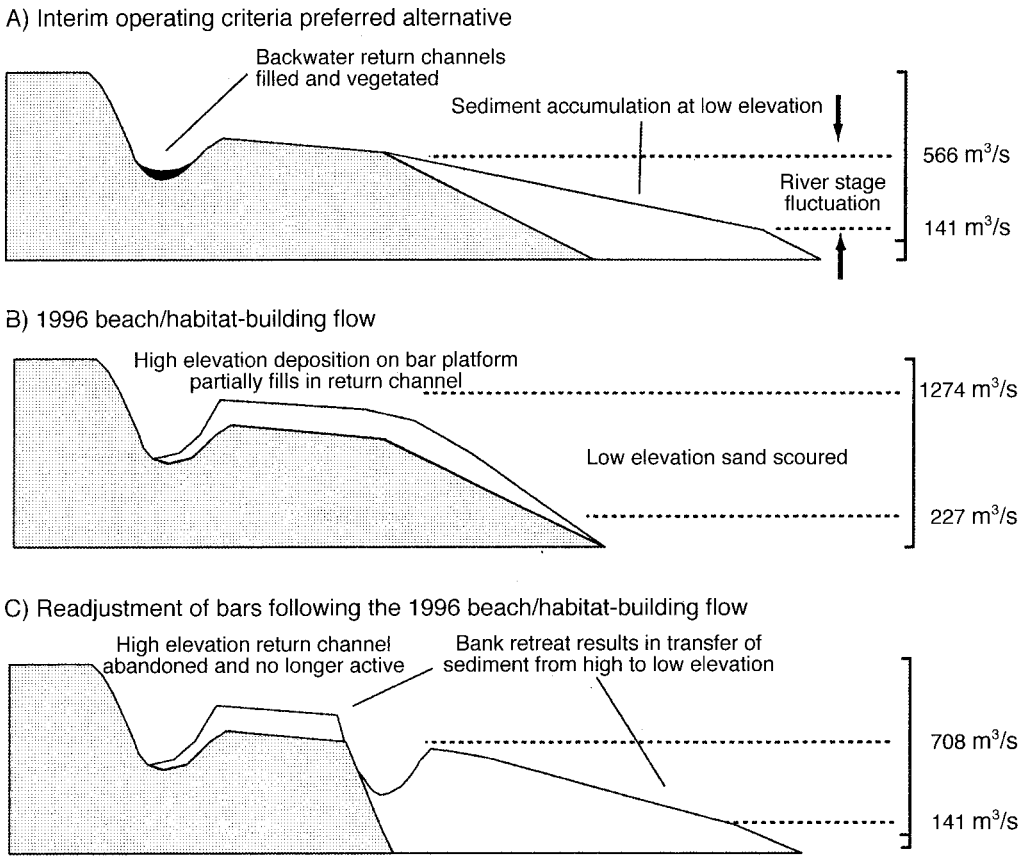

FIG. 7. Diagrams showing typical changes in bar topography and changes in backwater channels throughout Grand Canyon caused by the 1996 controlled flood. (A) During average flow conditions before the flood, river water did not inundate the bar or the return channel. The bar was eroding, and the return channel was infilling with vegetation. (B) Immediately after the flood, the bar platform had been aggraded, the return channel partially filled in, and the channel area offshore eroded and deepened. (C) In the 10 mo following the test flood, erosion from the high-elevation parts of the bar produced a sediment source for deposition in the eddy and main channel. A new return channel of lower elevation was established by bank retreat as eddy currents produced by the high steady flows after the test flow created and eroded the cut bank of the bar.

truth for the aerial photo imagery was established using up to three ground control points around each of 30 backwaters. We regressed remotely measured distances among these control points to MIPS measurements at these sites for each run. We adjusted MIPS area measurements using the mean regression equation for that run.

The abundance and area of backwaters detectable at a discharge of 226 m^3/s increased after the controlled flood (Fig. 8), consistent with the observations of Brouder et al. (1999) on a subset of backwaters. The total number of backwaters increased from 109 on 24 March to 164 on 6 April 1996, a 1.5-fold increase (Friedman's $t = 4.083$, $P = 0.043$, df = 1). Total backwater area also increased as a result of the test flood, from 6.09 ha to 13.95 ha, a 2.29-fold gain (Friedman's $t = 4.083$, $P = 0.043$, df = 1). However, backwater abundance only increased in Glen Canyon and Marble Canyon, and not in reaches further downstream, including places that are of most concern for native fish (Fig. 8). Thus, there was spatial variability in the response of backwaters to the flood. The number of backwaters increased in only a few reaches and not in the reaches most critical to the life history needs of the humpback chub.

The resumption of normal dam operations decreased the available area of backwaters, but not their abundance. The total number of backwaters increased during 1997, even though this was a period when there was widespread erosion of flood-deposited eddy bars. The total number of backwaters was 175 on 31 August 1997 (Fig. 8). However, backwater area dramatically decreased to 2.36 ha (Friedman's $t = 8.333$, $P = 0.004$, df = 1) during the first six months after the flood, and remained essentially unchanged through 1997. The loss of backwaters during the first six months constituted a 5.9-fold loss, and a 2.6-fold decrease in relation to the pre-flood backwater area (Fig. 8). These changes were probably related to the transfer of sand from high to low elevation, and the establishment of new flow pat-

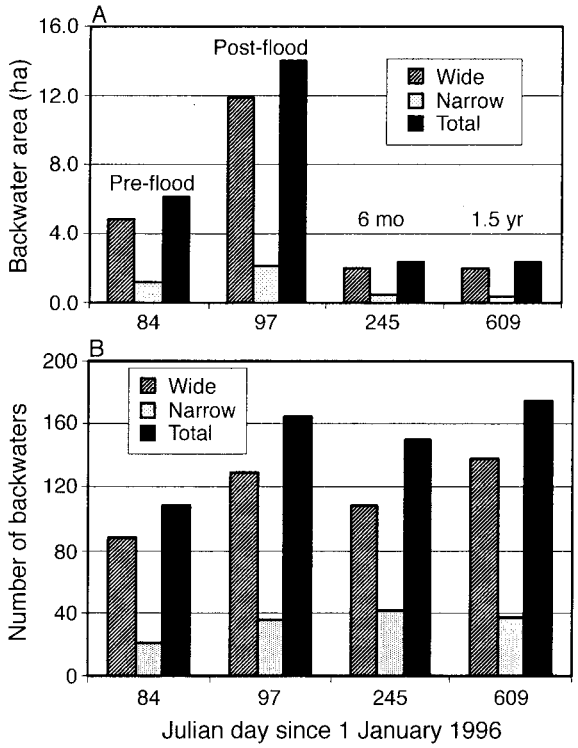

FIG. 8. (A) Backwater area and (B) number of backwaters before and after the flood in the Colorado River corridor between Glen Canyon Dam and Separation Canyon (river kilometer 386), on 24 March, 6 April, and 1 September 1996, and 31 August 1997, measured using Map Image Processing Software (MIPS) from aerial videographic images.

terns in eddies caused shifts in the location and shape of the primary eddy return-current channel. New eddy flow geometries developed on the channel side of the high elevation bars, creating new, lower elevation return-current channels which were isolated from the main stem only at very low flows (Fig. 7).

DISCUSSION AND CONCLUSIONS

The controlled flood was a small physical disturbance in relation to pre-dam river conditions in terms of its magnitude, total volume of water, duration, and in relation to the magnitude of the baseflows immediately before and after the flood. The flood was also unusual in its timing and occurred much earlier in the year than any previously measured high flow of this magnitude. Thus, this flood did not have the potential to rework physical habitats in a similar manner to pre-dam floods.

In terms of post-dam river conditions, the controlled flood was a much larger hydrological event. The flood was one of seven high flow events that have occurred since completion of Glen Canyon Dam in 1963. Post-dam floods of this magnitude previously occurred in 1965, 1980, and annually between 1983 and 1986. The flood had a recurrence of 5.1 yr, and the flood occurred after a 10-yr period when the flow did not exceed power-plant capacity. The flood inundated high elevation fine-grained alluvial deposits that had not been under water since 1986, and most of these deposits were extensively overgrown by riparian vegetation (Stevens 1989, Stevens et al. 1995). The dense riparian vegetation undoubtedly made erosion of these areas more difficult.

The sediment supply available for transport by the controlled flood was much less than pre-dam floods. The largest geomorphic effect of this flood was to redistribute fine sediment from low elevation to higher depositional sites along the channel margin; at the same time, some fine sediment was exported to Lake Mead. Fine sediment redistributed to high elevation represented one type of "improvement" to the ecosystem caused by the flood; fine sediment delivered to Lake Mead represented one type of "loss." Schmidt (1999) estimated that as much fine sediment was exported from Marble Canyon as was deposited along its banks and in eddies, and he estimated that the ratio of export to deposition increased further downstream. Upstream from the Little Colorado River (LCR), most of the sand in transport was eroded from low elevation parts of eddies; downstream from the LCR, most of the sand was derived from the bed.

The flood's water and sediment flux left their mark on the low elevation fine sediment components of the physical template of the riverine ecosystem, because fine sediment deposits are easily entrained at the velocities typical of the main current and in eddies at flood stage. In contrast, reworking of coarse-grained debris flow deposits was confined to a small subset of debris fans that had been aggraded in the decade prior to the flood. As with any river, the distribution of velocity exhibits a strong gradient from highest near the center of the main current and lowest at the bed and banks. In the fan–eddy complexes of Grand Canyon, very low velocities also occurred near the zones of flow separation and reattachment that occur at the upstream and downstream ends of eddies.

These spatial patterns of velocity change resulted in a spatially variable arrangement of areas of deposition and erosion caused by the flood. Fluvial marshes, which typically occur near the stage of the post-dam baseflows, were extensively eroded. Elsewhere, low elevation sandbars that create backwaters at low river stage were also extensively eroded. In contrast, nearshore deposition was widespread, because the net direction of sediment transport was from the channel center towards its banks and nearshore velocities were low. Thus, there was little erosion near the water's edge of the 1996 controlled flood, and riparian shrubs were buried and not scoured. Changes in flow patterns also caused the re-excavation of return-current channels. Erosion of these channels, along with deposition of the higher elevation parts of reattachment bars led to a net

increase in backwater habitat that persisted for at least six months after the flood.

Recovery follows disturbance in any fluvial system (Wolman and Gerson 1978), and the flood-induced changes only lasted a few years. Some flood-induced changes disappeared very quickly: bar faces were rapidly reworked, backwater area quickly decreased, and some riparian plant species quickly regrew on aggraded bars (Kearsley and Ayers 1999). Elsewhere, flood-induced changes had longer persistence: flood-deposited high elevation sand still is abundant along the river, but is now approaching its pre-flood sizes (Kaplinski et al. 1999). The number of backwaters in the river corridor was still larger in 1997 than the number immediately before the flood, but the areas of those backwaters had decreased greatly. There was enhanced soil nutrient availability for at least two years.

Other changes are of long-term consequence: the coarsened surface texture of the substrate has the potential to affect riparian vegetation successional dynamics. The 9- to 17-yr periods without floods allowed the proliferation of riparian vegetation (Turner and Karpiscak 1980, Johnson 1991, Stevens et al. 1995, Webb 1996). The creation of higher bars with a coarser texture than that which existed prior to the flood reduces potential recolonization by wetland and some riparian plant species (Stevens 1989, Stevens et al. 1995, 2001).

Deposition of new sediment occurred directly over pre-existing vegetation on reattachment bars. This burial initiated a unique pulse of nutrient availability in backwaters and bar soils that lasted for up to two years, and may have stimulated bar vegetation regrowth (Parnell et al. 1999). Rapid regrowth of buried clonal marsh plants (i.e., *Equisetum* spp., *Phragmites australis,* and *Scirpus pungens*) on steep bar faces may have reduced erosion rates during the two years following the test flood. Although the role of shrubs in preventing scour and fill along the channel banks was not studied, the low velocities of these areas makes it unlikely that scour would have been large, even in the absence of vegetation.

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AQUATIC FOOD BASE RESPONSE TO THE 1996 TEST FLOOD BELOW GLEN CANYON DAM, COLORADO RIVER, ARIZONA

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Abstract. We examined the impact of the 1996 test flood released from Glen Canyon Dam (GCD) on the aquatic food base in the Colorado River through Grand Canyon National Park, Arizona, USA. Benthic scour and entrainment of both primary and secondary producers occurred at all study sites along the 385-km river corridor. The majority of the organic drift occurred within the first 48 h of the test flood with the arrival of the hydrostatic wave. Recent macrophyte colonizers (*Chara, Potamogeton,* and *Elodea*) of fine sediment in the tailwaters were scoured from the channel bottom, with recovery to pre-flood estimates within 1–7 months depending on taxa. Macroinvertebrates and filamentous algae recovered within three months depending on taxa. The test flood removed suspended particles from the water column and increased water clarity, which enhanced benthic recovery. The test-flood hydrograph was designed primarily as an experiment in sand transport and occurred during a period of sustained high releases from GCD starting in June 1995 due to above-average inflow into Lake Powell. We discuss the implications of the hydrograph shape, pre- and post-riverine conditions, and the slow response time of biological resources for design of aquatic ecosystem experiments.

Key words: adaptive management; aquatic food base; Cladophora; *Colorado River; desert biome; discharge; disturbance; flood; Glen Canyon Dam; macroinvertebrates; organic drift; river regulation.*

INTRODUCTION

Variability in river discharge can affect the structure and function of benthic communities by altering the stability and availability of substrata (Power et al. 1988, Cobb et al. 1992), water velocity (Peterson and Stevenson 1992), aerial exposure (Blinn et al. 1995), light quantity (Duncan and Blinn 1989), and water quality (Scullion and Sinton 1983). Regulated rivers eliminate seasonal hydrographic changes and remove important life history cues for some aquatic insects, thereby reducing biodiversity (Power et al. 1988). Alterations in hydrologic patterns also modify community interactions that have developed over evolutionary time (Resh et al. 1988).

Statzner and Higler (1986) contend that changes in stream hydraulics are the major determinants of benthic invertebrate distribution, based on the intermediate disturbance hypothesis as outlined for lotic systems by Ward and Stanford (1983) and Reice and co-workers (1990). Under extreme discharge conditions (i.e., spring run-off), species numbers are relatively low, whereas during highly inconsistent conditions (i.e., zones of hydraulic transition) species richness is relatively high due to an overlap of species inhabiting the fringes of their niche requirements. These same hydraulic criteria may operate in the regulated Colorado River if flooding frequency is increased. Conversely, the exotic post-dam aquatic communities may not respond similarly to natural streamflow conditions because they now flourish under very unnatural flow regimes.

Studies in smaller lotic ecosystems in the Southwest have revealed the importance of floods in nutrient availability, particularly nitrogen (Grimm and Fisher 1986). Spates increase nutrient concentrations through hyporheic upwelling and run-off (Peterson and Grimm 1992). Particulate organic matter can also be released into the water column from the floodplain, transported downstream, accumulated in depositional zones, and mineralized for assimilation following high flows (Elwood et al. 1983). The flood pulse concept (Junk et al. 1989) describes the role of periodic floods in floodplain rivers and the subsequent organic enrichment and increase in habitat variability as the floodplain slowly drains following the flood. However, the Colorado River through Grand Canyon is a deeply incised channel with a minimal floodplain and does not allow for retention of floodwater.

The structure of the benthic community in the Colorado River through Grand Canyon has been altered by the construction of Glen Canyon Dam (GCD)

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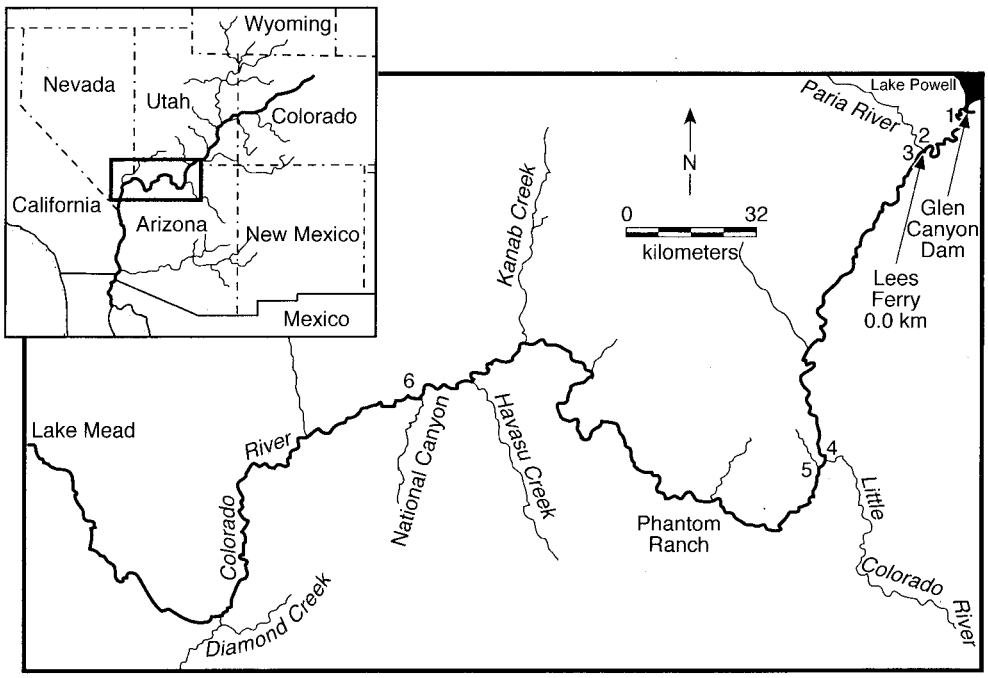

FIG. 1. Map of the Colorado River study area between Glen Canyon Dam and Lake Mead. General locations of collection sites are numerically listed along the river corridor. In numerical order these sites are named: 1, Glen Canyon Gage (River kilometer [Rkm] − 23.2); 2, Lees Ferry (Rkm 0.8); 3, Two-Mile Wash (Rkm 3.1); 4, Little Colorado River Island (Rkm 109.6); 5, Carbon Creek (Rkm 109.6); and 6, Lava Falls (Rkm 292.8).

through changes in river discharge, organic budget, suspended sediments, and water temperature (Blinn and Cole 1991, Stevens et al. 1997*b*). At present only discharge can be directly managed. Higher baseflows, reduced peak flow, and hourly fluctuation rates are the essential components of the selected discharge criteria from GCD as defined by the environmental impact statement process (U.S. Bureau of Reclamation 1995, Benenati et al. 2000). A similar reduction in flow regime implemented on the Patuxent River, Maryland, caused a doubling in benthic macroinvertebrate density and improved community condition (Morgan et al. 1991).

Construction and operation of Glen Canyon Dam (GCD) has created a food base alien to the desert Southwest. The food base community changes in composition and biomass with distance from the dam due to tributary release of suspended sediments (Blinn and Cole 1991, Stevens et al. 1997*b*). Discharge from GCD is stenothermic, averaging 10°C year-round, and is virtually free of suspended material, with water clarity routinely exceeding Secchi depths of 7 m in the tailwaters (Shannon et al. 1996*a*). Increases in water temperature are minimal through the 385-km study site, with the greatest increase in western Grand Canyon (≤17°C in early summer). Stevens et al. (1997*b*) estimated that an additional 520 km would be required to obtain the pre-dam annual high of 28°C. This protracted effect of hypolimnetic water released from GCD is due to the relatively large flow volume, confined channel, and reduced surface-area-to-volume ratio as the river traverses this seasonally hot, arid region of northern Arizona.

Tributary input of suspended sediments effectively alters the benthic community below the confluence of the Paria River, 28.1 km below GCD and 2.5 km below Lees Ferry, which is designated 0.0 km (Fig. 1). The Little Colorado River (98.6 km) also contributes seasonally high loads of suspended sediments. Average annual sediment input from these two tributaries is 8.25 $\times 10^6$ Mg, with the Paria River contributing one third of this amount. The Paria River has an average baseflow of only 0.77 m^3/s (Andrews 1991). This is an atypical example of a second order stream significantly altering the aquatic community of a fourth or fifth order river by reducing water clarity. Annual median discharge from GCD is 345 m^3/s (Stanford and Ward 1991); this can dilute the suspended sediments but not without negative consequences to the benthos. The high suspended loads of the Paria and Little Colorado rivers result from the erosion of soft sedimentary strata common on the arid Colorado Plateau (Beus and Morales 1990).

The Colorado River Management Plan in Grand Canyon National Park (NPS 1989) states that its resource management goals are "to preserve the natural resources and environmental processes of the Colorado River corridor and the associated riparian and river

environments . . . (and) to protect and preserve the river corridor environment" (NPS 1989:9). The Environmental Impact Statement (U.S. Bureau of Reclamation 1995) on the operation of GCD identified the aquatic food base as an "indicator resource" and important habitat for wildlife. Wildlife linked directly to the aquatic food base include native and nonnative fish, insectivorous birds and bats, reptiles, and waterfowl (Carothers and Brown 1991, Stevens et al. 1997*a*). Indirect links to the aquatic food base include endangered Peregrine Falcons feeding on waterfowl, insectivorous birds and bats, as well as Kingfishers, Great Blue Herons, Osprey, and Bald Eagles preying on fish. In response to the adaptive management guidelines from the GCD Environmental Impact Statement we investigated the impact and response of the aquatic food base from the 1996 test flood in the Colorado River below GCD by evaluating the following parameters: underwater light intensity, water quality, benthic standing mass of primary and secondary producers, and the biomass and composition of organic drift.

Materials and Methods

Study site

The cold and vacillating clear water habitat has selected for aquatic organisms normally found in nearctic regions such as various Chironomidae, *Simulium arcticum* complex, oligochaetes (including Lumbricidae, Lumbriculidae, Naididae, and Tubificidae), and an introduced amphipod *Gammarus lacustris* (Blinn and Cole 1991, Stevens et al. 1997*b*, Pomeroy et al. 2000). Recent colonizers since 1994, possibly as a result of reduced discharge variability, include Trichoptera (*Hydroptila arctia, Rhyacophila* spp., *Hydropsyche oslari*, and Limnephilidae), Diptera, (*Bibiocephala grandis, Wiedemannia* spp.), Ephemeroptera, (*Baetis* spp.), Coleoptera, (*Microcylloepus* spp.), Planariidae, and Hydracarina. Based on Merritt and Cummins (1984), these macroinvertebrates represent three functional feeding guilds: detritivores, filter feeders, and grazers.

Grazing macroinvertebrates consume epiphytic diatoms that colonize *Cladophora glomerata,* other filamentous algae, and aquatic macrophytes (Blinn and Cole 1991, Shannon et al. 1994). Recently *Cladophora* has been replaced seasonally in the tailwaters of GCD by other algal taxa including: Chlorophyta, (*Mougeotia* spp., *Oedogonium* spp., *Spirogyra* spp., *Stigeoclonium* spp.), Rhodophyta, (*Batrachospermum* spp., *Rhodochorton* spp.), a diatom mucilage matrix and the cyanobacterium, *Tolypothrix* spp. (Benenati et al. 1997). Benenati et al. (1997) suggested that changes in phytobenthos have resulted from an interaction between high inflow into upper Lake Powell which provided consistently high flows from GCD, lowered the specific conductance of lake water, and reduced nutrient concentrations. Soft bottom habitats in the tailwaters have been colonized by macroalgae and aquatic macrophytes (*Chara contraria, Potamogeton pectinatus,* and *Elodea* sp.) since modified flows have been released from GCD (Patten et al. 2001).

Discharge during the collection period ranged from 142 to 708 m^3/s, except for the test-flood peak of 1275 m^3/s. Discharges from GCD averaged $\leq$450 m^3/s, with minimal daily or monthly fluctuations from June 1995 to September 1996 as a result of above average inflow into Lake Powell, returning to fall fluctuating flows (227–424 m^3/s) in October.

Water quality

Water quality measurements of temperature (°C), specific conductance (mS), dissolved oxygen (mg/L), and pH were taken with a Hydrolab Scout 2 (Hydrolab, Austin, Texas) at the time of each sampling at Lees Ferry during the test flood and at all other collections. Water transparency was measured with a Secchi disk. We monitored light intensity at Lees Ferry and Carbon Creek during the test flood with submersible Onset data loggers (Onset HOBO, Pocasset, Massachusetts). These instruments were placed at a depth of 50 cm throughout the flood to measure light intensity at a uniform depth.

Benthic collections

Sampling was conducted in October 1995 and during March, June, and October of 1996 at four sites (0.8, 3.1, 109.6, and 326.4 km) in both pool and cobble habitats (Fig. 1). Sites were selected in conjunction with fish collection areas and also bracketed the two main tributaries with an additional site in western Grand Canyon. Test-flood collections were taken during pre- and post-flood steady 227 m^3/s flows and 2 and 6 mo after the Spike Flow (SF). In addition, 1 wk and 1 mo post-flood benthic collections were made at Lees Ferry Cobble (Rkm 0.8) and Two-Mile Wash (Rkm 3.1). Yount and Niemi (1990) reviewed 50 disturbance/recovery investigations and found that ~3 mo were required for complete recovery in lotic systems from spates. We based our collection intervals on this assumption.

Peterson or Petite Ponar dredges (Petite Ponar, Saginaw, Michigan) were used in pool habitats and Hess substrate samplers were employed on cobble bars. Six cobble and 12 pool samples were taken for abundance and mass determinations from transects established in 1990 (Stevens et al. 1997*b*). All samples were placed on ice and processed within 24 h. At the time of collection we recorded: depth, current velocity, relative distance to shore, time of day, and the discharge both estimated on site from local landmarks and verified from USGS gaging station data.

Biotic samples were sorted into the following 11 categories: *Cladophora glomerata,* cyanobacteria algal crust (*Oscillatoria* spp.), miscellaneous algae, detritus, chironomids, simuliids, *Gammarus lacustris,* gastro-

pods, lumbriculids and tubificids (Oligochaeta), and miscellaneous macroinvertebrates. Each category was oven-dried at 60°C to a constant mass. Ash-free dry mass (AFDM) conversions were estimated from dry mass to AFDM regression equations. We calculated an error of ±0.04 g AFDM per 100 samples composed primarily of very fine particulate organic matter (detritus). Quality control calculations based on 1208 samples determined an overall error rate of 1.1% for AFDM estimates.

Sediment (~500 g) was collected at pools sites with either a Peterson or Petite Ponar dredge to compare test-flood effects on sediment clast size. Samples were oven-dried at 60°C and mechanically sieved for percentage clast size using the Wentworth scale: gravel, coarse sand, sand, and silt/clay (Welch 1948). These data were collected in order to indicate scour and/or deposition caused by the test flood.

Upper tailwater (GCD to the Paria River) fine sediment habitats were evaluated for macrophyte composition and cover at 14 sites at the following intervals: March, April, July, and November 1996. Ordinal values (OV) were assigned for relative abundance: OV1 = low vertical growth, patchy, and sparse; OV2 = moderate vertical growth, occasionally patchy; and OV3 = higher vertical growth, extensive, and generally no patchiness.

Organic drift collections CPOM

Nearshore surface drift samples (0–0.5 m deep) were taken at each pool site and at Glen Canyon Gage (Fig. 1), during each trip for coarse particulate organic matter (CPOM). Collections were made with a circular tow net (48 cm diameter opening, 0.5 mm mesh) held in place behind a moored pontoon raft or secured to the riverbank. Sampling times were staggered across the test-flood hydrograph so that a particular parcel of water would be sampled at all sites (n = 336). CPOM collecting during the test flood occurred on the first and last days of the pre-and post-steady flows, as the hydrostatic wave arrived at each site, the initial pulse of water from Lake Powell and three times during the high steady flow period. Samples were placed on ice and processed live within 48 h and sorted into seven categories including: *G. lacustris,* chironomid larvae, simuliid larvae, miscellaneous invertebrates, *C. glomerata,* miscellaneous algae/macrophytes, and detritus. Miscellaneous invertebrates included lumbriculids, tubificids, physids, trichopterans, terrestrial insects, and unidentifiable animals. Detritus was composed of both autochthonous (algal/bryophyte/macrophyte fragments) and allochthonous (tributary upland and riparian vegetation) flotsam. Invertebrates were enumerated, oven-dried at 60°C, weighed, ashed (500°C, 1 h), and reweighed.

Current velocity was measured for volumetric calculations (mass·m^{-3}·s^{-1}) using a Marsh-McBirney electronic flow meter (model 201D, Marsh-McBirney, Gaithersburg, Maryland). The duration of all drift collections (n = 411) averaged 1.4 min (SE ± 0.06) with an average of 9.2 ± 0.5 m^3 of water sampled through nets. The seemingly low duration and volume of water filtered was due to the enormous amount of organic material drifting during the test flood. Had the sets not been limited to a few seconds in duration, the nets would have lost their effectiveness in collecting drift and samples would have been too large to process in a timely manner. The standard sampling error was within ±10% of the estimated mean total drifting mass (0.218 ± 0.024 g·m^{-3}·s^{-1}; Culp et al. 1994); therefore, collections were assumed to be consistent and representative of the study site.

We tested the hypothesis that organic drift was uniformly distributed across the river channel at Lees Ferry with simultaneous collections at two locations at the surface and at a depth of 3 m on 20 November 1995. Using the same drift nets as described above, two crews simultaneously made 25 collections at each location and depth (n = 100). Estimates of total drifting organic material were made by drying the entire sample at 60°C, combusting for 1 h at 500°C, and calculating ash-free dry mass (AFDM). Current velocity and duration of each set were recorded for volumetric calculations with the units reported as mg AFDM·m^{-3}·s^{-1}. Independent-samples t test indicated no significant differences in organic drift between sites at either the surface (4 ± 5 SD vs. 7 ± 5 mg·m^{-3}·s^{-1}; P = 0.07) or at a 3 m deep (7 ± 6 vs. 7 ± 5 mg·m^{-3}·s^{-1}; P = 0.9). Nor was there a significant difference at either depth between sites (P = 0.1). From this analysis we accept the hypothesis that single location collections are representative of the entire channel. This is probably the result of a restricted channel, which is common in the Colorado River below GCD. Surface collections had the most variability, possibly due to wind and erratic surface currents.

Drift samples were analyzed for size fractions after dry mass was obtained. Material from each collection interval and site was dry sieved into <1 mm, 1–10 mm, and ≥10 mm size fractions. Each sample was gently shaken by hand for 30 s, which allowed for the separation of size fractions without particulate degradation (Shannon et al. 1996*b*). This method was examined for accuracy by sieving known samples for 15, 30, and 45 s (n = 12). The 30-s sample had <3% error in mass. Precision was defined by sieving the same sample three times and we found <5% error in mass (n = 4). The errors were randomly distributed across the size fractions.

Organic drift collections FPOM

Fine particulate organic matter (FPOM) was collected during the test flood at the same time as CPOM. Surface drift collections (0–0.5 m deep) were made

with a circular tow net (30 cm diameter opening, 153 μm mesh) held in place behind a moored pontoon raft or secured to the riverbank. Samples were preserved in 70% ETOH and sorted in the laboratory with a dissecting microscope into the following categories for biomass: (1) zooplankton; Copepoda, (Calanoida, Cyclopoida, Harpacticoida), Cladocera, Ostracoda and (2) miscellaneous zooplankton; small Chironomidae, Oligochaeta, *G. lacustris*, Tardigrada, etc. Samples were filtered through a 1-mm sieve to remove coarse particulate organic matter (CPOM). Depending on zooplankton density, samples were sorted in their entirety or were split into 2-, 5-, or 10-mL subsamples from a 100-mL dilution. Three subsamples were taken from split samples and these values were averaged and extrapolated for the entire sample.

Zooplankton was sorted into vials for dry mass estimates, then converted to ash-free dry mass (AFDM) using a regression equation. Densities for all zooplankton categories were also recorded. The remaining organic material was filtered onto glass microfiber filters (Whatman GF/A, Whatman, Clifton, New Jersey) with a Millipore Swinex system. These filters were then oven-dried at 60°C and combusted for 1 h at 500°C to obtain an AFDM for all detritus. The condition, reproductive state, and presence of nauplii were documented. Volumetric calculations, mass·m^{-3}·s^{-1}, were determined in the same fashion as CPOM drift.

Large flotsam

Our CPOM sampling did not include large flotsam (>0.1 m) that was common during the up-ramping and during the first couple of days of 1274 m^3/s test flood. Understanding the role of large flotsam is important in the overall context of the flood which is attempting to return some aspects of the pre-impoundment condition. Large woody flotsam is a primary source of carbon above Lake Powell today (Haden et al. 1999) and was probably an important pre-dam organic source. In an effort to quantify this portion of the organic budget we examined interval photographs from the Grand Canyon beach survey program taken during the test flood for large CPOM (M. Manone, *personal communication*). Cameras that showed the complete river channel with a clear view not obstructed by rapids or canyon shadows were selected at about every 35 km, including km 12.8, 88.0, 166.4, 195.7, 232.8, 275.5, and 323.2. While viewing each frame on CD-ROM, which was enlarged to the best resolution possible, every noticeable particle of flotsam was scored. The location and time of the picture taken was compared to the test-flood hydrograph so the scores could be placed in relation to other drift collections.

Statistical analyses

Multivariate analyses of variance (MANOVA) were used to analyze categorical predictor variables (physical parameters) against multiple response variables (mass estimates of biotic categories) for significant temporal and spatial trends for both benthic and organic drift patterns ([ln + 1]-transformed data). Influence of the test flood, including pre- and post-collections, on benthic and organic drift estimates within collection sites were analyzed with the Kruskal-Wallis test. Ordinal ranks for macrophyte cover were analyzed with Kruskal-Wallis among sampling periods, while 227 m^3/s flows were compared with the Mann-Whitney *U* test. All calculations were performed with SYSTAT Version 5.2 computer software (SYSTAT 1992).

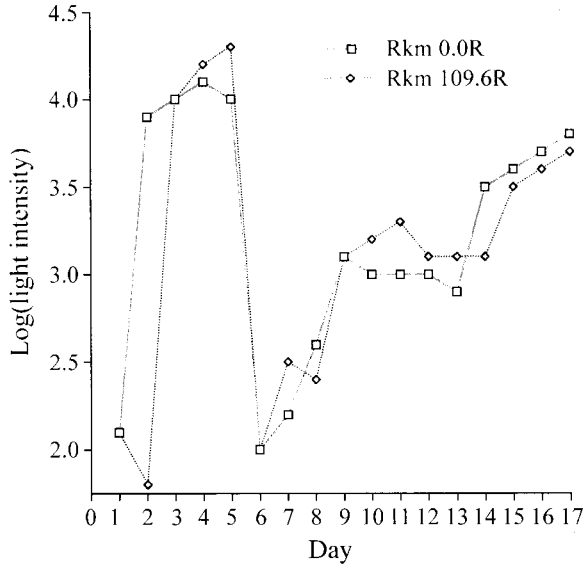

FIG. 2. Log of light intensity (measured in lumens per square meter) in the Colorado River at Lees Ferry (Rkm 0.0R [R following number refers to river right looking downstream]) and below the Little Colorado River (Rkm 109.6R) at 0.5 m depth prior to, during, and one week after the test flood (TF) below Glen Canyon Dam, Arizona. Day sequence on *x*-axis begins on 21 March and ends on 6 April 1996. Discharge at Lees Ferry for each day was as follows: day 2, five pre-227 m^3/s; day 6, 12 1274 m^3/s; day 13, 16 post-227 m^3/s. Values for the lower station were moved one day to the left because of lag time for the hydrostatic wave.

RESULTS

Water quality

Water clarity was the only water quality parameter monitored during the flood that varied outside of typical patterns (Shannon et al. 1996*a*, Stevens et al. 1997*b*). Light intensity measured at Lees Ferry and below the Little Colorado River revealed a similar pattern of diminishing light intensity as the test-flood hydrograph reached peak flow and then increased as the peak flow persisted (Fig. 2). The similarities in light intensities between sites, even though they are almost 110 km apart, is a reflection of how this river responded to the test flood. The reduction in light intensity 2 d

TABLE 1. Results of multiple analysis of covariance comparing pre- and post-flood benthic mass in the Colorado River through Grand Canyon in pool and riffle habitats for March (1995 and 1996) and June (1994 and 1996) collections.

Source	Wilks' lambda	Approximate *F* statistic	df	*P*	Response variable
Riffle habitats (March)					
Trip	0.6	6.8	11, 125	<0.0001	A,O,B,I
Site	0.6	7.2	11, 125	<0.0001	C,A,M,G,S,L,I
Pool habitats (March)					
Trip	0.9	2.2	11, 263	0.0162	D
Site	0.9	2.5	11, 263	0.0063	C,A,S,T
Riffle habitats (June)					
Trip	0.7	6.2	11, 125	<0.0001	A,D,M,B,L,T,I
Site	0.6	8.4	11, 125	<0.0001	C,A,M,G,S,B,T
Pool habitats (June)					
Trip	0.9	1.68	11, 263	0.07	M
Site	0.8	5.6	11, 263	<0.0001	D,M,I

Notes: Predictor variables of collection trip date covaried by collection site and were analyzed against response variables of biotic categories. Taxonomic categories include: *Cladophora* (C), *Oscillatoria* (O), miscellaneous algae/macrophytes (A), detritus (D), chironomids (M), *Gammarus* (G), gastropods (S), simuliids (B), lumbriculids (L), tubificids (T), and miscellaneous macroinvertebrates (I). Only significant univariate response variables are listed ($P < 0.04$). Overall Wilks' lambda, trip and site, was significant ($P < 0.0001$).

prior to the flood resulted from a spate that influenced the entire river corridor (Fig. 2). During the post-flood at a 227 m^3/s discharge, light intensity was increasing over time at both sites. Secchi depths, recorded at Lees Ferry, followed the same inverse relationship to discharge with a return to pre-flood depths by the end of the 1275 m^3/s release.

Water temperature released from GCD measured ~1 km downriver at Glen Canyon gage ranged from 9.1° to 9.5°C and pH ranged from 7.3 to 7.8. Dissolved oxygen (DO) concentrations at Glen Canyon gage during the pre-227 m^3/s were 8.8 mg/L at 86% saturation. As water was released through the four bypass tubes (~400 m^3/s) aeration increased the DO concentration to 13.8 mg/L, exceeding saturation at 122%. Conductivity increased from 0.71 mS in February at Glen Canyon gage to 0.87 mS during the test flood and returned to 0.72 mS by October.

Influence of test flood on sediment clast size in channel

A comparison of sediment clast composition during pre-flood (March) and post-flood (June) from five pool sites revealed that the flood removed silt from all sites and sand (very fine, fine, and medium) from Lees Ferry, exposing gravel. Coarse sand, including very coarse, decreased at all sites below Lees Ferry; it is unknown if it was buried with sand or scoured. This pattern explains the increase in tubificids in drift samples and the decrease in chironomid mass in pools, as we have found a significant positive relationship between silt/clay and macroinvertebrate biomass in pools (Blinn et al. 1994).

Sediment clast composition in pools collected in October 1996 showed that post-flood changes were site specific. At Lees Ferry the percentage of very coarse sand and sand both increased, while silt and gravel decreased. Sediment composition at Nankoweap and Tanner remained unchanged and were 100% sand. The Kanab Creek pool site (Rkm 203.4L [L refers to river left looking downstream]) was 100% gravel due to a flash flood from an adjacent drainage. The Spring Canyon (Rkm 326.5R [R refers to river right looking downstream]) pool site had more than regained the silt fraction lost to the test flood.

Benthic patterns: pre-flood

Discharges from Glen Canyon Dam (GCD) from June 1995 through the test flood were at the upper limits of allowable discharge. A comparison of the benthic community between March 1995 and March 1996 indicated an overall significant difference between these two periods for both riffle and pool habitats (Table 1). Evaluating the differences between these two periods is important in understanding the impacts of the test flood because the March 1996 trip established our system-wide baseline. We determined an overall significant difference between those two periods and for riffle habitats, but pools only varied significantly between sites and not between trips (Table 1).

Biomass in pools and riffles during March 1995 and March 1996 revealed a system-wide impact of a wetter than normal winter of 1995 (Table 1). Detrital loads in pools decreased by ~90% from March 1995 to March 1996 (Table 2). We observed evidence of spates or debris flows from every perennial tributary from Nankoweap Creek to Diamond Creek during our March 1995 monitoring trip (Shannon et al. 1996*a*). An influx of woody debris from these events, coupled with high discharges the following year, accounted for the removal of material by March 1996. In riffle habitats, *Oscillatoria* spp., miscellaneous algae/macrophytes/bryophytes (MAMB), and miscellaneous macroinver-

TABLE 2. Average system-wide benthic mass for pre-flood estimates from March 1996 and post-flood estimates from June 1996 in the Colorado River through Grand Canyon, for pool and riffle habitats.

Habitat	Taxonomic category	Non-flood		Flood	
		Date	AFDM†	Date	AFDM†
Pool	detritus	Mar 95	55.0 (32.6)	Mar 96	4.5 (1.7)
Riffle	*Oscillatoria*	Mar 95	0.244 (0.060)	Mar 96	3.123 (1.003)
	MAMB	Mar 95	0.215 (0.002)	Mar 96	8.994 (3.194)
	simuliids	Mar 95	0.022 (0.012)	Mar 96	0.006 (0.004)
	MM	Mar 95	0.005 (0.097)	Mar 96	0.025 (0.009)
Pool	chironomids	Jun 94	0.106 (0.012)	Jun 96	0.0001 (0.0001)
Riffle	MAMB	Jun 94	1.5 (1.4)	Jun 96	8.33 (3.46)
	detritus	Jun 94	1.22 (0.39)	Jun 96	8.45 (2.85)
	lumbriculids	Jun 94	0.146 (0.065)	Jun 96	0.037 (0.19)
	chironomids	Jun 94	0.093 (0.051)	Jun 96	0.08 (0.03)
	simuliids	Jun 94	0.005 (0.002)	Jun 96	0.014 (0.002)
	tubificids	Jun 94	0.012 (0.006)	Jun 96	0.045 (0.014)
	MM	Jun 94	0.024 (0.008)	Jun 96	0.113 (0.050)

Notes: June 1994 and March 1995 represent non-test-food patterns for comparison. All biotic categories listed are significantly different between trips ($P < 0.04$). MAMB = miscellaneous algae/macrophytes/bryophytes, and MM = miscellaneous maroinvertebrates.

† Values for ash-free dry mass (AFDM) estimates are expressed as grams per square meter with one standard error in parentheses.

tebrate (MM) AFDM estimates were all significantly higher in 1996 than 1995 collections (Table 2). However, estimates of simuliid larvae/pupae mass were significantly lower (~80%) during March of 1996 (Table 2). The biomass of the cyanobacterium, *Oscillatoria* spp. was more than 12-fold higher in 1996 over 1995, probably because we were sampling higher in the channel due to high flows. It is in the lower varial zone that *Oscillatoria* thrives with its ability to withstand periodic desiccation by storing moisture in its silt/clay matrix (Shaver et al. 1998).

Biotic categories also differed significantly by site between March 1995 and 1996, with pools being more resistant to annual change than riffles (Table 1, Fig. 3). The shift in dominance from the filamentous green alga *Cladophora glomerata* to miscellaneous algae and MAMB at Lees Ferry is noteworthy when comparing sites between years. MAMB also increased below the Little Colorado River confluence. Chironomid mass increased at many lower Grand Canyon sites and was less variable in collections during March 1996 than in March 1995. *Gammarus lacustris* mass showed an overall decrease in 1996 compared to March 1995 AFDM estimates except at Two-Mile Wash (km 3.1) and Little Colorado River Island (km 98.6).

Benthic patterns: during and post-flood

A comparison of benthic biomass in pool and riffle habitats between June 1994 and June 1996 showed more significant categorical differences within riffles than pools, with an overall increase in biomass in 1996 (Table 2). Some fine-sediment dwellers, such as chironomids and lumbriculids decreased in June 1996 collections, except for tubificids which increased by 80%. Faster turnover rates of tubificids in riffles as compared to chironomids or lumbriculids may be attributed to their use of detritus that collected from riffles in June 1996 but which was not available in June 1994.

Multivariate comparisons of benthic mass between June 1994 and June 1996 varied significantly by site, with riffles more susceptible to change than pools (Tables 1 and 2). June biomass estimates were higher overall at more sites in 1996 than in 1994 for *C. glomerata,* MAMB, chironomids, *G. lacustris,* tubificids, and gastropods; however, lumbriculid mass was lower.

Multivariate analysis of benthic biomass was conducted at five cobble sites (Lees Ferry, Two-Mile Wash, Little Colorado River Island, Tanner Cobble, and Lava Falls), with collection intervals designed to detect the impact and response of the benthos to the test flood. This analysis indicated significant change for both collection interval and site (Fig. 3, Table 3). Univariate analyses indicated that only MAMB, lumbriculids, and tubificids varied significantly for both collection interval and site. In order to assess the impact of the flood on the benthos, we compared Hess collections taken during both the pre- and post-flood steady 227 m^3/s discharges and determined that the biotic categories responded differently at each site.

Cladophora glomerata did not change significantly at Lees Ferry or Little Colorado River Island after the flood, but did at all other sites (Fig. 3, Table 4). The relative lack of suspended sediment at Lees Ferry probably did not scour *C. glomerata,* which was virtually eliminated at Two-Mile Wash, only 1 km downstream and below the Paria River confluence (Fig. 1). Recovery of *C. glomerata* was equaled or greater than that of the pre-flood estimates within 1 mo at Lees Ferry and within 2 mo at Two-Mile Wash and Tanner Cobble.

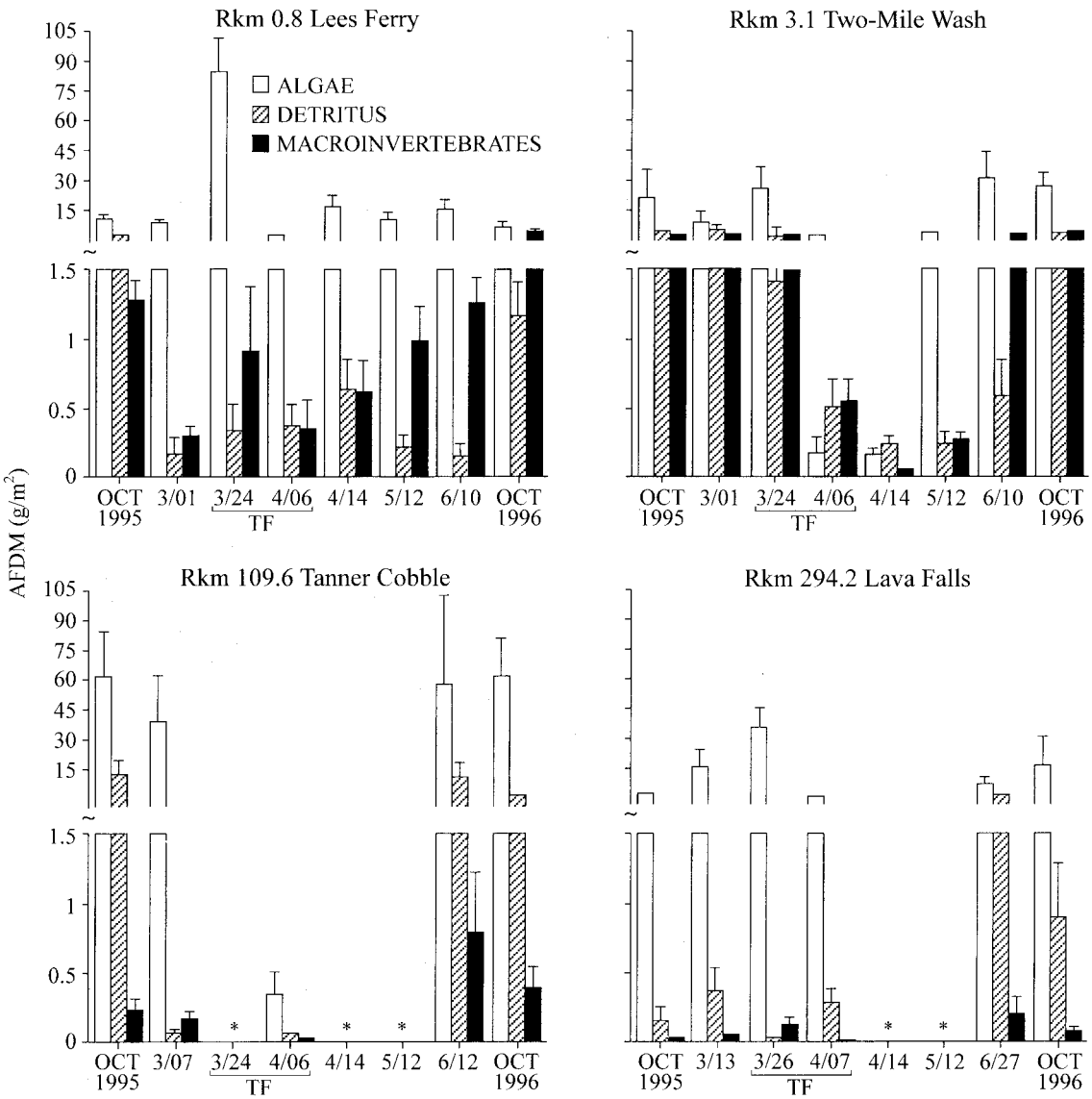

FIG. 3. Average standing mass (ash-free dry mass [AFDM] in grams per square meter; +1 SE) of aquatic benthos at selected sites along the Colorado River corridor for algae, macroinvertebrates, and detritus for selected periods prior to, during, and after the test flood (TF) below Glen Canyon Dam, Arizona, USA. Dates on *x*-axis are month/day; for example, 24 March is shown as 3/24.

A similar pattern of scour and recovery occurred for MAMB estimates.

There was little overall change in chironomid AFDM following the flood, but a steady increase in AFDM occurred over the 2-mo period for *G. lacustris.* We noted that many *G. lacustris* were stranded in pools as the water level dropped during the drawdown prior to the test flood, but egg masses and small size-class amphipods (<2 mm) were noted during 1-wk and 1-mo post collections. Whether this reproduction was a result of the flood or was normal for that time of year requires further investigation.

Macro-algae and aquatic macrophyte density was dramatically reduced following the test flood. Macrophyte ordinal values decreased from 1.5 (0.2) pre-flood to 0.6 (0.1) post-flood with full recovery by July, 2.1 (0.1) decreasing to 1.7 (0.1) by November. The November decrease can be attributed to a seasonal decrease in light availability and discharge through October and November (227–350 m^3/s). The macroalga, *Chara contraria,* was most vulnerable to the 1275 m^3/s experimental discharge and was co-dominant with *Potamogeton pectinatus* through the summer. *Elodea* was infrequently observed during surveys prior to No-

TABLE 3. Results of multiple analysis of variance comparing benthic biomass in the Colorado River through Grand Canyon from five cobble sites: Lees Ferry, Two-Mile Wash, Little Colorado River Island, Tanner Cobble, and Lava Falls.

Source	Wilks' lambda	Approximate *F* statistic	df	*P*	Response variable
Trip	0.3	2.4	55, 508	<0.0001	C,A,D,M,B,L,T,I
Site	0.7	4.1	11, 109	<0.001	O,A,G,L,T

Notes: Collection times were made to determine the influence of the spring test flood on benthic biomass, with all sites collected one month before the flood, during the steady 227 m^3/s flows both pre- and post-flood, and two months after the test flood. Lees Ferry and Two-Mile Wash were also sampled one week and one month after the test flood. Predictor variables of collection trip date covaried by collection site and were analyzed against response variables of biotic categories ([ln + 1]-transformed data, original units AFDM/m^2). Taxonomic categories include: *Cladophora* (C), *Oscillatoria* (O), miscellaneous algae/macrophytes (A), detritus (D), chironomids (M), *Gammarus* (G), gastropods (S), simuliids (B), lumbriculids (L), tubificids (T), and miscellaneous macroinvertebrates (I). Only significant univariate response variables are listed ($P < 0.04$). Overall Wilks' lambda, trip and site, was significant ($P < 0.0001$).

vember when it became dominant. These data indicate how variable and sensitive these soft bottom plants are to discharge.

Organic drift patterns: test flood

Multivariate analysis of coarse particulate organic matter (CPOM) in drift from five sites (Lees Ferry, Two-Mile Wash, LCR Island, Tanner Cobble, and Lava Falls) indicated a significant change for both collection interval and site (Fig 4, Table 5). All biotic drift categories varied significantly by collection interval, while only *G. lacustris* and miscellaneous macroinvertebrates varied significantly by site. Comparisons of CPOM in the hydrostatic wave vs. the actual flood discharge (1274 m^3/s) revealed a significant difference (Kruskal-Wallis; $P < 0.01$) with the hydrostatic wave carrying more organic material. These data indicated the greatest AFDM entrainment occurred during the up-ramp of the test flood and that duration was not a factor affecting either scour or entrainment.

TABLE 4. Results of Kruskal-Wallis tests comparing pre- and post-flood benthic biomass in the Colorado River through the Grand Canyon from five cobble sites: Lees Ferry, Two-Mile Wash, Little Colorado River Island, Tanner Cobble, and Lava Falls.

Site	Biotic category	Rank sum: Pre-flood	Rank sum: Post-flood	*P*
Lees Ferry (Rkm 0.8)	MAMB	57	21	0.004
	Oscillatoria	53	25	0.020
	MM	52	26	0.037
Two-Mile Wash (Rkm 3.1)	*Cladophora*	57	21	0.004
	MAMB	57	21	0.004
	Oscillatoria	54	24	0.005
	detritus	54	24	0.016
	chironomids	57	21	0.003
	tubificids	51	27	0.022
Little Colorado (Rkm 98.7)	simuliids	21	57	0.002
Tanner Cobble (Rkm 109.6)	*Cladophora*	53	25	0.025
	MAMB	54	24	0.016
	Oscillatoria	54	26	0.037
	MM	57	21	0.003
Lava Falls (Rkm 294.2)	*Cladophora*	25	53	0.004
	Oscillatoria	54	24	0.016
	detritus	25	53	0.020
	MM	54	24	0.007
	chironomids	57	21	0.004

Notes: Collections were made during the steady 227 m^3/s flows both pre- and post-flood from below the base discharge of 142 m^3/s. Except for the pre-flood, collections at Little Colorado River Island and Tanner Cobble were made on 6 and 7 March 1996, respectively. Only biotic categories that were significantly different between collections are listed ($P < 0.04$). For all categories, $n = 12$. Miscellaneous algae/macrophytes/bryophytes is abbreviated as MAMB and miscellaneous macroinvertebrates is abbreviated as MM.

Cladophora glomerata, MAMB, and detrital drift estimates all peaked during the hydrostatic wave and recovered or surpassed pre-flood drift mass at each site except for detritus which was probably swept through the river corridor to Lake Mead. Aquatic Diptera and miscellaneous macroinvertebrate drifting mass also peaked during the test-flood wave and recovered or surpassed that of pre-flood estimates after 1 mo at Lees Ferry and Two-Mile Wash. Miscellaneous macroinvertebrates were composed primarily of tubificid worms during the test flood which suggested disturbance and movement of the bedload. Terrestrial insects represented only 0.013% (36 out of 2600) of the miscellaneous macroinvertebrate category, which is low but two orders of magnitude higher than the values reported by Shannon et al. (1996*b*).

Percentage particle size of CPOM changed with site and collection interval with a decrease in the ≥10-mm size fraction during the steady 1274 m^3/s flows, whereas both 1–9 mm and the <1-mm size fraction increased. This pattern was consistent for all sites except for Lava Falls which may have resulted from the break-up of large flotsam as it moved through the rapids of middle and lower Grand Canyon. Lees Ferry and Two-Mile Wash sites regained the ≥10-mm size fraction within 1-wk after the flood, which coincided with the pattern for phytobenthos at these two sites.

Particle size of CPOM drift in June 1996 was pri-

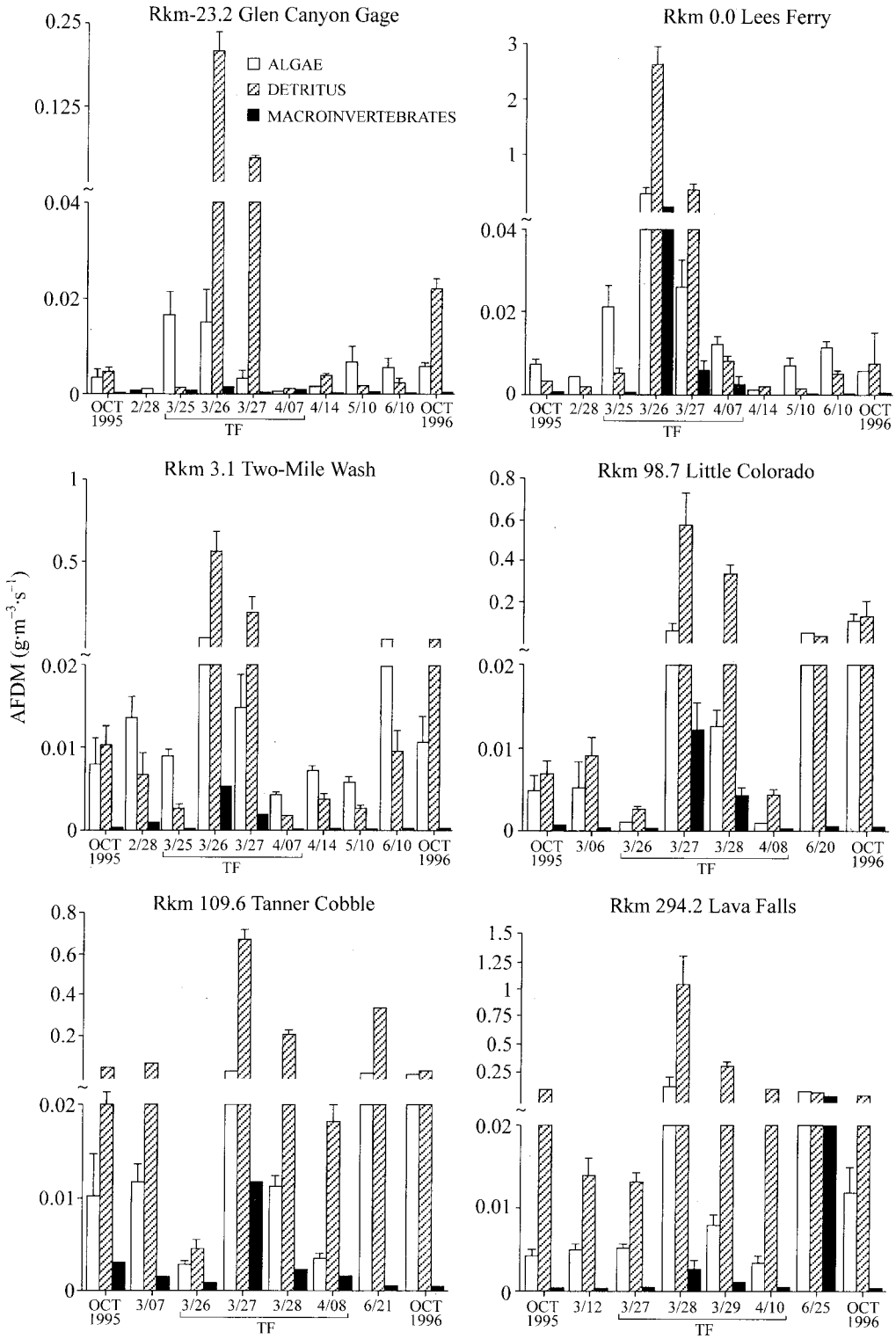

FIG. 4. Average standing mass (ash-free dry mass [AFDM] in grams per cubic meter per second; +1 SE) of organic drift at selected sites along the Colorado River corridor for algae, detritus, and macroinvertebrates for selected periods prior to, during, and after the test flood (TF) below Glen Canyon Dam, Arizona, USA. Dates on the *x*-axis are month/day; for example, 25 March is shown as 3/25.

TABLE 5. Results of multiple analysis of variance comparing coarse particulate organic matter (CPOM) in the Colorado River through Grand Canyon from five sites with collection times pre-, post-, and during the March 1996 test flood.

Source	Wilks' lambda	Approximate F statistic	df	P	Response variable
Trip	0.4	6.7	54, 2018	<0.0001	C,A,O,D,AD,G,I
Site	0.9	6.1	6, 395	<0.0001	G,I

Notes: Collection sites include Glen Canyon Gage, Lees Ferry, Two-Mile Wash, Little Colorado River Island, Carbon Creek, and Lava Falls. Collection times included one month prior to the test flood, during the pre-flood steady 227 m^3/s flow, during the hydrostatic wave from 1274 m^3/s test flow, actual water from the 1274 m^3/s test flow, during the post-flood steady flow from 227 m^3/s, one week and one month post-flood at only Glen Canyon Gage, Lees Ferry, and Two-Mile Wash, and two months post-flood at all sites. Predictor variables of collection date covaried by collection site and were analyzed against response variables of biotic categories. Taxonomic categories include: *Cladophora* (C), miscellaneous algae/macrophytes (A), detritus (D), aquatic diptera (AD), *Gammarus* (G), and miscellaneous macroinvertebrates (I) (n = 2060). Only significant univariate response variables are listed ($P < 0.04$). Overall Wilks' lambda, trip and site, was significant ($P < 0.0001$).

marily ≥10 mm and reflected the extensive growth of aquatic primary producers after the flood. Collections of CPOM in late October 1996 were highly variable, probably a result of monsoon spates and late fall storms. Both collection periods demonstrated a reach-based pattern for the distribution of organic matter drift. For example, in October, Nankoweap (Rkm [river km] 84.8) had no CPOM ≥10 mm in size, but the gage site above the Little Colorado River, only 14 km downriver, had 50% of the CPOM ≥10 mm in size.

Estimates for FPOM biomass varied significantly by collection date and site during the test flood. Zooplankton, miscellaneous zooplankton, detritus, and total FPOM exhibited similar patterns to CPOM; i.e., the highest FPOM concentrations occurred within the hydrostatic wave and decreased through the steady discharge. Lees Ferry collections carried the highest total FPOM (1.7 ± 18 $g \cdot m^3 \cdot s^{-1}$ AFDM) in the hydrostatic wave. The FPOM estimates at Lees Ferry increased by 92% while traveling the 24-km reach below Glen Canyon Dam, probably picking up riparian debris. At the post-227 m^3/s flow collections, FPOM estimates returned to pre-SF values at Glen Canyon (0.004 ± 0.0006 $g \cdot m^3 \cdot s^{-1}$ AFDM) and Lees Ferry (0.02 ± 0.003 $g \cdot m^3 \cdot s^{-1}$ AFDM). However, at Lava Falls FPOM estimates were 2.5 times higher at the post-flood collection than at the pre-SF collection. This may be a function of a higher discharge carrying more FPOM at Lava Falls during this collection interval because river discharge never dropped below 340 m^3/s, due to the draining of bank stored water. These areas generally have elevated FPOM concentrations in comparison to upriver sites (Shannon et al. 1996*a*).

Zooplankton biomass followed a similar pattern to that of FPOM during the flood with the hydrostatic wave carrying the most zooplankton, with a decrease downstream and through the test-flood hydrograph. Zooplankton composition was dominated by cyclopoid copepods at all sites and collection intervals except at Lees Ferry where the hydrostatic wave transported a high concentration of miscellaneous zooplankton (3073 animals/L ± 511 $m^3 \cdot s^{-1}$). This concentration of miscellaneous zooplankters corresponds with the relatively high biomass of secondary producers in the tailwaters.

Large flotsam

Examination of interval camera photographs during the flood showed an average of 1.4 large flotsam (>0.1 m) bundles photographed during the up-ramp, 2 bundles during the arrival of the water at 1274 m^3/s, 0.5 bundles during the steady 1274 m^3/s discharge, and 1.2 bundles during the post-flood. We made the assumption that each photograph represented a one-second time interval. No large CPOM bundles were sighted immediately prior to the test-flood steady flows. These data indicate entrainment of large flotsam, primarily tamarisk and some up-land vegetation, during the up-ramp that was stranded on beaches below the 1274 m^3/s stage.

Large flotsam contributed a considerably smaller mass to drifting organic material during the flood in comparison to FPOM and CPOM. Organic drift during the flood, including both pre- and post steady flows averaged 0.24 $g \cdot m^3 \cdot s^{-1}$ of CPOM. This extrapolates to ~1.06×10^6 kg of CPOM after multiplying the mass of organic drift by the total estimate of water discharged during the test flood. FPOM organic drift for the flood averaged 0.22 $g \cdot m^3 \cdot s^{-1}$ or 0.97×10^6 kg for the entire test-flood period. In contrast, we estimated ~2.3×10^4 kg of flotsam was transported by the flood. These values were calculated from an average of ~22.2 bundles that passed a given point every hour, calculated from an average of 1.5 bundles per 250-m camera view at a water velocity of 3.7 km/h and each bundle at 4 kg AFDM (n = 10), and then for the 11-d test flood when bundles passed by the cameras. To demonstrate how little large flotsam contributed to the organic drift mass we need to increase the mass estimate by threefold or 400 kg AFDM for each bundle to reach the

same order of magnitude of CPOM and FPOM (~2.3 × 10^6 kg).

Discussion

Test-flood effects

The test flood of March 1996 significantly altered the aquatic food base in the Colorado River throughout the river corridor of Grand Canyon National Park over the short term. Scour and entrainment of both primary and secondary producers occurred at all sites, but varied among biotic categories. Those biota associated with fine sediments in the river channel (e.g., aquatic macrophytes, tubificids, and lumbriculids) were more susceptible to disturbance compared to those associated with the surfaces and interstitial spaces of the more stable armored cobble (e.g., *Cladophora glomerata* and *Gammarus lacustris*). Phytobenthic fine sediment taxa were scoured and remained unstable as taxonomic shifts in dominance were documented eight months after the flood.

Our results indicated that >90% of the benthos was removed at the arrival of the hydrostatic wave or 24 h from the start of the test flood. Also, drift mass reached highest levels during the first 2 d of the flood and subsided after that period. Drift mass during the flood was also an order of magnitude higher than that reported by Shannon et al. (1996*b*) during normal dam operations. Angradi and Kubly (1995) reported on CPOM and FPOM mass in the Glen Canyon reach from September 1990 through December 1991, during the GCES Phase II Research Flows (Patten 1991). Both CPOM and FPOM values in their study were an order of magnitude lower than values during the test flood. These differences may be attributed to the highly fluctuating research flows, which may have flushed the study site of POM during high flows, and produced results similar to post-flood results. Also, Angradi and Kubly (1995) used an active collection system with diaphragm pumps and Miller Tubes from a moving boat which may have caused an under estimation of drift mass.

Test-flood recovery

Recovery of the phytobenthos on hard substrata to pre-flood conditions was complete after one month for some sites. This recovery was much faster than experimental results reported by Blinn et al. (1995) or Benenati et. al. (1998). Although the phytobenthos was scoured, cobbles were not completely barren of algal rhizoidal holdfasts, especially *C. glomerata.* This fact coupled with virtually no tributary input of suspended sediment, which resulted in optimum water clarity, allowed for relatively quick recruitment of the phytobenthic community. The test flood flushed the system of fine particles, also contributing to the relatively high transparency of the water column.

Macroinvertebrate biomass followed the same pattern as that of phytobenthos and recovered within two months at all sites. Furthermore, collections for primary consumers during the post-flood trip of June of 1996 included some of the highest biomass values and most diverse fauna ever recorded during a six-year monitoring program (Blinn et al. 1994, Shannon et al. 1996*a,* Stevens et al. 1997*b*). Other investigators have reported similar fast recruitment times for phytobenthos and invertebrates under optimum conditions following a major disturbance (Steinman and McIntire 1990, Yount and Niemi 1990, Peterson 1996).

However, it is not clear whether the rapid colonization of biota would have occurred without the high steady discharges and the extended period of high water clarity that followed the test flood. Our data indicate that steady flows, high or low, contribute to increases in the aquatic food base. Furthermore, discharges ≥450 m^3/s tend to mitigate the negative influence of suspended sediments, delivered by tributaries, on water clarity. The higher discharges also provide more wetted perimeter for colonization by benthos.

Estimates for drift mass during June 1996, after two months of near steady flows, reached levels reported by Leibfried and Blinn (1986) for fluctuating flows. These investigators suggested that a potential positive effect of fluctuating flows was the entrainment of drifting food for fish. Our data indicate that high phytobenthic production under near steady flows result in equal or higher drift mass for downstream fish, without the negative features of a widely fluctuating varial zone (Usher and Blinn 1990, Angradi and Kubly 1993, Blinn et al. 1995). Unfortunately, we were not able to document this pattern further because low steady flows (3 d at 142 m^3/s), conducted in August 1996 for post-flood aerial photo-documentation of river channel morphometry, resulted in desiccation of developing benthos in the varial zone.

Management implications

Was this test flood a worthwhile experiment in dam operations? Yes, in regards to what was learned and no in terms of lasting impact. This low magnitude flood (about half of the annual peak flow) did little to return pre-dam characteristics to the aquatic community. The fundamental aspects of the aquatic community structure prior to impoundment of the Colorado River included variable temperature regime, muddy water, allochthonous carbon sources, and consistent seasonal changes in discharge. An occasional test flood such as that released from GCD can not possibly return all the parts of the community structure that are now missing. River temperature did not change during the flood from normal operations at that time of the year. The water was muddy during the beginning of the test flood but cleared up toward the end of the flood. Allochthonous input did increase during the beginning of the test flood according to stable isotope analysis but was not sustained (Blinn et al. 1998). Scour of the benthos did

occur and recovered quickly, possibly in response to the consistent flows following the flood. However, benthic biomass estimates were higher than ever reported probably aiding recovery rates. Had the tributaries been running and the flows fluctuating on a daily, weekly, and monthly basis as usual, then recovery may not have occurred as fast and the test flood would have been a detriment to the aquatic food base.

The fundamental reason for the test flood in Grand Canyon, i.e., to move sand from the channel to the riverbanks to create larger beaches for the river-running industry, was accomplished. Managers need to define the natural resources that will benefit from a test flood and whether the ecosystem in general will benefit. It is possible that managing discharge in order to replace some pre-dam components will create more of a disturbance and reduce any ecosystem vitality. The aquatic food base in the Colorado River through Grand Canyon is an alien assemblage that responds more favorably to reduced daily fluctuations and may not benefit from the occasional test flood.

Conclusions

The hypothesis that regulated rivers can be managed for the benefit or protection of natural resources with higher than normal discharges was tested in March 1996 with a 7-d discharge of 1274 m^3/s from GCD. This experiment was conducted in response to the environmental impact statement on the operations of GCD, and was a component of the selected operating alternative. Effects of this experiment varied among resources, as this symposium issue has defined. The overall influence of the test flood on the aquatic benthos is not clear due to post-flood conditions of high steady flows with relatively high water clarity. We believe that both the antecedent and subsequent hydrograph conditions were as much, if not more responsible, for the rapid recovery of the benthic community.

Negative attributes of the test-flood hydrograph were the low steady 227 m^3/s flows that desiccated the varial zone at the expense of the biota and the timing of the flood. March and April are historically wet periods in northern Arizona, which results in elevated suspended sediment input from tributaries that would typically slow benthic recovery. The positive attributes of the flood include delivery of organic food into the water column for downstream fish during the first two days of the flood and the removal of fine sediments from shorelines which ultimately enhanced water clarity and benthic recovery. Consideration of pre- and post-flows are important when constructing hydrographs for managed high flows, especially when considering response times of biotic resources that are much slower than abiotic resources such as sand. Future test floods should experiment with shorter durations, higher peak flows, and take place on consecutive years with similar dam releases so natural variability can be assessed against dam operations.

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EFFECTS OF A TEST FLOOD ON FISHES OF THE COLORADO RIVER IN GRAND CANYON, ARIZONA

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Abstract. A beach/habitat-building flow (i.e., test flood) of 1274 m^3/s, released from Glen Canyon Dam down the Colorado River through Grand Canyon, had little effect on distribution, abundance, or movement of native fishes, and only short-term effects on densities of some nonnative species. Shoreline and backwater catch rates of native fishes, including juvenile humpback chub (*Gila cypha*), flannelmouth suckers (*Catostomus latipinnis*), and bluehead suckers (*C. discobolus*), and all ages of speckled dace (*Rhinichthys osculus*), were not significantly different before and after the flood. Annual spring spawning migrations of flannelmouth suckers into the Paria River and endangered humpback chub into the Little Colorado River (LCR) took place during and after the flood, indicating no impediment to fish migrations. Pre-spawning adults staged in large slack water pools formed at the mouths of these tributaries during the flood. Net movement and habitat used by nine radio-tagged adult humpback chub during the flood were not significantly different from prior observations. Diet composition of adult humpback chub varied, but total biomass did not differ significantly before, during, and after the flood, indicating opportunistic feeding for a larger array of available food items displaced by the flood. Numbers of nonnative rainbow trout (*Oncorhynchus mykiss*) <152 mm total length decreased by ~8% in electrofishing samples from the dam tailwaters (0–25 km downstream of the dam) during the flood. Increased catch rates in the vicinity of the LCR (125 km downstream of the dam) and Hell's Hollow (314 km downstream of the dam) suggest that these young trout were displaced downstream by the flood, although displacement distance was unknown since some fish could have originated from local populations associated with intervening tributaries. Abundance, catch rate, body condition, and diet of adult rainbow trout in the dam tailwaters were not significantly affected by the flood, and the flood did not detrimentally affect spawning success; catch of young-of-year increased by 20% in summer following the flood. Post-flood catch rates of nonnative fathead minnows (*Pimephales promelas*) in shorelines and backwaters, and plains killifish (*Fundulus zebrinus*) in backwaters decreased in the vicinity of the LCR, and fathead minnows increased near Hell's Hollow, suggesting that the flood displaced this nonnative species. Densities of rainbow trout and fathead minnows recovered to pre-flood levels eight months after the flood by reinvasion from tributaries and reproduction in backwaters. We concluded that the flood was of insufficient magnitude to substantially reduce populations of nonnative fishes, but that similar managed floods can disadvantage alien predators and competitors and enhance survival of native fishes.

Key words: Catostomus latipinnis; *Colorado River; endangered species; fathead minnow; flannelmouth sucker;* Gila cypha; *Glen Canyon Dam; humpback chub;* Oncorhynchus mykiss; Pimephales promelas; *rainbow trout; test flood.*

INTRODUCTION

Floods are a common feature of rivers in the American Southwest and usually occur as runoff from spring snowmelt or as late summer monsoonal rainstorms (Webb et al. 1991*a*, *b*, Collier et al. 1996). Floods reshape the channel, infuse large amounts of nutrients into the river, and maintain a dynamic equilibrium to which many unique and indigenous fishes have adapted (Petts 1984, Poff et al. 1997). Thirteen large main stem dams now control the flow of the Colorado River (Fradkin 1984), and in many regions of the basin, including

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For reprints of this Invited Feature, see footnote 1, p. 633.

Grand Canyon, floods are now a missing component of the hydrologic setting (Daudy 1991). The effect on native fish communities is only partly understood, but the absence of floods can impede life cycles of many species (John 1963, Meffe and Minckley 1987). Aside from the direct detriment to native species, the absence of rigorous and silt-laden floods can also allow for invasions of nonnative fishes, which prey on and compete with native forms (Minckley 1991, Ruppert et al. 1993). Returning floods as a feature of regulated southwestern rivers can benefit native fishes and disadvantage nonnative species. This investigation tested the hypothesis that a test flood of 1274 m^3/s would not significantly affect native or nonnative fish populations in the Colorado River through Grand Canyon.

A beach/habitat-building flow (the test flood) was released by the U.S. Bureau of Reclamation from Glen Canyon Dam down the Colorado River through Grand Canyon on 22 March 1996 through 7 April 1996. This test flood consisted of a steady high release (i.e., flood) of 1274 m^3/s for 7 d, preceded and followed by steady low releases of 226 m^3/s for 4 d each. The purpose of this test flood was to implement the concept of beach/habitat-building flows, a common element of the alternatives presented in the Final Environmental Impact Statement on the Operation of Glen Canyon Dam (U.S. Bureau of Reclamation 1995). Beach/habitat-building flows are ". . . scheduled high releases (i.e., floods) of short duration designed to rebuild high elevation sandbars, deposit nutrients, restore backwater channels, and provide some of the dynamics of a natural system." The following objectives were addressed to evaluate the effects of the test flood: (1) determine effects on the tailwater trout fishery; (2) determine effects on distribution, dispersal, and habitat use of native and nonnative fishes; and (3) determine effects on movement and food habits of humpback chub.

The Colorado River through Grand Canyon supports 15 species of freshwater fishes, including four native species and 11 nonnative species; an additional seven nonnative species occur in the Lake Mead inflow (Valdez and Ryel 1997). The native species are warmwater riverine forms that include the federally endangered humpback chub (*Gila cypha*); a species of special concern, the flannelmouth sucker (*Catostomus latipinnis*); and the bluehead sucker (*C. discobolus*), and speckled dace (*Rhinichthys osculus*). The razorback sucker (*Xyrauchen texanus*) is native to the canyon, but only hybrid intergrades (*C. latipinnis* × *X. texanus*) have been captured recently (Douglas and Marsh 1998). A blue-ribbon tailwater fishery for introduced rainbow trout (*Oncorhynchus mykiss*) occurs in ~25 km of the Colorado River from Glen Canyon Dam to Lees Ferry, and rainbow trout and brown trout (*Salmo trutta*) are locally common in tributaries and tributary inflows further downstream. Common carp (*Cyprinus carpio*) and channel catfish (*Ictalurus punctatus*) are also common downstream of the dam tailwaters. Fathead minnows (*Pimephales promelas*) and plains killifish (*Fundulus zebrinus*) are locally common in backwaters and tributaries from the Little Colorado River (LCR) to the Lake Mead inflow, where red shiners (*Cyprinella lutrensis*) are abundant, and channel catfish and striped bass (*Morone saxatilis*) occur in large numbers in spring and summer. Walleye (*Stizostedion vitreum*), yellow bullhead (*I. natalis*), largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), green sunfish (*L. cyanellus*), black crappie (*L. nigromaculatus*), and threadfin shad (*Dorosoma petenense*) are uncommon in Grand Canyon but are residents of the Lake Mead inflow. Many aspects of the life history of the fishes of the Colorado River in Grand Canyon are influenced by flow regulation through Glen Canyon Dam. Flow regulation results in the absence of floods; cold, clear hypolimnetic releases of 8°–10°C; and daily fluctuations of up to 227 m^3/s from hydropower production (Arizona Game and Fish Department 1996*b*, Valdez and Ryel 1997, Hoffnagle et al. 1999).

Methods

Short- and long-term effects of the test flood were evaluated on fish assemblages in four reaches of the Colorado River from Glen Canyon Dam to upper Lake Mead (Fig. 1). The reaches included: Reach 1, the tailwaters between Glen Canyon Dam and the Paria River (0–25 km downstream from the dam); Reach 2, the area near the LCR inflow (121–130 km downstream from the dam); Reach 3, the area near Hells Hollow (311–318 km downstream from the dam); and Reach 4, the area near Spencer Creek (414–424 km downstream from the dam). Reach 1 was sampled during the steady low releases of 226 m^3/s before (i.e., pre-flood, 22–26 March) and after (i.e., post-flood, 3–7 April) the test flood of 1274 m^3/s (26 March through 2 April). Reaches 2 and 4 were sampled before, during, and after the flood; and Reach 3 was sampled before and after the flood. Reaches 2, 3, and 4 were also sampled at flows of ~379 m^3/s about one month before the test flood (i.e., pre-experiment, 28 February through 14 March) and at ~521 m^3/s about one month after the test flood (i.e., post-experiment, 18 April through 3 May).

The tailwater trout fishery

Trout in the tailwaters were sampled with a 5.5-m electrofishing boat equipped with a 220-V generator and a Coffelt CPS Mark XX electroshocking unit (Coffelt Manufacturing, Flagstaff, Arizona, USA). Either 14 or 15 random fixed transects were electrofished at night (~2000 s/transect) between 0.5 and 19.5 km downstream of the dam during the pre- and post-flood steady releases (226 m^3/s), and in August (~425 m^3/s) and November, 1996 (~226 m^3/s). All fish were measured for total length (TL ± 1 mm), weighed (±0.1 g

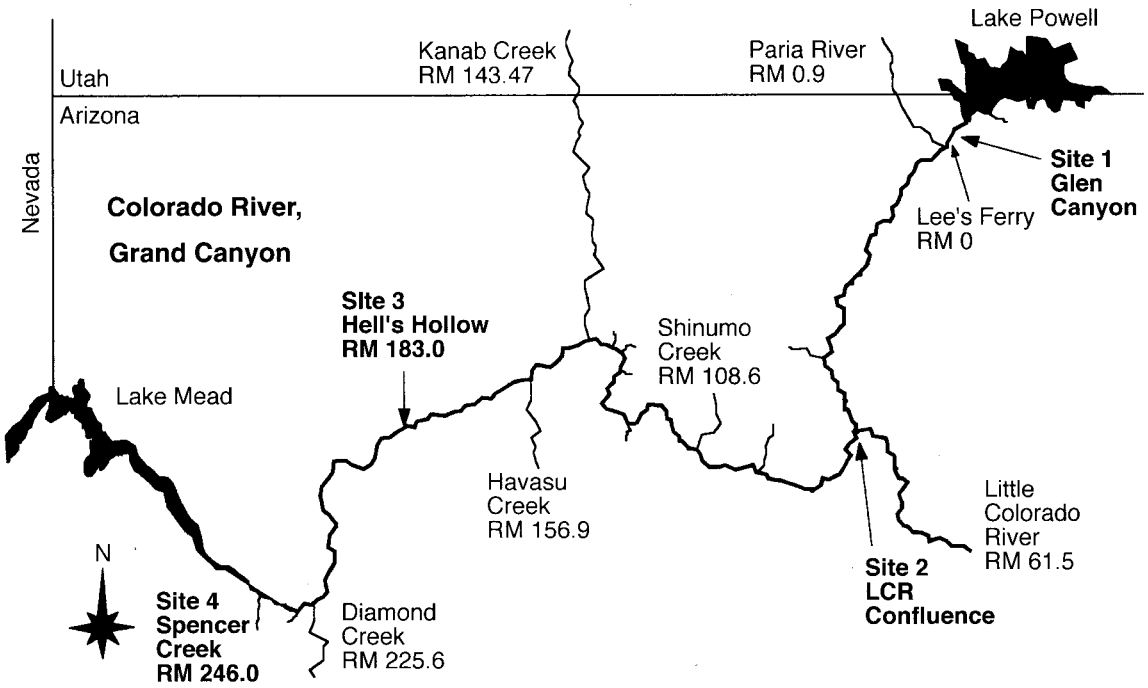

FIG. 1. The Colorado River through Grand Canyon and sample reaches used to evaluate effects of the test flood. One river mile (RM) equals 1.6 river kilometers.

for small [<10 g] fish, ±1 g for larger fish), and released alive at the point of capture unless collected for diet analyses. Stomachs of randomly selected rainbow trout were removed and preserved in 10% formalin, and contents were identified to the lowest possible taxonomic category and measured (±0.1 mL) by volumetric displacement. Analysis of variance (one-way ANOVA) was performed on means for lengths, mass, and condition factors (K = mass × 10^5/[total length]^3). Relative gut volume (RGV, the volume of stomach contents [for fish that had fed] in mL/fish length in meters; Filbert and Hawkins 1995) was compared using the Kruskal-Wallis test over all months and the Mann-Whitney U test between March (pre-flood) and April (post-flood). Planned (a priori) comparisons were conducted on data from the pre- and post-flood steady flows. Chi-square tests were used to compare frequency of occurrence of empty stomachs and of predominant taxonomic groups in the diet.

Distribution, dispersal, and habitat of native and nonnative fishes

Movements of 50 adult flannelmouth suckers were followed with the aid of crystal-controlled sonic transmitters (Model PRG-94 tags, 72–83 kHz; Sonotronics, Tucson, Arizona, USA), surgically implanted in the fish 10–14 d before the test flood. The majority of fish had prominent tubercles indicating near readiness for spawning; four males readily expressed gametes (Thieme 1997). Fish near the confluence of the Colorado and Paria rivers were tracked during pre- and post-flood steady releases from the riverbank with a mobile unit consisting of an underwater directional hydrophone (Sonotronics Model DH-2) and a digital receiver (Sonotronics USR-5W). Fish were similarly tracked from the riverbank during the flood in the lower Paria River, which was greatly expanded by inundation from the Colorado River. Sonic-tagged fish in the 25-km dam tailwaters were tracked from a boat.

Ten adult humpback chub were also surgically implanted with 11-g ATS radio transmitters (model BEI 10-18, Advanced Telemetry Systems, Isanti, Minnesota, USA) one month before the experiment and tracked before, during, and after the flood with Smith-Root SR-40 receivers (Smith-Root, Vancouver, Washington, USA) and model 2000 ATS programmable receivers (Valdez et al. 1993). These fish were captured and released near the confluence of the LCR, in Reach 2 and monitored for 2–5 d. During the test flood, fish were contacted on a daily basis to monitor movement and habitat use, and selected fish were monitored continuously for periods of up to 4 d. Fish were located by triangulating radio signals and locations of fish were plotted on 1:1200 aerial photographs.

Fish in Reaches 2 and 3 were sampled with electrofishing, trammel nets, minnow traps, and seines (Valdez et al. 1993, Arizona Game and Fish Department 1996*a*). Electrofishing was conducted from a motorized 4.8-m Achilles HD-16 hypalon sportboat (Achilles Corporation, Tokyo, Japan) equipped with a 220-V

generator and a Coffelt CPS Mark XX electroshocking unit with spherical electrodes. Electrofishing was conducted by the same crew to reduce variation from crew effect. Trammel nets were 22.9 m long with 3.8-cm inside mesh and 30.5-cm outside mesh. Unbaited commercial minnow traps, made of galvanized wire, were used for sampling shorelines, and backwaters were sampled with 10-m bag seines with 0.6-cm delta mesh.

Four major habitat types were sampled in Reaches 2 and 3 at the pre-flood and post-flood low releases and in Reach 2 during the flood, including shorelines, tributary inflows, large eddies, and backwaters. Main channel pools and runs were not sampled because of logistical difficulties and few fish reported in these habitats by previous studies (Valdez et al. 1993, Valdez and Ryel 1995). Shorelines were partitioned into debris fans, talus, and vegetation; these shoreline types have consistently yielded the highest densities of fish in Grand Canyon, including humpback chub (Valdez and Ryel 1997, Converse et al. 1998). For each of the three shoreline types, four similar shoreline sections, each 50–100 m long, were sampled twice during each pre-flood, flood, and post-flood release; hence 24 boat electrofishing samples were taken for each flow release (i.e., 3 types $\times$ 4 sections $\times$ 2 samples = 24). Minnow traps were set in groups of five in each of the three shoreline types and checked three times during each flow release, such that 180 minnow traps were set during each flow release (i.e., 3 types $\times$ 4 sections $\times$ 3 samples $\times$ 5 traps = 180). Catches from the group of five traps were pooled for analysis to reduce variation and approach normal distributions in catch rates. Large eddy complexes in Reaches 2, 3, and 4, and the LCR inflow were sampled with boat electrofishing and trammel nets. Large volumes of suspended debris trapped in eddies during the first two days of the flood hampered use of trammel nets, but the amount of suspended material lessened and netting was successful during the latter half of the flood. Backwaters were sampled with seines during the pre- and post-flood periods; no backwaters were present during the flood.

All fish were measured for total length (TL $\pm$ 1 mm), weighed ($\pm$0.1 g for small [<10 g] fish, $\pm$1 g for larger fish), and released alive at the point of capture. Native fish >150 mm TL were injected with PIT tags (Biomark, Boise, Idaho, USA) if no tag was detected by scanning, and associated data entered in a master Grand Canyon database. Adult humpback chub captured in trammel nets and by electrofishing during each of the three flow releases were examined for food contents with a nonlethal stomach pump (Wasowicz and Valdez 1994). Humpback chub gut contents were preserved in 70% ethanol. In the laboratory, gut contents were sorted into taxonomic groups (Pennak 1989), enumerated, and ash-free dry mass (AFDM) was determined for each taxonomic group. The same statistical analyses were used on diets of humpback chub as described above for rainbow trout.

Electrofishing catch-per-unit-effort (CPUE) was calculated by species as numbers of fish/10 min; for trammel nets as numbers of fish for 23 m of net/100 h; for minnow traps as numbers of fish for 5-trap groups/24 h, and for seines as numbers of fish/100 m^2 seined. Significant differences in mean CPUE were tested using the Mann-Whitney U test (Sokal and Rohlf 1987). Catch statistics are presented for Reaches 1 and 2, but low numbers of fish and high variability in catches at Reaches 3 and 4 precluded meaningful catch statistics. Hence, Reaches 1 and 2 were the most reliable statistical indicators of flood effects on native and nonnative fish assemblages.

Results

The tailwater trout fishery

Rainbow trout and flannelmouth sucker were the only fish species caught in Reach 1 before and after the flood (Table 1). Catch-per-unit-effort (CPUE) for rainbow trout of all sizes in Reach 1 did not differ significantly ($P > 0.05$) between the pre- and post-flood low releases, but the percentage catch of juvenile trout <152 mm TL was reduced by ~8% (Table 2). The proportional catch of rainbow trout <152 mm TL increased more than 20% in November (i.e., eight months after the flood), compared to previous months. The majority of these trout were young-of-year (YOY) hatched since the flood.

Rainbow trout caught during pre-flood (March) and post-flood (April), and following the experiment (i.e., August and November) ranged from 46 to 593 mm TL. Mean lengths and mass differed significantly ($P < 0.05$) among sampling periods (Table 2); i.e., trout caught in April were longer ($P < 0.001$) and heavier ($P < 0.05$) than those caught in March, confirming that there were fewer small fish in the sample following the flood. Mean length was less ($P < 0.05$) in November than in March, indicating that spawning success infused more small fish into the sample population. Mean mass did not differ significantly between March and November ($P > 0.05$), and mean condition factors did not differ significantly ($P > 0.05$) among sampling periods.

Stomachs of rainbow trout 121–538 mm TL showed that diet differed significantly ($P < 0.001$) among sampling periods, and percentage of individual components differed in patterns of change (Table 3). Green algae (*Cladophora glomerata*) dominated the diet by volume in all months, except November. Amphipods (*Gammarus lacustris*), chironomids, and gastropods (snails) were the principal macroinvertebrates in the diet, and other taxa (Diptera, oligochaetes, terrestrial invertebrates) generally comprised <2% each of stomach content volume. Univariate analysis showed that volume and percentage composition of individual taxa in the diet did not differ significantly ($P > 0.05$) between pre-

TABLE 1. Numbers of fish caught by species before, during, and after the test flood at four sample reaches of the Colorado River between Glen Canyon Dam and upper Lake Mead.

	Reach 1 (Dam tailwaters)†		Reach 2 (LCR inflow)			Reach 3 (Hells Hollow)†		Reach 4 (Spencer Creek)		
Common name	Before	After	Before	During	After	Before	After	Before	During	After
Natives										
Humpback chub	0	0	87	68	166	0	0	0	0	0
Flannelmouth sucker	12	3	7	2	8	35	37	2	0	0
Bluehead sucker	0	0	0	1	11	1	4	0	0	0
Speckled dace	0	0	105	139	291	13	29	4	0	3
Nonnatives										
Rainbow trout	1513	1685	62	36	164	1	4	0	0	0
Fathead minnow	0	0	169	11	154	4	30	9	67	50
Common carp	0	0	1	0	0	29	28	49	43	36
Channel catfish	0	0	0	0	0	11	3	20	22	40
Brown trout	0	0	2	2	1	1	1	0	0	0
Plains killifish	0	0	3	0	0	0	1	1	0	2
Striped bass	0	0	0	0	0	0	0	1	12	0
Threadfin shad	0	0	0	0	0	0	0	1	0	1
Yellow bullhead	0	0	0	0	0	0	0	1	0	0
Red shiner	0	0	0	0	0	0	0	100	72	55
Redside shiner	0	0	0	0	1	0	0	0	0	0
Largemouth bass	0	0	0	0	0	0	0	1	0	1
Black crappie	0	0	0	0	0	0	0	1	0	0
Bluegill	0	0	0	0	0	0	0	1	0	0
Green sunfish	0	0	0	0	0	0	0	1	0	1
Walleye	0	0	0	0	0	0	0	1	0	0
Totals	1525	1688	436	259	796	95	137	196	240	181

† Fish not sampled during the test flood.

and post-flood releases, but volume and percentage composition of *G. lacustris* ($P < 0.001$) and gastropods ($P < 0.02$) increased in November above pre-flood levels, while percentage composition of chironomids and *C. glomerata* decreased ($P < 0.001$).

RGV also differed ($P < 0.001$) among sampling periods (Table 3), increasing between pre-flood (March) and post-flood (April) steady releases ($P < 0.01$), remaining high in August ($P < 0.01$), but declining in November ($P < 0.002$) to pre-flood levels. Frequency of occurrence of empty stomachs did not differ ($P > 0.05$) among sampling periods, with only 9.0–22.9% of fish with empty stomachs.

Staging and spawning by flannelmouth suckers

The lower Paria River prior to the flood was characterized as narrow (<5 m wide) and uniformly shallow (<30 cm). During the flood, the waters of the Colorado River backed into the mouth of the Paria River, forming a slack water pool ~730 m long and up to 2.8 m deep. Normally, reproductively ripe flannelmouth suckers pass through this shallow portion of the Paria River as they proceed 2–12 km or more upstream to spawn during March and April (Weiss et al. 1998). However, during the test flood, 33 of 50 flannelmouth suckers implanted with sonic transmitters and released in the Colorado River before the flood were recontacted in the newly formed slack water pool at the Paria River mouth. An additional nine sonic-tagged fish were relocated in Reach 1 immediately following the flood. Of the remaining eight sonic-tagged fish, three were never recontacted, three were accounted for in Reach 1 within three months, and two were recontacted within two months at the LCR, 98 km downstream from the

TABLE 2. Total catch, mean length, mass, and condition factor (K), catch/min of electrofishing (CPUE), and number of catch <152 mm TL for rainbow trout during pre-flood (March), post-flood (April), and post-experiment sample periods (August, November) in the Glen Canyon Dam tailwaters, 1996.

Sample period	Numbers of fish	Total length (mm)†	Mass (g)†	Condition (K)†	CPUE	Number <152 mm‡
Pre-flood (March)	1513	230.8 (2.8)*	198.5 (5.7)*	0.961 (0.006)*	3.52	543 (35.9)
Post-flood (April)	1685	239.9 (2.6)**	211.2 (5.1)**	0.954 (0.005)*	3.58	477 (28.3)
Post-experiment (August)	1306	228.4 (3.2)*	232.0 (6.7)***	0.979 (0.010)*	2.61	477 (36.5)
Post-experiment (Nov)	1335	214.7 (3.2)***	208.2 (6.5)*	0.986 (0.010)*	2.58	655 (49.1)

Note: CPUE = catch-per-unit-effort, TL = total length.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
† Numbers in parentheses are standard errors.
‡ Numbers in parentheses are corresponding percentages.

TABLE 3. Frequency of occurrence and mean percentage composition by volume and relative gut volume of predominant items in stomachs of rainbow trout (121–538 mm TL) during pre-flood (March), post-flood (April), and post-experiment (August, November) sample periods from Glen Canyon Dam, 1996.

	March (N = 36)		April (N = 30)		August (N = 60)		November (N = 54)	
Food category	Frequency (%)	Percentage composition	Frequency (%)	Percentage composition	Frequency (%)	Percentage composition	Frequency (%)	Percentage composition
Gammarus lacustris	62.5	25.2 (6.1)*	74.1	38.1 (6.7)*	75.9	31.6 (5.1)*	82.4	71.6 (5.2)**
Chironomids	71.5	23.8 (6.7)*	54.6	8.0 (3.6)**	59.6	14.3 (3.5)*	15.8	8.3 (3.6)**
Gastropods	9.7	2.1 (1.3)*	7.8	0.1 (0.1)*	24.8	9.1 (2.9)**	35.1	6.0 (2.2)**
Cladophora glomerata	58.5	46.2 (7.8)*	62.4	50.1 (9.1)*	58.3	43.0 (5.6)*	12.3	7.1 (3.1)**
Relative gut volume		4.8 (1.0)*		11.8 (2.6)**		11.7 (1.4)**		3.9 (0.7)*
Percentage empty stomachs	16.7		16.7		9.0		22.9	

Notes: Numbers in parentheses in columns reporting percentage composition are standard errors. N = number of fish sampled, TL = total length.
* $P < 0.05$, ** $P < 0.01$.

Paria River. Possibly, these two fish were transported downstream by the flood, although Weiss (1993) documented movement of adult flannelmouth suckers between the two tributaries during operational flows in 1992. No sonic-tagged fish could be detected with a shore-based mobile receiver in the main stem in the vicinity of the Paria River confluence during the flood, despite the fact that this was an area of flannelmouth sucker congregation before and after the flood. Following the flood, a total of 576 YOY flannelmouth suckers were captured in the lower Paria River from mid-May to late September; the majority were in the warm mouth of this tributary.

Distribution, dispersal, and habitat of native and nonnative fishes

A total of four native and 16 nonnative fish species were captured during the test flood at the four sampling reaches between Glen Canyon Dam and upper Lake Mead (Table 1). Of 10 fish species caught in Reach 2, catch rates for backwater seining, minnow traps, electrofishing, and trammel nets between pre- and post-flood flows were significantly different for only three species, including plains killifish, rainbow trout, and speckled dace (Fig. 2, Appendix A). Mean catch rates for the three shoreline types were not significantly different within gear types (electrofishing or minnow traps) and data were pooled for these analyses. Mean CPUE in backwaters decreased significantly (P = 0.0352) for plains killifish from 0.12 to 0 fish/100 m seined, and increased significantly (P = 0.0371) for juvenile rainbow trout from 0.17 to 0.87 fish/100 m. Mean CPUE for speckled dace increased significantly (P = 0.0123) in minnow traps along shorelines from 1.39 to 2.71 fish/24 h, and mean CPUE for adult rainbow trout increased significantly (P = 0.0104) in trammel nets from 2.78 to 34.27 fish/100 h. Increased catch rates of speckled dace are attributed to local shifts in habitat use; mean CPUE for minnow traps in debris fans increased significantly ($P \leq 0.05$) from 0.52 fish/24 h (SD = 0.28) before the flood to 2.04 fish/24 h (SD = 1.43) 1 d after the flood, but returned to 0.54 fish/24 h (SD = 0.29) 2–3 d after the flood, indicating selection for debris fans during the flood. Though no significant changes in catch rates occurred for juvenile humpback chub, a similar shift in habitat use was seen from vegetation and debris fans to talus; significant increases occurred in catch rates ($P \leq 0.05$) in talus, from 0.08 fish/24 h (SD = 0.042) pre-flood to 0.37 fish/24 h (SD = 0.21) 1 d after and 0.37 fish/24 h (SD = 0.52) 2–3 d after the flood. Catch rates of fathead minnows were higher, but not significant, along vegetated shorelines 1 d after the flood at 0.28 fish/24 h (SD = 0.27), compared to 0.18 fish/24 h (SD = 0.23) before the flood and 0.15 fish/24 h (SD = 0.195) 2–3 d after the flood. These results suggest that fathead minnows also shifted habitat use to vegetated shorelines during the flood. However, concurrent significant increases in catch rates of fathead minnows at Reach 3 (190 km downstream) and Reach 4 (290 km downstream), also indicate downstream displacement of this species. Increased catch rates of juvenile and adult rainbow trout in Reach 2 (near the LCR) were concurrent with decreases in Reach 1 and also attributed to downstream displacement by the flood.

When compared over a longer period of time, from before the experiment (28 February through 14 March, 1996) to after the experiment (18 April through 3 May, 1996) (Fig. 3, Appendix B), significant decreases in shoreline catch rates near the LCR were indicated for bluehead suckers, fathead minnows, and plains killifish, with increases in juvenile rainbow trout. Catches of bluehead suckers decreased significantly (P = 0.0443) in backwaters from 0.46 fish/100 m (N = 22) to 0.05 fish/100 m (N = 4), and mean CPUE for plains killifish decreased significantly (P = 0.0065) from 0.86 to 0 fish/100 m. However, CPUE for juvenile rainbow trout in backwaters increased significantly (P = 0.0146) from 0.04 to 0.32 fish/100 m. The greatest change in CPUE was for fathead minnows, which decreased significantly (P = 0.0001) in minnow traps

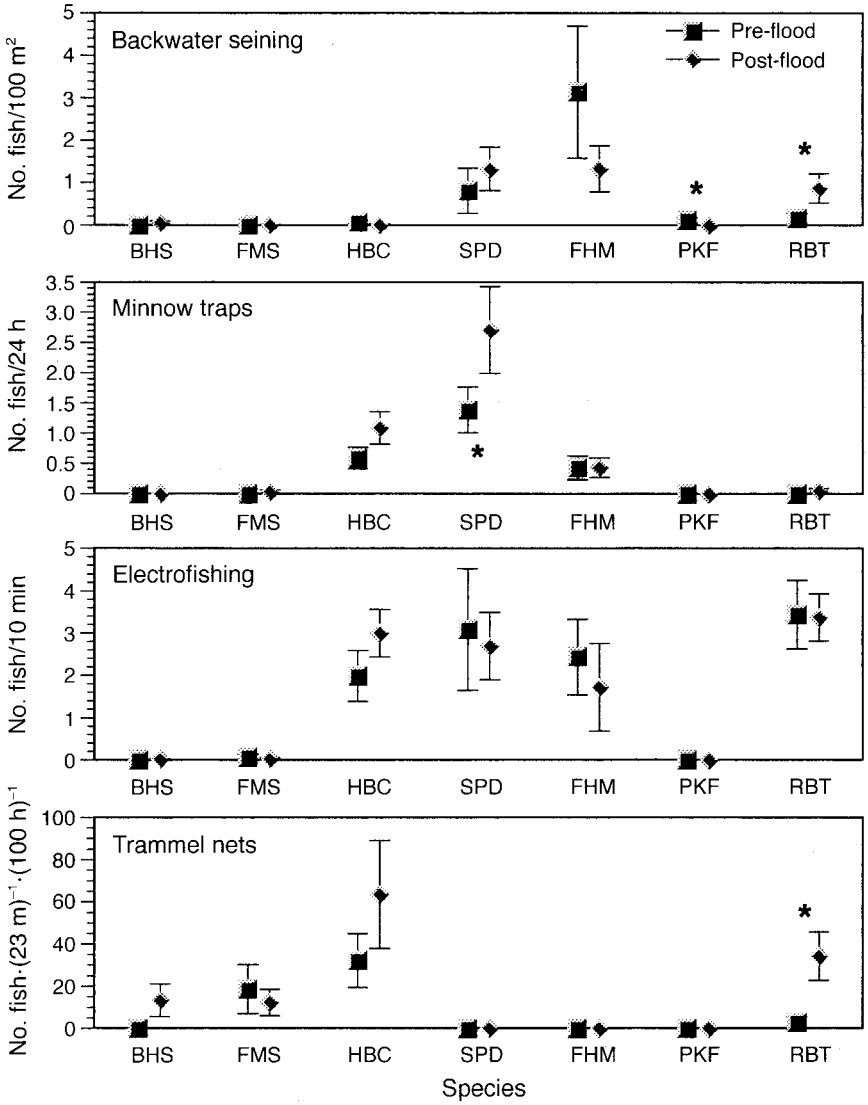

FIG. 2. Mean catch-per-unit-effort (CPUE) for fishes using various gear in the main stem Colorado River near the confluence of the Little Colorado River during steady pre-flood (22–26 March) and post-flood (3–7 April) flows. Error bars show ±1 SD. Species codes: BHS = bluehead sucker, FMS = flannelmouth sucker, HBC = humpback chub, SPD = speckled dace, FHM = fathead minnow, PKF = plains killifish, and RBT = rainbow trout. Asterisks indicate significant differences at $\alpha = 0.05$.

from 0.77 to 0.05 fish/24 h and in electrofishing (P = 0.0185) from 1.62 to 0.34 fish/10 min.

Movement and habitat use of adult humpback chub

Of 10 adult humpback chub surgically implanted with radio transmitters during 29 February through 2 March, 1996, nine were recontacted during the experiment of 22 March through 7 April, 1996; transmitter failure or extensive movement is suspected for the 10th fish. This recontact rate of 90% was similar to 91% reported by Valdez and Ryel (1995) for 76 radio-tagged humpback chub in the same area during 1990–1992. We believe few fish were contacted in the daytime during the pre- and post-flood low releases of 226 m/s because of reduced fish activity from high water clarity and lack of turbidity as cover (Valdez and Ryel 1995). Net movement (resultant distance from first to last contact) of the nine fish during the 16-d experiment (mean, 0.40 km; range, 0–1.24 km) did not differ significantly (t test, $P \leq 0.05$) from net movement of the same fish in the month preceding the experiment (mean, 1.26 km; range, 0.1–2.95 km; 26–39 d). No unusual movements or congregations of adult humpback chub were seen during the test flood. During descending flood flows, at ~989 m/s, one radio-tagged fish moved over a 2-h period upstream and into the lower channel of the LCR

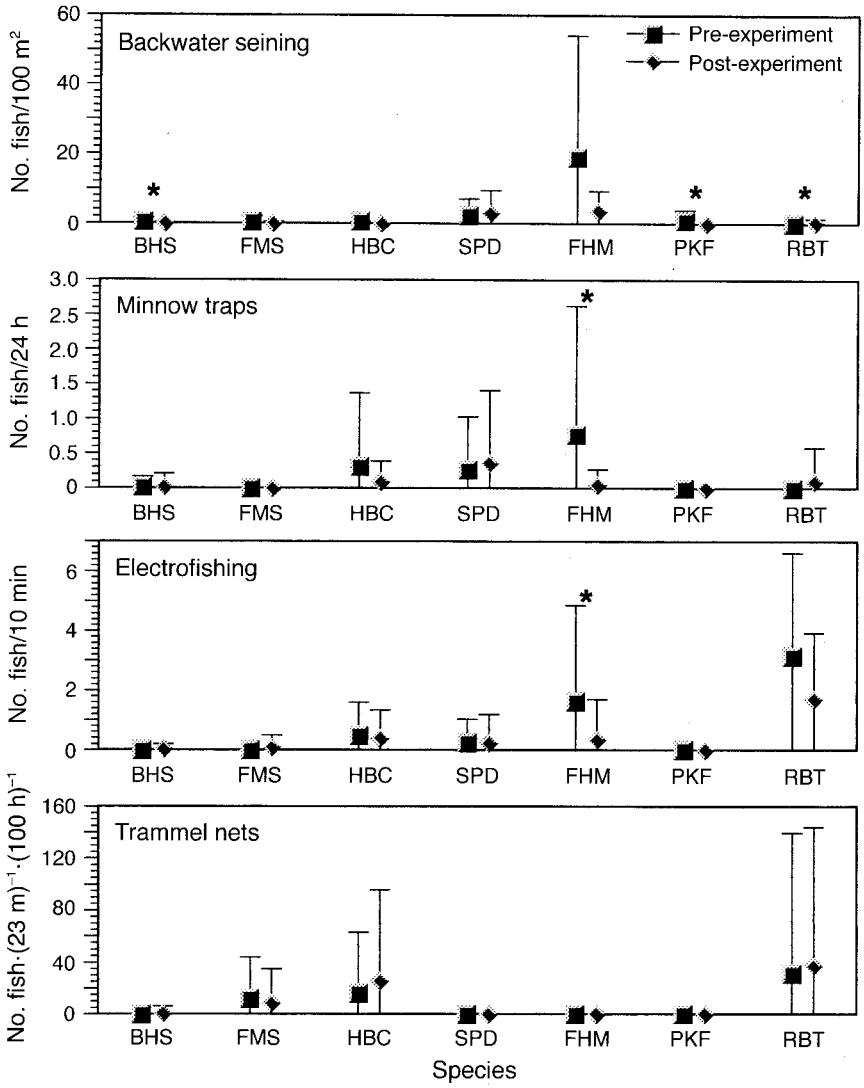

FIG. 3. Mean catch-per-unit-effort (CPUE) for fishes using various gear types in the main stem Colorado River near the confluence of the Little Colorado River during pre-experiment (28 February through 14 March) and post-experiment (18 April through 3 May) periods. Error bars are ±1 SD. Species codes: BHS = bluehead sucker, FMS = flannelmouth sucker, HBC = humpback chub, SPD = speckled dace, FHM = fathead minnow, PKF = plains killifish, and RBT = rainbow trout. Asterisks indicate significant difference at $\alpha = 0.05$.

for ~2.4 km in what appeared to be a normal spawning ascent. A second radio-tagged fish moved ~1.1 km between recirculating eddies during descending flows and returned 1.1 km to its original location. These observations constitute the greatest movements of radio-tagged adult humpback chub during the experiment.

Habitat used by the nine radio-tagged fish during the experiment was indicated by 73% of contacts from eddies and 27% from runs. Of total time observed during the experiment, the radio-tagged fish spent 97% of their time in eddies and only 3% of their time in runs. During the experiment, four fish were regularly contacted in the main stem, two were regularly contacted in the lower LCR, two were contacted irregularly in the main stem, and one was contacted only once in the lower LCR. Of the four fish contacted regularly in the main stem, all moved to the same type of habitat during the high release of 1274 m/s. The fish moved to the upstream end of large recirculating eddies to small triangular patches of quiet water formed near the separation point by the interface of the main stem downstream flow and the recirculating water reflecting off the shoreline. Representative movement and habitat use polygons during flood and post-flood releases are shown in Fig. 4 for a radio-tagged adult humpback chub ~126 km downstream of Glen Canyon Dam. The fish remained within these areas for the entire 4 d of observation each during and after the flood. These tri-

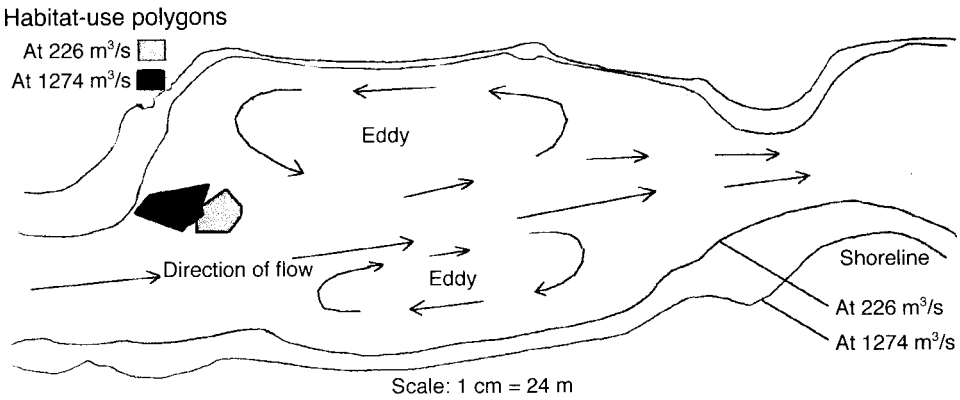

FIG. 4. Movement and habitat-use polygons for a radio-tagged adult humpback chub in the Colorado River, Grand Canyon, during the flood (1274 m^3/s) and post-flood (226 m^3/s) releases from Glen Canyon Dam, ~126 km downstream of the dam.

angular patches of water were usually 20 to 30 m along each side and were characterized by low velocity and low sediment deposition. In addition to adult humpback chub, flannelmouth suckers, bluehead suckers, rainbow trout, and carp were numerous-to-abundant in and near the low-velocity areas of these recirculating eddies.

Food habits of adult humpback chub

Gut contents of 45 adult humpback chub (250–450 mm TL, 143–815 g) captured during the experiment included 16 different types of food items, identified as five major food categories (Arizona Game and Fish Department 1996*b*). Simuliid larvae (blackflies), chironomid larvae, terrestrial insects (i.e., Coleoptera [beetles] and adult Diptera [true flies]), *G. lacustris*, and *C. glomerata* occurred in 98%, 93%, 91%, 81%, and 49%, respectively, of all fish examined. One side-blotched lizard (*Uta stansburiana*) was found in guts of each of two fish, and two of the 45 fish sampled had empty guts.

Gut contents were compared as mean AFDM for chubs sampled before (N = 9), during (N = 16), and after the flood (N = 18) (Fig. 5, Table 4). Ten food categories were consumed pre-flood, nine during the flood, and 14 post-flood. Simuliids dominated the diet with 68%, 25%, and 61% AFDW before, during, and after the flood, respectively. *Gammarus lacustris* comprised the greatest percentage of stomach contents during the flood (31%), but only 5% and 17% during pre- and post-flood sampling periods, respectively. Chironomids decreased from 14% before the flood to 2% and 6% during and after the flood, respectively. Terrestrial insects (i.e., Coleoptera and Diptera) increased from 1% pre-flood to 19% during the flood, but were only 6% of the diet post-flood. *Cladophora glomerata* composed 9% of the diet pre-flood and only 2% post-flood, but was not found in the diet during the flood. The only food items that changed significantly in mean AFDM were simuliids and *G. lacustris*, which decreased significantly from pre-flood to flood periods. Mean AFDM

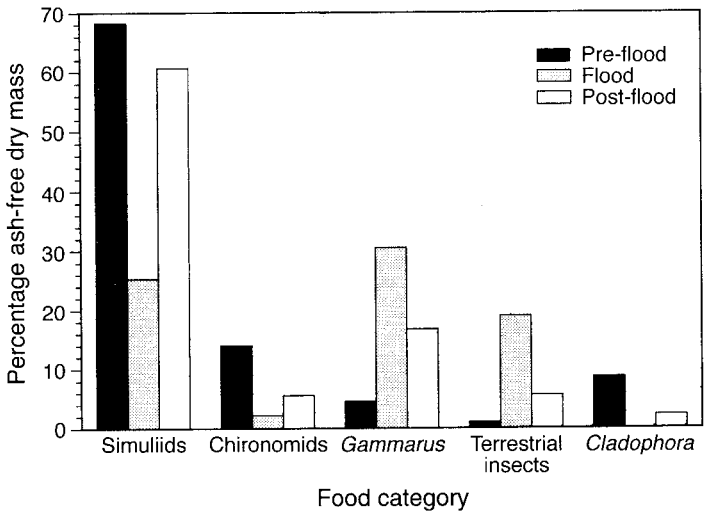

FIG. 5. Percentage ash-free dry mass of principal food categories from guts of 43 adult (>250 mm total length) humpback chub during pre-flood (n = 9), flood (n = 16), and post-flood (n = 18) sampling.

TABLE 4. Mean and one standard error (SE) for ash-free dry mass (mg) of food categories in gut contents of adult humpback chub during three phases of the 1996 test flood on the Colorado River through the Grand Canyon.

Category	Pre-flood (N = 9)		Flood (N = 16)		Post-flood (N = 18)		ANOVA (df = 2, 40)
	Mean	SE	Mean	SE	Mean	SE	
Simuliids	12[a]	10	3[b]	3	7[ab]	7	P = 0.0120
Chironomids	1	1	4	1	1	1	P = 0.3837
Gammarus lacustris	0.9[a]	1	5[b]	7	2[ab]	2	P = 0.0424
Terrestrial invertebrates	0.2	0.2	2	3	1	1	P = 0.0956
Other aquatic invertebrates	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	P = 0.5056
Total invertebrates	27	20	24	20	21	13	P = 0.6139
Cladophora glomerata	5	16	0	0	1	3	P = 0.2174

Notes: Superscripts indicate significant differences among flood phases for each taxon with a significant ANOVA. Identical letters indicate nonsignificance between means (Ryan-Einot-Gabriel-Welsch multiple F test; $P < 0.05$). The terrestrial category consisted of Coleoptera, Diptera (adults), Formicidae, Acarina, Orthoptera, and Lepidoptera. The other aquatic category consisted of Hydracarina, Culicidae, and Diptera larvae. Abbreviations are: N = number of fish sampled, df = degrees of freedom.

of both items was similar between pre-flood and post-flood periods.

DISCUSSION

The test flood had little effect on native fishes of the Colorado River in Grand Canyon and only short-term effects on some nonnative species (Valdez et al. 1999). The most dramatic effects were an approximate 8% reduction in electrofishing catch of juvenile rainbow trout (<152 mm TL) in the Glen Canyon Dam tailwaters, and a reduction in shoreline densities of fathead minnows and backwater densities of plains killifish near the LCR, 121–130 km downstream from the dam (Hoffnagle et al. 1999, McKinney et al. 1999). Concurrent downstream increases in numbers and densities of juvenile rainbow trout in sample reaches 100 and 290 km downstream from the dam tailwaters suggest that these fish were displaced downstream by the flood. These young trout may not have all originated from the dam tailwaters since reproducing trout populations occur in intervening tributaries. Other studies show that small size classes of fish can be more adversely impacted by flooding, primarily as a result of displacement by high water velocities and turbulence (Seegrist and Gard 1972, Harvey 1987, Lamberti et al. 1991). Samples eight months following the test flood showed a 20% increase in juvenile rainbow trout in the tailwaters, indicating survival and recruitment by recently emerged trout fry. These fry were hatched from eggs that were likely in river gravels during the flood. Flood impacts are usually greatest when eggs are in the gravel and when fry are emerging (Seegrist and Gard 1972, Hanson and Waters 1974, Pearsons et al. 1992). The flood also had little detrimental effect on the diet of adult rainbow trout. Increased food intake in the dam tailwaters immediately following the flood indicated opportunistic feeding associated with increased drift of macroinvertebrates (e.g., Elliott 1973, Scullion and Sinton 1983, Bres 1986, Brittain and Eikeland 1988, Filbert and Hawkins 1995). Nevertheless, composition of stomach contents was similar to that previously described for fish in the tailwaters (Angradi et al. 1992). We conclude that the flood did not significantly affect the rainbow trout population in the dam tailwaters.

The flood also did not appear to impede pre-spawning aggregations and spawning runs of flannelmouth suckers into the Paria River, ~26 km downstream from the dam (McIvor and Thieme 1999). Sonic-tagged adults sought refuge from high main stem velocities in the much-expanded Paria River mouth during the flood, returned to the main stem after the flood, and proceeded with a spawning migration up the Paria River, as in previous years (Weiss 1993). Ripe individuals of both sexes were found at known spawning locations 2–10 km upstream in the Paria River prior to and during the flood. We infer successful spawning from the capture of 576 young-of-year (YOY) flannelmouth suckers in a small slack water pool in the lower Paria River from mid-May to late September. This is the largest number of YOY captured in the lower Paria River for 1991–1996, and ranks second in annual CPUE for YOY in this tributary (Weiss 1993, McIvor and Thieme, *in press*; Arizona Game and Fish Department, *unpublished data*). We believe the success of the 1996 year class is due, in part, to the presence of the slack water pool during and after the flood and a lack of flooding in the Paria River during the rearing season.

Although shoreline catch rates of fathead minnows near the LCR decreased in backwaters, densities recovered eight months after the flood as a result of immigration from tributaries and reproduction in backwaters. Fathead minnows use a variety of habitats in Grand Canyon, including backwaters, vegetated and rocky shorelines, and seasonally warmed tributary inflows (Valdez and Ryel 1995, Arizona Game and Fish Department 1996*a*, Hoffnagle et al. 1999), and they are known to spawn in backwaters (Hoffnagle 1995). Although a warmwater species, fathead minnows are tolerant to cold temperatures and are found as far north as tributaries to Great Slave Lake, Canada (Scott and

Crossman 1973). The test flood inundated the primary backwater habitats (Brouder et al. 1999) and the high turbulent flows probably made main channel conditions unsuitable for the species. These fish were displaced downstream as indicated by increased abundance of fathead minnows near Hells Hollow (~315 km downstream of the dam) and near Spencer Creek (~415 km downstream of the dam) immediately after the flood. However, the flood was of insufficient magnitude to scour the entire width of the channel and there remained shelter along rocky shorelines and inundated vegetation. Incomplete displacement of fathead minnows and enclave populations in tributaries enabled the species to recover in eight months.

Similar effects were seen for plains killifish, which have become increasingly common in backwaters and tributaries of Grand Canyon in recent years (Arizona Game and Fish Department 1996*a*, *b*). Plains killifish are found primarily in shallow, quiet waters (Cross 1967 as cited in Minckley and Klassen 1969). Although plains killifish were common in backwaters prior to the flood, none were found following the flood at any sample locations, indicating substantial reduction in the main stem. It appears that this species was unable to find alternative habitats as the flood inundated backwaters, and individuals were either displaced entirely from the main stem or killed by the flood. Nevertheless, the species is common in tributaries of Grand Canyon and reinvasion and recovery began five months after the flood, via immigration and natural reproduction, and densities equaled or exceeded pre-experiment levels eight months after the flood.

Of the four native species exposed to the flood (i.e., humpback chub, flannelmouth sucker, bluehead sucker, and speckled dace), significant changes in catch rates occurred only for speckled dace along shorelines and juvenile bluehead suckers in backwaters (Hoffnagle et al. 1999). Unlike decreased densities of nonnative fathead minnows and plains killifish, changes in catch rates of speckled dace are attributed to local shifts in habitat use. Higher catches of speckled dace in debris fans during and 1 d after the flood suggest a switch from inundated mid-channel islands and riffles to shoreline debris fans, and a subsequent return to mid-channel habitats during lower flows. Speckled dace commonly inhabit swift water in streams and rivers (John 1963, Minckley 1973), including the Paria River where the species survives floods of high discharge and turbidity (Rinne and Minckley 1991). However, the species often prefers shallow habitats with moderate velocity (Rinne 1992). Apparently these conditions were reduced in mid-channel habitats during the Grand Canyon flood and individuals found alternative suitable habitats in debris fans, which are usually in close proximity to mid-channel riffles occupied by speckled dace at lower flows (Valdez and Ryel 1995).

Catch rates of juvenile bluehead suckers also decreased in backwaters during the flood, but this decrease is also attributed to habitat shift as an artifact of ontogenetic changes in the fish. Bluehead suckers are well adapted to swift water (Minckley 1991) and we find it unlikely that age-1 fish would have been displaced by the flood. Individuals exposed to the flood were ~50 mm TL, or the size at which individuals usually develop a cartilaginous ridge (radula) on the lower jaw for scraping algae and diatoms from rocks in swift water (Minckley 1973) and they move from quiet shorelines and backwaters to main channel riffles and runs (Arizona Game and Fish Department 1996*a*). Post-experiment sampling with electrofishing yielded juvenile bluehead suckers along deep shorelines indicating that the fish had moved from backwaters to deep shorelines.

Juvenile humpback chub remained nearshore, primarily along talus shorelines and debris fans during the flood. These rocky shorelines provide continuous interstitial habitat in which the young fish can find shelter from high velocities at various flow levels (Converse et al. 1998). These findings suggest great resilience by juvenile humpback chub for high velocities and turbulence associated with high river flows, and confirm that the species selects habitat with structure to provide low-velocity microhabitats (Valdez et al. 1990).

Mean net movement of 0.40 km (range, 0–1.24 km; 16 d) by nine radio-tagged adult humpback chub during the experiment did not differ significantly (t test, $P \leq 0.05$) from movement of 1.26 km (range, 0.1–2.95 km; 26–39 d) by the same fish in the month preceding the experiment. This movement was comparable to that of 69 radio-tagged adults tracked in Grand Canyon during 1990–1992 (mean, 1.49 km; range, 0–6.11 km; 30–170 d; Valdez and Ryel 1997), and similar to movements reported for the species from Black Rocks, Colorado by Valdez and Clemmer (1982) (mean, 0.8 km; $n = 8$) and Kaeding et al. (1990) (mean, 1.4 km; $n = 10$). We conclude that the flood had no effect on movement of adult humpback chub.

Habitat used by the nine fish during the experiment (i.e., 73% of contacts from eddies, 27% from runs) was also similar to previous studies (74% of contacts from eddies, 16% from runs, 7% from eddy return channels, 3% from pools, <1% from riffles [Valdez and Ryel 1997]). Fish in eddy habitats selected a small triangular patch of calm water bounded by swift downstream currents, moderate recirculating currents, and a point of land termed the "separation point" (Rubin et al. 1990). Observations during the flood indicated little movement from these habitats and characteristic positions in mornings and evenings, suggesting feeding on material entrained in the eddy. Despite substantial entrainment of material in this part of the eddy, bathymetry during the flood (M. Gonzales, *personal communication*) showed little sediment deposition, suggesting

that the fish were occupying areas of low velocity, low sediment deposition, abundant drifting and entrained food supplies, and suitable depth.

Humpback chub have been reported to be opportunistic in their feeding habits, consuming a variety of invertebrates of aquatic and terrestrial origin (Kaeding and Zimmerman 1983, Valdez and Ryel 1997), and are reported to engorge on terrestrial sources of insects, such as grasshoppers and locusts (Tyus and Minckley 1988). Diet of adult humpback chub during the flood indicates that the fish fed opportunistically on the large variety of foods dislodged during the high flows, including insects, crustaceans, algae, plant debris, and reptiles (two side-blotched lizards were found in guts of two fish). Simuliids, chironomids, *G. lacustris,* terrestrial invertebrates, and *C. glomerata* continued to be the principal food items, but with greater utilization of terrestrial insects and *G. lacustris* during and after the flood. The flood dislodged large numbers of *G. lacustris,* as reported by Leibfried and Blinn (1987) for smaller increases in flow, and Blinn et al. (1999) in 1996, making them available as drift, as evidenced by windrows of dead and dying amphipods with the descending flows of the flood.

Adult humpback chub, flannelmouth suckers, bluehead suckers, rainbow trout, and carp were also found in large numbers at the mouth of the LCR. It is not clear if these fish were attracted to the large pool formed by the flood or if these fish were aggregating for spawning ascents, which coincided with the time of the test flood. Regardless, the flood did not appear to impede staging and spawning ascents by adult humpback chub or flannelmouth suckers at the mouth of the LCR (Brouder and Hoffnagle 1997). Impounding tributary mouths by main stem floods may be beneficial to staging and ascending fish by creating a large pooled area with a moderate thermal gradient in which adults can rest and acclimate to warmer tributaries. This ponding effect may also be beneficial for thermal acclimation by recently hatched larvae and juveniles descending into the colder main stem. The flood stage at which this ponding effect is most suitable for habitat area and thermal gradient varies with tributary geomorphology and inflow. For the Paria River, the post-flood pool that functioned as a rearing area was formed by high (424–509 m/s) relatively steady flows in the Colorado River (Thieme 1997).

The collection of one juvenile redside shiner (*Richardsonius balteatus*), 53 mm TL, immediately following the flood is noteworthy because of its cold tolerance and predatory nature. The fish was caught in a minnow trap 128 km downstream from the dam during the post-flood release, and is the first record of this species from Glen and Grand canyons since 10 specimens were reported in 1981 by Kaeding and Zimmerman (1983). The species is present in Lake Powell and small numbers of individuals may have survived passing through the dam bypass tubes, although it is more likely that small numbers of redside shiners exist in springs or tributaries in Grand Canyon and were dispersed by the flood from areas not normally sampled. Also, one apparent *C. latipinnis* × *X. texanus* hybrid was caught in the lower LCR during synoptic sampling; numerous hybrid specimens have been caught in recent sampling (Douglas and Marsh 1998), but it appears that the razorback sucker is extirpated from Grand Canyon.

The effect of the 1996 test flood on fish assemblages was difficult to evaluate because of the lack of adequate baseline data and uncertainty related to natural seasonal and interannual variation. This lack of understanding of population demographics confined the evaluation to the data collected immediately before and after the experiment and precluded comparing population levels over a period of years. Such fish population data are needed for the main stem Colorado River in Grand Canyon to establish a baseline of information on species composition, abundance, age structure, mortality, and movements, as well as an understanding of interspecific competition and predation. This information is vital for evaluation of future test floods. We also believe that managed floods should be implemented without pre- and post-flood low steady releases, which tend to confound experimental results. For the 1996 flood, decreased densities of fish in backwaters could be attributed to desiccation of these habitats during low flows as well as to downstream transport during flood flows. Possibly the low flows provided a temporary reprieve for some nonnative fishes from the rigorous flood conditions. Elimination of these low flows will maintain relatively high main channel velocities that may inhibit displaced nonnatives from finding suitable habitats.

The test flood did not appear to affect native fish populations in the Colorado River in Grand Canyon, and caused only short-term reductions in some nonnative species. Meffe and Minckley (1987) and Minckley and Meffe (1987) showed that native fishes in small-to-midsize southwestern streams were largely unaffected by floods, but that numbers of nonnative fishes were reduced substantially when flows approached or exceeded two orders of magnitude greater than mean discharge. Whereas floods in small streams may be desirable and effective at controlling nonnative fishes, managed floods in the Colorado River through Grand Canyon are not likely to reach sufficient magnitude to significantly and permanently reduce numbers of nonnative fishes. At present, maximum releases through the power plant (940 m/s) and the bypass tubes (i.e., jet tubes, 425 m/s) will yield ~1365 m/s, or slightly higher flow than the test flood of 1274 m/s. The level required to inundate sheltered shorelines and provide sufficient velocities in the main channel to displace nonnative fishes remains unknown. It seems unlikely, with present dam management operations to minimize

the risk of uncontrolled releases, that a release of sufficient magnitude is possible from Glen Canyon Dam. Nevertheless, the results of the 1996 test flood suggest that properly designed and timed floods can be used to temporarily reduce numbers of predaceous and competing nonnative fishes to the benefit of native species.

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APPENDIX A

A table of mean catch-per-unit-effort and total catch of fishes during pre-flood (22–26 March) and post-flood (3–7 April) phases of the test flood in Reach 2 of the Colorado River is available in ESA's Electronic Data Archive: *Ecological Archives* A011-012-A1.

APPENDIX B

A table of mean catch-per-unit-effort and total catch of fishes during pre-experiment (28 February through 14 March) and post-experiment (18 April through 3 May) phases of the test flood in Reach 2 of the Colorado River is available in ESA's Electronic Data Archive: *Ecological Archives* A011-012-A2.

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

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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,

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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 to −
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 seepwillow (*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 m^3/s in 1983 and flows >1274 m^3/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 m^3/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 m^3/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 m^3/s stage (KAIMG 1997). A total of 1275 KAS were marked and moved above the 1274(+0.5) m^3/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.

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