Management of Discharge, Temperature, and Sediment in Grand Canyon for Native Fishes

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Abstract--The 1963 closure and subsequent operation of Glen Canyon Dam on the Colorado River altered downstream flow regimes, thermal characteristics, and sediment transport dynamics. These changes resulted in severe negative impacts to the native fish fauna in Grand Canyon. We contend that preservation of remnant native species and the success of any attempts to restore the predam fauna are predicated upon a return to environmental conditions approximating those present in the evolutionary history of this community. A protracted period, measured in generations of these long-lived fishes, will be necessary for restoration of the native species. Under existing water temperature and sediment regimes, we recommend flow modifications that (1) minimize daily fluctuations, (2) adjust seasonal hydrology to parallel natural discharge patterns, and (3) deliver controlled floods to maintain a favorable balance between native fishes and potentially detrimental introduced species. Water temperature modification and sediment augmentation are additional elements likely required to complete the restoration process. Incorporation of these elements into dam operations would provide greater flexibility and offer more opportunities to use the dam as an effective tool to foster the multiple uses for which it was constructed.

Introduction--We have prepared this document to present recommendations for operation of Glen Canyon Dam to optimize the long-term management, enhancement, and reestablishment of native fish populations in the Colorado River and its tributaries in the Grand Canyon region. As researchers and managers of native fishes in Grand Canyon, we believe that management goals for these populations are best achieved through maintenance and enhancement of their habitats by managing the dynamic processes that create and sustain those habitats. We contend that the only sensible basis for management of the native fishes is a clear understanding and acceptance of their evolutionary history, and adoption of an operational scheme that will function within the constraints of that history (see Meffe 1992). We argue that the present condition of the existing native fish fauna is primarily a result of degradation of historic habitats and disruption of processes that created and maintained these

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habitats during the course of the fishes' evolutionary history. We emphasize that the presence of predatory and competitory non-native fishes has contributed to, and indeed is a descriptor of, this habitat degradation.

Our objectives for enhancement of native fish populations in Grand Canyon include: (1) promote successful reproduction in the Colorado River and its tributaries; (2) increase survival of early life stages; (3) increase recruitment to adult, reproducing segments of populations, and; (4) minimize detrimental effects (competition, predation) of non-native fishes. Complete restoration of the native fauna must include reintroduction of those species eliminated from the system following closure of Glen Canyon Dam.

Structure of the Document--To allow managers and administrators with limited time and training in fisheries science the opportunity to consider our arguments, we begin this document with a relatively brief section that makes recommendations for the operational elements of hydrology, water temperature, and sediment. Hydrology initially is considered independently, because there are restrictions to any near term modification of the other elements that necessarily are imposed by the need for environmental compliance, further studies, planning, engineering, and construction of a multi-level intake structure or means of sediment augmentation. We assume that future annual water delivery will continue to conform to Colorado River Compact allocation of at least 8.23 million acre-feet. We stress that hydrology, water temperature, and sediment were inextricably related environmental variables in the evolutionary history of the native fishes. Failure to adequately recognize these interrelationships and integrate them into future operations of Glen Canyon Dam has been a major contributor to the recent impasse in selection of a preferred alternative.

For those readers with the time and training to critically evaluate our reasoning and judgment, we provide a subsequent, more lengthy background section. This section provides the basis for our position, which is rooted in scientific literature, unpublished results of ongoing studies, and our combined experiences with fishes and aquatic ecosystems in the Grand Canyon and elsewhere.

Statement of the Problem--The closure in 1963 of Glen Canyon Dam on the Colorado River above Grand Canyon drastically altered hydrological, physical, and biological functions and characteristics of the downstream riverine ecosystem (Carothers et al. 1981, Maddux et al. 1987, Andrews 1991, Blinn and Cole 1991, Carothers and Brown 1991, Minckley 1991, Stanford and Ward 1991). Flow patterns were modified dramatically from pre-dam conditions; a predictable pattern of seasonal flow variation was replaced by one of daily discharge fluctuations. Large reductions in the amount of sediment transported through Glen and Grand canyons occurred with entrapment of tens of millions of tons annually in upper reaches of Lake Powell. Cold water released from the depths of Lake Powell altered physical characteristics in the downstream river, further disrupting the seasonality of environmental conditions by reducing the annual range and mean of water temperatures.

These changes modified the temporal pattern of environmental conditions in the post-dam river, altering linkages between the native fishes and their habitats. Perennial low water temperatures from deep reservoir releases limited or eliminated successful reproduction and decreased growth rates of native fishes in the Colorado River. The physical barrier presented by Glen Canyon Dam restricted their seasonal movements and migrations. Food sources and feeding relationships in the mainstem were altered following near cessation of particulate organic matter transported from the Upper Colorado River Basin. In combination, these changes altered relationships between the mainstem and its tributaries, both of which are important in the life histories of the native fishes.

Populations of most non-native fishes present in the mainstem prior to 1963 persisted following closure of the dam, although distributions and abundances of some species were altered. The non-native assemblage was increased by massive new sportfish stocking programs initiated in Lake Powell and in the tailwater below the dam to exploit the recreational opportunities in newly created systems both upstream and downstream. These actions were taken with little regard for their impacts on native fishes.

The endangered Colorado squawfish (*Ptychocheilus lucius*) and bonytail chub (*Gila elegans*), and the roundtail chub (*G. robusta*) were eliminated from Grand Canyon within a decade of the closure of Glen Canyon Dam. The endangered humpback chub (*G. cypha*) reproduces only in a single tributary, and its mainstem distribution has contracted. Another endangered species, razorback sucker (*Xyrauchen texanus*), is extremely rare in Grand Canyon (although possibly never abundant), with no current evidence of reproduction. Successful mainstem reproduction by the remaining, more common native fishes, also was reduced or eliminated.

RECOMMENDATIONS

Recommended Hydrology in the Absence of Temperature Modification--We contend that an approximation of the hydrological pattern under which the native Colorado River fishes evolved (Figure 1) is one of the major prerequisites for successful maintenance and enhancement of these populations in Grand Canyon. This contention is a tenet of the flood pulse concept (Junk et al. 1989), which was developed to explain adaptations of aquatic and terrestrial faunas in large floodplain rivers. We argue that these adaptations transcend the geomorphic differences between classical floodplain rivers and the canyon-bound Colorado River. In the U.S., reestablishment of natural hydrological patterns has been advocated for restoration of the Missouri River (Hesse and Mestl 1993) and Green River fish communities (Lindell 1992).

Benefits to native fishes from such a discharge pattern include the recreation of historic interactions among hydrology, aquatic habitat and native fish life histories, and suppression of non-native fish populations. Continued release of perennially cold waters will largely preclude successful mainstem reproduction by native fishes, and may restrict the potential of recommended flows to improve conditions for increased growth and survival of progeny. With this precaution, we offer the following recommendations for hydrology in the absence of water temperature modification.

We recommend replacing daily fluctuations with seasonal adjustments in discharge to produce a single peak hydrograph. Beginning in March, discharge levels should be raised above autumn-winter low flows. These base flows preferably should be held at a minimum of 5,000 cfs. The ascension of spring flows should be scheduled to arrive at a peak as high as practically possible (near 30,000 cfs) in May or June, so that high, but not necessarily maximum, flows are present through the period of major reproduction by native fishes in tributaries. Even higher flows might be desirable, but we recognize there are legal constraints on annual releases and that a sediment balance must be maintained.

We believe that increasing spring flows to a sustained maximum will serve four purposes: (1) provide an environmental cue for gonadal maturation and aggregation of mainstem fishes prior to their ascension into tributaries for reproduction; (2) back up the waters of canyon-bound tributaries forming ponded rearing habitats in their mouths and reduce the transport of early life stages from tributaries into the mainstream; (3) create and maintain nearshore rearing habitats for early life stages entering the mainstem, and; (4) reduce the populations of mainstem non-native fishes through downstream displacement, disruption of reproduction, and lowering survivorship of early life stages.

Minckley (1991) suggested that the key to reestablishment of the native fish fauna of Grand Canyon lies with the suppression of non-native fishes. This objective can be accomplished in part by exploiting the inability of non-native fishes to cope with large floods carrying heavy sediment loads (Minckley and Meffe 1987). We anticipate that the effectiveness of controlled floods to displace non-native fishes will be a function of both magnitude and duration. Thus, in years when water releases in excess of 8.23 MAF are scheduled and sufficient sediment is available, we advocate that additional supplies be programmed into spring releases to further exploit the negative effects of floods on non-native fishes. We recognize that this effect is temporary, but the limitation can be offset by periodic repetition of the treatment.

The descending limb of spring peak flow discharges should progress in monthly steps, but be concentrated in several successive days of each month to allow relatively long periods of stable flows in interim periods. Return to base flows should be accomplished by September, and these flows optimally should be maintained through February. The level of base flows should be between 5,000 cfs and 10,000 cfs to provide large numbers of mainstem rearing habitats and to allow sufficient water to meet spring-summer needs.

The proposed scenario for declining flows will afford young native fishes in lower tributary reaches the greatest possible opportunity to remain in these areas, yet retain relatively extended periods of stability in nearshore mainstem rearing habitats for individuals that enter this more hostile environment. The major advantages accrued by young native fishes from their persistence in these relatively stable habitats are increased growth and survivorship due to warmer water temperatures, lower current velocities, and increased availability of food resources. These advantages will be multiplied to the extent that competitory and predatory non-native fishes have been successfully displaced.

Recommended Hydrology in the Presence of Temperature Modification--Further optimization of Glen Canyon Dam operations to benefit native fishes should include serious consideration of a multi-level intake structure (MLIS) to control water temperature. At a minimum, temperature modification is the only way to alleviate the known restriction by cold water temperatures to successful mainstem reproduction by native species. We propose a gradual increase from hypolimnetic (deep water) release temperatures beginning in spring when epilimnial (near surface water) temperatures exceed those of the hypolimnion in Lake Powell. Epilimnial releases should be scheduled to achieve a high of approximately 15°C from June through September or October, followed by a rapid return to hypolimnetic release temperatures in November through February. This pattern would provide sufficient temperature elevation to allow for mainstem reproduction, and survival and accelerated growth of young. We suggest altering the specific pattern of temperature modification among years to mimic the variability inherent in the pre-dam ecosystem.

Based on best available information, these actions would elevate downstream summer temperatures an additional 2°C at the Little Colorado River (LCR) (122 km downstream) and by nearly 7°C at Diamond Creek (386 km downstream) above release temperatures due to downstream warming (Ferrari 1988). Thus, releases of 15°C in June and July should warm to 19-20°C--optimum for spawning, incubation, and rearing--in the mainstem reach beginning some 200 km below the dam. Attainment of these temperatures would provide an opportunity for successful reproduction by aggregations of humpback chub collected in that reach in recent years, while minimizing disruption of reproduction by individuals that presently reproduce in the LCR. Since the minimum temperature of successful incubation and hatching is near 15°C, conditions that would allow some successful reproduction would also occur in upper reaches during this period. Both tributary-spawned fish entering the mainstem and mainstem-spawned fish would experience temperature conditions better suited to faster growth. Such a temperature regime likely would also benefit the Lee's Ferry tailwater fishery by providing more optimal temperatures for trout growth (Lechleitner 1992).

Installation and operation of a MLIS to warm the Colorado River in Grand Canyon and introduce seasonality of water temperatures may affect several aquatic and riparian ecosystem components. Potential effects include: (1) alteration of algal species composition and productivity; (2) alteration of invertebrate species composition and productivity; (3) invasion and enhancement of additional non-native fishes from Lake Mead, Lake Powell, or internal tributaries, and; (4) increases in the incidence of fish diseases and parasites. We emphasize, however, that proposed maximum release temperatures are only 5-6°C higher than present, and that hypolimnial releases will continue to be delivered during autumn and winter months.

Greatest concern expressed to date for unintended effects of increasing water temperatures is for the possible invasion and establishment of additional non-native fishes or entrenchment of existing species, which could potentially offset the benefits of a MLIS. We believe that a lack of important environmental requirements, other than water temperatures, serves to restrict the distribution and abundance of non-native fishes in Grand Canyon (Valdez 1992). These conditions should continue to exert negative effects on invasion and expansion of the non-natives. Furthermore, as discussed above, the recurring impacts of periodic flood events should serve as a major control agent in the system.

Increasing and seasonally adjusting water temperatures in Grand Canyon would remove a known impediment to successful reproduction by native fishes in the mainstream and improve survival and the potential for rapid growth by young fishes. If these impediments from cold water temperature are relieved, we believe the optimal scenario for mainstem hydrology will be altered, and there can be more flexibility in the delivery of water. For example, a major reason for maintaining high flows during reproductive and early growth periods under existing conditions is to retain most young fishes in tributaries. If mainstem reproduction is successful and young-of-the-year fishes experience faster growth and greater survivorship in warmer Colorado River waters, the importance of mainstem habitats, both reproductive and rearing, will increase relative to tributary habitats. Thus, mainstem hydrology should be modified accordingly to increase the advantage to young fishes occupying these habitats.

Based on the timing of native fish reproduction in the Upper Colorado and Green rivers relative to hydrology and water temperature, we believe that mainstem reproduction in Grand Canyon (excepting razorback sucker) will begin on the descending limb of the hydrograph once water temperatures exceed 15 C. Given the suspected limits to warming with a MLIS, requisite mainstem temperatures could be reached in early June, a time when tributary reproduction by native fishes typically is waning. Therefore, provision of a potentially important environmental cue for reproduction could be facilitated by flows that are descending at a rate approximating the pre-dam pattern during June and July. High flows could be maintained for a shorter period, because of the decreased emphasis on retaining young fishes in tributaries, and flow reductions could occur more rapidly to open rearing habitats following the reproductive period.

Existing knowledge of nearshore mainstem rearing habitats, particularly backwaters, relative to river stage in Grand Canyon suggests that the number of these habitats presently is maximized in the range of 5,000-10,000 cfs. Thus, we recommend that dam discharges be lowered at a more rapid rate beginning in early July to reach this range. Decreasing mainstem flows admittedly will dewater rearing habitats at higher stages and form those at lower stages, resulting in some displacement of young fishes. In reality, there will be variation in the pattern of summer flows brought about by unpredictable tributary floods from monsoonal storms. This condition was common in the evolutionary history of these fishes, however, and we believe the negative effects of such displacements will be diminished considerably in warmer mainchannel waters. In addition, a relatively steep descent to base flows following the peak hydrograph may serve as an important spawning cue.

Increased growth rates of young native fishes during the extended period of warm water from June-October will place these individuals at a larger size more able to cope with the return of cold waters in November. As juvenile big-river fishes reach total lengths 100-150 mm, they begin to occupy deeper waters in eddies less affected by diel flow fluctuations. This change in habitat use provides an opportunity to use hydrology during winter months to further disadvantage non-native fishes, should this action be necessary. We believe that diel winter flow fluctuations, of an order similar to those presently in place, could be used to destabilize nearshore habitats used by some non-native fishes during this period. Such fluctuations could be used to particular advantage as a tool against small-bodied non-natives, such as fathead minnow and red shiner, that largely depend upon nearshore habitats during their entire life cycle. We understand that these fluctuations would also be an advantage to hydroelectric production.

Sediment Augmentation Element--The final ingredient to best simulate historic environmental patterns for the betterment of native fish populations would be to implement sediment augmentation. The best time for this application would be during the highest flows in spring when sediment would be most easily mobilized and distributed to the higher levels of nearshore habitats within the system. Augmentation would restore the functional role that sediment historically fulfilled in the temporal and structural formation of instream habitats, and would help assure that a sediment balance would be maintained in Grand Canyon. The latter factor is particularly important, because our ability to use controlled floods as an element in the control of non-native fishes and the creation and maintenance of nearshore rearing habitats is predicated on the availability of sufficient sediment in the system.

At this time the precise quantity and best method of delivery of augmented sediment is unknown, but we believe the elaborate, costly, and environmentally questionable pipeline proposed previously would not be necessary. Hydrological and sediment transport models presently under development by physical scientists, in conjunction with the improving knowledge of sediment storage, should be applied to resolve these issues. One important characteristic of sediment introduced to the system is that it include silts and clays, as well as sand. Approximately 70% of the pre-dam suspended load in spring floods was in the sand-size range, and the remainder was silt-clay (Howard and Dolan 1981). Grain sizes transported during tributary floods are dominated by fine-grained clays and silts.

Turbidity produced by fine-grained sediments in transport has been indicated as an important cover element for native fishes (Kaeding and Zimmerman 1983, Valdez et al. 1992), and diminished water transparency can limit the effectiveness of sight feeding non-native predators. Silts and clays also are the primary sources of the important plant nutrient phosphorus, which appears to be limiting to primary productivity in the Colorado River in Grand Canyon (Evans and Paulson 1983).

Augmentation of sediment supplies to Grand Canyon, with the attendant advantages to native fishes, should allow even further flexibility in the use of hydrology to maintain the important balance between native and non-native fishes. We advance the working hypothesis--and advocate its testing--that sediment augmentation in conjunction with water temperature modification would allow additional periods of controlled floods or diel fluctuations to be used as elements of destabilization to negatively impact non-native fishes. Optimal use of Glen Canyon Dam as a tool to maintain, enhance, and restore the native fish community in Grand Canyon will be realized when the combined elements of hydrology, water temperature, and sediment can be used to maximize the flexibility of dam operations for that purpose. This flexibility should also allow best use of the dam as a tool to promote the mixture of multiple uses for which it was originally constructed.

BACKGROUND INFORMATION

The Pre-dam Environment--Scarcity of detailed pre-dam habitat descriptions for the Colorado River in the Grand Canyon region hinders our discussion of historic habitats, although considerable information exists regarding the environmental processes that acted to form those habitats (Leopold and Maddock 1953, Leopold et al. 1964, Leopold 1969, Dolan et al. 1978, Howard and Dolan 1981, Rubin et al. 1990). For comparative purposes, we rely upon relevant information from areas upstream in the Colorado River basin that remain relatively unimpacted by flow manipulations (e.g., Cataract Canyon), and other more general references.

The annual hydrograph of the pre-dam Colorado River in Grand Canyon typically was unimodal, and the single peak in flow was produced from snowmelt waters carried from high mountains in the upper basin. Based on U.S. Geological Survey (USGS) gaging station records near Phantom Ranch in the 20 years before closure of the Glen Canyon Dam (1942-1962), mean monthly flows varied between approximately 5,000 and 10,000 cubic feet per second (cfs) from September through February (Figure l). Spring flows rose to a mean of approximately 50,000 cfs in June. Peak flows then receded relatively abruptly and approached base levels by August. Considerable variation in the timing, magnitude, and duration of these discharges occurred among years, but the overall flow pattern was predictable.

Hydrological patterns of the major sediment-producing tributaries in Grand Canyon generally exhibited two peak periods of discharge; one associated with spring snowmelt and the other with runoff from late summer convective ("monsoon") storms. As exemplified by USGS flow records at the Cameron gauge on the Little Colorado River (LCR), the timing, magnitude, and duration of tributary discharge inputs were more variable than mainstem discharges (Figure 1). Discharge at the mouth of the Paria River is similar to the LCR pattern (Figure 1). The extreme temporal and spatial variability of late summer precipitation events in watersheds of these streams are well documented (Sellers and Hill 1974).

Mean suspended sediment discharge through Grand Canyon was 66.1 million tons per annum at Lee's Ferry, and approached 86 million tons at Phantom Ranch (Andrews 1991; Figure 2). The Paria and Little Colorado rivers, entering the Colorado between these points, contributed annual means of 3.0 and 9.3 million tons of sediment, respectively. Colorado River sediment transport patterns at Lee's Ferry more closely approximated the seasonal pattern of hydrology than these tributaries (Figure 2), where sediment inputs were disproportionately associated with late summer precipitation events (Andrews 1991). The tributaries also contributed a much greater proportion of sediment load to the Colorado River than water discharge levels would indicate (Andrews 1991).

High spring flows inundated canyon-bound tributary mouths and created large, ponded areas with low current velocities at inflows and in rare unconfined reaches of channel where river terraces were overtopped (Howard and Dolan 1981). Terrace deposits were repeatedly reworked by these annual discharge events. Massive gravel-boulder debris fans that were periodically deposited at the confluence zones following high magnitude tributary flood events created steep gradient rapids characterized by extreme turbulence and current velocity (Leopold 1969, Graf 1979, Kieffer 1985). Large pools formed immediately upstream of these channel constrictions. Pool bottoms were filled with fine inorganic materials transported by the sediment-rich pre-dam river. Flow separation and reattachment patterns below debris fan constrictions formed large eddy complexes of recirculating flow, and low-velocity return channels or backwater habitats (Rubin et al. 1990, Schmidt 1990).

The ascending limb of the spring peak flow in the mainstem scoured peripheral and midchannel habitats dominated by fine-grained substrates, such as eddies, eddy return channels, and pool bottoms above and below rapids (Howard and Dolan 1981). Sediments were deposited on the descending limb from a complex interaction between hydrology and sediment load and particle size (Howard and Dolan 1981). Spring high flows were of sufficient velocity to scour and redeposit larger substrates such as gravels, pebbles and cobbles, and rework tributary debris fans (Leopold 1969, Graf 1979, Howard and Dolan 1981, Kieffer 1985).

Late summer and early autumn tributary floods transported large amounts of fine sediments to the mainstem, where they were mostly aggraded on channel bottoms (Howard and Dolan 1981). Highest suspended sediment concentrations in the pre-dam Colorado River occurred during tributary flood events, occasionally exceeding 28,000 parts per million (Dolan et al. 1974).

Seasonal changes in water temperature lagged behind the patterns of hydrology and sediment. Mean monthly temperatures of the pre-dam Colorado River varied from 3°C during January low flows to near 25°C in July and August on the descending limb of the peak flow hydrograph (Figure 3). Temperatures typically began to rise in February and began declining in September.

Only a limited water temperature record is available for the LCR below Blue Spring, the stream's lower perennial source 21 km above the mouth. Temperatures during the period 1990-1993 rarely approached minima or maxima exhibited in the pre-dam mainstem (Figure 3). Constant temperature of Blue Spring (20.6°C) and other springs in the lower LCR (Loughlin 1983) ameliorate the effects of extreme air temperatures in the lower perennial reach. The pattern of seasonal temperature change in the LCR and Paria River are similar to the pre-dam Colorado River (Figure 3).

Metabolism in the pre-dam river was driven by heterotrophic processes during periods of high discharge and sediment load, where light limitation and scouring precluded most algal productivity. Vast volumes of allochthonous organic matter transported from upstream terrestrial sources likely provided the major source of biological nutrition during these periods, as occurs in other southwestern streams (Rinne 1975, Minckley and Rinne 1985). Backwaters and sites with woody debris could have supported diverse and abundant invertebrate communities (Carlson and Muth 1989). Autotrophic production may have been considerable as suspended sediment and organic materials settled upon return to base flow conditions or during droughts.

Adaptations of the Native Fish Fauna--Native fishes of the Grand Canyon area evolved with and adapted to the habitats and habitat-forming processes of the pre-dam Colorado River and its tributaries. The most obvious adaptations are the morphological specializations common to much of the fauna (reviewed by Minckley 1991). Adult body sizes are large (excepting speckled dace, *Rhinichthys osculus*), and their shapes are fusiform and streamlined. Presumed adaptations to turbulence and high current velocities include the evolution of depressed crania; large predorsal humps or keels; elongated, thin caudal peduncles; and large falcate fins. There is a nearly uniform presence of small eyes; small, deeply embedded scales; and thick, leathery skin that maximizes streamlining characteristics and minimizes abrasion from suspended sediment.

Native fishes developed wide physiological tolerances to temperature (approximately 0-30 C; reviewed by Lechleitner 1992); tolerances of embryos (Hamman 1982, Marsh 1985) and larvae (Lupher and Clarkson 1994) are more restricted. Longevity allowed large-bodied species to live beyond many short-term but common climatic events that rendered conditions unsuitable for successful reproduction (Minckley 1991). The native fishes specialized behaviorally to cope with problems associated with floods, including avoidance of abrasive forces and current velocities of these events (Meffe and Minckley 1987, Minckley and Meffe 1987). Timing of reproductive activity to coincide with periods of benign environmental conditions promote increased survivorship of offspring (Tyus and Karp 1989). Aberrations in discharge patterns during reproductive periods have been demonstrated to result in pronounced increases in mortality of early life stages (Harvey 1987, Clarkson and Robinson 1993).

Large-bodied native fishes utilize the larger rivers for spawning in the upper basin (Tyus 1987, 1990, Tyus and Karp 1989, Kaeding et al. 1990). There is evidence of post-dam mainstem spawning by some native species in Grand Canyon, but recruitment has been considered largely unsuccessful (Kaeding and Zimmermann 1983, Maddux et al. 1987, Hoffnagle 1994). Lack of successful reproduction in the Colorado River in Grand Canyon has been attributed primarily to low temperatures that retard or preclude embryonic and larval development (Hamman 1982, Marsh 1985). The Colorado River in Grand Canyon otherwise contains habitat characteristics similar to those successfully used for reproduction by humpback chub and other native species in the upper basin (Kaeding et al. 1990, Valdez 1993).

Reproductive strategies of the native fishes are intimately integrated with the patterns of hydrology, sediment transport, water temperature, and trophic processes. Spawning by native fishes in the major rivers of the upper Colorado River basin is initiated when temperatures rise above 16 C (Vanicek and Kramer 1969, Seethaler 1978, Nesler et al. 1988, Tyus and Haines 1991), although razorback sucker can utilize lower temperatures for reproduction (Tyus 1987, Bozek et al. 1991). Excepting razorback sucker (Tyus and Karp 1989, 1990), the major period of mainstem spawning typically coincides with the descending limb of the peak flow, usually in May-August (Vanicek and Kramer 1969, Tyus and Karp 1989, Karp and Tyus 1990, Tyus 1990). The predictable flood pulse patterns of large rivers favors the development of ethological and other adaptations by aquatic organisms (Junk et al. 1989).

Spring-summer flow patterns in combination with temperature serve as an environmental cue to culminate gonadal maturation and release of gametes in Colorado squawfish (Vanicek and Kramer 1969, Nesler et al. 1988), and association of spawning with specific hydrograph patterns for other native fish species suggests a more general influence. However, most Colorado River species can reproduce successfully when confined in the absence of hydrological stimuli (Johnson and Jensen 1991). Photoperiod undoubtedly plays a large role in the sequences of reproductive physiology and behavior of native fishes (Hontela and Stacey 1990). Scouring (cleaning) of substrates following flood events may also serve as an environmental cue to trigger spawning activity (John 1963, Mueller 1984), as may reduced turbidity levels (Deacon and Minckley 1974). Although the mechanisms that historically stimulated native fishes toward reproduction (gonadal maturation, staging, release of gametes) are not precisely known, the ichthyofauna did respond, and persisted for millennia under the natural hydrograph and associated conditions.

Reproduction and survival of native fishes in Grand Canyon are enhanced by seasonal interactions between the discharge patterns of the Colorado River and its tributaries. Tributary reproduction peaks in April-June in most tributaries (Suttkus and Clemmer 1976, Kaeding and Zimmermann 1983, Maddux et al. 1987, Maddux and Kepner 1988, Clarkson and Robinson 1993, Robinson et al. 1994). This feature historically allowed utilization of canyon-bound tributary mouths backed up by high mainstem flows in May-July by rearing larvae and early post-larvae. Larvae drifting (Valdez et al. 1985, Angradi et al. 1992, Robinson et al. 1994) into lower reaches of tributaries encountered conditions of warmer, clearer water with slowing currents that deposited drifting invertebrates and particulate organic matter. These conditions provided an excellent rearing environment for the young native fishes. By the time mainstem flows began to recede in July, young-of-year fishes were of sufficient size to increase their probability of survival as they passed into the mainstem.

These conditions have occasionally occurred in the post-dam era. During high water years of 1984-1986, numerous young-of-year humpback chub were observed in the confluence zone of the LCR (Maddux et al. 1987, W.R. Persons, AGFD, personal communication). Relatively few early life stage fishes were found there at lower regulated mainstem flows during 1991-1993 (AGFD data).

It is unknown if historically there were separate genetic components among pre-dam mainstem native spawners and tributary spawners. Mainstem spawning may have been an adaptation that served to maximize the probability of successful reproduction of individuals by spreading the outlay of sexual products across both environments, i.e. fishes may have released a portion of their eggs in tributaries (LCR) early and released the remainder later in the mainstem. Alternatively, distinct mainstem and tributary-spawning stocks may have existed.

Adaptations by larvae of some species (e.g. Colorado squawfish) to drift from hatching sites to more suitable downstream rearing sites probably served to enhance survival and growth (Tyus 1986). The timing of mainstem reproduction also takes advantage of the presence of newly formed, relatively productive (Grabowski and Hiebert 1989, Kubly 1990) backwater habitats for use by developing native fish larvae and young-of-year juveniles of most species (Tyus 1987, Tyus and Karp 1989, 1991, Tyus and Haines 1991, Valdez 1990).

The Post-Dam Environment--Magnitudes, ranges, and seasonal patterns of the hydrograph were changed significantly from the historic situation following closure of Glen Canyon Dam (Figure 4). Except during years of exceptional runoff, maximum discharges normally did not exceed 31,500 cfs, the maximum powerplant capacity of the dam prior to generator uprating. The annual range in discharge typically did not exceed 30,000 cfs, but daily discharge fluctuations approaching that range were possible under routine powerplant operations. With the recent establishment of "interim" flows, this range has contracted somewhat, but the pattern of daily flow fluctuation remains.

The persistent pattern of a large daily range in discharge is a phenomenon unseen in pre-dam days. One of the most noticeable effects of this pattern is on backwater and shoreline habitats, which are inundated and desiccated on a daily basis as a result of changes in river stage. Such temporal instability precludes the level of biological productivity that is characteristic of backwaters in the absence of daily changes in stage. In addition, weak-swimming larval and post-larval fishes are forced from these refugia and exposed to higher mainstem current velocities and often colder temperatures, where they are subjected to increased physiological stress, lowered growth rates, and presumably elevated mortality rates (Kaeding and Osmundson 1988, Thompson et al. 1991, Lupher and Clarkson 1994). Fishes may be isolated and desiccated as habitats are dewatered and dried, or subject to lethal temperature, oxygen, or salinity levels where isolated pools persist. Some of these energetic effects also may be imposed upon older fishes that inhabit larger habitats such as tributary mouths, eddies, runs and riffles.

Emplacement of Glen Canyon Dam greatly curtailed sediment input from the Upper Colorado River Basin. The remaining sediment load reaching Grand Canyon, a loss of approximately 77%, or 66 million tons per year at Phantom Ranch (Andrews 1991), is essentially accounted for by tributary inputs below the dam (Figure 4). The 25 km reach between the dam and Paria River almost never receives sediment input, and a net loss of fine-grained materials from that area has resulted in substrate armoring (Pemberton 1976, Howard and Dolan 1981, Kondolf et al. 1989, Angradi et al. 1992). Concern for a net loss of sediment over time in Glen and Grand canyons has been expressed (Dolan et al. 1974).

Altered post-dam hydrology and sediment transport dictate that geomorphological adjustments in the river channel are inevitable (Leopold et al. 1964, Dawdy 1991). High water terrace deposits are no longer inundated and are now being modified by vegetation and eolian changes (Turner and Karpiscak 1980, Howard and Dolan 1981). Flushing of fines from and comminution of large particles within high gradient reaches (especially rapids) is now less frequent due to reduced flood magnitudes (Howard and Dolan 1981, Kieffer 1985, O'Brien 1987). Variable (aggradation and erosion) reach-wide and site-specific changes to fine-grained streambed and bank deposits have occurred due to interactions among patterns of water discharge, rate of stage change, and antecedent sediment storage conditions (Howard and Dolan 1981, Beus and Avery 1993).

Islands, sand bars, and beaches that are no longer scoured by spring high flows have been invaded by exotic saltcedar (*Tamarix chinensis*) (Turner and Karpiscak 1980). This species has trapped and stabilized sediment, causing an average reduction in channel width of 27% in the Green River in and near Canyonlands National Park, Utah (Graf 1978; but see Everitt 1979). This reduction of transportable sediments and expansion of stable deposits has decreased the ability of the channel there to adjust to substantial fluctuations in discharge (Graf 1978).

Seasonal variations in water temperature practically ceased following releases from Lake Powell through hypolimnial penstocks. Mainchannel temperatures are now seasonally and perennially cold, rarely ranging beyond limits of 7-15 C (Figure 4). Peripheral backwater habitats partially isolated from mainchannel flows are one of the few habitats that warm above these levels, but only seasonally during diel cycles and as a result of the combined effects of stage fluctuations and levels of incident solar insolation (Maddux et al. 1987, Kubly 1990, Angradi et al. 1992). Effects of lowered temperatures on native Grand Canyon fishes include reduced growth rates and metabolism (Lupher and Clarkson 1994), decreased survival to sexual maturity (Kaeding and Osmundson 1988), reduced condition, lipid stores, and size that result in elevated overwinter mortality for young-of-year fishes (Thompson et al. 1991), lowered egg production by adults (McAda and Wydoski 1983), and reduced survival of developing embryos (Marsh 1985).

As a result of post-dam hydrology, temperature, and sediment changes, major trophic shifts have occurred in the mainstem Colorado River. Standing crops of attached algae in the relatively stable, clear, armored, and nutrient-rich tailwater increased relative to pre-dam conditions (McConnell and Sigler 1959, Zimmerman and Ward 1984). Sediment inputs from the Paria River, 25 km downstream from Glen Canyon Dam, abruptly reduce standing biomass of the periphyton community (Angradi et al. 1992, Usher et al. 1987, Blinn et al. 1992).

High densities and biomass of invertebrate populations contrast with low species diversity in the Glen Canyon Dam tailwater (Leibfried and Blinn 1986). Thermal constancy and low absolute water temperatures disrupt cues necessary for the completion of life cycles of many macroinvertebrates (Ward 1976, Hauer and Stanford 1982). The transitory character of nearshore habitats has rendered them largely unsuitable for colonization by desiccant-intolerant algae and invertebrates (Usher and Blinn 1990, Angradi et al. 1992).

Disturbances to pre-dam habitats and fluvial processes have been detrimental to most native and non-native fishes. Native forms, however, fared the worst; three species were extirpated and others are threatened with extirpation. As forcefully argued by Minckley (1991), the introduction of non-native fishes to the Colorado River Basin is the most critical factor affecting the long-term status of native forms. The canyon now supports populations of at least 10 non-native fishes (Maddux et al. 1987, Valdez et al. 1992) and several non-native macroinvertebrate taxa (Blinn and Cole 1991), the latter including the fish parasites *Lernaea cyprinacea* (Carothers et al. 1981) and *Bothriocephalus achielognathi* (Angradi et al. 1992, Clarkson 1992, Clarkson and Robinson 1993). The sometimes subtle ways that non-native species may displace and eliminate native forms through competition and predation were discussed by Minckley (1991) Ruppert et al. (1993), and Douglas et al. (1994).

Legal History--Prior to construction of Glen Canyon Dam, evaluation of its potential impacts on fishery resources was limited to expectations for sport fisheries development in Lake Powell and in the downstream tailwater (U.S. Bureau of Sport Fisheries and Wildlife 1958). Native suckers and the Colorado squawfish were mentioned only in passing, even though the latter species and razorback sucker already were declining rapidly in the lower Colorado River basin (Minckley 1973). The three chubs (bonytail, humpback, and roundtail) were not considered, perhaps in part because of the confusion surrounding their taxonomic differentiation (Holden and Stalnaker 1970).

Conversion of the U.S. Bureau of Sport Fisheries and Wildlife to the U.S. Fish and Wildlife Service (USFWS), passage of the Endangered Species Preservation Act of 1966, and public recognition of the plight of species in danger of extinction provided impetus for federal listing of rare Colorado River fishes (Holden 1991). In March of 1967, humpback chub and Colorado squawfish were included in a list of endangered species (32 FR 4001). Passage of the Endangered Species Act of 1973, and subsequent inclusion of these species, afforded them greater protection. Bonytail chub was listed as endangered in April 1980 (45 FR 22710-27713). A formal proposal to list razorback sucker as threatened was put forth in 1978 (43 FR 17375-17377), but withdrawn in 1980. Following a petition for listing by the Sierra Club Legal Defense Fund in 1989, USFWS submitted a new proposal listing and the species was listed as endangered in October 1991 (56 FR 54957-54966).

Recognized threats to the continued existence of the "big river fishes" of the Colorado River consistently have included fragmentation of populations, restriction of movements, and loss of habitats from emplacement of dams (Colorado River Fishes Recovery Team 1990, 1991, 58 FR 65178-65966). In anticipation of modifications to Glen Canyon Dam, the Bureau of Reclamation in 1977 formally requested Section 7 Consultation with USFWS concerning effects of dam operations on federally listed species. The following year, USFWS rendered a jeopardy opinion for humpback chub and also indicated to Reclamation that dam operations were limiting the potential recovery of Colorado squawfish (USFWS 1978). No reasonable and prudent alternatives were provided with the opinion, but USFWS recommended that Reclamation undertake studies to better understand the effects of dam operations on humpback chub. Due in large part to the concern expressed by AGFD that increased water temperatures would unintentionally promote increases in non-native fish populations in Grand Canyon (USFWS 1978), USFWS suggested that studies should be conducted before recommending actions that would raise the temperature of the river downstream of Glen Canyon Dam using multiple penstocks such as at Flaming Gorge Dam.

In 1979 Reclamation held public meetings on proposed peaking power modifications to operations at Glen Canyon Dam. The proposal met with considerable public opposition, and was dropped. An accompanying proposal for uprating and rewinding the dam's generators was continued, however, and in 1982 Reclamation determined a Finding of No Significant Impact (FONSI) for that action. Public opposition was sustained, and even though the Commissioner of Reclamation concurred with the FONSI, he determined that concern over the impacts of current operations was sufficient to warrant studies of those operations. Uprate and rewind of the generators was undertaken, and in December of 1982 the Commissioner directed that Glen Canyon Environmental Studies should begin.

During the course of the initial phase of GCES, Reclamation again requested formal Section 7 Consultation with USFWS on operation of Glen Canyon Dam. A draft jeopardy biological opinion, with reasonable and prudent alternatives, was submitted to Reclamation in August of 1987, but the two agencies subsequently agreed to develop seven Conservation Measures in lieu of reasonable and prudent alternatives.

In July of 1989, the Secretary of Interior agreed to National Environmental Policy Act evaluation of the operation of Glen Canyon Dam and the preparation of an Environmental Impact Statement (EIS). Although it was recognized that much of the research conducted under the Conservation Measures would not be completed, the EIS was scheduled to be finished in 24 months and USFWS agreed to render a biological opinion on the preferred alternative put forth in that document.

Summary and Conclusions--The operational scenario described above has sufficient scope and flexibility to utilize the dam as a powerful tool to effect enhancement of the native fish community, allow establishment of a balance between native and non-native fishes, and benefit other natural resources of Grand Canyon. We are confident, within the limitations of our imperfect knowledge of species and processes, that return of the Colorado River below Glen Canyon Dam to a semblance of its natural state through creative changes in discharge, thermal regime, and sediment augmentation will ultimately enhance native fishes in Grand Canyon. Our recommendations are not to be viewed as a trial-and-error approach to ecosystem management. Rather, once capability to implement these major changes is in place, operational flexibility will become the key to optimizing conditions for all resources. Within this context, water management (exclusive of emergency situations and as otherwise constrained by law) will be responsive to requirements of the native ichthyofauna.

We envision an implementation schedule that emphasizes dynamic flexibility and experimentation in all phases of operation, coupled with systematic, programmed and opportunistic monitoring of changes in downstream habitats and biota. Discharge regimens should initially be fixed (within applicable legal constraints but also with the priority of native fish management) to eliminate daily fluctuations and mimic the natural seasonal hydrograph for a period of years adequate to document downstream enhancement of the native fish community. Contemporaneous research on seasonal thermal modification via MLIS should be instituted and conducted as quickly as possible to determine the advisability of this action. Finally, sediment augmentation could be brought on line to complete the steps toward restoration of natural habitats and the native fish community. The appropriate combination of hydrology, temperature, and sediment that optimizes conditions for native fish cannot now be predicted, but will be determined only by creative experimental manipulations, a process that may take decades to resolve. Status assessment of native fishes would be directed continuously into a feedback loop to water managers to allow integration of operations with species requirements.

Because year class strength of the larger native fishes likely was variable in response to historical pre-dam environmental conditions, operations under this new scenario would not necessarily have to optimize conditions in all years. Opportunities would exist in some years to adjust operations specifically to suppress non-native fishes (e.g., flushing flood flows, temperature changes to preclude reproduction, etc.), benefit other natural resources, or for other purposes. As biological information becomes more reliable and species responses more predictable, the system should be fine-tuned to sustain both natural and human resource demands. While the time frame to complete this process will be protracted, we believe the stated goals and objectives are realistic and can be successfully attained.

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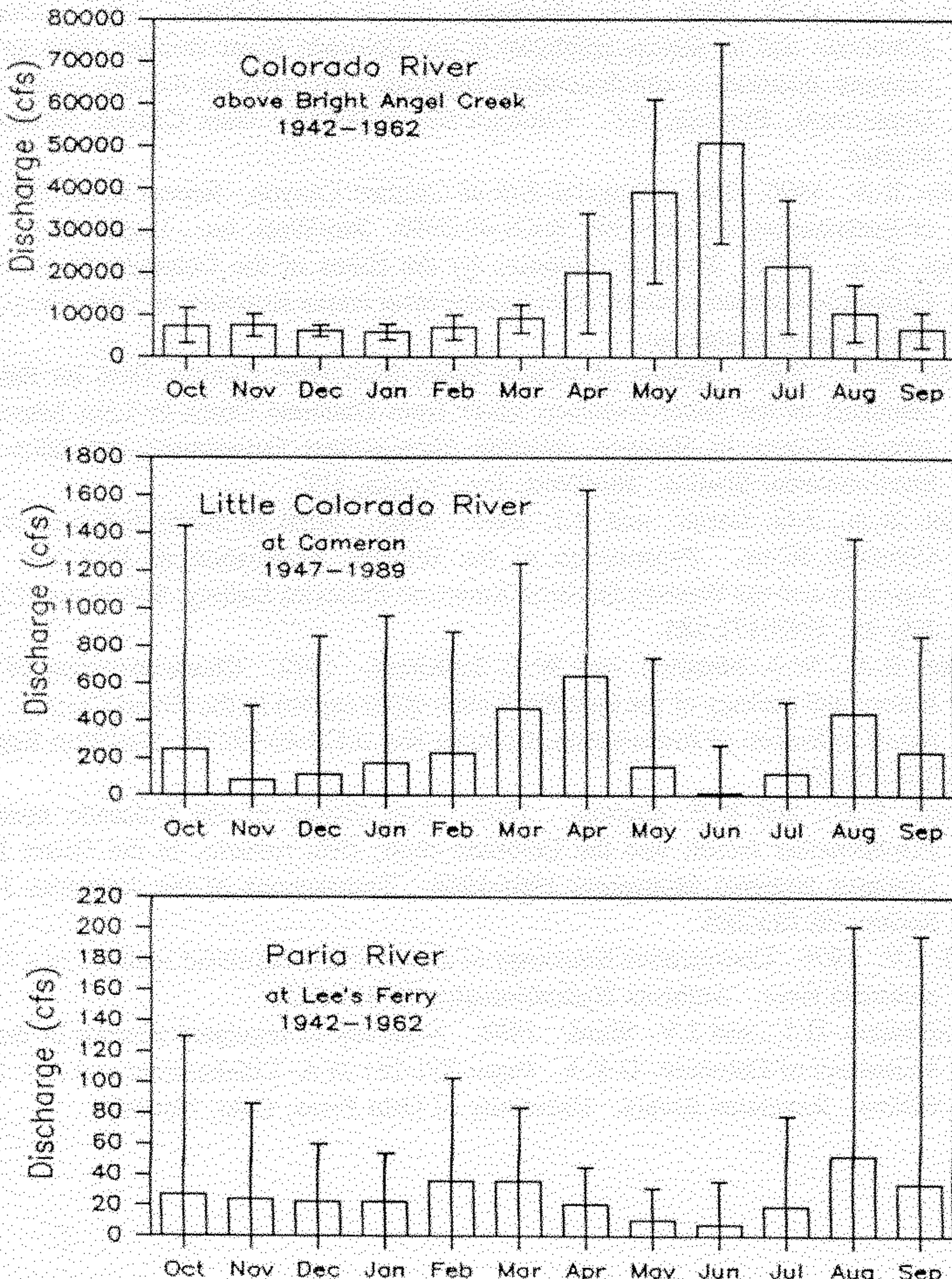

FIGURE 1. Mean daily water discharges (open bars) of the pre-dam Colorado River near Phantom Ranch, Little Colorado River near Cameron, and Paria River at Lee's Ferry, Arizona, based on U.S. Geological Survey gauge station records. Vertical brackets represent ± 1 standard deviation of the monthly means.

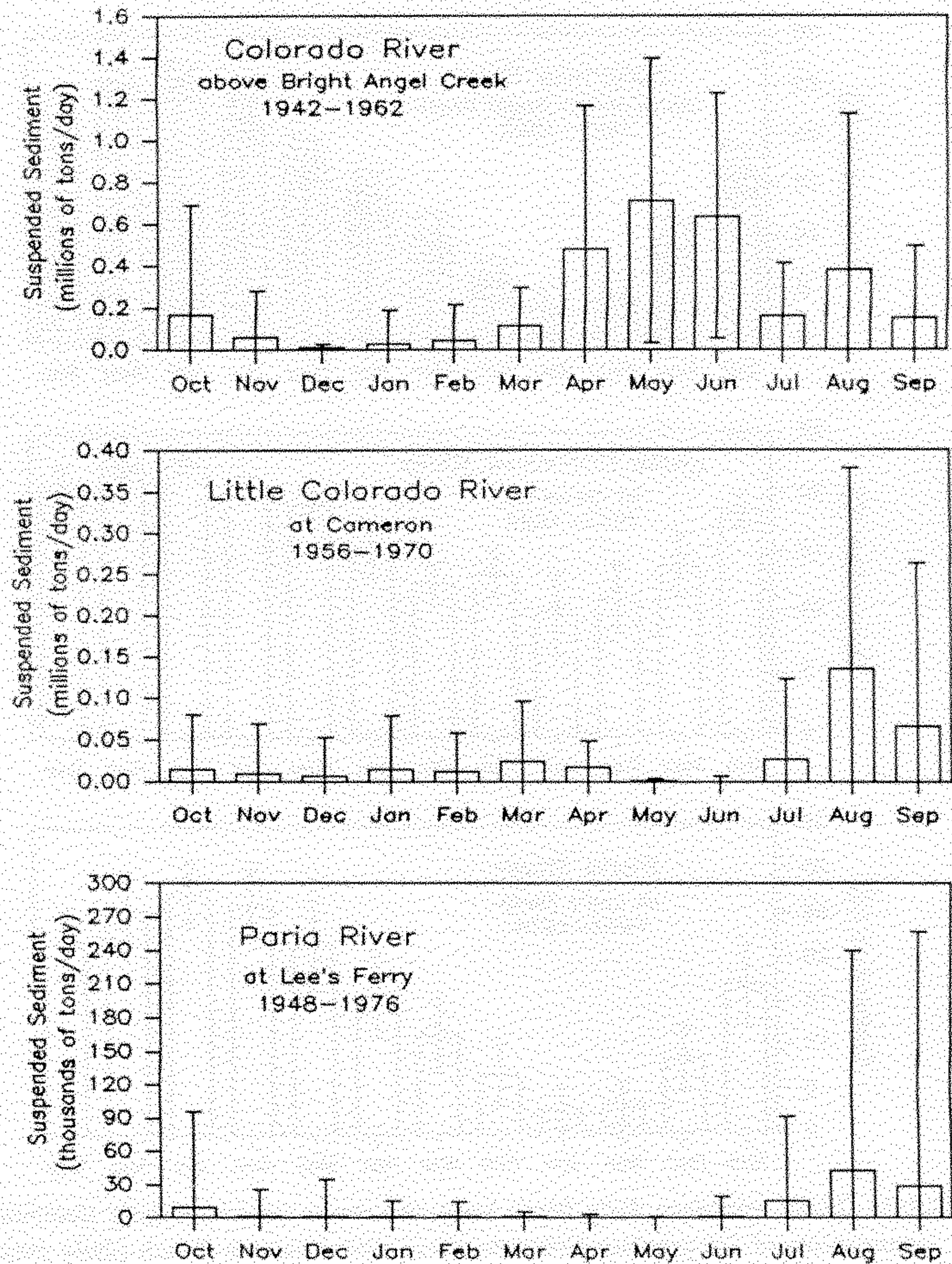

FIGURE 2. Mean daily suspended sediment discharges (open bars) of the pre-dam Colorado River near Phantom Ranch, Little Colorado River near Cameron, and Paria River at Lee's Ferry, Arizona, based on U.S. Geological Survey gauge station records. Vertical brackets represent ± 1 standard deviation of the monthly means.

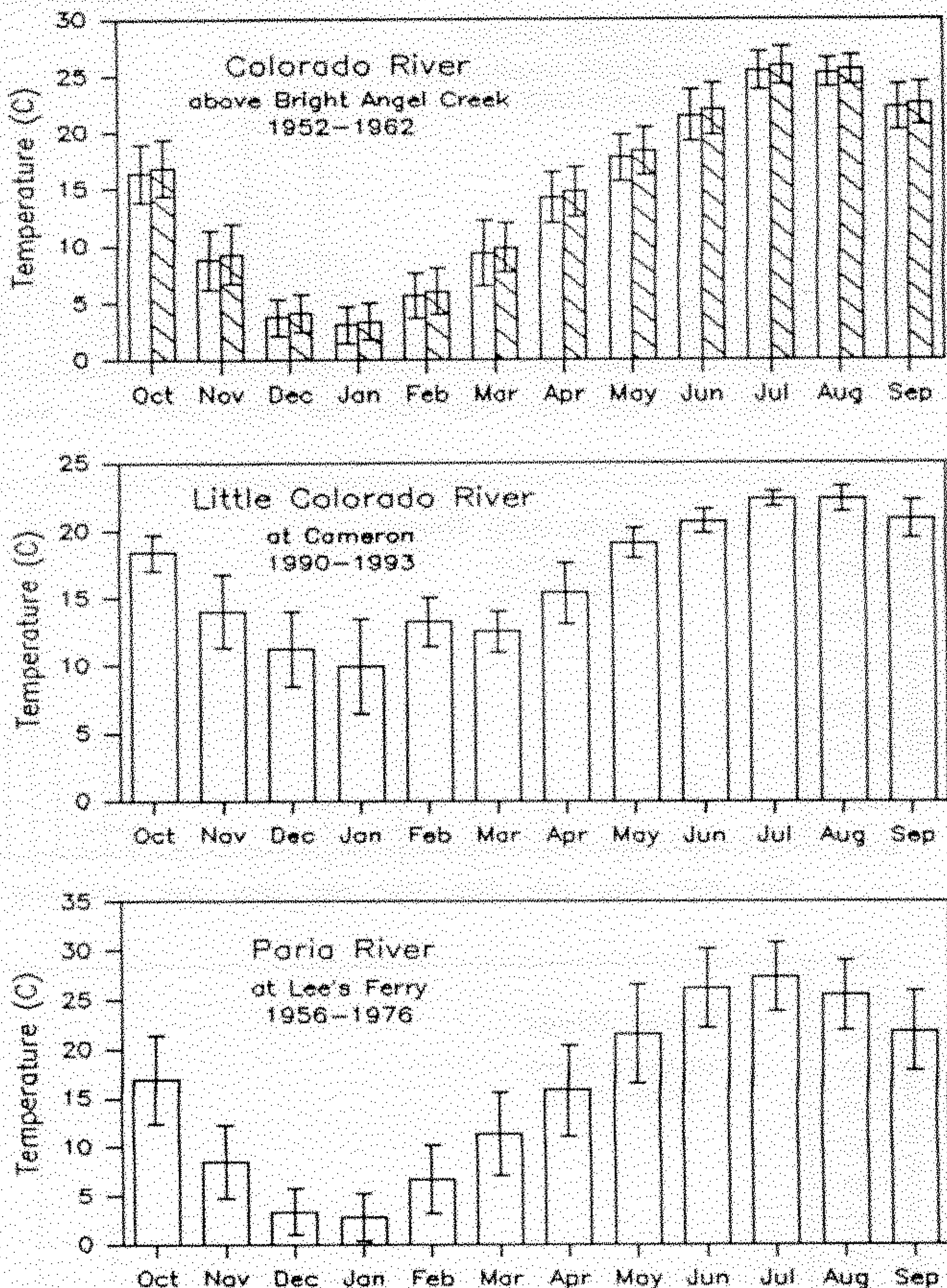

FIGURE 3. Mean minimum daily (open bars) and mean maximum daily (hatched bars) water temperatures of the pre-dam Colorado River near Phantom Ranch (daily means not available), mean daily water temperatures (open bars) of the Little Colorado River approximately 1 mile above the mouth, and mean instantaneous daily water temperatures (open bars) of the Paria River at Lee's Ferry, Arizona, based on U.S. Geological Survey gauge station records. Vertical brackets represent ± 1 standard deviation of the monthly means.

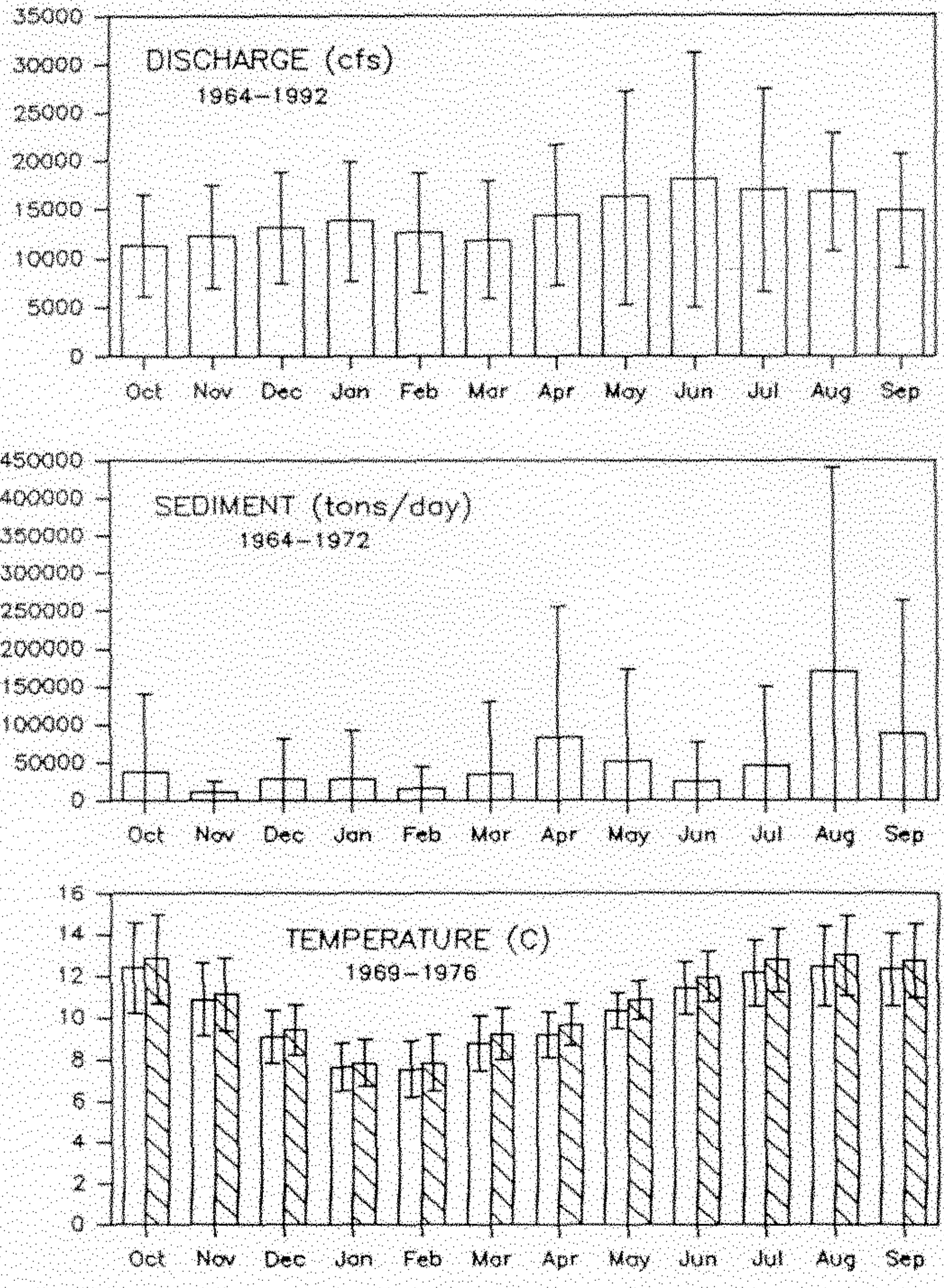

FIGURE 4. Mean daily water discharge and suspended sediment discharge (open bars), and mean minimum daily (open bars) and mean maximum daily (hatched bars) water temperatures (daily means not available) of the post-dam Colorado River near Phantom Ranch, Arizona, based on U.S. Geological Survey gauge station records. Vertical brackets represent ± 1 standard deviation of the monthly means.