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Abstract

to be added

Rhithron - headwater reaches of a river continuum characterized by cold, clear water, bedded gravel and cobble substrata on the river bottom and alternating canyon (constrained) and intermontane floodplains (less constrained).

Potamon - the downstream zone of a river continuum characterized by warm, often turbid waters, sandy, unstable bottoms and complex channels that may be partially constrained in canyon segments but more often meander through broad valley or coastal floodplains (after Illies and Botosaneanu 1963 and Stanford and Ward 1993).

Ecosystem -- the totality of ecological, social and economic processes (function) that interconnect organisms (structure), including humans, with their environment in a given place and time period. Ecosystem boundaries are permeable with respect to energy and materials flux and often are best determined by the nature of the ecological issue or question of concern.

I. Introduction

Endangered Fishes of the Upper Colorado River

Four endemic fishes (Colorado squawfish (*Ptychocheilus lucius*), bonytail chub chub (*Gila elegans*), humpback chub (*Gila cypha*) and razorback sucker (*Xyrauchen texanus*) of the Colorado River are protected under the Federal Endangered Species Act, and a recovery program for these fishes has been established by the U.S. Fish and Wildlife Service (Wydoski and Hamill 1991). These endemic, big-river fishes were abundant throughout the potamon reaches of the Upper Colorado River during settlement and initial development of the basin (*circa* 1870s-1950s) (Minckley 1973, Quartarone 1993). However, current population size and recruitment of these fishes are reduced substantially, underscoring the rationale for their listing under the Endangered Species Act. Bonytail chubs and razorback suckers are virtually extirpated in the Upper Colorado River. Reproducing populations of humpback chubs are known only in three isolated canyon areas. Squawfish remain comparatively abundant, but their distribution is restricted by dams and diversions (Figure 1). The decline of these fishes is attributed primarily to habitat loss and other environmental changes associated with construction of reservoirs and reduced and regulated flows in the remaining potamon reaches of the fragmented river system (Stanford and Ward 1986a). Predation by numerous introduced species (Minckley et al. 1991, Tyus 1991a and b) and toxic effects of selenium from irrigation return flows (Stephens et al. 1992) also have produced documented pressures on the survival of these fishes.

The recovery program emphasizes reregulation flows and obtaining water rights to insure long-term stability of flows so that documented environmental needs of the fish can be met over the long term (U.S. Fish & Wildlife Service 1987a, 1993). Flow regimes have been formally recommended for the Green River (U.S. Fish & Wildlife Service 1992), Yampa River (U.S. Fish & Wildlife Service 1990) and the 15-mile reach of the mainstem Colorado River in the Grand Valley near Grand Junction, Colorado (Kaeding and Osmundson 1989, Osmundson and Kaeding 1991). However, provision of instream flows is contentious, owing to the high value of water development entitlements owned by Colorado, Utah and Wyoming per the Colorado River Compact. Indeed, the recovery program is predicated upon development of these entitlements. Contention also has arisen with regard to the efficacy of technical or scientific methods used to justify flow recommendations.

Objectives of the Study

In Part III of this report I review the salient aspects of the ecology of the Upper Colorado River system that pertain to provision of instream flows needed for recovery of the four endangered fish species. In Part IV, I examine the rationale and methods used by the Fish and Wildlife Service in recommending specific flow regimes in specific river segments, and I identify critical uncertainties and technical and non-technical issues related to provision of flows to assist recovery of the fishes. Finally in Part V, I recommend an action plan for resolving technical and policy issues related to quantifying instream flow needs of the endangered fishes. These objectives could not be met without a thorough reading of the literature describing the biogeochemistry of the river system; thus, I offer perspective on the quality and completeness of the ecological information base in the context of flow provisions to protect and enhance the fish populations of concern.

Acknowledgments

I was assisted in this analysis by advice and comment from an expert panel consisting of Edmund D. Andrews (U.S. Geological Survey, Boulder, CO), William J. Matthews (University of Oklahoma Biological Station, Kingston, OK) and James V. Ward (Colorado State University, Fort Collins, CO). Their help is gratefully acknowledged. I also thank W. Brad Vickers (Bureau of Reclamation, Salt Lake City, UT) for providing flow data and hydrographs on the Green and Yampa Rivers.

II. Methods and Approach

Review of Information

I located and read peer-reviewed publications and unpublished reports ("grey" literature) pertaining to the ecology of the fishes, along with documents providing rationale and data for flow provisions recommended by the Fish and Wildlife Service. Also, I discussed data, rationale and issues related to flow provisions with researchers, management personnel and persons with detailed knowledge of issues pertaining to provision of instream flows. Literature cited in the body of this report are those works that I determined to be most pertinent to an informed discussion of instream flow provisions in the context of the Upper Colorado River system and its rare, endemic fishes. Additional literature that I read but did not cite herein, and people with whom I discussed my study, are listed in Appendices 1 and 2.

I emphasize that time and money did not permit me to independently examine raw data, with the exception of some discharge data. My analysis is limited to review of documents and discussions of data with researchers. Data presented in the figures included herein are presented as they were given in the publications from which they were drawn. Therefore, judgments and conclusions depend on the quality and quantity of data presented in the documents or provided to me in unpublished form. However, I noted from the outset that many of the key observations about these fishes and the rivers in which they live have been published in peer-reviewed literature. Indeed, the occurrence of juried papers is quite high in relation to the dollars invested in research on these fishes and in comparison to other multimillion dollar programs I have reviewed recently (i.e., Glen Canyon EIS; Columbia River Fish and Wildlife Program). Reviewed publication does not guarantee accuracy of data or interpretations, but it is the best standard of credibility we have in science.

Throughout the report, citations are given whenever information from a publication is used in my interpretations. In all cases citations refer to the text preceding a specific citation in the report, as per usual scientific protocol. In some cases I cited people with whom I had discussions; such personal communications are cited only in cases where new data or technical observations not currently in print were discussed and I felt corroboration was warranted.

Peer Review and Schedule

During the study period, which began in October, 1992, I reported monthly to the Instream Flow Subcommittee of the recovery program to facilitate communication and understanding of the objectives of the study, my approach and understanding of issues. I maintained a log of people with whom I had discussions pertaining to the study.

Assembly and review of literature and dialog with persons working on the problem were completed in May, 1993.

I met with the expert panel April 18 - 19, 1993, in Grand Junction, Colorado. I provided the panel with an abbreviated version of this report, we viewed sites on the Colorado and

Gunnison Rivers from aircraft, visited sites in the 15-mile reach with Doug Osmundson (Fish and Wildlife Service, Grand Junction, CO) and discussed my review and preliminary conclusions.

A first draft of this report was provided to the Instream Flow Subcommittee and the expert panel on May 7, 1993, for their review. Written reviews of the first draft by the expert panel were provided to me by June 15, 1993, (see Appendix 4), and the report was revised per their concerns and with consideration of other comments received.

Ecological Context for Instream Flow Analyses

My approach to this project emphasizes that the complex biogeochemistry of river ecosystems is naturally variable. The essence of ecology is understanding processes that control observed variability in the distribution and abundance of biota. I hope that readers will agree that we seek not to describe the river as it exists today; rather, we seek an understanding of how the river is changing in response to natural and human influences in order to protect and enhance the fishes of concern. Quantification of the structure and function of complex systems, like the Upper Colorado River ecosystem, in time and space must be based on long-term empiricisms. Like most scientists, I view model building and logistic descriptions of dynamic events in ecology as mechanistic tools for formalizing a better understanding of what is known about a system; such tools should not be used in an attempt to predict the future. Predicting the consequences of environmental change is the ultimate challenge of contemporary ecology. This must be resolved through strong inferences based on properly scaled measurements of biophysical variables that integrate the myriad of system-specific ecological processes that are spatially and temporally dynamic (see also Magnuson 1990, Stanford and Ward 1992a). In other words, the problem of instream flow provision must be resolved from strong inferences derived from long-term trends in ecological processes and responses of the river ecosystem in which the endangered fishes live.

III. River Ecology and The Effects of Regulation on the Endangered Fishes of the Upper Colorado River: Review and Synthesis

Ecology of the Endangered Fishes

Information about the endangered fishes is very detailed, given that they are relatively rare fishes; several detailed reviews of the scientific information have been published (e.g., Stanford and Ward 1986b, Minckley et al. 1991, Tyus 1991a). Therefore, I repeat here only salient points of particular importance to my review of the flow recommendations made by the U.S. Fish and Wildlife Service. The reader is encouraged to consult the review articles for detailed descriptions of the many years of study devoted to these interesting fishes.

As noted above, the historical range of the four species included the potamon and transitional reaches of the Green and Colorado River systems, including most of the larger tributaries, in particular the Yampa, White, Dolores and Gunnison Rivers. However, bonytail chubs are close to extirpation, but are being cultured along with humpback chubs, squawfish and razorback suckers at the Dexter National Fish Hatchery, Dexter, New Mexico (Johnson and Jensen 1991). Because of their comparative rarity in the wild, ecological information on their historical range is more fragmentary than for the other species of concern. A few specimens of bonytail chubs were collected in the 1970s in the Green and Yampa Rivers (Kaeding et al. 1986), but their phenology (life history) and exact cause of disappearance in the Upper Colorado River system are unknown.

Humpback chubs are found only in whitewater canyon segments (Figure 1). Migrations are limited, and it may be that humpback chubs were always restricted to specific canyon segments, at least as adults. Spawning in the Upper Colorado River occurs on the declining limb of the spring runoff event in association with the 20°C isotherm. Humpback chubs interact behaviorally and probably hybridize with congeneric, endemic roundtail chubs, which are more abundant throughout the Upper Colorado (Kaeding et al. 1990, Karp and Tyus 1990). Life cycles of humpback chubs in the Upper Colorado appear to be similar to phenology documented in the Little Colorado River near its confluence with the Colorado River within the Grand Canyon (Kaeding and Zimmerman 1983; Richard Valdez, BioWest Inc, Logan, UT, personal communication).

Lanigan and Tyus (1989) estimated that only 978 ± 232 adult razorback suckers remained in the Green River above Desolation Canyon during 1981-86. The population appears to have declined since 1986 based on recaptures of fish tagged in the earlier study. However, annual population estimates are biased by differential tag retention and the efficacy of estimates are currently being examined. Moreover, young razorback suckers have been collected in the Green River in recent years. Some recruitment may be occurring, perhaps related to higher flows. Whether stable or declining, the population of razorback suckers in the Green - Yampa system likely has not exceeded more than 1,000 fish in the last two decades (Tim Modde, U.S. Fish and Wildlife Service, Vernal, UT, personal communication). Most of the very few other razorback suckers captured in the Upper Colorado are old fish and no recruitment of razorback suckers has been clearly documented since the 1960s.

Razorback suckers have been observed spawning, or in spawning condition (ripe) during the rising limb of the spring runoff at temperatures 5-10°C below (McAda 1980, Tyus 1987) the experimentally observed optimum range (20-22°C) for reproduction (Inslee 1982, Hamman 1985, Marsh 1985). Razorback suckers were commonly (50 or more per year) collected in the 15-mile reach of the Colorado River in the early 1970s, mostly in a gravel pit connected to the river near Grand Junction, CO (McAda 1980, Valdez and Wick 1983). That gravel pit washed out in the 1984 spring flood of record, and only incidental captures were made subsequently (Osmundson and Kaeding 1991). However, in the spring of 1993, 67 razorback suckers were taken from another gravel pit; these fish were all the same age, perhaps spawned in the gravel pit during the

1984 flood (Frank Pfieffer, U.S. Fish and Wildlife Service, Grand Junction, CO, personal communication).

In addition to their propensity to inhabit man-made gravel pits that are at least ephemerally connected to the river, razorback suckers are most often captured in low velocity habitats in the channel (Figure 2) and wetland ponds connected to the channel (McAda 1980, Tyus et al. 1987). Bulkley and Pimentel (1983) showed that razorback suckers preferred temperatures of 22-25°C in shuttle box experiments. In the potamon reaches of the Upper Colorado River, shallow, backwater and wetland habitats are typically closer to the preferred temperatures than is the river channel, especially in the upstream reaches where razorback suckers are most commonly found. Indeed, Wick et al. (1983) showed that backwaters flooded by spring runoff on the Yampa River were significantly warmer than the channel, thereby offering more degree days for maturation of spawning condition. Naturally functioning backwaters (i.e., not influenced by erratic, regulated flows) also contain food sources, such as zooplankton, invertebrates associated with macrophytes and microbially-rich detritus, needed to mediate growth of razorback suckers (Wick et al. 1982, Wick 1991).

The reproductive bottleneck that is preventing recruitment of razorback suckers in the Upper Colorado River is unknown. Clearly, these suckers prefer lacustrine environments, owing to their proclivity for low velocity habitats, especially flooded gravel pits and backwaters during high flows. River flow regulation, wetland revetments, diversion dams (which limit migratory pathways, see Figure 1) and presence of abundant native and nonnative predators (also discussed below with regard to similar influences on squawfish) may prohibit the fish from using wetlands in a manner that will allow recruitment to occur annually. Indeed, in Lake Mohave on the Lower Colorado River, where a large population of razorback suckers has persisted for many years but did not recruit in spite of apparent spawning success each year, the recruitment bottleneck was attributed to predation of larvae and early juveniles by nonnative minnows and sunfish (Marsh and

Langhorst 1988, Marsh and Minckley 1989, Papoulias and Minckley 1992). The recruitment bottleneck for razorback suckers in the Upper Colorado River very likely relates to the current paucity of low velocity, warm, food-rich and non-predator dominated habitats during spring and summer.

Instream flow recommendations (discussed below) predominantly are based on ecological knowledge of Colorado squawfish, which are the most abundant and best known of the endangered big river endemics. Squawfish occur most abundantly in the potamon reaches of the Yampa, Green, White, Gunnison (i.e., downstream from the Redlands diversion dam; a few are isolated upstream) and mainstem Colorado Rivers (downstream from the Grand Valley diversion dams) (Figure 1).

Colorado squawfish are long-lived piscivores that grow to more than a meter in length and exhibit long migrations (e.g., between White and Yampa Rivers) (Tyus 1990) associated with 15-20°C isotherms (my interpretation based on data in Tyus 1984, 1990). The fish spawn on chute channels (Harvey et al. 1993) that form on specific alluvial bars in the Yampa and Green Rivers (Figure 2) in association with the decline of spring runoff and spates (Nesler et al. 1988, Tyus 1990). Eggs of squawfish hatch within about 5 days after spawning at 20-22° C, which is the critical temperature for successful reproduction (Hamman 1981, Haynes et al. 1984, Tyus and McAda 1984, Marsh 1985). Upon hatching, larvae drift downstream (Figure 3) where they are entrained in backwater nursery areas (Figure 1). In lab experiments young of the year (YOY) prefer and grow best at 25°C (Black and Bulkley 1985). The YOY and juveniles are most often found in specific low velocity environments, created by the complex relationship of flow and channel geomorphology (Figure 2). These nursery and rearing sites also are inhabited by native and nonnative fishes, particularly flannelmouth suckers (*Catostomus latipinnis*), roundtail chubs (*Gila robusta*), green sunfish (*Lepomis cyanellus*), red shiners (*Cyprinella lutrensis*), sand shiners (*Notropis stramineus*) and channel catfish (*Ictalurus punctatus*), that compete with the endangered fishes for available food resources or prey upon them directly (Valdez and Wick 1983, Karp and Tyus 1990). Adult squawfish also prefer areas of the channel that are braided and complex, where low velocity habitats (e.g., eddies, pools and slow runs) are abundant. Like razorback suckers, adult squawfish tend to move in and out of large backwaters that form on downstream ends of backbar channels and terrace- or wall-based channels (Figure 2), which remain connected to the main channel at baseflows. They may feed in these environments (Valdez and Wick 1983) or simply move into low velocity habitats to avoid the higher flow of the main channel (Doug Osmundson, U.S. Fish and Wildlife Service, Grand Junction, CO, personal communication). Growth is optimum at 25°C, based on experimental studies; Kaeding and Osmundson (1988) showed that growth in the 15-mile reach of the Colorado River was reduced, because maximum temperatures were less than optimum for maximum growth year around. Warmer temperatures in backwater environments could offset the cold water effect (Wick et al. 1983), assuming food supply is adequate and small squawfish can avoid predation.

Long-term monitoring data strongly indicate to researchers in the recovery program that recruitment of larvae and YOY squawfish and subsequent year classes are highest when intermediate (about the long-term average) peak flows occur during spring runoff. Recruitment was substantially lower on years of very high spring flows (e.g., flow peaks of record in 1983 and 1984 at the State line gauge, Figure 4) (Osmundson and Kaeding 1991), owing either to poor spawning conditions or mortality associated with flushing effects of high runoff. Low recruitment on low flow years may be related to lack of suitable habitat, either for spawning, or rearing or both. An alternate interpretation of Figure 4 is that the extremely high flows of 1983-84 created substantial amount of new spawning habitat which was available but gradually deteriorating during 1985-88. Regardless of how the relationship is interpreted with respect to the peak (1983-84) and low (1982) events, it is fairly clear that squawfish recruitment can occur over a very wide range of spring flows (i.e., the recruitment threshold is very wide). I conclude that squawfish spawning may be much less site-specific than is suggested by the literature or a very wide range of preferred spawning conditions exist on the spawning bars where squawfish are routinely found (e.g., Cleopatra's couch bar on the Yampa).

The life history strategy of squawfish appears to be strongly influenced by the propensity of the larvae and juveniles to flush far downstream from the spawning site; survivors subsequently move back upstream as they mature. Adults, especially large fish (Figure 5), are most commonly found at or near the potamon-rhithron transition zone in the Yampa and Colorado Rivers. Recruitment also was lower on low flow years, presumably because predation rates were higher. This relationship between year class strength and peak discharge seems to hold for both the Green River and Colorado River (Tyus and Karp 1989, 1991, Osmundson and Kaeding 1991) and also applies to humpback chubs in the Grand Canyon (R. Valdez, BioWest Inc, Logan, UT, personal communication). Recruitment is weak on very high and low flow years and relatively good on years of long-term average flows.

Dynamic Relationships Between Flow, Channel Geomorphology and Food Webs

The distribution, abundance and life histories of the endangered fishes appear to be strongly influenced by availability of physical habitats that are created and maintained by flow dynamics in time and space (Figure 6). Indeed, squawfish only spawn on clean cobble on specific bars in the sediment-laden river segments of the Upper Colorado system. Hence, a fundamental process-response relationship involves the movement of the fish to the bars in concert with flows that first form the bars and then flush sediment off of cobble substratum so that the fish can spawn successfully (Figure 2) (Tyus 1990, Harvey et al. 1993). Humpback chubs only occur in eddies and other hydraulically complex habitats found in constrained channels in the steeper gradient segments within canyons (Figure 2) (Kaeding and Zimmerman 1983, Kaeding et al. 1990, Karp and Tyus 1990). Squawfish and razorback suckers are almost always captured in low or zero velocity habitats (Tyus 1984, Osmundson and Kaeding 1989). Squawfish (Tyus 1991a and b), and perhaps razorback suckers as well (Minckley et al. 1991), must have access to low velocity environments to mature. This strongly implies that low velocity habitats are important feeding, or resting areas or both.

Low velocity environments are formed and maintained by complex hydrologic processes that involve the frequency and duration of peak flows and associated flux of sediment through the stream segment (cf., Andrews and Nelson 1989). Numbers and area of low velocity environments used by squawfish larvae, juveniles and sometimes adults in the aggraded Jensen and Ouray areas of the Green River (Tyus and Haines 1991) apparently are maximized at a given time at river discharge of 1381 cfs (numbers) and 1687 cfs (area) (Pucherelli et al. 1990). However, it must be kept in mind that a river stage-backwater relationship observed on a particular year is determined by the volume and duration of the peak flow events that occurred during spring runoff or other intense spates of that year, or the year or two immediately preceding the measurements. Instream flows designed to provide maximum access for endangered fishes to low velocity habitats must be based on long-term measures of the relationship between peak flows and channel and backwater configuration, even in river segments where delivery of sediments is equal to export (quasi-equilibrium systems). This is especially true in segments that may be aggrading, as in the Escalante Bottom and Ouray areas of the Green River (Andrews 1986), because channel configurations may change dramatically in response to variable peak flows. In other words, as the channel morphology changes from year to year, a given discharge will vary in its inundation of backwaters which can profoundly influence fishes and other biota that must move into backwaters and other low velocity habitats from the channel and back again in short (diel) and long (seasonal) time frames.

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Efforts to build process-response models of flow and physical habitat relationships (e.g., Harvey et al. 1993) therefore must take into account that flow and substratum relations in most riverine environments are stochastic and cannot accurately be described by linear or logistic functions. Indeed, complex channels which promote occurrence of low velocity habitats are virtually always characterized by non-uniform flows in time and space, whereas many models (discussed in more detail below) often assume uniform flow.

Given that a relationship exists between flow dynamics and availability of various physical habitats preferred by the fish, what role do these habitats play in the trophic ecology of the river? Except during periods of high turbidity, the Upper Colorado River system in general is intensely autotrophic and capable of supporting very productive benthic food webs on cobble substratum of riffles in the steeper segments (Annear and Neuhold 1983, Carter and Lamarra 1983, Ward and Stanford 1991). Although it is not conclusively documented in the Upper Colorado River system, backwater environments, which are most abundant in the aggraded segments, are apparently very productive after spring runoff owing to: a) the flux of clear, nutrient rich water through them from hyporheic sources (Figure 2) and b) warmer temperatures than occur in the channel, both of which are associated with the approach of baseflows in summer. However, channel areas in aggraded segments are not likely as productive, owing to the unstable nature of the sand and mud bottoms (Ward et al. 1986, Ward and Stanford 1991). Moreover, as one moves downstream toward Lake Powell on either the Colorado River or the Green River, recruitment of fine sediments increases. The lower reaches of both rivers are characterized by extensive deposits of silt and clay (E. D. Andrews, U.S. Geological Survey, Boulder, CO, personal communication), which may limit zoobenthos production. Indeed, zoobenthos species richness and biomass declines downstream from the rhithron-potamon transition as the river bottom changes from coarse to fine substratum (Carter and Lamarra 1983, Ward and Stanford 1991).

These studies and discussions with researchers suggest that food webs are more stable, complex and productive in the upstream reaches of the potamon, associated with cobble substratum within the channel (e.g., Yampa Canyon, 15-mile reach, lower Gunnison River). In the aggraded segments of downstream reaches on both the Green and Colorado Rivers, productive food webs may only be present in low velocity backwaters. Studies to date are inconclusive as to exactly how productive backwater environments actually may be, but algae, zooplankton and mud-loving midge (chironomidae) larvae are present in backwaters on the Green River (Grabowski and Hiebert 1989). I would expect that naturally functioning backwaters (i.e., seasonally flooded and continuously connected to the channel) contain rooted aquatic vegetation (i.e., as opposed to encroaching riparian vegetation, discussed below) which provide substratum for algae, odonates, snails, mayflies and caddisflies, in addition to forms living on the bottom (e.g., oligochaetes and midges). Organic detritus originating in the river channel (e.g., periphyton, drifting leaves) also may be deposited in low velocity habitats providing substratum for detritivorous insects and fishes. Hence, backwater food webs typically have abundant forage for small fish, such as YOY squawfish, that are in turn available to larger predators. A large body of literature supports the concept that naturally functioning floodplain wetlands of rivers are very productive and an essential component of the life history of fishes that migrate between channel and floodplain wetlands (Junk et al. 1989, Ward 1989).

Because they fringe the channel, backwaters and associated wetlands are more ephemeral than cobble bars, which remain inundated even at the lowest flows. Moreover, backwater environments in many unconstrained (floodplain) areas of the Upper Colorado River have been ecologically disconnected from the river channel either by man-made revetments or by sand bars or encroaching riparian vegetation that are no longer scoured owing to truncation of peak flows by regulation (e.g., Graf 1978, Stanford and Ward 1986). Indeed, I believe loss of productive backwater environments may in part explain why humpback chubs are found only in canyon segments and why razorback suckers and squawfish move around a great deal. Food webs associated with gravel bars are very likely more productive and permanent (e.g., Ward and Stanford 1991), and the larger razorback suckers and squawfish adults must search for these more productive sites, owing to their large size and need for abundant, large forage items. Squawfish adults may be most commonly found in or near the rhithron-potamon transition zone (Figure 5) because the transition zone is the only area with sufficient productivity and a permanent food web to support the life history energy balance of this large predatory animal. Indeed, other native fishes that are the natural prey of adult squawfish, especially roundtail chubs and bluehead suckers (*Catostomus discobolus*), are more abundant in or near the transition zones (Doug Osmundson, U.S. Fish and Wildlife Service, Grand Junction, CO, personal communication) where algae and zoobenthos forage likely is most abundant.

This trophic, dynamic nature of the potamon reaches of the Upper Colorado River and interactive influences with geomorphic controls is a poorly understood aspect of the ecology of the endangered fishes. On the one hand, it is apparent that these fishes prefer low velocity habitats; on the other hand, these low velocity habitats may not be as productive as higher velocity reaches owing to fluctuating flows caused by regulation. Measurements are needed to more firmly establish cause and effect. The problem is complicated by the fact that site-specific velocities vary with flow, which is precisely why channel geomorphology is so complex and dynamic in time and space. I conclude that throughout their life cycle these fishes are highly adapted to variations in flow velocity, depth, turbidity and food web structure and function associated with this spatially and temporally-dynamic biophysical interaction. They simply move around as flow varies, constantly seeking the best energy return on energy invested in foraging. In the case of squawfish, their large size apparently allows considerable movement to efficiently use a highly variable environment. Anthropogenic activities, such as revetment of floodplains and erratic regulation of baseflows by dams and diversions, change the natural biophysical variability and reduce the variety of habitats available, thereby compromising the life history energy balance of the fishes (Ward and Stanford 1989).

Influences of Stream Regulation

Flows in both the Green and Colorado River systems have been depleted by diversions and further regulated by hydroelectric releases from large storage reservoirs (Figures 1, 7 - 9). Of the larger tributaries, only the Yampa remains essentially free flowing. In order to examine the rationale for provision of flows to recover the endangered fishes, it is necessary to understand how the river ecosystem has been changed by regulation. The ecological effects of stream regulation have been extensively reviewed and summarized (cf., Ward and Stanford 1979, Lillehammer and Saltveit 1984, Petts 1984, Stanford and Ward 1986b, Craig and Kemper 1987, Carlson and Muth 1989, Gore and Petts 1989). As above, I discuss only salient aspects of the problem here.

Alteration of Flow, Temperature and Sediment Regimes

Regulation has reduced the spring peaks of the snowmelt-dominated rivers of the Upper Colorado River system and increased the baseflows (see Figures in Stanford and Ward 1983, Andrews 1986). Hydroelectric operations also have increased short-term flow variability (e.g., Figures 10 and 11). Rivers regulated by hypolimnial (bottom) release dams (e.g., Aspinall Units on Gunnison) are cooler in the summer and warmer in winter for many miles downstream from the dam than was the case before impoundment (Stanford and Ward 1983), although Flaming Gorge Dam was retrofitted with a selective withdrawal system to ameliorate negative effects of cold temperatures on fish growth downstream from the dam (Stanford and Ward 1986a).

Retention of sediments within impoundments such as Flaming Gorge and the Aspinall Units has reduced suspended and bedloads downstream from the dams. Moreover, loss of peak flows has reduced the transport power of the river. Sediment discharges from tributaries downstream from the point of regulation therefore are more persistent; alluvium and colluvium entering the river channel are not moved downstream with predam efficiency. Thus, riverine sediment budgets and channel elevations may change dramatically after regulation. In the Green River, mean annual sediment discharge decreased by 54% at Jensen and 48% at Green River, 105 and 290 river miles downstream from Flaming Gorge Reservoir (Andrews 1986). A new quasi-equilibrium between sediment supply and transport has been attained in the Green River (Lyons and Pucherelli 1992) resulting in a decrease in the bankfull channel of 6% (Andrews 1986) to 10% (Lyons and Pucherelli 1992). Loss of channel area is attributed to formation of new islands and increased island size and loss of side channels which filled with bed materials (Lyons and Pucherelli 1992). In the Gunnison Gorge of the Gunnison River downstream from the Aspinall Units, summer thunderstorms in 1991-92 caused debris flows in normally dry side flow channels. This episodic inflow of rocks and soil created large alluvial fans out into the river, which have persisted owing to insufficient peak flows to flush alluvium downstream (Elliott and Parker 1992).

Channel Encroachment by Riparian Plants

The inability of the regulated river to redistribute alluvium allows encroachment of vegetation into the river channel. Dense vegetation down to the low water mark (i.e., minimum flow channel) is an ecological feature that now characterizes the river corridor of the regulated segments of the Gunnison (Stanford and Ward 1984), Colorado (Graf 1978, Stanford and Ward 1986b, Osmundson and Kaeding 1991) and Green Rivers (Fisher et al. 1983). However, Fisher et al. (1983) also provided very clear evidence that vegetation along the shoreline of the Yampa River has not substantially changed in over 100 years because the Yampa remains unregulated. Unvegetated, bare sandbars and backwaters evident in photographs taken in 1871 were amazingly unchanged in photos of the same spots in 1983. Record high flows in 1983 did not change this interpretation (Potter 1984). Clearly, the scouring effect of spring floods does limit the distribution of riparian plants into the channel and backwaters on the Yampa River, whereas riparian vegetation composed primarily of nonnative species such as reed canary grass (*Phalaris arundinacea*), salt cedar (*Tamarix pentandra*) and Russian olive (*Elaeagnus angustifolia*) is gradually choking the regulated segments of the Upper Colorado River system.

Two interactive processes are involved in the long-term succession of regulated stream riparia. First, stabilization of flows allows encroachment of riparian vegetation into the channel, backwaters and floodplain wetlands, if the latter two are still hydrologically functional after regulation. The riparian zone of regulated rivers is small but continually rehydrated. Second, nonnative plants are more competitive in the stabilized environment that exists in the narrow saturated zone next to the river channel and backwaters, and they tend to dominate the community. Native plants are adapted to deal with extreme variations in flow and soil saturation, conditions that do not occur in the dynamic fashion that characterizes unregulated hydrographs in the Colorado River system. That is, in the predam environment, the riparian zone was large and only periodically or seasonally flooded. Hence, the natural plant succession that followed scouring flood events has been curtailed or lost along regulated streams as reflected in the narrow, undisturbed riparian corridor along the wetted perimeter of the river and its backwaters (Gregory et al. 1991).

Maintenance of cottonwood (*Populus deltoides; P. fremontii*) gallery forests, that once characterized the floodplains of the pristine Upper Colorado River, were dependent upon seasonal flooding and drying in the riparian zone. Seeds produced by cottonwoods in the spring were deposited with debris on the floodplain surfaces as flows declined after the spring spate. Gradually drying soils of fine riverine alluvium provided ideal substratum and water supply for germination and growth of seedlings. As a result of this unique coupling of the tree's life cycle with the annual hydrograph, trees of even age can be used to date the extent of past high flow events. Moreover, cottonwood leaves dropped in the fall and blown into the river provide an important allochthonous source of nutrients for riverine food webs. Only remnant forests remain today in the Upper Colorado River system, owing to regulation of flow which limits distribution of seeds and conditions required for germination. Agricultural activities such as grazing and tillage, and floodplain revetments also prevent establishment of cottonwood seedlings. Replacement of riparian forests of naturally reproducing cottonwoods and associated native plants by nonnative plants in a narrow fringe along the river corridor is a classic symptom of the severing of dynamic spatial and temporal connections between the river channel from its floodplain (Stanford and Ward 1986a, 1992, 1993).

Two questions require resolution with regard to riparian ecology and imposition of re-regulated flows in the Upper Colorado River. First, how much flooding and what frequency of flooding does the riparian zone require in order to maintain native riparia? Fisher et al. (1983) showed that the Yampa corridor remains largely unchanged, although salt cedar has invaded throughout the lower half of the river. The 1983-84 high floods allowed cottonwoods to reseed along the upper Green River (personal observation). Other flows over the last several decades have not produced cottonwoods. Second, how much of an effect will encroachment of vegetation into the river channel have on reconfiguration of the channel, if peak flows are reinstated? Studies are needed because the linkage between lack of peak events and loss of riparian communities on the Upper Colorado River seems clear.

Loss of Food Web Function in the Varial Zone: The Problem of Baseflow Instability

Hydropower operations have produced erratic baseflows on the Gunnison (e.g., Figure 11) and on the Green River (Figure 10) that are especially problematic because they destabilize food webs in the "varial zone" of the river. The varial zone is the shallow area of the shoreline (as opposed to the middle or thalweg of the channel) that is inundated and dewatered by the peak flow events. Hence, the varial zone includes riparia as well as portions of the primary and secondary channels and backwaters not normally considered part of the riparian zone. In an unregulated river the varial zone may be quite large and dynamic in the context of natural geomorphic variability described by Figure 2, or in the context of the gallery forest discussed above. The varial zone in a regulated river often is smaller, owing to reduction in peak flows, but more importantly, the varial zone of a regulated river usually is repeatedly watered and dewatered by dam operations for hydropower generation. As markets for hydropower vary, so does water output from the dam. The result on the Green and Gunnison Rivers is reflected in high spikes above baseflow (e.g., at points of initiation shown by arrows in Figure 11) often lasting several days (e.g., note also sudden changes in flow in Figure 10). Regulated flows below hydropower dams also often reflect the consequences of the dam operator's need to control electrical load ("peaking" operations), as on the Green River in 1992 (i.e., much lower, diel cycles evident in Figures 12 and 13). Peaking and other short-term operations water and dewater the varial zone of a regulated river with much greater frequency than would occur under natural conditions.

Constant flushing of the varial zone prevents establishment of food webs and resting areas for small fish that are required to support riverine fisheries. Weisberg et al. (1990) demonstrated that standing crops of zoobenthos increased 100 fold in one year in a regulated river after eliminating peaking operations at the dam and thereby reducing the devastating ecological effects of unnatural, short-term flushing of the varial zone. Repeated flushing also removes plant growth nutrients and alters the natural thermal insolation of shallow backwaters that are especially important for bioproduction of low velocity food webs in general, and for growth of squawfish and razorback suckers specifically. In spite of the laudable reregulation effort by operators of Flaming Gorge Dam to stay within flow windows (Figure 14) determined to maximize areas of backwater habitats in the aggraded nursery areas of the Green River during summer and fall, 1992, peaking operations still caused considerable diel fluctuation of river stage. Hence, I infer from Figure 14 that backwaters were flushed daily during the critical baseflow period of late summer (Figures 12 and 13). The data presented by Graboski and Heiber (1989) suggest that the food webs in the backwater environments of the Green River are not very productive. As noted above, these backwaters should contain rooted aquatic plants and a biodiverse, productive invertebrate and fish food web. I realize that the fluctuations shown in Figures 12 and 13 are considerably reduced from operations in the past. Nonetheless, development of stable, productive food webs in the backwaters probably have not occurred as a consequence of reregulation of the Flaming Gorge releases. Moreover, they will not likely ever be very productive, unless flow fluctuations can be eliminated. Empirical information with which to firmly judge the productivity of backwater food webs as influenced by regulated baseflow regimes throughout the Upper Colorado River is sorely needed and should be approached in the trophic dynamic context described above.

Peaking operations at Flaming Gorge are attenuated in relation to distance downstream from the dam. Therefore, baseflow instability (Figures 12 and 13) progressively worsens upstream from Jensen and may be severe in the Echo and Brown Park reaches. Elsewhere between Jensen and the dam, the river is constrained in canyons and the problem may be ameliorated by geomorphology. However, peaking flows are known to interrupt insect emergences that feed the trout fishery in Red Canyon immediately downstream from the dam (my observation and Larry Crist, Bureau of Reclamation, Salt Lake City, UT, personal communication). Similar effects were observed on the Missouri River below Holter Dam in Montana and outcry from fly fishermen caused load control operations to be shifted to another dam. The effect was a translocation of stream regulation effects from one river to another, thereby confounding management objectives (Stanford and Hauer 1992). This illustrates the potential difficulty of changing operations to meet the needs of endangered fishes in potamon reaches of the Upper Colorado River system, if rhithron trout fisheries might be influenced in the process.

Stream Regulation Mediates Invasions of Nonnative Predators and Complicates Provision of Instream Flows to Protect Endangered Fishes

Introduction of trout and other nonnative fish in regulated streams is an enormously confounding problem in the interpretation of the ecology of regulated streams because the native species virtually always seem to decline in the presence of exotics, whether the river is regulated or not. This pervasive ecological problem has been reviewed exhaustively (e.g., Mooney and Drake 1986). Clearly, predation of natives, including endangered fishes, by exotics does occur in the Upper Colorado River system; and red shiners (*Cyprinella lutrensis*), fathead minnows (*Pimephales promelas*), walleye (*Stizostedion vitreum*), northern pike (*Esox lucius* Linnaeus), channel catfish (*Ictalurus punctatus*), largemouth bass (*Micropterus salmoides*) and green sunfish (*Lepomis cyanellus*) are especially problematic invaders (cf., Karp and Tyus 1990, Tyus 1991b, Tyus and Haines 1991). However, Meffe (1984) and Minckley and Meffe (1987) showed that intense flooding in rivers in the southwestern United States was positively correlated with diversity and abundance of native fishes and negatively correlated with diversity and abundance of nonnative fish. The strong inference is that the nonnatives are maladapted to survive intense and frequent (annual, at least) flooding in contrast to the natives. Having fewer predators increases recruitment of natives, and over time allows the natives to persist in greater abundance than nonnatives (Figure 15). The work of Meffe and Minckley included the Virgin River and other tributaries of the Colorado River, but none in the upper basin. Thus, while the data are not directly applicable, the relation probably holds. Indeed, Hawkins and Nesler (1991) correlated lower ratios of nonnatives to natives with high peak flows in the Yampa River.

The prediction that flooding will limit predation mortality of endangered fishes is used as one rationale in the recovery program for reinstatement of peak flows. I note that introduced species, red shiners for example, are native in rivers that experience floods (of bankfull or greater) rather frequently, which might suggest that flow augmentation might not work very well in controlling some nonnative species. However, the complex interactions described above that are associated with major disturbance events, like flooding, may not manifest the same in all rivers or all river reaches, even if they are prone to flooding. The relationship needs to be examined and compared in constrained and unconstrained reaches.

Stream Regulation in an Ecosystem Context: Occurrence of Ecological Discontinuities

The cumulative effect of regulation, especially when deep release dams control the flow downstream, is that the rhithron-potamon transition zone is pushed downstream, producing an ecological discontinuity (*sensu* Ward and Stanford 1983). Biophysical conditions characteristic of headwater (rhithron) segments manifest in reaches that were characterized by warm water conditions before regulation. Very productive cold water food webs, including stenotherms such as stoneflies and trout (Figure 1), establish in waters that were inhabited by potamon species prior to impoundment.

Regulation of the Gunnison River by the Aspinall Units (Figure 9) has produced a classic and well documented ecological discontinuity. The position of the rhithron-potamon transition has shifted downstream 40 - 50 miles (Ward and Stanford 1991) as a consequence of reduced peak flows and colder water temperatures. Indeed, bankfull discharge of 11,000 cfs in the Gunnison Gorge downstream from the dams occurred every 3.2 years before regulation. Given the storage capacity of the Aspinalll Units, the historical water yield of the catchment and current regulation regime, bankfull discharge will occur only once in 40 years in the future (Elliott and Parker 1992). Moreover, baseflows are high and variable (e.g., Figure 11) owing to hydropower operations, and the hypolimnial releases have cooled the river at the confluence of the North Fork (Figure 1) by nearly 10°C during summer (Stanford and Ward 1983). A reproducing (wild) rainbow and brown trout fishery (Nehring 1988) developed in association with a biodiverse and very productive cold water zoobenthos community from Crystal Dam through the Gunnison Gorge to below the confluence of the North Fork (Figure 16) (Hauer et al. 1989, Stanford and Ward 1989, Ward and Stanford 1990, 1991, Stanford and Ward 1992b). Hence, the rhithron-potamon transition zone, which occurred within the Gorge prior to regulation, now occurs below the North Fork confluence. Creation of this substantial ecological discontinuity, coupled with construction of the Redlands and Hartland diversion dams which blocked migration pathways many years ago (Quaterone 1993), undoubtedly has contributed to the demise of squawfish and razorback suckers in the Gunnison River where they were formerly abundant (Tyus 1984, Minckley et al. 1991, Tyus 1991a).

However, the new rhithron community in the regulated Gunnison River is extremely fragile owing to the responsiveness of the ecological discontinuity to flow and temperature as controlled by reservoir releases. Indeed, the new rhithron food web, including the valuable trout fishery, was severely damaged by the episodic side flows (described above) that occurred during the summer of 1991-92, when the regulated flows were at or near the 300 cfs minimum. Benthos and fish were smothered by fine sediments (Stanford 1989). Recent experimental flows to help determine flow recommendations for endangered fishes in the Gunnison River reached 4,000 cfs in 1992 but were insufficient to rearrange alluvium entrained in the river channel (Elliott and Parker 1992). Due to the interactive effects of 1) a lack of spring peaks or other flushing flows, 2) an extended period of minimum flow (both 1 and 2 due to drought), 3) warmer temperatures associated with low flows and 4) episodic loading of the channel from ephemeral side flows, the position of the discontinuity moved upstream during 1991-92 and side channels and eddies filled in with fine sediments and vegetation. Today the riparian corridor of the river is densely vegetated, and, thus, surface and groundwater exchange with critically important backwater systems (Figure 2) has been altered or lost (Stanford and Ward 1992b). The food web in the lower part of the Gunnison Gorge remains impaired, owing to persistent fine sediments within and upon the substratum of the river bottom which prevents establishment of a productive biofilm and restricts attachment sites for zoobenthos.

This Gunnison River case history is a classic response to stream regulation. Similar results have been recorded elsewhere (e.g., Petts 1986, Stanford and Hauer 1992). Indeed, an upstream discontinuity clearly exists on the Colorado River (Voelz and Ward 1991) and the Green River (Pearson 1968), although the latter is significantly reset toward predam potamon conditions by the Yampa River (Annear and Neuhold 1983).

Conclusions Based Upon Review of the Ecological Literature Pertaining to the Endangered Fishes and the Regulation of Flow

1) The distribution, relative abundance, life histories and some important physical habitat preferences of squawfish, humpback chubs and razorback suckers (in that order) are reasonably well known (Figure 6) and documented in peer-reviewed literature. I found no compelling arguments against the scientific validity of this information. But, the influences of river hydraulics, sediment transport and riparian controls on the longitudinally dynamic food web are

not so well understood. In other words, the data upon which current flow recommendations are based primarily describes the ecology of the fishes, not the ecosystem that supports them.

2) Strong linkages between trophic (food web) and geomorphic attributes of the Upper Colorado River ecosystem are dynamic, or variable, in time and space. For example, algae (periphyton) and zoobenthos communities are more productive on cobble bars than sand, but substratum size on river bars is highly variable in time and space as a function of the dynamic sediment transport and deposition processes that occur as the river fluctuates between peak and baseflows (Figure 2). Another example, though not well documented, is the propensity for high benthic and planktonic production in subchannels (backwaters) and floodplain water bodies that were (predam) seasonally pulsed and predictable. These different, yet interactive, space and time scales that produce natural biophysical variation are the essence of the ecosystem in which the endangered fishes evolved.

3) Studies to date in the Upper Colorado River strongly infer that flow regulation, specifically reduction of the amplitude between peak- and baseflows, is a likely contributor to the decline of the native fishes. But, cause and effect are not simple relationships. For example, it appears that years of regulated flows, coupled with construction of revetments, have reduced the availability of backwaters and wetlands as nursery habitats that support larval and juvenile squawfish. Although extremely high flows appear to be associated with weak cohorts of Colorado squawfish and humpback chubs, extreme flooding needed to maintain channel morphology and channel-floodplain interactions likely are critical for long-term survival of the fishes. Indeed, the only recent incident of successful recruitment of razorback suckers occurred when high flows reconnected riparian gravel pits to the mainstem Colorado River. Presence of nonnative predators and reduced complexity of habitats needed by the different life history stages of the endangered fishes (due to severing of channel-floodplain connections and encroachment of riparian vegetation into the channel) further confound determination of cause and effect. The fundamental problem

with respect to provision of flows to recover the endangered fishes is balancing the many interactive effects in a manner that will favor the native fishes over the long term (i.e., decades).

4) The phenologies (life histories) of the endangered fishes, as well as zoobenthos which also have been studied in detail, are either directly or indirectly controlled by flow magnitude and timing and the association between flow and temperature. However, relationships between flow, channel configuration and thermal heterogeneity (cf., Ward 1984) have not been well integrated conceptually or empirically or in the context of the various life history stages of the fishes. A squawfish life history energetics model, for example, likely would be very helpful in this regard.

5) Stream regulation has introduced serial discontinuities (i.e., downstream extension of cold water or rhithron environments) within the river continuum of the Upper Colorado River system. The location and persistence of these discontinuities are directly related to flow, and largely determine where the endangered and other native fishes can achieve a positive life history energy balance (i.e., complete the life history with net recruitment of young at or above minimum viable population size). Bear in mind that these fishes are adapted to potamon conditions and the length of the potamon zone has decreased as a consequence of the downstream extension (discontinuity) of the rhithron zone through regulation of flow from the deep storage reservoirs. The concept of ecosystem "resets" and discontinuities (sensu Ward and Stanford 1983), coupled with the notion that connected channel and floodplain (backwaters, wetlands) components of the riverscape are seasonally pulsed by flooding (Ward 1989), robustly integrate the myriad of biophysical processes that are influenced by stream regulation. Strong inferences about how a river ecosystem may respond to alternative flow management actions must be derived in this ecosystem context. The downstream shift in the position of the rhithron-potamon transition is an ecosystem-level measure of change wrought by regulation and is a basis for adjusting flows to maximize conditions known to be favorable to both potamon (e.g., endangered fishes) and rhithron (e.g., trout) fisheries.

6) River ecosystems are too complex to be described by simple deterministic models or constructs of individual attributes. Ecosystem components are N-dimensional, inherently variable (stochastic) in time and space and interact in complex ways that cannot be predicted from simple logistical equations. Construction of an ecosystem model that describes all of the dynamic processes discussed above is likewise unreasonable as a predictive tool.

IV. Methods, Rationale and Critical Uncertainties in the Derivation of Recommended Flows to Protect the Endangered Fishes: Review and Synthesis

Review of Instream Flow Methodology

For well over two decades many different researchers have toiled to derive a general (easy to use), precise (gives same answer in repeated tries) and real (accurately describes the many interactive processes that occur in nature) model to predict stream flows to protect fish and invertebrates. Considering the myriad of factors that influence the distribution and abundance of endangered fishes in the Upper Colorado River system described above, and further considering how intractable controlling factors become when many different river systems and biota are of interest, the search for such a model is formidable indeed.

Nonetheless, instream flow modeling has been fostered by the extreme value of water and the unwillingness of water development interests to "experiment" with flows on a river-by-river or even segment-to-segment basis. Much litigation has resulted over the need to maintain flows within river segments to protect biota plus channel and floodplain features at the expense of flow depletion (abstraction) for other human uses or at the expense of less flexibility for hydropower operations.

Flow Threshold Models

A two-volume proceedings (Orsborn and Allman 1976) of a special symposium on rationale and approaches to instream flow methodology sponsored by the American Fisheries Society and the American Society of Civil Engineers set the stage for this endeavor to couple management-oriented aquatic science with the physical mechanics of water flow in stream channels. From the outset a fundamental tenet of the evolution of instream flow methodology was that something simpler (less mathematical) and more intuitive (to field personnel working for management agencies) than full-blown ecosystem simulation was needed. As a consequence, the methodology has tended to focus on economically important fishes and their habitat "preferences" as determined by flow. This should not be surprising since a primary objective of wildlife and fisheries management for decades has been to protect and enhance species-specific habitats in order to maximize carrying capacity, and hence, maximize harvest of surplus biota.

The first widely used methods were entirely based upon the fact that below some flow threshold, physical habitat becomes limiting to fish and other stream biota during some part of their life cycle. The most commonly used of these is the "Montana" method (Tennant 1975 and various modifications, see Weische and Rechard 1980 for review) which attempts to relate perceived problems, though rarely quantified (my observation, but also see Morhardt 1986), of the regulated flows to the historical flow regime that occurred on the average. This approach to habitat optimization, though still widely used (Reiser 1989), does not consider the importance of flow variation and its complex relationship to channel geomorphology described above.

Statistical Approaches

Many studies have attempted, with widely varied success, to statistically relate some measures of the biophysical attributes of rivers and streams to the disturbance effect of flow variation. Most of these studies are basic science where the intent was to document aspects of the structure and function of stream ecosystems with respect to flow changes. Much of the work was focused on demonstration of relationships between the distribution, abundance and behavior of aquatic biota and important physical variables using various regression and multivariate analyses in natural (regulated situations compared to unregulated controls) and experimental designs (experimental manipulations designed to simulate flow effects) (cf., Kroger 1973, Reice 1985, Perry et al. 1986, among many others). However, very few studies actually demonstrate a statistically valid relationship between biomass or some other abundance measure and flow variables that apply to different streams or even different stream segments. Indeed, Morhardt 1986 reviewed and annotated 72 studies that attempted to derive a general instream flow model that would accurately predict productivity to flow variables in different streams. Only one (Binns and Eiserman 1979) produced a statistically valid result, and Morhardt (1986) concluded that was because the streams were in the same region and were biophysically very similar. Armitage (1989) was able to predict the occurrence and biomass of macroinvertebrates from a suite of environmental variables using gradient analysis (TWINSPAN) in regulated streams in England. But again, these streams are rather homologous in comparison to the Upper Colorado River system, and the distribution of zoobenthos in English rivers, which have been regulated for centuries, is well known. Clearly, in small streams where flow processes are relatively uniform (non-stochastic) and distribution and abundance of biota are well known, relationships can be demonstrated with statistical accuracy and precision. Detailed presentations of the science of stream ecology with respect to the effects of flow and hydraulics are given by Resh et al. (1988) and Statzner et al. (1988).

In rivers that are large and complex most studies are site specific by design because it is widely recognized that unbiased replication of sites across streams is difficult, if not impossible, owing to the stochastic nature of large rivers. In fact, it is very difficult to replicate within a stream segment because flow mechanics produce so many different microhabitats that it is almost impossible to take enough samples to describe biotic distributions. Pseudoreplication is a problem in many studies. All streams are ecologically different and therefore mechanistic models must compromise reality to gain generality. The alternative is essentially a trial and error approach. In other words, multivariate analyses may show that certain flow variables influence biotic productivity in a regulated stream; therefore, a particular flow pattern should optimize productivity. The only way to verify that prediction is to implement the flow regime and monitor productivity.

Incremental Flow Modeling

In spite of the inherently variable nature of lotic ecosystems, the need to describe continuous functions between flow and habitat is widely perceived, along with the assumption that aquatic biota in rivers are primarily limited by availability of physical habitat. Physical variables, such as temperature, velocities, size of gravel, cover, etc., obviously vary with flow. So models were developed in an attempt to describe change in these habitat variables in increments of flow. This vastly more complicated approach still implies that as habitat increases so will fish carrying capacity, and hence, fish populations.

By far the most used (Reiser et al. 1989) and most sophisticated incremental method is that developed by the U.S. Fish and Wildlife Service (Bovee 1982). This concept is called the Instream Flow Incremental Methodology (IFIM) and is a collection of computer programs and analytical procedures designed to predict changes in fish or invertebrate habitats in a "representative" stream reach due to flow changes. The IFIM has three major components: 1) Transects across a "representative" reach are divided into cells (intervals) in which depth, velocity, cover value and often substratum roughness or quality are measured or simulated. These are assumed to be independent variables. 2) The range of velocities, depths and cover or substratum used by the biota are determined by relating occurrence of various life history stages (e.g., YOY, juveniles, adults, spawners) of target species to the "hydraulic" variables. In other words, life stages of target biota are sampled or otherwise monitored (fish preferences are often determined from animals fitted with radio transmitters) across the range of the hydraulic variables to derive "habitat suitability curves." Intuitively this is a logical approach, but it is often biased by sampling error, especially in large, deep and often turbid rivers where the biota are difficult to capture or see. 3) The net suitability of use of a given locality (transect cell) is quantified by a parameter called weighted usable area (WUA), which is a derived relationship between plan area of the transect cell (area available) and the habitat preference indices (from suitability curves) for velocity, depth and substratum. The WUA is calculated cell by cell and summed for the entire reach and over a range of discharges. Hence, increments of WUA for a stream become a continuous function of discharge. Easy to read and more detailed descriptions of IFIM are given by Gore and Nestler (1988) and Nestler et. al (1989). This procedure has been widely used to justify flow provisions in regulated streams throughout North America, in some cases leading to state statutes to guarantee protection of aquatic biota (Reiser et al. 1989).

Even though IFIM has become an industry standard (Reiser et al. 1989), it has a number of faults that are not widely recognized or understood within the management circles. Concern exists with respect to use of suitability curves as probability functions (Patten 1979, Mathur et al. 1985, Moyle and Baltz 1985), the assumption of independence of depth, velocity and substratum (Patten 1979, Malthur et al. 1985), the lack of a demonstrated relationship between WUA and a meaningful measure of productivity or biomass (Mathur et al. 1985, Bowlby and Roff 1986, Conder and Annear 1987, Scott and Shrivell 1987) and lack of any relationship with regard to many other ecosystem processes, such as predation and other density dependent relations, that clearly influence population structure (Moyle and Baltz 1985, Bowlby and Roff 1986, Orth 1987, Stanford and Ward 1992). To my knowledge none of these criticisms have been resolved, nor is it likely they will be. However, these criticisms have been placed in perspective with respect to the rationale and intent of the IFIM, which is often misunderstood, misrepresented and misused (Gore and Nestler 1988). For example, the model was not intended to predict biomass. It is a physical habitat simulator. Even when the model is applied properly, a variety of problems may emerge depending on input choices, which necessitates a clear understanding of how the model works. The simulator can use a variety of hydraulic predictors (e.g., the HEC-2 flow model of the U.S.

Army Corps of Engineers), each of which has biases and therefore will result in different WUA calculations (Gan and McMahon 1990). Suitability curves not derived on site (i.e., curves given in the literature) are often used, which can also bias output (Gore and Nestler 1988).

The IFIM was used in an attempt to derive flow recommendations for the Upper Colorado River with respect to the endangered fishes. However, in the analysis WUA often was maximized for various life history stages of squawfish and humpback chubs at very low flows that in the historical record were exceeded most or all of the time (Rose and Hann 1989). Such output is nonsense because the ecological data for these fishes clearly shows the importance of backwaters and eddies that occur at much higher flows. The problem here is that IFIM probably should never have been used in the big river reaches of the Upper Colorado River system. When low velocity habitats are abundant, as they are throughout the potamon of the Colorado River system, the simulator underestimates the WUA; in fact, the model cannot deal with zero flow habitats. This explains why IFIM works well only in small streams where the channel is characterized by uniformly varying flow (e.g., the low velocity profile reflects steady, uniform flow which is also an assumption of the HEC-2 hydrology simulator that is often used in IFIM, my observations). Also, habitat suitability curves were probably biased because the fish were difficult to observe or collect in the usually turbid, deep water of the Yampa and Green Rivers (Rose and Hann 1989) which is precisely why the adult monitoring program (U.S. Fish & Wildlife Service 1987b) emphasizes shallow, shoreline habitats that can be effectively sampled by electrofishing. However, the fishes routinely use deep water habitats (e.g., Tyus and McAda 1984, McAda and Kaeding 1991), and movement between habitats (e.g., channel, backwaters) on a diel basis cannot be accounted for in the method. A final point to keep in mind is that the utility of IFIM evolved a great deal during the period that data were being gathered in the Upper Colorado River studies, and deficiencies in the method with regard to the Colorado River perhaps were not apparent at the time much of the data were gathered.

Are There Other Options?

Certainly strong inferences can be derived from careful measures of channel processes that influence habitats important to the fishes. Reiser et al. (1989) recently described the physical relationships between hydraulics and movement of sediments with respect to deriving flushing flows to remove fine sediments entrained within the bottom of an alluvial river, as described above for the Gunnison River. These principles of flow mechanics can be used to derive other formalized approaches to manage flows for the purpose of maintaining channel forms the fishes use. Sediment transport mechanics depend upon detailed information on sediment gradation, channel geomorphology and channel slope. If data needed to calculate sediment mass balance are available and are coupled with detailed topographic information, derived either from air photos or surveys over the period before and after regulation, the morphological dynamics of the channel can be documented (cf., Andrews 1986, Lyons and Pucherelli 1992) and informed approaches to flow negotiations can proceed. However, regime analyses too often rely on untested assumptions that some flow volume and rate relationship, usually bankfull flow, is the dominant channel-forming flow. Determination of bankfull flow is problematic owing to local variations in channel morphology coupled with usually too few data on hydraulics of the reach during peak flow events.

The preferred approach in my view is a thorough, empirical understanding of sediment gradation, channel geomorphology and channel slope, with which movement of sediment, and hence the dynamics of many physical habitats important to aquatic biota, can be estimated as a function of the duration of peak flow events. Andrews and Nelson (1989) used this approach to document topographic responses of a large bar complex in the Green River over a history of flow events. A major advantage of the model is that, although it is deterministic, flows, sediment supply and to some extent the topography can be stochastic. The model is being used to predict dynamics of sediment transport and channel topography in response to flow variation elsewhere in the Colorado River system. Model development and verification is greatly assisted by recent improvements in automated field surveying equipment (total stations) that allow rapid and very accurate measurements of local topography (E. D. Andrews, U.S. Geological Survey, Boulder, CO, personal communication). However, as concluded by Reiser et al. (1989), the most certain method to determine relations between peak flow events and channel features in a regulated river is to tag an array of bed materials, carefully survey channel topography (*sensu* Andrews and Nelson 1989) and relate movement of materials and changes in topography to different flow events carefully controlled by reservoir releases. However, the flow peaks have to be high enough to move the tagged bed materials, which can be approximated *a priori* using standard hydraulic calculations.

From a more biological perspective, a number of alternative approaches are possible. Binns and Eiserman (1979) predicted trout biomass in Wyoming streams with a habitat quality index (HQI) in which 11 habitat variables, including baseflow and annual change in discharge, thought to influence trout populations were subjectively rated. The predictions were significantly correlated with actual measures of biomass. The Delphi rating schedules used in this technique apparently resolved much of the nonlinearity usually observed in relationships between habitat descriptors and fish biomass. However, Bowlby and Rolf (1986) were not as successful in using the method in Ontario streams because trout density changed within stream segments when habitat variables remained the same. Other biophysical indices of habitat quality have been proposed (cf., Osborne et al. 1992); they have been used to establish relative influences of stream regulation in different streams, but to my knowledge they have not been used to examine incremental effects of flow.

A general (simple application in different streams) incremental flow - biomass model that is statistically precise (repeatable) and accurate (describes reality) is likely not attainable, especially in large rivers like the Upper Colorado where ecosystem structure and function is complex and poorly known. It is feasible, however, to approach the problem from a multidisciplinary perspective, where strong inferences about how the endangered fishes are likely to respond to reregulated flow regimes can be derived from process-oriented studies that demonstrate key biophysical relationships. Linking hydrology, geomorphology and limnology in an ecosystem context is the key (Stanford and Ward 1992), and I recommend below a new approach for reaching an ecosystem level of understanding with respect to flow provision in potamon reaches of the Upper Colorado River.

<u>Flow Regimes Recommended to Protect and Enhance Endangered Fishes in the Upper Colorado River</u>

In this section I attempt a very concise presentation of the flow recommendations that were made by the U.S. Fish and Wildlife Service to provide context for my summary of problems with these recommendations, which follows in the next section. Flow recommendations have not been made for tributaries other than the Yampa.

Yampa River (U.S. Fish & Wildlife Service 1990):

- The "historical" flow pattern ("percentile flows that occur naturally"), based on derived monthly regime that includes 68.8 K acre feet depletion of historical flow, will be maintained.

Green River (U.S. Fish & Wildlife Service 1992):

- Between April 1 and May 15 releases from Flaming Gorge ramp upward (< 400 cfs/day) with the trend measured in the Yampa. Releases from Flaming Gorge will correspond to the peak flow in the Yampa to yield flow between 13,000 - 18,000 cfs for 1 (dry year) - 4 (wet year) weeks between May 15 and June 1. This may require release of 4,000 - 4,700 cfs from Flaming Gorge for the duration of the peak; if peak flow in the Yampa is < 9,000 cfs (very dry year), release from Flaming Gorge will be 4,000 - 4,700 cfs for one week corresponding to the Yampa peak flow.
- Releases from Flaming Gorge will ramp down (< 400 cfs/day) to 2,000 cfs for at least one week and then to 1,100 - 1,800 cfs at Jensen (first gauge below the Yampa-Green confluence)

by ca. June 20 on dry years, July 10 on normal years and by July 20 on wet years (target dates can be adjusted as new information on larval drift and entrainment in nursery areas becomes available). Hourly flows at Jensen will be maintained at 1,100 - 1,800 cfs (±25%) until ca. September 15; compensation for freshets from the Yampa (natural events) is not required. Water released from Flaming Gorge during this period will be from the warmest strata possible in the reservoir to produce temperatures in the Green River at Jensen that are no more than 5°C colder than temperatures in the Yampa at its confluence with the Green.

- From September 15 to November 1 flows will be as above, except during wet years when a range of 1,100 - 2,400 cfs (±25%) will be allowed.

- From November 1 flows will remain stable through the ice formation and spring breakup period, except as necessary to produce storage in Flaming Gorge that will ensure spring through autumn flows given above. If ice is not present, flows may vary within constraints of the U.S. Bureau of Reclamation agreement with Utah (i.e., 800 - 4,700 cfs). Section 7 consultation will occur if emergency events impact Reclamation's ability to comply with the above for more than 20 hours during any month.

- Beginning in spring 1992 "research flows" will be allowed. These experimental flows will be used to refine the current recommended flows as per priorities annually agreed upon by the U.S. Bureau of Reclamation, the U.S. Fish and Wildlife Service and Western Area Power Administration. The effects of winter baseflow to full peaking power fluctuations will be evaluated, along with one year of stable winter releases at or below 2,000 cfs and one year of spring flows utilizing jet tube bypass at the dam. Other research concerns listed were temperature control by selective withdrawal, feasibility of retrofitting bypass tubes for generation to allow bigger spring peaks, and mechanisms of legal protection of instream flows presumably through appropriation of conditional instream flow rights. Various studies underway in FY 93 are summarized in Bureau of Reclamation et al. (1992) and include studies of larval drift of squawfish, razorback suckers and humpback chubs, overwinter survival of squawfish YOY, geomorphic classification and ecology of backwaters, nonnative fish management and wetlands rehabilitation (Old Charley Wash).

- Flows that actually occurred in 1992 under the interim agreement (U.S. Fish & Wildlife Service 1992) are given in Figures 14 and 17.

Colorado River above Confluence with the Green River (Kaeding and Osmundson 1989, Osmundson and Kaeding 1991):

- At the state line gauge:
  a) maintain or increase the current 25% peak flows (high day of the year) at 30,000 - 40,000 cfs (squawfish recruitment peaks);
  b) increase the frequency of years with peak flows in excess of 40,000 cfs from one in twelve years (8%, the current condition) to one in four years (25%) (i.e., flushing peaks); and
  c) the rest of the time (50%) maintain peak flows equal to or exceeding 22,000 cfs (minimal recruitment peak).
- Within the 15-mile reach provide peak flows as given in Table 1.

Table 1. Recommendations for spring flows (in cfs) in the 15-mile reach (from Osmundson and Kaeding 1991).

Frequency (percent years)	Peak day	Mean monthly discharge		
		April	May	June
≥ 25%	> 23,500	> 3,900	> 12,900	> 16,300
≥ 25%	20,500 - 23,500	3,200 - 3,900	10,800 - 12,900	12,800 - 16,200
≤ 50%	14,800 - 20,500	2,400 - 3,200	8,300 - 10,800	10,000 - 12,800

- Maintain July - September flows from 700 - 1,200 cfs on normal or wet years and 600 cfs minimum on dry years within the 15-mile reach.
- Maintain current (1954 - 1989) base (winter) and transition (October and March) flows (ca. 1,000 - 2,000 cfs) in the 15-mile reach.

Problems with the Flow Recommendations of the U.S. Fish and Wildlife Service

Yampa River

Recommendations made for the Yampa River specify maintenance of historical flows. I support that objective, although I did not verify the baseline and I do not think it is appropriate to use monthly means in such analyses. The daily flow duration curve for the period of record would more accurately reflect the real baseline.

The Yampa clearly is a critical habitat for the endangered fishes. Recruitment of populations in the Green River may depend upon spawning sites in Yampa Canyon. Most importantly, the Yampa River is the only reasonably pristine tributary remaining in the Upper Colorado River system. Hence, I view it as a "control" for evaluating the success or failure of interim flows adopted on the regulated reach, which will be a critical assessment to be made in the future.

Green River

Recommendations on the Green River were based on inferences from ecological studies of the endangered fish, which I summarized above (not necessarily in support of the recommended flows), and the backwater area to discharge relation determined by Pucherelli et al. (1990). The main intent of the peak flow recommendation apparently was to add volume to the peak flows derived from the Yampa River to create an annual spring peak sufficient to flood and maintain connectivity of the channel to backwater environments and floodplain wetlands in the aggraded reaches near Jensen and downstream.

Rationale for duration and amplitude of the spring peak was not given, except with regard to constraints on releases at Flaming Gorge Dam (i.e., only 4,000 cfs can be discharged through the generators plus an additional 4,000 cfs can be passed through bypass or jet tubes without opening flood gates). The fact that the Yampa and Green Rivers historically peaked at different times was not clearly addressed, nor were the proposed ramping rates on the rising and falling limbs of the hydrograph in either the context of the discharge to backwater area relationship of Pucherelli et al. (1990) or the need to establish ecologically functional wetlands on the floodplain (e.g., at Escalante Bottom). Also, the recommended flow regime allows a great deal of fluctuation at baseflow (late summer and winter - see Figures 10 and 12 - 14), which I believe will compromise maintenance of food webs needed in backwaters within the varial zone of the river. The flow-backwater relationship of Pucherelli et al. (1990), upon which the baseflow recommendations were made, is valid only for current channel morphology and will likely change with onset of new peak flows.

The ecological basis of the temperature criterion (i.e., < 5°C change at Jensen relative to Yampa River temperatures at the confluence) was not established for either the channel or the backwater environments. I argue in Part III above that temperature pattern in the channel and backwaters is critical to the ecology of the river, and hence, survival of the fishes. Temporal and spatial patterns of temperature in the Green River depend upon the release level at Flaming Gorge, volume, distance from the dam, ambient air temperatures, channel morphology and amelioration effects by side flows, especially the Yampa. This relation apparently can be partially controlled by the selective withdrawal system at the dam, at least to Jensen.

These concerns are clearly problematic with respect to legitimacy of the flow recommendations for the Green River. Some of my concerns may be resolved by the ongoing five-year research program, although work plans I reviewed were too brief to allow judgment on that issue. Moreover, integration among projects on the Green River and with recovery projects elsewhere in the Upper Colorado River is lacking or unclear. Research objectives ought to be fairly uniform throughout the Upper Basin, given that the same fishes and ecological issues are involved in all of the tributaries.

However, my greatest concern with recommendations for the Green River is that peak flows are not very high and the baseflows are not very low by predam standards (i.e., the ratio of peak to baseflow is 40 based on predam flows of record, whereas the recommended ratio is 12). Hence, the flow recommendations may not do much ecological good, especially if the peaks do not accomplish much channel reconfiguration and baseflow fluctuations for hydropower operations do indeed compromise stability of the food webs.

Colorado River

On the Colorado River, IFIM and a FWS flow-temperature model were used to predict July - September baseflows that 1) maximized runs, riffles and pools (not backwaters) used by adult squawfish and 2) increased temperatures 1 - 2°C over 1978-86 observed values (with the thought that age-0 fish would grow faster). Discharge, backwater and temperature relations therefore may be suspect, owing to the tendency of IFIM to over-emphasize the importance of low flows as preferred habitats. However, the analysis may be generally correct by default, because Kaeding and Osmundson (1988) argue convincingly that the 15-mile reach is suboptimal habitat thermally. Certainly lowered summer flows should allow the water to warm up more. However, backwaters might be too shallow to support food webs that also are needed. I understand that work is underway to provide a better estimate of flow-backwater relationship in the key reaches of the Colorado River. In general, the rationale for baseflows is much more refined and data-based than on the Green River.

Spring flows on the Colorado rivers were recommended on the basis of departure from historical records and the need to flush the rivers to revitalize low velocity habitats that are thought to be critical to the survival of the fishes. I support the intent based on my review and synthesis of the ecology of the river given above. However, the spring flow recommendations were also rationalized in part on the perceived need to provide intermediate flows 50% of the time to foster favorable recruitment of squawfish (i.e., frequency of peak flows were based on data in Figure 4). (Similar data were not presented to support this flow recommendation on the Green River, although I understand that 1983-84 cohorts were low in relation to flows of record, Tim Modde, U.S. Fish and Wildlife Service, Vernal, UT, personal communication. The flow-recruitment relationship should be thoroughly examined and presented in the context of adult captures over the long-term flow record in both rivers). I noted in Part III above my concerns with the flow-recruitment relation of Figure 4; but, if the general relationship of Figure 4 is valid, and I think these are indeed pivotal data, clearly a tradeoff exists. High flows in the Colorado River (and elsewhere) may be expected to produce in- and off-channel habitats that are critical to squawfish and razorback suckers at the expense of recruitment of squawfish. Intermediate flows may produce stronger squawfish cohorts as habitat quality in general deteriorates, and perhaps, dramatically influences survival of razorback cohorts because wetlands or gravel pits they need cannot be accessed. I think the recommended flows, if implemented as interim flows over a reasonably long (five years) time period, can allow the consequences of this tradeoff to be clarified.

Peak flows exceeded 30,000 cfs at the state line 23 years out of 51 in the period of record used to rationalize flow recommendations for the 15-mile reach. So, the recommendation that high flows occur 25% of the time is somewhat confusing. According to Doug Osmundson (U.S. Fish and Wildlife Service, Grand Junction, CO, personal communication) this really means that at least one year in four should have peaks of 30,000 - 40,000 cfs and, currently, that is indeed the case. However, peak flows at the state line gauge are due in large part (47%) to discharge from the

Gunnison River, and it is not clear how that system fits into the picture. This seems problematic if different flows are ultimately derived for the Gunnison River. Currently, squawfish recruitment is not measurable in the Gunnison River, even though they are known to persist above the Redlands diversion dam. Reregulated flows and removal of the diversion dams, provision of bypass devices or introduction of cultured stocks may allow the squawfish and razorback suckers to recover in the Gunnison River. (The same applies to the Colorado River with respect to the Palisade diversion dams that delimit the upstream end of the 15-mile reach. Conditions seem very favorable for squawfish and razorback suckers upstream from these structures). Because peak flows also are needed on the Gunnison to rebuild habitat, the recommendations for the 15-mile reach may be higher than needed. Similar concerns may apply to other tributaries, especially the Dolores and White Rivers. However, the flow recommendations for the Colorado River are more solidly rationalized and data-based than recommendations for the Green River in the context of my review and synthesis of the river ecology of the Upper Colorado River and the interactive effects of regulation. The recommended peaks and baseflows more closely reflect predam conditions, in spite of the dramatic depletions that have occurred in the Colorado River above the Gunnison River confluence (Figure 8).

Differing Methodologies and the Role of "Professional Judgment"

Because I was asked to review the methods for assessing instream flows, it appears that the efficacy of the various instream flow methodologies was not fully understood while studies leading to the recommended flows were being conducted. Heavy investment in IFIM was made, and it clearly was not warranted. The method as currently formulated should not be used in the future in the potamon reaches of the Upper Colorado River, owing to the problems I detailed above. The recommendations should have been based primarily on inferences from long-term qualifications of energetics, habitat preferences, recruitment, channel geomorphology and food web composition and stability and simple correlations with the highly variable flows that eventuated over the decade of the 1980s. Had that been done, I think the flow amplitude recommended by the U.S. Fish and

Wildlife Service on the Green River would have been higher (higher spring peaks, lower baseflows) and more consistent with my synthesis of the existing information. The Colorado River recommendations probably would not be much different than were proposed, because they were logically based on the available information in spite of the fact that IFIM data were included.

Moreover, reliance on "professional judgment" is overemphasized as rationale for the flow recommendations of the U.S. Fish and Wildlife Service, given the general high quality of the ecological studies that have been done. That a high peak to baseflow ratio should be reflected in the recommended flow regimes to protect the endangered fishes is strongly inferred by the available science, and is not simply professional judgment. However, segmenting the ecosystem to make flow recommendations and using different approaches to similar problems in the three segments for which flow recommendations have been made clearly undermined the credibility of the science (see also University of Colorado, Denver, 1993). However, ongoing work seems responsive to criticisms and it appears that the depth of understanding and methods are converging within the system. One purpose of this review is to foster that convergence and to focus on the larger issue of critical uncertainties with the state of the knowledge base, not just the problems associated with some methods.

Critical Uncertainties in the Recovery Program with Respect to Provision of River Flows to Protect Endangered Fishes

In a program with a scope the size of the recovery program for endangered fishes in the Upper Colorado River system, uncertainties are inevitable. However, uncertainties must be recognized and resolved if program goals are to be reached. Based on my review of the ecological information and recognizing the problems in the methodological approaches that were used to derive flow recommendations to protect these fishes, I list here uncertainties that appear to be critical to the goal of establishing flow regimes that will recover the endangered fishes. Uncertainties always occur in two basic, but very different, forms that are interwoven in any natural resource management process: those that relate to the technical understanding and those that relate to policy implementation.

Critical Uncertainties at the Program (Policy) Level of Organization

1) Flow seasonality and its correlates (e.g., temperature and physical habitat) may not be the factor(s) limiting recovery of the native fishes. For example, food web interactions may be preventing recruitment of YOY in a manner that is ecologically complex, but independent of flow. Or, recruitment might be limited by chronic effects of selenium or some other pollutant. Given the data currently in hand, this seems to be an unlikely scenario, but a successful management process requires careful consideration of, and planning for, unexpected alternatives.

2) Given the high societal value placed on tailwater trout fisheries, and the high priority placed on meeting entitlements under the Colorado compact and current water law (i.e., the "law of the river"), water volume in the Colorado and Green Rivers may be insufficient to produce flows required to recover the fishes upstream from Lake Powell. This is the tough one and it follows that a firm, common understanding of water supply and legal allocation is required so that valid alternatives can be derived. Confidence in water supply predictions is equally as important as predictions of water needed to recover the fishes. Both of these issues will evolve as more information is available, so it is wise to keep them in the same context.

Critical Uncertainties at the Information (Scientific) Level of Organization

1) Channel morphology in time and space is not a simple stage-area relationship. Formation and maintenance of low velocity habitats (e.g., chute channels and other backwaters, see Figure 2) are critical for successful recruitment of YOY and juveniles of all four endangered fishes. Flushing flows are clearly needed to scour sediment and vegetation from low velocity habitats and remove fines entrained in cobble bars to increase benthic production. However, the tradeoff between very high peaks (near flows of record) of short duration versus lower peaks of

longer duration (as is now proposed) have not been examined in enough detail. The role of interstitial flow in forming and maintaining low velocity habitats and food web dynamics have not been investigated at all. Given that predictive models of incremental flows and bioproduction have not been forthcoming, a new approach is needed (see below).

2) What is the tradeoff between propensity of endangered fish larvae to drift downstream and the need for high flows to maintain connectivity between the channel and backwaters and wetlands? Larval drift appears to be tightly coupled with flow volume and availability of low velocity habitats. If flows are implemented that are too low to create complex channel features that retain passively drifting larvae, they may be swept out of the areas where they can mature. On the other hand, reformation of wetlands could create additional or new habitat that is favorable to nonnative predators, thereby swamping the gains made by implementing peak flows. Keep in mind that the observation that peak flows compromise nonnative fishes was primarily made in constrained reaches (e.g., Yampa Canyon) where refugia from the scouring effects of high flows are more limited.

3) Can food webs re-establish in the varial zone to the extent needed to recover the fishes, given the windows permitted or needed for hydropower operations? The pervasive influence of baseflow changes is not well documented and may in fact be the factor limiting riverine productivity. This also has policy ramifications because it is possible for the Bureau of Reclamation to limit peaking and load operations at Flaming Gorge and the Aspinall Units to produce more uniform flows if the payoff in more productive food webs is realized as is predicted from experience elsewhere.

4) Can the endangered fishes expand their range and productivity given the downstream shift in the rhithron-potamon transition, and is the locality of the transition zone likely to stay constant as reregulated flow regimes are implemented? This uncertainty is discussed in detail

above and clearly the result of reregulation can be inferred from existing data on each of the river segments for which flows have been or will be recommended. This has not been done, except on the Gunnison. However, it appears that the combination of temperature and bed materials of the predam rhithron-potamon transition no longer occur. Seasonal and annual temperature patterns have shifted downstream and sand domination of bottom substratum has shifted upstream.

Conclusions with Respect to Provision of Flows

Habitats of Endangered Fishes are Suboptimal and Maintenance of Current Flow Conditions Will Not Facilitate Recovery

Environmental change caused by operation of on-channel reservoirs manifests in the form of ecological discontinuities that likely control distribution and abundance of the endangered fishes. As a consequence, adult squawfish, razorback suckers and humpback chubs are most abundant in stream reaches where maximum summer temperatures seldom reach or exceed 23-25°C in the channel. Moreover, other physical attributes of the system that the fish clearly depend upon have been subjected to a wide array of environmental change (e.g., increased baseflow variation owing to regulation, revetment of backwater areas, higher water clarity from reservoir entrapment of sediments, introduced species, etc.). I agree with Tyus (1992) that considerations of instream flow provisions are based on ecological information obtained in suboptimal habitats of these fishes. However, that is the only information that is available, owing to extensive environmental change before ecological studies were begun. Given that the fishes have been studied in suboptimal environments, knowledge about large floodplain rivers on other continents (cf., Welcomme 1979, Dodge 1989, Petrere 1991) should be carefully considered. Some convergent evolution probably has occurred in relationships between fish faunas and floodplain river dynamics that can be extremely useful in decision-making processes in the Colorado River.

Provisions of flow must be predicated on the strong inference that maintaining current conditions will not contribute to recovery of the fishes. Squawfish, and perhaps humpback chub, populations may have stabilized to some extent in response to existing conditions, but their long-term persistence may not be likely because environmental change will continue to add negative influences on the fishes (e.g., with the expert panel and Doug Osmundson, I witnessed on our field trip in April, 1993 new revetment projects which further constrained the channel within the 15-mile reach).

Implement Interim Flows that Re-establish Functional Backwater Habitats in the Key Aggraded Segments and Allow the Fishes to Recover Naturally

The specifics of how exactly to reregulate flows to recover the endangered species remain problematic for lack of an approach or method that can relate incremental flows in ~~an~~ integrative way to the structure and function of the ecosystem. However, the fishes will not recover if flow fluctuations continue to uncouple floodplain and channel components of the ecosystem and compromise persistence of food webs in the varial zone. There is a risk that higher amplitude (peak to baseflow) regimes may be implemented and fishes will not respond or a number of years may be required before a response can be quantified. However, this is one of several critical uncertainties that cannot be resolved without implementing higher peak to baseflow regimes and determining effects on fishes as well as compact entitlements.

How much higher? I don't know, exactly. But it is clear that the fishes may be most compromised by poor availability of high quality (i.e., productive food webs dominated by native fish), low velocity habitats. The existing information strongly infers that the primary problem is inability of existing flow regimes to scour sediment, thereby constraining and simplifying channel morphology. Higher peak flows (e.g., within 5% of the flows of record) of shorter duration than what have been recommended to date will transport more sediment. I conclude that it would be better to go as high as possible without inducing excessive flooding of human inhabitations for a shorter period (2-5 days) to build a greater range of physical complexity in the channel (i.e., channels will scour deeper, bars will build higher and the channel will develop more complexity and surface roughness as flows decline).

The flow recommendations made by the U.S. Fish and Wildlife Service clearly are better than the *status quo* and the need for further ecological and geomorphic data discussed herein should not deter implementation, at least on an interim basis. The recommended flows are a reasonable starting point but must be refined as ecological responses are evaluated with rigorous statistical designs (see below). Experimental flows, scheduled for the Green and Gunnison Rivers, must be properly conducted to allow concerns about the efficacy of the interim flows to be resolved. Careful attention to the many matters discussed in this report with respect to ecosystem structure and function will be required.

Reregulation is especially needed to re-create low velocity, backwater habitats and natural food web function, both temporally and spatially and with reliable frequencies. To do this we need to do five things: 1) firmly understand how peak flows reconfigure the channel and flush out fine sediments in relation to food web structure and function and the spawning requirements of the endangered fishes (e.g., much should be learned from the high runoff in the spring of 1993; if not, the recovery program is not functioning properly); 2) do away with (in large part) late summer and winter power generation for peaking to stabilize baseflows and channel-backwater connections (the preferred tradeoff is higher volume for greater stability, sometimes referred to as "baseloading"); 3) permanently open revetted and/or naturally blocked backwaters and wetlands in the aggraded segments of the Green (e.g., Escalante and Ouray reaches), Colorado (e.g., Walker reach) and Gunnison Rivers (e.g., Escalante reach); 4) eliminate on-channel diversion dams (e.g., Redlands, Hartland, Palisade, Cameo, DeBeque) that block migration pathways either by physical removal or construction of effective fish passage devices; and 5) monitor ecological indicators of response to reregulation in an adaptive manner that will allow flows to be refined as new information becomes available. I caution against fish culture operations (stocking) in lieu of these five actions. The fishes should recover naturally and at less cost in the long run through proper reregulation of flows and habitat enhancement.

A Community Ecology Approach Should Complement Standardized Monitoring

The standardized monitoring program (U.S. Fish & Wildlife Service 1987b) is sufficiently developed to demonstrate trends in the populations of the endangered fishes. Continuation of this data base is absolutely essential as a performance check on the recovery program. More accurate population estimates should be a top priority by permanently tagging a large proportion of endangered fishes. Passive integrated transponder tags (PIT tags, 11 mm) have proven effective and should continue to be used; new, smaller tags will be available soon to allow very small fish to be permanently tagged (citation needed). Systematic procedures are needed to insure that tags are implanted in all new fish captured and recorded by all researchers working in the Upper Colorado River Basin. Proper mark/recapture analysis designs should be used upon consultation with fisheries biometricians (e.g., Kenneth Burnham, Colorado State University).

It also is essential that the trophic ecology of the rivers become better understood in order to approach flow provisions adaptively, and my studies with J. V. Ward on the zoobenthos demonstrate the utility of understanding the distribution and abundance of species throughout the river continuum. Presence of healthy populations of the mayfly, *Traverella albertani*, and the Dobson fly, *Corydalus cornutum,* clearly indicate the existence of healthy potamon food webs. The salmon fly, *Pteronarcys californica,* is a firm indicator of the downstream end of the rhithron (Ward et al. 1986, Ward and Stanford 1991, Ward 1992). These insects are easily recognized and will be present in kick samples on clean cobble runs and riffles. If they are not present, something is wrong with the food web. Moreover, strong inferences about the potential for recovering endangered fishes may be derived from examination of other native species. After all, flannelmouth, blueheads, speckled dace and roundtail chubs also segregate within the various river segments and may be declining in areas where the interactive effects of regulated flows are most pervasive (my observation).

The condition of native fishes (e.g., flannelmouth and bluehead suckers, roundtail chubs) that are not now considered threatened or endangered should be monitored to provide more information on the resiliency of the native fish community to environmental change. Indeed, all of the data gathered to date strongly suggest that future evaluations should be framed from a full community ecology perspective that, of course, emphasizes the endangered fishes. Total community stability, colonization-extinction relations, trophic cascades, strong interactions and other determinations of dynamics in the community properties of food web theory have been articulated in a great body of literature (e.g., Lowe-McConnel 1987, Matthews and Heins 1987, Kitchell 1992) that does not seem to be a part of the recovery program. Current studies are too focused on populations of individual species instead of the assemblages of all fish species as the key ecosystem component of the recovery program.

Understanding the importance of the rhithron-potamon transition to these fishes will be especially insightful. Repeated measures analysis of variance and other multivariate statistics (e.g., Gelwick and Matthews 1992) can be used to better estimate the spatial and temporal variation in the fish communities at some key monitoring sites.

Provide Better Understanding of Water Availability

Finally, a clear need exists for a common understanding of water availability. The "Guru II" process (University of Colorado, Denver 1993) is encouraging, and hopefully, resulting policies will be responsive to the implications of this report. On the technical side, development of more accurate hydrologic models that focus on the process of water and sediment routing is critical to refinement of the flow recommendations. A good example is the compartmental model currently under development in the Gunnison River catchment by the U.S. Geological Survey (citation needed). This model uses climatic data to confidently predict water yield and should be very useful in forecasting water availability and thereby allow flow regimes on the Gunnison River to be refined annually.

However, I return to my caveat at the outset of this study. Modeling is not a panacea nor should it be the primary goal. Mathematical and conceptual constructs are useful mechanisms for formalizing what is known from empirical study. The goal is to understand the complexity and stochasticity of the ecosystem that is influencing the distribution and abundance of the endangered fishes. Also, geomorphology by itself will not allow flows to be refined, nor will fish biology be sufficient. Rather, we must empirically link biophysical conditions with the factors that influence fish production in time and space as strong interactors within the ecosystem encompassed by the catchment of the Upper Colorado River.

V. Recommendation: An Ecosystem Approach to Refinement of Flows to Protect Endangered Fishes in the Upper Colorado River System

The main premise of recovery of endangered fishes identified in this report is that higher amplitude (peak to baseflow) annual flow regimes need to be implemented, monitored and refined with respect to uncertainty about ecological effects and influences on water supply within the Upper Colorado River system. However, a new approach is needed to increase the confidence that responses to flow regimes can be demonstrated empirically. The primary goal is to thoroughly understand how different annual flow patterns influence distribution and quality of food webs from the rhithron-potamon transition to Lake Powell and thereby influence the recovery of the endangered fishes. However, I emphasize that I do not propose a new, long-term research program that has to be completed before flows can be implemented. On the contrary, I advocate imposition of the flows currently recommended by the U.S. Fish and Wildlife Service with the proviso that the effects of those flows be evaluated in an adaptive management context.

The proposed methodology has three fundamental elements: 1) implementation of interim flows as recommended by the U.S. Fish and Wildlife Service, but if possible, with higher peaks (at the expense of duration, if necessary) and minimal short-term variations for hydropower peaking during baseflow periods; 2) resolution of effects of seasonally variable flows on linkages between channel-floodplain morphology and riverine food webs in selected stream reaches; 3) correlation of these results with the standardized monitoring program to draw inferences about status of endangered fishes within the stream continuum from the dams to Lake Powell; and 4) implementation of an adaptive management process to refine the flow provisions as interpretations of flows and ecosystem responses are made.

Arguments for provision of modified interim flows are given above, but the Gunnison River should be included as it is a critically important tributary. The Yampa River is the unregulated control for interpreting responses in the regulated tributaries. At some point the Dolores and White Rivers should be included in the study design.

Reaches for empirical study and modeling should be limited at the outset to sites in aggraded segments because a greater range of habitats occur in association with larger floodplain surfaces and the area of the varial zone is larger than in the canyons. Moreover, it is intuitive that refining flows for the aggraded segments likely will produce favorable results (not necessarily optimal) in the constrained reaches of the system. Sites known to be important to the endangered fishes should be emphasized (e.g., Cleopatra's couch bar on the Yampa; Ouray reach on the Green; complex channel areas above and below the Gunnison confluence in the 15-mile reach; Camel Switch area on the Gunnison and at least one lower river site on the Colorado and Green Rivers).

The modeling approach of Andrews and Nelson (1989) should be used to establish topographic and substratum changes, but at some point expanded to include analysis of interstitial flow, with respect to discharge variation that occurs on short (daily to weekly) and long (seasonal and interannual) time scales. Distribution and abundance of zoobenthos (cf., Ward and Stanford 1991), zooplankton (backwaters, Wetzel and Likens 1979) and fish (all species, cf., Gelwick and Matthews 1992, Meador and Matthews 1992) should be stratified within the reach as determined by the diversity of detailed topographical features. Emphasis should be given to understanding backwater food webs and relationships to discharge-mediated connectivity with the river channel. If possible, estimates of some measure of the primary producer community (e.g., organic matter standing crop in size fractions, community P/R, chlorophyll *a*, macrophyte diversity and dry weight biomass) should be made in relation to at least pre- and post-spate conditions, also stratified within the reach. Reaches need to be instrumented with multiple temperature sensors in various habitats (thalweg, shoreline, backwaters, air, hyporheic zone). Discharge measures must be made on site to calibrate USGS data to the site as input to the topographical model and other interpretations.

Interactions of flow and biophysical variables between and within reaches should be examined using appropriate statistical (cf., Gelwick and Matthews 1992) designs planned and peer reviewed *a priori*. Much more attention needs to be given to variance estimates and hypothesis testing. All parties need to carefully discuss the environmental, biodiversity and societal concerns related to Type I and II errors in statistical design and rationale for setting alpha levels (p-values) for falsifying hypotheses. The tendency to rely on inferences from means must be resisted, and proper statistical planning should be implemented prior to the initiation of field work. The approach recommended here involves expertise in geomorphology, hydrology, and fisheries; biometrics expertise should always be a priority.

The entire river system should be periodically stereo-photographed at 1:6000 (e.g., after, not during, every near record flow event) or other appropriate scale to allow inferences at the local study sites to be related to changes observed systemwide. This is also a good way to document changes in the riparian community and non-flow sources of environmental change, such as revetments. I caution that technology is rapidly approaching the point that near real-time data (e.g., using low altitude, multi-spectral video imaging, time lapse photography) may provide a better approach to regionalizing locally-derived (ground-truthed) data. Currently, however, interpretation of stereo color photos remains state-of-the-art.

Sampling of zoobenthos and fish communities should be done at additional locations to better establish longitudinal trends in the distribution of biota and the relative stability of food webs. These data are also needed to describe responses to environmental change in the ecosystem context of serial discontinuities. Continued attention to the accuracy of sampling is warranted. Quality control checks (for example, by releasing tagged fishes and invertebrates within the sampling zone and determining percent recovery) should be part of the standard protocol. This will help resolve concerns about how to handle such things as skewed distributions of various species and zero catches, which have been contentious in the monitoring program to date. In all respects, always link the physical and biological work at the outset, and integrate results often.

Adaptive ecosystem management in the context of this study design involves 1) determination of alternative flow regimes based upon all ecological data and a clear understanding of water availability, 2) formal assessment of the risk of failure of alternative regimes, either directly or through interference with unrelated actions (e.g., downstream provision of flows for squawfish that compromise trout fisheries near the dam), 3) design, implementation and peer review (outside of the recovery program!) of a monitoring and research program that will demonstrate ecosystem-level effects of the management action (i.e., interim flows as recommended), 4) implementation of a preferred action (interim flows) and 5) existence of a management process that can effectively implement an alternative regime, if monitoring indicates that current flows are failing to protect the fish of concern or jeopardizing water development entitlements (Hollings citations needed). The current recovery program has only some of these elements. However, the most obvious missing ingredient is the ecosystem context and the need for a more integrative monitoring program. Initially, the research proposed above is needed to establish cause and effect and to clarify long-term monitoring needs. In the interim, the existing monitoring program should be maintained. The protection of entitlements can be approached in the same adaptive fashion.

I appreciate the idealism in this approach, and I am not convinced that existing entitlements can be developed and at the same time maintain adequate peak to baseflow regimes needed to recover the fishes. However, it does formalize the elements that are critically needed. Perhaps with better empirical information about flow effects on ecosystem attributes that critically influence the endangered fishes, parties in contention can find middle ground. However, the experimental flows and adaptive management approach to evaluation need an unambiguous endorsement. Although I have pointed out major holes in the data regarding the basic environmental requirements of the endangered fishes, I am satisfied that the state of the ecological knowledge in the Upper Colorado River Basin is sufficient to justify endorsement of interim flows.

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Figure Legends

Note: All figure legends are at the bottom of the figures with the exception of the legends for Figures 10 and 14 (below).

Figure 10. Fall and winter flows on the Green River (at Flaming Gorge Dam, red line, and at Jensen, blue line) in relation to unregulated flows from the Yampa River (green line). Data from W. Brad Vickers, (U.S. Bureau of Reclamation, Salt Lake City, UT).

Figure 14. Summer and fall baseflows on the Green River (at Flaming Gorge Dam, red line; and at Jensen, blue line) in relation to unregulated flows from the Yampa River (green line). Lines delineating 1800 cfs (black) and 1350 cfs (grey) represent baseflow operational windows recommended for recovery of endangered fishes (U.S. Fish & Wildlife Service, 1992) as derived from the stage-backwater relationship determined by Pucherelli et al. (1990) and Lyons and Pucherelli (1992). Data from W. Brad Vickers, (U.S. Bureau of Reclamation, Salt Lake City, UT).

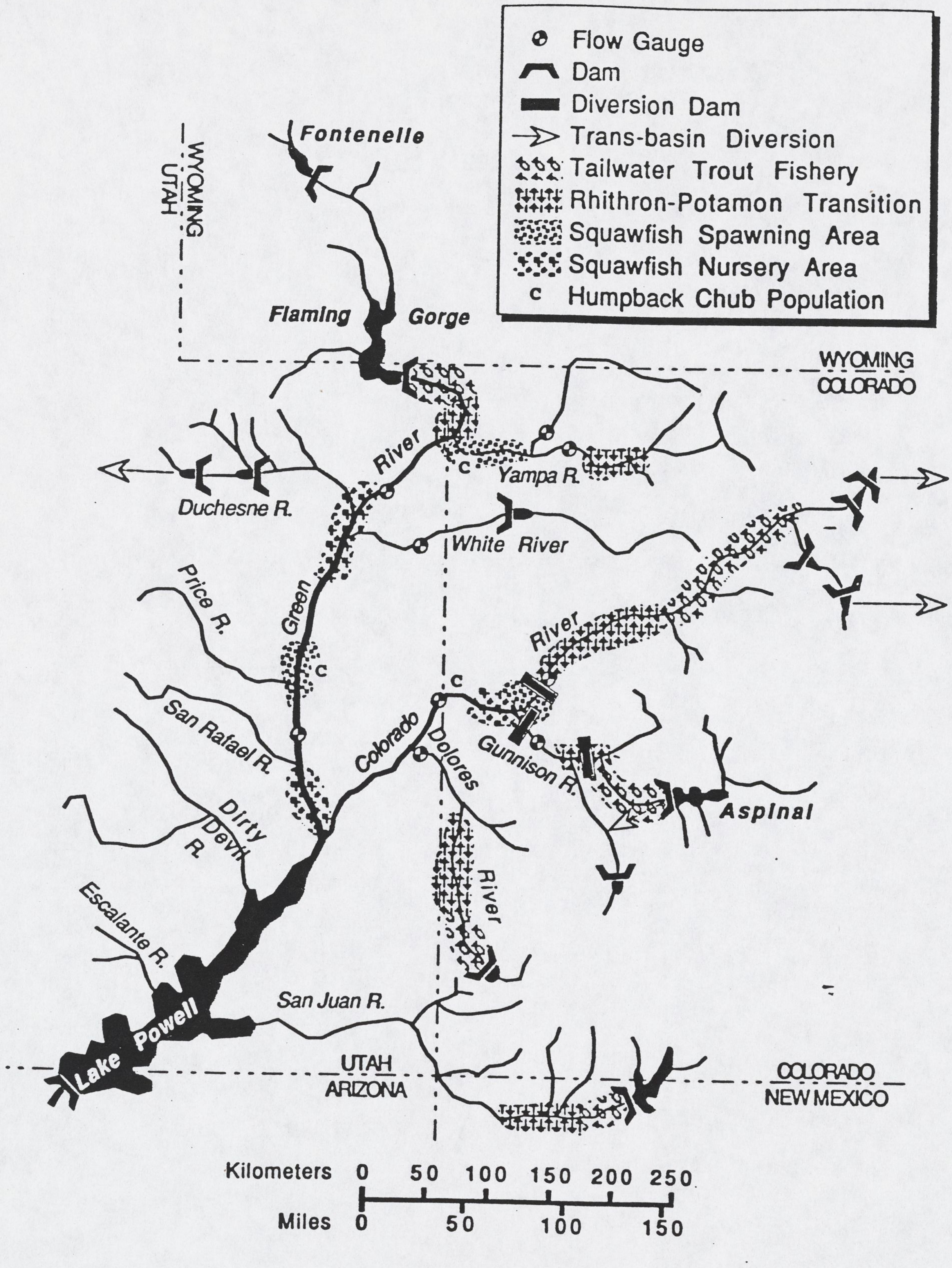


Figure 1. The Upper Colorado River system upstream from Lake Powell, showing rhithron-potamon transition zones on the largest tributaries, localities of reproducing humpback chub populations, localities of squawfish spawning and nursery areas, hydroelectric dams and diversions that regulate discharge and block squawfish and razorback migrations, and localities of economically important tailwater trout fisheries (modified from Stanford and Ward 1984, 1986b, Tyus and Karp 1991).

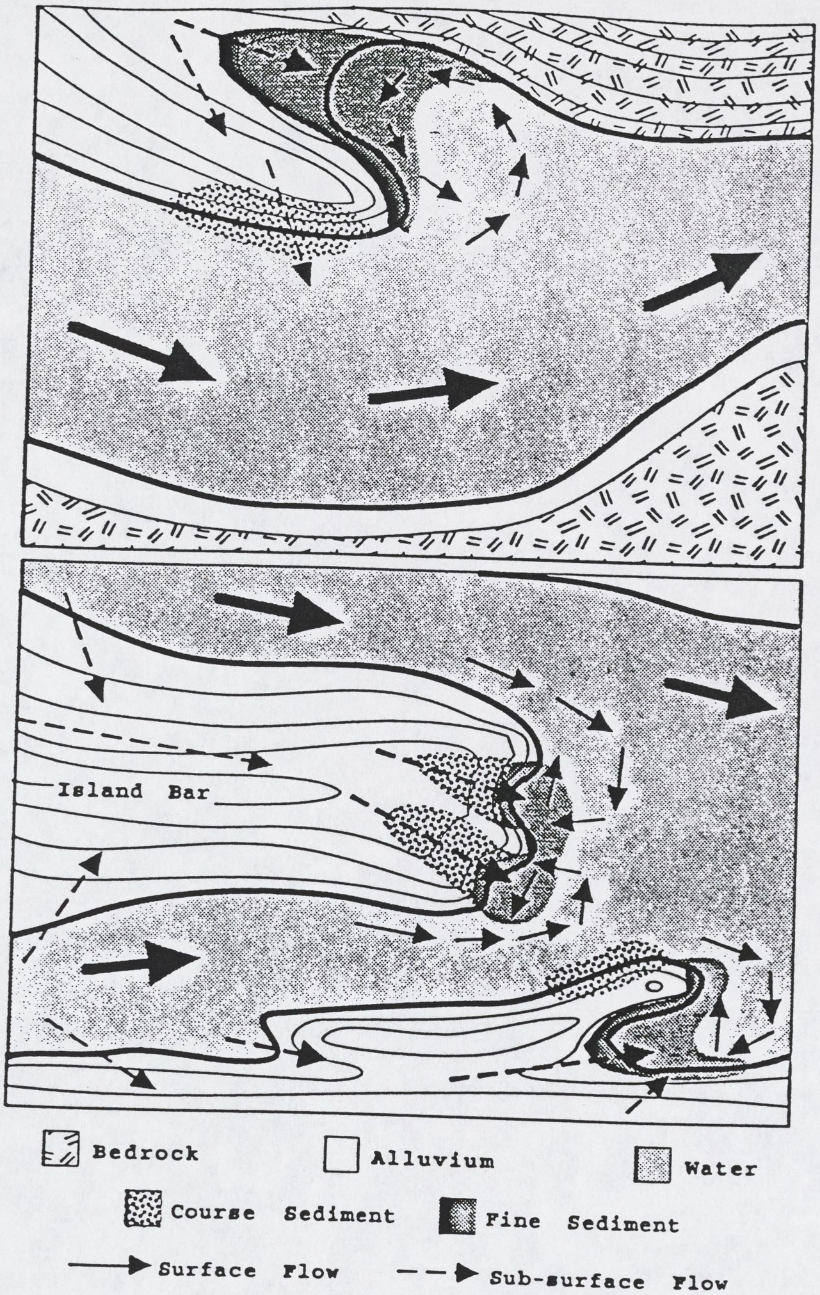


Figure 2. Schematic representation of geomorphic processes that form low velocity habitats in constrained (canyon, top panel) and unconstrained, aggraded (floodplain, bottom panel) reaches of the Upper Colorado River system where endangered fishes are routinely found. In both panels the current condition is baseflow. In the top panel a wall-based channel formed during a higher flow period, creating an eddy which persists and causes deposition of fine sediment in the backwater at the downstream end of the channel. Declining flows from the preceding high discharge period also increased the velocity of water draining across the point bar thereby leaving clean, course cobble. In the bottom panel a midchannel or island bar and a back-bar channel were built during high flow, allowing low velocity habitats to form on the downstream ends. Chute channels of clean cobble formed on the steep, leading edge of the island bar, as velocity increased with declining volume of flow over the bar. At baseflows, fine sediments deposited on the aggraded portion of the bar front in relation to river stage. The backbar channel and point bar function similarly to the wall-based channel. In all cases river water penetrates the alluvium at the upstream end of the bar creating interstitial, subsurface flow that discharges into the low velocity environments and the river as change in elevation reverses the piezometric (downward) gradient to the water table. Hence, habitats used by endangered fishes are dynamic in time and space and are controlled by sediment supply and size, channel morphometry (especially slope and relative constrainment by bedrock) and the volume and duration of the previous peak flow events (modified from Tyus 1984, Harvey et al. 1993).

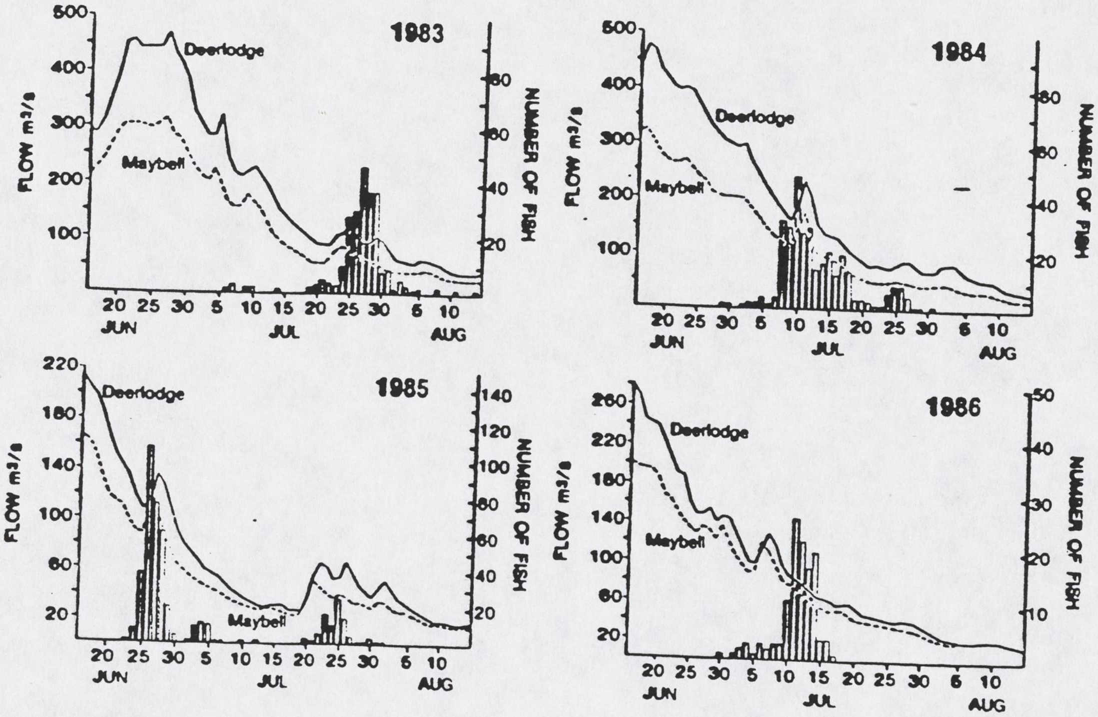


Figure 3. Relationships of Colorado squawfish spawning dates (vertical bars, data derived from larval drift rates that were adjusted for hatching time) to Yampa River flows measured at the Deerlodge and Maybell gauges on 4 different years. Number of fish represents number of larval fish sampled and distributed according to estimated spawning date (from Nesler et al. 1988).

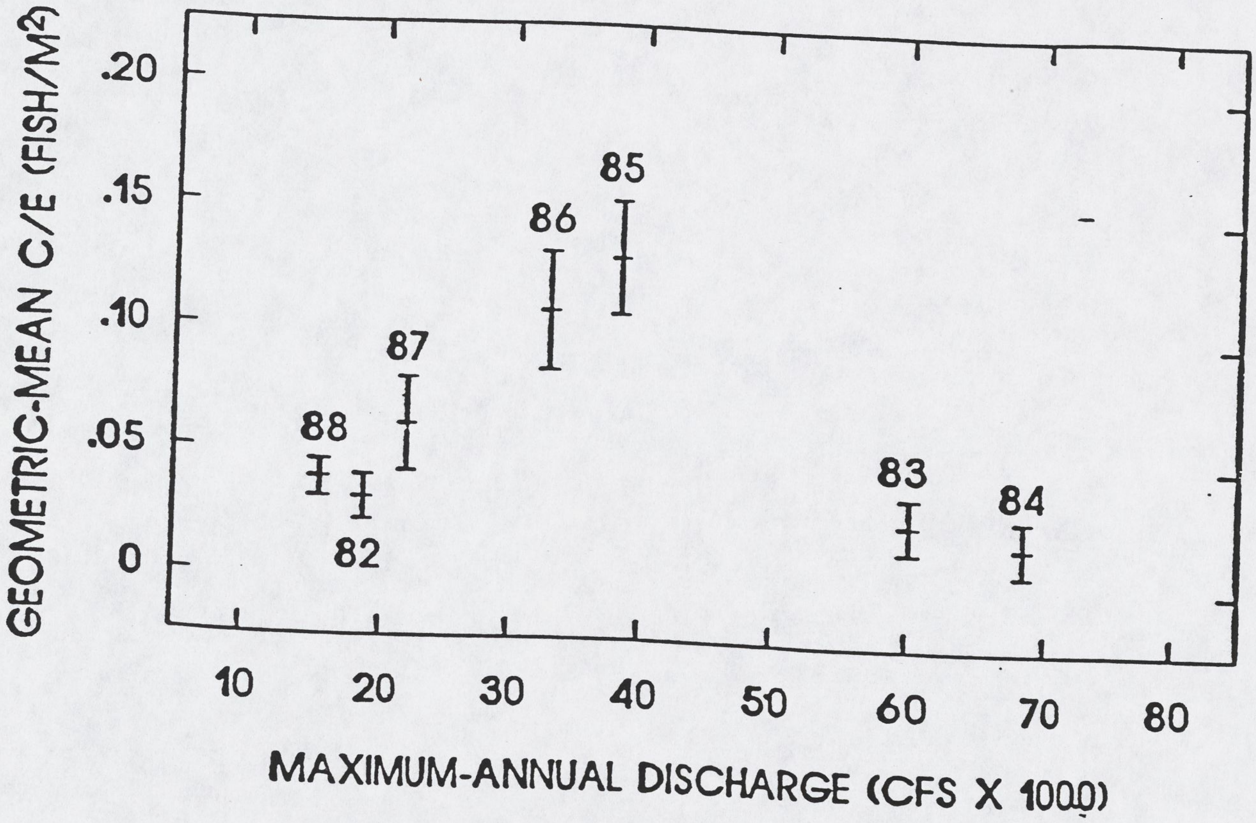


Figure 4. Catch per effort of post larval squawfish as related to maximum annual discharge for the Colorado River. Data are geometric means ± 1 standard error for fish collected in backwaters using the standardized sampling protocol (U.S. Fish & Wildlife Service, 1987b) during October between the Westwater Canyon (mile 110) and confluence with the Green River (mile 0). Thus, the data are a relative measure of recruitment from spawning that occurred during the high flow periods each year (from McAda and Keading 1989, also included in Osmundson and Keading 1991). Data collected in 1989 - 1991, which were low to average water years, are consistent with this relationship (C. McAda, Fish and Wildlife Service, Grand Junction, CO, unpublished data).

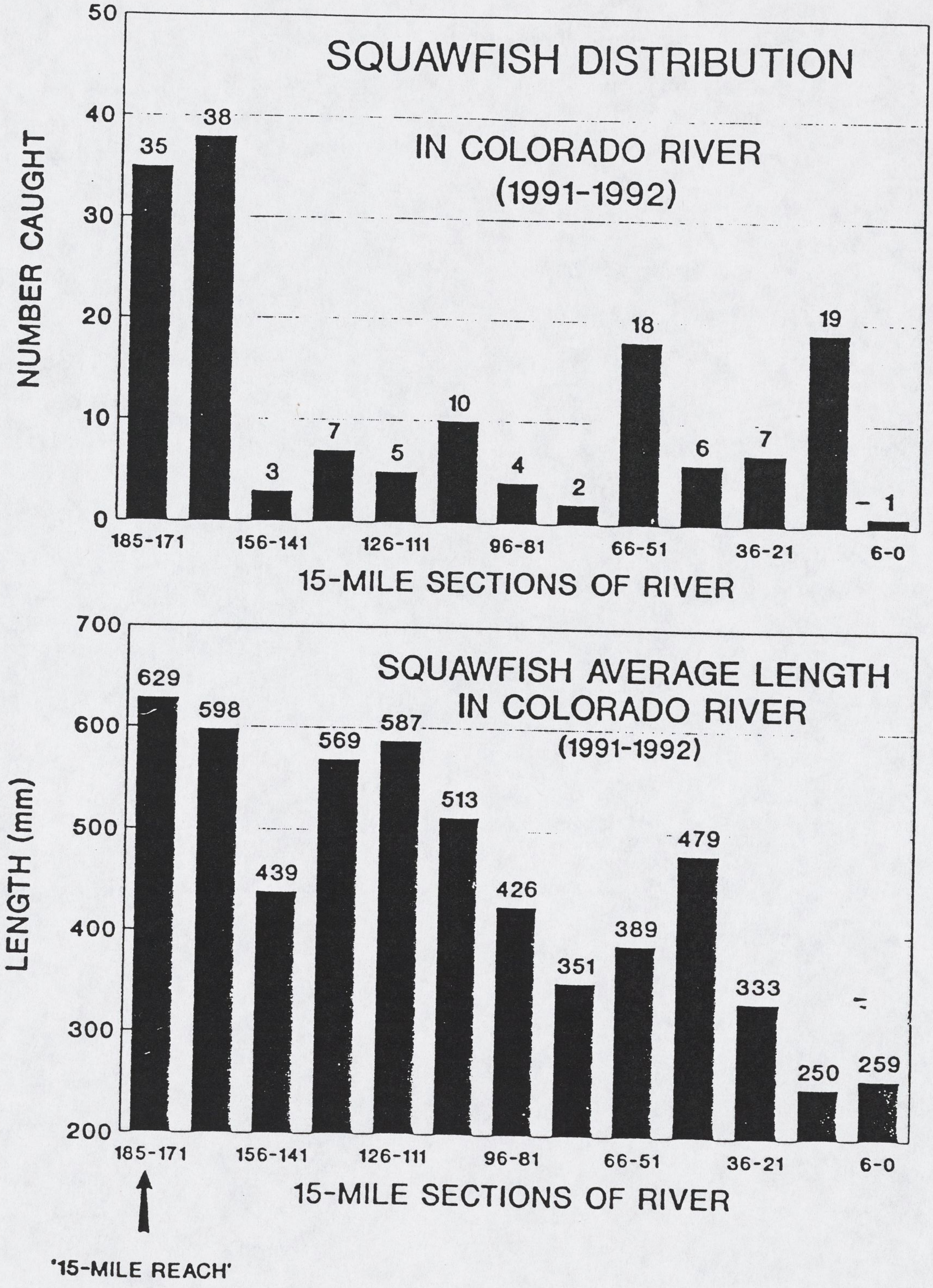


Figure 5. Distribution of squawfish by size and number caught in the Colorado River from the Green River confluence (mile 0) to the Grand Valley diversion dam at the top of the 15-mile reach during the 1991 - 1992 standardized sampling program. This relationship, although variable, is remarkably consistent from year to year; the upstream areas inhabited by larger adults are consistently devoid of YOY squawfish relative to the river segment below Westwater Canyon and the confluence with the Green River (mile 111 - 0) (C. McAda, Fish and Wildlife Service, Grand Junction, CO, unpublished data).

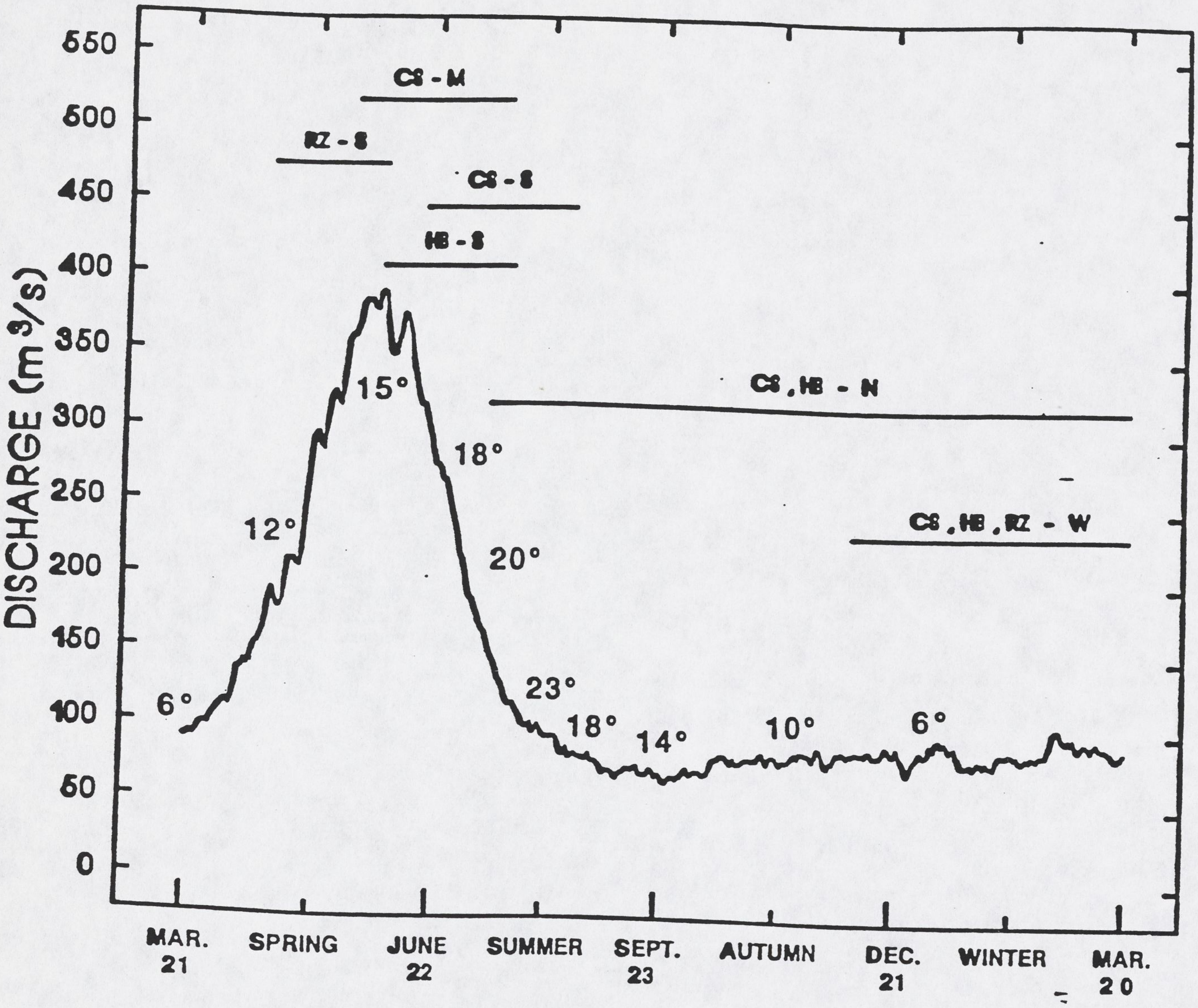


Figure 6. Generalized relationship between average flows in the Green River (Jensen gauge), river temperatures (°C) and the timing of life history events (M=migration to spawning sites, W=adult overwintering, N=brooding in nurseries, S=spawning), of squawfish (CS), humpback chubs (HC) and razorback suckers (RZ) (modified from Tyus 1990, Tyus and Karp 1991).

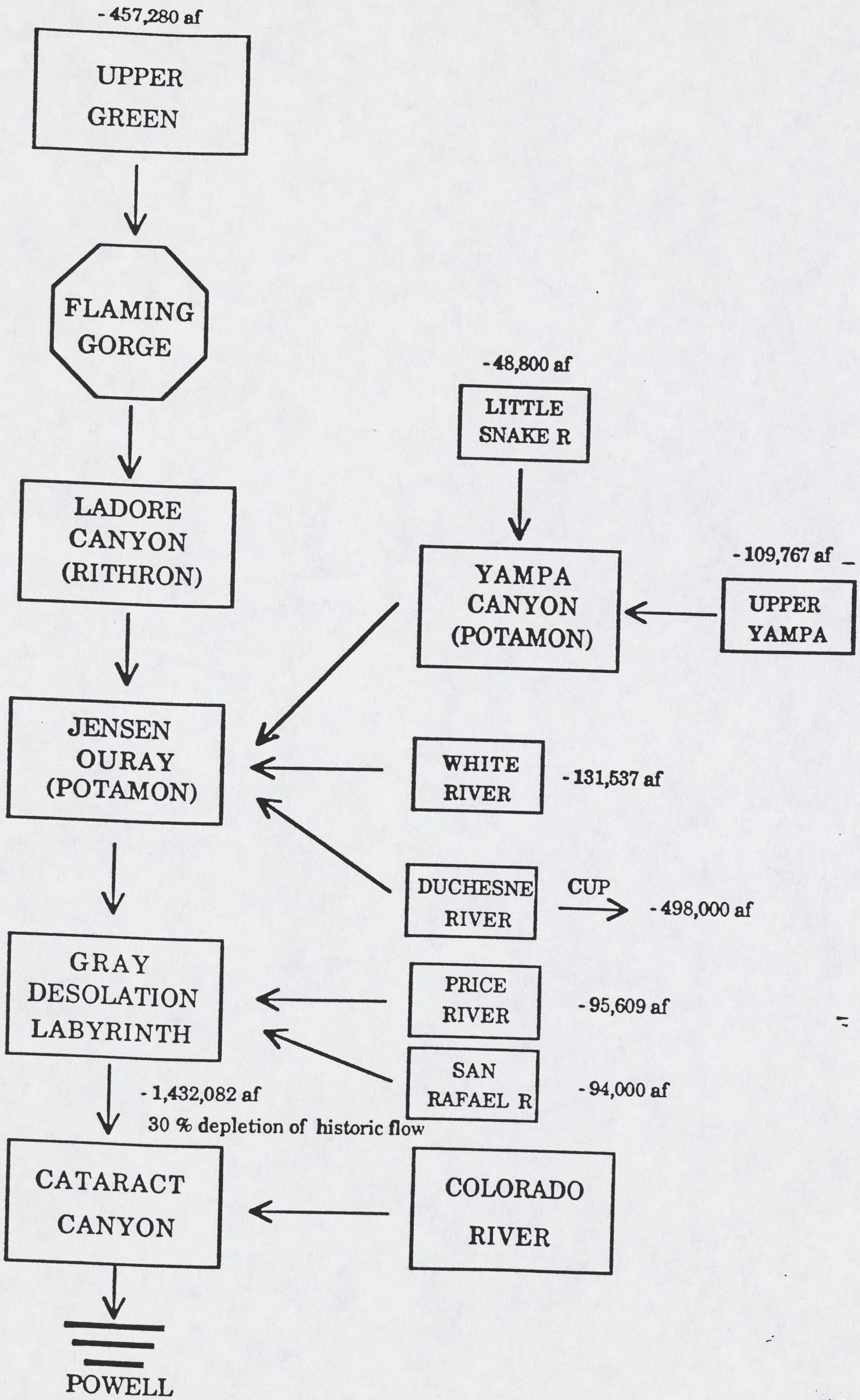


Figure 7. Regulation of flow in the Green River system. Octagons represent storage reservoirs and reversed arrows indicate transcatchment diversions.

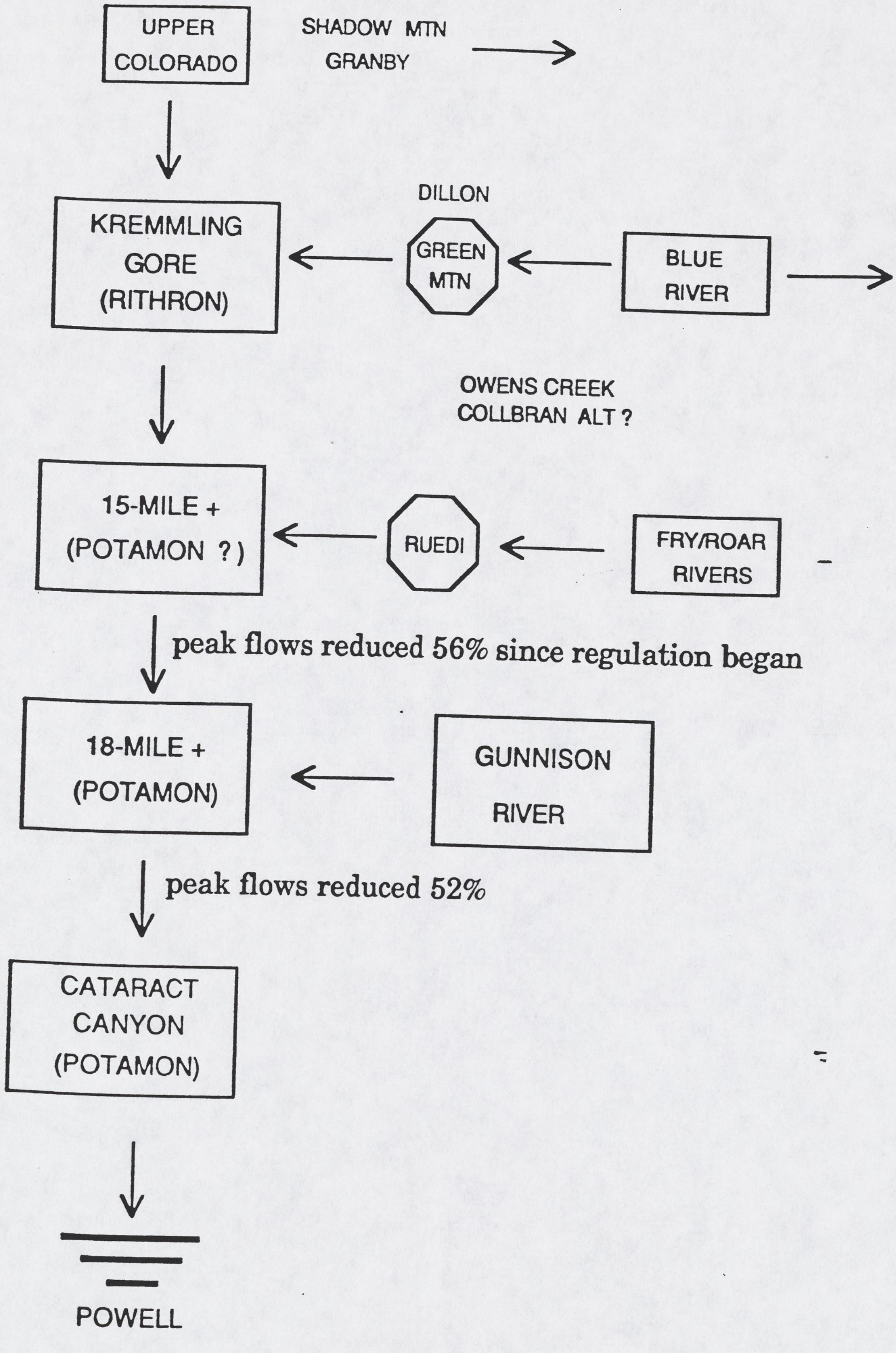


Figure 8. Regulation of flow in the Colorado River system, upstream of the confluence with the Green River. Octagons represent storage reservoirs and reversed arrows indicate transcatchment diversions.

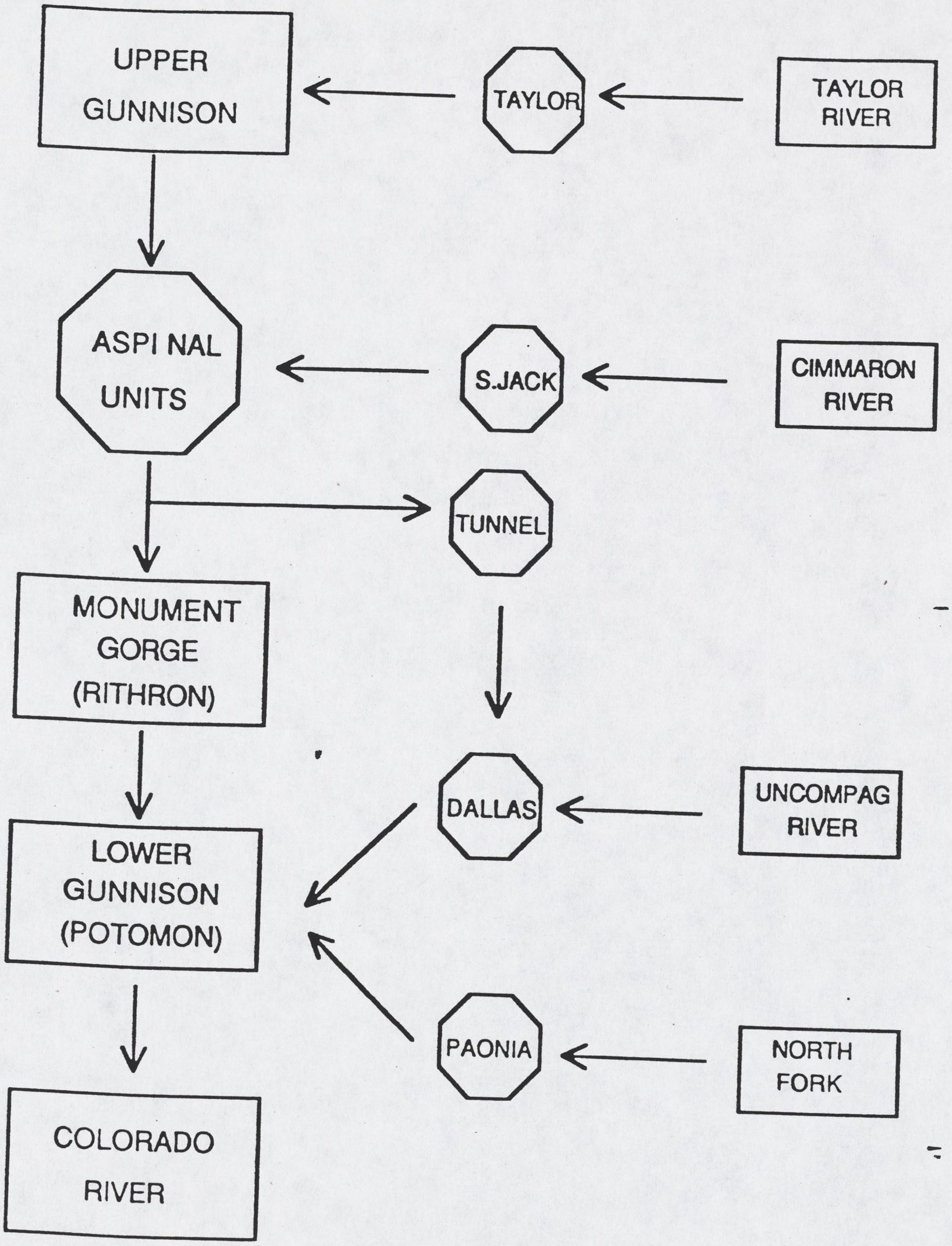
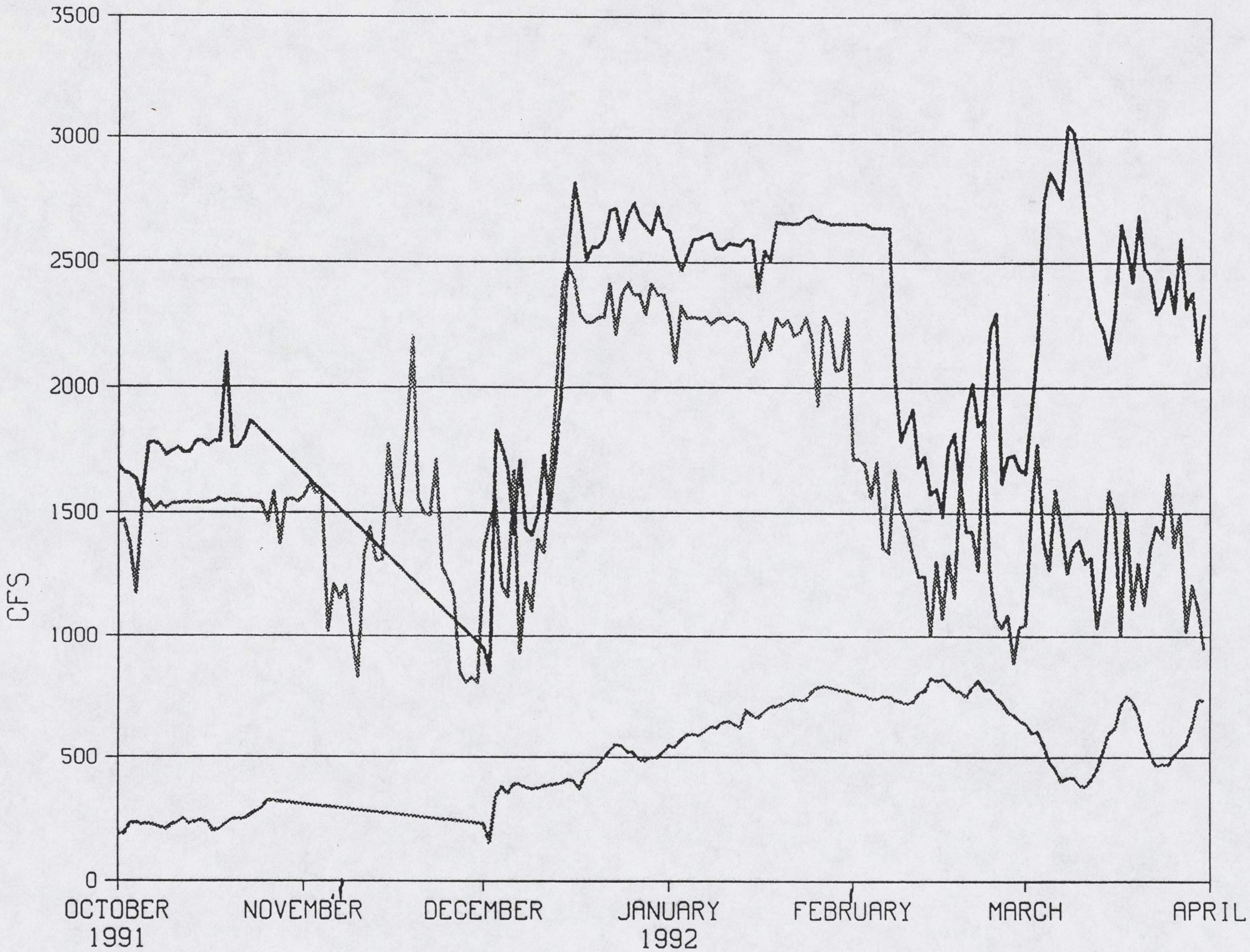


Figure 9. Regulation of flow in the Gunnison River. Octagons represent storage reservoirs and reversed arrows indicate transcatchment diversions (I do not know what the depletions are in this river, can anyone provide those data? No one offered on the first draft...help needed).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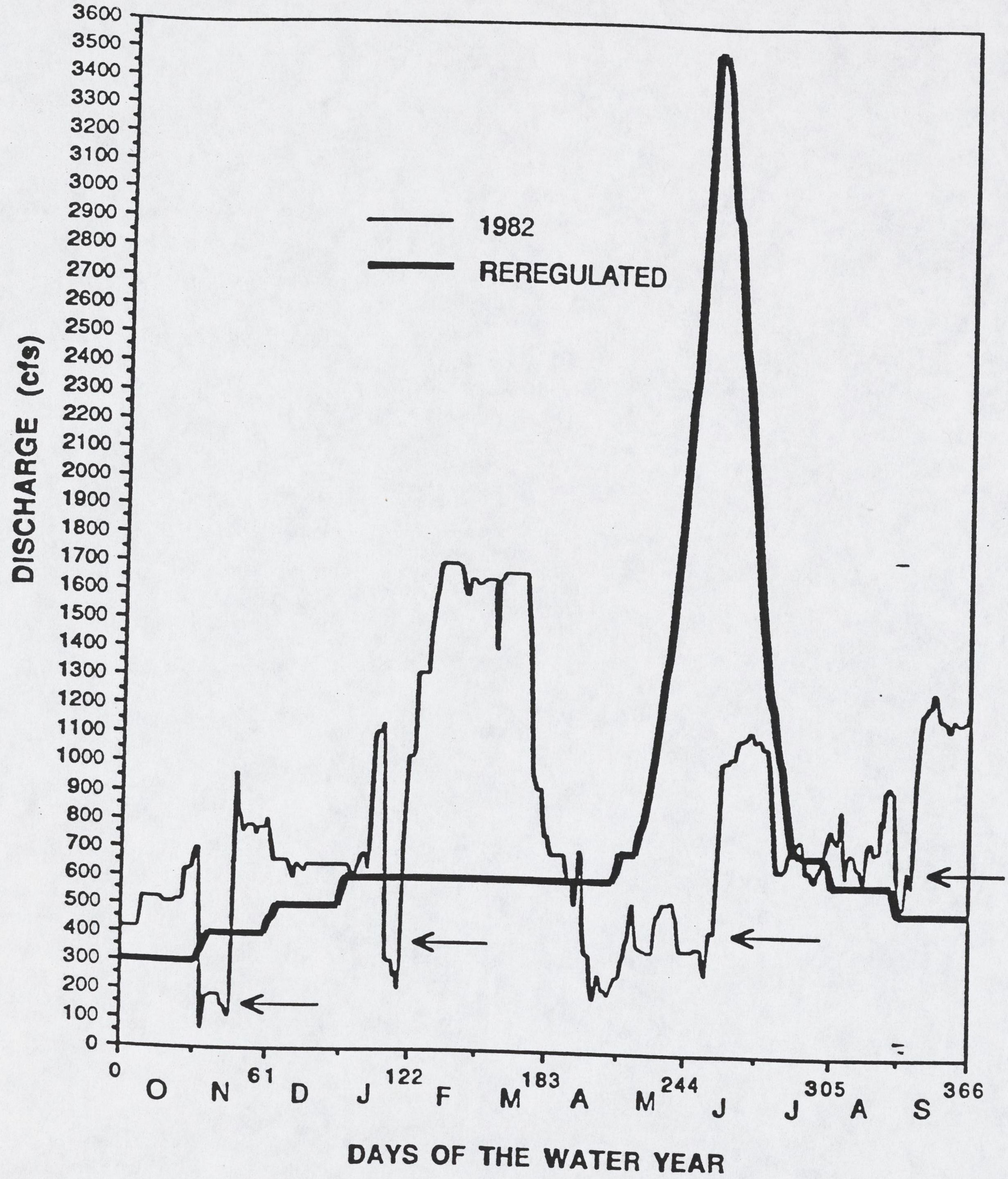


Figure 11. Variability of flows on the Gunnison River (East Portal gauge) as a consequence of regulation by the Aspinal Units during the 1982 water year and as reregulated to simulate the predam hydrograph (from Stanford and Ward 1992b).

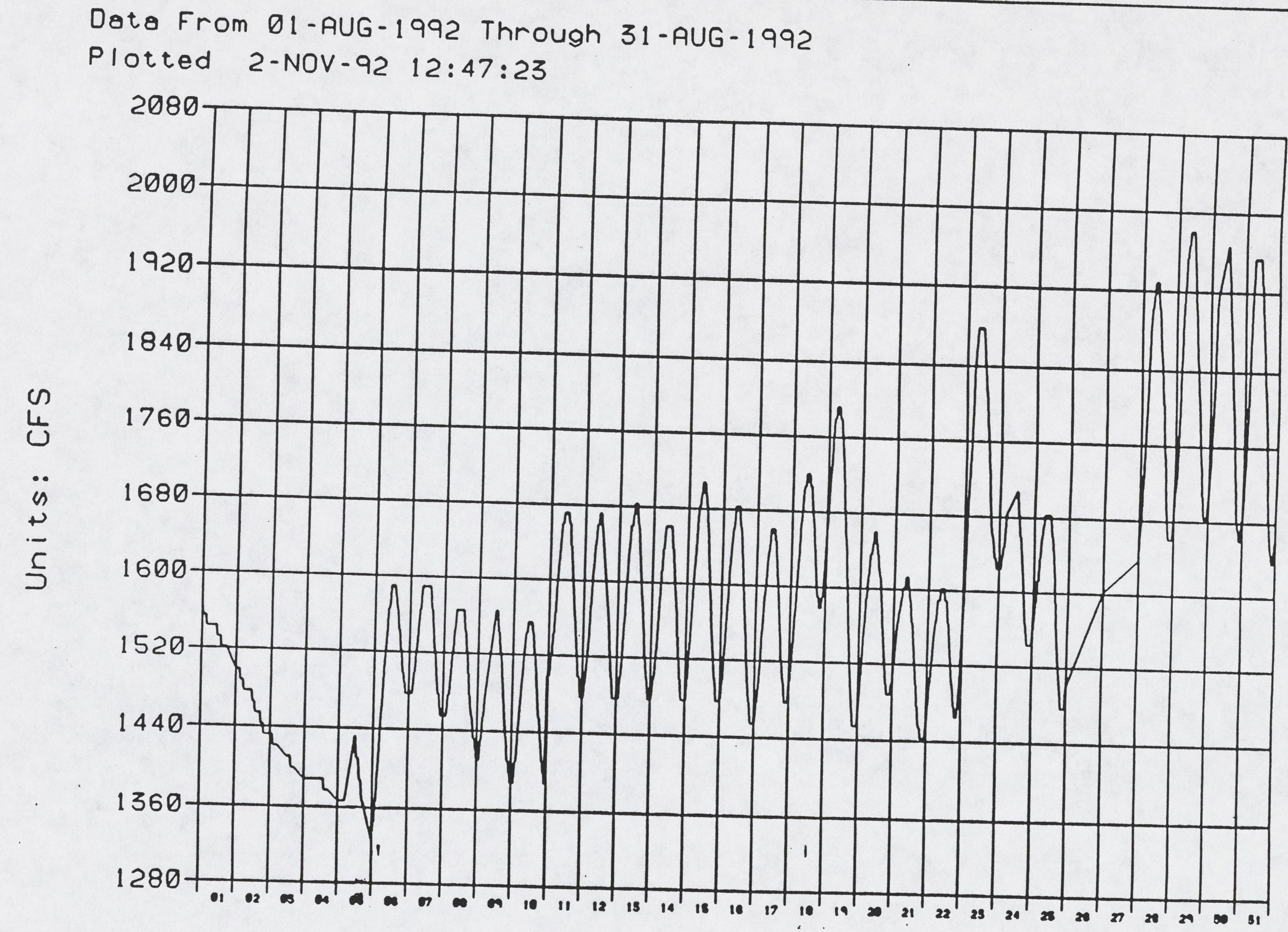


Figure 12. Hourly discharge measured on the Green River at the Jensen gauge during August, 1992. Data from W. Brad Vickers, (U.S. Bureau of Reclamation, Salt Lake City, UT).

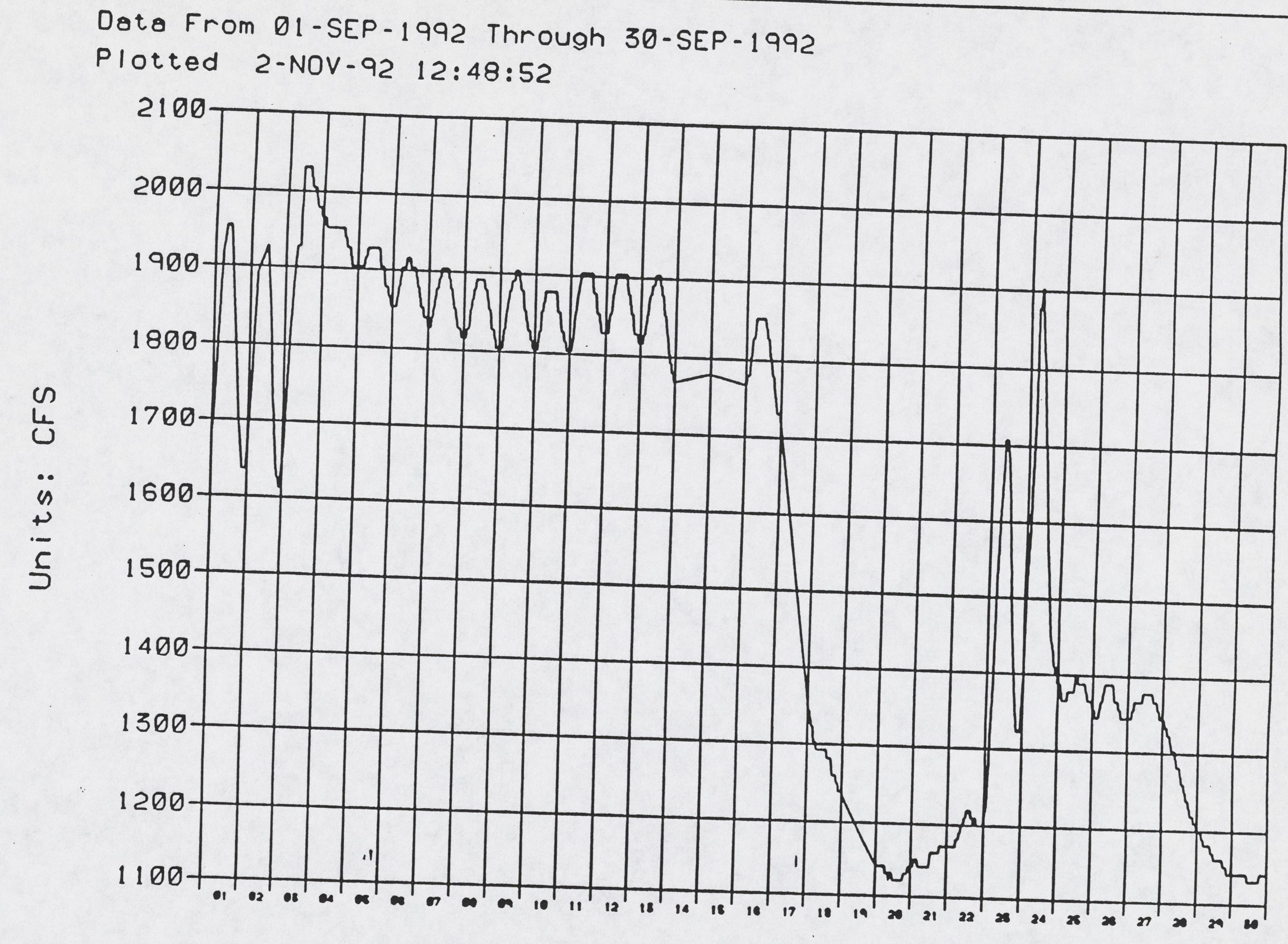
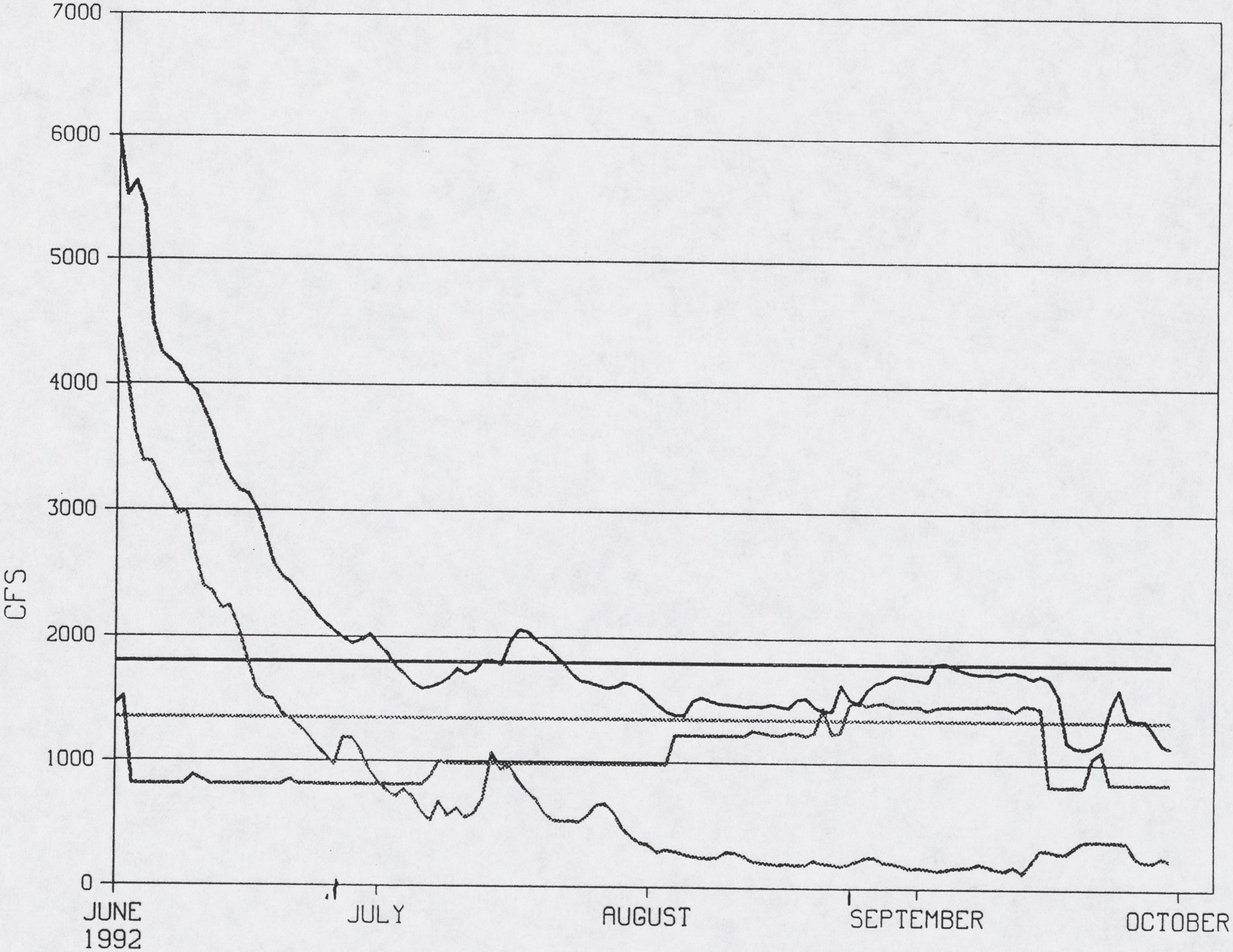


Figure 13. Hourly discharge measured on the Green River at the Jensen gauge during September, 1992. Data from W. Brad Vickers, (U.S. Bureau of Reclamation, Salt Lake City, UT).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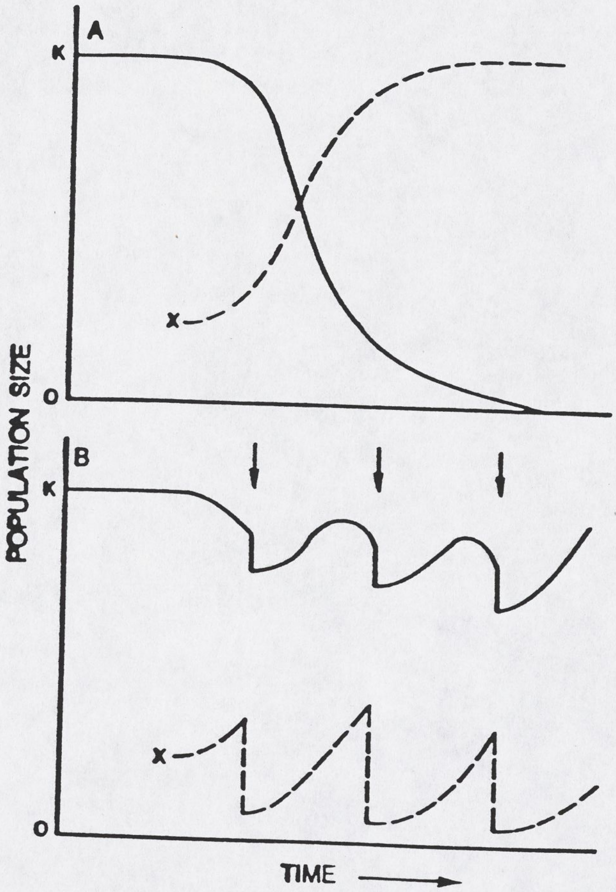

Figure 15. Graphic models of the dynamic relation between native and non-native fishes in regulated (A) and unregulated (B) arid-land streams. A: In a regulated stream, native fishes (solid line) typically decline and disappear upon introduction (x) of non-native fishes (dashed line). B: In a free-flooding stream, native fishes similarly decline after non-natives appear, but flooding (arrows) reduce the latter to levels that permit recovery of native fishes. During interflood periods, population size and range of non-native fishes again expand and negatively impact native species until the next flood. If flooding occurs frequently enough, long-term coexistence may occur as a dynamic equilibrium. K = carrying capacity of the stream for native fishes.

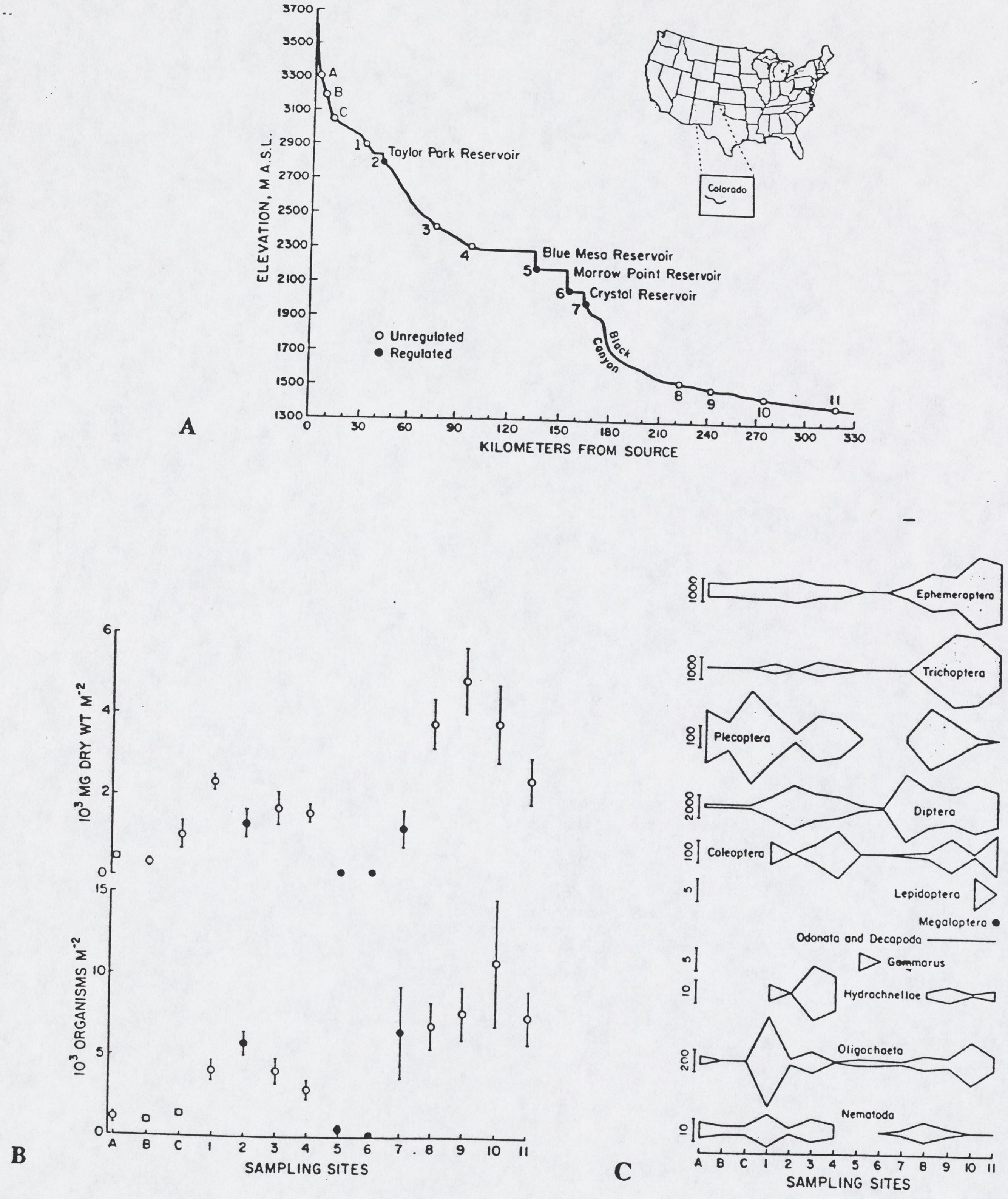

Figure 16. A. Longitudinal profile of the Gunnison River system. B. Biomass and density (mean and s.e. bars) of total zoobenthos in the Gunnison River from headwaters to mouth. Sites 1 - 11 (located in A) were sampled in 1979-80. C. The contribution of major groups to the total number of zoobenthos collected per site (located in A) in 1979-80. (from Ward and Stanford 1991).

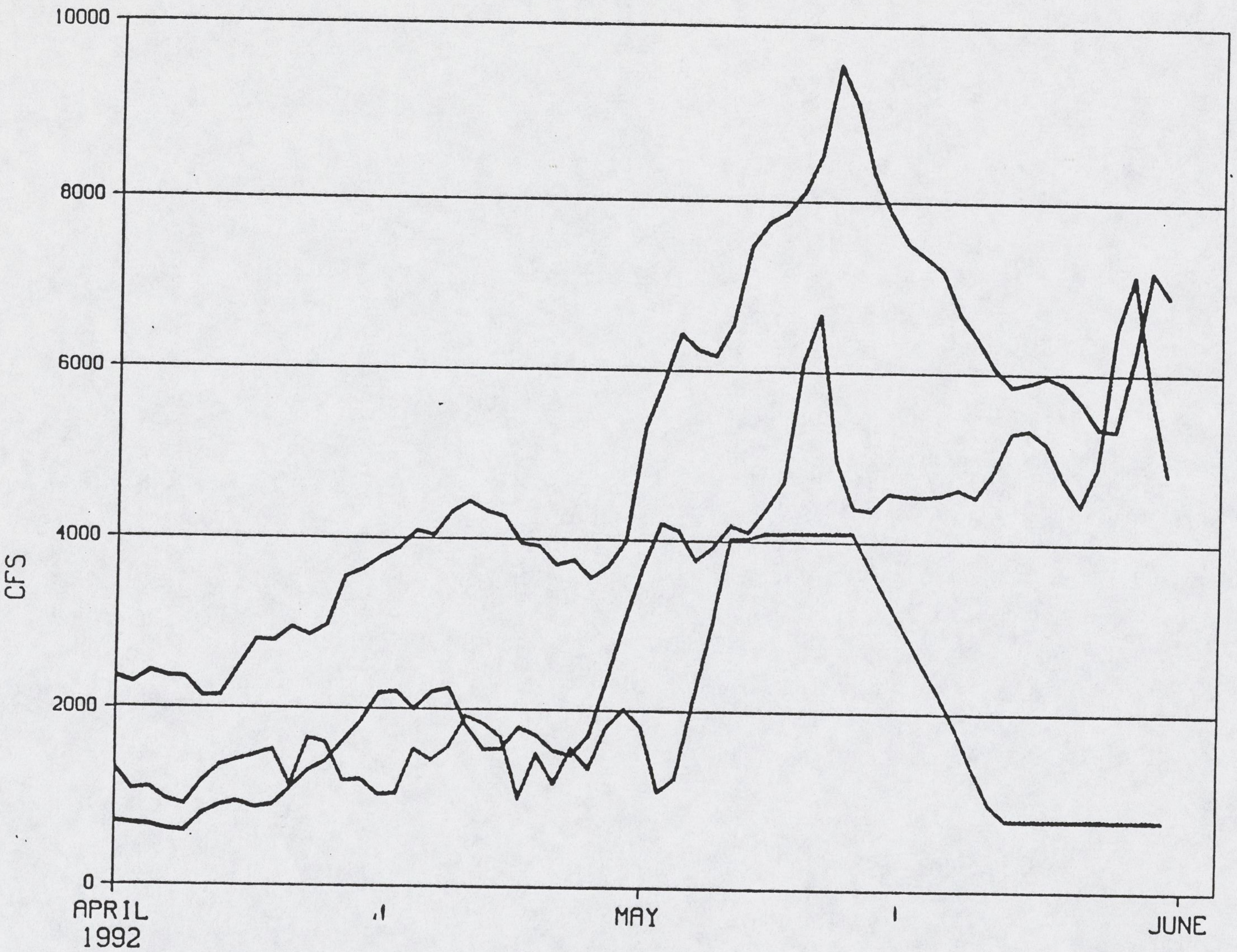

Figure 17. Spring 1992 flows on the Green River (at Flaming Gorge Dam, bottom line; and at Jensen, top line) in relation to unregulated flows from the Yampa River, middle line). Data from W. Brad Vickers (U.S. Bureau of Reclamation, Salt Lake City, UT).

APPENDIX 1

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APPENDIX 2

Persons Contacted During this Study

Gene Jencsok, Colorado Water Conservation Board, Denver, Colorado	303/866-3441
Tom Pitts, Tom Pitts and Associates, Loveland, Colorado	303/667-8690
Grady McNeill, Colorado Division of Wildlife, Denver, Colorado	303/291-7280
Jay Skinner, Colorado Division of Wildlife, Denver, Colorado	303/291-7260
Rick Gold, Bureau of Reclamation, Salt Lake City, Utah	801/524-5592
Larry Crist, Bureau of Reclamation, Salt Lake City, Utah	801/524-5498
Dan Luecke, Environmental Defense Fund	303/440-4901
Robert Wigington, The Nature Conservancy, Boulder, Colorado	303/444-1060
John Hamill, U.S. Fish and Wildlife Service, Denver, Colorado	303/236-2985
Lee Mills, U.S. Fish and Wildlife Service, Denver, Colorado	303/236-8154
Larry Shanks, U.S. Fish and Wildlife Service, Denver, Colorado	303/236-7398
Barry Saunders, Utah Division of Water Resources, Salt Lake City, Utah	801/524-3522
Dr. Harold Tyus, U.S. Fish and Wildlife Service, Denver, Colorado	303/236-7398
Messrs. Doug Osmundson, Chuck McAda and Frank Pfeifer, U.S. Fish and Wildlife Service, Grand Junction, Colorado	303/245-9319
Dr. Tom Nesler, Colorado Division of Wildlife, Fort Collins, Colorado	303/484-2836
Mr. Larry Crist, Bureau of Reclamation, Salt Lake City, Utah	801/524-5498
Dr. Richard Valdez, Biowest, Logan, Utah	801/752-4202
Drs. Clair Stalnaker and Ken Bovee, National Ecology Research Center, Fort Collins, Colorado	303/226-9331
Mr. Pat Nelson, U.S. Fish and Wildlife Service, Denver, Colorado	303/236-7398
Mr. George Smith, U.S. Fish and Wildlife Service, Denver, Colorado	303/236-5322
Mr. Mike Pucherelli, Bureau of Reclamation, Denver, Colorado	303/236-4300
Mr. Joe Lyons, Bureau of Reclamation, Denver, Colorado	303/236-3786
Mr. Henry Maddux, U.S. Fish and Wildlife Service, Salt Lake City, Utah	801/975-3620
Mr. William E. Davis, Chandler, Arizona	602/963-0382
Dr. Robert Muth, Larval Fish Lab, Fort Collins, Colorado	303/491-5255
Dr. Lynn Kaeding, U.S. Fish and Wildlife Service, Yellowstone National Park, Wyoming	
Mr. Kevin Bestgen, Larval Fish Lab, Fort Collins, Colorado	303/491-5255
Drs. Tim Modde and Bruce Haines, U.S. Fish and Wildlife Resources, Salt Lake City, Utah	801/789-0354
Mr. Leo Lentsch, Utah Dept. of Natural Resources, Salt Lake City, Utah	801/538-4756
Mr. Tom Chart, Div. of Wildlife Resources, Price, Utah	801/637-3310

APPENDIX 4

Reviews of the First Draft Report by the Expert Panel

Colorado State University

Department of Biology
Fort Collins, Colorado 80523
(303) 491-7011
FAX: (303) 491-0649

17 May 1993

Dr. Jack A. Stanford, Director
Flathead Lake Biological Station
311 Biostation Lane
Polson, MT 59860

Dear Dr. Stanford:

Your draft report on the endangered fishes of the upper Colorado River system is impressive indeed. The ecosystem approach that you propose is the perspective that is needed.

I have reviewed the document and provide numerous comments on the attached sheets for your consideration. Phone me if any of my comments are not clear or if you wish me to elaborate on any points made in my review of the document.

Sincerely,

JVWard

J. V. Ward
Professor

/n
Attachment

J. V. Ward's review of (First Draft) "Instream Flows to Assist the Recovery of Endangered Fishes of the Upper Colorado River System: Review and Synthesis of Ecological Information, Issues, Methods and Rationale" by Jack A. Stanford.

Page	Paragragh	Comments
2	last	can demography (birth & death rates, emigration, immigration) be reduced? Would populations be a better term here?
3	1st Full ¶	The word stability could be misconstrued. I would delete "long-term stability of flows so" and add "over the long term" at the end of the sentence.
10	1st	Low recruitment during low flow years may relate to the fact that suitable habitat is not inundated — i.e., most of the water is in the channel proper, especially as the river is now (channelized, etc.).
—	—	Some figures would profit by having an explanatory legend (other figures are self explanatory). I found the figure legends. They should be moved so that they precede the figures.
10	First Full ¶	Is this statement too strong? It implies that there are few or no unknowns in the basic environmental requirements of these species. That is not the impression I get from Kevin Bestgen, for example.
11	First Full ¶	You say that "Instream flows designed to provide maximum access for endangered fishes to slackwaters must be based on long-term measures. . . ." Yes, but as the channel morphology changes from year-to-year, a given discharge will vary in its inundation of backwaters. This is stated earlier in the paragraph, but might be worth restating in a different way after the "long-term measurement" sentence (i.e., short-term adjustments in required discharge, based on long-term measurements).
13	first 2 lines	Do macrophyte beds develop in backwaters during summer? If so, I would expect a diverse and abundant invertebrate fauna associated with the plants (odonates, snails, mayflies, caddis, oligochaetes, chironomids, etc.). Has anyone looked at this?

14	line 2	add ", reduce the variety of habitat types available,"
—	—	Do you want to cite our 1989 paper — "Riverine Ecosystems: The Influence of Man on Catchment Dynamics and Fish Ecology"?
18	—	Mooney & Drake (1989) not in References.
19	end of 1st ¶	"Meffe 1984" is the correct spelling — incorrectly spelled as "McFee" in text and as "Mefee" in References.
19	First ¶	Bottom line is that unpredictable flooding prevents exotic species from eliminating native species. As we discussed in Grand Junction, apparently this phenomenon only applies to canyon-constrained segments. pick up on page 38.
21	Number 1	I feel that there are still major holes in knowledge of basic environmental requirements of these fishes (but you are the one who has read all the literature). — pick up on page 48 - JW.
21	Number 2	Another example, probably not documented, is the high benthic & planktonic production in side channels and floodplain water bodies that was (pre dam) seasonally pulsed and predictable.
22	Number 3	The major interactive pathways are reviewed in my keynote address on "Riverine-Wetland Interactions." Also, even though very high flows are associated with weak year classes, extreme flooding may still be necessary to maintain the channel morphology and channel-floodplain interactions critical for the long-term survival of these fishes.
23	Number 6	For these fishes, it may be necessary to integrate the Serial Discontinuity concept (longitudinal dimension) with the lateral dimension (e.g., our LARS paper).
28	—	Also, importance of migration/movement is not considered.
33	—	It seems that examining benthic & planktonic assemblages in backwaters under different flow scenarios would be an important research goal. pick up on pg 46

36	—	Having a major section on "Critical Uncertainties" is excellent!
38	Number 4	Are you using the word "reregulated" here and elsewhere in two contexts (i.e., to moderate severe flow fluctuations as Crystal Dam does for the Gunnison <u>and</u> to establish new flow regimes)?
41	—	Evaluating the effectiveness of actions for the fish may not be feasible (in an annual time frame) given the probable time frame for measurable responses (decades?).
42	—	Regarding the fact that flow provisions are based on ecological information obtained in <u>suboptimal</u> habitats for these fishes — I feel that what is known about the fishes of floodplain rivers on other continents should be more fully considered in drawing conclusions for the endemic fishes of the Colorado River system. Some convergent evolution has undoubtedly occurred in the relationship between fish faunas and floodplain river dynamics.
46	—	In last paragraph on food web sampling, stress sampling benthos and plankton in backwaters (and isolated – at low flow – floodplain water bodies?).

RECEIVED JUN 10 1993

United States Department of the Interior

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TAKE PRIDE IN AMERICA

June 8, 1993

Professor Jack Stanford
Flathead Lake Biological Station
311 Bio Station Lane
Polson, Montana 59860-9659

Dear Jack:

You will find enclosed a copy of your draft manuscript "Instream Flows to Assist the Recovery of Endangered Fishes of the Upper Colorado River System: Review and Synthesis of Ecological Information, Issues, Methods and Rationale" with my review comments. You have done an excellent job synthesizing a large quantity of sometimes incomplete or contradictory information. Your conclusions are supported and well-reasoned. My review comments, written in the manuscript margins, are primarily editorial questions concerning the significance of a particular report or study you have reviewed.

You will see that I have made a number of comments concerning figure 4. It presents a nice story, however, I have several reservations. As figure 4 stands, I don't believe that it proves the point that flows of about 30,000-40,000 ft^3/s are best for spawning. The conclusions may be correct, but it has not been proven. Clearly, the relation between streamflow and spawning success is a central question, and the implications of figure 4, if correct, are substantial. Therefore, I feel the relation shown in figure 4 needs more work. For example, is peak discharge really important? The implication is that extremely large flows carry larval fish far downstream. Should not one use the mean daily flow during the period of larval fish emergence? Lateral separation zones, eddies, increase in size and complexity as discharge increases. Consequently, there are undoubtedly plenty of backwater refuges available to drifting larval fish at discharges greater than 40,000 ft^3/s. Furthermore, the flow velocity, either mean or surface, is only 20-30 percent greater at 70,000 ft^3/s than 40,000 ft^3/s. Is this difference significant? The time of travel for a water parcel between Westwater Canyon and the Green-Colorado confluence is only about 48 hours at 40,000 ft^3/s, versus perhaps 35-40 hours at 70,000 ft^3/s. The springs of 1983 and 1984 were unusually late and cold. Perhaps, water temperature is actually the cause of low spawning success rather than discharge. Alternatively, the high flows of 1983 and 1984 may have created a substantial area of quality spawning beds which were gradually degraded by the intermediate-to-low flows of 1985-1988. So much for speculation. My point is that the relation shown in figure 4 may not be the explanation for year-to-year variations on spawning success. I suspect that the additional years of information 1989-1993 inclusive together with additional information (eg. temperature) for the previous years would significantly reduce the range of possible primary causes of the variation in annual recruitment.

Your principal conclusion is that it is time to begin a regime of experimental flow, especially high spring flows as well as reduced daily fluctuations during the summer. I agree fully. We have enough information currently to plan and initiate a program of experimental releases. Furthermore, without such a program, I believe it will be very difficult to identify and support a regime of instream flows which will assist the recovery of endangered fishes in the Upper Colorado River Basin.

Respectfully,

Ned

E. D. Andrews

25 May 1993

REVIEW OF DR. J. A. STANFORD'S REPORT ENTITLED, "INSTREAM FLOWS TO ASSIST THE RECOVERY OF ENDANGERED FISHES OF THE UPPER COLORADO RIVER SYSTEM: REVIEW AND SYNTHESIS OF ECOLOGICAL INFORMATION, ISSUES, METHODS AND RATIONALE" (FIRST DRAFT OF 30 APRIL 1993), PREPARED FOR THE INSTREAM FLOW SUBCOMMITTEE OF THE ENDANGERED FISHES RECOVERY PROGRAM, UPPER COLORADO RIVER

By: William J. Matthews, Professor, Biological Station and Department of Zoology, University of Oklahoma, HC 71 Box 205, Kingston, OK 73439; Telephone 1-405-564-2463, FAX 1-405=564-2479, E-mail NA0591@UOKMVSA (Bitnet or Internet).

Summary:

Dr. Stanford has reviewed a huge amount of peer-reviewed and agency literature, and appears to have interacted in detail with all principal players in these complex issues. He provided an excellent summary for the expert panel at our meeting in April. I endorse his conclusion that the presently recommended peak flows be provided (at a minimum), and that higher spring runoff peaks should be implemented, with adequate experimental examination of results. The conclusion that high peak flows are required and critical for the large river fishes, from the perspective of forming and maintaining critical backwater habitat, seems reasonable. It seems imperative that frequent fly-overs be used to document carefully all changes in channel morphology with peaking flow events, that USFWS monitoring of fishes continue uninterrupted, and that studies be designed to carefully assess results of experimental peak flows. I agree with Dr. Stanford that an ecosystem perspective, to include food web analyses, is a most appropriate approach to assuring the long-term benefit of the target (endangered or threatened) fish species. I concur with his recommendations for expanded studies of the entire fish assemblage, including non-natives, and recommend that approaches from the discipline of community ecology as well as food web theory be incorporated. I suggest that the food web analyses suggested by Dr. Stanford be expanded to include alternate pathways through detrital or grazing processes, and that the total food web supporting the large-river fishes, and its response to flows, will be best understood if all food web pathways are evaluated. Food web pathways in backwaters also need careful evaluation separate from (but integrated with) mainstream studies. I recommend that services of highly skilled statisticians be secured early in the planning process for any design and analyses of biological and physical channel responses to experimental flows, and that careful attention be given to adequacy of sampling from the perspective of experimental power, and in selecting ANOVA, regression, or multivariate techniques or a combination of same.

I. Documentation:

Appendices 2 and 3 provide a detailed and informative log of Stanford's activities, indicating that he has discussed these complex issues with a wide variety of local and regional managers and individuals familiar with the issues of endangered fishes, flows, fluvial geomorphology, etc.

II. Specific comments on text: Amplification of points in text; minor questions marked in text.

Page 10, and in Figure 5. Error bars about means are needed.

Page 12. Information on zooplankton production, primary or secondary productivity, or similar measures, e.g., diurnal oxygen curves, in the backwater habitats would be helpful, and should be incorporated in future studies.

* Page 13. Food webs can be thought of at one spatial scale as delimited to particular habitats, e.g., gravel bars; however, at a larger spatial scale they may all integrate into a more comprehensive "river-reach" food web. Also on page 13, alternate food web paths could be important in these systems, e.g., that periphyton produced on gravel bars can die without being consumed, forming detritus, and leading to a microbially mediated "detritus" loop that lengthens the links in food web or delays upward transition of a carbon atom to a top predator, or (2) be directly consumed by algae or biofilm-eating fishes, forming a direct PPR-algae-herbivore-predator link. All of the food web paths could be important in understanding mechanisms in the system.

* Page 27: Regarding IFIM, I would also argue that these models don't include potential habitat needs for some fish species for differing activities, e.g., some fish may feed in one part of stream, "rest" in another, and use yet another (e.g., deeper pool, cover) as escape habitat. Further, like most studies, these river fish studies are in daytime. Some fish benefit from slow-moving habitats at night when they become rather inactive, and if possible (within limits of investigator safety) studies of fish habitat use at night should be conducted.

Page 30 et seq. All of the discussions about need for major flows to move bed material seem reasonable. It would seem that without occasional major flows the silting in of backwater accesses, and encroachment of vegetation could be a major problem.

Page 42. The need for monitoring of non-endangered native fishes, as well as non-natives, could best be framed in studies from a community ecology perspective, with long-term views of total community stability, colonization-extinction, determination of dynamics in community properties, etc., all of which would nicely complement food web studies. Strong consideration should be given to multivariate analyses of long-term data, providing objective views of trajectories of community change, as well as indications of any rapid changes. There exists a whole body of literature by fish or stream ecologists including Moyle, Grossman, Fisher & Grimm, Cashner, Ross, myself, and others, that provides a wide array of approaches for assessing changes in fish communities. I see no evidence that this body of information is being incorporated at this time, largely because studies are focused at present on populations of individual species instead of communities or "assemblages" of all the fish species. This literature should be examined for potential application in the Upper Colorado River monitoring programs.

Page 42, bottom. Re. risk that flows may be implemented and fish "not respond". I think it important that all parties understand that it may take some number of years to have fish "respond" in a meaningful fashion. Again, statistical planning in advance of the studies, using existing data for variance estimates, can provide a reasonable estimate of what magnitude of changes are detectable, given certain levels of sampling effort and numbers of years. In other words, the Colorado River fish project should let the statistics (evaluated in advance) drive the process of evaluation of experimental flows, rather than gathering a lot of data across years and hoping that statistics can sort our patterns *a posteriori*.

Page 43. Based on my brief discussions with Charles McAda, the fish sampling program seems valid. However, I have not reviewed original "methods" document. Assurance should be provided that the studies have adequate statistical power to detect (or reject) differences. A really good statistician should be on the team, particularly if the team moves to set up studies of response of fish to experimental flows. Careful planning of study design, statistics, experimental power, etc. at this point could make a difference between collecting a lot of data leading to no firm conclusions vs. collecting data in an efficient design that optimizes return of statistical power for dollars spent. Only with adequate power and replication (at least within reaches) can the experimental period yield robust answers.

I do strongly agree (page 43) that whatever monitoring is ongoing should be continued, as these data are "golden" regardless of any quibbles about details.

Page 44: The rather simple two-way ANOVAs in my papers (Matthews 1990 and Matthews and Meador 1992) can be improved upon. For one thing, if fixed sampling is used (as I assume it would be) this should be set up as a repeated measures model, with replication within reaches. In that way, there is no need to use the interaction term as the error term, as I was forced to do in Matthews (1990). Additionally, it would be beneficial if future studies also focus on asking "what % variance is related to flow modification?" relative to "what % of total variance is related to other variables", rather than just testing for effects of flow modification.

Page 47: All parties need to carefully discuss the environmental, biodiversity and societal concerns related to Type I and Type II errors in statistical design in future studies and analyses, and a discussion of and balance of Type I and II errors depending on the real risks involved in being "wrong" in an outcome. More attention needs to be given overall to evaluation of statistics, setting acceptable alpha-levels (p-values) for decision making, etc. I get the feeling that a lot has been done by just "looking at means". I think that for something as big and complex-and important as the Upper Colorado River it is essential that interested parties agree to consult with very highly skilled statisticians, either from outside agency or academic sectors. These complex studies will require statistical support from the very best of available statisticians in order to maximize return for dollars spent. I cannot emphasize strongly enough that without adequate statistical planning there could be huge amounts of money wasted on studies that cannot ultimately be used to answer the questions!

III. Figures: All comments on figures (below) made while inspecting figures and figure legends before reading text of report, to determine if figures are explanatory, clear, and "stand alone".

Figure 2. Generally clear to me as a non-geologist, but clarity or agreement between figure and legend is needed re. terminology for "coarse sediment" or "coarse cobble".

Figure 3 and elsewhere. Discharge units should be standardized among all studies and agencies.

Figure 4 refers to a "relationship" between maximum discharge and CPUE of postlarval squawfish. However, there is a gap in knowledge for any maximum discharges from 40,000 to 60,000 CFS, thus there could be a threshold as to what is "good" for squawfish production anywhere in that range. It may not be a smooth curve peaking at 1985 date.

Figure 5 requires belief on faith that relationships exist from year to year. If data exist to support this statement, then it should also be possible to put some standard error bars on the histograms so readers can judge for themselves if the relationship is "constant". This is especially true in lower panel. Include error bars around mean size so readers can determine constant the relationship is. Some means alone are unconvincing, especially with the very small sample sizes for some reaches (i.e., a mean of 351 mm is of little value with a sample size of 2 fish, as in the reach from mile 67-80. One fish could have been 551 mm and the other only 151 mm and you would get the stated average--which would be biologically meaningless.) Error bars of some kind are essential here.

Figure 15: Even in a general model, I am suspicious of any fixed K (carrying capacity) for fishes in a western stream. Surely this is highly variable from year to year regardless of introduction of exotic fishes. Next, if introduced fishes harm natives by something <u>other</u> than competition, say, predation, then the carrying capacity will have nothing to do with anything. (However, the relationship graphed in Figure 15 could still hold). As one example, it is thought that introduced red shiners, green sunfish, and others, in many parts of the west may have more impact by predation on young of natives than by competition, etc. There is quite an ongoing debate on this point by some of the principal players in Arizona and New Mexico, for example.

APPENDIX 5

Policy and Technical Issues Gleaned from Ad Hoc Discussions

One of the objectives of this study was to discuss issues with researchers and others to determine how people active in the recovery program (see Appendix 2) view the problem of instream flow provision, the adequacy of the science that bears on provision of flows and the utility of the data collected to date. Most of the important technical and key policy issues that came up are reflected in the critical uncertainties given part IV of the report. However, a number of other interesting, insightful and ancillary issues did emerge from the discussions. These are listed in no particular order and briefly discussed as follows.

- Many of the non-research people insisted that the flows be based on "sound science" and some expressed concern that the present flow provisions were based on different approaches and rationale, and therefore are not soundly science-based. Part of the frustration with regard to this basic issue is that incremental water allocation is very difficult to link in the same manner to the needs of the fishes.

- Concern exists that this review may focus too much on the gaps in scientific data and rationale that were used to develop flow recommendations, allowing the provision of flows to be stymied while additional data are gathered. A majority of the people I talked to agreed that too little has been done to date to protect the fishes and that the flow recommendations that are on the table, while somewhat scientifically tenuous, should be implemented under interim agreements and modified as new data become available.

- Some researchers are troubled with the way in which funding priorities are developed in the recovery process. They perceive little cohesiveness in terms of coupling the life histories of the fishes with ecological ramifications of various flow scenarios. This may be a result of the power the biological opinions have in determining how money for gathering new information is spent. Or, it may relate to to the fact that the recovery program itself has become a bureaucracy that is too large. People suggested that the recovery subcommittee structure may be redundant and a better job of coordinating recovery could be done by a single advisory group to the Fish and Wildlife Service (e.g., "Some people are on all of the committees, so why have them"). Moreover, there needs to be a more responsive process, again perhaps by a single committee, that develops research priorities before proposals are prepared. On the other hand, several people indicated that technical issues should be left to the technical people.

- Several people suggested that this report may represent the last best shot to get science involved in the determination of instream flows.

- Habitat enhancement flows (e.g., spring peak hypothesis) have been negotiated at Flaming Gorge, Navajo and Glen Canyon; and Aspinall operations are being evaluated for the same purpose. Some suggested that flows should be evaluated at only one dam; if habitat enhancement via flow provision works at one site, then it can be pursued at other sites. If not, then less energy is lost to the system than if failure occurs at all sites.

- The issue of "sufficient progress" came up several times. As I understand it, this issue relates to the desire for guarantees in the recovery process: 1) instream flow agreements must insure the future so that water development entitlements can be firmly and clearly met and 2) the FWS recovery program must be set or firm and not always changing. An ancillary issue relates to how progress toward recovery will be evaluated in the future and when is recovery sufficient to guarantee the fishes can survive without further management actions (i.e., will Section 7 surface time and time again).

• For the fish, a major issue is volume of water during a spring "peak" period, the shape of the transition curve to and from the spring peak and the nature of a minimum or baseflow regime. A major issue for power producers is timing of flows relative to need to generate power for load control, load following and meeting peak demands, in addition to providing the maximum steady output possible given water availability. Some argued that the limitations of these two concepts of constraints on the system are not understood by all parties at the table.

• Some agreed with the concept of adaptive management in the context of new science as well as entitlements. This means that management (e.g., provision of flows) should evaluate alternative actions and risks and proceed on the basis of current knowledge, but with the provision of a monitoring program that can evaluate the effectiveness of actions for the fish as well as with respect to meeting water development entitlements. If flows are not producing "sufficient progress" toward recovery, then an alternative must be found.

• A great deal of uncertainty exists with respect to water availability each year, and current models are not very useful according to some. In general, most people are operating with the assumption that enough water exists, but everyone recognizes that hard choices are coming. The mainstem Colorado River (e.g., 15 -mile reach and upstream) may be the most problematic of the reaches in this respect.

• On the Green River and the Gunnison River, flow provisions from the dams also influence National Park values other than with respect to endangered fishes. Some expressed concern that flow provisions and the recovery program in general disregard this interactive reality.