ECOLOGICAL VALUE OF FLOODPLAIN HABITATS TO RAZORBACK SUCKERS IN THE UPPER COLORADO RIVER BASIN

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DISCLAIMER

EXECUTIVE SUMMARY

This report reviews the ecological value of floodplain habitats to recovery of the razorback sucker and the anticipated responses of other endangered, native, and nonnative fishes to floodplain habitat enhancement/restoration activities in the Upper Colorado River Basin (Upper Basin). It is intended to serve as a reference document for persons working on habitat enhancement projects related to the Recovery Implementation Program for Endangered Fishes in the Upper Colorado River Basin (Recovery Program).

The conclusions summarize highlights of the information reviewed in the report and the recommendations are based on rationale provided in the text that are supported by the literature cited.

The report emphasizes the need for integration of all Recovery Program elements, especially streamf low management, habitat development and maintenance, management of nonnative fishes and sport fishing, and captive propagation/stocking that must be done concurrently to achieve self-sustaining populations (i.e., recovery).

Conclusions:

1. The declining numbers of some endemic Colorado River fishes including the razorback sucker is attributed to extremely low or complete lack of recruitment. Although long-lived razorback sucker can spawn successfully in some years and produce larvae, high mortality during the early life stages limits recruitment in Upper Basin razorback stocks to the point that they are no longer self-sustaining.

2. Habitat alteration and nonnative fish introductions were considered to be the two most important factors in the extinction of 40 native North American fishes (27 species and 13 subspecies) during the past century. These two factors also appear to be extremely important in the decline of razorback sucker stocks in the Upper Basin and are undoubtedly related to the decline of the other three endangered Colorado River fishes.

3. Shifts in survival during early life stages of fish populations most often result in a decline of populations in altered aquatic habitats. Recruitment of fishes is curtailed primarily from mortality during the larval stage from either starvation, predation, or both.

4. Razorback larvae are 9-11 mm TL at swimup and larvae between 11 and 12 mm TL with a mean age of 12-17 days predominated light trap captures in the middle and lower Green River from 1992 to 1996. Approximately 20% of all razorback larvae captured in the Green River were larger than 12 mm TL with the two largest specimens at 20 and 24 mm TL. The oldest larva was 34 days old at capture. These results demonstrate that high mortality occurs in the early life stages.

   Similar results have been reported in the Lower Colorado River Basin. Most razorback sucker larvae captured in Lake Mohave were less than 20 days old and averaged 11.4 mm TL where mortality from starvation was estimated to be between 23% and 78% from 1992 to 1995, depending upon the year of capture and nutritional index used. The remaining razorback larvae succumb to predation by nonnative fishes, resulting in no recruitment from natural reproduction in Lake Mohave.

5. The density of zooplankton required for survival of larval razorback suckers during the "critical period", when larvae are making the transition from endogenous (yolk sac) to exogenous (mostly small invertebrates) nutrition, was 30-60 organisms per fish per day based on work completed at the Dexter National Fish Hatchery, New Mexico. The

"point of no return" or "point of irreversible starvation" occurred between 19 and 22 days.

6. The first food organisms of larval razorback suckers are diatoms, rotifers, algae, and detritus. Soon afterward, razorback larvae begin to select larger zooplankton organisms, primarily cladocerans and copepods. Razorback larvae collected from shallow backwaters in Lake Mohave in the Lower Basin and the Green River in the Upper Basin also ate early instar chironomids and trichopterans. However, it must be recognized that fish larvae as well as zooplankton and free-swimming benthic invertebrates are captured in light traps, suggesting that the razorback larvae were opportunistic in feeding on the concentrated benthic organisms. As razorback larvae increase in size, they will select larger zooplankton and small benthic organisms as food. Zooplankton and benthic invertebrates are eaten by all life stages (larvae, juveniles, and adults) of razorback suckers.

7. Nutrition and subsequent growth rate of larval fishes is extremely important because smaller fish that are in poor condition (i.e., starved) with limited locomotive ability are more susceptible to predation for a longer period of time. Razorback sucker larvae that were deprived food in the laboratory showed an initial increase in length as they utilized remaining yolk reserves but they were significantly less in total length and weight than larvae fed ad libitum at temperatures of 14, 18, and 23 C.

   Razorback sucker and other fish larvae, including razorback sucker, exhibit compensatory growth and can recover quickly from short periods of starvation if they encounter high prey densities before they reach the "point of irreversible starvation".

8. Zooplankton densities in the main channel never reached densities required for larval razorback suckers to survive their critical period. Zooplankton densities that were adequate for larval razorbacks during the critical period were found in only two of the largest backwaters sampled (Intersection Wash in the middle Green River and Millard Canyon in the lower Green River). However, zooplankton densities, necessary for survival during the critical period, were reached consistently in floodplain habitats.

9. Only a portion of the zooplankton or benthic invertebrate biomass is available to razorback larvae since their mouths are gape-limited and they tend to select the largest organisms that will fit into their mouths. Aquatic organisms normally found in the water column such as zooplankton also occur in benthic samples and benthic organisms that are either free-swimming or emerging pupae also occur in the water column. Larval fishes, including razorback suckers, feed on both benthic and planktonic food organisms of the right size.

10. Razorback suckers spawn in the spring on the ascending limb of the hydrograph when extremely low densities of small food organisms first used by larvae occur in the main river channel and backwaters, suggesting that the life history strategy of this species evolved to utilize the high productivity of floodplain habitats. Therefore, starvation may be an important factor in survival of larval razorbacks during their critical period.

    Drifting razorback larvae during the spring runoff are also highly vulnerable to predation by nonnative fishes since razorback larvae constitute the largest portion of drifting aquatic organisms entering backwaters used by nonnative fishes.

11. In addition to being effective predators on larval endangered fishes, juvenile nonnative fish species are more than likely significant competitors with larval and juvenile endangered fishes.

Competition by two species occurs when food resources are limited, the food is shared, and one of the species is adversely affected. Competition among freshwater fish species is often difficult to document because these fishes lack specialization in food habits so that much overlap occurs in their food habits. However, the extremely low densities of zooplankton during the spring runoff that serve as food for larval razorback suckers and the high percentage of nonnative fishes in backwaters of Upper Basin rivers provide evidence that competition may also reduce survival of razorback larvae.

12 Laboratory and pond studies conducted at the Dexter National Fish Hatchery, New Mexico documented that about 2 months are required for larval razorback suckers to achieve 25 mm TL (1 in). Flooding of terraces or depressions for a short period of time (i.e., 7 to 10 days) will not be adequate for larval razorback suckers to reach 25 mm TL when they would no longer be vulnerable to abundant adult red shiners based on size of the mouth-gape from studies conducted through Utah State University. However, gape size is irrelevant to predation by the fathead minnow because this species attacked catostomid larvae as a school, tore the prey into pieces, and consumed the pieces in a Pacific Northwest study. It is not known if other small nonnative fish species in the Upper Basin are capable of tearing larvae into pieces and consuming the pieces.

Red shiners and fathead minnows compose 90% or more of the fish that occupy backwater habitats in Upper Basin rivers based on the Recovery Program's Interagency Standardized Monitoring Program. When levees were removed to reconnect floodplain habitats with Upper Basin rivers, nonnative fishes quickly colonized and dominated these habitats in the Upper Colorado and middle Green rivers.

13. Starvation of larval razorback suckers during their critical period from the loss of productive floodplain habitats through regulated streamflows combined with a high vulnerability to predation by nonnative fishes appear to be the most important factors limiting recruitment in the Upper Basin.

14. Reconnecting floodplain habitats with rivers in the Upper Basin is expected to benefit razorback suckers since these habitats will provide adequate quantity and quality of food organisms that are required by larval razorback suckers to survive their "critical period". Larvae and juveniles of other fishes including the other endangered species (Colorado squawfish, humpback chub, and bonytail) are also expected to benefit from zooplankton and benthic macroinvertebrates that enter the main channel and backwaters from floodplain habitats.

Predation and competition from nonnative fishes on native fish larvae and juveniles can be reduced in floodplain habitats with high densities of zooplankton and benthic food organisms that can serve as alternate food items. Floodplain habitats with rooted aquatic vegetation or other structure also provide protection to razorback larvae and juveniles that readily use such cover when available. In contrast, there is little to no survival of larval razorback suckers in the present low velocity habitats (primarily backwaters without cover) in Upper Basin rivers.

15. Historically, the continuum concept and the flood pulse concept both applied to nutrient cycling in the turbid, unproductive rivers of the Upper Colorado River Basin. However, fragmentation of Upper Basin rivers

disrupted nutrient cycling through the continuum process. Although the flood pulse process was an integral part of the natural river-floodplain ecosystem, it is even more important for productivity in the present fragmented ecosystem.

Reduction of historic peak streamf lows and extensive levees prevent the connectivity in this river-floodplain ecosystem. Reconnection of the floodplain with Upper Basin rivers will reestablish some of the lost integrity and productivity of the river-floodplain ecosystem.

16. The long-lived and highly fecund razorback suckers may not require successful recruitment annually to develop self-sustaining populations. The frequency of successful recruitment to produce self-sustaining populations of razorback suckers is unknown but can be determined through field evaluations. It is possible that successful recruitment every five to ten years may be sufficient to naturally maintain the razorback sucker since this species lives to 44 years or possibly longer. However, it would be desirable to have recruitment every year or as often as possible until target Recovery Program objectives are achieved.

Recommendations:

1. Continue acquisition and enhancement/restoration of floodplain habitats in the Upper Colorado River Basin because reconnection of rivers with floodplain habitats will improve the productivity of the ecosystem for zooplankton and benthic invertebrates required for survival by the early life stages of the razorback sucker.

   Acquisition with the intent of preserving existing floodplains that are still functional will help maintain the existing integrity of the river-floodplain ecosystem.

   Reconnection of floodplain habitats appears to be critical to increase larval razorback sucker survival during their critical period so self-sustaining populations (i.e., recovery) can be developed. Also, adult razorback suckers may benefit from feeding on zooplankton and benthic invertebrates in the productive floodplain habitats to regain their body condition after spawning. Mature razorbacks may spawn in floodplain habitats that would benefit natural reproduction when streamf lows at normal river sites are unsuitable for spawning.

   Any enhancement or restoration endeavors must be made through experiments that are thoroughly evaluated using a systems approach that incorporates adaptive management processes. Areas that are enhanced/restored should be thoroughly evaluated to determine the responses of the endangered and nonnative fishes to such efforts and refinements made as necessary to achieve desired goals and objectives.

2. Continue to focus on levee removal to reconnect floodplains with Upper Basin rivers and consider excavating present floodplain terraces that are higher in elevation than present streambanks.

   Regulated streamflows can be managed to inundate floodplain habitats for a longer period of time to increase survival of razorback sucker larvae. Several large-river ecologists emphasize the importance of mimicking historic hydrographs to reestablish integrity of river-floodplain ecosystems. Field experiments to evaluate increasing streamflows will have to deal with private land issues and streamflow variability will have to be increased incrementally to minimize flood hazards to private agricultural or occupied floodplain areas.

The timing of flows through regulated water releases from dams is important to ensure that (1) flows and substrate in the main channel are suitable for razorback sucker spawning and (2) flows will inundate floodplains so that larval razorbacks have access to productive floodplains during their critical period.

Removal of levees that are located on the lowest floodplain terraces (public property or acquired private property) is an alternative way to reconnect mainstem and tributary rivers with productive floodplain habitats. Such removal should be done on properties that can be easily reconnected with the main channel and inundated with existing or slightly enhanced streamflows.

Since the existing floodplain terraces were deposited when natural streamflows were high, floodplain terraces in prime areas that can be easily inundation are limited. It may be necessary to excavate existing terraces so that present and/or restored streamflow regimes can inundate floodplains where levees are breached.

3. The river discharge necessary to provide an adequate frequency of inundation of floodplain habitats should be initially made on an annual basis or as often as possible. However, long-lived fish species that have exhibited strong year-class strength such as the razorback sucker or Colorado squawfish may only require inundation of floodplains in 1 out of 5 to 10 years to maintain self-sustaining populations after populations have been reestablished.

4. The use of depression ponds in the floodplain should be considered as prime habitats for rearing wild razorback sucker larvae or captive-reared razorback suckers. Shallow floodplain depressions may require excavation to increase the water depth to prevent winterkill if the razorback suckers are reared to a larger size.

   Excellent growth of razorback suckers in floodplain habitats has been demonstrated in the Upper and Lower Basins of the Colorado River system. Floodplain depression ponds provide habitat where razorback suckers can reach a size when predation by nonnative fish species would be considerably reduced as razorbacks gain access to the river on subsequent high streamflows.

   If frequency and duration of flooding through managed streamflows cannot be restored, then floodplain depressions may be the only course of action left for maintaining razorback sucker stocks from extinction until solutions are found for recovery.

5. Design and conduct appropriate field experiments as Recovery Program funds are available to determine the control method(s) that will be adequate to reduce or manage selected nonnative fish species where the floodplain has been reconnected with the main channel.

   Control of nonnative fishes on a largescale basis in a large river system is not practical based on the published literature. Therefore, nonnative fish management should be emphasized in river reaches that are immediately upstream or downstream of floodplain habitats that are already connected or are reconnected to the river.

6. Continue reintroduction stocking of captive-reared razorback suckers in the upper Colorado River and augmentation stocking in the middle Green River.

   Floodplain ponds in the vicinity of suitable spawning bars in adjacent rivers can be used to rear wild razorback sucker larvae or captive-reared juveniles. The use of such ponds would expose fish to waters that provide olfaction cues in the event that imprinting behavior is important. Exposure to feeding on natural food organisms may also be important to survival after release into Upper Basin rivers. The average size of razorback suckers at the end of the first growing season in the Upper Basin is about 100 mm TL (- 4 in) and about 300 mm TL (- 12 in) at the end of the second growing season in off-channel habitats. The best survival of captive-reared razorback suckers in the Upper Basin has been from larger stocked fish.

It is highly recommended that razorback suckers be reared for two growing seasons and stocked when they are about 300 mm TL (- 12 in) or larger. Although augmentation stocking is not recovery, it provides a mechanism to maintain adult razorback suckers in the Upper Basin until a solution is found to achieve self-sustaining populations (i.e., recovery).

Evaluate factors that may affect survival of razorback suckers after stocking, including (1) use of floodplain ponds as a "half-way" habitat where captive-reared razorback suckers can become conditioned to eating natural food organisms before release, (2) importance of physical conditioning to various water velocities prior to release, (3) size of fish at release, (4) time of release, etc.

If the provisions of (1) nursery habitat with adequate food and cover and (2) adequate control of nonnative fishes cannot be achieved, human intervention may be required to rear razorback suckers in predator-free off-channel habitats so that their populations can be either reestablished through reintroduction stocking or bolstered (i.e., jump-started) through augmentation stocking.

I. INTRODUCTION

Human alteration of the main rivers and tributaries in the Upper Colorado River Basin (Upper Basin) had a major negative impact on some native fishes -- to the point where the razorback sucker (Xyrauchen texanus), bonytail (Gila elegans), Colorado squawfish (Ptvchocheilus lucius), and humpback chub (Gila cypha) are now listed as endangered under the Endangered Species Act. Other native fish species (e.g., flannelmouth sucker, Catostomus latipinnis and bluehead sucker, Catostomus discobolus) are still able to maintain self-sustaining populations, despite the drastic altered condition of the historic river environment. In less altered river reaches, native fish species still dominate the fish fauna (Anderson 1997; Burdick 1995) while, in more altered reaches, nonnative fish species are more abundant demonstrating that they are highly adaptive and can quickly dominate a fish community (Miller et al. 1982; Tyus et al. 1982).

Many riverine fish species exhibit seasonal movements into inundated floodplain habitats for spawning, rearing, and foraging (Copp 1989; Finger and Stewart 1987; Lambou 1963; Ross and Baker 1983). Seasonal flooding is important in sustaining various fish species that are characteristic of river channels (Baker and Killgore 1994). Baker and Killgore emphasize that the pattern of flooding appears to be of paramount importance in structuring wetland fish communities and that fish may spread over large areas of the floodplain during high streamf lows. The lateral movement of fish on the floodplain decreases exponentially with reductions in streamf low (Kwak 1988) and recruitment may not occur if water levels remain low (Starrett 1951). Dramatic declines of Age 0+ fish, that were correlated to the loss of floodplain habitat, were reported by Coop (1990). A higher riverine fish standing stock was associated with high spring floods in the Atchafalaya floodplain in the lower Mississippi River whereas the standing stock was lower following low spring floods (Bryan and Sabins 1979). Because of floodplain importance to fisheries, the American Fisheries Society adopted a position to "encourage restoration of historic floodplain and upland wetlands to regain stormwater retention, conveyance, and low-flow augmentation capabilities of the watershed, focusing on efforts to restore large 'functioning' floodplain wetlands" (Rasmussen 1996).

Habitat alteration and nonnative fish introductions were considered to be the two most important factors in the extinction of 40 native North American fishes (27 species and 13 subspecies) during the past century (Miller et al. 1989). These two factors also appear to be extremely important in the decline of razorback sucker stocks in the Upper Basin and are undoubtedly related to the decline of the other three endangered Colorado River fishes.

One of five major elements that are being addressed through the "Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin" (Recovery Program) is habitat development and maintenance (U.S. Fish and Wildlife Service 1987). The declining numbers of some endemic Colorado River fishes is attributed to the lack of recruitment. Although the long-lived endangered fishes spawn successfully and produce larvae, high mortality during the early life stages limits recruitment. Most Recovery Program participants believe that the lack of recruitment in the razorback sucker is related to the lack of adequate nursery habitat and predation/competition by nonnative fishes.

This report summarizes the published literature on the ecological value of floodplains to riverine fish communities and relates this literature to reports on the ecological requirements of razorback suckers that have been developed through the Recovery Program and management endeavors of biologists in the Lower Colorado River Basin. It emphasizes the need for concurrent integration of Recovery Program elements, particularly streamf low management, habitat development and maintenance, management of nonnative fishes, and captive propagation because these elements are closely interconnected.

II. FACTORS LIMITING ABUNDANCE OF SOME ENDEMIC FISHES

The Colorado River and its tributaries flow through 2,317 km (1,440 miles) of arid land (Carlson and Muth 1989) and serves over 15 million people with water for various uses including municipal use, irrigated agriculture, industry, and mining (Utah Water Research Laboratory 1975; Bishop 1971). Bishop emphasizes that these various uses of water have resulted in conflicts. This river flows through arid or semi-arid land that is supplied by only about 2.9 hectare-meters per square kilometer (60 acre-feet of water per square mile) of surface water annually which is less than any other major river in the United States (Utah Water Research Laboratory 1975).

During the past century, water development in the Upper Colorado River Basin to serve agricultural, domestic, industrial, and mining activities altered the natural river ecosystem (Carlson and Muth 1989; Maddux et al. 1982; Miller et al. 1982; Wydoski 1980; U.S. Fish and Wildlife Service 1990a,b, 1991). Dam construction and water storage to serve human needs changed the natural hydrograph through dam operations that released water for irrigated agriculture (seasonal) or for generating power during peak use periods (daily). Historic spring peaks in the hydrograph in the Green River (Vanicek 1967) and in the Colorado and Gunnison rivers (McAda and Kaeding 1991) were decreased and streamflows were increased when the rivers would become naturally low after the spring runoff. Changes in the hydrograph have, in turn, altered aquatic habitats, particularly backwater and floodplain habitats that are considered vital to survival during the early life stages of some native fishes. Coldwater releases from dams reduced water temperatures of the natural and historic warmwater aquatic ecosystem. Water depletions from the system increased through irrigated agriculture. Nonnative fish species were introduced in the rivers and manmade reservoirs, both intentionally and accidentally, that changed the species composition of the fish community. While native fishes in the Colorado River system have apparently been on the decline since the 1800's (Miller 1961), they declined more rapidly in the Upper Basin since the 1960's from habitat alterations of the river and colonization by nonnative fishes (Miller et al. 1982; Carlson and Muth 1989).

Although native Americans along the Colorado River constructed canals to divert water for irrigating crops around 1000 A.D. (Graf 1985; Powell 1961), irrigated agriculture via small diversions was not renewed until the middle to late 1800's (Fradkin 1983) and did not become extensive until the 1920's (Hunt and Huser 1988). Broad river valleys in the Upper Basin were colonized by people who began to construct levees for flood control (Fradkin 1983). As dams were constructed in the Upper Colorado River Basin -- particularly after the completion of Flaming Gorge Dam on the Green River in 1963 and the Wayne Aspinall Storage Unit on the Gunnison River in 1978 (Carlson and Muth 1989), the historic peak spring streamflows decreased that allowed people to construct levees that more easily controlled overbank flooding. Marshes and floodplain habitats disappeared as levees were built to control the river from regularly flooding agricultural lands. The connectivity of the river with floodplains was severely reduced and dramatically disrupted the natural function of the river/floodplain ecosystem that depended upon floodplains for productivity. Many large, highly productive, floodplain areas in broad, alluvial valleys along the Upper Colorado River Basin rivers are no longer connected with the river.

The geologic isolation of the Colorado River and its tributaries from other watersheds resulted in a fish fauna where 64% of the native species are endemic to the Colorado River system (Miller 1961). In addition to being unique, the fish fauna of the Colorado River Basin is very depauperate when compared with other North American river basins. The native fishes of the Colorado River system were adapted to dynamic natural aquatic conditions that included extremely variable streamflows and high sediment loads. These fishes evolved together and, more than likely, formed a stable fish community where competition and predation were balanced. The main natural predator on the native fishes in the Upper Colorado River Basin was the Colorado squawfish. The other native species occupied various habitats (i.e., niches) that reduced competition for food resources.

Today, the fish fauna in most areas of the Colorado River Basin bears little resemblance to the fish community that occurred historically. Nonnative fish species now compose 76% (42 of 55 species) of the fish community in the Upper Colorado River Basin (Tyus et al. 1982). Since the nonnative fishes did not evolve with the endangered fishes, mechanisms to balance predation and competition to allow co-existence have not developed so nonnative fishes predominate in the present fish community. This change in the fish community is consistent with ecological theory where species that are more efficient in capturing and converting food into biomass (i.e., nonnative species) will persist over other species (i.e., native species) as resources become scarce (Tilman 1982).

III. ECOLOGICAL IMPORTANCE OF FLOODPLAINS

The importance of the land-water interface to the productivity of lotic systems has been recognized for over twenty-five years (Allan 1995; Hynes 1970; Hynes 1983; Schlosser 1990, 1991; Ward 1989). However, interpretation of the complexity of biological responses and importance of geomorphological or hydrological processes has occurred only recently.

Historically, the ecological concepts of the river continuum (Vannote et al. 1980) and flood pulse (Junk et al. 1989) applied to the Upper Colorado River Basin. The river continuum concept applied to the headwaters and high gradient, restricted meander, canyon reaches while the flood pulse concept applied to low gradient, unrestricted reaches that form floodplains in broad valleys. Lotic systems not only transfer organic matter from upstream reaches in arid or semi-arid regions (i.e., continuum concept) but also deposit this material in floodplains where these nutrients aid in high productivity of invertebrates that periodically transfers food organisms to the main channel of the river (i.e., flood pulse concept). Most of the productivity in a large river-floodplain ecosystem occurs in the floodplain and is dependent upon the duration of inundation and the area of inundation (Junk et al. 1989). With dam construction, river ecosystems became fragmented (Ward and Stanford 1983, 1995) so that the continuum concept of energy transfer has been greatly disrupted. Although the flood pulse concept was probably more important to energy transfer than the continuum concept before Upper Basin rivers were altered, the flood pulse concept is even more important today to productivity of the present fragmented river ecosystem where extensive levees continue to separate much of the floodplain habitat from main channels. The major zone of productivity in a floodplain is the "moving littoral" (i.e., a shallow zone that extends from the edge of the waterline to several meters in depth) because it covers the maximum area of a floodplain for a given flood as it traverses the floodplain during inundation and draining (Junk et al. 1989).

Floods and floodplains are now understood to be essential components of large river systems (Bayley 1991; Petts and Maddock 1994; Sedell et al. 1989; Welcomme 1995). The energy dynamics of large rivers is strongly influenced by floodplain habitats (Sedell et al. 1989) where productivity is higher than in river channel habitats (Hynes 1970; Welcomme 1985; Welcomme 1989). Floodplains provide a greater opportunity for retention and processing of nutrients and organic matter than main river channels (Sparks 1995). The spawning strategies of fishes in many tropical and temperate areas are correlated with the flood pulse that is associated with high productivity in shallow, flooded areas (Copp 1989; Junk et al. 1989). Ephemeral wetlands in arid regions (e.g., floodplains, arroyos, and playa lakes) are not included in classification systems for wetlands and surface waters yet these wetlands are extremely important habitats for plants and animals that are adapted to the sporatic availability of water (National Research Council 1992).

Welcomme (1995) and Ward and Stanford (1995) emphasized that the diversity, resilience, and integrity of large river ecosystems are related to the connectivity of the main channel and its associated floodplain. However, there is an increasing trend in regulating streamflows of large river systems to increase productivity of basins for agriculture and make them safer for human occupation. Generally, such modification of aquatic environments adversely affects the fish stocks in large river systems. Welcomme (1985) stated that the majority of riverine fish species are extremely sensitive to modifications in the flood cycle and other environmental alterations caused by regulated streamf lows. Welcomme emphasized that substantial shifts in composition of the fish community result from introduction of nonnative species that poses uncertainty of restoring native fish assemblages by simple natural processes. Therefore, river management planning must include floodplains that are essential to maintaining the productivity and integrity of large river systems.

A. Relation of Nutrients, Sunlight Penetration, and Warm Water Temperatures to Primary Production. Primary production is the basis for development of a food web through phytoplankton and periphyhton standing crops that increase in concert with higher inputs of nutrients regardless of latitude. Carbon, nitrogen, and phosphorus are key elements for phytoplankton production. Phosphorus is the most limiting element in north temperate and subarctic waters (Schindler 1978). Nitrogen is the most abundant element in the atmosphere and is generally not limiting. Also, abundant carbon dioxide in the atmosphere provides the necessary carbon. Therefore, phytoplankton production and standing crop in north temperate freshwaters is generally proportional to the phosphorus input. Particulate phosphorus, either chemically desorbed or actively mobilized by microbiota, is not readily available in rivers with a high sediment load because most of the phosphorus is bound to the sediments (Ellis and Stanford 1988). Watts and Lamarra (1983) determined that between 21% and 49% of the total phosphorus in Colorado River water at the bridge upstream from Moab, Utah in September and October 1978 was available as an extractable form of calcium-bound phosphorus and they concluded that algae production was inversely related to river turbidity.

Turbidity from suspended fine sediments in Upper Colorado River Basin rivers is high and affects primary and secondary production. Production of phytoplankton and zooplankton that form the basis for a food pyramid are extremely low in the these rivers (Grabowski and Hiebert 1989; Cooper and Severn 1994 a, b, c, and d; Mabey and Shiozawa 1993). High turbidity in the river channel obstructs the penetration of sunlight that is needed for phytoplankton production. However, backwaters and embayments along the main river channels and marshes, wetlands, ponds, and lakes in floodplains provide favorable conditions for phytoplankton production. Sediments that are deposited in low water velocity areas provide nutrients and sunlight penetrates the clearer water allowing phytoplankton and periphyton to flourish as primary producers and to stimulate development of the food chain. Low velocity off-channel habitats also become warmer than the riverine environment in the Upper Basin that also aids phytoplankton production (Kaeding and Osmundson 1988). The combination of nutrients, sunlight penetration of the water column, and warmer water temperatures in low velocity off-channel habitats provide the best conditions for phytoplankton and zooplankton production in the Upper Basin.

B. Importance of Floodolain Habitats to Secondary Production. Low velocity habitats are also important to secondary production of zooplankton in large riverine environments (Welcomme 1985). The most comprehensive studies of plankton communities in rivers and floodplains have been made in tropical rivers of Venezuela (Saunders and Lewis 1988a, 1988b, 1989; Twombly and Lewis 1987, 1989). Mean densities of cladocerans and copepods (the most abundant taxa) were 421 organisms per liter in a floodplain (Laguna la Orsinera). Welcomme (1985, 1989) summarized the range of zooplankton densities (combined species) in floodplains ranged between 0.2 and 24,000 per liter. Various studies have reported zooplankton densities that were 30 (Welcomme 1989) to 100 (Hamilton et al. 1990) times greater in floodplain habitats than in the adjacent river channels. The differences in zooplankton densities are due to seasonal pulses by different species (Welcomme 1985).

Information on zooplankton densities in temperate rivers of North America are limited. The mean number of zooplankton in backwaters of the Missouri River between April and October was 6.7 organisms per liter (Kallemeyn and Novotny 1977). Data for zooplankton in floodplains of the Missouri River were not available because extensive channelization has eliminated periodic inundation of the floodplain. Only one study included rotifers among the zooplankton taxa studied in the Upper Colorado River Basin. Grabowski and Hiebert (1989) sampled rotifers in 1988 using a 25 micron plankton net and reported between 0 and 0.1 rotifers per liter in the main channel of the middle Green River and between 0 and 14.9 rotifers per liter in backwater habitats along this river reach. They did not sample floodplain habitats during their study.

Although direct comparisons of zooplankton densities in the Upper Colorado River Basin cannot be made because different sampling methods were used by the various investigators, the trends in zooplankton density by habitat are the same with the lowest density in the main river channels, higher in backwaters, and highest in floodplain habitats (Tables 1 and 2). The following discussion focuses on cladocerans and copepods since these two taxa constitute the most abundant prey items in the upper basin for which data are available. The upper value in mean number of cladocerans and copepods per liter in main channels of the Upper Basin was 1.3, 13.1 for backwaters and 81.5 for floodplain habitats (Table 1). This summary of Upper Basin zooplankton studies demonstrates that habitats with lower water velocities (backwaters and floodplains) are more productive than habitats with higher water velocities (main channels) and that floodplains are the most productive habitats.

While the seasonal dynamics of zooplankton have been documented in the literature (Hynes 1970; Welcomme 1985), few studies have been done on this aspect of zooplankton dynamics in Upper Basin river/floodplain habitats. The number of zooplankton (combined species) in a 147-ha wetland depression (Old Charley Wash) along the middle Green River were highest (43 [1995] to 54 [1996] organisms/liter) in June during the descending limb of the spring runoff (Figure 17 of Modde 1997). During the summer of 1991, the mean number of zooplankton increased from - 200 per liter in June to nearly 700 per liter in August in the same wetland depression (Mabey and Shiozawa 1993; Table 2). However, the mean number of cladocerans and copepods per liter was higher in the main channel of the middle Green River during July, 1991 (1.3/1) than in August, 1991 (0.3/1) and in a small backwater, 7.1/1 in July and 1.4 in August (Table 2) The higher mean values in the backwaters in July were probably due either to (1) escapement of zooplankton from floodplain habitats when they are connected by high spring streamf lows or (2) displacement into the river from off-channel habitats as the streamflows subsided (Kallemeyn and Novotny 1977; Welcomme, 1985, 1989).

Table 1. Range of the mean number of zooplankton (cladocerans and copepods) from investigations of various habitats in the Upper Colorado River Basin 1/

Habitat	Range of the mean number of organisms/liter
Main Channel 2/	0 - 1.3
Backwaters	0 - 13.1
Floodplain Habitats	4.2 - 81.5

1/ The mean number of zooplankton were obtained from the following studies: Grabowski and Hiebert (1989); Cooper and Severn (1994a), b, c, d, and e; Mabey and Schiozawa (1995). The number of samples taken, sampling gear used, seasons (late spring and summer) and years of sampling differed so ranges are used to illustrate the relative productivity of zooplankton.

2/ Most (4) of the investigations were made on the Green River. However the data include two investigations on the Colorado River and one investigation on the Gunnison River, a major tributary of the Colorado.

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Table 2. Mean number of zooplankton (cladocerans and copepods) from various habitats in or along the Green River, Upper Colorado River Basin, illustrating seasonal differences. 1/

Habitat	Month/Year	Range of the mean number of organisms/liter
Main Channel	7/91	1.3
	8/91	0.3
Backwater (Large)	6/91	63.4
Backwater (Small)	7/91	7.1
	8/91	1.5
Floodplain Habitat 2/	6/91	205.9
	7/91	311.4
	8/91	690.2

1/ Data summarized from Mabey and Schiozawa (1995).

2/ This habitat is a 147 hectare depression wetland that fills during high streamf lows and retains water by a dike and water control structure at the former natural outlet.

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More detail of the mean numbers of zooplankton in different habitats of the Upper Basin are summarized in Appendices 1 and 2. Grabowski and Hiebert (1989) reported 0.2 to 0.136 cladocerans and copepods per liter in the middle Green River main channel and 0.02 to 0.289 in backwaters during

1987 and 1988. Mabey and Shiozawa (1993) documented zooplankton densities in the middle Green River as 0.3 to 1.3 organisms per liter, 1.5 to 7.1 in the Ouray backwater, 63.4 at Intersection Wash (a large backwater), and 206 to 690 in an floodplain depression (Old Charley Wash) along the middle Green River (Appendix 1).

In an open water habitat of the Moab Slough along the Colorado River immediately upstream from Moab, Utah, the density of cladocerans and copepods averaged about 2 per liter for backwater sites and about 36 per liter for an open water wetland during the summer of 1993 (Appendix 2; Cooper and Severn 1994a). Cooper and Severn did not collect any zooplankton during their sampling from the main channel in this reach of the Colorado River. Samples of cladocerans and copepods from the Escalante Ranch site on the middle Green River, upstream from Jensen, Utah, contained 0 per liter for the main river channel, a mean of 41 per liter for backwaters, and a mean of 71 per liter for an open water wetland (Appendix 2; Cooper and Severn 1994b). The mean number of cladocerans and copepods from a backwater of the Gunnison River at the Escalante State Wildlife Area, about 5 miles downstream from Delta, Colorado, was 11 per liter and the mean number from an open water wetland was 25 per liter (Appendix 2; Cooper and Severn 1994c). Cladocerans and copepods samples from a floodplain depression (Old Charley Wash) in the middle Green River on the Ouray National Wildlife Refuge contained a mean of 31 per liter in 1993 (Appendix 2; Cooper and Severn 1994d). Samples taken from the main channel and a backwater on the refuge did not contain any cladocerans or copepods when sampled (Appendix 2; Cooper and Severn 1994d). The density of cladocerans was 26 per liter and the density of copepods was 28 per liter in a gravel-pit pond along the Colorado River in October, 1993 (Appendix 2; Cooper and Severn 1994e). These studies document that the highest zooplankton densities in the Upper Basin were in floodplain habitats. Seasonal dynamics of zooplankton were not made in the studies summarized above.

The mean number of aquatic organisms captured in 5 vertical tows with a 20.3 cm plankton net in backwaters of the lower Green River in 1997 varied between 2.4 to 124.1 organisms (combined zooplankton and free-swimming benthic invertebrates) per liter, depending upon site and date of collection (Table 3; Nance 1997). The mean numbers of aquatic organisms increased in the lower Green River between May and July that corresponded to warmer water temperatures (Table 3). The four major taxa represented in lower Green River samples were Nemotoda, Oligochaeta, Rotifera, and Copepoda. Several of the minor taxa included Cladocera and Chironomidae.

Microcrustaceans that form zooplankton communities are also found in substrates of aquatic habitats as benthos. Mabey and Shiozawa (1993) reported between 1,000 and 6,300 benthic microcrustaceans (Cladocera, Copepoda, and Cyclopoida) per square meter in the main channel of the middle Green River through the Ouray National Wildlife Refuge, between 4,900 and 6,000 organisms per square meter for a backwater, 23,000 per square meter at Intersection Wash and between 8,600 and 263,000 per square meter in Old Charley Wash. The mean number of aquatic organisms collected in five 1.85 cm bottom cores from backwaters in the lower Green River varied from 65,200 to 562,200 organisms per square meter, depending upon the site and date of collection (Nance 1997).

C. <u>Production of</u> <u>Benthic Macroinvertebrates</u> <u>in Various Aquatic Habitats.</u> Various factors affect the microdistribution and habitats of benthic invertebrates in streams including water velocity and substrate size such as rock, cobble, gravel, silt, and detritus (Rabeni and Minshall 1977). The experimental results of Rabeni and Minshall (1977) are supported by

Table 3. Mean number of aquatic organisms per liter (combined species of zooplankton and free-swimming benthic invertebrates) collected in five vertical tows with a 20.3 cm plankton net from three backwaters in the lower Green River during 1997. 1/

Date	Millard Canyon	Anderson Canyon	Holeman Canyon
May 1	6.2	2.4	6.6
May 8	0.5	5.8	5.2
May 15	8.4	3.6	3.4
May 22	29.0	7.6	6.2
May 29	30.9	6.8	6.8
Jun 5	53.7	7.6	14.9
Jun 12	124.1	19.2	26.2
Jul 10	95.8		

1/ Data from Nance (1997); mean values were rounded.

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the literature of benthos in running waters (Hynes 1970; Welcomme 1985) that document a higher species diversity and often larger numbers of benthic macroinvertebrates occur in riffles with large rock, cobble, or gravel substrates than river reaches with sand and silt substrates. Benthic invertebrates that inhabit riffles colonize downstream reaches by movement through the substrate, displacement by high streamf lows, and drift. However, upstream movement is hindered by long reaches of sand-silt substrates and streamf lows 12 cm/s or greater (Luedtke and Brusven 1970). Generally, upstream movement by benthic invertebrates is 5 to 30% of the downstream drift (Bishop and Hynes 1969). Benthic invertebrates produced in floodplain habitats move or are carried by currents and can provide a substantial part of the food base for fish in the main channel and backwaters (Eckblad et al. 1984).

Although species diversity of benthic invertebrates in low velocity habitats with sand and silt substrates of the Upper Colorado River Basin is less, the numbers of certain taxa (e.g, chironomids) can be very high. Chironomids constitute a significant part of the diets of larger larvae, juveniles, and even adult endangered fishes in low velocity habitats of the Upper Basin so that taxon is emphasized in this discussion of benthic production. The upper part of the range for chironomids was 4,150 per m^2 in the main channel, 31,125 per m^2 in backwaters, and 23,055 per m^2 in floodplain habitats of Upper Basin rivers (Table 4). More detail of the mean numbers of chironomids in different habitats of the Upper Basin are summarized in Appendices 1 and 2.

The numbers of chironomids, found in the main channel of the middle Green River, ranged between 360 to 4,645 organisms/m and the numbers ranged from 4,820 to 28,860 organisms/m^2 for backwater habitats in 1987 (Appendix 1; Grabowski and Hiebert 1989). In 1988, Grabowski and Hiebert reported the range in numbers of chironomids between 280 and 5,000 organisms/m^2 for the main channel of the river and between 3,330 and 28,890 organisms/m^2 in backwater habitats. Obviously, the backwater habitats were more

Table 4. Range of the mean number of chironomids from investigations of various habitats in the Upper Colorado River Basin. 1/ 2/

Habitat	Range of the mean number of organisms/m
Main Channel	20 - 4,150
Backwaters	83 - 31,125
Floodplain Habitats	0 - 23,055

1/ The mean number of chironomids were obtained from the following studies: Grabowski and Hiebert (1989); Cooper and Severn (1994a), b, c, d, and e; Wolz and Schiozawa (1995). The main channel, backwaters, and floodplain habitats contained primarily sand and silt at the sites sampled so chironomids were used as a measure of relative abundance of benthic macroinvertebrates. The number of samples taken, sampling gear used, seasons (late spring and summer) and years of sampling differed so ranges are used to illustrate the relative productivity of chironomids.

2/ Most (4) of the investigations were made on the Green River. However the data include two investigations on the Colorado River and one investigation on the Gunnison River, a major tributary of the Colorado.

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productive in chironomid production than the main channel. Another study evaluated macroinvertebrate densities in the main channel, side (ephemeral) channel, and two types of backwater habitats in the middle Green River, downstream of Vernal, Utah. The numbers of chironomids in the main channel ranged between 3,500 and 4,200 organisms/m, the range for the side (ephemeral) channel was between 2,300 and 8,100, in one large backwater (basically a riverside lagoon) the range of chironomids was between 9,000 and 23,000, and in the other backwater, the range was between 22,800 and 31,100 organisms/m (Appendix 2; Wolz and Shiozawa 1995). Four baseline studies were conducted of wetland habitat sites in bottomlands of rivers in the Upper Basin. The wetland at Escalante Ranch along the middle Green River, upstream from Jensen, Utah, produced a mean of 17 chironomids/m in the main channel, 17 organisms/m in a backwater, and 31 organisms/m for an open water wetland (Appendix 2; Cooper and Severn 1994b). At another wetland site, Cooper and Severn (1994a) reported a mean of 11 chironomids/m^2 in the main channel of the Colorado River immediately upstream from Moab, Utah, 4 in a backwater site and 11 in an open water wetland. The Gunnison River at the Escalante State Wildlife Area, about five miles downstream from Delta, Colorado, contained a mean of about 496 chironomids/m, a backwater contained 1,141 and an open water wetland contained 1,092 (Appendix 2; Cooper and Severn 1994c). The mean number of benthic chironomids/m^2 in a floodplain depression (Old Charley Wash) was 33, 21 in a backwater, and 10 from the channel of the middle Green River adjacent to the floodplain on the Ouray National Wildlife Refuge, Utah (Cooper and Severn 1994d).

The mean number of aquatic organisms (combined species) collected in five 1.85 cm bottom cores from backwaters in the lower Green River varied between 65,200 and 562,200 organisms/e, depending upon the site and date of collection (Nance 1997).

D. <u>Relation of Food to Larval Fish Survival and Year-Class Strength.</u> Larval fish must initiate feeding during the first few weeks after swimup when they are making the transition from endogenous nutrition (yolk sac) to exogenous feeding (invertebrates) before the larvae reach "a point of no return" or the "point of irreversible starvation" that is termed the "critical period" (Hjort 1914; Houde 1987; Li and Mathias 1982; Miller et al. 1988). The timing, density, size, and duration of zooplankton availability must "match" the timing of the swimup stage of fish larvae. High mortality of larval fish can occur from starvation or reduced growth if food resources are limited and/or intra- and interspecific competition is high (Leggett 1986; May 1974; Welker et al. 1994). Horn (1996), Lasker (1981), Lawler (1965) and others emphasize that the growth rate of larval fishes is extremely important because smaller fish that are in poor condition (i.e., starved) with less locomotive ability (Rice et al. 1987) are more susceptible to predation (Leggett 1986). The highest survival of larval fish occurs when high densities of zooplankton are present during the time when larvae begin exogenous feeding (Hjort 1926; Leggett 1986). Fish larvae can recover quickly from short periods of starvation through compensatory growth if they encounter high densities of zooplankton before they reach their "point of irreversible starvation" (Miglavs and Jobling 1989).

Starvation as factor in mortality was suggested by Marsh and Langhorst (1988) for razorback sucker larvae in Lake Mohave and documented for the razorback sucker larvae in the laboratory (Papoulias and Minckley 1990). Razorback sucker larvae of about 10 mm total length were maintained in the laboratory at 18 C. Unfed razorback larvae died in 10 to 30 days. Razorback larvae must find food of the right size and density between 8 and 19 days to survive. The "point of no return" or "point of irreversible starvation" when the fish died even though sufficient food of the right size became available occurred between 19 and 23 days for razorback sucker larvae. Papoulias and Minckley reported that the minimum quantity of food required for survival of the razorback sucker larvae during the critical period was 30-60 brine shrimp nauplii per fish per day to survive. Razorback sucker larvae had good survival (80-90%) if the number of food organisms available to each fish was 58 per day or higher (upper diagram; Figure 1). However, the best growth during 50 days after swimup occurred when the number of food organisms was 527 per fish per day or higher (lower diagram; Figure 1).

In earthen ponds, razorback sucker larvae had excellent survival from swimup to 8 weeks of age (67.4-89.8%) when the mean number of zooplankton per liter was between 12.5 and 43.3 (Papoulias and Minckley 1992; upper diagram, Figure 2). There was no significant difference among treatments. However, growth of razorback sucker larvae during the eight-week period increased significantly with the density of zooplankton (lower diagram, Figure 2). In another study, the survival of razorback sucker fry in hatchery ponds at the Dexter National Fish Hatchery, New Mexico, increased from 10.8-35.7% to 87.8-98.6% with increases in fertilization and lower stocking rate of fry (Hamman 1987).

Recruitment of long-lived fishes with high fecundity is curtailed primarily from mortality during the larval stage from either starvation, predation, or both (Houde 1987; Hunter 1981; Lasker 1981). Razorback sucker larvae that were deprived food in the laboratory showed an initial increase in length as they utilized remaining yolk reserves. However, they were significantly less in total length and weight than larvae of the same age fed <u>ad libitum</u> at temperatures of 14, 18, and 23 C (Horn 1996). Many razorback sucker larvae in Lake Mohave survive to swimup but often have empty guts suggesting starvation is a factor in early life mortality (Marsh and Langhorst 1988) or reduced growth due to insufficient food keeps the larvae within a vulnerable size to predation for a longer period

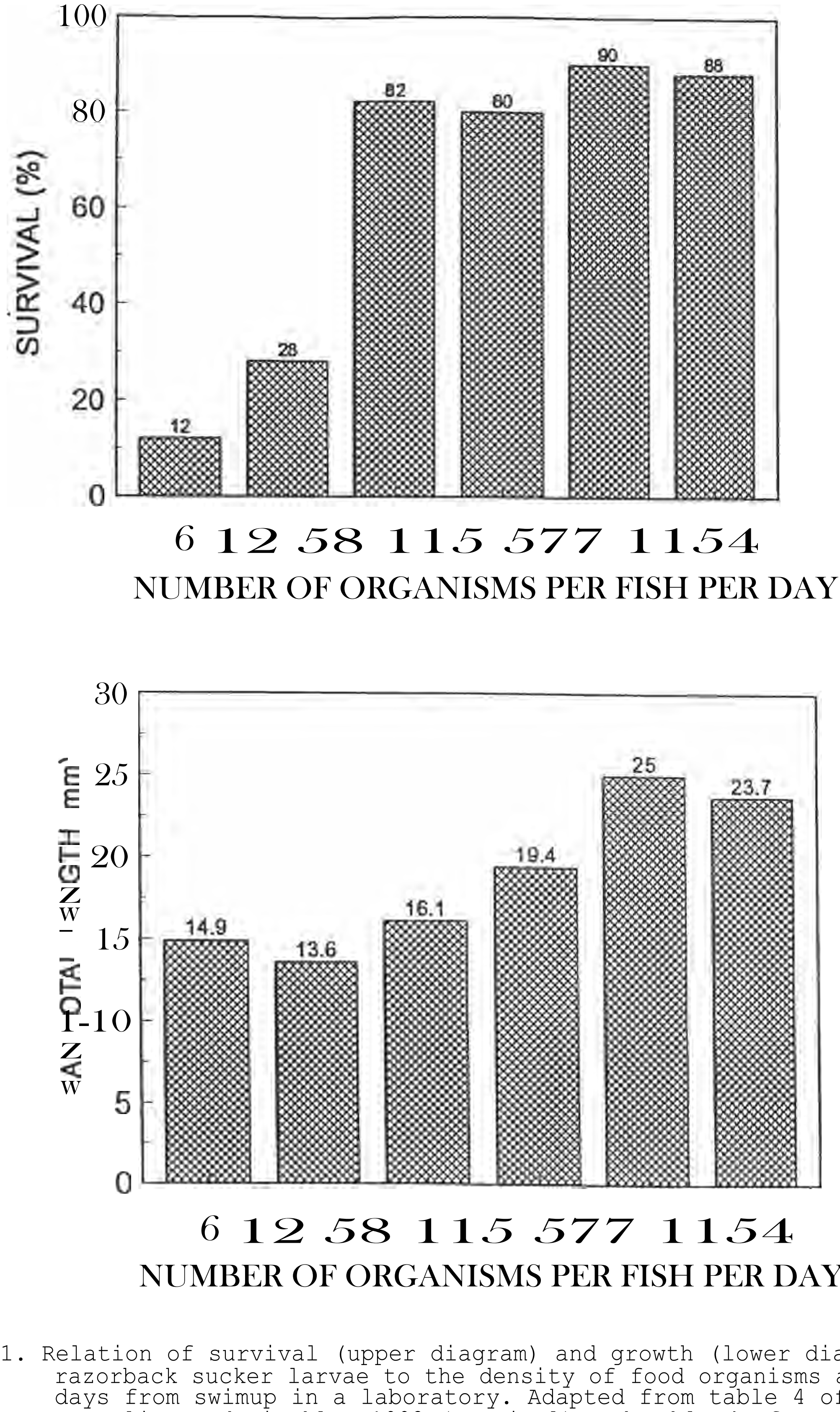


Figure 1. Relation of survival (upper diagram) and growth (lower diagram) of razorback sucker larvae to the density of food organisms after 50 days from swimup in a laboratory. Adapted from table 4 of Papoulias and Minckley 1992 (survival) and Table 4 of Papoulias and Minckley 1990 (growth).

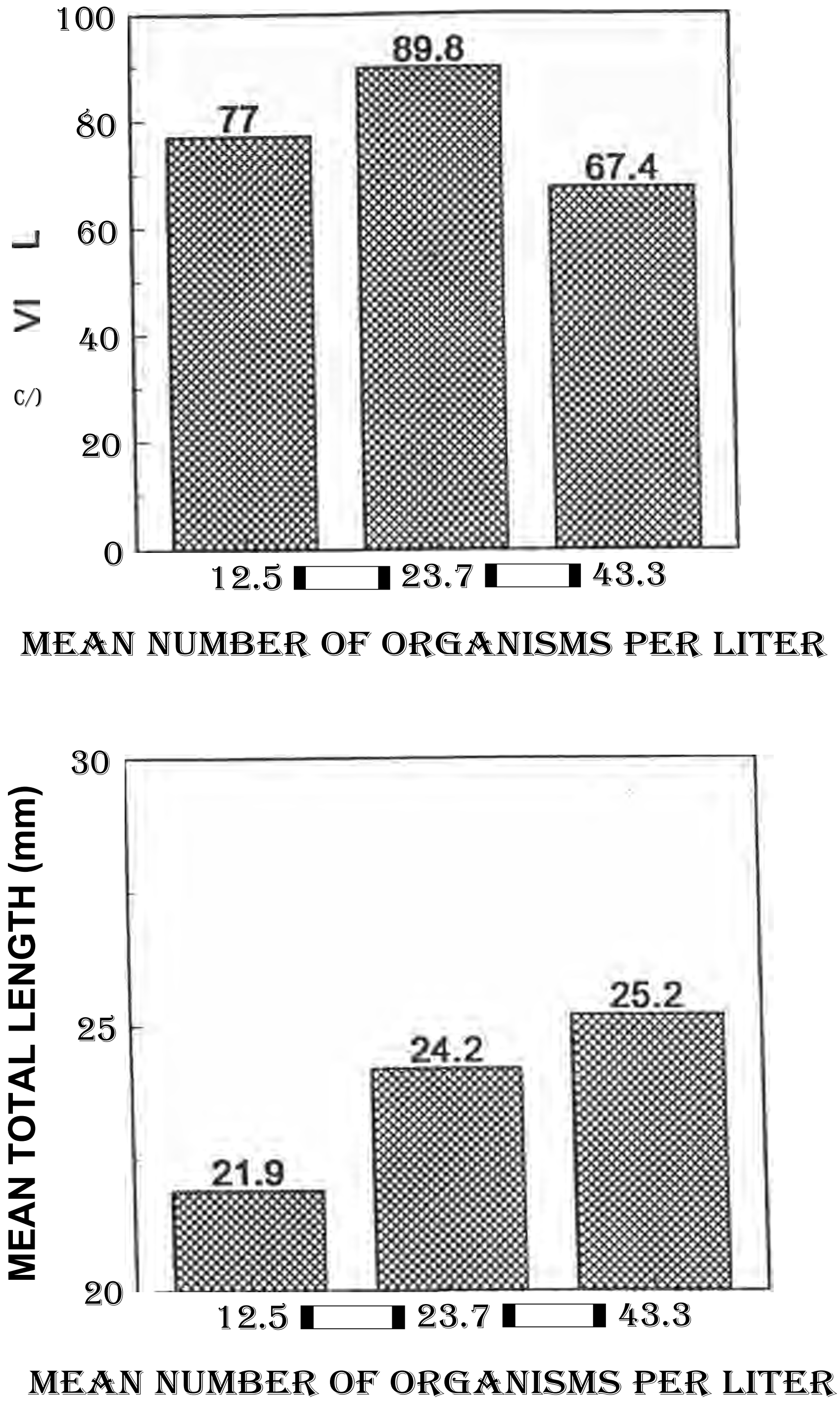


Figure 2. Relation of survival (upper diagram) and growth (lower diagram) of razorback sucker larvae to the density of food organisms after 8 weeks from swimup in earthen ponds. Adapted from text (survival) and Table 2 of Papoulias and Minckley 1992 (growth).

of time with the result that larvae, surviving starvation, are apparently completely consumed by piscivorous fishes in Lake Mohave (Horn 1996; Minckley et al. 1991). Shifts in survival during early life stages of fish populations most often result in a decline of populations in altered aquatic habitats (Houde 1987; Lasker 1981; Lawler 1965).

The average size of 1,735 razorback sucker larvae with a mean age of 12-17 days from the middle Green River was 12 mm TL (range 8 - 24) and the average size of 440 larvae from the lower Green River was 13 mm TL with a range between 10 and 20 mm (Muth et al. 1998). Muth et al. reported that only 20% of the razorback larvae collected from the Green River, Utah were larger than 12 mm TL with the two largest larvae at 20 and 24 mm TL.

Larger, faster-growing razorback sucker larvae are more likely to be captured in light traps because they are more mobile but may not be representative of the actual size structure among all larvae (Horn 1996). Razorback sucker larvae are 7-9 mm TL at hatching and 9-11 mm at swimup (Muth et al. 1998). Most razorback sucker larvae captured in Lake Mohave were less than 20 days old and averaged 11.4 mm TL while larvae reared in the laboratory reached a length of about 15 mm in 20 days at 18 C and nearly 16 mm in 20 days at 14 C (Horn 1996). Horn's estimates of mortality from starvation in Lake Mohave were between 23% and 78% between 1992 and 1995, depending upon the year of capture and nutritional index used. Therefore, most razorback sucker larvae collected in both the Upper and Lower Colorado River Basins are of a size (11-12 mm TL) when they are just converting to exogenus feeding during their critical period when they disappear from samples.

The larvae and juveniles of all endangered Colorado River fishes feed on zooplankton (U.S. Fish and Wildlife Service 1987, 1990a, 1990b, 1991). The first foods of larval razorback suckers in ponds were diatoms, detritus, algae, and rotifers (Bestgen 1990; Papoulias and Minckley 1992). Soon afterward, razorback larvae begin to select larger zooplankton organisms,primarily cladocerans. Marsh and Langhorst (1988) reported that razorback sucker larvae, less than 21 mm TL, fed on rotifers, cladocerans, and copepods in the open water of Lake Mohave and that the diet of razorback larvae in backwaters included larval chironomids and trichopterans. Older and larger razorback sucker larvae in Lake Mohave occupied small inlets or bays that were shielded from wind and wave action where a broader spectrum of small prey occur and are eaten by the larvae (Horn 1996).

Muth et al. (1998) reported that small food items generally composed between one-half to two-thirds (range 49-68%) of the total volume in the digestive tracts of razorback sucker larvae between 11 and 14 mm TL from the middle and lower Green River and that early instar chironomids composed between 32 and 51% of the total volume. Most of these razorback larvae were collected in light traps from shallow backwaters. The volume of digestive tracts composed of chironomids in Muth et al. (1998) may be an artifact because free-swimming invertebrates are attracted to light traps (Ervin and Haines 1972) and chironomids are larger than zooplankton so a few organisms would compose a large percentage of the total volume of food. It is likely that razorback sucker larvae were opportunistic in eating the early instar benthic organisms that were attracted to and accumulated in light traps. Gradually, late larvae and early juveniles feed on larger benthic organisms when they are available.

The diet of adult razorback suckers in reservoirs consisted largely of zooplankton that they obtained from the water column (Marsh 1987) but, in river habitats, the diet of adults consists of benthic materials, mainly immature Chironomidae, Ephemeroptera, and Trichoptera along with algae and detritus (Bestgen 1990). The density of zooplankton required for larval razorback sucker survival (30-60 organisms per fish per day; Papoulias and Minckley 1990) occurred in floodplain habitats along the Green River but rarely reached that density in backwaters, and never reached it in the main channel of Upper Basin rivers (Tables 1 and 2; Cooper and Severn 1994 a,b,c,d,e; Grabowski and Hiebert 1989; Mabey and Shiozawa 1993). Only two large backwaters in the Upper Basin contained zooplankton densities that were adequate for razorback sucker larvae during their critical period -- Intersection Wash in the middle Green River (Mabey and Shiozawa 1993) and Millard Canyon in the lower Green River (Nance 1997).

It is important to point out that only a portion of the zooplankton or benthic invertebrate biomass is available to razorback larvae since their mouths are gape-limited but they select the largest organisms that will fit into their mouths (Marsh and Langhorst 1988). Another important point is that aquatic organisms normally found in the water column such as zooplankton also occur in benthic samples and benthic organisms that are either free-swimming or emerging pupae also occur in the water column. Larval fishes, including razorback suckers, feed on both benthic and planktonic food organisms that are available and of the right size.

The year-class strength of fish species is often determined by environmental conditions such as suitable water temperature as well as the quality and quantity of food organisms available to larval fish within the first few weeks of hatching (i.e., critical period; Hjort 1914, 1926; Houde 1987). During years with optimum environmental conditions, high survival of larval and juvenile fish produces strong year classes. The timing, extent, and duration of flooding greatly influences fish species that use floodplain habitats and these factors may exert a moderate to strong control in year-class strength of some fishes (Lambou 1963; Baker and Killgore 1994).

The endangered Colorado River fishes are long-lived and are known or believed to produce strong year classes (Henrickson and Brothers 1993; Kaeding and Zimmerman 1983; McCarthy and Minckley 1987, Miller et al. 1982; Minckley et al. 1991; Osmundson and Burnham 1996; Vanicek and Kramer 1969). The ultimate year-class strength of many riverine fishes depends on the magnitude and duration of overbank flooding (Bayley 1991), suggesting that reconnection of floodplains with Upper Basin rivers (i.e., re-establishing the flood pulse) may be a key strategy in recovery of the razorback sucker.

E. Use of Floodplain Habitats by Adult Razorback Suckers. During high spring runoff, adult razorback suckers in the Upper Colorado River Basin were captured in large eddies at the mouths of rivers, off-channel ponds that have a connection to the rivers, and wetlands in floodplain areas (Modde 1997; Tyus 1987; Tyus and Karp 1990; Valdez and Wick 1983). These investigators believed that adult razorback suckers used these low water velocity habitats to escape the high water velocities that occur in the main channel during high spring streamf lows. Since adult razorback suckers were also found in wetlands in floodplain areas and off-channel ponds after the spawning season on the descending limb of the hydrograph, some investigators suspected that adult fish also used these productive habitats to regain body condition after spawning. Although adult razorback suckers feed on benthic and drifting invertebrates, algae, and detritus in rivers (Bestgen 1990), their diet in reservoirs (and probably floodplain habitats) consists largely of zooplankton filtered from the water column (Marsh 1987).

Floodplain habitats may also be used as spawning sites by adult razorback suckers in the Upper Colorado River Basin (Kennedy 1979; Osmundson and Kaeding 1989; Tyus and Karp 1990). Ripe female razorback suckers were collected from a large embayment on the Walter Walker Wildlife Area along the Colorado River near Grand Junction, Colorado (McAda and Wydoski 1980; Valdez and Wick 1983). Valdez and Wick (1983) also reported collecting ripe razorback suckers of both sexes from "Clifton" Ponds along the Colorado River near Clifton, Colorado. These fish may have used the floodplain habitat for staging but actually spawned in the adjacent river channel. However, there is a possibility that they actually spawned in the floodplain.

Kidd (1996) reported that he observed spawning razorback suckers in significant numbers between 1971 and 1980 at five sites on the upper Colorado River: (1) the Mesa County DeBeque gravel pit, (2) the Colorado River Overflow near DeBeque, (3) the Palisade Labor Camp slough, (4) the 32 1/4 Road backwater/gravel pit, and (5) the Walter Walker Wildlife Area. These sites were all greater than 2 ha (5 ac) in area, more than 457 m (1,500 ft) long, generally 0.9-1.5 m (3-5 ft) in depth, and did not depend entirely upon the river to maintain water levels. Kidd attributed the rapid decline of the razorback sucker population in the upper Colorado River to the loss of the Colorado River Overflow spawning site near DeBeque, Colorado during the high flood events of 1983 and 1984.

Spawning of razorback suckers in Lake Havasu in 1950 was described by LaRivers (1962). Adult razorback suckers spawned naturally and successfully in isolated coves along the shore of Lake Mohave (T. Burke, 1994, personal communication; Mueller et al. 1993). Jonez and Sumner (1954) described spawning of razorback suckers in Lake Mead and spawning of both razorback suckers and bonytail in Lake Mohave. Jonez and Sumner stated that both species were broadcast spawners that were observed in large schools. In reservoirs, razorback suckers congregate and spawn on flat or gently sloping shoreline areas over gravel, cobble, or mixed substrate (Bozek et al. 1990; Douglas 1952). In Lake Mohave, razorbacks spawned in water from 0.5 to 5.0 m deep (Minckley et al. 1991). However, they were observed to spawn in water from 10 to 15 m deep in Senator Wash Reservoir (Medel-Ulmer 1983). Captive razorback suckers also spawned in earthen ponds at the Dexter National Fish Hatchery, New Mexico (J.H. Williamson, 1998, personal communication).

Although cobble and gravel bars are used as spawning sites for razorback suckers in rivers, floodplains may also be used for spawning under certain conditions. Sparks (1995) pointed out that "A floodplain depression that is ordinarily dry during moderate floods may become a spawning site during record floods, when traditional sites are unusable because of excessive water velocities or sediment loads".

F. Streamf low Management - A Critical Habitat Component in River-Floodplain Ecosystems. The natural streamf low regime of virtually all rivers is inherently variable and this variability is critical to maintaining the integrity of river-floodplain ecosystems (Poff et al. 1997). The morphology of a river channel is dependent upon lateral and vertical controls based on the geology of the region and physiographic setting of the river (Church 1992). The productivity of rivers in the Upper Colorado River Basin was historically provided through energy transfer by the river continuum and the flood pulse. The sediment load of these rivers limited primary and secondary productivity in the main channels so that nutrients were provided longitudinally from terrestrial sources upstream and laterally from the inundation of floodplains during high streamf low events. Dams have fragmented major rivers in the Upper Basin so that productivity from upstream sources (i.e., the river continuum concept) was disrupted (Ward and Stanford 1983, 1995). Because of fragmentation by dams, Upper Basin rivers are now more dependent upon the productivity of aquatic organisms from lateral floodplain sources (i.e., the flood pulse concept). Recent protocol from large-river biologists (Stanford et al.

1996) requires "restoring peak flows needed to reconnect and periodically reconfigure channel and floodplain habitats".

Large-river ecologists recommend mimicking the natural hydrograph as a first step in habitat enhancement/restoration (Bain et al. 1988; Poff et al. 1997; Stanford 1994; Stanford et al. 1996; Ward 1989). Overbank flooding is required to reconnect floodplains with rivers. However, overbank flooding is a controversial issue with the public because of potential economic loss in agricultural crops and private property as well as sociological issues such as (1) increases in mosquitoes and potential for encephalitis outbreaks and (2) spread of noxious introduced weeds (U.S. Bureau of Reclamation and U.S. Fish and Wildlife Service 1998).

If overbank flooding does not occur, the lateral floodplain productivity is curtailed with the result that the productivity of Upper Basin rivers are adversely affected. As streamf lows increase and subside during the spring runoff, various aquatic habitats are produced that are used by the different life stages of native fishes (Schlosser 1990, 1991). Low velocity habitats in streams and floodplains can be maintained only by preserving fluvial geomorphological processes of watersheds (Kellerhals and Miles 1996). Kellerhals and Miles also stated that efforts to restore fish habitat in river channels and floodplains have resulted in low success in rivers that have been extensively altered. Regulation of streamf lows through dam releases for irrigated agriculture and peak power generation reduces the diversity of aquatic habitats -- some of which may be required by various life stages of the razorback sucker for successful recruitment (Wick 1997). Stanford et al. (1996) stated that reregulation of most rivers can be accomplished without substantially compromising storage or power generation.

If economic, political, and sociological pressures prevent increasing streamf lows to restore the river-floodplain integrity, then it will be necessary to excavate floodplain habitats to aid in the recovery of the endangered fishes. Many of the existing floodplain terraces in broad alluvial valleys of Upper Basin rivers were deposited during much higher peak streamf lows than presently occur. Excavation of floodplain habitats would allow inundation at lower river elevations so that private property along Upper Basin floodplains that are either occupied by humans or used for agriculture will not be adversely affected. Modde (1997) reported that some recruitment of razorback suckers occurred in floodplain depressions along the middle Green River.

Most known historic spawning aggregations of razorback suckers in the Upper Colorado River Basin were located upstream from river reaches with broad floodplains where rivers meandered without restriction. The best example is "Razorback Bar" on the middle Green River that is located just downstream of Dinosaur National Monument. A broad floodplain extends about 90 km (56 mi) downstream from "Razorback Bar" to Pariette Draw. The razorback sucker population using this bar was estimated to be about 500 adult razorback suckers (Modde et al. 1995). About half of the adult razorback suckers captured by electrofishing at Razorback Bar in 1998 were marked fish, suggesting that the population is declining (L. Shanks, 1998, personal communication).

The timing of streamf low was found to be important in maintaining a cobble bar (Razorback Bar) that is a primary spawning site for razorback suckers in the middle Green River, upstream from Jensen, Utah. Twelve cross-sections at "Razorback Bar" during 1993 and again in 1996 indicated that this site was subject to a backwater effect and significant sedimentation occurred at discharges exceeding 340 m3/s (12,000 cfs). Some sedimentation of the site began at a discharge of 200 m^3/s (- 7,000 cfs) and resulted in 0.6 m (- 2 ft) of sand deposition as streamf lows approached 650 m^3s/s (- 23,000 cfs; Wick and Cluer 1998). At lower streamf lows, the backwater effect does not occur and the channel becomes narrower so that higher water velocities can scour sand from the cobble substrate to make it suitable for razorback sucker spawning. Wick and Cluer (1998) suggested the low catch rate of razorback sucker larvae in light traps from the middle Green River during 1995 reported by Muth et al. (1998) may have been caused by excessive sedimentation in the cobble and gravel substrate at Razorback Bar that resulted in poor reproductive success. Although razorback suckers spawn in rivers on the ascending limb of the hydrograph and can spawn in floodplain ponds or isolated lagoons that may not have gravel or rubble substrate, these observations demonstrate the magnitude and timing of releases from Flaming Gorge Dam are crucial to Razorback Bar, the primary razorback spawning site in the middle Green River. Therefore, the magnitude and timing of regulated water releases from Flaming Gorge Dam are important to ensure that (1) the substrate at Razorback Bar is clean and suitable for razorback sucker spawning, and (2) flows will allow inundation of floodplains so that larval razorbacks at swimup have access to productive floodplains during their critical period. Lower releases from Flaming Gorge Dam are needed to maintain suitable conditions on "Razorback Bar" for spawning but higher releases are needed shortly afterward to inundate floodplains and provide access for swimup razorback larvae to productive nursery areas.

IV. ROLE OF PREDATION AND COMPETITION IN SURVIVAL OF LARVAL ENDANGERED FISHES

Stanford et al. (1996) reported that one of three general principles of stream ecology related to streamflow regulation is that "native biodiversity decreases and nonnative species proliferate". Predation and competition by nonnative fishes have been demonstrated to have an adverse impact on native fishes in various North American waters (Moyle et al. 1986). These two factors are also believed to be significant in the decline of the endangered Colorado River fishes. The responses of both native (including endangered) and nonnative fishes will have to be monitored closely with habitat enhancement of floodplains in the Upper Colorado River Basin.

Minckley et al. (1991) considered predation by nonnative fishes to be the single-most important factor in recruitment failure of razorback sucker in Lake Mohave in the Lower Colorado River Basin. Jonez and Sumner (1954) reported that carp (Cyprinus_carpio) fed on the eggs of razorback suckers in Lake Mohave and young bass (Micropterus salmoides) and sunfish (Lepomis sp.) fed on razorback larvae. Researchers also believe that predation by nonnative fishes is an important factor in the Upper Basin (Tyus and Saunders 1996). Reference to predation by nonnative fishes is most often related to fish species that are known to be piscivorous such as members of the Families Centrarchidae, Ictaluridae, and Esocidae. However, the most numerous fishes in backwaters of the Upper Basin are nonnative minnows that may be more important predators than more widely recognized piscivorous species.

Although predation on endangered fishes in the Upper Basin occurs by nonnative, piscivorous fishes in the Family Centrarchidae such as the green sunfish (Lepomis_cyanellus), smallmouth bass (Micropterus dolomieui), largemouth bass, the Family Ictaluridae primarily in the channel catfish (Ictalurus punctatus), and one member of the Family Esocidae, the northern pike (Esox lucius), several nonnative minnows (particularly, fathead minnows, Pimephales promelas and red shiners, Cyprinella lutrensis) may be even more important predators on the endangered Colorado River fishes and may also be important competitors with the endangered fishes.

A. Predation. Predation on larval fish significantly decreases their survival (Leggett 1986). Although razorback sucker gametes are viable and larvae are produced through successful natural reproduction in the Upper Basin (Muth et al. 1998), the swimup larvae are highly vulnerable to predation by nonnative fishes because food organism availability is low in the main channel and backwaters of Upper Basin rivers.

Nonnative red shiners and fathead minnows are often the most abundant fish species in backwaters of the Upper Basin rivers. For example, Cranney (1994) reported that red shiners constituted 66.5% and fathead minnows 31.9% of 3,599 fish collected in 13 seine hauls in the lower Duchesne River, a tributary to the middle Green River. Only one native fish (a bluehead sucker) was captured during that sampling effort. Red shiners and fathead minnows constituted 90.4% of 149,489 fish collected between 1986 and 1994 from primary backwaters of the Colorado and Green rivers during the Interagency Standardized Monitoring Program (McAda et al. 1994a, 1994b, 1995). In 1996, nonnative minnows (combined species) comprised 92-99% of the total number of fish seined from backwaters of Upper Basin rivers during standard monitoring (McAda et al. 1997).

Adult red shiners were found to be predators on fish larvae in the Yampa and Green rivers (Ruppert et al. 1993). Adult red shiners (36.1 mm TL) consumed all 100 razorback sucker larvae and terminated a cage experiment in a wetland to determine competition between the two species (Modde and Wick 1997). Fathead minnows have also been documented to be predators on catostomid larvae (Dunsmoor 1993). Therefore, it is reasonable to assume that nonnative minnows such as the red shiner and fathead minnow are important predators on razorback sucker larvae. The razorback sucker spawns on the ascending limb of the hydrograph and their larvae drift downstream during May and June when zooplankton and benthic invertebrate numbers are low in backwaters in the turbid waters of Upper Basin rivers. Razorback sucker larvae would be highly susceptible to predation at that time by abundant nonnative minnows.

The composition of fish species in existing backwaters along six reaches in the middle Green River was made up primarily of nonnative minnows. Fathead minnows composed between 37.7 and 88.1% of fyke net catches in 1997 and red shiners composed 6 to 48.5% of the catches at these six sites (G. Birchell, 1998, personal communication). In backwaters that were reconnected with the main channel along the same six river reaches, fathead minnows composed over half (50.4 - 72.4%) of fyke net catches and red shiners comprised between 3.1 and 18.3% of the catches in 1997.

Although successful natural spawning of razorback suckers occurs on wave-swept rubble along the shoreline of Lake Mohave, survival of larvae only occurs in habitats such as predator-free isolated coves (Minckley et al. 1991). However, in the absence of predaceous fish, large numbers of odonate nymphs were produced in these coves and they replaced fish predators (Mueller et al. 1993). Horn et al. (1994) reported that odonate nymphs were very effective in capturing and consuming razorback sucker larvae in the laboratory. Larger juvenile razorback suckers are now stocked into the isolated coves to reduce or eliminate predation by odonate nymphs.

Nonnative fishes quickly occupy floodplain habitats that are reconnected to the main channels of Upper Basin rivers (G. Birchell, 1998, personal communication; Burdick et al. 1997). For example, nonnative fishes invaded and colonized a gravel-pit pond in the floodplain of the upper Colorado River within four months after the pond was drained, all nonnative fishes removed, and the pond reconnected with the river (Burdick et al. 1997) and, within eight months, five species of nonnative fishes successfully reproduced in the pond. This pond had a irregular bottom that was below the streambed of the main channel and did not drain as streamf lows from the spring runoff subsided. Burdick et al. recommended that deep gravel-pit ponds be rehabilitated by reshaping and sloping the bottom so that such ponds drain as high streamf lows subside to provide ephemeral floodplain habitats rather than permanent ones.

Four floodplain terraces and four floodplain depressions were reconnected with the middle Green River as part of the Recovery Program Habitat Enhancement/Restoration Subprogram. Nonnative minnows dominated the catches of fyke/trammel net catches from these sites in 1997. Fathead minnows composed between 14.9 and 76.2% of these catches and red shiners accounted for 3.1 to 30.8% in the four terrace sites (G. Birchell, 1998, personal communication). In one site, sand shiners dominated at 48.1% of the catch but this species made up only a small portion (1.1 to 9.1%) of the catches at the three other terrace sites. In the four floodplain depressions that were reconnected with the middle Green River, fathead minnows composed between 28.5 to 70.2% of fyke/trammel net catches in 1997 (G. Birchell, 1998, personal communication). Red shiners were not very abundant in the reconnected depressions with catches that ranged between 0 and 9.5%. Green sunfish composed over one-fourth (25.2 and 26.5%) of the catches at two depression sites but formed a relatively small portion of the catches (2.6% and 9.8%) at the other two sites. Black bullheads (Ictalurus melas) also made up from one-fourth to nearly one-third (24.3% and 31.9%) at the same two sites where green sunfish were numerous but were absent from one of the other reconnected depressions and made up 9.4% of the catch at the remaining site. Carp composed nearly one-third of the catch in one reconnected depression (29.3%) but were nearly absent at the other three sites (0, 1.1, and 1.4% of the catches).

B. Competition. Although competition for food among larval and juvenile fishes in the Upper Colorado River Basin has not been well documented (Hawkins and Nesler 1991), the main reason is because competition among freshwater fish species is often difficult to document due to the lack of specialization in food habits by freshwater fish, resulting in much overlap in their food habits (Larkin 1956). However, the extremely low densities of zooplankton in backwaters during the spring runoff where larval razorback suckers are now found and the high percentage of nonnative fishes provides evidence that competition may also be an important factor in the Upper Basin. Competition would probably be reduced if productive floodplain habitats, with higher densities of alternate food organisms occur, are reconnected with the main channels.

Beyers et al. (1994) documented in the laboratory that competition between larval Colorado squawfish and larval fathead minnow occurred where growth of both species was reduced through competition. Beyers et al. reported that the "negative competitive effects were quantitatively greater and more frequent for Colorado squawfish than for fathead minnows". Adult nonnative minnows and juvenile razorback suckers feed on the same food organisms so that nonnative minnows are not only predators on larval razorback suckers but may also be important competitors with juvenile razorbacks.

Competition by two species occurs when food is limited, the food is shared, and one of the two species is adversely affected by sharing food (Connell 1983; Crombie 1947; Elton 1946; Hardin 1960; Larkin 1956; Li and Moyle 1993; Moyle et al. 1986; Schoener 1982; Tilman 1982; Underwood 1986). Species that are more efficient at capturing and converting food into biomass will persist for a longer time as food resources become scarce (Schoener 1982; Tilman 1982). Such competitive interactions can change the structure of a fish community (Werner 1984). Density-dependent processes are often reflected in reduced growth rather than direct mortality in juvenile and adult fish (Schoenherr 1977).

Dietary overlap was reported between nonnative and native fishes in the Upper Basin (Jacobi and Jacobi 1982; Grabowski and Hiebert 1989; Muth and

Snyder 1995). Slightly over 3% of 53,750 larval or early juvenile fish captured in the middle Green River during 1992-1996 were razorback suckers and less than 1% of 59,220 larval and early juvenile fish in the lower Green River were razorback suckers (Muth et al. 1998). Nonnative cyprinids (red shiner, sand shiner NotroDis stramineus, carp CvDrinus carpio, and fathead minnow dominated the total light trap catch during 1993 (88%) and 1995 (70%) and native catostomids (bluehead and flannelmouth suckers) dominated the light trap catches in 1994 (97%) and 1996 (63%) in the middle Green River (Muth et al. 1998). Muth et al. (1998) stated that "Annual initiation of razorback sucker spawning in the Green River during our investigation [1992-1996] was probably triggered by a suite of interacting environmental cues that could not be detected in our analysis of individual water temperature and discharge parameters." The high percentage of nonnative cyprinids in certain years (such as 1993 and 1995) could be significant competitors with razorback sucker larvae because food resources are limited in the main channel and backwaters of the middle Green River.

A field experiment in backwaters of the middle Green River with complete, partial, or no fish exclosures demonstrated that fish can significantly reduce planktonic and benthic food resources and that diet overlap by nonnative fishes could result in competition with native fishes (Collins and Shiozawa 1994). These findings are consistent with results from studies on smaller streams where invertebrates in low velocity habitats with soft substrates have been reduced by fish predation (Angermeier 1985; Gilliam et al. 1989; Schlosser and Ebel 1989). Similar studies of large rivers were not found in the literature.

V. IMPORTANT FLOODPLAIN HABITATS IN THE UPPER COLORADO RIVER BASIN

Floodplain habitat sites (135 sites in the Green River Subbasin [Green River - 132 sites; potential area of 7,458 ha or 18,430 ac, Yampa River - 1 site; potential area of 8.9 ha or 21 ac, and White River - 2 sites; potential area of 256 ha or 634 ac] and 158 sites in the Colorado River Subbasin [Colorado River -110 sites; potential area of 4,948 ha or 12,222 ac] and Gunnison River - 48 sites; potential area of 1,305 ha or 3,223 ac) that could provide nursery areas for recovery of the razorback sucker and perhaps other endangered fishes were inventoried and classified during 1993 (Irving and Burdick 1995).

A. Green River Subbasin. Most floodplain habitat sites along the Green River are located between Pariette Draw upstream to Escalante Ranch (Irving and Burdick 1995; RK 383-499 [RM 238-310]; 2,466 ha [6,093 acres]). Floodplain terraces comprised the vast majority (75% of 99) of habitat in the Green River Subbasin while floodplain depressions comprised the remaining 25% of sites. Four percent of the 132 potential floodplain sites along the Green River were separated from the river by natural levees while 11% were separated by levees constructed by humans. Approximately 32 km (20 mi) of the Green River consisted of natural and human-constructed levees at 20 sites.

In early 1998, floodplain areas were evaluated based on three criteria: (1) Biological importance to the endangered fishes.; (2) Opportunities for floodplain enhancement/restoration.; and (3) Focus on areas that flood or could be made to flood under present streamf lows (P. Nelson, 1998, personal communication). In the Green River Subbasin, high priority reaches included RK 185 to RK 212 (RM 115 to RM 132 [Green River, Utah]) and RK 383 (RM 238; Pariette Draw) to RK 515 (RM 320; Dinosaur National Monument).

B. Colorado River Subbasin. Most floodplain habitats along the Colorado and Gunnison rivers were scattered in four general areas (Irving and Burdick 1995): (1) Colorado River between Debeque and Rifle, Colorado (RK 327-386

[RM 203-240]); (2) Grand Valley reach of the Colorado River between Loma and Palisade, Colorado (RK 245-298 [RM 152-185]); (3) Colorado River between McGraw/Hotel Bottoms and the Cisco boat landing (RK 159-177 [RM 99-110)); and (4) the Gunnison River near Delta, Colorado (RK 81-87 [RM 50.2-54.21). Floodplain habitat sites in the Colorado River Subbasin consisted of 37% terraces, 21% gravel-pit ponds, and 20% side channels. Natural levees separated 23.6 km (14.6 mi) of the 158 floodplain habitat sites along the Colorado and Gunnison rivers while 56.3 km (34.9 mi) were separated by levees constructed by humans.

The 1998 evaluation of river reaches identified RK 204 (RM 127; Westwater Canyon) to RK 386 (RM 240; Rifle, Colorado) on the Colorado River and RK 80.5 (RM 50; Escalante State Wildlife Area) to RK 120.7 (RM 75; North Fork of the Gunnison River) as high priority reaches based on the three criteria described above (P. Nelson, 1998, personal communication).

Arrangements are being made with state and federal agencies that have floodplain habitat in public ownership along the Colorado and Green rivers to experimentally remove levees to evaluate zooplankton and benthic invertebrate production and responses by endangered as well as other native and nonnative fishes. Acquisition of floodplain habitat sites in private ownership is being explored to protect areas that flood with present streamf lows and to reconnect other sites with the river by breaching levees (U.S. Bureau of Reclamation and U.S. Fish and Wildlife Service 1998).

VI. CONSIDERATIONS IN ENHANCING OR RESTORING FLOODPLAIN HABITATS IN THE UPPER COLORADO RIVER BASIN

The principles of hydrology, fluvial geomorphology, and systems ecology must be integrated into planned river enhancement to prevent inadequate analysis of water and sediment transport, morphology of the channel and its associated floodplain, and ecological requirements of organisms (National Research Council 1992). Such planning must recognize the ongoing physical processes in the river and work with these processes rather than against them (Heede and Rinne 1990). Important concepts in river enhancement planning are that (1) a river is the product of the drainage basin or watershed, (2) the integrity of river systems is influenced by watershed management practices, and (3) the terrestrial environment closest to the river (i.e., riparian zone) has the greatest impact on potential responses in the floodplain. Many past failures in ecological enhancement of rivers and streams resulted from inadequate analysis of physical conditions and establishment of realistic and measurable objectives for biological responses (National Research Council 1992).

The dynamic equilibrium of a physical system in a river creates various ecological habitats that results in a corresponding dynamic equilibrium of the biological system. River enhancement should begin with improved land management practices in a watershed that will allow the river to re-establish the dynamic equilibrium of its physical system. The goal of ecological enhancement of rivers is to improve the dynamic equilibrium of the physical, chemical, and biological systems together (National Research Council 1992).

The basic ecological requirements of space, water quality, streamf low, cover, and food must be reviewed by life stage for each endangered fish species in recovery efforts since all are important in producing and maintaining self-sustaining populations. Various biological, chemical, and physical factors must be considered in evaluating floodplain habitats that have the potential for enhancement or restoration (Table 5). Because rivers have a one-way downstream movement, preservation or enhancement efforts requires careful planning and management of the entire stream network and the surrounding landscape (Shelton 1988).

Economic, political, and sociological factors are also important and must be considered concurrently with the biological, chemical, and physical factors (Table 5). Nearly all large rivers in the northern third of the Earth have been dammed and regulated to provide water for irrigated agriculture, flood control, hydro-electric power, industry, and domestic use (Dynesius and Nilsson 1994). Humans settled in the corridors of these large rivers largely because the rivers provided transportation and floodplains provided productive agricultural areas and prime areas for industrial development. Humans have and will continue to have a dominating influence on watersheds and river ecosystems that dramatically influences environmental integrity, productivity, biodiversity, and heterogeneity (Frissell et al. 1993). Cairns (1995) emphasized that, to be successful, ecological integrity of aquatic systems must include the sustainable use of water resources by humans. Restoration of large river-floodplain ecosystems to a pristine or virgin state is probably not possible for highly altered systems that are used by humans (Welcome 1989, 1995). Instead, Gore and Shields (1995) suggest that the logical approach is to recover some of the ecological functions and values.

Habitat enhancement or restoration involving river margins (Large and Petts 1994) must consider biological, economic, political, and sociological factors (Wydoski 1977) and decisions should be made through negotiated adaptive management (Brown 1993; Ludwig et al. 1993; Walters 1986; Walters and Hillborn 1978). Because of strong economic, political, and social pressures from humans for multiple-use of large river-floodplain systems for hydro-electric power, agriculture, industry, and municipal uses, it is doubtful that restoration or returning rivers to an original state is possible (Bradshaw 1996). However, it is entirely possible to mitigate (i.e., to moderate), to remediate (i.e., to rectify), or to enhance (i.e., to improve) environmental conditions in a river ecosystem (Stanford et al. 1996).

The restoration of large floodplain rivers will require at least partial recovery of the natural hydrograph based on the current knowledge of such systems (Bayley 1991; Hesse 1995; Poff et al. 1997; Stanford et al. 1996; Ward and Stanford 1995). However, Dolan et al. (1974) stated that the historic natural hydrograph of Colorado River System can no longer be restored because of human alterations and the river system is rapidly approaching a new state such that the future of river bars and floodplain terraces is unclear. Yet restoration of large river ecosystem integrity requires full consideration of the river continuum and flood pulse concepts of energy transfer (Walker et al. 1995). Walker et al. emphasized that the greatest conflict occurs between the supply and demand of water from dryland river systems and believe that the integrity of large dryland rivers will be maintained only if users use water that is surplus to maintenance requirements of the riverine ecosystem. Site-specific efforts will not restore the ecological integrity of large rivers.

Many of the floodplain habitats flooded ephemerally under historic riverine conditions. For example, Cooper and Severn (1994d) estimated that streamflows between 481 and 566 m^3/s (17,000 and 20,000 cfs) were required to inundate the floodplain along the middle Green River on the Ouray National Wildlife Refuge. A streamflow of 566 m^3/s (20,000 cfs) occurred 17 times during the 47-year period of record (1946-1993) but only 7 times since the completion of Flaming Gorge Dam in 1964 (29 years). This floodplain was inundated only 6 times during the 47-year period for over 20 days. More recently, FLO Engineering, Inc. (1995) estimated that a streamf low of 575 m^3/s (20,300 cfs) was required for extensive inundation of the middle Green River floodplain on the Ouray National Wildlife Refuge. To reconnect the river with the floodplain will either require breaching the levees to produce inundation under present streamf lows or excavation of the floodplain terraces to lower the elevation so that floodplain inundation can occur without overbank flooding of private lands.

Table 5. Primary considerations for maintaining or enhancing the ecological integrity of aquatic habitats.

Physical Considerations

Water Supply (Quantity of Surface Water or Groundwater)
Frequency of Inundation
River Elevation and Discharge
  when Floodplain becomes Inundated
Water Depth and Duration
Control of Water Exchange and Levels in Floodplain Habitats
Water Temperature (Range and Potential for Manipulation)
Sediment Deposition and Erosion

Biological Considerations

Ecosystem Approach
Goals and Objectives for Preservation or Enhancement
  of River-Floodplain Ecosystem
Status and Trends of Native and Nonnative Species
Reintroductions of Captive-Reared Animals
  Maintaining Genetic Integrity and Diversity
  Need for Imprinting Larval or Young Fish to Source Water
  Batch Marks to Identify Captive-Reared Animals
  Size of Captive-Reared Animals at Release
  Timing of Release (Diel and Seasonal)
Proper Food (e.g., Size and Abundance) for Various Life
  Stages; Availability for Reintroductions
Access and Exit Routes for Animals
Vegetative Cover
Control of Predators and Competitors
  Nonnative Fish, Macroinvertebrates, Birds,
  Mammals, or Other Animals

Chemical Considerations

Acceptable Water Quality
  Chemistry, Dissolved Oxygen, Potential for Nitrogen
    Supersaturation from Well Water
Potential Contaminants
  Selenium, Heavy Metals, Pesticides or Herbicides

Economic, Political, and Sociological Considerations

  Uses of Floodplain Habitats (Human Occupation,
    Agriculture, Livestock Grazing, Gravel Mining, etc.)
  Legal Mandates, Human Pressures, Lobbying
  Cultural Attitudes, Perceptions, Values

Other examples of ephemeral flooding include the Escalante State Wildlife Area on the Gunnison River, downstream of Delta, Colorado (Cooper and Severn 1994c) and Moab Slough on the Colorado River, immediately upstream from Moab, Utah (Cooper and Severn 1994a). Cooper and Severn estimated that a streamflow of 340 to 425 m^3/s (12,000 to 15,000 cfs) was required for overbank flooding at that site. A streamflow of 425 m^3/s (15,000 cfs) occurred 31 times during a 97-year period of record (1896-1993). The duration of flooding at this streamf low occurred only 8 times for over 25 days. Pre-dam (1897-1965) streamflows that were greater than 283 m^3/s (10,000 cfs) on the Gunnison River were about 3 weeks in duration but the post-dam (1966-1993) streamf lows were less than 1 week at flows greater than 283 m^3/s (10,000 cfs). Cooper and Severn (1994a) estimated that streamflows of 1,133 m^3/s (40,000 cfs) were required for overbank flooding at Moab Slough along the Colorado River. This flow occurred 26 times during the 70-year period of record (1924-1993) but only 6 times between 1963 and 1993. The duration of inundation at Moab Slough over 25 days occurred only 5 times.

Even floodplain habitats that become inundated for a short time can produce relatively high densities of zooplankton as in the flooded willow habitat of Moab Slough along the Colorado River described by Cooper and Severn (1994b; Appendix 2) that benefit fish in backwaters and main river channels. However, a short duration of inundation on floodplain terraces is probably not sufficient for survival of larval razorback suckers and subsequent population recruitment today because the larvae will not have adequate time to grow large enough to escape predation by nonnative fishes when they enter backwaters of the rivers as streamf lows subside.

VII. INTEGRATION OF RECOVERY PROGRAM ELEMENTS

It is imperative to integrate all Recovery Program elements, especially streamflow management, habitat enhancement/restoration, control of nonnative fishes, and captive propagation and stocking of razorback suckers.

A. Streamflow Management. Streamf low management must consider the magnitude of discharge, frequency of occurrence, duration of specific flow conditions, timing of flows, predictability of flows of a defined magnitude, and rate of flow change (Poff et al. 1997). If possible, it would be ideal to mimic the natural hydrograph with streamflows high enough to flood existing terraces (Stanford 1994). Although ecologically sound, this strategy will have to take into account private lands that are occupied by humans or used for agriculture would be flooded and could result in loss of human lives or economic losses to agricultural crops. Streamf lows and habitat requirements for endangered Colorado River fishes were described for the Green River (Tyus and Karp 1991), Yampa River (Tyus and Karp 1989), and "15-mile reach" of the upper Colorado River (Osmundson et al. 1995).

If increasing streamf lows is not feasible in the Upper Basin because of economic, political, or sociological constraints, then excavation of existing terraces may be necessary so that the floodplain can be inundated within the present streamf low regime. Field experiments to evaluate increasing streamf lows would probably preclude extremely high releases and may have to be made incrementally to minimize flood hazards to private agricultural areas or to ensure the safety of humans living on floodplains.

Gore (1985) pointed out that substrate composition, critical to macroinvertebrate abundance and diversity, can be easily manipulated through streamf low management. He emphasized that "benthic macroinvertebrates comprise a large and diverse faunal community in most undisturbed running water ecosystems" and that benthic organisms provide a critical pathway for energy transport and utilization within stream ecosystems. An example of enhancement in a benthic invertebrate community through establishment of a minimum flow from a hydroelectric plant was described by Weisberg et al. (1990).

B. Habitat Enhancement/Restoration. All enhancement or restoration endeavors must be made through well designed experiments that will allow a thorough evaluation using an adaptive management approach. Evaluation of habitat enhancement includes the Recovery Program element of monitoring and research. Areas that are enhanced/restored should be thoroughly evaluated to determine the responses of the endangered and nonnative fishes to such efforts and refinements made as necessary to achieve desired Recovery Program goals and objectives. Enhanced areas will either have to be large enough or numerous enough to ensure that responses by fishes can be detected.

Larval and juvenile razorback suckers apparently require inundated floodplains to grow and survive (Mueller 1995; Mueller et al. 1993; Tyus and Karp 1989, 1990, 1991). Rapid growth of razorback sucker juveniles in off-channel habitats was reported by Osmundson and Kaeding (1989) and Mueller et al. (1993). Reconnecting floodplain habitats with rivers in the Upper Colorado River Basin is expected to benefit razorback suckers most since these habitats will provide an adequate quantity of food of the right size and at the right time for survival of larval razorback suckers during their critical period. Larvae and juveniles of other native fishes including the three other endangered species (Colorado squawfish, humpback chub, and bonytail) will also benefit from floodplain production of zooplankton and benthic invertebrates that enter the river when streamflows subside after spring flooding, enhancing the productivity of the main channel and backwaters of Upper Basin rivers.

Adult razorback suckers are flexible in their use of habitats. Although this species evolved in large riverine systems, adults have survived well in both lacustrine (Wallis 1951, Marsh and Langhorst 1988, Minckley et al. 1991) and lotic (Miller et al. 1982; Tyus 1987) habitats. During high spring runoff, adult razorback suckers in the Upper Colorado River Basin congregated in large eddies at the mouths of rivers, off-channel ponds that have a connection to the rivers, and wetlands in floodplain areas (McAda and Wydoski 1980; Modde 1997; Tyus and Karp 1990; Valdez and Wick 1983). The use of low velocity habitats by adult razorbacks may be to escape the high velocities associated with the spring runoff and possibly to feed after spawning to regain their body condition.

Razorback suckers spawn annually on clean cobble and gravel in rivers (Tyus and Karp 1990; Wick and Cluer 1998) and on the wave-swept rubble shoreline of Lake Mohave (Minckley et al. 1991). It is possible that floodplain habitats may have been used more extensively for spawning in the past by razorback suckers (Osmundson and Kaeding 1989) when they had access to them and riverine conditions were unsuitable as suggested by Sparks (1995) for other riverine fish species.

Breaching Levees. Removal of levees that are located on the lowest floodplain terraces (public property or acquired private property) is the most practical way to reconnect mainstem and tributary rivers with productive floodplain habitats using present streamflows. Such removal should be done on properties that can be easily reconnected with the main channel where thorough evaluations can be made of zooplankton/benthic invertebrate production and responses by native and nonnative fish species.

Ideally, reconnection of floodplain habitats with main river channels should simulate natural conditions where possible and be relatively maintenance free.

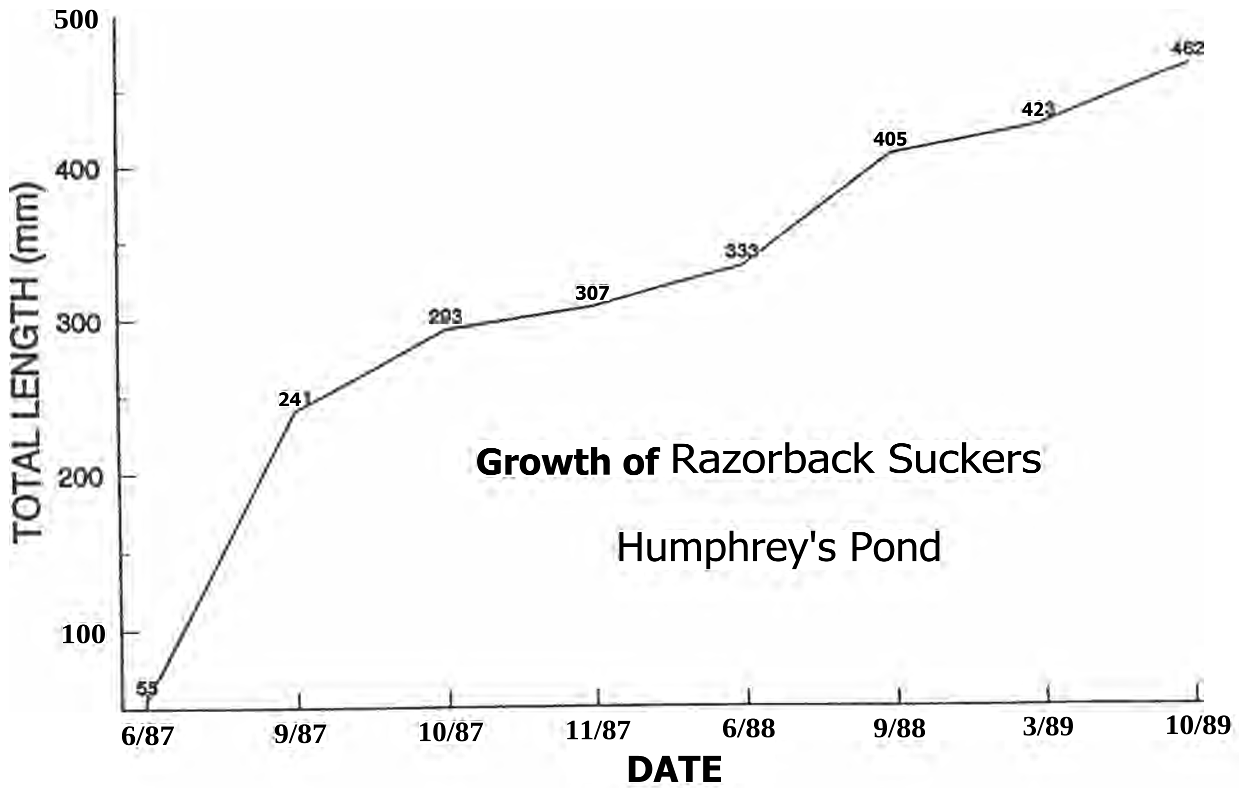
Floodplain Terraces. Existing floodplain terraces were deposited by high peak streamflows that occurred before high dams were constructed and the streamflows were regulated (i.e., peak streamflows that resulted in inundation, scouring, and deposition of floodplains were lost). Existing streamflow conditions may not permit annual inundation of the floodplain by simply removing levees. It may be necessary to excavate existing terraces so that present streamflow regimes can inundate floodplains where levees are breached. Reconnection of breached areas on lowered floodplains could be made without enhancing streamflows that may cause economic losses or social issues.

Depression Ponds. Depression ponds in the floodplain provide habitat where good to excellent growth of larval and juvenile razorback suckers and juvenile Colorado squawfish have been demonstrated (Osmundson and Kaeding 1989). In Humphrey's Pond along the Upper Colorado River, razorback suckers grew from 55 to 307 mm TL (-2 to 12 inches) from June until November, 1987 (Figure 3; Osmundson and Kaeding 1989). This growth is similar to the growth in hatchery ponds. For example, razorback suckers grew from 44 to 255 mm TL (- 2 to 10 inches) from April until October, 1993 in Wahweap State Fish Hatchery (Lake Powell), Utah (Figure 3). Twenty-eight Age-O razorback suckers from Old Charley Wash along the Middle Green River averaged 94 mm TL (- 4 inches) in September and October, 1995 (Modde 1997). Forty-five Age-O razorbacks from Old Charley Wash averaged 66 mm TL (- 2.5 inches) in August, 1996. In 1997, 95 juvenile razorback suckers were collected from Old Charley Wash. The razorback suckers collected from Old Charley Wash were survivors of wild larvae that entered the wetland during high spring streamf lows. Eleven wild razorback suckers captured in a wetland (Leota Bottom wetland complex along the middle Green River) in 1994 were between 250 and 370 mm TL or -10 and -15 inches (Modde and Wick 1997). These fish were yearlings based on scale analysis and probably entered the wetland in the spring of the previous year when it was filled with Green River water. A large number of mature razorback suckers were found in a gravel-pit pond (Etter's Pond) along the Upper Colorado River in 1990 that apparently gained access to the pond as larvae during the 100-year floods of 1983 and 1984 (F. Pfeifer, 1994, Personal Communication). However, it is also likely that these razorbacks were progeny from the spawning of only a few adult razorback suckers that entered the pond during these floods, based on mtDNA analysis (B. DeMarais and T. Dowling, 1994, personal communication). Razorback suckers from the Ouray National Fish Hatchery, Utah, that were surplus to Recovery Program needs, were stocked into golf course ponds at Page, Arizona where they grew from an average length of 115 mm TL (- 4 inches) to 383 mm (- 15 inches) between May, 1996 and August, 1997 (Mueller and Wick 1998). Larval razorback suckers stocked into depression ponds along Lake Mohave have exhibited good growth to large sub-adults that are stocked into Lake Mohave (Minckley et al. 1991; Mueller 1995; Mueller et al. 1993).

If frequency and duration of flooding discussed below cannot be restored, then captive-rearing of razorback suckers in predator-free floodplain depressions may be the only course of action left for maintenance of razorback sucker stocks in the Upper Basin to prevent their extinction.

Required Frequency of Flooding. The frequency of floodplain inundation required for recovery of razorback suckers is unknown. Numerous floodplains have been separated from the rivers for a long time so their potential nutrient levels and productivity are unknown. The flood pulse concept of nutrient cycling (Junk et al. 1989) provides the productivity of present Upper Basin rivers because of fragmentation of river reaches by dams. Therefore, reconnection of rivers may be required more often in the future than when the Upper Basin ecosystem was unaltered.

The river elevation necessary to provide an adequate frequency of inundation of floodplain habitats should initially be made on an annual basis or as often as possible to assist razorback suckers through their "critical period" that, in turn, should increase survival and recruitment.



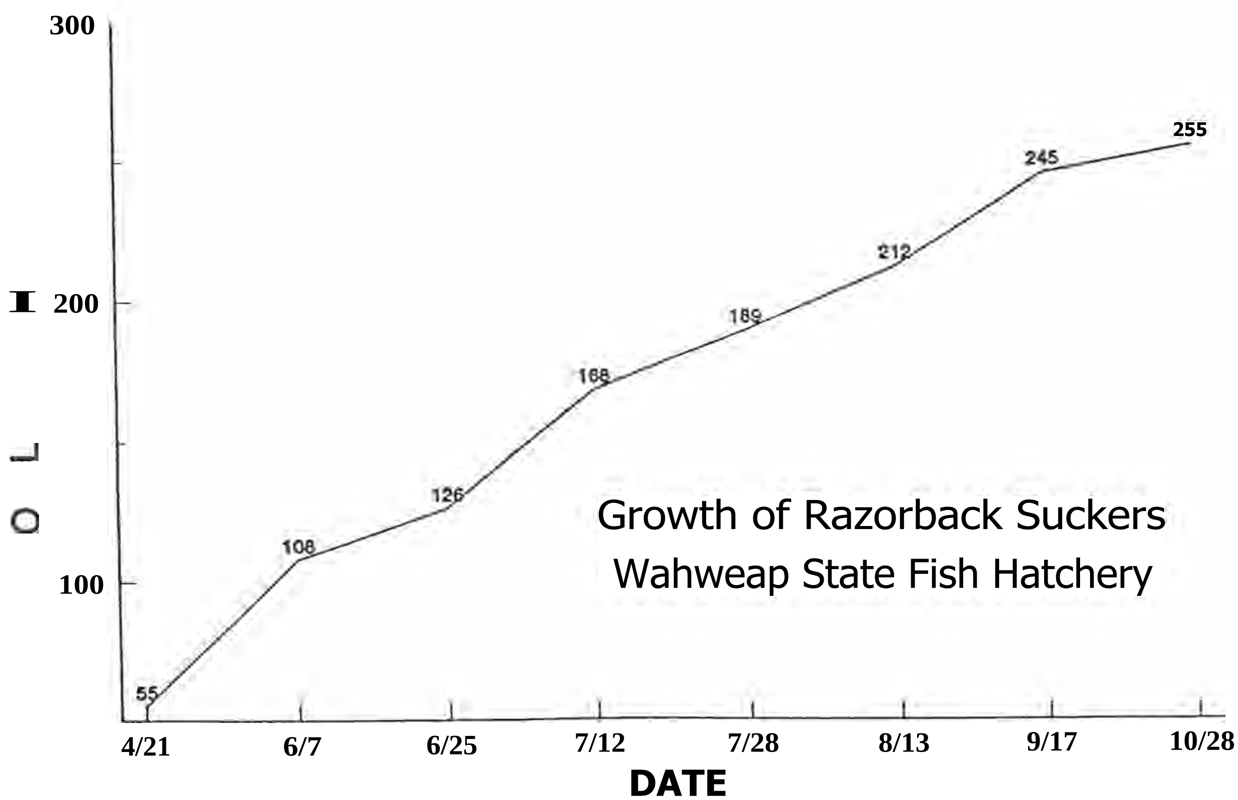


Figure 3. Growth of razorback suckers in Humphrey's Pond along the Colorado River near Grand Junction, Colorado in 1987-88 (upper diagram) and a pond at Wahweap State Fish Hatchery near Big Water, Utah in 1993 (lower diagram). Data adapted from Osmundson and Kaeding (1989) for Humphrey's Pond and from A.W. Gustaveson, Utah Division of Wildlife Resources for Wahweap State Fish Hatchery.

However, successful recruitment every five to ten years may be sufficient for a long-lived species such as the razorback sucker that lives to **44** years (McCarthy and Minckley 1987) or possibly longer, once the species is recovered. Sparks (1995) stated that creating an ideal water regime annually may be unnecessary for certain species because the reproductive potential of most warmwater fishes enables them to produce strong year classes. The four endangered Colorado River fishes are known to be long-lived (Henrickson and Brothers **1993**; Kaeding and Zimmerman **1983**; Miller et al. 1982; McCarthy and Minckley **1987**; Vanicek and Kramer 1969). The Colorado squawfish and bonytail were reported to produce strong year classes that were correlated with streamf lows (Vanicek and Kramer 1969). Vanicek and Kramer also reported strong year classes in the roundtail chub (Gila <u>robusta</u>) that is endemic to the Colorado River system but is not federally listed as threatened or endangered. McCarthy and Minckley (1987) concluded that 24 to 44 year-old razorback suckers in Lake Mohave were hatched prior to or coincidental with the construction and filling of the reservoir and that some year-classes were stronger than others. Finally, Kaeding and Zimmerman (1983) provided evidence of differences in numbers of humpback chub juveniles between years. Therefore, recruitment of the endangered Colorado River fishes was not an annual event but occurred when environmental conditions favored survival of larval and juvenile fishes. Endemic fish species may have evolved a life history strategy where strong year-classes sustained stocks in the dynamic, natural streamf low of the upper Colorado River and its tributaries.

<u>Duration of Flooding.</u> Flooding depression ponds along Upper Basin rivers should provide an adequate duration of time for razorback sucker to survive to the juvenile or subadult life stage when they would be large enough to escape predation and competition by most nonnative fishes. Razorback suckers should grow to 100 and 200 mm TL (- 4 to 8 in) in one growing season and 300 mm TL (- 12 in) in two growing seasons, based on present information (Figure 3).

If the duration of inundation in floodplain terrace habitats is short, razorback suckers will not grow to a size where predation and competition by nonnative fishes is no longer a principal factor in their survival. If the duration of flooding these habitats is longer, nonnative fishes may flourish and continue to adversely affect larval and juvenile razorback suckers through predation and competition (Nelson et al. 1995).

<u>Contaminants</u> may cause high mortality of larval and Age-O razorback suckers in some depression floodplain ponds. Bioaccumulation through the food chain in floodplain habitats may increase mortality of Age-O razorback suckers (Hamilton 1995; Hamilton et al. 1996) and elevated levels in milt and eggs may inhibit successful reproduction in adult razorback suckers (Hamilton and Waddell 1994).

C. <u>Control of Nonnative Fishes.</u> In Section IV, predation on and competition with endangered fishes by nonnative fishes were identified as important problems (Tyus and Saunders 1996) that must be addressed concurrently with other Recovery Program actions. Nonnative fishes in floodplain habitats and backwaters along the main channel will also benefit from increased production from enhanced/restored floodplain habitats (Nelson et al. 1995). Recovery of the endangered fishes is dependent on sufficient survival of larvae and juveniles that will provide adequate recruitment to develop and maintain self-sustaining populations. Therefore, adverse nonnative fish interactions may limit the recovery of the razorback sucker unless adequate control measures can be implemented in immediate upstream reaches, and particularly in downstream reaches of the main channels, where advanced larvae or early juvenile razorbacks occupy backwater habitats upon leaving floodplain habitats.

Only 43 of 250 fish control projects were considered to be successful in a comprehensive review by Meronek et al. (1996). Total control of nonnative fishes is impossible in the Upper Colorado River Basin because these fishes are well established with self-sustaining populations (Wiley and Wydoski 1993). However, attempts to remove nonnative fishes should help to increase the numbers of razorback suckers in Upper Basin rivers. Minckley and Meffe (1987) believed that even temporary removal or suppression of nonnative predators or competitors may enhance native fish populations. Although biologists are often intimidated by the inefficient and labor-intensive methods of fish control and possible negative public reaction, there is a necessity to reduce (or eradicate if possible) nonnative fish species because of the magnitude of the problem in certain waters (Temple 1990). Ultimately, the endangered fishes must be able to sustain their populations with the established nonnative fishes in the Upper Basin, if recovery is to be realized. Otherwise, periodic or continuous human intervention will be required to control nonnative, warmwater fishes because compensatory growth and survival of nonnative fishes will allow rapid resiliency (Wiley and Wydoski 1993).

Mechanical control methods are most practical for management of nonnative fishes in the Upper Colorado River Basin. Chemical control in the main channels or connected habitats would be undesirable based on numerous accidental fish kills that have occurred in running waters. Chemical control is a viable option for control of nonnative fishes in floodplain ponds and is being implemented to reduce chronic escapement from gravel-pit ponds along the upper Colorado and Gunnison rivers (U.S. Fish and Wildlife Service 1998). Biological control generally uses predatory fish species that will consume any suitable fish species including endangered fishes. Increasing the numbers of Colorado squawfish in the Upper Basin would provide some biological control of nonnative fishes. The use of other fish species as predators and the use of pathogens (e.g., a virus specific to channel catfish) are not viable options because of high risk. Partial control using mechanical control methods (e.g., removal with various gear, increased water velocity, increased streamflows, etc.) is the only option that reduces risks but this control method often does not generally remove an adequate proportion of the nonnative fish population and compensatory mechanisms of increased growth and fecundity will allow rapid repopulation (i.e., resiliency) by nonnative fishes (Wiley and Wydoski 1993). Osmundson and Kaeding (1991) suggested that streamflow manipulations might be used to manage nonnative fishes while enhancing native fishes. However, Valdez (1990) concluded that regulation of streamflows may not be an effective long-term method to reduce nonnative fishes that are adapted to river environments or with a high reproductive potential. Valdez reported that red shiners were reduced in numbers during a year with high streamflows in Cataract Canyon of the Colorado River but exhibited a high resiliency during the following year with a lower streamf low. Partial control of nonnative fishes should be evaluated in river reaches where experimental floodplain enhancement or restoration is completed to determine the responses of native (including endangered) and nonnative fishes. All habitat enhancement or restoration endeavors and nonnative fish control measures should be implemented concurrently by applying adaptive management (Walters 1986; Walters and Hillborn 1978) that allows actions to be taken even when there is a great deal of uncertainty (Ludwig et al. 1993).

Cover requirements for fish varies by species and life stage that may differ diurnally and seasonally (Gore and Shields 1995). Cover reduction in river ecosystems may reduce fish populations up to 80% (Wesche 1985). Mortality of Age-0 razorback suckers may be less in depression ponds with rooted aquatic vegetation that serves as escape cover along the middle Green River (Modde 1997). However, there is no escape cover in gravel-pit ponds without rooted aquatic vegetation along the upper Colorado

River (Burdick et al. 1997) but artificial cover could be placed on the gravel substrates of such ponds. Juvenile razorback suckers readily use rooted aquatic vegetation as cover in the Lower Colorado River Basin based on SCUBA observations (G. Mueller and T. Burke, 1994, personal communication). Aquatic vegetation in Leota Bottoms and Old Charley Wash may have been a factor in the survival of Age-O razorback suckers. Abundant red shiners in Old Charley Wash were captured in open water so they would were spatially separated from the larval and juvenile razorback suckers that used vegetative cover in the littoral zone (Modde 1997). Sonic-tagged subadult razorback suckers stocked into Lakes Mohave and Powell quickly occupied backwaters with cover (Mueller and Marsh 1998). In Lake Mohave, 40% of the fish used Sago pondweed as cover and about 14% used cavities in rubble and cobble substrates. In Lake Powell, a high percentage (up to 86%) of the fish used flooded Tamarisk as cover. Some recruitment of razorback suckers was documented in Lake Mead where fish between 318 and 381 mm TL (one dead fish was determined to be 4 years old) were captured (P.B. Holden, 1998, personal communication). Holden attributed the recruitment of razorback suckers in Lake Mead to higher densities of zooplankton, presence of more cover as rooted aquatic vegetation and flooded Tamarisk, and stable water levels, compared to Lake Mohave where such conditions do not exist and recruitment has not occurred.

If management of the nonnative minnows, green sunfish, channel catfish, smallmouth bass, and juvenile largemouth bass is possible in the general vicinities of enhanced or restored floodplain habitats (particularly downstream to reduce numerous nonnative fishes in backwaters), razorback suckers may be able to develop self-sustaining populations. However, the size attained by razorback suckers is only about 25 mm TL in 8 weeks (Figures 1 and 2). The body of a 25 mm razorback sucker is deep and wide enough to preclude predation by adult red shiner based on the gape size of adult red shiner mouths (T. Crowl, 1995, personal communication). A razorback sucker of 25 mm may still be vulnerable to fathead minnows since these minnows tear their prey apart and eat the pieces (Dunsmoor 1993). In addition, razorback larvae of 25 mm as well as larger juveniles would still be highly vulnerable to predation by juvenile and adult green sunfish, channel catfish, smallmouth bass, and largemouth bass.

D. Captive Propagation/Stocking of Razorback Suckers. The razorback sucker was considered the highest priority species for propagation among the four endangered Colorado River fishes by the Biology Committee (Wydoski 1994) because the stocks are declining and little or no recruitment has been documented for this species in the Upper Colorado River Basin. A dramatic decline in razorback suckers occurred between 1974 and 1991 in RK 245.9-297.8 (RM 152.8-185.1) of the upper Colorado River (Burdick 1992). A high capture of 206 razorback suckers in this reach during 1974 declined and no fish were captured during 1989-1992. Three adult razorback suckers were captured in this reach in 1993, one in 1995, and none in 1996 and 1997 (C. McAda, 1998, personal communication). The Recovery Program Biology Committee also agreed that augmentation stocking was required in the middle Green River to increase and stabilize the present population (Wydoski 1994) that is estimated to be about 500 razorback suckers (Modde et al. 1996).

Captive propagation and stocking of razorback suckers should be considered a fishery management tool and not a solution to recovery. Captive propagation and stocking are needed to (1) reestablish or augment stocks in Upper Basin rivers until other problems are solved, (2) accelerate the rate of recovery, and (3) have fish in the rivers to evaluate various recovery actions. Ultimately, the integrity of river-floodplain ecosystem of the Upper Colorado River Basin must be restored if recovery of the endangered fishes is to be achieved.

Re-introduction stocking of razorback suckers in the upper Colorado and Gunnison rivers and augmentation stocking in the middle Green River should be continued following approved stocking plans and genetics conservation measures (Williamson and Wydoski 1994) to increase numbers of razorback suckers in those rivers. Although augmentation stocking is not recovery, it provides a mechanism to maintain adult razorback suckers in the upper Colorado River Basin to prevent extinction until a solution is found to achieve self-sustaining populations (i.e., recovery).

Evaluate factors identified in a stocking plan that may affect survival of captive-reared fish including (1) use of floodplain ponds as a "half-way" habitat where captive-reared razorback suckers can become conditioned to eating natural food organisms, (2) importance of physical conditioning to various water velocities prior to release, (3) size of fish at release, (4) time of release, etc. Experimental stocking in the Green and Gunnison rivers with captive-reared fish of 100 mm TL (- 4 in) has not been successful. Few of the fish were recovered shortly after stocking and recaptures have not been made. However, seven razorback suckers were recaptured in 1997 from 1,068 that were stocked as larger fish (209-308 mm TL; - 8-12 in) into the middle Green River in 1996 (T. Pruitt, 1998, personal communication).

Recaptures of razorback suckers stocked into the San Juan River (F. Pfeifer, 1997, personal communication) suggested that larger fish may survive better than small fish. Although survival of juvenile razorback suckers that were stocked at 113 mm TL (- 4 in) into the Gila River, Arizona increased because of less predation by ictalurids, Marsh and Brooks (1989) recommended stocking fish that are 300 mm TL (12 in) or larger in the Lower Colorado River Basin. Recaptures of fish stocked at 300 mm TL has been considered successful in Lake Mohave (G. Mueller, 1996, personal communication). The former Recovery Program Propagation Coordinator (RSW) recommended that fish 300 mm TL (- 12 in) or larger should be stocked in the Upper Colorado River Basin. Razorback suckers in floodplain ponds along Upper Basin rivers will grow to 300 mm TL (- 12 in) by the end of the second growing season (Figure 3). Fish that are reared in floodplain ponds would reach 400 mm TL (16 in) or larger by the end of the third growing season. Fish stocked after three seasons of growth in the fall should mature and produce larvae in Upper Basin rivers the following spring.

In conclusion, the Recovery Program elements of (1) streamf low, (2) habitat enhancement/restoration, (3) control of nonnative fishes and (4) captive propagation/ stocking of razorback suckers must be integrated conscientiously and concurrently because these four Recovery Program elements are closely interconnected and are expected to affect the responses of native (including endangered) and nonnative fishes.

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APPENDIX 1

Mean zooplankton (cladocerans and copepods) and benthic chiromonid densities in various aquatic habitats of the middle Green River. Data on cladocerans and copepods adapted from Figures 46-62 for 1987 and from Table 28 for 1988; data on chironomids for 1987 and 1988 adapted from Figures 21 and 22, respectively, of Grabowski and Hiebert (1989).

Habitat		Jun-Oct 1987 Zooplankton densities cladocerans (no./l)	Jun-Oct 1987 Zooplankton densities copepods (no./l)	Jun-Oct 1987 Benthic chironomids (no./m)	Jun-Oct 1988 Zooplankton densities cladocerans (no./l)	Jun-Oct 1988 Zooplankton densities copepods (no./l)	Jun-Oct 1988 Benthic chironomids (no./m^2)
Main Channel (Island Park)	RM 333.0	0.020	0.025	40	0.01	0.02	500
Main Channel (Jensen)	RM 300.6	0.020	0.020	470	0	0.02	200
Main Channel (Ouray)	RM 251.1	0.020	0.080	20	0	0.53	20
Backwater	RM 333.2	0.044	0.136	2,430	0.01	0.03	1,730
Backwater	RM 332.2	0.060	0.020	1,400		-	-
Backwater	RM 327.6	-	-	-	0.01	0.05	1,670
Backwater	RM 300.6	-	-	-	0.02	0.02	900
Backwater	RM 300.5	-	-	-	0	1.24	2,300
Backwater	RM 300.3	0.111	0.141	2,230	-	-	-
Backwater	RM 298.6	0.027	0.056	1,790	0.01	0.13	2,900
Backwater	RM 298.4	-	-	-	0.01	0.06	370
Backwater	RM 251.0	0.033	0.256	1,400	0	0.25	2,470
Backwater	RM 250.8	0.020	0.127	2,770	0	0.07	2,400
Backwater	RM 250.7	-	-	-	0.01	0.18	1,800
Backwater	RM 249.7	0.020	0.077	1,530	-	-	
Backwater	RM 249.4	-	-		0	0.23	1,900

APPENDIX 2

Mean zooplankton (cladocerans and copepods) and benthic chironomid densities in various aquatic habitats of the Upper Colorado River Basin. 1/ 2/

River/ Habitat	Date	Zooplankton density cladocerans (no./l)	Zooplankton density copepods (no./l)	Benthic chironomids (no./m^2)	Reference
Middle Green River					
(Ouray National Wildlife Refuge)					
Main Channel	7/91	0.025	1.288	4,150	1/ Mabey and Schiozawa 1993
	8/91	0.008	0.308	3,516	
					1/ Wolz and Schiozawa 1995
Large backwater (Intersection Wash)	6/91	0.188	63.17		
Ephemeral side channel	6/91	-	-	2,325	
	7/91		-	8,185	
Backwater (Ouray)	7/91	1.263	5.857	31,125	
	8/91	0.484	0.985	22,863	
Floodplain	6/91	30.77	175.12	903	
(Old Charlie Wash)	7/91	3.99	307.41	23,055	
	8/91	3.42	686.77	3,955	
Colorado River					
(Moab Slough)					
Main Channel	6-10/93	0	0	156	2/ Cooper and Severn 1994a
Backwater	6-10/93	0.98	0.49	82.5	"
Bullrush	6-10/93	28.6	10.3	447	"
Open Water	6-10/93	19.7	14.8	241	"
Flooded Willows	6-10/93	12.8	4.43	-	"
Middle Green River					
(Escalante Ranch)					
Main Channel	6-10/93	0	0	349	2/ Cooper and Severn 1994b
Backwater	6-10/93	7.19	2.6	349	"
Bullrush	6-10/93	2.70	1.0	349	"
Open Water	6-10-/93	10.6	11.2	631	"
(Escalante State Wildlife Area)					
Main Channel	6-10/93	0	0	486	2/ Cooper and Severn 1994c
Backwater	6-10/93	0.70	2.73	486	"
Bullrush	6-10/93	2.81	0.78	1,663	"

APPENDIX 2 (Continued)

River/ Habitat	Date	Zooplankton density1/ cladocerans (no./l)	copepods (no./l)	Benthic chironomids2/ (no./m^2)	Reference
Gunnison River (Escalante State Wildlife Area; Continued)					
Open Water	6-10/93	10.9	7.41	1,074	"
(Ouray National Wildlife Refuge)					
Main Channel	6-10/93	0	0	197	2/ Cooper and Severn 1994d
Backwater	6-10/93	0	0	420	"
Flooded Cottonwood	6/93	51.41	3.10	0	"
Bullrush	6-10/93	10.28	10.62	107	"
Open Water	6-10/93	15.48	30.08	644	"
Colorado River (29 5/8 Mile Pond)	10/93	26	28	-	Cooper and Severn 1994e

1/ Data for cladocerans and copepods were adapted from Appendix Table 4 of Mabey and Schiozawa (1993). Data on benthic chironomids adapted from Tables 2, 3, 4, and 5 of Wolz and Schiozawa (1995).

2/ Data for cladocerans and copepods adapted from Figures 22, 22, 22, and 15 of Cooper and Severn 1994a, b, c, and d, respectively. Data for chironomids were adapted from Figures 27, 21, 23, and 16 of Cooper and Severn 1994a, b, c, and d, respectively.