

**AN EVALUATION OF RECOVERY NEEDS FOR ENDANGERED FISHES
IN THE UPPER COLORADO RIVER,
WITH RECOMMENDATIONS FOR FUTURE RECOVERY ACTIONS**

Final Report

by

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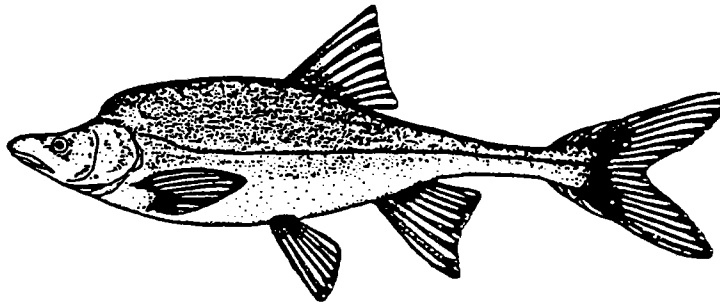
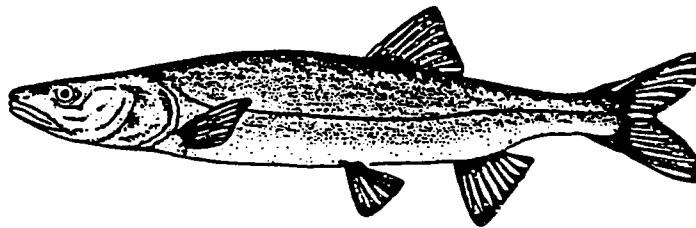
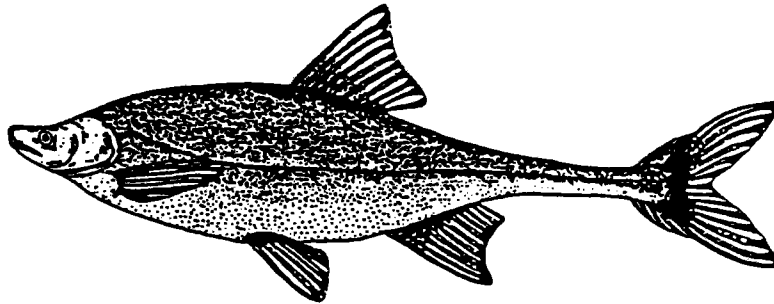
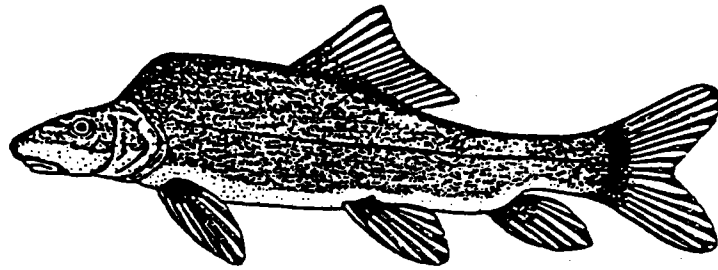
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FRONTISPIECE. The four endangered big river fishes of the Colorado River: razorback sucker (top), bonytail, Colorado squawfish, and humpback chub (bottom). (Original drawings by James M. Beard)

PREFACE

Efforts to recover populations of endangered fishes in the upper Colorado River are proceeding in an environment that has been, and is continuing to be altered by human activity. Recovery efforts for the fishes also involve many stakeholders, representing varied and sometimes incompatible interests. These two issues: continuing change in river habitat and conflicting viewpoints among stakeholders, has made it difficult to identify and to agree on needed recovery actions. The Recovery Implementation Program for recovery of Colorado River fishes in the upper Colorado River Basin (RIP), a consortium of federal and state agencies, and private stakeholders is charged with management of the recovery effort. The RIP serves as a forum to discuss and, hopefully, to resolve conflicts between the perceived needs of the fishes and the desire for continued resource development.

In general terms, this report provides a review and synthesis of existing information on the life history requirements and habitat needs (physical and biological) of the endangered species comprising the big river fish community in the upper Colorado River. The review and synthesis provides a basis for evaluating recovery alternatives with the goal of promoting recovery of these endangered species through successful recovery actions. It is hoped that this report will be helpful to the RIP in identifying recovery options and resolving conflicts.

Subsequent to submission of an earlier version of this report in January 1998, a lengthy peer-review process was undertaken by the project sponsor. This final report incorporates that peer review in a contemporary sense (i.e., a complete rewrite to include all information that was produced after 1997 was not undertaken). In the two year period following completion of the draft report, many of recommendations provided have been addressed in some meaningful fashion. However, two major recommendations, i.e., development of a multispecies or ecosystem recovery plan, and the need to explore physical habitat modifications as an alternative to flow manipulations for improving the quality of fish habitat, have not been addressed in any substantive way. Both of these recommendations are considered critical to the recovery effort, and we hope the release of this final document will encourage further consideration of these recommendations and other findings.

Further information about the rare and endangered Colorado River fishes can be obtained from the Colorado River Coordinator, USFWS, P.O. Box 25486 Denver Federal Center, Denver, Colorado 80225. Project Manager for this contract was Mr. Ray Tenney, Colorado River Conservation District, P.O. Box 1120, Glenwood Springs, CO 81602.

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EXECUTIVE SUMMARY

Native fishes of the upper Colorado River (UCR) basin are declining in abundance due to anthropogenic alterations to physical and biological components of the natural riverine environment. Two primary agents of environmental change have been water resource development and the introduction of nonnative fishes. Construction and operation of many dams, reservoirs, and diversions throughout the UCR basin have altered the historic hydrograph, fragmented habitat by blockage, converted riverine to lacustrine habitat, and changed water quality characteristics (especially temperature and sediment transport). Concurrent with water resource development, many nonnative fish species have been introduced in the Colorado River system. Some of the introduced species are aggressive competitors and predators that occupy habitats essential for native riverine fishes. Although water resource development undoubtedly has taken a toll on the physical habitat of the native fishes, the presence, proliferation, and continued addition of nonnative fishes to the river system is arguably the greatest threat to native fish populations.

The big river fish community has been greatly affected by recent habitat change. As a result, four species of have declined so greatly in abundance and geographical distribution that they are now listed as endangered under provisions of the Endangered Species Act. Efforts to recover these four fishes are led by the U.S. Fish and Wildlife Service, which established recovery teams, completed recovery plans, and determined critical habitat pursuant to provisions of the Act. However, recovery issues related to physical habitat have been contentious. Perceived recovery needs have constrained future water development in an area where seven state governments participate in water allocation through interstate compacts and other legal agreements. Issues related to control of nonnative fishes also have been nettlesome, in part due to jurisdictional concerns of state agencies. Resolution of these issues, in part, will require clarifying the scientific rationale for recovery and by establishing priorities for future actions.

Much has been learned about the life history requirements of endangered big river fishes during the past twenty years. However, despite large investment in research and numerous management actions, there has been no apparent success toward recovery, if judged on the basis of increasing the abundance and distribution of endangered fishes. Instead, another fish (razorback sucker) has been listed during this period and natural bonytail populations have virtually disappeared. The razorback sucker has suffered from poor or no recruitment for many years, and the number of fish in the wild has declined sharply, especially in the UCR where very few individuals remain. There are so few bonytail remaining in nature that for all practical purposes the species is functionally extinct, i.e., it is essentially extirpated from the upper Colorado River basin. The remaining two species have fared better. Extant populations of humpback chub appear to be relatively stable in size, but the species now has a very restricted geographical distribution. The number of Colorado pikeminnow (formerly Colorado

squawfish) also appears to be relatively stable, although strong year classes are infrequent and populations in the UCR are small.

Clearly there is a need to maintain or increase the size of extant populations, and to accomplish this management actions have focused typically on improving physical habitat conditions. In particular, attention has been devoted to establishing a flow regime that will benefit adult fish. A serious shortcoming in these management actions has been the lack of emphasis on biotic factors, especially introduced nonnative fishes. To date, no successful program has been developed to control or reduce the abundance of nonnative fishes, and it is doubtful if recovery will be successful until that happens.

Addressing biotic factors alone is no guarantee of successful recovery, however. In general, recovery will require a more comprehensive view of limiting factors for a given species, which will vary spatially and temporally. Moreover, biotic (biological) and abiotic (physical and chemical) limiting factors may operate simultaneously. Thus, successful application of management action at the local level will require a view of limiting factors that considers all life history stages and the habitat used by each stage. In addition, managers must determine when action deemed necessary for recovery may not be sufficient. For example, creating and maintaining optimal physical habitat is a condition necessary for recovery, but it may not be sufficient where nonnative predators have the capacity to eliminate recruitment.

This study emphasizes that a more holistic approach is needed in the recovery program, and recommends development and formal adoption of a multispecies or ecosystem recovery plan. Such a plan would encompass all fishes in the big river community throughout their range as the best mechanism for implementing a broader and more comprehensive perspective on recovery of the four listed fishes. By incorporating geographic priorities, such a plan could guide local recovery efforts, and aid communication and coordination with recovery efforts in other locations as well. Such an approach also would aid in monitoring the status of other species at risk and insure that other species would not need to be listed in the future.

The following additional conclusions and recovery recommendations address present recovery efforts for each specific initiative of the RIP, and have been drawn from the review and synthesis of existing information:

Instream Flows:

The need for suitable instream flows for all life stages of the endangered fishes has long been recognized, but more effort is needed to understand how instream flows affect the fishes, and how adverse effects can be minimized or avoided.

- The relationship between flows and the amount of nursery habitat for Colorado pikeminnow in the UCR should be more fully evaluated, because this information could provide important guidance for developing flow management strategies.
- Flows required by the young of the other endangered fishes are virtually unknown. More effort should be expended to obtain habitat needs for these fishes as well, and to determine the role of instream flows during this critical life stage.

Habitat Development and Restoration:

- Physical habitat modifications should be explored as an alternative to flow manipulations, such as improving adult habitat for Colorado pikeminnow in the 15-Mile Reach, or in other locations where water supplies are limited or other constraints warrant such an approach.
- The abundance of “preferred” prey may be more important than physical habitat quality for determining the abundance of adult Colorado pikeminnow in the 15-Mile Reach, yet past studies seem to ignore this possibility. The relationship between food and physical habitat needs to be more fully explored.
- Adult Colorado pikeminnow make use of upstream areas that support abundant populations of native prey species. Access should be provided to areas upstream of the 15-mile reach in the UCR, because if the fish gain access to upper reaches (containing preferred prey), individuals may grow faster and the population may increase in numbers.
- The locations of actual and potential spawning habitat is not known adequately and should be determined for Colorado pikeminnow in the UCR.
- If nursery habitat is found to be limiting for Colorado pikeminnow in the UCR, physical habitat modifications may offer a means of augmenting nursery habitat.

Stocking of Endangered Fishes:

- Previous reintroductions have not been very successful in terms of increasing demonstrably the sizes of populations of endangered fishes. Future reintroductions should reflect a better appreciation of life history needs.
- Stocked fish may behave differently than wild fish, and this has important ramifications for implementing recovery actions. Future reintroduction protocols need to be designed to anticipate this possibility.
- Habitat in, and above, Debeque Canyon offers potentially important habitat for translocating juvenile or adult Colorado pikeminnow and humpback chub, and should be evaluated for this purpose.

- Reintroduction in the UCR will be an essential component of plans to recover the razorback sucker. The prospects for successful reintroduction may be enhanced by a local facility that can pay adequate attention to site adaptation.
- Protocols should be refined for tracking all individuals from any future introductions.
- Translocations should be given a higher priority for establishing populations of listed fishes.

Control of Introduced Fishes:

- Nonnative fishes that are abundant in Colorado pikeminnow nursery habitat may be the most significant impediment to increasing recruitment of that species. Effective control measures need to be developed and implemented.

Research, Monitoring, and Data Management:

- The recovery program would benefit from broader review, synthesis, and dissemination of research, not only in the Colorado River Basin, but to a broader audience as well.
- There is a fundamental need for an assessment tool that will measure progress toward recovery. The current ISMP is not adequate for this purpose.
- Knowledge of carrying capacity could help set realistic expectations on recovery targets.
- Recovery plans for each species should specify the number of populations needed for recovery, their location, and target size. The current IMO targets should be considered preliminary.

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PART 1. INTRODUCTION

Native fishes of the upper Colorado River (UCR) basin are declining in abundance. The most likely cause of their decline is anthropogenic alteration of the natural environment. Habitat of the native Colorado River fishes has been changed greatly during the last 100 years by human actions including physical alterations and the introduction of nonnative species. Alterations to the physical environment are associated primarily with construction of water development projects that began in the early 1900s (Fradkin 1984, Carlson and Muth 1989). By the 1960s, more than 50 dams and major diversions had been constructed on mainstream river (Figure 1), and impoundment of flow by these structures converted many river reaches into lacustrine habitat. Operation of the dams has altered substantially the natural timing, duration, and magnitude of annual flood flows in the Colorado River. Flow regulation and the presence of structures have also caused changes in water temperature, sediment load, nutrient transport, and other facets of water quality (Carlson and Muth 1989). In some reaches, silt load has been reduced 90% (Fradkin 1984). Most existing mainstream habitats are now different than the historic habitats in which the native fishes evolved, and some have been modified so extensively that native fish can no longer survive in them.

Physical changes in the riverine habitat were accompanied by the introduction and proliferation of nonnative fish species, including many that are predaceous, highly competitive, and harmful to the native fish fauna (reviewed by Tyus and Saunders 1996a). Some introduced fishes have become very successful under the environmental conditions that now prevail in the Colorado River system. Although the native fishes were well adapted to their natural environment, alterations to the physical habitat may have created conditions that are now more favorable to many of the introduced species. Even where physical habitat has been altered relatively little, nonnative fish abundance has increased, and the abundance of native fishes has been reduced. Most habitat used by the native fishes also is occupied now by introduced species (Minckley 1982, Tyus et al. 1982a, Carlson and Muth 1989).

Changes in the physical and biological characteristics of riverine habitat have contributed to the endangerment of four native fish species (Colorado pikeminnow, humpback chub, bonytail, and razorback sucker). These and other fishes native to the main channels of the Colorado River system ("big river fish community") have disappeared from most of their original habitat. Their endangerment is attributable to a suite of environmental factors that is essentially the same for all four species. The problem exists at the ecosystem level because an entire fish community is threatened and threats include biotic and abiotic factors.

Concern about the decline and endangerment of four species from the big river fish community resulted in Federal and state listings. Actions to recover species listed under provisions of the Endangered Species Act are guided by recovery plans prepared by the U.S. Fish and Wildlife Service (USFWS) for each species. Each of the four

endangered fishes in the Colorado River system has a separate recovery plan, but there is no comprehensive plan addressing recovery of the community, or ecosystem, as a whole. Experience has shown, however, that a broader perspective could be beneficial (Clark et al. 1994). In fact, the USFWS has determined recently that a "multispecies" or ecosystem approach that combines several species in one recovery plan could "...improve the rate, fiscal efficiency, and effectiveness of recovery actions for listed species and...eliminate the need to list candidate species" (USFWS 1994b). In case of the Upper Colorado River (UCR), such an approach would address the needs of all species in different geographic areas.

In the Colorado River system, the foundation for adopting an ecosystem-oriented approach to recovery efforts was set in 1994 when the USFWS designated critical habitat for the four listed species of the big river fish community (Maddux et al. 1993, USFWS 1994a). The Razorback Sucker Recovery Plan (USFWS 1998), completed subsequent to designation of critical habitat, recognizes explicitly the new ecosystem framework. Formal adoption of a multispecies approach would represent a major step in the evolution of ideas and policies governing recovery of the Colorado River fishes. A preliminary draft of a multispecies plan was prepared for the USFWS, but was not accepted by the Colorado River Fishes Recovery Team (S.J. Petersburg, personal communication) and developing a framework that would be acceptable to all interests would be a difficult task. Although it may take several more years to develop, a formal plan for multispecies recovery is likely to guide recovery efforts in the future. Consequently, it would be advantageous to begin evaluating recovery needs in that context.

The goal of this report is to facilitate recovery of fishes native to the UCR by focusing on major recovery needs identified through a new synthesis of available information. The main focus geographically extends from the confluence with the Green River upstream to Rifle, Colorado. Contributions made by many individuals from diverse institutions and agencies have provided the basis for characterizing the abundance and distribution of the endangered fishes in the UCR basin, and their life history requirements. The next step involves an assessment of those environmental factors most likely to present obstacles to increasing the abundance of these endangered species. In concept at least, identifying obstacles to population expansion should guide recovery efforts. To some extent, this has already occurred, but a review of previous efforts is warranted. Finally, recommendations for future recovery actions are made on the basis of what is needed and what might work.

PART 2. ENDANGERED FISHES IN THE UPPER COLORADO RIVER BASIN

Background

The upper Colorado River basin (UCRB) consists of about 254,000 km², and it drains parts of Colorado, Wyoming, Utah, New Mexico, and Arizona (Iorns et al. 1965). It has

been divided into three major hydrologic sub-basins - the Green River, upper mainstem Colorado River, and San Juan River (Iornes et al. 1965, Carlson and Carlson 1982) - all of which have been altered significantly by human activities. Most of the water in the system is snowmelt that originates in high mountain streams generally above 10,000 ft amsl. Tributary streams at lower elevations add comparatively little water, but can be important for contributions of sediment and for seasonal inputs of water. The natural hydrograph reflects the regular and prominent influence of spring runoff in May and June (Maddux et al. 1993, Stanford 1994), when peak flows produced extensive seasonal inundation of the floodplain. High discharge and erodible substrate produce very turbid water seasonally. Smaller tributaries, generally at lower elevations, are prone to flash flooding after unpredictable summer storms. Storm events contribute to turbidity in the main river during the base flow period. As a consequence, native Colorado River fishes have had a long evolutionary history of adaptations to a river system characterized by extreme seasonal variations in flow and by generally turbid water.

The ancient Colorado River watershed was a much wetter environment than now exists (Smith 1981). The evolution of native fishes was strongly influenced by an ecological history of long pluvial episodes, each lasting about 100,000 years, that were separated by short interpluvial episodes of desert climates lasting only 10-20,000 years. During pluvial episodes, portions of the river system included extensive lacustrine habitat (Stanford and Ward 1986a, Minckley et al. 1986), and the fossil record demonstrates that ancestral Colorado River fishes used this habitat. In recent times, the climate of the basin has been extremely arid. Nevertheless, the native fishes persisted and thrived even during such dry periods. Evolutionary forces have produced a fish community adapted to a riverine system, but flexible enough to make use of conditions ranging from lacustrine to riverine. The fishes are extreme generalists that exploited every available natural habitat and evolved some complex life histories that have facilitated survival in the harsh environment of the Colorado River (e.g., see Minckley and Deacon 1991, Smith 1981, Minckley et al. 1986).

Three different stream zones are recognized in the basin (Joseph et al. 1977, Minckley et al. 1986), and each contains a characteristic native fish fauna, albeit with overlap. At high elevation, the Headwater Zone is a productive region of cold water, high gradient streams that have rocky substrate and support coldwater fishes (predominantly salmonids). The Intermediate Zone, which may receive input from the coldwater streams, has streams of lower gradient and finer substrate. The water is warmer and more turbid, and productivity remains substantial, but benthic fauna are limited to rocky outcrops. Streams of the Intermediate Zone are dominated by cyprinids and catostomids, but some coolwater salmonids (e.g., whitefish) also occur. Streams of the Lower Zone, also called the large-river zone, are characterized by even lower gradients and warmer, more turbid water. In the Colorado River, this Lower Zone is composed of two major habitats: canyons and alluvial reaches. Native fishes in this region were exclusively minnows and suckers. The inhabitants of the main channels comprised the big river fish community.

The native fish fauna of the Colorado River is characterized by a high level of endemism. Of the 46 native fishes (species and subspecies) present in recent times, 38 are endemic (Miller 1958, Stanford and Ward 1986b). The high level of endemism was heavily influenced by the Quaternary history of the intermountain area of western North America. Populations were isolated by desertification, and faunal composition was changed by local extinctions during the Pleistocene (Smith 1978, Stanford and Ward 1986b). At one point, native Colorado River fishes consisted of only 32 to 36 species, depending on taxonomic interpretation (Stanford and Ward 1986b, Carlson and Muth 1989). River systems of similar size elsewhere (e.g., Missouri River) typically have an order of magnitude more fish species.

Present Distribution and Abundance

Four of the big river fishes, the Colorado pikeminnow (*Ptychocheilus lucius*), razorback sucker (*Xyrauchen texanus*), humpback chub (*Gila cypha*), and bonytail (*Gila elegans*) (Frontispiece), once populated warmwater reaches of the mainstream rivers of the Colorado River basin from Wyoming to Mexico. The abundance and distribution of these fishes have been drastically reduced, and the species are now threatened with extinction. As part of the effort to recover these species, government agencies have invested heavily in surveys establishing the present distribution and abundance of each species. The results of these surveys provide the basis for assessing essential aspects of life history needs (e.g., habitat preference, migrations, etc.), and, in time, progress toward recovery goals.

Beginning in 1979, the USFWS initiated an ambitious program for monitoring the abundance of endangered fish species throughout the UCRB. Not only was spatial coverage thorough in a statistical sense, but several types of sampling gear were used to optimize collection of all species and life history stages. Sampling efficiency was optimized by selecting river reaches (strata) representing different habitat characteristics. The results of this comprehensive program, summarized in W.H. Miller et al. (1982d), provide an excellent baseline record of fish abundance in the UCRB.

Subsequent monitoring efforts have been less comprehensive in terms of spatial coverage and sampling gear, but can detect major trends in abundance (McAda et al. 1994). However, identifying trends in fish abundance has been hampered by high variability in capture data among years, because local changes in the riverine environment and stochastic events can affect population size. In addition, elucidation of trends in the UCRB is complicated by the migratory habits of species like the Colorado pikeminnow, and by the difficulties of identifying early life history stages of the endangered species, especially when those stages may be segregated spatially from the adults.

A number of investigators have used standardized methods to sample fish populations in the various rivers of the UCRB and have described the physical habitat in which the

fishes were captured. A summary of the geographical distribution of the endangered fishes with physical descriptions of the strata sampled is given in the Appendix. However, study results may not be directly comparable, because the different geographic areas may have been sampled by different protocols and in different seasons or years.

Colorado pikeminnow

The Colorado pikeminnow is now restricted to the UCRB and persists in only four populations, which are located in the Yampa River, the Green River below its confluence with the Yampa River, the upper Colorado River (including the lower Gunnison River), and the lower San Juan River (USFWS 1991, 1994a). The present distribution and abundance of the Colorado pikeminnow in the upper Colorado River has been documented thoroughly by Valdez et al. (1982) and Osmundson and Burnham (1996). The distribution appears to have changed little from the time of earlier surveys conducted by Holden and Stalnaker (1975) and Seethaler (1978). The ISMP has provided additional information on abundance and short-term population fluctuations (McAda et al. 1994a,b,1995; Osmundson et al. 1996), and there is some evidence of recent, and relatively high levels of recruitment during some years.

Although the Colorado pikeminnow is classified as a warmwater species, adults are cold tolerant (Wick and Hawkins 1989). Most adults move to upstream reaches after spawning and establish home ranges in cooler tributary streams for most of the year. Evidence for this pattern in the Green River basin includes tag returns, dead fish, photos by anglers, and other unpublished records on file at the USFWS office in Vernal, UT. In unblocked streams, some adult fish move as far upstream as the lower portions of coldwater trout reaches (e.g., Steamboat Springs in the Yampa River and Swallow Canyon in the upper Green River), although most of the adult fish select slightly warmer areas for residence during most of the year (e.g., Yampa River from Williams Fork to Juniper Springs, Colorado; USFWS 1987).

The two largest extant populations occur in the Green River basin: one that spawns in the lower Yampa River, and one that spawns in the lower Green River. Adult pikeminnow occupy about 520 mi of river channel divided almost equally between the Green River (240 mi) and its two main tributaries, the Yampa and the White rivers (280 mi). Adults are found in the Yampa River from its mouth to Craig, in the White River from its mouth to Meeker, and in the Green River from the Yampa confluence upstream to Swallow Canyon in Browns Park. The Green River mainstream below its junction with the Yampa River was once thought to contain about 8,000 adult fish, or about 23 fish per mile (Tyus 1991), and the Green River basin (including Green, Yampa, and White rivers) probably supports twice that many adults.

The Colorado pikeminnow population in the UCR consists of approximately 600 - 650 subadult and adult fish (Osmundson and Burnham 1996). McAda and Kaeding

(1991a) speculated that there have been no major changes in population size since the 1970s. Because strong year classes are infrequent, recruitment may not support the present numbers over a long period of time (Osmundson and Burnham 1996). Most of the adult fish are found in the upper 60 mi of river below the Grand Valley diversion (Valdez et al. 1982, Osmundson et al. 1995, 1997). Adults also occur in the lower Gunnison River (Burdick 1995), and spawning was confirmed by capture of larvae in 1994, 1995, and 1996 (Anderson, unpublished data). The younger fish tend to occupy lower river reaches (Valdez et al. 1982, Osmundson et al. 1997).

The San Juan River contains a small population of Colorado pikeminnow, and collections of young fish indicate that the population is reproducing (Platania et al. 1991, Ryden and Ahlm 1996).

In general, each of the known populations is associated with a primary nursery area that harbors larvae from one or more spawning sites. In the Colorado River, the Green River system, and the San Juan River, adults are most prevalent in river reaches at, or upstream of, spawning areas (Tyus 1986, Tyus and Haines 1991, Osmundson and Burnham 1996, Ryden and Ahlm 1996). However, the present concentrations of adults may be restricted to river reaches below barriers that block migrations. Examples of such blockages include Flaming Gorge Dam on the Green River (Vanicek 1967) and Taylor Draw Dam on the White River (Trammell et al. 1993).

Humpback chub

Information about the historical distribution of humpback chub is sparse, in part, because the fish was not described as a species until relatively recently (Miller 1946, Valdez and Clemmer 1982). The largest extant population of humpback chub occurs in the Grand Canyon in the vicinity of the confluence of Little Colorado River (LCR) and Colorado River. Recent estimates of the population place the number of adults in the range of 4,500 to 10,400 fish (Douglas and Marsh 1996), which includes about 2,680 to 4,280 in the mainstream (Valdez and Ryel 1995). The humpback chub was first reported in the UCRB in the 1970s (Holden 1977, Valdez and Clemmer 1982), however museum collections document the existence of a population in the Yampa River in 1948 (Tyus 1998). The humpback chub has persisted in the Colorado and Green river systems, and is reproducing successfully in the Yampa and upper Colorado rivers (Tyus et al. 1982, Archer et al. 1985, Kaeding et al. 1990, Karp and Tyus 1990). In the upper Colorado River, Valdez et al. (1982) captured 238 humpback chub, but nearly all (229) came from Black Rocks and Westwater Canyon. The population in Westwater Canyon probably consists of several thousand fish, but the precision of the estimate is very poor (B. Burdick, personal communication; T. Chart, unpublished data).

Population size of humpback chub in Black Rocks and Westwater canyons is thought to be relatively stable (Kaeding et al. 1990, McAda et al. 1994).

Razorback sucker

Razorback suckers were historically common in the portions of the UCRB, including the mainstream Green and UCR (reviewed by Minckley et al. 1991). In the UCR, fish have been reported from Moab, UT to Rifle, CO (Kidd 1977, Burdick 1992, Westwater Engineering 1996). Juvenile razorbacks were captured near Moab in the 1960's (Taba et al. 1965). More recent collections (Valdez et al. 1982, Archer et al. 1985, Osmundson and Kaeding 1989) have shown very low and declining numbers below Palisade. Above Palisade, a few individuals have been reported from Highline Lake and isolated ponds near Rifle and Debeque (Burdick 1992).

The largest remaining population of razorback suckers occurs in Lake Mohave of the lower basin of the Colorado River. Because recruitment is very low, the population continues to decline in abundance (Marsh 1995). The only remaining riverine population occurs in the Green River near the confluence with the Yampa River; it consists of less than 1,000 fish and may be declining (Lanigan and Tyus 1989, Modde et al. 1996). A few individuals also have been collected in the mainstream Colorado River and in the lower San Juan River. In the upper Colorado River, 47 razorback suckers were collected during the two years of the baseline survey, but most of these (79%) came from two flooded gravel pits: Walter Walker State Wildlife Area (RM 164) and Clifton Pond (RM 118; Valdez et al. 1982). Captures of razorback suckers declined in the UCR from 1974 to 1988 (Osmundson and Kaeding 1991), and only one individual was captured in six years of the ISMP (McAda et al. 1994). The species has probably been extirpated from the UCR. Furthermore, there is no indication that recruitment is adequate to support existing populations (McAda and Wydoski 1980; Meyer and Moretti 1988; Lanigan and Tyus 1989; Modde et al. 1995).

Bonytail

The bonytail was apparently common in some portions of the UCRB, including the Green River (USFWS 1990a), but it may never have been common in the UCR (Westwater Engineering 1996). It is thought to have been extirpated from the UCRB (Valdez and Clemmer 1982). The last individuals reported in the basin were one fish captured near Black Rocks (Kaeding et al. 1986) and five captured in Cataract Canyon (Valdez and Williams 1993). The few individuals that have been captured in Lake Mohave may represent the last of the species in nature. All other individuals exist as hatchery stocks. Virtually nothing is known about the life history of this species except that it inhabited the main channel of large rivers and also could survive in reservoirs (USFWS 1990a).

Life History Requirements

A thorough knowledge of life history requirements is essential for guiding recovery efforts, because it establishes the environmental (abiotic and biotic) conditions that each life history stage needs for survival and growth. Ideally, one would begin by assembling a comprehensive spatial and temporal map of habitat use, incorporating information such as the path and timing of migrations, location and time of spawning, location of nursery areas and time of occupation, and the habitats occupied by juveniles and adults at different times of the year. In riverine habitat, the timing of most life history events is closely connected with flow in the river (Tyus and Karp 1989, Tyus 1990; Figure 2). The effects of annual changes in temperature and photoperiod, which also may be involved in the timing of life history events, are very difficult to separate from flow events like spring runoff. It seems likely that there may be interactions among the environmental variables that provide cues for life history events. Flow also plays a significant role in the availability of certain types of habitat (e.g., habitat in the floodplain will only be inundated during peak flows), and in the physical dimensions of habitat (higher flow usually means deeper, wider habitat).

Superimposed on the spatial and temporal map of physical habitat are the biological dimensions of habitat, which are defined largely by predator-prey or competitive interactions. The endangered fishes must have access to an abundance of suitable food species, but not be exposed excessively to predation (both topics will be addressed in more detail in a later section).

A less obvious biological aspect that influences habitat selection and use is learned and/or instinctive (genetic) behavior. These behaviors tend to have a phylogenetic basis, and thus are commonly shared among related taxa. Examples include a propensity for selecting certain habitats, prey selection, extent and direction of migrations, and orientations to flow, temperature or substrate. Learned responses, such as imprinting, are essential to some migratory species (e.g., acipenserids, clupeids, salmonids, and catostomids), which may rely on subtle environmental cues, such as chemical composition of the water, to guide them back to the spawning areas from which they emerged several years earlier. Concern about the role of these cues is raised whenever the natural habitat, or access to it, is altered.

Determining the life history requirements of endangered species is inherently difficult because so few individuals exist in the wild. There are simply not enough opportunities to associate individuals of different life history stages with preferred habitat. The situation in the UCRB is further complicated by extensive alterations to physical and biological characteristics of the natural habitat. Thus, for example, if adult Colorado pikeminnow are now found in deep runs, is it because eddies or "slack" waters are no longer available? Or, is it because they have been displaced from other, more suitable, habitat by aggressive, introduced fishes?

Despite legitimate concerns about the extent to which present-day field studies of rare species will provide an accurate representation of their life history requirements, there is no alternative but to make the best use of such information. Field studies conducted where a species is relatively abundant, and where the habitat is altered least (all habitat now occupied by the endangered fishes has been altered some), are most likely to provide an accurate view of life history requirements (discussed by Tyus 1992). The optimal remaining habitat is closest to the conditions in which the native species evolved, and presumably are the conditions in which the species are most likely to maintain adaptive advantage over introduced species. Field studies in the UCRB have tended to be very localized in focus, with the result that populations (or subpopulations) of one species are treated almost as if they were separate species. A narrow geographic focus for field studies can lead to a fragmented view of recovery needs. Although local adaptations can and do occur, recovery efforts in general could benefit from generalizations about and synthesis of life history needs, leading to a conceptual model of life history.

The Green River system in the upper basin has long been identified as perhaps the most suitable location to determine management measures necessary for recovery of Colorado pikeminnow and razorback sucker, because it supports the largest riverine populations of these species and because habitat in a major tributary, the Yampa River, remains largely unaltered. Flow in the mainstem of the Yampa River is regulated little and access to upstream habitat has not been blocked. The Grand Canyon in the vicinity of the Little Colorado and Colorado rivers is the logical place to study the life history needs for the humpback chub, because there is a large population sustained by natural recruitment. Information obtained from the more "natural" locations can be supplemented, albeit cautiously, with observation from sites where habitat has been altered, but where the species is relatively abundant. A good example is Lake Mohave, AZ-NV, which supports the largest extant population of razorback sucker. The bonytail presents a special challenge because it is not sufficiently abundant anywhere in nature to afford opportunities for meaningful study.

Observations of behavior or habitat use for individuals at different stages of development represent fragments of life history that must be assembled into a cohesive story. The task is difficult because the subjects are hard to locate and there are confounding factors, as mentioned previously. Nevertheless, a complete understanding is important for the recovery effort because it can help identify obstacles to recovery of existing populations and sites with potential for restoring populations. The remainder of the text in Part 2 of this report summarizes what is known about the life history requirements of each of the four endangered fish species.

Colorado pikeminnow

There is more information available for the life history requirements of Colorado pikeminnow than for requirements of the other three endangered species. Because there is so much information, it is both feasible and prudent to divide the presentation into several parts. The first section deals with the requirements of adult pikeminnow when they are not engaged in behavior related to reproduction. The second section covers adults during the relatively short period of time in which they migrate to spawning areas and reproduce. The third section reviews what is known about the requirements of larvae and postlarvae (age-0) from hatching until they leave the nursery areas. The fourth section covers juveniles until they mature and join the adult segment of the population. The final section is a narrative that integrates the main attributes of the life history in the context of the annual hydrograph.

Adult, nonspawning. For most of the year, adult Colorado pikeminnow are not engaged in behavior directly related to reproduction. After spawning, most adult Colorado pikeminnow occupy individual home range areas that are located predominantly in upstream reaches (Tyus 1990), and that may be many miles from the major spawning areas. The other adults will take up residence in home ranges that are close to the spawning areas, or move downstream. Most of the fish tend to remain in the adult habitat areas from late summer until mid-spring (Valdez and Masslich 1989, Wick and Hawkins 1989), when they undertake their spawning migrations (Tyus 1990). In terms of the annual hydrograph, the nonspawning period is associated chiefly with baseflow conditions. Adults spend much of their time in low velocity habitat (e.g., pools, eddies, backwaters, etc.) adjacent to the main channel. At high discharge, low velocity habitats are more likely to be flooded shoreline or overbank areas (Tyus and Karp 1989, Tyus 1990).

Adult Colorado pikeminnow in the Yampa, White, and Green rivers occupy a variety of habitats in mid-to-late summer, but are captured most commonly in eddies, pools, runs, and shoreline backwaters, over sand and silt substrates (Tyus et al. 1984, 1987). Visual observations of fish in shallow water indicate that adults also used lower velocity microhabitats behind boulders, flooded vegetation, or other cover, when available. Many radio-tagged fish were located in deep shoreline habitats in the summer and their local movements in these habitats suggested heavy use of the eddy-run interface (Tyus et al. 1987). Physical habitat used by radiotagged adults varied with location; water depths and velocities used by adults were different in the mainstream Green River (mean depth=1.4 m, mean velocity=0.2 m/s) than in the tributary Yampa (mean depth=0.9 m, mean velocity=0.1 m/s) and White (mean depth=0.7 m, mean velocity=0.5 m/s) rivers (Tyus et al. 1984). The high degree of variability among rivers suggests that factors other than depth and velocity may also influence habitat selection.

Habitat use during the winter appears to be quite variable and may be influenced by factors such as water level, ice conditions, and food sources (Wick and Hawkins 1989, Valdez and Masslich 1989). The fish remain active all winter, but do not tend to stray

from home ranges. In the Green River, adult Colorado pikeminnow used the following habitats in rank order: slow runs, slackwaters, eddies, and backwaters, where depths averaged 2.5 to 4.5 feet and velocities were 0 to 1.0 fps. In the unregulated Yampa River, the fish occupied off-channel backwater and embayment habitats that were probably sources of food organisms (Wick and Hawkins 1989). The fish were found in depths that varied between habitats, averaging 2 to 3.5 feet in backwaters, embayments and runs, and 5 to 9.5 feet in eddies (Wick and Hawkins 1989). Movement of the fish into backwater habitats was attributed, in part, to feeding (Wick and Hawkins 1989). Winter habitat use was similar in the 15-Mile Reach, where pools and runs were used 77-95% of the time (Osmundson et al. 1995).

In spring and early summer, when rivers are rising, but prior to spawning migration, habitat use by adult Colorado pikeminnow depends on water conditions. The fish were most often located in seasonally-inundated shorelines, including backwaters or bottomlands (Tyus 1990). Radiotracking data indicated use of shoreline backwater habitat in a low-flow year (1981) and use of flooded bottomlands during a high-flow year (1983) (Tyus and Karp 1989). Flooded shorelines were also used by adult Colorado pikeminnow during the two high-flow years, 1983 and 1984 (Tyus et al. 1987). Seasonally-flooded bottoms were used from late April to May of 1985 and 1987, during flow events that represent average annual high flow events (i.e., 226 - 283 m³/s). Wick et al. (1983) noted in 1982 (an average-flow year), that adult Colorado pikeminnow used flooded shoreline areas in spring, but moved to backwater habitats as the river level dropped.

Habitat use also is influenced by flow regime. Under moderate flow conditions, adults in the UCR were found in backwaters, eddies, and pools 90% of the time, and in runs only 10% of the time (Osmundson et al. 1995). When flows were low, adults were found in runs 97% of the time. The apparent shift in preference is probably the result of changes in habitat availability caused by changes in flow (e.g., inundated gravel pits simply do not exist at low flow; Osmundson et al. 1995).

The availability of inundated gravel pits in the UCR can create a distorted view of the general habitat requirements for the species. In the UCR, Valdez et al. (1982) reported that the average water depth where adults were captured was about 6 ft, which is much deeper than the average depth recorded for adults in the Green River. The difference probably reflects the importance of inundated gravel pits, which are present in the UCR, but not in the Green River.

Adult Colorado pikeminnow are piscivorous (Vanicek 1967), but will consume other prey (Beckman 1953, USFWS 1991). Their natural prey were native suckers and chubs, which are readily consumed. They also will consume nonnatives, but occasionally with deleterious consequences; there are several accounts of pikeminnow choking on the spines of channel catfish (Vanicek 1967, McAda 1983, Pimental et al. 1985, Quarterone 1993).

Migration and Spawning. The initiation of spawning migration is an important event in the reproductive cycle of the Colorado pikeminnow. Because most home ranges are upstream of spawning areas, migrations usually begin in the downstream direction, but upstream migrations also occur (Tyus et al. 1987, Tyus 1990, Irving and Modde 1995). In fact, the longest migration on record occurred when a fish tagged in Lake Powell moved 318 km upstream in about one month to join an aggregation of other fish in the UCR. Based on radio tracking data, fish in the Green River begin spawning migrations about June 21 (range: May 23rd to July 22nd) and fish in the Yampa River migrate about June 15 (range: May 27th to July 13th). The timing of migrations in the UCR and the San Juan River is similar to that reported for the Green River, occurring from late June through early August (Archer et al. 1985, Ryden and Ahlm 1996).

Spawning migrations begin just after peak runoff and are initiated earlier in low water years than in high water years (Tyus and Karp 1989). The time between the date of peak runoff and the initiation of migration is negatively correlated with the date of peak flow; in the Green and Yampa rivers, there were statistically significant correlations in which earlier dates of peak flows were associated with longer time intervals before the migration occurred (Tyus 1990). The potential importance of flow is highlighted by the recent hypothesis that flow spikes from spring rainstorms may influence ovulation and spawning (Nesler et al. 1988). Temperature may also influence the timing of migration because temperatures must be at least 9°C (average 14°C) before migration occurs.

The annual pattern of spawning migrations of Colorado pikeminnow in the Green River basin demonstrates a clear capacity for homing to particular sites (Tyus 1985, 1990). The precise mechanism by which adults locate these sites is not understood fully, but circumstantial evidence supports natal imprinting (Wick et al. 1983, Tyus 1990). Electron microscopy has revealed that larvae possess a functional olfactory mechanism (R. Muth, personal communication). Not only are the receptors present, but a burst of hormones in the early larval stage suggests that imprinting is occurring (Scholz et al. 1993). Furthermore, recent studies with adult fish that have been exposed to hormones have shown an extremely acute sense of smell (A. Scholz, personal communication).

The pattern of movement of adults in the Green River basin is too complex to be explained as a response to gradients in environmental variables or to odors from conspecifics. Individual fish may travel long distances to spawning grounds, and fish with adjacent home ranges may go to different spawning reaches that are separated by many miles. Each fish appears to use only one spawning area (Wick et al. 1983; Tyus 1985, 1990; Irving and Modde 1995), but fish migrating to one location may pass through another one. Moreover, before fish begin these migrations, they are dispersed widely in the Green, White, and Yampa rivers, and may be upstream or downstream of their destinations.

It is possible that Colorado pikeminnow migrate to and spawn in locations where they were hatched (i.e., homing to natal areas), however this has never been proven. Orientation to olfactory cues provides an explanation consistent with the observed

homing behavior, and the fish possess the biological "equipment" necessary for responding to those cues. The chemical cues could govern the direction of fish movements by eliciting positive (upstream) or negative (downstream) responses, for example. Chemical inputs, such as natural organic matter, from tributaries, seeps, or flooded lands may provide gross cues for locating a spawning reach, and more subtle cues, such as reproductive byproducts from previously hatched young, may guide the fish to more specific locations within the spawning reach (reviewed by Tyus 1990).

Spawning probably occurs within a very small part of the range inhabited by each population of the Colorado pikeminnow. The location of each spawning site could be established unequivocally if spawning activity were observed directly. However, direct observation is unlikely because mature adults are rare and the rivers they inhabit are usually so turbid that the substrate is obscured. Consequently, most evidence supporting the case for spawning at a particular site will be circumstantial. Deductions can be based on the movements and reproductive status of adults, as well as the geographic distribution of larvae. Because newly-hatched larvae have virtually no ability to swim against river currents, their presence establishes a downstream limit on the area within which spawning must have occurred. Captures of larvae can be used to delineate a "suspected" spawning area, according to USFWS criteria (USFWS 1987). The boundary is imprecise insofar as the larvae can drift far from the spawning area in just a few hours after hatching.

The movements of mature adults at the time of spawning also can provide circumstantial evidence for the location of spawning sites. Radiotracking of adults has shown convergence of individuals on a particular river reach (e.g., Tyus 1985, 1990). Tracking data can define a "suspected" spawning area, but the boundaries of the river reach are likely to be overly broad because it may be very difficult to distinguish staging areas from the actual sites of egg deposition.

Collection of adults in "ripe" condition indicates that a spawning area is in close proximity, although adults can still move some distance when in ripe condition (cf. Tyus et al. 1987). The presence of ripe males is sufficient for defining a "suspected" spawning area (USFWS 1987). Females in "running ripe" condition are close enough to the time of egg laying that they are unlikely to move far. Thus, the USFWS (1987) has set the presence of running ripe females as the only acceptable criterion for "confirming" the location of a spawning site.

The best documentation of spawning sites has come from the Green River system. The reproductive ecology of Colorado pikeminnow in the Green River basin was studied intensively over a 10-year period (1980-90), in which studies encompassed many facets of reproduction including the timing of pre- and post-spawning movements, the extent and duration of spawning, and habitat use (Haynes et al. 1984, Nesler et al. 1988, Tyus 1990, Tyus and Haines 1991). Thousands of larvae and juveniles were captured, the movements of 150 radio-tagged adults were monitored, and 233 fish were captured in breeding condition. In the Yampa River, evidence supporting a suspected spawning

area has been collected from RM 4 to RM 30. However, the area where spawning has been confirmed by presence of running ripe females is much smaller, extending from Cleopatras's Couch (RM 16) to Harding Hole (RM 19) in Yampa Canyon. In Green River, the suspected spawning area in Gray Canyon extends from RM 142 to RM 187, and spawning has been confirmed from Three Fords rapid (RM 154 to RM 156).

All other spawning areas in the UCRB fall in the "suspected" category. In the UCR, larval Colorado pikeminnow have been captured between RM 155 and RM 171 in most years since 1982 (Osmundson and Kaeding 1989, McAda and Kaeding 1991a, Osmundson and Burnham 1991, R. Anderson unpublished data). Larvae have also been collected above RM 171 (Gunnison River confluence) in 1982 (McAda and Kaeding 1991a) and 1995 (Anonymous 1996b; R. Anderson unpublished data). Aggregations of adult fish during the presumptive spawning period have been recorded between RM 176 and RM 179 (McAda and Kaeding 1991a), and at RM 169 when running ripe males (but no running ripe females) were captured from a pool at the base of a newly formed riffle (D. Osmundson, unpublished data). In the Gunnison River, an aggregation of radiotagged fish was observed between RM 30 and RM 35 in 1993 and 1994 (Burdick 1995), and larvae were captured downstream of this reach in 1994, 1995, and 1996 (R. Anderson unpublished data). Movements of radio-tagged fish suggest that spawning may occur near Black Rocks, and in the lower Colorado River in Professor Valley (Archer et al. 1985). In the San Juan River, a suspected spawning area has been detected near the "Mixer" (RM 209-215) on the basis of radiotracked movements of 6 fish and the presence of one ripe male (Ryden and Ahlm 1996).

Breeding Colorado pikeminnow are most often concentrated in river reaches containing deep pools and eddies used for staging, and submerged cobble/gravel bars used for egg deposition. Within a spawning reach of several miles, the fish may select one or more localized areas for spawning. Radio-tagged fish move from pools or eddies to presumably spawn on bars and then return to the former habitat (Tyus and McAda 1984, Tyus 1990). Similar behavior has been recorded for spawning northern pikeminnow (Beamesderfer and Congleton 1981). Turbid riverine conditions have precluded direct observation of egg deposition. However, cobbles removed from spawning substrate in the Yampa River during this time of year are clean of sediment and algae (Archer and Tyus 1984; USFWS, unpublished data, Vernal, UT). There are substantial field and laboratory data suggesting that Colorado pikeminnow, and other pikeminnow species, require clean cobble surfaces for successful adhesion of eggs (Patten and Rodman 1969; Hamman 1981). Hamman (1981) also noted hatching of Colorado pikeminnow larvae from cobble surfaces. Spring scouring, a gradual decrease in summer flows, and a concomitant decrease in sediment load minimize siltation of cobble bars. Recent studies (Harvey et al. 1993, Harvey and Mussetter 1996) argue that spawning areas for Colorado pikeminnow in the Yampa River have a well-defined set of hydraulic and geomorphologic characteristics, and these characteristics seem to apply to spawning areas in the San Juan River (M. Harvey, pers. comm., 1997).

The annual spawning period for Colorado pikeminnow has been determined in the Green River system from migrations of radio-tagged fish, collections of ripe fish, and back-calculated dates of larval emergence. Average temperatures during the spawning period were in the range of 22-25°C (Haynes and Muth 1984, Nesler et al. 1988, Tyus 1990). The spawning period, which typically lasts 4 to 5 weeks, generally occurs earlier in low-water years, and later in high-flow years, presumably in response to varying flow and temperature conditions (Vanicek and Kramer 1969, Tyus and Karp 1989). USFWS data from 1981 to 1988 indicated that spawning occurred when flow was decreasing and temperature was increasing following spring peak runoff (Tyus 1990). This generally occurred 26 days (range: 17 - 33 d) following migration. Spawning of Colorado pikeminnow is not triggered by a single flow or temperature event, but by the interaction of abiotic and biotic influences (Tyus 1990).

The sex ratio of ripe Colorado pikeminnow on spawning grounds shows a consistent bias toward males. Captures in the Green River basin yielded about 15 males for each female (Tyus 1990). A similar bias has been reported for the northern pikeminnow. Patten and Rodman (1969) used scuba to observe spawning of northern pikeminnow and reported the number of males exceeded the number of females by a factor of about 50 to 200. Casey (1962) also reported that male northern pikeminnow outnumbered females. Most capture data suggest that a biased sex ratio is typical in the genus *Ptychocheilus*. The reason for the biased sex ratio has not been established firmly, but may be the result of spawning behavior or sex-related differences in the age of first reproduction. Radiotracking data show that adults, especially females, do not return every year to the same spawning bar, and that no Colorado pikeminnow have been found spawning on more than one spawning bar. The clear implication is that females do not spawn every year. If females spawn less often than males, there will be fewer ripe females than ripe males in a given year, other things being equal.

A sex-related difference in the age of first reproduction may also contribute to a biased sex ratio. If it is assumed that the sex ratio is 1:1 at hatching, and that mortality is not sex-related, the sex ratio for ripe fish will depart from 1:1 if females mature later than males. Application of age-length data from Hawkins (1991) to ripe Colorado pikeminnow collected on spawning grounds shows that males begin reproducing at approximately age eight and females begin reproducing at approximately age ten. For the two years during which maturation of females is delayed relative to males, females are still exposed to mortality. Thus, the number of mature females will be less than the number of mature males.

Larvae and Postlarvae. Larval Colorado pikeminnow emerge as sac-fry from cobble bars and begin drifting downstream rapidly (Haynes et al. 1984, Nesler et al. 1988). The yolk sac contains enough energy reserve to support the new fry for several days, after which exogenous feeding becomes necessary. The larvae tend to frequent shorelines with lower velocities and eventually become concentrated in shallow backwater habitats of alluvial reaches (Tyus et al. 1982b, Haynes et al. 1984, Tyus and Haines 1991, Valdez et al. 1982). Once in the backwaters, larvae begin feeding on

zooplankton and benthic organisms, and postlarvae as small as 30 mm have been observed consuming other fish (Muth and Snyder 1995).

Late summer and autumn is a critical period for growth and survival of young Colorado pikeminnow. The abundance and growth of young pikeminnow in the Green River are favored by relatively low flows, and impaired by high flows that inundate and damage backwater habitat: catch and growth rates during late summer and autumn were higher in the low flow years (1979-1980) and lowest in years with unusually high releases (1983-1984) from Flaming Gorge Dam (Tyus et al. 1987). This relationship suggests that the flows that optimize growth and survival of small pikeminnow vary with time of year and that postlarval survival depends on the availability of backwater nursery habitat (Tyus and Haines 1991).

Most larvae produced by one population will use one nursery area downstream (Figure 3). Larvae produce in the Grand Valley region of the UCR drift downstream to a nursery area in the vicinity of Moab, UT (Valdez et al. 1982). In the Green River, there are two nursery areas; one is 130-150 km downstream from the Yampa River spawning reach, and the other is 130-150 km downstream of the Green River spawning reach (Tyus et al 1982b and 1987, Tyus and Haines 1991). The nursery habitat is created with the gradually decreasing flows that follow spring runoff and persists through the summer and early autumn. Increased releases from reservoirs in autumn and winter may inundate this habitat. The quantity and quality of these habitats are thought to be crucial to successful recruitment.

Aerial photography and videography have been used to assess the relationship between nursery habitat conditions and flow in the river. In the Green River, aerial studies coupled with ground interpretation have shown that maximum area of backwaters occurs at flows in the range of 30 to 50 m³/s (Pucherelli and Clark 1989). Flows above or below this level reduce the number of backwaters available as nursery habitat. However, it is clear that a simple flow vs. backwater area relationship does not exist. Instead, the area and number of backwaters depends on a complex relationship that is sensitive to the timing, duration, and magnitude of flow and sediment inputs, as well as the physical characteristics of the riverine habitat. Other studies of the relationship between backwater habitat and flow are being conducted by the Bureau of Reclamation and the Utah Division of Wildlife Resources for the UCR (Fenton 1996), but results are not yet available.

Nutrient dynamics in the backwater nursery habitats have not been studied thoroughly, but some studies have been done in the Green River. Backwaters in the Ouray area, where larval pikeminnow were abundant, were richer in food than similar habitat upstream. Reduced fluctuations in water level near Ouray may have resulted in more stable backwater habitats and possibly reduced exported nutrients and food (Grabowski and Hiebert 1989).

Large, age-0 Colorado pikeminnow are most abundant in shoreline backwaters, but they also use other habitats, presumably in response to changing water temperature. Larval pikeminnow in the UCR (RM 26.8) used backwaters that were warmer than the river channel (Valdez et al. 1982). Similar findings are reported from mark-recapture studies in the Green River, where young fish were observed making diel movements between backwaters and the main channel (Tyus 1991b). The movements appear to be associated with temperature because fish occupied warmer backwaters in the day, but moved into the main channel as water temperature decreased in the backwaters at night. The young fish also are sensitive to changes in water level; they move into shallow backwaters as water level increases (Tyus 1991b) and move out of shallow areas when water recedes, thereby avoiding being trapped in isolated pools (Valdez et al. 1982). Abundance and growth of age-0 fish showed a negative correlation with flows in the river and a positive correlation with water temperature (Tyus and Haines 1991). Thus, the larvae appear to do better when river flow is low and water temperature is high, at least during some times of the year.

Juvenile pikeminnow (age 0 and age 1) appear to be very tolerant of winter conditions. In laboratory studies that simulated winter conditions, Thompson (1989) found that most of the larvae survived 210 days of starvation at 3-4°C, and Thompson et al (1991) determined that overwinter survival of age-0 pikeminnow was related to large size and fat content at the onset of winter. A more recent study also supports the premise that healthy young fish are tolerant of starvation (Bestgen 1996). Healthy larvae would be able to survive winter under normal flow conditions, even with relatively little food (Tyus and Haines 1991).

Juveniles. Juvenile Colorado pikeminnow tend to leave the nursery habitat during the next spring runoff, when they are greater than 60 mm long, and gradually move upstream toward adult habitat. The process takes time, and the juveniles (60-200 mm) and subadults (200-400 mm) become spread throughout the system (cf. Valdez et al. 1982). Most of the movement probably occurs during the late juvenile or subadult stage, because only large-sized fish are found in the upper Yampa River, and the highest concentration of juveniles is found in the lower Green river (Tyus 1986 and 1990, Tyus et al. 1987). Osmundson et al. (1997) reported that this movement occurs in the UCR when the fish reach a size of about 450 mm. Fifteen of eighteen fishes that entered the Gunnison River via the new Redlands fish passageway were juveniles that came from the lower part of the UCR (F. Pfeifer, personal communication). The search for new habitat is probably associated with a change in diet. The condition of juveniles seems to decline with age if they remain in the lower part of the UCR, whereas condition improves with age in the upper part of the river (Osmundson et al 1997). Sexual maturity can be attained as early as 5-6 years under artificial conditions (Hamman 1981), but probably not until about 8 years in nature (Tyus 1990, Hawkins 1991, Seethaler 1978).

Integration of Life History. The life history of the Colorado pikeminnow has been studied in greater detail than that of the other three endangered fishes, and much

information is available. The life cycle of the Colorado pikeminnow is relatively complex, including spatial separation of life stages and energetically-costly migratory behavior (Tyus 1986, 1990). These components are part of the life strategy and tactics that have maximized fitness of the Colorado pikeminnow over millions of years. The foregoing review has been assembled from many sources, each reporting on a small facet of life history. There is a lot of "noise" in the compilation of facts, because it is based in part on actions of individual fish and their response to environmental factors. Consequently, this collection of facts lacks cohesiveness. The following narrative seeks coherence and cohesiveness for the most important features of the life history, but the cost of simplifying complex phenomena is the loss of detail.

In general, adult Colorado pikeminnow spend most of the baseflow period (Sep-Apr) in upper river reaches that extend as far as the downstream edge of coldwater trout habitat. Each fish occupies a relatively stable home range located in areas that have high densities of native suckers and chubs. Physical habitat conditions are variable, and habitat selection is probably related to prey abundance. Adults exhibit considerable tolerance to cold and remain active throughout the winter.

Adults become very active in spring when snowmelt cause the rivers to rise. Rising flow, increasing temperatures, and other environmental influences stimulate gonadal development and reproductive behavior. During peak runoff, usually in May, adults begin migrating to spawning areas. Homing, guided presumably by olfactory cues, takes the adults to the same spawning site from which they emerged as sac-fry, perhaps more than a decade before. Spawning activity occurs over a 3-4 week period when flows are declining after peak runoff, and when water temperatures are in the range of 22-25°C. Adult females may use overbank areas for staging, and the higher temperature in these habitats may hasten the maturation of ova.

The adhesive eggs are deposited on cobble bars and develop for 7-10 days before hatching. The newly emerged sac-fry drift downstream and soon reach suitable nursery habitat about 100 km of the spawning area. The young fish may continue to move downstream another 20 km, or more, during the next few months.

Backwater nursery habitat is created by the declining flows that follow peak runoff. If peak flows are low, few backwaters are formed. If flows remain high, potential backwaters are inundated. However, past studies have demonstrated that a simplistic flow/backwater area relationship does not occur; instead, the duration, timing, and magnitude of flows and sediment inputs seem to be implicated. In the nursery area, the larvae and postlarvae feed on zooplankton and benthos. As they grow in size, they begin to consume fish as well. Postlarvae continue to feed actively throughout the winter, but can withstand extended periods of starvation, if food is unavailable. The juvenile fish (60-200 mm) occupy backwater areas in the spring of their first year, but are difficult to find after spring runoff, apparently because they begin using other habitats.

By the time the fish have reached subadult size (250 - 400 mm), they become increasingly piscivorous. Gradually, the subadults begin moving upstream, perhaps drawn to better habitat and more suitable food. Over a period of years, these fish move into adult habitat many miles upstream of the nursery area. Because the movement is so gradual, they become widely distributed in the system. Male Colorado pikeminnow mature when they are about 8 years of age, and females mature when they are about 10 years old.

Razorback Sucker

Most of the following text is based on data obtained from studies of razorback suckers in riverine habitat of the UCRB. Despite the fact that most of the razorback suckers remaining in nature are found in Lake Mohave, AZ-NV, rivers are likely to be the focus of restoration efforts in the UCRB. Consequently, the body of information on life history, behavior, and habitat use in lacustrine habitat will be used only sparingly.

In winter, razorback suckers in the Green River occupy slow runs, slackwaters, eddies, and backwaters of the main channel (McAda and Wydoski 1980, Valdez and Masslich 1989). The fish are cold-adapted and remain active in winter; local movements increase with increased discharge and flow fluctuations (Valdez and Masslich 1989). Razorback suckers also have been observed using large backwaters in some locations during early spring (Westwater Engineering 1996).

Razorback suckers in unrestricted riverine habitat exhibit both local and long-distance movements in spring and summer (Tyus 1987; Tyus and Karp 1990; Modde et al. 1995), although these movements are not as extensive as those observed for the Colorado pikeminnow. During spring migrations, fish may move 50 to 190 km to spawning sites in the Green and Yampa rivers (Tyus and Karp 1990). Radiotracking studies and recaptures of tagged fish on spawning grounds have documented homing to specific spawning sites, to which the fish show fidelity. Similar homing movements are known for other catostomids, where at least 95% of the spawning fish migrate to their home stream (see Dence 1948, Werner 1979). Recent studies have implicated olfactory imprinting as the mechanism by which razorback suckers locate spawning areas. Scholz et al. (1992, 1993) confirmed that a burst of thyroxine occurred during the sac-fry stage, immediately before the larvae swam up from the cobbles and entered downstream drift. Thyroxine activity in other fishes has been associated with a period of sensitivity in which olfactory imprinting can occur (Hasler and Scholz 1983, Scholz et al. 1992, 1993).

The RIP has supported two studies of olfactory imprinting in razorback suckers. Fish exposed to two different chemicals during the sac-fry stage were later tested in a maze when they were adults. In the first study, most fish moved and oriented to the correct chemical (Haines et al. 1996). Results were less clear in a subsequent study where fewer fish oriented to either chemical (A. Scholz, personal communication), but behavior may have been confounded by the presence of ripe females. In both studies,

however, almost all fish that moved, oriented to the chemical to which they had been exposed, and presumably imprinted, as larvae.

Razorback suckers in the UCR basin spawn in spring, when flows are increasing and water temperatures in the main channel are about 14-15°C (Tyus 1987, Tyus and Karp 1990), but there appears to be some plasticity in both timing and temperature (Minckley et al. 1991). Early in the spawning season, razorbacks congregate in flooded shorelines, flooded bottomlands and gravel pits, and in the mouths of tributary streams. These areas, which are probably used for staging, resting, or feeding, have higher temperatures (mean: 19.6, range: 17.5-21 C; Tyus and Karp 1990) than the main channel, and the warmer conditions may enhance maturation of gametes or otherwise prepare the fish for reproductive activities.

There has been some controversy in the literature about the habitat that razorback suckers select for spawning (see Minckley et al. 1991 for review). The issue is significant because it provides part of the justification for major investments by the RIP for acquisition of bottomlands. The typical spawning substrate for catostomids consists of gravel or cobble (Breder and Rosen 1966). This is true of suckers in the western US (Moyle 1976), including obligate lacustrine suckers that ascend streams to spawn on gravels and cobbles (Scoppertone and Vinyard 1991). The razorback sucker conforms to the general catostomid pattern: it deposits eggs in flowing water over substrate that is predominantly gravel or cobble (reviewed by Minckley et al. 1991). Even in Lake Mohave, spawning adults aggregate over areas of coarse substrate (cobble mixed with gravel), and the spawning fish sweep away fine materials before creating the depressions in which the eggs are deposited. There is no indication that razorback suckers deposit eggs over flooded vegetation in Lake Mohave, nor is it likely that they will do so in flooded bottomland where the substrate may be vegetated or composed of fine material. Except for induced spawning of captive fish in hatchery ponds (e.g., Dexter NFH, Dexter, NM), catostomids do not deposit eggs over vegetation or fine substrate.

Confusion about the sites chosen by razorback suckers for egg deposition may be due in part to the extended period of time during which the females remain ripe. It has been speculated that razorback suckers spawn in silty backwaters, flooded pasture, river oxbows, and flooded bottomlands (Valdez et al. 1982, Osmundson and Kaeding 1991). To be sure, razorback suckers in an advanced reproductive state (tuberculate with expressible sex products) have been found in habitats of that kind, leading to the logical conclusion that egg deposition also occurs there. However, egg deposition has not been observed in those habitats, and it would not be expected based on the reproductive biology of that or related species. A more likely explanation is that the fish used those habitats for staging, and that the advanced reproductive state was a misleading clue. Because razorback suckers remain ripe for a long time, ripe fish captured in the staging area would still have time to move into the main channel and spawn over coarse substrate; this behavior has been documented previously (McAda

and Wydoski 1980, Tyus 1987, Tyus and Karp 1990, USFWS unpublished records on file in Vernal, UT).

The capture of larval razorback suckers in upper and lower reaches of the Green River (seine collections; R. T. Muth and D. Snyder, personal communication) suggests that razorback suckers spawn successfully in the Green River basin. However, the razorback suckers in the Green River are primarily old fish (Minckley, pers. comm.); very little annual recruitment has been documented since the 1960s (Lanigan and Tyus 1989, Modde et al. 1996). The timing coincides roughly with the closure of Flaming Gorge Reservoir. Although operation of the reservoir reduced flooding and decreased availability of inundated shorelines and overbank habitat, it is not clear that this alone is responsible for the absence of recruitment to the razorback population. The question remains open, because present operation of the reservoir still permits inundation of bottomlands that should be sufficient for some recruitment. Perhaps operation of the reservoir leads to more stable habitat conditions that favor nonnatives. In the UCR, similar flooded areas that were once used by razorback suckers in the spring have been lost, including areas that reportedly supported razorback suckers in spawning condition (Archer et al. 1985). Reproducing populations of razorback sucker persisted in the UCR above Debeque Canyon for more than 60 years after the construction of dams blocked fish movement downstream, but habitat destruction has been cited as the cause for the demise of this population (Westwater Engineering 1996).

Integration of Life History. Although the life history of the razorback sucker has been documented in less detail than that of the Colorado pikeminnow, there is still a large body of information derived from years of research. The following narrative seeks to describe the general life cycle in a cohesive manner, patterned after the comparable section for the Colorado pikeminnow. As before, this overview simplifies by intentionally ignoring details that distract from a coherent view.

Adult razorback suckers spend most of the baseflow period (Sep-Apr) in low velocity habitats (e.g., backwaters, eddies, etc.) of the main channel. They remain active even in cold water, but movements are local. In the spring, when flows increase during runoff, the adults begin spawning migrations. Movements appear to be guided by olfactory cues, which lead each fish to the spawning area where natal imprinting occurred. Main channel temperatures are 14-15 °C at this time. The fish move into off-channel staging areas (backwaters, oxbows, flooded bottomlands), where warmer temperatures (17.5-21 °C) probably facilitate the final maturation of gametes. Females remain ripe for an extended period of time (perhaps weeks), and they move into the main channel and deposit eggs in flowing water over coarse (gravel and cobble) substrate.

The rest of this narrative becomes speculative, because there is little documentation of life history. Hatching occurs during, or slightly before, peak runoff. Historically, larvae would have access to flooded bottomlands and probably spent a few weeks there.

When water levels receded in the overbank areas, the larvae returned to the main channel.

Humpback Chub

In contrast to the Colorado pikeminnow and razorback sucker, humpback chub are relatively sedentary and occupy restricted river reaches for most or all of the year (Valdez and Clemmer 1982; Valdez and Ryel 1995, 1997). The fish may remain in or near specific eddies for extended periods of time, and may return to the same eddy for spawning (Karp and Tyus 1990b). Radio-tagged fish from the UCR at Black Rocks stayed almost entirely within a 1.8 mile reach (Archer et al. 1985, Kaeding et al. 1990). Behavior is similar in the Grand Canyon, where 60 tagged fish were recaptured only about one mile from their original capture location (Valdez and Ryel 1995). Although remaining in one reach for most of the year, the fish tends to make use of microhabitats where there is a natural flow regime. Humpback chub in the Yampa River were forced to move into deeper pools as water levels dropped in summer (Karp and Tyus 1990b) and similar behavior was noted in the Little Colorado River (Gorman 1994).

Ontogenic shifts in humpback chub habitat use have been reported by Valdez and Ryel (1995, 1997) in the Grand Canyon, with subadult fish (50– 200 mm TL) using primarily shallow shoreline habitats and adults using deeper offshore habitats. Microhabitats preferred by adult humpback chub during warmer months are large recirculating eddies and slow runs (Valdez and Clemmer 1982, Karp and Tyus 1990b).

Humpback chub reproduction occurs shortly after peak runoff when water temperatures exceed 16°C (Valdez et al. 1982). In the UCR, spawning has been recorded between mid-June and late July (Archer et al. 1985), although the two years of study were both characterized by unusually high flows that may have delayed spawning. Ripe fish are captured mainly in deep shoreline eddies, but spawning presumably occurs in mid-channel and lateral cobble bars. Virtually nothing is known about habitat preferences of the larvae.

Postlarval chubs are most often captured in shoreline habitats, including backwaters, small eddies, side channels, and embayments (Valdez et al. 1990), however as the fish grow larger than about 40mm TL they begin to move into deeper and swifter habitats. This ontogenic shift in habitat use was dramatic in the Grand Canyon, where younger fish (larvae through subadults (less than 200mm) occupied in shallow shorelines, but adults used deeper offshore habitats (Gorman 1994; Valdez and Ryel 1995, 1997).

Habitats used by humpback chub are greatly affected by flows. Higher flows tend to maintain the recirculating eddies used primarily as habitat for adults. An insectivore, the chub benefit from higher flows that provide allochthonous inputs, including terrestrial insects.

Other fishes occupy humpback chub habitats, and there is some anecdotal information that suggests that the chub may have been displaced from some habitats due to interactions with channel catfishes and other introduced fishes (Tyus 1998). Direct predation has been observed in Grand Canyon, where introduced catfish and trout consumed large numbers of the fish (Valdez and Ryel 1995; Marsh and Douglas 1996)

Bonytail

Life history information about the bonytail is scant (USFWS 1990a), and its habitat requirements are virtually unknown. Very few fish have been reported in the UCRB and it is not known if the fish was ever abundant there (Tyus et al. 1982; but see photo in Quarterone 1993, which suggests that the fish may have been abundant locally). The last bonytail reported from the UCRB was captured on 17 July 1984 near Black Rocks (Kaeding et al. 1986). Some bonytail have persisted in large reservoirs of the lower basin (e.g., Lake Mohave and Lake Mead), indicating an ability to live in lacustrine habitat (Minckley 1973, Valdez and Clemmer 1982, USFWS 1990a). Results of a radiotracking study of adult bonytail chub introduced into the upper Green River in 1988 and 1989 indicate that the fish exhibit crepuscular movements, and are relatively quiescent during the day and night (S. Cranney, Utah Division of Wildlife Resources, pers. comm.). Studies are in progress to determine basic ecological requirements that may be needed for successful reintroduction (Crowl et al. 1996).

PART 3. ENVIRONMENTAL FACTORS LIMITING RECOVERY

General

The abundance of a natural population is determined by the balance of individuals gained through reproduction and those lost to mortality. If recruitment to the breeding population does not equal or exceed loss to all sources of mortality, other factors being equal, the population will decline. For endangered species, it is a foregone conclusion that loss has significantly exceeded recruitment in the past. Successful recovery will depend on enhancing recruitment relative to loss (or reducing loss relative to recruitment).

The factors contributing to recruitment and loss may be abiotic (physical or chemical), biotic, or both. Physical factors could include the quality or abundance of habitat required for one or more life history stages. For example, loss of habitat through channelization, or degradation of substrate by sediment accumulation, will reduce the number of larvae produced. Other things being equal, a drop in production of larvae would decrease recruitment. The condition of the physical habitat also is strongly influenced by the hydrologic regime because of relationships between flow and extent of habitat, or between flow and sediment transport, for example. Water quality, another abiotic factor, could cause mortality via pollutants, or reduce recruitment by more subtle

effects like delay of spawning due to colder water temperatures. In general, however, water quality effects other than temperature have been studied little. Biotic factors are most likely related to predation or competition from nonnative fishes, but may also include food supply.

Environmental factors that regulate the abundance of a life history stage, or a population, are considered "limiting factors." There are biotic and abiotic factors that regulate growth and mortality, and the relative importance of these limiting factors may vary in time (e.g., with season or with life history stage) or space (habitat occupied by a particular life history stage at a particular time of year). Especially for species that are endangered, and thus rare, it may be difficult to define rigorously the factors limiting population size. A certain amount of inference based on best professional judgment therefore becomes necessary.

Identifying limiting factors is the first step in developing plans for enhancing recovery of the endangered fishes. The next step is assigning priorities for alleviating the limitations imposed by each of the factors. Ideally, priorities for management actions should be established based on the number of fish that will be added to the population. It probably will not be sufficient to address problems one at a time, because multiple factors may be acting in concert.

In the review that follows, limiting factors are examined on two overlapping scales: basin-wide and species-specific. Limiting factors that exist on the basin-wide scale will affect some or all life history stages of one or more of the endangered fishes. These include abiotic factors such as flow and temperature (which are linked to some extent), and biotic factors such as the abundance of nonnative fishes. Basin-wide factors will be reviewed separately because it is easier to understand their origins and the pervasiveness of their effects. It is also necessary to examine limiting factors from a species-specific perspective because it provides the temporal and spatial focus necessary for developing recovery plans efficiently. For each species, limiting factors will be reviewed in the context of life history because limiting factors may be different at each stage, especially where the stages occupy different habitat (e.g., Colorado pikeminnow).

Basin-wide Limiting Factors

Abiotic

The construction of dams and diversion structures in the Colorado River basin has converted much riverine habitat into reservoirs and smaller lacustrine habitat. Loss or alteration of habitat has been extensive and is documented elsewhere (e.g., Carlson and Muth 1989, Minckley and Deacon 1991). This loss is, for practical purposes, irreversible. The presence of these structures and their role in regulating flows have other, albeit less direct, effects on fish habitat. Structures in the channel may constitute

physical barriers to dispersal and seasonal migration. The importance of barriers to fish movement will be discussed in connection with species-specific limiting factors.

The operation of reservoirs and other components of the water storage and distribution system affects fish habitat by altering water depth, water velocity, and sediment load, properties that are critical for the creation and maintenance of fish habitat. The quantitative hydrodynamic connection between flow alterations and loss of fish habitat in the main channel is poorly understood, with the notable exception of work on Colorado pikeminnow spawning habitat (Harvey et al. 1993). The relationships are complex and probably better to explore in the context of needs for specific life history stages (e.g., nursery backwaters for larval pikeminnow).

The operation of reservoirs also has had some effect on temperatures in the rivers. Reservoirs store cold meltwater in spring and, even though the surface layer of each reservoir will warm during the summer, the release of water from near the bottom of each reservoir will yield cold water through much of the summer. The result is a depression of water temperatures below reservoirs during the months when the native fishes have spawned historically. Colder temperatures could affect spawning as well as the growth and survival of young larvae in the drift (Berry 1988). The association between water temperature and initiation of spawning is relatively well known for the Colorado pikeminnow (Tyus and Karp 1989, Tyus 1990), but less so for the other species.

Lower temperatures may have implications for other life history stages, but less is known, and some of the research results seem contradictory. Early lab studies provided information about preferred temperatures of young life history stages of Colorado pikeminnow, from hatching success to optimum temperatures for growth of young of the year (Hamman 1981, Black and Bulkley 1985, Marsh 1985, Bozek et al. 1984). Studies also were done to determine how temperature changes might affect survival and behavior of young fishes (e.g., Berry 1988, Childs and Clarkson 1996). Findings of these laboratory studies have been applied to the river system with varying results. For example, Kaeding and Osmundson (1988) used main channel temperatures to evaluate habitat suitability for Colorado pikeminnow. More recent studies have shown that endangered fishes in riverine habitat may not select the temperatures conditions predicted as optimal by laboratory studies (e.g., spawning temperatures for razorback sucker: Tyus and Karp 1989, 1990).

One factor that may mitigate the effect of lower temperatures is the capacity of all life history stages to move toward suitable temperatures in the river. Young pikeminnow can and do move between habitats such as backwaters, eddies, and main channel shorelines in response to differences in temperature regime (e.g., Valdez et al. 1982, Tyus 1991b). Adult pikeminnow and razorback suckers use a wide range of off-channel habitats such as semi-isolated backwaters, gravel pits, and cut-off side channels, and they may move into shallow, flooded habitats in spring (Wick et al. 1983, Tyus 1987 and 1990, Tyus and Karp 1990). It is thought that active selection of a preferred

temperature regime is at least part of the reason for those movements. Finally, winter studies show that the native fishes remain active through the coldest months, seeking different habitat conditions of flow and temperature, and displaying a higher degree of cold tolerance than is characteristic of many warmwater fishes (Wick and Hawkins 1989, Valdez and Masslich 1989).

The research available on the temperature requirements of the endangered fishes does not lead to unambiguous conclusions about the effects that lower river temperatures have had on fish in the wild. Specifically, it has proven difficult to apply the results of laboratory studies of temperature preference to fish in the riverine environment. The natural habitat is complex and the range of temperatures actually available to wild fish is greater than would be expected on the basis of temperatures recorded in the main channel (cf., Valdez et al. 1982, Tyus 1991). Behavioral considerations that allow the wild fish to select from the range of temperatures available in the different habitats in or adjacent to the main channel provide a mechanism for ameliorating the adverse effects of low temperatures in the main channel. The egg is probably the stage most vulnerable to lower river temperatures because eggs are deposited at specific locations in the main channel and have no capacity to seek more favorable temperatures. Thus, with the possible exception of the egg stage, changes in main channel temperatures may not have had a large effect on habitat that otherwise remains natural.

Biotic

For at least 50 years, scientists have been concerned about the role nonnatives have played in the decline of native fishes. Dill (1944) was one of the first to suggest that nonnatives were responsible for declines observed in native fish populations in the lower Colorado River basin. He recognized that the decline began about 1930, and that it was coincident with a large increase in the abundance of nonnative fishes, especially channel catfish and largemouth bass. By 1960, populations of the big river fishes had been reduced greatly. Miller (1961) noted "drastic changes" in the fish fauna and observed that replacement of native fishes by introduced fishes in the lower Colorado River offered the "most impressive documentation for changing fish fauna" ever recorded. Schoenherr (1981) considered the evidence "overwhelming" for replacement of native fishes by aggressive introduced fishes, and he provided examples in which predation resulted in extirpation. More recent studies and reviews add to the case for a decline in the abundance of native fish species as nonnative species have increased in abundance (Joseph et al. 1977, Osmundson and Kaeding 1989, Quarterone 1993). It is not unusual now for nonnative fishes to comprise a significant portion (>25%) of standing stock in most areas, and to comprise up to 90% in backwaters (McAda et al. 1994).

An increasing body of evidence characterizes the negative interactions of nonnative fishes with the endangered big river fishes (Hawkins and Nesler 1991, Minckley et al. 1991, Maddux et al. 1993, Lentsch et al. 1996a). Evidence in many of the reports is indirect in the sense that they lacked direct observations or absolute proof of predation

on natives. Such indirect evidence may include inferences from field data or results of laboratory studies. Direct evidence of predation includes native fishes obtained from stomach contents of the nonnative fishes and by visual observation of predation.

Indirect evidence strongly suggests a link between the decline of native fishes to the proliferation of nonnative fishes has been given by many workers (Dill 1944, Wallis 1951, Jonez and Sumner 1954, Miller 1961, Vanicek 1967, Rinne 1971, Vanicek and Kramer 1969, Baxter and Simon 1970, Moyle 1976, Holden 1977, Joseph et al. 1977, Allan and Roden 1978, Deacon 1978, Miller et al. 1982 and references therein, Kaeding and Zimmerman 1983, Minckley 1983, Wick et al. 1983, Bestgen and Propst 1989, Marsh and Minckley 1989, Tyus and Karp 1989, Tyus and Beard 1990, Tyus and Nikirk 1990, Valdez et al. 1990, Minckley and Deacon 1991 and references therein, Propst and Bestgen 1991, Rinne 1991, Rinne and Minckley 1991, Scoppertone 1993, Ruppert et al. 1993, Trammell et al. 1993, and Valdez and Ryel 1995). Other workers have studied dietary overlap and postulated that competition for food and/or space was occurring (Jacobi and Jacobi 1982, McAda and Tyus 1984, Grabowski and Hiebert 1989, Muth and Snyder 1995, Valdez and Ryel 1995). Laboratory studies have documented agonistic behavior, resource sharing, and vulnerability to predation (Papoulias and Minckley 1990, Karp and Tyus 1990, Johnson et al. 1993, Beyers et al. 1994).

Direct observations, including stomach content analyses, of predation by nonnative fishes have been reported for many species native to the Colorado River basin, including Colorado pikeminnow, razorback sucker, and humpback chub (Table 1). The list is extensive and should leave no doubt that predation by nonnatives is a powerful force. The number of predator species is great, especially for the early life history stages of the razorback sucker. However, it has been difficult to document predation on larvae in nature. Part of the difficulty in documenting predation in early studies is that the rapid digestion of some of the centrarchid fishes was not appreciated. Langhorst and Marsh (1986) found that razorback sucker larvae were only distinguishable in stomachs of green sunfish (*Lepomis cyanellus*) for about 30 minutes. After that time the larvae essentially were dissolved. The table is supplemented by reports of humpback chub with characteristic bite marks that have been attributed to channel catfish. These marks could not have been made by native cyprinids or catostomids because they lack jaw teeth (Kaeding and Zimmerman 1983, Karp and Tyus 1990).

The nonnative fishes can be divided roughly into three assemblages based on the threat posed to recovery of the endangered fishes. The first is comprised of small cyprinid species (e.g., red shiner, sand shiner, and fathead minnow) that are abundant mainly in backwater habitats of the warmer, low-gradient river reaches. Although these cyprinids are small, they are very aggressive and will prey on larvae in the backwaters that serve as nursery habitat for the Colorado pikeminnow (Dunsmore 1993 and 1996, Muth and Snyder 1995). The second group consists of centrarchid fishes (e.g., largemouth bass, green sunfish) that occupy deeper and more permanent pools that

may or may not be connected with the channel at low water, but which can be connected at high water. These piscivorous fishes can displace native fishes and will consume juveniles of the native fishes (Burdick 1996, Osmundson 1987). The third group of nonnatives is a diverse collection of species (including channel catfish, black bullheads, common carp, walleye, and northern pike) that are better adapted for riverine existence, and which may prey on native fishes in main channel habitat for part or all of the year. Several of these nonnative species that pose problems in the UCRB have been implicated in the demise of native fishes nationwide (ANSTF 1994).

The body of evidence documenting the deleterious effect of nonnatives on the native fishes of the Colorado River system is sufficiently compelling to have convinced most experts in the region. Hawkins and Nesler (1991) polled regional fisheries experts and found that 81% believed nonnative fishes were responsible for significant problems. Maddux et al. (1993) reviewed issues related to the recovery of four endangered Colorado fishes and reported that interactions with nonnatives were the primary factor limiting recovery in some areas. Lentsch et al. (1996a) identified the nature of negative interactions of many nonnatives with the endangered species. The nonnative fish issue has been studied thoroughly (see review by Tyus and Saunders 1996a) and the conclusions are clear that introduced species have played, and continue to play, a significant role in the decline of the native big river fish community.

Species-specific Limiting Factors

Colorado pikeminnow

The specific factors regulating the growth and survival of adult Colorado pikeminnow are not well known. Adults are probably not subject to predation because they are too large for other piscivores to handle. Because the options for reducing adult mortality are limited, the most feasible prospects for increasing the number of adults may lie in improving or increasing their habitat, and this requires an understanding that habitat has biological, as well as abiotic dimensions.

Adult nonspawning habitat. Studies in the UCR have shown that the best adult habitat accessible to the extant population is in the reach from Westwater to Palisade (RM 125-186). This conclusion was derived from data on fish abundance and condition from the upper and lower portions of the Colorado River (Osmundson et al. 1997). Larger fish move out of the lower UCR as they become subadults, and the few that remain tend to be in poorer condition. In contrast, fish occupying the upper part of the UCR tend to improve in condition as they grow larger. The logical inference is that the upper portion (the 15-Mile Reach) offers better habitat conditions for the growth of adults than does the remainder of the accessible portion of the UCR. That does not necessarily mean that conditions in the 15-Mile Reach are optimal.

An examination of habitat use by adult Colorado pikeminnow shows that preferences vary seasonally in the 15-Mile Reach (Osmundson et al. 1995). However, results of

habitat use studies in the UCR should be interpreted carefully because habitat alteration has been extensive and because so few fish were available for study. Therefore, it would be prudent to compare habitat preferences in this part of the basin with those of other populations, especially in the Green and Yampa rivers where there are fewer barriers to fish movement. As indicated previously, habitat use in the unregulated portion of the basin is somewhat variable, and appears to differ from that reported for the 15-Mile Reach.

In general, the larger (subadult and adult) Colorado pikeminnow will move into upper river reaches when there is opportunity. For example, adult pikeminnow in the Yampa River frequently travel as far upstream as Craig, and have been reported as far upstream as Steamboat Springs. In the White River, before Taylor Draw Dam was closed, pikeminnow traveled up river as far as Meeker. Historical records from the Gunnison River basin place Colorado pikeminnow in the lower Uncompahgre River, and data from the recently-completed Redlands fish passage structure show that subadults from the lower UCR are now moving into the lower Gunnison River (F. Pfeifer, personal communication). In all three instances adult Colorado pikeminnow were occupying, or seeking, habitat that is comparable to the Colorado mainstem above Palisade; such adult habitat may be higher quality, in terms of physical and biological features, than that found further downstream. The shortage of high-quality nonspawning habitat may hinder expansion of the number of adult Colorado pikeminnow in the UCR.

The conclusion that high quality adult habitat is limited in the 15-Mile Reach in low-flow years also has been reached by the USFWS (Osmundson et al. 1995). Their proposed remedy involves optimizing adult habitat by providing higher minimum flows. Underlying the USFWS proposal are the following assumptions that are standard for instream flow methodologies: (1) the observed pattern of physical habitat use is indicative of requirements, and (2) satisfying the apparent physical habitat requirements will increase the carrying capacity of the riverine environment leading to an increase in the number of adult Colorado pikeminnow, unless the population is really held in check by another limiting factor. Both assumptions merit review.

Physical habitat conditions are obviously important, but may not be the primary factor constraining the abundance of adult pikeminnow. The historic prey of adult pikeminnow were native suckers and chubs. These prey species are more abundant in the upper river reaches (e.g., the Yampa above Maybell, the White River above Rangely, and the Colorado River above Palisade; (W.H. Miller et al. 1982bc, Tyus et al. 1982a, Valdez et al. 1982). Where adult pikeminnow have access to upper river reaches, they tend to be more abundant where the prey are more abundant. Flannelmouth suckers and adult Colorado pikeminnow congregated below Taylor Draw dam after it was closed, presumably because they sought access to "preferred" habitat upstream (Chart and Bergersen 1992, Trammell et al. 1993). The tendency of the adult Colorado pikeminnow to be distributed in river reaches that contain their preferred prey is well supported by the data, and argues that, for most of the year, physical habitat may be of less direct importance to the Colorado pikeminnow than the distribution of the prey. As

long as the physical habitat is appropriate for maintenance of the native prey population, it is probably adequate for adult Colorado pikeminnow.

It is of considerable significance to the recovery effort that the preferred prey items are less abundant in the UCR below Palisade. Adult Colorado pikeminnow may be congregating in the 15-Mile Reach simply because it receives input of prey species from upstream reaches and because it is as close as those fish can get to habitat that contains the preferred prey. The possibility that adult Colorado pikeminnow abundance is prey-limited in the 15-Mile Reach has significant ramifications for the recovery effort. It suggests that, unless food supply can be increased, improvements to physical habitat may not do much to increase the number of fish present. The area with suitable prey for the large adult pikeminnow will be extended greatly when barriers to Debeque Canyon are made passable.

Adult migration and spawning habitat. Lack of access to spawning grounds has been implicated in the decline of the Colorado pikeminnow (Joseph et al. 1977, Tyus 1984). Little is known, however, about the historical distribution and abundance of spawning sites. Spawning habitat has been located in the Yampa, Green, and San Juan rivers, and the presence of larvae shows that spawning also occurs in the UCR and the lower Gunnison River. Habitats in the Yampa and San Juan rivers appear to conform to a specific geomorphologic profile. The hydraulic and sedimentologic conditions necessary for the creation and maintenance of habitat with those characteristics have been defined recently by studying bar-forming events at two Colorado pikeminnow spawning sites in the lower Yampa River (Harvey and Mussetter 1996, Harvey et al. 1993). At present, there is no obvious reason to suspect that the quality or quantity of spawning habitat in these three rivers is limiting reproduction of the pikeminnow.

Less is known about spawning habitat in the UCR, in part because there have been only limited observations of adult pikeminnow occupying spawning ground, and no running ripe females have been collected (D. Osmundson, personal communication). Pikeminnow continue to spawn in the UCR despite the fact that some of the possible spawning sites have been severely altered by land and water development (Valdez et al. 1982, McAda and Kaeding 1991b). To the extent that habitat in the UCR may conform to the geomorphic profile that has been established for other spawning sites, it may be possible to infer the location of the habitat. Supplementary data on the distribution of larvae and ripe adults may help narrow the possibilities for spawning sites. It will be very difficult to determine if spawning habitat may limit reproduction or recruitment in the UCR until the location of the habitat is confirmed. In addition to possible spawning sites in the Grand Valley and in the lower Gunnison River, there is physical habitat in Debeque Canyon that appears to match the proposed geomorphologic profile (see Anderson 1996). However, the site in Debeque Canyon is not yet accessible to adults in the UCR because there are barriers to migration.

Adult population size. The minimum size required for maintaining a "viable" natural population of any of the endangered fishes should be an important consideration for

establishing recovery goals. Estimating minimum viable population (MVP) size is a difficult task, however, requiring information on the population and its environment. On the basis of theoretical considerations and empirical observations, the MVP is probably in the range of a few thousand to ten thousand individuals for most animal populations (Soule' 1987, Thomas 1990). The targets for populations of endangered fishes in the UCR should be set high until enough is known about the species in question to justify a smaller MVP.

One effort to address this issue in the UCRB was a "population viability analysis" of the Colorado pikeminnow (Gilpin 1993). Although that study did not specify a value for the MVP, it did conclude that the existing population was viable, albeit with reservations about the supporting data. Over and above concerns about the data set, there are important issues, not addressed by Gilpin, regarding uncertainty in environmental conditions. The frequency of anthropogenic alterations to the historic environment in the UCRB, and the fact that some of the change has been directional, undermine a key assumption about the predictability of the environment. Increasing uncertainty in the environment generally increases the size that a population must attain to be considered viable.

Recently, as part of an effort to establish Interim Management Objectives (IMO) for the endangered fishes, a computer model was developed for predicting trends in population size over time for each species on the basis of the information available on population dynamics (Crowl and Bouwes 1997). The model was used "to determine the number of adults that would be required to endure (with 95% certainty) that each subpopulation of each species would reach an effective population size of at least 500." The task was very ambitious and well-intentioned, but it became clear that the supporting data are not yet available. The modeling effort shows clearly what data are needed, and future data collection should be guided by those needs. The level of confidence in the population size targets obtained with those models is very low, however. There is no basis for choosing MVPs with more precision than the very broad range (2-10,000) offered by Thomas (1990).

Larvae and Postlarvae. Each population of Colorado pikeminnow appears to have a relatively well-defined and geographically restricted nursery habitat consisting of backwaters. It is not known how much habitat is necessary for supporting the larvae produced by any of the existing populations. It is known that the amount of backwater habitat is related to the hydrologic regime. If a relationship between flow and habitat could be developed for the UCR, it would be possible to determine the optimal flow regime, and to show how the amount of habitat might be affected by departures from the optimal flow regime.

The tendency of larval pikeminnow to seek out quiet shoreline habitat makes them vulnerable to stranding when water levels decline rapidly. Larvae are collected routinely from pools that have become isolated from the main channel when water level dropped (USFWS, unpublished data). Natural fluctuations in river level usually occur slowly

enough to afford larvae an opportunity to escape from the pool. In regulated rivers, however, changes in water level may occur more abruptly and strand larvae, thereby increasing their exposure to mortality due to predation, high temperature, or dessication.

A major problem confronted by larval pikeminnow in nursery areas of the UCR is the presence of nonnative fishes. All of the nursery habitat is occupied by aggressive nonnative fishes that are known to prey on pikeminnow larvae. Even for those larvae that escape predation, there is likely to be competition for food and space in the backwaters. The continued dominance of backwaters by nonnative fishes is probably incompatible with recovery of the pikeminnow.

The backwaters which provide nursery habitat for larval Colorado pikeminnow also support the adults and young of more than twenty nonnative fish species (Haines and Tyus 1990, McAda et al. 1994). ISMP data from the UCR indicate that nonnative fishes may comprise 95%, or more, of the standing stock in backwater habitats (McAda et al. 1984). All of the nonnative species are predacious and are known to eat larval and postlarval fishes of all kinds (Ruppert et al. 1993, Duns Moor 1993 and 1996). For those larvae that escape predation, there is likely to be competition for food and space. Introduced fishes such as channel catfish, green sunfish, and red shiner occupy the same habitat and consume the same food as young Colorado pikeminnow (Jacobi and Jacobi 1982, McAda and Tyus 1984, Muth and Snyder 1995). Growth and survival of larval pikeminnow may also be adversely affected by the aggressive behavior of introduced fishes such as green sunfish, red shiner, and fathead minnow (reviewed by Tyus and Saunders 1996a).

Concerns also have been raised that mortality of young fish is high during the winter months (Lentsch et al. 1996c). No source of mortality has been proposed for the overwinter losses, and there is ample evidence that the young fish are very tolerant of normal winter conditions. Furthermore, the evidence for overwintering mortality is not unequivocal. Studies conducted in the Green River showed no significant decline in abundance in three winters (Tyus and Haines 1991). For those instances where catches declined over the winter months, it is not clear to what extent the results could have been biased by downstream movements of the fish. It remains to be seen whether winter mortality is any higher than mortality experienced at other times of the year.

Juveniles. Juvenile Colorado pikeminnow remain at risk to predation until they reach a size of at least 130 mm (Crowl personal communication; Tyus and Saunders 1996a). Young pikeminnow stocked in the Verde River, AZ, were subject to predation by yellow bullhead (*Ameiurus natalis*) and large-mouth bass (*Micropterus salmoides*) (Hendrickson and Brooks 1987). Young pikeminnow in gravel pits near the Colorado River were prey for large-mouth bass, green sunfish, black crappie, and black bullhead (Osmundson 1987). Channel catfish have been observed preying on young pikeminnow in the Dolores River (Coon 1965).

Razorback sucker

Only one riverine population of the razorback sucker remains in the UCRB. The population or populations that used to exist in the UCR have essentially disappeared in the last fifteen years. Even in the Green River system, where ripe fish are collected routinely, very few juveniles are captured. The general consensus among researchers is that recruitment is very low or nonexistent throughout the Colorado River Basin (Holden 1977, McAda and Wydoski 1980, Minckley 1983, Tyus 1987, Marsh and Minckley 1989, Tyus and Karp 1990). The apparent lack of recruitment has been attributed to predation by nonnative fishes (reviewed by Tyus and Saunders 1996a), loss of spawning and rearing habitat (Westwater Engineering 1996), and lower water temperatures (Marsh 1985). Because nonnative predators are abundant and are widely distributed in the UCRB, they may be the primary factor limiting recruitment of razorbacks.

The potential role of water temperature in limiting the razorback sucker is difficult to evaluate, in part because almost all individuals remaining in nature are adults. One reach from which razorback suckers have been virtually eliminated is in the Green River from Flaming Gorge Reservoir to the Yampa River confluence, where main channel water temperatures have been altered as the result of reservoir operation. Changes in temperature, along with habitat reduction during the filling of the reservoir, may have precipitated extensive hybridization between razorback suckers and two other native sucker species (HMT, personal observations). The optimal temperature for hatching razorback suckers is about 20°C (Marsh 1985, USFWS unpublished data in Vernal, UT), but the remaining riverine population in the Green River spawns at much lower temperatures (Tyus and Karp 1990). Hatching success declines at lower temperatures and is very poor at 11°C. For larger life history stages that can move to preferred conditions, warmer temperatures might be available in shoreline areas. However, the amount of flooded bottomlands and shoreline habitats has been reduced by flow regulation and drainage, and diking has removed connections to the river. Access to warmer temperatures may no longer exist in some areas.

Humpback chub

Reasons for the decline of the humpback chub have been attributed to a combination of factors, including stream alteration (i.e., construction and operation of dams, diversions, and channelization), competition and predation with introduced species, pollution, and other factors (reviewed by USFWS 1990). Very little is known about the factors that may presently limit the abundance of the humpback chub in the UCR, although predation by channel catfish has been implicated elsewhere (Marsh and Douglas 1997, Tyus 1998). The populations in the UCR at Black Rocks and Westwater appear to persist in a habitat that is deep and restricted by the canyon geomorphology; the habitat is not very sensitive to changes in discharge. For example, flows of 2,000 cfs, which would be about half of the present baseflow, would not greatly alter physical conditions (Prewitt et al. 1982). Some benefit may be gained from comparing requirements of

humpback chub in the UCR with those of populations in the Yampa River and the Lower Colorado River, where the habitat is very different. One of the benefits of studying the species in the more shallow habitat of the Yampa and Little Colorado rivers is that it sets the stage for establishing a new population in a place such as Debeque Canyon, where there may have been a population until relatively recently (see Valdez et al. 1982). In such a setting, the importance of maintaining shallow habitat for the fish would merit study. There is recent evidence suggesting nonnative fish predation can have serious impact on populations of humpback chub (e.g. Douglas and Marsh 1996) and several predaceous species have been implicated (Table 1) It is not known with certainty whether nonnative fishes have been a major cause of decline, but there has been speculation that absence of the fish from some locations where they were historically present may be due to negative interactions with nonnative fishes (Tyus 1998).

Bonytail

Very few individuals remain in the wild and almost nothing is known about the requirements of the species. In absence of other information, it may be inferred that the same factors affecting other members of the big fish community also have negatively affected bonytail.

PART 4. RECOVERY PROGRAM AND RECOVERY ACTIONS

Successful recovery of endangered species has proven to be an elusive goal. Since the Endangered Species Act (ESA) was passed by Congress in 1973, about 1,000 species have been listed as threatened or endangered. Once a species was listed, the ESA requires preparation of recovery plans for guiding the recovery process. Ideally, careful execution of detailed recovery plans would lead to recovery and delisting of endangered species. Despite an enormous investment of effort on the part of professionals, recovery plans have been completed for only about half of the listed species, and recovery efforts have been successful for only 1% of the listed species (USFWS 1994b).

Much has been written about the perceived failure of recovery efforts. In general the criticisms have centered on narrowness of focus, inflexibility of the recovery plans, and lack of external participation and review (Clark et al. 1994, USFWS and NMFS 1994). Recovery plans tend to focus on recovery needs for a single species. More recent policy statements (USFWS and NMFS 1994) have stressed the need to consider a multispecies approach or an ecosystem approach in situations where more than one species may have been endangered as a result of a common set of factors. This broader approach is very appealing because it acknowledges the interactions of each species not only with the other species in the community, but also with the physical and chemical factors that comprise the abiotic setting.

Recovery efforts in the UCRB are undoubtedly complicated by the need to involve stakeholders, the many federal and state jurisdictions, and to comply with existing state and federal water agreements. To deal with the complexity of this situation, an interagency program (Recovery Implementation Program, RIP) was established for the UCRB (USFWS 1987, Rose and Hamill 1988). Primary responsibility for implementing step-down efforts defined in the individual recovery plans rests with the RIP, whose mandate extends for 15 years (1989 - 2003). The program has management authority for recovery actions in the UCRB, including the Green River and its tributaries from Flaming Gorge dam to the confluence with the Colorado River, and the Colorado River and its tributaries above the confluence with the San Juan River. The program oversees recovery activities in the UCRB, provides funds for evaluating habitat requirements of the fishes, and seeks ways to obtain water needed by the fish.

Final recovery plans have been written for all four of the endangered big river fishes (USFWS 1990a, 1990b, 1991, 1998). The individual plans make it clear that factors thought to be responsible for the endangerment of each species are generally common to all four species. It is now USFWS policy to develop a multispecies, or ecosystem, recovery plan when a suite of factors causes the decline of several species in one community. However, neither the USFWS nor the RIP has approved such a plan. Recovery plans suggest that the UCRB is important for recovery of the Colorado River fishes, in part because the UCRB contains the largest amount of free-flowing river reaches in the Colorado River basin still occupied by fishes of the big river community. However, neither the plans nor the critical habitat designation provides geographic prioritization of the areas most important for single or multispecies recovery.

Management Actions

The effectiveness of most management actions can be judged on two levels: proximate and ultimate. In the proximate sense, each action targets a factor that is thought to limit recovery of one or more of the endangered fishes. For example, increased flows might be proposed for improving the quality of habitat for adult Colorado pikeminnow. The action could be judged successful in a proximate sense if higher flows actually provided better habitat. In an ultimate sense, an action must increase the size of the population before it constitutes a successful step toward recovery. Assessment of the proximate level of success should be relatively simple. Demonstrating success in an ultimate sense is likely to be much more difficult for at least three reasons: 1) obtaining suitable data on fish abundance is problematic, 2) linking a change in population size to a particular management action is difficult at best, and 3) the action may provide relief that is necessary, but not sufficient alone, for recovery. The third reason bears elaboration because it highlights the need for an integrated approach to recovery.

The following hypothetical example helps illustrate the difference between necessary and sufficient conditions for recovery. Let us assume that the amount of spawning habitat is very small and is identified as a limiting factor for a listed species. A plan is

designed and carried out to increase the amount of spawning habitat. More adults are observed spawning and, presumably, more eggs are deposited. In a proximate sense, this would be judged successful because it relieved an apparent limitation to reproduction. Over the next few years, recruitment is monitored and found to be unchanged despite consistently higher levels of reproduction. Upon closer inspection, it is found that eggs and larvae are being consumed in vast quantities by nonnative predators. In an ultimate sense, the action of improving spawning habitat was a necessary step because it relieved a limitation, but was not sufficient by itself to promote recovery. An integrated approach to recovery would link the increase in spawning habitat with other actions designed to reduce the abundance of nonnatives. Those actions in concert should be sufficient to meet the ultimate goal of increasing population size.

During the last 20 years, considerable effort has been directed at recovering the listed fishes in the UCRB. Years of diligent research have produced substantial insights regarding the life history and needs of the endangered fishes. The RIP has avoided a piecemeal approach to management actions by creating an organizational framework that contains five elements: 1) provision of instream flows, 2) habitat development and maintenance, 3) stocking of native fish species, 4) nonnative species and sportfishing management, and 5) research, monitoring, and data management (Rose and Hamill 1988). The same framework provides a useful organizational approach for a review of previous management actions.

Provision of Instream Flows

The life histories of the native riverine fishes are closely tied to the annual pattern of river flow and the associated changes in physical habitat. Flow regulation has altered significantly the historic hydrograph in all rivers in the UCRB except the Yampa River. Changes in flow and sediment regime have resulted in alterations to physical habitat, such as narrower channels (Andrews 1986) and reduced flooding of bottomland (e.g., Stanford 1994). Consequently, there is now a need for managing flows to facilitate recovery of the endangered fishes. There can be little argument that the fish need water in the river, and that they have evolved in a setting where each step of the life cycle is connected with a particular phase of the annual hydrograph. The chief difficulty in evaluating the effectiveness of flow management strategies is that providing flow at the right time of year is a necessary condition for recovery (in the sense that suitable physical habitat is needed), but may not be a sufficient condition (in the sense that populations will not increase) without some additional management actions such as control of nonnative fishes. It is no small task to provide flows that are consonant with the life history needs of the fishes while at the same time meeting societal obligations for delivery of water.

The primary example in the UCRB for managing flows that will be helpful for recovery of the fish is Flaming Gorge Reservoir on the Green River. Operation of the reservoir altered natural conditions of importance to the native fishes by reducing peak flows in

the spring and reducing turbidity, among other things. At the same time, high releases from the reservoir during the time of year when larval Colorado pikeminnow should occupy the nursery areas has been implicated in the virtual loss of 1983-84 year class. To some extent, flow from the unregulated Yampa River ameliorates those problems downstream. As a result of biological consultation under Section 7 of the ESA, a major study was initiated of the operation of Flaming Gorge Reservoir and its effects on the listed fishes. This continuing program is a major force in providing habitat for young Colorado pikeminnow in an altered river.

The operation of large reservoirs upstream of endangered fish habitat has potential for aiding recovery by providing instream flows for the endangered fish in the present altered system. The Bureau of Reclamation, the USFWS, and others have been cooperating in several studies designed to evaluate the impacts upon the endangered fishes associated with operation of various reservoirs. These studies, performed under interagency agreements pursuant to Section 7 of the ESA, have resulted in recommendations for reservoir operation to offset impacts on the fishes. These include seasonal flow and non-flow related recommendations that have been developed from analysis and interpretation of empirical data.

A proposal for managing flows in the UCR also has been advanced for improving habitat considered important for Colorado pikeminnow and razorback sucker (Osmundson et al. 1995). Evaluations of summer flow needs in the 15-Mile Reach relied on a system that weighted each of the eight habitat types based on availability and use by the fish. The frequency of habitat use was determined from radiotelemetry data obtained at four study sites from 1986-88. Habitat availability was determined from aerial mapping at different river flows (557-11,200 cfs). The work characterized "mesohabitats" used by adult Colorado pikeminnow and recommended flows that produced water levels that maximized "preferred" habitat types, with the assumption that increasing the amount of preferred habitat in the 15-Mile Reach would increase the capacity for supporting pikeminnow in the river (Osmundson et al 1995). A flow of 1,630 cfs was recommended for summer and winter because it would produce the greatest amount of "preferred" habitat. Final flow recommendations for adult Colorado pikeminnow in the 15-Mile Reach were tempered by the reality that the proposed optimum flows may not be available in all years due to existing water commitments. In summer, the revised flow recommendations call for 1240 cfs in years of below average flow, but only 810 cfs in drought years.

Recommendations have also been developed for peak flows in the spring, because the magnitude of peak flows has been reduced. Prior to most flow regulation, flows of at least 23,000 cfs occurred about 70% of the time; now flows of that magnitude occur in only 20% of the years. Spring flows are important for Colorado pikeminnow and razorback suckers in the 15-Mile Reach, because these flows maintain habitat complexity in the channel, clean cobble in spawning habitat, and scour and flush fine sediment from low-velocity habitats. Over a four year period, depth measurements indicated that a spring flow of 14,800 to 12,900 cfs, depending on the type of water

year, would remove the fine sediment from backwaters in the 15-Mile Reach and transport it downstream.

Flows needed for fish recovery in the UCR are still being studied and recommendations will no doubt be refined as other alternatives are evaluated more fully. Only a few areas in the UCR have been evaluated for recovery of the fishes, and there is concern that provision of flows only for selected life history stages of one or two species will not help the fish community. In addition, there is a real lack of water at certain times of the year in the UCR (especially in the 15-Mile Reach). One option for increasing the amount of water in the Grand Valley would be to reduce the amount of water diverted for agriculture; one proposal claims that about 28,500 AF may be made available in this way (Norman 1996b). In addition, the Bureau of Reclamation is studying how to coordinate reservoir releases to provide better flow conditions (Wilson 1996).

The focus of virtually all flow management actions is the creation or maintenance of physical habitat. By managing flow over an annual cycle, it is possible to create and maintain the physical habitat needed by each life history stage, when the fish need that habitat. However, the endeavor is not simply a matter of ensuring proper depth of water. The considerations are complex and require knowledge of site-specific features including, but not limited to, bed topography, sediment supply and distribution, hydrology, and hydraulics. The task probably requires extensive geomorphologic modeling to demonstrate that the proposed flows are likely to create and maintain the desired habitat in the proper location. Furthermore, improved knowledge of channel geomorphology may make it easier to evaluate prospects for non-flow alternatives, which have yet to receive much attention for improving habitat.

Habitat Development and Maintenance

Development and maintenance of new habitat and providing access to new areas are priority recovery goals (USFWS 1987). Because creation and maintenance of habitat in the channel depends on having the proper flow regime, it is difficult to discuss habitat without discussing flow. Consequently, much of the relationship between flow and habitat was treated in the preceding section. The distinction made here, as a matter of convenience, involves segregating those habitat-related activities that may require no manipulation of flows from those that do. For the most part, this means providing access to habitat that is not presently accessible to the fish. For example, passage through some of the major barriers to migration, or restoring access to low-lying areas, would be in this category.

Access to seasonally-flooded habitat has been lost due to reservoir operation or diking. Restoring access has received much attention lately, including formulation of a RIP initiative for evaluating restoration of bottomland areas (Nelson et al. 1995), but the concept remains controversial (Nelson et al. 1995, Wydoski and Wick 1996). A demonstration project in the Green River basin has restored access to Old Charley Wash, providing off-channel habitat for rearing larval razorback suckers (Modde 1996).

The habitat has proven to be very productive, but, unfortunately, the resident fish community is dominated overwhelmingly by nonnatives; only 28 juvenile razorback suckers were collected from this site (Modde 1996). Unchecked competition and predation from at least 17 nonnative fish species (Nelson et al. 1995) may render overbank habitat useless for the intended beneficiaries. Creating new overbank habitat, or providing access to old overbank habitat, has been proposed for some locations (Nelson et al. 1995, Irving and Burdick 1995), and these may have potential for enhancing recovery if the abundance of nonnatives can be controlled either directly through manipulation of abundance, or indirectly by controlling the duration of off-channel flooding (Wydoski and Wick 1996).

Gravel pit ponds in the Grand Valley also have been considered for enhancing habitat of the native fishes. The ponds could be connected with the river and thus water level would fluctuate with river level. If the ponds drain completely when river level falls, problems with nonnatives appear to be diminished (F. Pfeifer, personal communication).

Construction of dams and diversions in the UCRB has created barriers that block or impede fish migrations. Blockage of migrations has the potential to reduce the population of a migratory fish by blocking access of some or all individuals to spawning areas, or limiting the availability of adult habitat, for example. The Colorado pikeminnow, which migrates over long distances, has experienced habitat fragmentation, as indicated by reports of congregations below obstructions during the spawning season (McDonald and Dotson 1960, Seethaler 1978, Trammel et al. 1993). Removal of the barrier is rarely an option, but construction of passageways through existing structures may restore migration routes for the fish. The only fish passage facility in the UCRB was constructed at the Redlands diversion dam in the lower Gunnison River. A preliminary evaluation of the structure is encouraging. It shows that approximately 25,000 fish, of which 94% were native species, have used the structure, including 19 Colorado pikeminnow (Pfeifer 1996).

The technical issue of designing stream passageways for Colorado pikeminnow is in a very early stage of research and development. It would be logical to construct and test a passageway in an area that now supports a large migration, but such activity is unlikely because of provisions in the ESA. In the case of the Redlands facility, testing is being performed at a location where there is no established migration route and there are few endangered fish that use it. Thorough testing should demonstrate the capacity of this structure to permit movement of adults in both directions, and of other life history stages in the downstream direction. A better understanding of design characteristics in relation to fish behavior is particularly important in view of existing plans for fish passage structures through the Price-Stubb and Grand Valley diversion dams (Flo Engineering 1997, Norman 1996a,b, Norman and Wernke 1996).

Stocking of Endangered Fishes

Adding individuals to a population is an obvious and direct way to increase its size. For a species like the bonytail that is virtually nonexistent in the wild, or the razorback sucker that has been essentially extirpated from the UCR, reintroduction is necessary for recovery. Consequently, it is important to review information available from previous stocking efforts and seek ways in which reintroductions can be made more successful.

Colorado pikeminnow. Colorado pikeminnow have been stocked into the UCR on several occasions. About 1,500 six-year old hatchery fish marked with dangler tags were released near Moab, UT in 1980 (Valdez et al. 1982), and an additional 76,000 young of the year (50-125mm) fish, tagged with coded wires, were released at various locations upstream from 1982-1984 (Archer et al. 1985). There has also been an undetermined number of fish that escaped from ponds where nearly 23,000 fish were held (USFWS unpublished records, Grand Junction, CO). These releases should have resulted in a significant increase in the number of pikeminnow in the system (the six-year olds would have more than doubled the extant adult population, and the young fish might have increased the extant population by 100-fold), but there has been no measurable increase in the numbers of Colorado pikeminnow in the UCR. That is not to say there has been no survival, because some stocked fish have survived in the UCR. From 1990-1994, 411 adult Colorado pikeminnow captured during spring sampling were checked for coded wire tags, and 5 (1.2%) fish carried the tags (D. Osmundson personal communication). The survival rate was probably higher than 1.2%, because only about half of the captured fish were large enough to have been in the population at the time the tagged fish were released. The apparently poor success of stocking has not been explained, but one clue is available from work done on White River, where 96,597 fingerling Colorado pikeminnow (age 1) were stocked in Kenney Reservoir in 1988. Most of these fish quickly left the site of stocking by passing over the dam, and continuing to travel downstream (Trammell et al. 1993). None of the stocked Colorado pikeminnow were captured after 3 years, and the stocking was called a failure. No Colorado pikeminnow have been stocked since 1990, and no specific plans have been developed for future stocking (Pitts and Cook 1997).

Problems in re-establishing populations of Colorado pikeminnow also have been experienced elsewhere. In 1985, the Arizona Game and Fish Department and Dexter National Fish Hatchery re-introduced 600,000 Colorado pikeminnow into the Salt and Verde rivers of the lower Colorado River basin, from which the Colorado pikeminnow had been extirpated (Hendrickson and Brooks 1987). About 400 of the fish were recaptured within a few months after stocking, but few or none are thought to have survived in the long term, except for some fish placed in isolated habitat from which emigration was not possible (Hendrickson 1992). As in the UCR, none of these efforts produced viable populations of the target species (Minckley et al. 1991). However, at least the reason for failure is clear from the lower basin efforts: predation from introduced catfishes and other species have taken a heavy toll (reviewed by Tyus and Saunders 1996).

Humpback chub. The only attempt at stocking humpback chub in the UCR occurred in 1980 when about 7,600 one-year old fish were nose-tagged with coded wire tags and released at Rapid 11 in Cataract Canyon (Valdez et al. 1982). The addition of this number of fish should have increased the size of the humpback chub population by as much as ten-fold, but subsequent surveys indicated little change in population size (Archer et al. 1985).

Razorback sucker. Several thousand razorback suckers have been stocked in the Green River since 1987 (Pitts and Cook 1997), but survival probably has been very low because few fish have been recaptured. A small number of razorback suckers have been released into the UCR and its tributaries, including 20 radiotagged in the UCR and 21 in Gunnison River, but mortality is thought to have been nearly 90% during the period of study (Burdick and Bonar 1997). An additional 316 razorbacks were stocked in the Gunnison River in 1995. Reintroductions of razorback suckers in the lower basin have been no more successful than efforts in the UCRB. More than twelve million fish were stocked from 1981 to 1990, but few if any have survived. At least 118 fish survived in the smaller tributaries for a short time, but none of the millions of fish stocked in other areas, including the mainstem rivers, has been recaptured (Minckley et al. 1991). Nonnative predators are thought to have been the main source of mortality.

A stocking plan has been drafted for introducing about 140,000 razorback suckers into the UCR and Gunnison River from 1996-2000. The plan called for 13,100 fish in 1996, but shortfalls in hatchery production restricted stocking in the Gunnison River to 282 fish in 1996 (Pitts and Cook 1997). Efforts were more successful in 1997 when 3,753 fish were stocked (F. Pfeifer, personal communication).

Bonytail. In the Green River, 86 adult fish were stocked, but the action failed due to a high mortality rate. In the UCR, about 2000 bonytail were stocked near Dewey bridge (TL 90-172 mm). Plans call for stocking 5,000 fish in the Green River and 5,000 fish in UCR in 1997 and 1998, plus another 2,000 to 5,000 fish at each of two other locations not yet named (Pitts and Cook 1997).

Summary. To date there is no indication that stocking has increased significantly the size of any extant population of the endangered fishes, or resulted in the establishment of any new populations. This should constitute adequate warning to managers that there are serious shortcomings in the approaches now used. It would not be surprising to learn that stocked individuals of small size were eliminated by predators; without protection from nonnatives, it is unlikely that larval, or even small juvenile, fish can be stocked successfully. Even when the fish that have been stocked were large enough that predation should not have been a major threat, stocking has not been successful. More creative approaches to stocking are greatly in need, because stocking will remain an integral part of recovery efforts at least for the razorback sucker and the bonytail. Part of the problem involves a dilemma: the fish must be released at a very early age to allow on-site conditioning (such as imprinting) but they must be released at a large size to escape predation by nonnative fishes.

Nonnative Species and Sportfishing

Nonnative fishes arguably pose the greatest threat to recovery of the endangered fishes today. Much has been written about the problem (e.g., Hawkins and Nesler 1991, Lentsch et al 1996a), including a strategic plan (Tyus and Saunders 1996a), but little has been done to control the nonnative fishes. Recently however, new fish stocking agreements have been signed by the Secretary of the Interior (USDI 1996) and the States of Colorado, Utah, and Wyoming. These agreements would limit introductions of problematic fish species into habitat designated critical for the endangered fishes, place restrictions on the types of fishes stocked in ponds in the 50 year floodplain, and limit future introductions.

One novel idea advanced for the control of small nonnatives in the UCRB would involve the manipulation of river flows (Valdez 1990; McAda and Kaeding 1991). Reduced abundance and suppressed reproduction of small cyprinids have been correlated with high discharge (McAda and Kaeding 1991, Osmundson and Kaeding 1991, Muth and Nesler 1993). Proposals have been advanced (Osmundson and Kaeding 1991, Lentsch et al. 1996a) for managing flows to take advantage of this "inhibitory effect." In desert streams, it has been observed that floods of 1-2 orders of magnitude higher than annual conditions are necessary for removing non-native fishes (Minckley and Meffe 1987). This observation seems substantiated by recent flow studies in Grand Canyon, where a spring flow of 45,000 cfs had no significant affect on nonnative fishes (R.A. Valdez, personal communication 1999). Unfortunately, very high flows can be detrimental not just to small cyprinids, but to all small fish including larvae and postlarvae of most native fishes in the Green River (Tyus and Haines 1991). Also, lack of selectivity in the technique makes it undesirable. Moreover, the inhibitory effect on small cyprinids appears to be very short-lived; populations of nonnative minnows tend show explosive growth in low flow years (Osmundson and Kaeding 1991).

Research, Monitoring, and Data Management

The RIP has invested heavily in basic and applied research that has advanced the state of knowledge about these fishes and their environment. The efforts have been productive and have resulted in many reports. Some of the research has been published in refereed journals, and more such publication should be encouraged because it requires external review and disseminates information to a wider audience. In general, however, scientists in the program do not receive adequate support or incentives for preparing their work for submission to refereed journals. There is also a wealth of unpublished information and "gray" literature that can be difficult to obtain. Problems in obtaining unpublished reports have also been noted in other recovery programs (NRC 1996). The focus of most studies tends to be narrow with respect to geographic scope and the species covered, and this is understandable from a logistical perspective. Nevertheless, the many small-scale studies can provide the fuel for major synthesis efforts that could benefit the recovery program by stimulating more progress.

Unfortunately, there has been little effort (with the notable exception of Miller et al. 1982 and USFWS 1987) directed at synthesis.

Monitoring the abundance of the listed fishes is also a key element of data collection for the recovery program. Ostensibly, monitoring should provide the evidence for trends in abundance that can demonstrate the effectiveness of recovery efforts. In the absence of suitable monitoring data, it can be difficult or impossible to reach useful conclusions about progress toward recovery. The USFWS and the Bureau of Reclamation initiated monitoring in 1979 with a basin-wide sampling effort that had a firm statistical basis for assessing abundance. Baseline data for all species were collected from all habitats in the mainstream Green and Colorado rivers from 1979 to 1981 (Miller et al. 1982), and portions of the program were continued through 1985 (Archer et al. 1985, Tyus et al. 1987).

Primarily for reasons of cost, the scope of the monitoring program was reduced with creation of the Interagency Standardized Monitoring Program (ISMP), which began sampling in 1986. The ISMP made good use of information from the baseline studies regarding the distribution of endangered fishes in the UCRB and the gear used to collect those fish, and devised a program more narrowly focused on selected population trends. Large reference areas were sampled annually for Y-O-Y and adult Colorado pikeminnow, and the Blackrocks-Westwater area of the Colorado River was sampled every three years for humpback chub (McAda et al. 1994). Results of the ISMP work appear annually, and the first few years (1986-92) were summarized in one report. Although the ISMP data can be important for detecting major trends in populations of some of the listed fishes, it has been criticized for various reasons (McAda et al. 1994, Stanford 1994). The most serious criticism is the inability of the ISMP to produce population estimates for the target species; it only produces indices of change for two of the four species. Furthermore, the ISMP is not a system-wide program.

After nearly 20 years of recovery efforts, reliable population estimates have been made for few populations of the endangered fishes. Moreover, there is little certainty, in most cases, whether populations have grown or declined in that time. Indeed, there remains confusion about the number of extant populations. The RIP should address the issue of the desirability of continuing the ISMP in its present form; there is little economy in making such a large investment in data that cannot document population size or trends. A useful model for future monitoring would be the population estimates developed by Osmundson and Burnham (1996) for Colorado pikeminnow in the UCR.

The recovery program requires an extensive management system to organize, store, and make available collected data. Development of the RIP in 1987 included provisions for regular meetings of a technical review group, and an annual review of past work in which needed studies and information are prioritized and funds are allocated. The USFWS has been given the lead under the RIP, for cataloging and maintaining the extensive amounts of data collected by Federal, State and private

agencies, and individuals. In addition, an annual research meeting has been conducted by cooperators each year since the early 1980s to aid in increasing awareness, sharing information, and reducing isolationism.

PART 5. CONCLUSIONS

Recovery of endangered species presents a formidable task, in part because it is an emerging field of science. Based on the number of species recovered relative to the number listed since passage of the ESA, the chance of success is about 1 in 100. After 20 years of effort in the UCRB, none of the four species has been recovered. At best, the Colorado pikeminnow and the humpback chub are holding even, or declining slightly. The razorback sucker has declined and the bonytail is gone. At the same time, much has been learned about the life history requirements of these species, and the factors that may limit them at each life history stage. The conclusions that follow represent the distillation of a vast amount of information. Some conclusions have been stated elsewhere, and some recommendations may be in place now, but all are presented here for the sake of maintaining a comprehensive view.

The pursuit of effective recovery of the big river fishes is frustrated by the large size of the Colorado River basin and its ecological, scientific, and political complexity. Not only are life histories of the endangered fishes complex, but low numbers of the fish and the difficulties of sampling in a large, turbid, and seasonally (and geographically) violent river, has made it difficult to obtain information needed to build a program. Just as important, funding and programs have lacked consistency and there has been a high turnover in researchers, managers, and administrators. From a scientific standpoint, it has been observed by several workers that many hypotheses and ideas developed years ago have been abandoned only to be rediscovered by a new generation of scientists who have unfortunately in some cases "reinvented the wheel". All of the above demonstrates lack of integrated, basin-wide approaches.

Much has been learned about the listed fishes during the last 15 years, but most of this consists of fragmentary bits of knowledge and isolated implementation of management actions throughout the basin. One of the most important things that could be improved in the recovery program is the adoption of a broader view of the task. There are now four separate recovery plans that treat the four endangered species as if they were entirely independent. Yet, all four species are part of the same community of native fishes, and all have been endangered by the same suite of factors related to alteration of the natural environment. At present, the recovery effort lacks a multi-species, or ecosystem, view capable of encompassing all four species as well as the other native species in the community. Such an approach is badly needed for the UCRB where the potential for community recovery is relatively high (at least compared with that in the lower basin).

Studies and recommendations in support of the recovery effort have not taken a very broad view in time and space. The temporal context is set by the annual hydrograph

which determines the major events related to the life cycle. The life histories of these riverine fishes are closely tied to the annual hydrograph. The timing for each step in the reproductive cycle (i.e., gonadal development, migration, and spawning), and each major transition in the life cycle occurs when flow conditions are correct, and thus the calendar date may vary from year to year. The hydrograph also determines the availability of habitat used by each life history stage. Successful recovery will depend on proper integration of life cycle events with the timing, magnitude, and duration of an altered hydrograph.

The pattern of habitat use by each life history stage determines the spatial boundaries necessary for recovery of each fish species. In the case of a migratory species like the Colorado pikeminnow, which may require 150 to 200 river miles to encompass all habitats used during its life cycle, the required geographic view is very broad. Focusing on smaller geographic units (e.g., 15-Mile Reach) may be necessary for logistical reasons and may yield significant information about a particular life history stage, but is not likely to be adequate alone for a full understanding of the needs of a particular species.

Compared with the considerable effort that has been expended on determining the physical habitat requirements of the fishes, the biological dimension of habitat has been neglected in the recovery effort. At least three major components of the biological dimension have been identified in this report: nonnative fishes, food supply, and imprinting. It is our opinion that nonnative fishes pose the single greatest threat to the endangered fishes, especially for the early life history stages. There is little hope for successful recovery unless meaningful efforts are made to reduce the abundance of nonnative fishes.

The composition and abundance of the food supply is obviously a determinant of adult habitat quality. However, most conclusions about the habitat requirements of adults have been reached on the basis of abiotic characteristics, with little attention being given to food requirements. To some extent this is because direct assessment of diet is essentially precluded by the endangered status of the fish. Nevertheless, there is mounting evidence that the distribution, abundance, and habitat use of adult Colorado pikeminnow is strongly influenced by the distribution and abundance of preferred prey. This may help explain why habitat use by adult Colorado pikeminnow appears to be so variable in terms of the abiotic attributes. The subject clearly warrants more attention.

Insufficient attention has been paid to the importance of learned behavior, such as imprinting, to the life histories of the endangered fishes. Attention to imprinting could benefit the recovery effort by maximizing reproduction and thus recruitment to the adult population. Failure of earlier stocking efforts may eventually be linked to a lack of environmental conditioning for hatchery fish. Spawning migrations of Colorado pikeminnow provide *prima facie* evidence of homing to natal areas, and laboratory studies of razorback suckers suggest that the presence of conspecific pheromones from ripe females also may be a factor in selecting spawning areas. Because hatchery

fish have had no learning experience in selecting spawning areas, they may spawn in areas that will not result in recruitment for various reasons including poor spawning habitat, exposure to predators, exposure to fluctuating water levels, or lack of suitable nursery habitat downstream. There is a risk that stocked fish will consume resources and compete with wild fish, but not contribute new individuals to the population.

Successful recovery will depend on a more comprehensive and integrated approach to alleviating the limitations imposed by environmental factors. More attention should be paid to the biotic factors limiting recovery, and to the differences in the relative importance of biotic and abiotic factors limiting the individual life history stages. A more comprehensive view of limiting factors in space and time leads to the position that addressing limitations individually is not enough for recovery. Management actions must support an integrated approach allowing for simultaneous control of factors that are both necessary and sufficient for recovery.

The distinction between necessary and sufficient factors is crucial for developing management actions for the endangered fishes, and it can be explained best through the following example. Adequate physical habitat is needed by each life history stage, and this entails providing flows that create and maintain habitat in the proper geographical location at the proper time of year. Creation and maintenance of suitable physical habitat is therefore necessary for recovery, but may not be sufficient alone. For example, even if physical habitat is optimal for all life history stages of the Colorado pikeminnow, recovery could still be threatened by recruitment failure if nonnative fishes are not controlled in nursery habitat. Conversely, the abundance of nonnative fishes might be controlled, but recovery prevented if nursery backwaters are not maintained by the proper flow regime. Provision of adequate physical habitat and control of nonnatives together should be sufficient actions that will lead to an increase in population size.

Management objectives have not been well defined in terms of expectations for increasing the size of the target population. Furthermore, some actions (e.g., improvements to physical habitat for adults) may be intended primarily for maintaining, rather than increasing, the existing population. Although maintenance actions are important and useful, they will not be enough to effect recovery because population size is not increased.

When a management decision requires an increase target population size, it is not possible to determine if the goal is realistic, or adequate, in terms of the number of populations and individuals that can be supported in the UCRB. Most of the recovery plans specify the number of populations required for downlisting and delisting, but it is not clear that such an outcome is achievable given the physical constraints of habitat in the UCRB. For example, there are four extant stocks of Colorado pikeminnow in the UCRB, and there may be potential for establishing one or two more. The number of possibilities is constrained by the configuration of habitat that must be available to support each population; as much as two hundred river miles may be needed for the

individuals in a population to complete the life cycle. Recovery plans do not specify the target number of individuals for each population, and there is virtually no information on carrying capacity with which to decide if the target is realistic. For adult Colorado pikeminnow, which are piscivorous, the sustainable density will be lower than that of suckers or chubs, which are lower on the food chain. Current IMO efforts propose a protocol for setting target population sizes, but flaws in the population model and inadequacies in existing population data base preclude the estimation of meaningful numbers for those targets.

On the other hand, the numbers that are achievable must be compared with the population size needed to maintain adequate genetic diversity. Not enough is known yet about the minimum population size that must be maintained in these wild stocks, but the hypothetical situation can be proposed where the minimum viable population size was determined to be 5,000. If the habitat could support only 2,000 individuals, there would be a gross mismatch between what is needed for recovery and what is possible in the natural setting.

Reintroduction of endangered fishes is frequently seen as a panacea for increasing the abundance of fish in nature. However, previous reintroductions in the UCRB appear to have done little or nothing to increase abundance, even when older fish were stocked. The previous lack of success implies an inadequate understanding of the problems faced by newly-introduced fishes. Where there are extant populations, stocking is not an attractive option. In addition, the presence of stocked individuals in a natural population may confound studies of behavior in the wild. For behavioral studies, translocation may offer a better option. Stocking protocols cannot be as passive as simply releasing the fish and hoping for the best. In those cases where reintroduction provides the only option for establishing a population as specified by the recovery plan, attention to imprinting and conditioning to local environmental characteristics may be essential.

PART 6. RECOMMENDATIONS FOR FUTURE RECOVERY EFFORTS

Multispecies Recovery

A central theme in this report is the need for broader perspectives in all facets of the recovery effort. There has been a tendency in the past to focus too narrowly on a particular river reach, time of year, species, life history stage, or limiting factor without making connections that could further enhance recovery for one or more of the listed fishes. Thus, our first recommendation addresses the best mechanism for implementing a broader perspective: preparation and formal adoption of a multispecies or ecosystem recovery plan. Because such a plan could deviate from existing plans and programs in the prioritization of recovery areas, it could lead to a rethinking of research ideas and approaches.

However, our previous efforts to draft a multispecies recovery plan that would be acceptable to various interests has made it clear that such a plan will be difficult to get approved. The principle reason appears to be that multispecies priority areas would be different than those for single species recovery, so that recovery funds may be re-prioritized in the basin. As a result, there is a fear that single-species recovery efforts may be de-emphasized.

Present Recovery Program

Recommendations concerning present recovery programs have been drawn from conclusions reached during a review and synthesis of existing information on the endangered big river fishes of the UCRB. In particular, emphasis has been placed on information derived from the review of limiting factors. In all cases, we have benefitted enormously from the years invested in research and management by various agencies and individuals.

Recommendations will be organized according to the five major initiatives in the RIP. The expectation is that well-defined questions and tasks will focus effort and result in a more efficient recovery process. Some of the recommendations take the form of questions that have been posed to help define options available to decision-makers. There also will be specific tasks defined to assist the recovery process.

As with any endeavor where resources are scarce, there is a need for assigning priorities to individual tasks. Many factors may influence decisions affecting the allocation of resources, but the central concern should be the capacity of a proposed action to increase the number of breeding fish in the population. Thus, for example, efforts to reduce the abundance of nonnatives should receive a high priority because of the potential to enhance recruitment of the endangered fishes. Plans to increase access to high-quality adult habitat might be assigned the next lower priority because the immediate effect on recruitment may not be as high, but the long-term potential for increasing the population is high. Finally, tasks related to determining the target population size for downlisting or delisting are less critical in the short term, because the immediate need for the information is low.

Instream Flows

What is the relationship between flows and the amount of nursery habitat for endangered fishes in the UCR? A study of flow levels and backwater availability established some links for Colorado pikeminnow in the Green River, and proved crucial in making recommendations for instream flows. A study of backwaters in the UCR has been undertaken, but it is not yet known if the study will provide the appropriate information. Given the importance of nursery habitat for successful recruitment, determining this relationship is pivotal for the recovery effort. Although a simplistic relationship between flows, sediment input, and backwater habitat is not anticipated, it

will be very important to understand what factors are important in producing backwater habitat in the UCR. Such knowledge might make it possible to define the hydrologic regime that optimizes habitat during the months when larvae and postlarvae occupy the nursery areas. This philosophy could be extended for other species as well, however, little is known about flow requirements for nursery habitat of the other endangered species.

Habitat Development and Restoration

Determine if physical habitat modifications can provide an acceptable alternative to regulation of instream flows for manipulating the availability of habitat for adult Colorado pikeminnow. In the 15-Mile Reach, there is much concern about the adequacy of existing physical habitat for adult Colorado pikeminnow. Flow recommendations for the 15-Mile Reach were based in part on a desire to manipulate the relative abundance of different habitat types to favor those habitats used by adult Colorado pikeminnow. By increasing flows during the low water period, the depth of water would be increased and the proportion of desired habitat also increased. However, existing water supplies are inadequate to provide the optimum habitat configuration in all years and compromises have been necessary. An efficient alternative to increased flow might involve engineered solutions that provide deeper or larger habitat (i.e., simple changes to the physical dimensions of the habitat) in specific locations. It will be important to define how physical habitat modifications offer viable alternatives to manipulation of instream flows, and for which species. If habitat can be improved through implementation of engineering alternatives, it may obviate the need for some flow manipulation. Furthermore, by localizing improvements, it should be practicable to monitor responses of fish to the availability of "improved" habitat. A study should be commissioned for determining the best locations for modifying a substantial area of habitat (perhaps as much as 1-5 miles). Biological monitoring of the improved habitat at the selected sites would be used to evaluate the potential for further habitat improvements. Consideration should also be given to effects on other fish species (e.g., Would the change enhance conditions for channel catfish or degrade conditions for roundtail chub?). A similar approach might be applied to habitat used by other life history stages in other parts of the river, and other fishes should be evaluated for potential application as well.

Determine the relative importance of physical habitat quality and prey abundance as determinants of the abundance of adult Colorado pikeminnow. Management decisions regarding habitat needs (e.g., flow) are being made now with the tacit assumption that the distribution of adult Colorado pikeminnow is governed chiefly by suitability of the physical habitat. An alternative view might be that prey abundance becomes the primary determinant after some minimum conditions are met for physical habitat. Existing information on the seasonal spatial distribution of adult pikeminnow and their native prey could help determine the relative importance of the two kinds of factors. Attention should be focused on those rivers where access to upper reaches is

(or was) unimpeded (e.g. Yampa River and White River, prior to closure of Taylor Draw dam). If the abundance of native prey seems to be the primary determinant of Colorado pikeminnow abundance a logical follow-up task might be: Determine the habitat requirements of the native prey? If pikeminnow distribution is related to the abundance of native prey, the link between physical habitat and pikeminnow abundance may be difficult to define. Within some limits, the primary considerations for physical habitat may be those factors that promote the abundance of the native prey. In that case, the next step could involve determining how to increase physical habitat for prey, with the assumption that it would result in an increased abundance of adult Colorado pikeminnow. The scope and urgency of this task will be influenced by the outcome of the translocation studies. A report evaluating the relationship between abundance of Colorado pikeminnow adults, physical habitat use and prey abundance prepared from existing data would be a valuable interim objective.

If preferred prey constitutes a significant dimension of habitat for adult pikeminnow, access to those prey should result in better conditions for the growth of adults and/or greater biomass per unit area. **Will adult Colorado pikeminnow with access to upper reaches (containing preferred prey) increase in numbers or grow faster than pikeminnow for whom such access is blocked?** A suitable comparison would involve fish with access to the upper Yampa River and fish in the 15-Mile Reach. Condition indices are probably a good way to observe the net effect of better conditions for growth. However, there are many factors that must be considered when making comparisons, (e.g., time of year, crowding, regression approach versus straight comparison of size classes, etc.). Moreover, individual growth benefits of access to high-quality habitat may be undermined if the density of fish rises above the level that can be supported by the existing food base.

Determine where Colorado pikeminnow spawn in the UCR. Colorado pikeminnow are known to spawn in the 15-Mile Reach, but the precise location of the spawning area has not been confirmed (by USFWS criteria). Consequently, it is not possible to target management attention on this critical unit of habitat. Existing information on larval drift, on the seasonal movements of radio-tagged fish, and field observations of fish aggregations has located areas where spawning is likely to have occurred. In conjunction with larval drift data, a reconnaissance investigation of the 15-Mile Reach should be undertaken to identify locations where the PRM criteria appear to be met. Combined geomorphic, hydraulic, sedimentologic, and biologic investigations could then be conducted to specifically identify the spawning sites. Once the geographic scope of possibilities has been narrowed, monitoring efforts can be directed more efficiently until a site or sites can be confirmed. When spawning areas have been identified, it will be possible to protect the sites, and evaluate their quality.

There may not be enough nursery habitat for recovery of the Colorado pikeminnow population in the UCR. **Can nursery habitat for the Colorado pikeminnow be augmented by installation of groins or other habitat modifications?** A related

issue is whether, given a fixed total surface area of backwaters, recruitment is favored by many small backwaters, or by fewer larger backwaters.

Stocking of Endangered Fishes

How successful have previous reintroductions been for adding to the populations of endangered fishes? Many fish have been introduced during the past fifteen years, including some that were introduced inadvertently. The location and number of fish released and recaptured have not been compiled in a record that can support an evaluation of success. For those fish that were tagged before introduction, there has been no comprehensive assessment of their fate (e.g., how many have been captured, where and when were they captured). Such an assessment is made difficult because that tags are lost at rates known only imprecisely, it should nevertheless be possible to make general statements about the relative numbers of stocked individuals thought to remain wild. Knowledge of the relative abundance of stocked individuals is crucial for interpreting results of studies purporting to reveal the behavior of wild fish, and for guiding future stocking efforts.

Determine if stocked fish behave differently than wild fish, and if so, modify plans for implementing recovery actions. One of the biggest uncertainties associated with potential reintroduction efforts is the extent to which fish behavior may confound the best intentions of managers. Past stockings may not have bolstered recruitment because the fish were not adapted to local conditions. Fish reared on artificial or different foods may have difficulty switching to another diet. Hatchery-reared fish that have not been exposed to the correct conditions as larvae may not reproduce successfully as adults. The presence of stocked fish would therefore place demands on resources (food and habitat) without adding to the population through reproduction. Strong circumstantial evidence suggest that imprinting can aid successful recruitment in some species. Radiotelemetry studies often demonstrate a "fright" response to a new environment, with fishes moving downstream in riverine introductions. There also is concern that other facets of behavior may not be represented accurately in studies that include stocked individuals.

Translocate Colorado pikeminnow and humpback chub into, or above, Debeque Canyon and into the Gunnison River. For many years, major physical barriers have blocked migration of Colorado pikeminnow into the UCR above Palisade and the Gunnison River above Redlands. Significant steps have been taken recently to eliminate those barriers. A passageway through the Redlands diversion dam now allows Colorado pikeminnow to move upstream on the Gunnison River and a passageway is under construction at the Grand Valley diversion on the UCR. In addition, plans are being prepared for passageways through the other two structures that block movement into Debeque Canyon. The assumption was made that subadult and adult Colorado pikeminnow will use habitat above the barriers, and monitoring at

the Redlands passageway supports this contention. Translocating juvenile or subadult Colorado pikeminnow could hasten the repopulation of the upstream reaches. Translocations would also provide an opportunity for studying behavior of wild fish, especially habitat use, in the newly occupied habitat. Observations about passageway design and habitat use could make it easier to decide if a passageway through the Hartland diversion on the Gunnison River would be warranted and how it might be designed.

There is also a strong justification for considering translocation of humpback chub. Anderson (1996) viewed Debeque Canyon as a suitable location for two other members (Colorado pikeminnow and razorback sucker) of the big river fish community. Collections made by Valdez et al. (1982) suggest that a population existed there relatively recently. Juveniles or subadults could be taken from the Black Rocks population so that there would be no concern about "contaminating" existing genetic stock. Studies of the Black Rocks population indicate that these fish do not move much, a behavioral trait which should facilitate establishing a population in the new location.

Support local facilities for rearing razorback suckers and develop site-adapted reintroduction plans that satisfy all life history needs. Translocation of some endangered fish may provide an option to site adaptation, but razorback suckers can only be restored in the UCR by reintroduction. Best results for reintroduction probably depend on having a local facility for rearing the fish because intensive management will be needed. Water from the UCR could be used and fish could be released at an early age into protected areas. Fertilized eggs can be hatched with water from a preselected spawning site, then released at that site, or returned to the facility for rearing. Such facilities should be located close to the planned reintroduction site to minimize transport problems.

Define protocols for tracking all individuals from any future introductions. There are two principle reasons for wanting to know the fate of all stocked individuals: (1) assessing success of stocking efforts, and (2) avoiding confounding results in studies where the behavior of stocked individuals may differ from that of wild individuals. There may also be potential benefits in terms of the relative success of different genetic stocks. The prospects for successful tracking will vary with the age of the individuals used, and with the nature of the device (e.g., tagged or transmitter) that records the identity of the stocked individuals. Previous efforts have not provided a very reliable or durable record. Recent experience with pit tags (now used on stocked Colorado pikeminnow) suggests that they can provide a satisfactory record.

Control of Introduced Fishes

Develop an effective nonnative fish control program. As evidence builds, there is little remaining doubt that nonnative fishes constitute a great constraint to recovery or perhaps all of the listed big river fishes. However, no successful program has been developed and implemented to control nonnative fishes to date. This remains a critical recovery need.

Remove nonnative fishes from known Colorado pikeminnow nursery habitat. Current information suggests very strongly that predation by nonnative fishes on early life stages is presently the most significant factor in reducing or preventing recruitment of the endangered fishes. The larval stage is probably the most vulnerable to predation, and they usually occupy backwater habitat. If the abundance of nonnatives can be reduced significantly in backwater habitat, there should be a measurable increase in recruitment of the endangered fishes that use backwaters as nursery areas. The task of removing the nonnatives is not trivial in terms of effort, but neither is the technology difficult or sophisticated. A trial project should be initiated in backwaters that are used as nursery habitat by the Colorado pikeminnow. If the removal effort is to have the desired effect, the abundance of **all** nonnatives (including small nonnative cyprinids like red shiners, fathead minnow, and sand shiners) should be reduced by at least 50% for several months. A certain amount of trial and error learning will be necessary for tailoring the removal techniques in terms of timing and amount of effort, which would begin before the small cyprinids reproduce and continue until age 0 pikeminnow are present. A detailed protocol and plan should be written, and a three year pilot program should be established for refining the methodology. Monitoring should assess the change in nonnative abundance and to compare larval abundance with prior ISMP efforts per river segment.

Research, Monitoring, and Data Management

Encourage broader review, synthesis, and dissemination of research. Because endangered fish recovery is a new and developing field, there is a critical need to share information and to seek outside contributions and to share with others, especially between upper and lower basin workers. There also is a compelling need for more synthesis that will lead to new approaches. For example, a research effort should be supported to synthesize existing information and develop conceptual life history models for the listed species. These conceptual models can be used to evaluate the behavior of species in different geographic locations with the goal of developing more effective recovery measures. When fish behavior (e.g., migrations, choice of spawning habitats, general habitat preferences) at a particular site does not correspond to the conceptual model, a thorough review is warranted to insure that all steps are taken to increase recovery potential. The recovery program invests substantial resources in research every year, but only a small fraction of that work makes it into the open literature. The program could benefit from an opportunity to showcase the work that has been done

and the studies in progress. One possible forum for such an undertaking would be a structured AFS symposium that would summarize research done in the 20 years since the 1981 Colorado River Symposium (Miller et al. 1982). One or more participants should have the task of synthesizing results from the symposium, and proposing new directions for recovery efforts. Another option might involve convening a NRC review panel like that used for the recent Glen Canyon studies.

Develop a program that will estimate existing population sizes for each endangered species. There is a fundamental need for an assessment tool that will measure progress toward recovery. This means estimating population sizes with sufficient precision that trends over time are detectable. The current ISMP was not designed for this purpose, and the data from ISMP surveys cannot be used to obtain population size estimates. The problem can be addressed by establishing a program that employs methodology comparable to that used by Osmundson and Burnham (1996) for estimating the size of the Colorado pikeminnow population in the UCR. Sampling should be repeated at a fixed time interval (e.g., every 5 years) until recovery goals have been met. Because sampling on this scale requires a large investment of effort, sampling of reaches within the UCRB could be scheduled on a rotation within the 5-yr interval. It will be critical, however, that the reaches sampled in one field season represent the full range of habitats used by the target populations. Thus, sampling in the UCR would have to extend from the Grand Valley diversion to the mouth of the Green River. Five years is probably the maximum time interval that will provide a useful assessment of progress and an opportunity to redirect efforts if goals are not being achieved.

How many Colorado pikeminnow can be supported in the UCRB? It is thought that there are no more than 4 or 5 stocks of Colorado pikeminnow remaining in the wild (Green River, Yampa River, upper Colorado River, San Juan River, and perhaps the Gunnison River). Given the specific requirements for spawning and nursery habitat (in terms of physical characteristics and spatial arrangement), it seems unlikely that the number of stocks can be increased by more than one or at the most two (UCR and Dolores River). The number of breeding fish in each population may be limited by the availability of high-quality adult habitat. If abundance in the Yampa River population can be taken as an indication of the level that can be sustained, the maximum number of adults is probably 20 to 25 per mile, although it is quite plausible that carrying capacity will vary among rivers. An inventory of suitable adult habitat could help establish the potential for supporting the fish in the UCRB, and specifically in the Colorado River above the Green River confluence.

Determine the population size and number of populations for long-term persistence of each endangered species. The chance of a species persisting over a long period of time is influenced strongly by the number of extant populations and the number of individuals in each population. A minimum number of breeding adults required for long-term maintenance of a natural population probably can be estimated on the basis of genetic arguments regarding minimum viable population size, provided

that there is adequate consideration for biased sex ratios and other factors that tend to diminish the effective size of natural populations. In particular, a margin of safety should be included for the role of stochastic events such as chemical spills. A recent interim management objective (IMO) document presents a methodology for setting minimum population size, and the approach is a good point of departure for future efforts. The IMO work also supported development of a spreadsheet model intended for estimating the size each population must maintain for a reasonable probability of persistence. The idea is good and the modeling effort will provide direction for future data collection efforts. However, current model predictions are of little use because of flaws in the model (especially in regard to the representation of reproduction) and inadequacies of the input data (few parameters are known with any certainty). Some progress can be made now by improving the existing modeling framework and by making better use of the available information.

The number of populations required for recovery probably will be greater than the number of extant populations for each of the endangered fishes. To some extent there may be tradeoffs whereby increasing the number of populations may reduce the number of individuals required for persistence of the species. This subject can and should be investigated through modeling techniques that have been applied to other species. Adding new populations is not a simple matter, however. Selection of suitable locations that do not now support populations may be aided by historical distribution data or may depend more on direct evaluations of physical and biological dimensions of habitat. Attention should be given to a practical assessment of the number of individuals that can be supported by the habitat within which each stock will complete its life cycle. Establishing populations in locations where they do not exist now will require stocking on a large scale. Considerable lead time is necessary to build hatchery stocks to the desired level.

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PART 8. BIBLIOGRAPHY OF PUBLISHED AND UNPUBLISHED SOURCES

- Allan, R.C., and D.L. Roden. 1978. Fish of Lake Mead and Lake Mohave. Nevada Department of Wildlife, Biological Bulletin 1:1-105,
- Anderson, R. 1996. An evaluation of fish community structure and habitat potential for Colorado squawfish and razorback sucker in the unoccupied reach (Palisade to Rifle) of the Colorado River, 1993-1995. Draft Report. Federal Aid in Wildlife Restoration Project SE-22, Colorado Division of Wildlife, Fort Collins. 81pp.
- Andrews, E.D. 1986. Downstream effect of Flaming Gorge Reservoir on the Green River, Colorado and Utah. Geological Society of America Bulletin 9:1012-1023.
- Anonymous. 1996a. Fish "ladder" now gateway to Gunnison River. Newsletter of the Recovery Program for the Endangered Fishes of the upper Colorado River. Fall 1996. U.S. Fish and Wildlife Service, Denver, Colorado. 8 pp.
- _____. 1996b. Squawfish spawn in Gunnison River. Newsletter of the Recovery Program for the Endangered Fishes of the upper Colorado River. Fall 1996. U.S. Fish and Wildlife Service, Denver, Colorado. 8 pp.
- Aquatic Nuisance Species Task Force (ANSTF). 1994. Findings, conclusions and recommendations of the intentional introductions policy review: Report to Congress. U.S. Fish and Wildlife Service, Washington, DC 53pp.
- Archer, D.L., L.R. Kaeding, B.D. Burdick, and C.W. McAda. 1985. A study of the endangered fishes of the upper Colorado River. Final Report. Colorado River Fishery Project. U.S. Fish and Wildlife Service, Grand Junction, CO.
- Baxter, G.T., and J.R. Simon. 1970. Fishes of Wyoming. Wyoming Game and Fish Department Bulletin 4:1-168.
- Beamesderfer R.D. and J.L. Congleton. 1981. Spawning behavior, habitat selection, and early life history of northern squawfish with inferences to Colorado squawfish. Pages 47-127 In Miller, et al. Colorado River fishery Project, Final Report, Volume 3. U. S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah
- Beckman, W.C. 1953. Guide to fishes of Colorado. Colorado State Museum, University of Colorado at Boulder. 110 pp. (Reprinted 1970).
- Berry, C.R. 1988. Effects of cold shock on Colorado squawfish larvae. Southwestern Naturalist 33:193-197.
- Bestgen, K.R. 1996. Growth, survival and starvation resistance of Colorado squawfish larvae. Environmental Biology of Fishes 46:197-209

- _____, and D.L. Probst. 1989. Distribution, status, and notes on the ecology of *Gila robusta* (Cyprinidae) in the Gila River Drainage, New Mexico. *Southwestern Naturalist* 34:402-412.
- Beyers, D.W., R.T. Muth, and M.S. Farmer. 1994. Experimental evidence of competition between larvae of Colorado squawfish and fathead minnow. Final Report to the Upper Colorado River Recovery Implementation Program. Larval Fish Laboratory, Colorado State University, Fort Collins.
- Black, T., and R.V. Bulkley. 1985. Preferred temperature of yearling Colorado squawfish. *Southwestern Naturalist* 30:95-100.
- Bozek, M.A., L.J. Paulson, and J.E. Deacon. 1984. Factors affecting reproductive success of bonytail chubs and razorback suckers in Lake Mohave. Final Report. U.S. Fish and Wildlife Service Contract 14-16-0002-81-251. University of Nevada, Las Vegas.
- Breder, C.M., Jr., and D.E. Rosen. 1966. Modes of reproduction in fishes. TFH Publications, Garden City, New Jersey. 961pp.
- Brooks, J.E. 1986. Annual reintroduction and monitoring report for razorback sucker (*Xyrauchen texanus*) in the Gila river basin, Arizona. Arizona Game and Fish Department, Phoenix. 22p.
- Burdick, B.D. 1992. A plan to evaluate stocking to augment or restore razorback sucker in the Upper Colorado River. Final Report. U.S. fish and Wildlife Service, Grand Junction, Colorado. 56 pp.
- _____. 1994. Conceptual management plan for habitat enhancement in flooded bottomlands. U.S. Fish and Wildlife Service, Grand Junction, Colorado 25 pp.
- _____. 1995. Ichthyofaunal studies of the Gunnison River, Colorado, 1992-1994. Final Report. U.S. Fish and Wildlife Service, Grand Junction, Colorado.
- _____. 1996. Flooded bottomlands restoration project: site 29-5/8 road gravel pit. Project #CAP-6-GP. FY 96 Annual Report of the Colorado River Recovery Program,. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.
- _____. 1997. Minimum flow recommendation for passage of Colorado squawfish and razorback sucker in the 2.3-mile reach of the lower Gunnison River: Redlands Diversion Dam to the Colorado River confluence. Final Report. Recovery Implementation Program for the Endangered Fishes of the Upper Colorado River Basin. U. S. Fish and Wildlife Service, Grand Junction, Colorado. 39 pp + 9 app.

- _____, and R.B. Bonar..1997. Experimental stocking of adult razorback sucker in the upper Colorado and Gunnison rivers. Recovery Program Project 50, Final Report. U.S. Fish and Wildlife Service, Grand Junction, CO. 28 pp + 2 app.
- Cada, G.F. and M.J. Sale. 1993. Status of fish passage facilities at nonfederal hydropower projects. *Fisheries* 18(7):4-7.
- Carlson, C.A., and E.M. Carlson. 1982. Review of selected literature on the Upper Colorado River system and its fishes. pages 1-8, *in* W.H. Miller et al. *Fishes of the Colorado River System: Present and Future*. American Fisheries Society, Bethesda, Maryland.
- Carlson, C.A. and R.T. Muth. 1989. Colorado River: Lifeline of the American Southwest. Pages 220-239 *in*: D.P. Dodge (editor). *Proceedings of the International Large Rivers Symposium*. Canadian Special Publication of Fisheries and Aquatic Sciences 106.
- Casey, O.E. 1962. The life history of the northern squawfish in Cascade Reservoir. M.S. Thesis, University of Idaho. 61 pp.
- Chart, T.E., and E.P. Bergerson. 1992. Impact of mainstream impoundment on the distribution and movements of the resident flannelmouth sucker (*Catostomidae: Catostomous latipinnus*) population in the White River, Colorado. *Southwestern Naturalist*: 37:9-15.
- Childs, M.R. and R.W. Clarkson. 1996. Temperature effects on swimming performance of larval and juvenile Colorado squawfish: implications for survival and species recovery. *Transactions of the American Fisheries Society* 125:940-947.
- Clark, T.W., R.P. Reading , and A.L. Clark. 1994. *Endangered species recovery: Finding the lessons, improving the process*. Island Press. Washington, DC, 450 pp.
- Colorado Division of Wildlife, et al. 1996. *Procedures for stocking nonnative fish species in the Upper Colorado River Basin*. U. S. Fish and Wildlife Service , Denver, Colorado. 25 pp.
- Coon, K.L. 1965. Some biological observations on the channel catfish, *Ictalurus punctatus* (Rafinesque), in a polluted western river. M.S. Thesis, Utah State University, Logan.
- Courtenay, W.R., Jr. 1993. Biological pollution through fish introductions. Pages 35-61 *in*: B.N. McKnight (editor). *Biological pollution: The control and impact of invasive exotic species*. Indiana Academy of Sciences, Indianapolis. 261 pp.

- Courtenay, W.R. Jr. and C.R. Robins. 1989. Fish introductions: Good management, mismanagement, or no management? *Reviews in Aquatic Sciences* 1:159-172.
- Crowl, T.A. and L. Lentsch. 1995. Estimating pike predation on Colorado River squawfish. Project F-47-R, study 8. FY 96 Annual Report of the Recovery Program for endangered fishes in the Upper Colorado River. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.
- _____, and N.W. Bouwes. 1997. Modeling population dynamics of Colorado squawfish, razorback sucker, and humpback chub for management objectives development. Ecology Center, Department of Fisheries and Wildlife, Utah State University, Logan.
- _____, L.D. Lentsch, P. Thompson, and Y. Converse. 1996. Ecological aspects for the reintroduction of bonytail *Gila elegans* in the upper basin of the Colorado River. *Proceedings of the Desert Fishes Council* 1995:30-31 (Abstract).
- Deacon, J.E. 1978. Endangered and threatened fish of the West. *Great Basin Naturalist Memoirs* 3:41-64.
- Dence, W.A. 1948. Life history, ecology, and habits of the dwarf sucker, *Catasomus commersoni utawena* Mather, at the Huntingdon Wildlife station. *Bulletin of the New York State College of Forestry at Syracuse University* 21(3):79-150.
- Dill, W.A. 1944. The fishery of the lower Colorado River. *California Fish and Game* 30:109-211.
- Douglas, M.E. and P.C. Marsh. 1996. Population estimate/population movements of *Gila cypha*, an endangered cyprinid fish in the Grand Canyon region of Arizona. *Copeia* 1996:15-28.
- Dunsmoor, L. 1993. Laboratory studies of fathead minnow predation on catostomid larvae. Research Report KT-93-01. Natural Resources Department, The Klamath Tribes, Chiloquin, Oregon. 16 pp.
- _____. 1996. Predation by planarian flatworms and fathead minnows on embryos and larvae of endangered suckers in Oregon. *Proceedings of the Desert Fishes Council* 1995: 35-36.
- Fenton, K.H. 1996. Remote sensing support for the Recovery Implementation Program research. Project 30. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.

- FLO Engineering. 1997. Concept development report, Grand Valley irrigation company diversion dam fish passage structure, Palisades, Colorado. Report to the U.S. Bureau of Reclamation, Contract 1425-6-CA-40-1730A. Breckenridge, Colorado. 44 pp.
- Fradkin, P.L. 1984. A river no more: The Colorado River and the West. The University of Arizona Press, Tucson. 360 pp.
- Gilpin, M. E. 1993. A population viability analysis of the Colorado squawfish in the Upper Colorado River Basin: A report to the U.S. Fish and Wildlife Service, Denver, CO. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado. 53 pp.
- Grabowski, S.J., and S.D. Hiebert. 1989. Some aspects of trophic interactions in selected backwaters and main channel of the Green River, Utah, 1987-1988. U.S. Bureau of Reclamation, Denver, CO.
- Gorman, O.T. 1994. Habitat use by the humpback chub, *Gila cypha*, in the Little Colorado River and other tributaries of the Colorado River. Final report for Glen Canyon Environmental Studies, Phase II. U.S. Fish and Wildlife Service, Flagstaff, Arizona.
- Haines, B., et al. 1996. Umbrella Project: Chemoreception, imprinting, and propagation of Colorado squawfish and razorback sucker. Project 31. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.
- Hamman, R.L. 1981. Spawning and culture of Colorado squawfish in raceways. *Progressive Fish Culturist* 43(1):173-177.
- Harvey, M.D., R.A. Mussetter, and E.J. Wick. 1993. A physical process-biological response model for spawning habitat formation for the endangered Colorado squawfish. *Rivers* 4(2):114-131.
- Harvey, M.D., and R.A. Mussetter. 1996. Evaluation of the required flow of bar forming events and 2-dimensional hydrodynamic modeling at Colorado squawfish spawning sites in the lower Yampa Canyon Colorado. Prepared for the Colorado River Water Conservancy District, Project 95-09. Mussetter Engineering Company, Fort Collins, Colorado. 6 Sections and 2 App.
- Hasler, A.D., and A.T. Scholz. 1983. Olfactory imprinting and homing in salmon. *Zoophysiology* 14:3-38.

- Hawkins, J.A. 1991. Age and growth of Colorado squawfish from the Upper Colorado River Basin, 1978-1990. Final Report to the U.S. Fish and Wildlife Service, Contract 60181-0-1431. Colorado Division of Wildlife, Fort Collins. 64 pp.
- Hawkins, J.A. and T.P. Nesler. 1991. Nonnative fishes of the upper Colorado River basin: An issue paper. Final Report. Colorado State University and Colorado Division of Wildlife, Fort Collins, CO. 72 pp.
- Haynes, C.M., T.A. Lytle, E.J. Wick, and R.T. Muth. 1984. Larval Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River basin, Colorado, 1979-1981. *Southwestern Naturalist* 29:21-33.
- _____, and R.T. Muth. 1984. Reproduction of Colorado squawfish (*Ptychocheilus lucius*) in the Yampa River, Colorado (1980-1983). *Proceedings of the Desert Fishes Council* 15:297.
- Hendrickson, D.A. 1993. Arizona stockings of razorbacks and squawfish: History and future research and management challenges. *Proceedings of the Desert Fishes Council* 1992:70.
- _____, and J.E. Brooks. 1987. Colorado squawfish reintroduction studies. *Proceedings of the Desert Fishes Council* 18 (1986):207-208.
- Hesse, L.W. 1994. The status of Nebraska fishes in the Missouri River. 3. Channel catfish (*Ictaluridae: Ictalurus punctatus*). *Transactions of the Nebraska Academy of Sciences* 21:73-87.
- Hill, T.D., W.G. Duffy, and M.R. Thompson. 1995. Food habits of channel catfish in Lake Oahe, South Dakota. *Journal of Freshwater Ecology* 10(4):319-323.
- Holden, P.B. 1977. A study of habitat use and movement of the rare fishes in the Green River from Jensen to Green River, Utah, August and September, 1977. *BIO/WEST Report PR-13-1*, Logan, UT.
- Holden, P.B., and C.B. Stalnaker. 1975. Distribution of fishes in the Dolores and Yampa River systems of the upper Colorado Basin. *Southwestern Naturalist* 19:403-412.
- Horn, M.J., P.I. Marsh, G. Mueller, and T. Burke. 1994. Predation by odonate nymphs on larval razorback suckers (*Xyrauchen texanus*) under laboratory conditions. *The Southwestern Naturalist* 39:371-374.
- Jornes, W.V., C.H. Hembree, and G.L. Oakland. 1965. Water resources of the upper Colorado River Basin. U.S. Geological Survey, Professional Paper 441.

- Irving, D.B., and B.D. Burdick. 1995. Reconnaissance inventory and prioritization of existing and potential bottomlands in the upper Colorado River basin, 1993-1994. U.S. Fish and Wildlife Service, Denver, Colorado 57 pp + 9 App.
- _____, and T. Modde. 1995. Migrational behavior and stock differentiation of Colorado squawfish in the White River. Proceedings of the Desert Fishes Council (1994):107-108.
- Jacobi, J.E., and M.D. Jacobi. 1982. Fish stomach content analysis. Pages 285-321 in: U.S. Fish and Wildlife and Bureau of Reclamation. Colorado River Fisheries Project. Part 3. Salt Lake City, UT.
- Johnson, J.E., M.G. Pardew, and M.M. Lyttle. 1993. Predation recognition and avoidance by larval razorback sucker and northern hog sucker. Transactions of the American Fisheries Society 122:1139-1145.
- Jonez, A. and R.C. Sumner. 1954. Lakes Mead and Mohave investigations: A comparative study of an established reservoir as related to a newly created impoundment. Federal Aid to Fisheries Restoration Project Completion Report, F-1-R, Nevada Fish and Game Commission, Reno, NV. 186 pp.
- Jordan, D.S. 1891. Report of explorations in Utah and Colorado during the summer of 1889, with an account of fishes found in each of the river basins examined. Bulletin of the U.S. Fish Commissioner 9:1-40.
- Joseph, T.W., J.A. Sinning, R.J. Behnke, and P.B. Holden. 1977. An evaluation of the status, life history and habitat requirements of endangered and threatened fishes of the Upper Colorado River Basin. Report FWS/OBS-77/2, U.S. Fish and Wildlife Service, Fort Collins, Colorado.
- Kaeding, L.R., and D.B. Osmundson. 1988. Interaction of slow growth and increased early life mortality: an hypothesis on the decline of the Colorado squawfish in the upstream regions of its historic range. Environmental Biology of Fishes 22:287-298.
- _____, and M.A. Zimmerman. 1983. Life history of the humpback chub in the Little Colorado and Colorado Rivers of the Grand Canyon. Transactions of the American Fisheries Society 112:577-594.
- _____, B.D. Burdick, P.A. Schroeder, and C.W. McAda. 1990. Temporal and spatial relations between the spawning of humpback chub and roundtail chub in the upper Colorado River. Transactions of the American Fisheries Society 119:135-144.

- _____, P.A. Schroeder, and W.R. Noonan. 1986. Recent capture of a bonytail (*Gila elegans*) and observations on this nearly extinct cyprinid from the Colorado River. *Copeia* 1986:1021-102.
- Karp, C.A. and H.M. Tyus. 1990a. Behavior and interspecific interactions of Colorado squawfish *Ptychocheilus lucius*, and five other fish species. *Copeia* 1990:25-34.
- Karp, C.A. and H.M. Tyus. 1990b. Humpback chub (*Gila cypha*) in the Yampa and Green rivers, Dinosaur National Monument, with observations on roundtail chub (*G. Robusta*) and other sympatric fishes. *Great Basin Naturalist* 50(3):257-264.
- Kidd., George. 1977. An investigation of endangered and threatened fish species in the upper Colorado River as related to Bureau of Reclamation projects. Final Report, North West Fisheries Research, Clifton Colorado. 37 pp. and 4 app.
- Langhorst, D.R. 1989. A monitoring study of razorback sucker (*Xyrauchen texanus*) reintroduced into the lower Colorado River in 1988. Final Report. (Contract FC-9494). California Department of Fish and Game, Blythe.
- Langhorst, D.R. and P.C. Marsh. 1986. Early life history of razorback sucker in Lake Mohave. Final Report to the U.S. Bureau of Reclamation, Order no. 5-PG-30-06440. Arizona State University, Tempe. 34 pp and App.
- Lanigan, S.L., and H.M. Tyus. 1989. Population size and status of razorback sucker in the Green River basin, Colorado and Utah. *North American Journal of Fisheries Management* 9:68-72.
- Lentsch, L.D., R. Muth, P.D. Thompson, T.A. Crowl, and B.G. Hoskins. 1996a. Options for selectively controlling non-indigenous fish in the upper Colorado River basin. Final Report. Publication 96-14, Utah Department of Natural Resources, Division of Wildlife Resources, Salt Lake City.
- _____, M. Trammell, and T. Chart. 1996b. Aspinal Unit Studies: Flow effects on humpback chub population in Westwater Canyon. Project 46. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.
- _____, R. Valdez, and B. Cowdell. 1996c. Flaming George Study: Effects of flow regulation and ice on overwinter nursery habitat of age O Colorado squawfish in the Green River below Flaming George Dam. Project 41, FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.

Maddux, H.R., L.A. Fitzpatrick, and W.R. Noonan. 1993. Colorado River endangered fishes critical habitat: Biological Support Document. U.S. Fish and Wildlife Service, Salt Lake City, UT. 225 pp.

Marsh, P.C. 1985. Effect of incubation temperature on survival of embryos of native Colorado River fishes. *Southwestern Naturalist* 30:129-140.

_____. 1995. Abundance, movements and status of adult razorback sucker, *Xyrauchen texanus* in Lake Mohave, Arizona and Nevada. *Proceedings of the Desert Fishes Council* (1994):24-35.

_____. and D.R. Langhorst. 1988. Feeding and fate of wild larval razorback sucker. *Environmental Biology of Fishes* 21:59-67.

_____, and J.L. Brooks. 1989. Predation by ictalurid catfishes as a deterrent to re-establishment of introduced razorback suckers. *Southwestern Naturalist* 34:188-195.

_____, and M.E. Douglas. 1997. Predation by introduced fishes on endangered humpback chub and other native species in the Little Colorado River, Arizona. *Transactions of the American Fisheries Society* 126:343-346.

_____, and W.L. Minckley. 1989. Observations on recruitment and ecology of razorback sucker: lower Colorado River, Arizona-California-Nevada. *Great Basin Naturalist* 49:71-78.

McAda, C.W. 1983. Colorado squawfish, *Ptychocheilus lucius* (Cyprinidae), with a channel catfish, *Ictalurus punctatus* (Ictaluridae), lodged in its throat. *Southwestern Naturalist* 28:119-120.

_____. 1991a. Movement of adult Colorado squawfish during the spawning season in the Upper Colorado River. *Transactions of the American Fisheries Society* 120:339-345.

_____. 1991b. Physical changes in the Gunnison and Colorado River resulting from construction of the Aspinall Unit and related projects, with hypotheses to assess the effects on the endangered fishes. Final Report. U.S. Fish and Wildlife Service, Grand Junction, Colorado. 60pp.

_____, and H.M. Tyus. 1984. Resource overlap of Age-0 Colorado squawfish with other fish species in the Green River, 1980. *Proceedings of the Bonneville Chapter, American Fisheries Society* 1984:44-54.

- _____, and L.R. Kaeding. 1989. Relations between maximum annual river discharge and relative abundance of age-0 Colorado squawfish and other fishes in the Upper Colorado River. Final Report. U.S. Fish and Wildlife Service, Grand Junction, Colorado. 25 pp.
- _____, and R.S. Wydoski. 1980. The razorback sucker, *Xyrauchen texanus*, in the upper Colorado River Basin, 1974-1976. U.S. Fish and Wildlife Service Technical Paper 99:1-15.
- _____, J.W. Bates, J.S. Cranney, et al. 1994a. Interagency Standardized Monitoring Program. Summary of results, 1986-1992. Final Report. Recovery Implementation Program for the Endangered Fishes of the Upper Colorado River Basin. U. S. Fish and Wildlife Service, Denver, Colorado. 73 pp + 2 App.
- _____. 1994b. Interagency Standardized Monitoring Program. Summary of results, 1993. Final Report. Recovery Implementation Program for the Endangered Fishes of the Upper Colorado River Basin. U. S. Fish and Wildlife Service, Denver, Colorado. 16pp + 3 App.
- _____, W.R. Emblad, T.E. Chart, et al. 1995. Interagency Standardized Monitoring Program. Summary of results, 1994. Final Report. Recovery Implementation Program for the Endangered Fishes of the Upper Colorado River Basin. U. S. Fish and Wildlife Service, Denver, Colorado. 17 pp + 3 App.
- McDonald, D.B., and P.A. Dotson. 1960. Fishery investigations of the Grand Canyon and Flaming Gorge impoundment areas. Utah Department of Fish and Game, Information Bulletin 60-3:1-70.
- Medel-Ulmer, L. 1983. Movement and reproduction of the razorback sucker (*Xyrauchen texanus*) inhabiting Senator Wash Reservoir, Imperial County, California. Proceedings of the Desert Fishes Council (1980) 12:106(Abstract).
- Meffe, G.K. 1985. Predation and species replacement in American southwestern fishes: A case study. Southwestern Naturalist 30:173-187.
- Meronek, T.G., P.M. Bouchard, E.R. Buckmen, T.M. Burri, K.D. Demmerly, D.C. Hatkeleli, R.A. Klumb, S.D. Schmidt, and D.W. Coble. 1996. A review of fish control projects. North American Journal of Fisheries Management 16:63-74.
- Miller, R.R. 1946. *Gila cypha*, a remarkable new fish from the Colorado River in Grand Canyon, Arizona. Journal of the Washington Academy of Sciences 36:409-415.
- _____. 1958. Origins and affinities of the freshwater fish fauna of western North America. Pages 187-222 in: C.L. Hubbs (editor). Zoogeography. Publication 51, American Association for the Advancement of Science, Washington, DC.

- _____. 1961. Man and the changing fish fauna of the American Southwest. Papers of Michigan Academy of Sciences, Arts, and Letters 46:365-404.
- Miller, W.H., D.L. Archer, H.M. Tyus, and K.C. Harper. 1982a. White River fishes study. Final Report. U. S. Fish and Wildlife Service, Salt Lake City, Utah.
- _____, D.L. Archer, H.M. Tyus, and R.M. McNatt. 1982b. Yampa River fishes study. Final Report. U. S. Fish and Wildlife Service, Salt Lake City, Utah.
- _____, H.M. Tyus, and C.A. Carlson (editors). 1982c. Fishes of the upper Colorado River System: present and future. American Fisheries Society, Bethesda, MD. 131 pp.
- _____, J.J. Valentine, D.L. Archer, H.M. Tyus, R.A. Valdez, and L.R. Kaeding. 1982d. Colorado River fishery project. Final Report. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah (3 volumes).
- Minckley, W.L. 1982. Fishes of Arizona. Arizona Game and Fish Department, Phoenix.
- _____. 1982. Trophic interrelations among introduced fishes in the lower Colorado River, Southwestern United States. California Fish and Game 68(2):78-89.
- _____. 1983. Status of the razorback sucker, *Xyrauchen texanus* (Abbott), in the lower Colorado River Basin. Southwestern Naturalist 28:165-187.
- _____, and J.E. Deacon. 1991. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson. 517 pp.
- _____, D.A. Hendrickson, and C.E. Bond. 1986. Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism. Pages 519-614 in: C.H. Hocutt and E.O. Wiley, (editors). The zoogeography of North American freshwater fishes. John Wiley and Sons, New York, NY. 866 pp.
- _____, P.C. Marsh, J.E. Brooks, J.E. Johnson, and B.L. Jensen. 1991. Management toward recovery of the razorback sucker. Pages 303-357 in: W.L. Minckley and J.E. Deacon (editors). Battle against extinction: native fish management in the American Southwest. University of Arizona Press, Tucson. 517 pp.
- Modde, T. 1996. Juvenile razorback sucker (*Xyrauchen texanus*) in a managed wetland adjacent to the Green River. Great Basin Naturalist 56:375-376.

- _____, K.P. Burnham, and E.J. Wick. 1996. Population status of the razorback sucker in the middle Green River (U.S.A.). *Conservation Biology* 10(1):110-119.
- Moyle, P.B. 1976. *The inland fishes of California*. University of California Press, Berkeley, CA.
- Mueller, G. 1995. A program for maintaining the razorback sucker in Lake Mohave. *American Fisheries Society Symposium* 15:127-135.
- Muth, R.T. and T.P. Nesler. 1993. Associations among flow and temperature regimes and spawning periods and abundance of young of selected fishes, lower Yampa River, Colorado, 1980-1984. Contribution 58, Colorado State University Fish Laboratory, Fort Collins, 50 pp.
- _____, and D.E. Snyder. 1995. Diets of young Colorado squawfish and other small fishes in backwaters of the Green River, Colorado and Utah. *Great Basin Naturalist* 55:95-104.
- Nesler, T.P., R.T. Muth, and A.F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. *American Fisheries Society Symposium* 5:68-79.
- Nelson, P.C., C.W. McAda, and D. Wydoski. 1995. The potential for nonnative fishes to occupy and/or benefit from enhanced or restored floodplain habitat and adversely impact the razorback sucker. An issue Paper. Recovery Implementation Program for Endangered Fish Species in the upper Colorado River Basin. U.S. Fish and Wildlife Service, Denver, Colorado. 8 pp + papers.
- Norman, B. 1996a. Fish passage at the Grand Valley Irrigation Company diversion dam. Project number CAP 17. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.
- _____. 1996b. Grand Valley water management. Project number CAP 11. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.
- _____ and M. Wernke. 1996c. Passage at the Price/Stubbs diversion dam. Project number CAP 5. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.

- Osmundson, D.B. 1987. Growth and survival of Colorado squawfish (*Ptychocheilus lucius*) stocked in riverside ponds, with reference to predation by largemouth bass (*Micropterus salmoides*). M.S. Thesis, Utah State University, Logan, UT.
- _____ and K.P. Burnham. 1996. Status and trends of Colorado squawfish in the upper Colorado River. Final Report. U.S. Fish and Wildlife Service, Grand Junction, CO. 35 pp.
- _____, and L.R. Kaeding. 1989. Studies of Colorado squawfish and razorback sucker use of the "15-mile reach" of the upper Colorado River as part of conservation measures for Green Mountain and Ruedi Reservoir water sales. Final Report. Colorado River Fishery Project, Grand Junction, Colorado
- _____. 1991. Recommendations for flows in the 15-mile reach during October-June for maintenance and enhancement of endangered fish populations in the Upper Colorado River. Final Report. Colorado River Fishery Project, Grand Junction, Colorado.
- _____, P. Nelson, K. Fenton, and D.W. Ryden. 1995. Relationships between flow and rare fish habitat in the '15 mile reach' of the upper Colorado River. Final Report. U.S. Fish and Wildlife Service, Grand Junction, CO. 71 pp. + 9 App.
- _____, M. Tucker, B.D. Burdick, W.R. Emblad, and T.E. Chart. 1997. Non-spawning movements of subadult and adult Colorado squawfish in the upper Colorado River. Draft Report. U.S. Fish and Wildlife Service, Grand Junction, CO.
- Papoulias, D. and W.L. Minckley. 1990. Food limited survival of larval razorback suckers in the laboratory. *Environmental Biology of Fishes* 29:73-78.
- Patten, B.G., and D.T. Rodman. 1969. Reproductive behavior of northern squawfish (*P. oregonensis*). *Transactions of the American Fisheries Society* 98:108-111.
- Pfeifer, F. 1996. Evaluation of effectiveness of the fish passage structure at the Redlands Diversion Dam and flow requirements in the 2.3 mile reach of the lower Gunnison River. Project number CAP 4b. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.
- Pimental, R., R.V. Bulkley, and H.M. Tyus. 1985. Choking of Colorado squawfish, *Ptychocheilus lucius* (Cyprinidae), on channel catfish, *Ictalurus punctatus* (Ictaluridae), as a cause of mortality. *Southwestern Naturalist* 30:154-158.

- Pitts, T. And M.J. Cook. 1997. Propagation and stocking activities of the Recovery Implementation Program for the Endangered Fishes of the Upper Colorado River Basin: Summary, status, assessment. Hall, Pitts, and Associates. Loveland, Colorado. 53 pp.
- Platania, S.P., K.R. Bestgen, M.A. Moretti, D.L. Propst, and J.E. Brooks. 1991. Status of Colorado squawfish and razorback sucker in the San Juan River, Colorado , New Mexico, and Utah. *Southwestern Naturalist* 36:147-150.
- Prewitt, C.G., K.A. Voos, and T. Waddle. 1982. IFG study of physical-chemical conditions on the Green and Colorado rivers, in Colorado and Utah. Pages 1-45 in W.H. Miller, et al., editors, Colorado River Fishery Project, Final Report, Part Three: Contracted Studies. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.
- Probst, D.L. and K.R. Bestgen. 1991. Habitat and biology of the loach minnow, *Tioroga cobitis*, in New Mexico. *Copeia* 1991:29-38.
- Quartarone, F. 1993. Historical accounts of upper Colorado River basin endangered fish. Colorado Division of Wildlife, Denver, Colorado. 66 pp.
- Rinne, J.N. 1971. The life history of *Lepidomeda mollispinis mollispinis* (the Virgin River spinedace), a unique western cyprinid. M.S. Thesis. University of Nevada, Las Vegas, NV. 109 pp.
- Rinne, J.N. and W.L. Minckley. 1991. Native fishes of arid lands: a dwindling resource of the desert Southwest. U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station General Technical Report 206, Fort Collins, Colorado.
- Rinne, J.N. 1991. Habitat use by spikedace, *Meda fulgida* (Pisces: Cyprinidae) in the southwestern streams with reference to probable habitat competition with red shiner, *Notropis lutrensis* (Pisces: Cyprinidae). *Southwestern Naturalist* 36:7-13.
- Rose, S., and J. Hamill. 1988. Help is on the way for rare fishes of the upper Colorado River basin. *Endangered Species Technical Bulletin* 8(3):1-7. U.S. Fish and Wildlife Service, Washington, DC.
- Ruppert, J.B., R.T. Muth, and T.P. Nesler. 1993. Predation on fish larvae by adult red shiner, Yampa and Green rivers, Colorado. *The Southwestern Naturalist* 38:397-399.
- Ryden, D.W., and L.A. Ahlm. 1996. Observations on the distribution and movement of Colorado squawfish (*Ptychocheilus lucius*) in the San Juan River, New Mexico, Colorado , and Utah. *Southwestern Naturalist* 42:161-168.

- Scholz, A.T., R.J. White, S.A. Horton and V.A. Koeler. 1992. Measurement of egg and larval thyroxine concentrations as an indication of the critical period for imprinting in razorback sucker *Xyrauchen texanus* (Abbott): implications for endangered stocks in the Colorado River basin. Report to the U.S. Bureau of Reclamation (Cooperative agreement No. 2-FC-40-11830). Salt Lake City, Utah.
- Scholz, A.T., R.J. White, S.A. Horton, M.B. Tilson, C.I. Williams, and B. Haines. 1993. Thyroxine concentrations and chemical imprinting of razorback sucker (*Xyrauchen texanus*) and Colorado squawfish (*Ptychocheilus lucius*) eggs and larva raised at Dexter National Fish Hatchery, New Mexico. Report to the U.S. Bureau of Reclamation (Cooperative agreement No. 2-FC-40-11830). Salt Lake City, Utah.
- Schoenherr, A.A. 1981. The role of competition and the replacement of native fishes by introduced species. Pages 173-203 in: R.J. Naiman and D.L. Soltz (editors). Fishes in North American Deserts. Wiley-Interscience, John Wiley and Sons, New York. NY.
- Scoppertone, G.G. 1993. Interactions between native and nonnative fishes of the upper Muddy River, Nevada. Transactions of the American Fisheries Society 599-608
- Seethaler, K.H. 1978. Life history and ecology of the Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River Basin. M.S. thesis, Utah State University, Logan.
- Smith, G.R. 1978. Biogeography of intermountain fishes. Pages 17-42 in: K.T. Harper and J.L. Revel (editors). Intermountain Biogeography: A symposium. Great Basin Naturalist Memoirs 2.
- Smith, M.L. 1981. Late Cenozoic fishes in warm deserts of North America: A reinterpretation of desert adaptations. Pages 11-38 in: R.J. Naiman and D.L. Soltz (editors). Fishes in North American Deserts. Wiley-Interscience, John Wiley and Sons, New York, NY.
- Soulé, M.E. 1983. What do we really know about extinction? Pages 111-124 in: C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas (editors). Genetics and conservation: A reference for managing wild animal and plant populations. The Benjamin/Cummings Publishing Company, Menlo Park, CA. 722 pp.
- Stanford, J.A. 1994. Instream flows to assist the recovery of endangered fishes of the upper Colorado River basin. Biological Report 24:1-47, U.S. National Biological Survey. Washington, D.C.

- Stanford, J.A. and J.V. Ward. 1986a. The Colorado River system. Pages 353-374 in: B.R. Davies and K.F. Walker (editors). The ecology of river systems. Dr. W. Junk, Publishers, Dordrecht, The Netherlands.
- Stanford, J.A. and J.V. Ward. 1986b. Fish of the Colorado system. Pages 385-402 in: B.R. Davies and K.F. Walker (editors). The ecology of river systems. Dr. W. Junk, Publishers, Dordrecht, The Netherlands.
- Taba, S.S., J.R. Murphy, and H.H. Frost. 1965. Notes on the fishes of the Colorado River near Moab, Utah. Proceedings of the Utah Academy of Science, Arts, Letters 42:280-283.
- Thomas, C.D. 1990. What do real population dynamics tell us about minimum viable population sizes? Conservation Biology 4(3):324-327.
- Thompson, J.M., 1989. The role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. M.S. Thesis, Colorado State University, Fort Collins. 87 pp.
- Trammell, M.A., E.P. Bergersen, and P.J. Martinez. 1993. Evaluation of an introduction of Colorado squawfish in a main stem impoundment on the White River, Colorado. Southwestern Naturalist 38:362-369.
- Tyus, H.M. 1984. Loss of stream passage as a factor in the decline of the endangered Colorado squawfish. Pages 138-144 in: Issues and technology in the management of impacted western wildlife; proceedings of a national symposium. Technical publication #14, Thorne Ecological Institute, Boulder, CO.
- _____. 1985. Homing behavior noted in Colorado squawfish. *Copeia* 1985:213-215.
- _____. 1986. Life strategies in the evolution of Colorado squawfish (*Ptychocheilus lucius*). Great Basin Naturalist 46:656-661.
- _____. 1987. Distribution, reproduction, and habitat use of the razorback sucker in the Green River, Utah, 1979-1986. Transactions of the American Fisheries Society 116:111-116.
- _____. 1990. Potamodromy and reproduction of Colorado squawfish *Ptychocheilus lucius*. Transactions of the American Fisheries Society 119:1035-1047.
- _____. 1991a. Ecology and management of the Colorado squawfish. Pages 379-402 (Chapter 19) IN: Minckley, W.L. and J.E. Deacon (eds). Battle against

extinction: Native fish management in the American Southwest. University of Arizona Press. 517 pp

_____. 1991b. Movements and habitat use of young Colorado squawfish, *Ptychocheilus lucius*, in the Green River of Utah. *Journal of Freshwater Ecology* 6:43-51.

_____. 1992. An instream flow philosophy for recovering endangered Colorado River fishes. *Rivers* 17:30-32.

_____. 1998. Early records of the endangered fish *Gila cypha* Miller from the Yampa River of Colorado, with notes on its decline. *Copeia* 1998:190-193.

_____, and C.A. Karp. 1989. Habitat use and stream flow needs of rare and endangered fishes, Yampa River, Colorado. U.S. Fish and Wildlife Service Biological Report 89(14):1-27.

_____. 1990. Spawning and movements of razorback sucker, *Xyrauchen texanus* (Abbott), in the Green and Yampa rivers, Colorado and Utah. *Southwestern Naturalist* 35:427-433.

_____, and C.W. McAda. 1984. Migration, movements, and habitat preference of Colorado squawfish, *Ptychocheilus lucius*, in the Green, White and Yampa Rivers, Colorado and Utah. *Southwestern Naturalist* 29:289-299.

_____ and G.B. Haines. 1991. Distribution, abundance, habitat use, and movements of young Colorado squawfish *Ptychocheilus lucius*. *Transactions of the American Fisheries Society* 120:79-89.

_____, and J.F. Saunders, III. 1996a. Nonnative fishes in the upper Colorado River basin and a strategic plan for their control. Final report to the Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin. Cooperative Agreement 14-48-0006-95-923. Center for Limnology, University of Colorado at Boulder. Pp. I-vii, 1-84 + app.

_____, and J.F. Saunders, III. 1996b. Multispecies recovery plan for four endangered fishes of the mainstream Colorado River. Draft Report to the Denver Regional Office of the U. S. Fish and Wildlife Service. Center for Limnology, University of Colorado at Boulder. 126 pp + 3 app.

_____ and J. M. Beard. 1990. *Esox lucius* (Esocidae), and *Stizostedion vitreum* (Percidae) in the Green River basin, Colorado and Utah. *Great Basin Naturalist* 50(1):33-39.

- _____ and N.J. Nikirk. 1990. Growth, diet, and status of channel catfish, *Ictalurus punctatus*, in the Green and Yampa rivers, Colorado and Utah. *Southwestern Naturalist* 35(2):233-244.
- _____, B.D. Burdick and C.W. McAda. 1984. Use of radiotelemetry for obtaining habitat preferences of Colorado squawfish. *North American Journal of Fisheries Management* 4:177-180
- _____, B.D. Burdick, R.A. Valdez, C.M. Haynes, T.A. Lytle, and C.R. Berry. 1982. Fishes of the upper Colorado River Basin, distribution, abundance, and status. Pages 12-70 in: Miller, W.H., H.M. Tyus, and C.A. Carlson (editors). *Fishes of the upper Colorado River System: present and future*. American Fisheries Society, Bethesda, MD. 131 pp.
- _____, C.W. McAda, and B.D. Burdick. 1982. Green River Fishery Investigations: 1979-1981. Pages 1-99, IN: U.S. Fish and Wildlife Service and Bureau of Reclamation, Colorado River Fishery Project, Part II. Salt Lake City, UT. 365
- _____, R.L. Jones, and L.A. Trinca. 1987. Green River rare and endangered fish studies, 1982-1985. Final Report. Colorado River fishes monitoring program. U.S. Fish and Wildlife Service, Vernal, Utah.
- U.S. Department of the Interior. 1996. Procedures for stocking nonnative fish species in the upper Colorado River basin. U.S. Fish and Wildlife Service, Denver Colorado. 25 pp.
- U.S. Office of Technology Assessment (USOTA). 1993. Harmful nonindigenous species in the United States. U.S. Congress Office of Technology Assessment, Publications OTA-F-565 (Report) and 566(Summary). U.S. Superintendent of Documents, Washington, DC. 391 + 47 pp.
- U.S. Fish and Wildlife Service (USFWS). 1987. Recovery implementation program for endangered fish species in the upper Colorado River Basin. U. S. Fish and Wildlife Service, Region 6, Denver, CO. 82 pp.
- _____. 1990a. Bonytail chub recovery plan. U.S. Fish and Wildlife Service, Region 6, Denver, CO. 35 pp.
- _____. 1990b. Humpback chub recovery plan. U.S. Fish and Wildlife Service, Region 6, Denver, CO. 43 pp.
- _____. 1991. Colorado squawfish recovery plan (revised). U.S. Fish and Wildlife Service, Region 6, Denver, CO. 56 pp.

- _____. 1998. Razorback sucker *Xyrauchen texanus* recovery plan. Region 6, Denver, CO. 77pp.
- _____. 1994a. Determination of Critical Habitat for four Colorado River Fishes; Final Rule. U.S. Fish and Wildlife Service, Federal Register 59(54):13374-13400.
- _____. 1994b. Report to Congress: Recovery program, Threatened and endangered species. U.S. Government Printing Office, Washington, DC.
- _____ and National Marine Fisheries Service. 1994. Notice of interagency cooperative policy for peer review in Endangered Species Act activities. Federal Register 59(126):34273-34271.
- Valdez, R.A., and E.J. Wick. 1983. Natural VS. Manmade backwaters as native fish habitat. Pages 519-536, IN: V.D. Adams and V.A. Lamarra (eds), Aquatic resources management of the Colorado River ecosystem. Ann Arbor Scientific Publishers, Ann Arbor, Michigan.
- _____, and G.H. Clemmer. 1982. Life history and prospects for recovery of the humpback and bonytail chub. Pages 109-119, in W.H. Miller, H.M. Tyus, and C.A. Carlson (editors). Fishes of the upper Colorado River system: Present and future. American Fisheries Society, Bethesda, MD.
- _____, and R.D. Williams. 1993. Endangered fish of Cataract Canyon. Final report to the U.S. Bureau of Reclamation. BIO/WEST, Incorporated. Logan Utah
- _____, and R.J. Ryel. 1995. Life history and ecology of the humpback chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona. Executive summary to the Bureau of Reclamation, Salt Lake City, Utah. Contract No. 0.CS-40-09110. 23 pp.
- _____ and W.J. Masslich. 1989. Winter habitat study of endangered fishes, Green River. BIO/WEST Report 136-2. Logan, Ut. 184 pp.
- _____, W.J. Masslich, and A. Wasowicz. 1992. Dolores River native fish habitat suitability study. Final Report to the Utah Division of Wildlife Resources, Contract 90-2559. BIO/WEST Inc., Logan Utah.
- _____, P. Mangan, R. Smithy, and B. Nilson. 1982. Upper Colorado River investigation (Rifle Colorado to Lake Powell Utah). Pages 101-279, IN U.S. Fish and Wildlife Service and Bureau of Reclamation, Colorado River Fishery Project, Part II. Salt Lake City, UT. 365 pp.

- _____, W.J. Masslich, R. Radant, and D. Knight. 1990. Status of the Virgin spinedace (*Lepidomeda mollispinis mollispinis*) in the Virgin River drainage, Utah. BioWest Report PR-197-1. 43 pp.
- Vanicek, C. D. 1967. Ecological studies of native Green River fishes below Flaming Gorge Dam, 1964-1966. Ph.D. thesis, Utah State University, Logan, UT. 125 pp.
- Vanicek, C.D. and R.H. Kramer. 1969. Life history of the Colorado squawfish (*Ptychocheilus lucius*) and the Colorado chub (*Gila robusta*) in the Green River in Dinosaur National Monument 1964-1966. Transactions of the American Fisheries Society 98:193-208.
- Wallis, O.L. 1951. The status of the fish fauna of the Lake Mead National Recreation Area, Arizona-Nevada. Transactions of the American Fisheries Society 80:84-92.
- Werner, R.G. 1979. Homing mechanisms of spawning white suckers in Wolfe Lake, New York. New York Fish and Game Journal 26(1)48-58.
- Westwater Engineering. 1996. Technical Memorandum: Endangered fish of the upper Colorado River, observations from 1970 through 1995: George T. Kidd. Appendix C. Technical memorandum IN: Camp Dresser and McKee, Inc.: Replacement of the Plateau River pipeline: Biological Assessment. Denver Colorado ..
- Wick, E.J. and J.A. Hawkins. 1989. Colorado squawfish winter habitat study, Yampa River, Colorado, 1986-1988. Contribution 43, Larval Fish Laboratory, Colorado State University, Fort Collins. 96 pp.
- Wick, E.J., C.W. McAda, and R.V. Bulkley. 1982. Life history and prospects for recovery of the razorback sucker. Pages 120-126 in: W.H. Miller, H.M. Tyus, and C.A. Carlson (editors). Fishes of the upper Colorado River system: Present and future. American Fisheries Society, Bethesda, MD.
- _____, D.L. Stoneburner, and J.A. Hawkins. 1983. Observations on the ecology of Colorado squawfish (*Ptychocheilus lucius*) in the Yampa River, Colorado, 1982-1988. Technical Report 83-7, Water Resources Support Laboratory, U.S. National Park Service, Fort Collins, Colorado. 55 pp.
- Wilson, M. 1996. Coordination of reservoir operations. Project CAP 14. FY 96 Annual Report of the Recover Program for Endangered Fishes of the Upper Colorado River Basin. Unpublished report on file with the U.S. Fish and Wildlife Service, Denver, Colorado.

Wydoski, R.S., and E.J. Wick. 1996. Ecological value of flooded bottomland habitats to endangered fishes in the Upper Colorado River Basin. U.S. Fish and Wildlife Service, Denver. 33 pp.

Native Species	Introduced Predator	Reference
Razorback sucker	channel catfish	Medel-Ulmer 1983, Minckley 1983, Bozek et al. 1984, Brooks 1986, Langhorst 1987, Marsh and Langhorst 1988, Marsh and Brooks 1989, Marsh and Minckley 1989
	common carp	Jonez and Sumner 1954, Medel-Ulmer 1983, Minckley 1983, Bozek et al. 1984, Brooks 1986, Langhorst 1987, Marsh and Langhorst 1988, Marsh and Brooks 1989, Marsh and Minckley 1989
	green sunfish	Langhorst and Marsh 1986, Medel-Ulmer 1983, Minckley 1983, Bozek et al. 1984, Brooks 1986, Langhorst 1987, Marsh and Langhorst 1988, Marsh and Brooks 1989, Marsh and Minckley 1989, Muth and Beyers, in press
	sunfishes	Mueller 1995
	largemouth bass	Mueller 1995
	flathead catfish	Medel-Ulmer 1983, Minckley 1983, Bozek et al. 1984, Brooks 1985, Langhorst 1987, Marsh and Langhorst 1988, Marsh and Brooks 1989, Marsh and Minckley 1989
Colorado squawfish	channel catfish	Coon 1965, Muth and Beyers, in prep.
	green sunfish	Osmundson 1987, Muth and Beyers, in prep.
	largemouth bass	Osmundson 1987
	smallmouth bass	Hendrickson and Brooks 1987, Hendrickson 1993
	black crappie	Osmundson 1987
	bullheads	Taba et al. 1965, Hendrickson and Brooks 1987, Osmundson 1987
	northern pike	Crowl and Lentsch 1995
	flathead catfish	Hendrickson 1993
Humpback chub	channel catfish	Valdez and Ryel 1995, Douglas and Marsh 1996
	bullheads	Taba et al. 1965
	brown trout	Valdez and Ryel 1995
	rainbow trout	Valdez and Ryel 1995, Douglas and Marsh 1996

Table 1. Summary of citations for direct evidence of predation by nonnatives on native fishes in the Colorado River Basin.

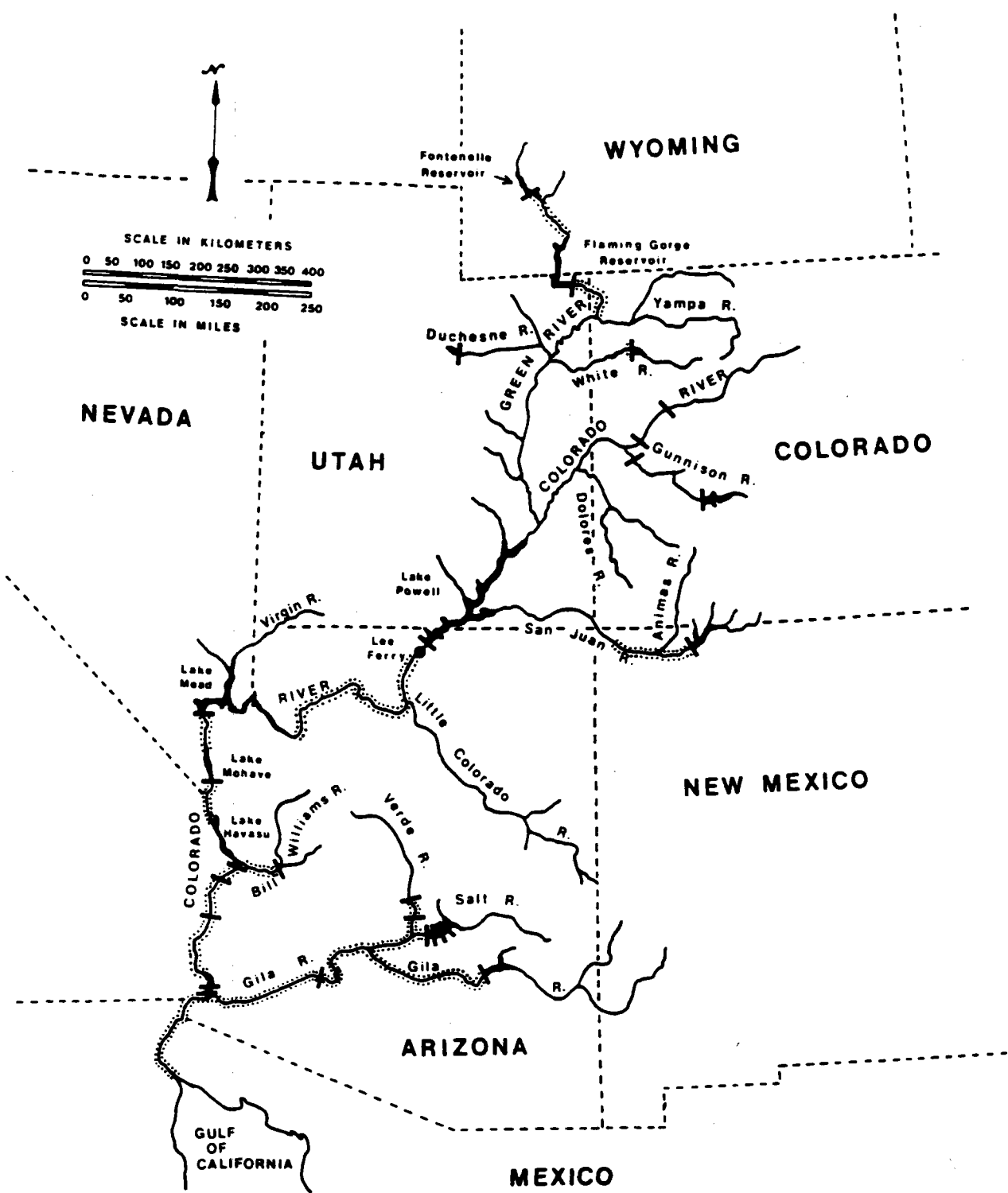


Figure 1. Mainstream barriers and their impacts in the Colorado River basin (after Tyus 1984). Solid bars perpendicular to channel indicate location of barriers, darkened sections of channel above barriers show impoundments, and stippling indicates extent of downstream impact.

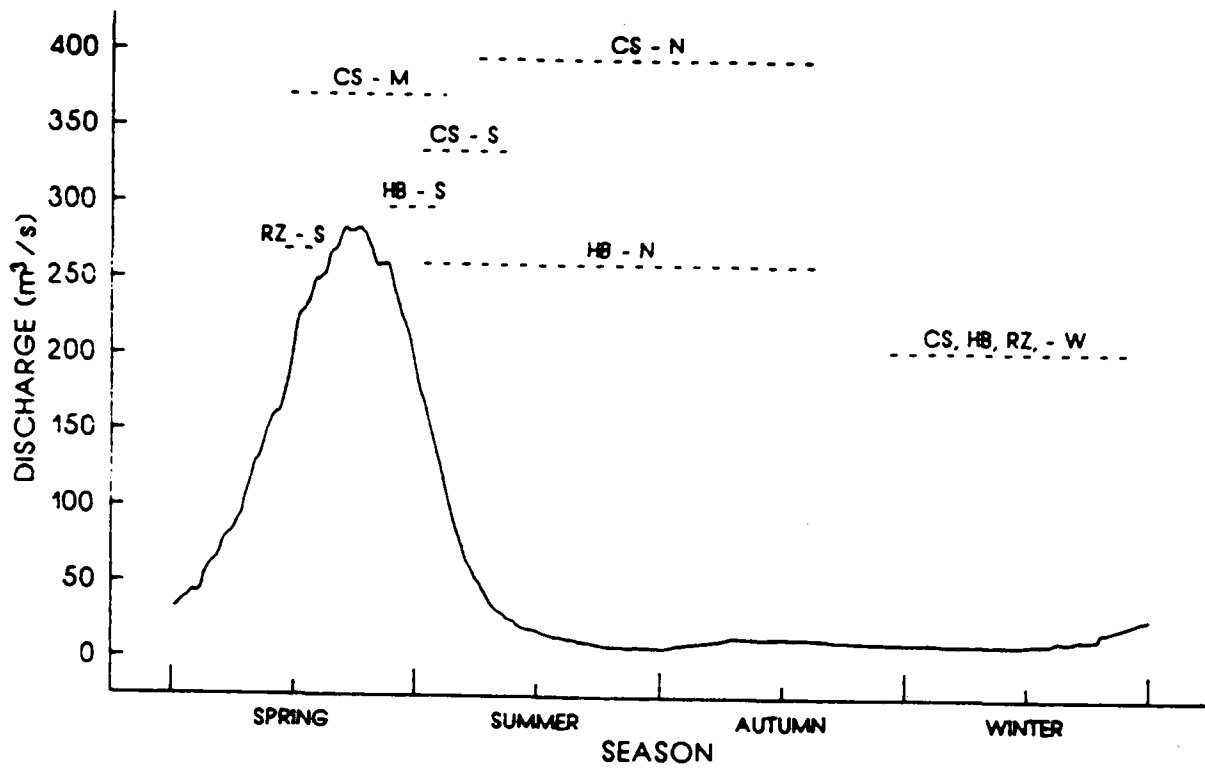


Figure 2. Conceptual relationship between the natural hydrograph and the timing of events (M=migration, S=spawning, N=nursery, W=winter) in the life history of Colorado squawfish (CS), razorback sucker (RZ), and humpback chub (HB). (After Tyus and Karp 1989).

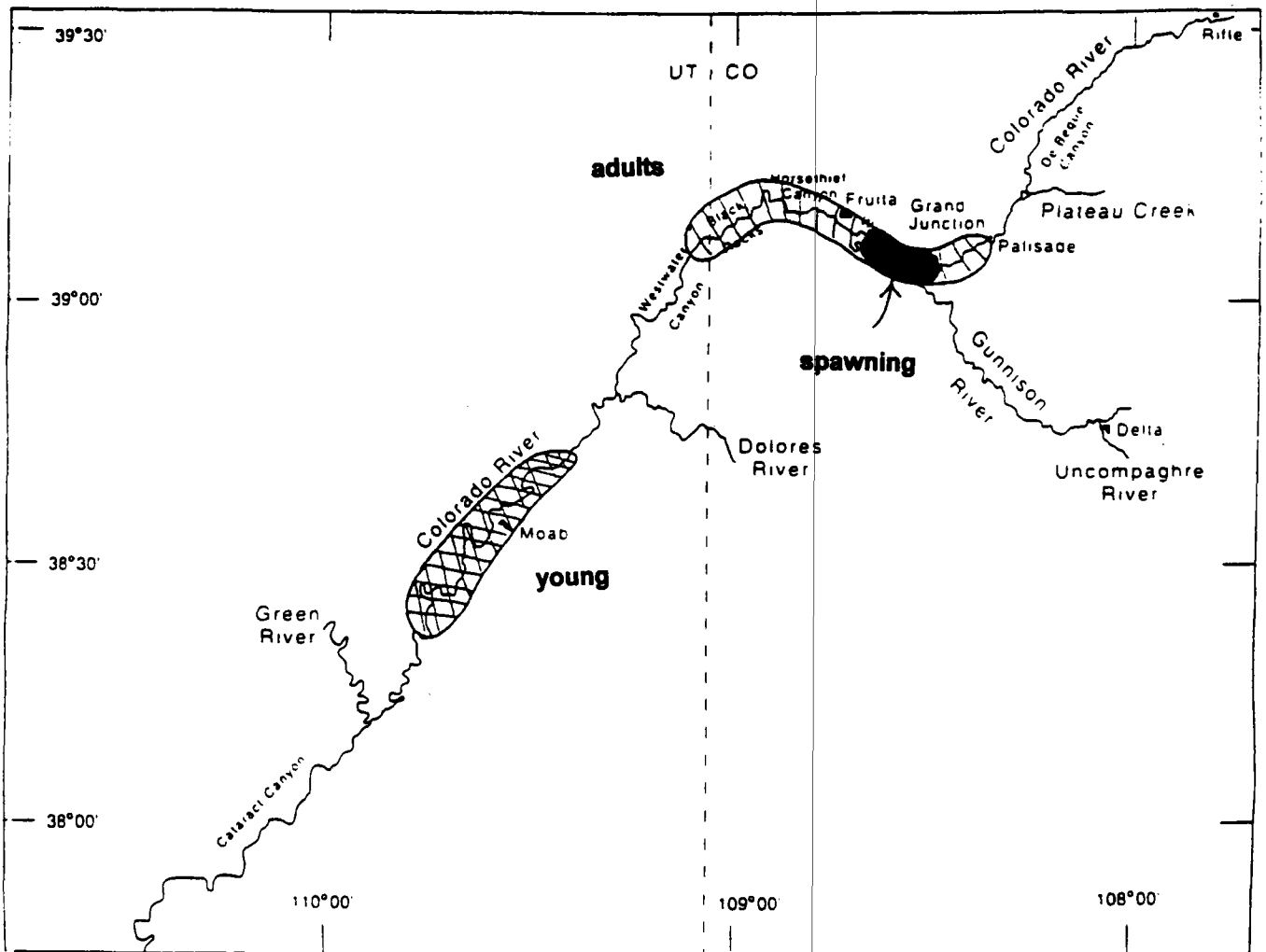


Figure 3. The locations of spawning habitat and areas of high density for young and adult Colorado squawfish in the upper Colorado River.

APPENDIX

Major River Reaches

The focus of this review is the Colorado River and its major tributaries between its confluence with the Green River and Rifle, Colorado. For convenience, and for historical reasons, the mainstem will be divided into two major reaches (in order moving upstream): (1) confluence with the Green River to Palisade, Colorado, and (2) Palisade to Rifle, Colorado. The two main tributaries, Gunnison and Dolores, will be treated separately. For each of the reaches and tributaries, this review will cover the major physical and hydrologic features, significant aspects of water quality, suitability of habitat, and historic and recent occurrence of the endangered fishes.

Upper Colorado River from the Green River to Palisade (RM 0 to 190). This section of the river has been designated as critical habitat for all four of the listed fishes. Although adult and juvenile squawfish are found throughout this reach, adult Colorado squawfish tend to be more common above Westwater Canyon (RM 125), while younger fish were more common downstream (Valdez et al. 1982, Archer et al. 1985, McAda et al. 1994). Humpback chub were common only in Westwater and Black Rocks, and razorback sucker were captured in gravel pits in the Grand valley area. No bonytail were captured.

Flow in this reach is regulated chiefly by dams and diversions upstream on the Colorado and Gunnison rivers. Upstream flow regulation has reduced the average instantaneous flows to only 48% of historic conditions (Osmundson and Kaeding 1989), and annual average flows have been reduced about 30% (M. Harvey, pers. comm.). There is no major flow regulation within the reach. The Gunnison and Dolores rivers are tributary to the reach, adding about 40% of the average annual water volume. Because there are no dams or major diversions, there are no significant barriers to fish migration. The reach is typically low-gradient alluvial habitat, but it is not entirely uniform. The reach includes two significant areas of canyon habitat, Black Rocks and Westwater, and is sufficiently heterogeneous that it was divided into 7 distinct strata for fish sampling, abstracted as follows from Valdez et al. (1982):

Stratum C. The lowest stratum in the UCR extends 47 miles from the mouth of the Green River to Potash. In this reach, the river meanders through a wide floodplain. The river is shallow (average depth of about 1 foot) and contains the highest number of backwater habitats (11.5 per 10 km; 33%) in the UCR. This reach contains the most important nursery (rearing) habitat for young Colorado squawfish in the UCR. Shallow runs were the most common habitat. Juvenile and adult squawfish also were captured in this reach. A total of 18 fish species occur, and nonnative common carp (the most abundant large fish), red shiner, sand shiner, and channel catfish were abundant. Two adult razorback suckers were captured in Stratum C.

Stratum D. River conditions change upstream of Potash. The 24 mile section above Potash flows through an open valley, where the river channel is more defined, but backwaters (7.4/10 km; 21%) and eddies were common. As in stratum C, 18 species of fishes were collected, and native flannelmouth sucker were abundant. Bluehead sucker and roundtail chub were common. The same nonnative fishes

were abundant as in stratum C, but largemouth bass increased in number. All life stages of Colorado squawfish occur in Stratum D, and one razorback sucker also was captured.

Stratum E. Stratum E encompasses the next 15 mile reach where the river flows through Moab Canyon, an area of steep canyon walls and some small open valleys. The river consists mostly of deep runs and pools with an average depth of about 7 feet. Adult and juvenile squawfish occur in Moab Canyon, but shallow habitats are limited (e.g., 0.5 backwaters/10m km; 1%). Eighteen fish species were reported, and native roundtail chub were numerous. Carp was the most abundant large species.

Stratum F. Above Moab Canyon the river meanders through 25 miles of shallow canyons and foothills. Predominant habitats were runs and eddies, and average depths were less than 5 feet. Of 16 species reported, some native fishes (Flannelmouth sucker, blue head sucker, and roundtail chub) were more common. Colorado squawfish adults and young were reported. Backwaters were numerous (9/10 km; 26%), but substrates were rock and sand.

Stratum G. Westwater Canyon, one of the deepest reaches of the UCR, extends 14 miles upstream of agate wash. The river channel is narrow and deep (average depth 8 feet), and a series of rapids creates turbulent conditions. Humpback chub exist in this area, and habitats are primarily deep runs, eddies and pools. Backwaters are few (3/10 km; 9%) and only 13 fish species were reported. Roundtail chub was the most abundant large fish.

Stratum H. Upstream of Westwater Canyon, the UCR flows 29 miles through alternating areas of sagebrush parks and open canyons, including Horse thief and Ruby Canyons. Substrates are gravel/rubble and sand/silt, and habitats are runs, with some pools and eddies. Backwaters are few (0.8/10 km; 2%). Average depth was 4 feet. Seventeen fish species were reported, including Colorado squawfish, humpback chub, and razorback sucker. This reach included Black Rocks, an area that supports a large population of humpback chub. Flannelmouth sucker was the most abundant large fish.

Stratum I. The uppermost reach in this river section extends from Loma to Palisade, a distance of 31 miles. It passes through developed land, including the city of Grand Junction. The Gunnison River enters midway through this stratum. The river is extensively braided and there are many gravel islands. A series of inundated gravel pits occur in this reach, including Walter Walker State Wildlife Area, and Clifton Pond. Average water depth is about 4 feet. Seventeen fish species were reported; Bluehead and flannelmouth suckers were the most abundant species, comprising about 87% of the total electrofishing/trammel net catch.

The Grand Valley, which occurs within Stratum I of this reach, has been identified as important to recovery efforts for the listed fishes (e.g., Archer et al. 1985, Osmundson et al. 1995), principally due to the numbers of Colorado squawfish and razorback sucker captured there. The Grand Valley has been divided into two separate sections: a 15- Mile Reach and an 18-Mile Reaches by USFWS (Archer et al. 1985). The 15-Mile Reach, which has figured prominently in recent discussions of recovery efforts, extends from the confluence with the Gunnison River upstream to the Grand Valley diversion dam at Palisade (Osmundson and Kaeding 1989, 1991). Most of the reach lies within the Grand Valley, which contains the largest urban area in the upper Colorado River basin. Consequently, it is heavily influenced not only by urbanization in Grand Junction, but also by extensive agriculture in the Grand Valley.

Flows in the 15-Mile Reach have been greatly altered by dams and diversions upstream. The mean peak flow is now only about 56% of historic, and flows in June have been reduced to 55% of historic levels (Osmundson and Kaeding 1989, 1991). The effects of water resource development on the hydrology and geomorphology of this part of the river were studied recently by Van Steeter (1996). In general he found that

the areas of complex riverine habitats had decreased 12 to 29% after major reservoirs were brought on line. Changes to physical habitat included loss of shoreline habitat, diking, and riprap. Although there are no major dams or diversions within the 15-mile reach, the Grand Valley diversion at the head of the reach prevents upstream migration of fish.

The significance of this reach to recovery of endangered fishes in the upper Colorado River and the need for instream flows to support those fishes have been a topic of several recent reports (Kaeding and Osmundson 1989, Osmundson and Kaeding 1991, Osmundson et al. 1995, Osmundson 1996, USBR 1992). Although this reach of the upper Colorado River comprises only about 8% of habitat used by endangered fishes, it is considered extremely important by the USFWS because of the high catch rates of native fishes, high catch rates of adult Colorado squawfish, and historic use of the area by razorback suckers in spring (Osmundson et al. 1995). According to the USFWS, the most critical habitat issue in the reach is the adequacy of instream flows. The USFWS believes that it is necessary to acquire or appropriate additional water in order to have sufficient flow for the endangered fishes, and have made flow recommendations to aid in maintaining the present population of Colorado squawfish (Kaeding and Osmundson 1989, Osmundson and Kaeding 1991, Osmundson et al. 1995). Alternatives for providing water to meet these recommendations have recently been studied, but low flows may not be at a dependable or desirable level (USBR 1992).

The 15-Mile Reach, and downstream portions of the Grand Valley contained historical spawning sites of the Colorado squawfish and razorback sucker, but this area has been heavily influenced by gravel mining operations (Valdez et al. 1982, Archer et al. 1985). Colorado squawfish spawning has only been documented twice in the last 14 years, when small larvae were captured. Apparent recruitment failure in this reach of the Colorado River is probably linked to the abundance of introduced nonnative fishes. Altered habitats in the 15-Mile Reach have been extensively colonized by nonnative fishes. This is especially true of gravel pit ponds which can be important sources of piscivorous fishes (Burdick 1994, Osmundson 1987).

Another reach that has been given special status is the 18-Mile Reach below the mouth of the Gunnison River. The 18-Mile Reach is greatly influenced by flows of the Gunnison River, which supplies about 40% of the total annual flow (Burdick 1997). The evidence for spawning of Colorado squawfish in this reach includes collections of very young fish, presence of ripe adults, and radiotelemetry data (Valdez et al. 1982, Archer et al. 1985, McAda et al. 1994). In addition, ripe razorback sucker were historically numerous, and may have spawned in inundated gravel pit habitats (Valdez et al. 1982). The 18-Mile Reach also contains the most important bottomland habitats in the UCR. The most important bottomlands include the Walter Walker State Wildlife Area (Irving and Burdick 1995). Bottomlands may be significant for future recovery efforts.

Colorado River from Palisade to Rifle (RM 190 to 240). This reach of the river is relatively high gradient although it has a lower gradient section near Rifle. Although spring flows have been reduced by about 40% in this reach, baseflows have been increased by 20% (Anderson 1996). The changed hydrologic regime has resulted in a

narrowing of the channel. In addition, channelization has eliminated floodplain and bottomland habitat. Fish migrations are blocked partially or completely by the Grand Valley diversion (RM 185.4), the Price Stubb Dam (RM 188.3), and the Government Highline dam (RM 193.6). This section of the river is included in critical habitat designation (USFWS 1994).

Recent surveys of fish abundance have shown that native fishes predominate (>80%), especially in Debeque Canyon (Valdez et al. 1982, Anderson 1996). Flannelmouth and bluehead suckers were the most abundant native species. Roundtail chub were abundant in Debeque Canyon (RM 194-197) and common upstream. The collection of putative humpback-roundtail chub hybrids in Debeque Canyon led Valdez et al. (1982) to suggest that these fish were remnants of a once larger population of humpback chub. Colorado squawfish and razorback sucker are known to have occupied this reach in the past (Valdez et al. 1982, Westwater Engineering 1996). Studies of larval drift at Parachute and Palisade have shown extensive reproduction of native fishes (Valdez et al. 1985).

Adult Colorado squawfish habitat was judged excellent in the riverine section upstream of Debeque due to the abundance of forage fishes, including native suckers and whitefish. There were numerous pools and deep runs during the baseflow period, as well as ample backwaters and eddies during spring flows. Except for a few trout and centrarchids, no large native or nonnative predators were common in the electrofishing surveys. The Colorado Division of Wildlife concluded that this reach has habitat suitable for reintroduction of adult Colorado squawfish and razorback sucker (Anderson 1996).

Once again relying on the work of Valdez et al. (1982), the characteristics of the major strata in this reach can be described as follows:

Stratum J. Fish habitat in the 25-mile stratum from Palisade to Debeque Canyon consists mainly of runs, small pools, and a few backwaters. Some areas adjacent to I-70 and the tracks of the Union Pacific Railroad have been altered by use of riprap to protect the shoreline. Where riprap has been used, the river channel tends to be deep (avg. of 6 ft), more stable, and with higher water velocity. Fish populations were dominated by native suckers, but common carp and roundtail chub also were abundant. Colorado squawfish and razorback sucker were captured downstream of the Highline dam, which is a 17-foot barrier.

Stratum X. In the 31-mile section from Debeque to Rifle, the river is less confined and more natural in appearance. It flows through open cropland and sagebrush foothills. The average depth is about 2 feet, but deeper areas occur as the river winds through erodible substrates and areas that have been mined for gravel. The upper part of this stratum is a zone of transition between habitat occupied by warm-water fishes and that occupied by cool-water fishes. Native suckers, common carp, and roundtail chub were the most abundant species. Most of the fish habitats were reported to be runs and riffles with some pools and eddies. Some overbank flooding occurs in the spring.

Tributaries

Gunnison River. Historic flows of the Gunnison and its tributaries have been greatly altered by water development projects. Private development began in about 1880 and federal involvement began in 1909 with construction of the Gunnison Tunnel. Major projects on the main stem of the Gunnison include the Taylor Park Dam which was completed in 1937 and the Aspinall unit reservoirs which began with construction of Blue Mesa in 1966 and concluded with the Crystal Reservoir in 1976. These reservoirs have resulted in extreme alteration of the historic flows in the Gunnison River. The Redlands Diversion, which was constructed in 1918, posed a complete barrier to fish migration until 1996 when a fish ladder was completed (Anonymous 1996a).

The Colorado squawfish and the razorback sucker were once common or abundant in the Gunnison River (Jordan 1891, Jordan and Evermann 1896). Both species were reported from the Gunnison in the 1930s and the 1950s (Chamberlain 1936, Kidd 1977). Colorado squawfish were still present in the lower Gunnison River by the 1980s, but the razorback sucker had virtually disappeared (Valdez et al. 1982). More recent studies of the Gunnison River have documented spawning by Colorado squawfish (Anderson 1996), and individuals of a remnant population of Colorado squawfish (Burdick 1995). Flow recommendations have been made by USFWS to assist fish in passing upstream through the Redlands Diversion during low flow periods (Burdick 1997).

Physical habitat and fish community composition in the lower Gunnison River have been evaluated recently by Burdick (1995). The following accounts are based on electrofishing samples taken during Burdick's work with some supplemental information from Valdez et al. (1982):

Stratum 1. The first reach extends three miles from the mouth of the Gunnison River to the Redlands diversion dam, which forms a barrier to fish migration for most of the year. Operation of the diversion results in occasional dewatering of the reach. During the drier periods, most fish occupy a large pool immediately downstream of the diversion structure. The unfavorable hydrologic regime makes this an atypical reach. Gradient is high (7 feet per mile) and fish habitat consists mainly of shallow riffles and runs during the drier months.

Stratum 2. The second reach extends 12 miles from the Redlands diversion to Whitewater. The river is bounded by a wide floodplain which contains gravel pits and quarries. Stream gradient is high (5.7 feet per mile) and average depth is 4.3 ft. Fish habitat consists mainly of riffles, slow runs, and a few backwaters. About 90% of the fish captured were native species.

Stratum 3. The next 15 miles of the river, from Whitewater to Bridgeport, flows primarily through canyon habitat. The gradient is 5.9 feet per mile and the average depth is 4.3 feet. Fish habitat consists mainly of main channel runs with few riffles or side channels. About 90% of the fish captured were native species.

Stratum 4. In the 12 miles from Bridgeport to Escalante, the Gunnison has a braided channel that is bounded by historic floodplain, part of which supports fruit orchards. The gradient is 6.5 feet per mile and the average depth is 3.3 feet. The channel contains two small rapids and two rock structures for diverting irrigation flows. A suspected spawning area for Colorado squawfish occurs between RM 30 and 35. More than 90% of the fish captured were native species.

Stratum 5. In the 18 miles from Escalante to the Hartland diversion, the river flows through an extensive floodplain. The channel is braided and it contains diverse fish habitat including runs, riffles, and

backwaters. The gradient is 9.3 feet per mile and the velocity is relatively high. About 80% of the fish captured were native species. Several pike, which probably had escaped from Paonia Reservoir, were also captured in this reach.

Stratum 6. In the seven miles above the Hartland diversion, the braided channel of the Gunnison River flows through a large floodplain. Some vegetated islands occur in this stratum. The gradient is very high (12.5 feet per mile) and the water flows swiftly. Habitat complexity is higher in this stratum than in the others. Habitat consists of riffles, runs, and backwaters. Part of the channel (3.3 miles) has been modified extensively by dikes and gravel mining operations. About 60% of the fish captured were native species. The most abundant nonnative fishes were white sucker, brown trout, rainbow trout, and white sucker hybrids.

Stratum 7. The uppermost reach extends 8 miles to the confluence of the North Fork. The river flows through an open canyon and has a gradient of 8.8 feet per mile. Part of the adjacent floodplain supports fruit orchards. About 40% of the fish captured were native species. The most abundant nonnative species were white sucker, brown trout, rainbow trout, and white sucker hybrids.

Dolores River. Flows in the lower portion of the Dolores River have been greatly altered by dams and diversions to the extent that nearly all water is removed at times of high demand. Under those conditions, the San Miguel River provides most of the flow that appears in the lower part of the Dolores. Habitat in the lower part of the river was evaluated recently; although physical habitat may be suitable at some times of the year, flow regulation and pollution present serious problems (Valdez et al. 1992). Uranium, gold, and salt mining have resulted in severe pollution and fish kills as recently as the 1960s (Joseph et al. 1977). In one account, most of the fish in the lower 60 miles of the river were killed by mine pollution (Valdez et al. 1992). Fishes tissues contained elevated levels of heavy metals (Kunkle et al. 1983).

In addition to problems with physical habitat, biological conditions also are degraded by the presence of nonnative fishes. In a recent study, 70 to 80% of the fish captured over a 2-year period were nonnatives (Valdez et al. 1992). Little is known about the historical abundance of the endangered fishes in the Dolores River, but neither the Colorado squawfish nor the razorback sucker has been reported in the last 20 years, with the exception of 4 squawfish captured in the lower 2 km of the river in 1991 (Valdez et al. 1992). Poor water quality and severe flow depletions appear to make the Dolores River poorly suited for the four endangered fishes (Valdez et al. 1992). However, water quality may be improved by cleanup efforts now mandated by regulatory agencies (Valdez et al. 1992).

A recent survey by Valdez et al. (1992) divided the river into 6 strata, the details of which are summarized below:

Stratum 1. In the 22.7 miles from the mouth of the Dolores to the UT-CO state line, the river traverses 2 different regions: a deep upper region bounded by a canyon and a shallow lower region bounded by a floodplain. Fish habitat was varied and included slow runs, pools and small rapids. Almost all of the fish were nonnative species of which common carp, red shiner, and fathead minnow were abundant.

Stratum 2. In the next 18.6 miles to the confluence of Salt Creek, the Dolores has a braided channel that is bounded by a wide floodplain. Most of the fish habitat consisted of slow runs, but there were also riffles and small rapids. The native flannelmouth sucker was the most abundant of the large fishes.

Stratum 3. The next 23.1 miles, extending to the confluence of the San Miguel, flows through deep, narrow canyons. Fish habitat consists chiefly of small riffles, rapids, and deep pools. Native flannelmouth suckers were very abundant.

Stratum 4. From the San Miguel to Paradox Valley (10.4 miles), the Dolores flows through a narrow canyon with shallow riffles and runs, and an open valley with a wide floodplain. Flannelmouth suckers comprised almost 60% of the fish community.

Stratum 5. This stratum extended for almost 54 miles and included narrow canyons where the fish habitat consisted of riffles and pools, and small valleys where the fish habitat consisted of slow runs and shallow eddies. The dominant large fish was the rainbow trout.

Reach 6. The final 48 miles flowed mainly through a narrow canyon. Fish habitat consisted of pools, riffles, and runs. Rainbow trout were the predominant large fish.