RESOURCE USE BY NATIVE AND NON-NATIVE FISHES OF THE LOWER COLORADO RIVER: LITERATURE REVIEW, SUMMARY, AND ASSESSMENT OF RELATIVE ROLES OF BIOTIC AND ABIOTIC FACTORS IN MANAGEMENT OF AN IMPERILED INDIGENOUS ICHTHYOFANA

DRAFT REPORT

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SUMMARY OF KEY FINDINGS

Native and non-natives fishes that occupy the lower Colorado River overlap broadly in their physical habitat and resource uses. Spatio-temporal overlap was evident at all life stages (larval, juvenile, and adult). Common resource uses involved critical life-history functions such as feeding (subsuming maintenance and growth); however, a substantially greater number and proportion of non-native fishes than native species are piscivorous predators. Spatial, temporal and thermal aspects of spawning were comparable among native and non-native fishes, notwithstanding requirements of cold-vs warm-water taxa. Faunas were distinctive in mode of reproduction: native species all are broadcast spawners without parental care, while non-natives are predominated by nest-building and some level of parental protection of eggs and young.

No attribute of physical habitat or resource use can be identified that markedly or marginally favors one group of fishes over another, and we cannot envision habitat manipulations or features that could be made to accomplish such a goal. Rather, the evidence supports an hypothesis that presence of non-native fishes alone precludes successful life-cycle completion by components of the native fauna. This array of non-native fishes now present has feeding, behavioral, and reproductive attributes that allow it to displace, replace, or exclude native kinds.

The lower Colorado River is physically altered and hydrologically regulated. New habitats created by dams include impoundments that represent large lakes, and thermally depressed, downstream tailwaters. These are dramatically different from the lower Colorado River before dams. Nonetheless, there is ample evidence to support an argument that these habitats would be occupied by native fish communities, and these native fishes would find resources necessary to life-cycle completion and population maintenance, if there were no non-native fishes. It is absurd to suggest that the Colorado River would be devoid of fishes if alien species had not been introduced to the system.
Given these compelling arguments and the preponderance of available information, we recommend segregated management of native and non-native fishes in the lower Colorado River. Native fish management should focus on providing aquatic habitats free of and protected from non-native fishes, and populated with native populations or assemblages derived from appropriate, genetically defined stocks. Development of a comprehensive management plan to implement this recommendation should be accomplished by resource management entities in cooperation with species experts and other interested parties. Because the status of the imperiled native fish fauna of the Colorado River continues to decline, responsible parties are urged to act decisively and expediently in this new direction. Non-native fish management recommendations relative to physical habitat and resource uses are beyond the scope of this report.
INTRODUCTION

The ichthyofauna of the present-day Colorado River mainstream is a unique assemblage predominated by naturalized populations of non-native species (Minckley 1978, U.S. Fish and Wildlife Service [USFWS] 1980). In the lower river (below Grand Canyon) the entire freshwater fish fauna has been essentially replaced, including five, large-bodied endemic species which either are extirpated (humpback chub [Gila cypha], Colorado squawfish [Ptychocheilus lucius] and flannelmouth sucker [Catostomus latipinnis]), or severely depleted in numbers and reduced in range (bonytail [Gila elegans] and razorback sucker [Xyrauchen texanus]) as a result of human development of water resources. These fishes once were widely distributed and abundant (Minckley 1973, 1991), but all except flannelmouth sucker now are federally listed as endangered (U.S. Fish and Wildlife Service [USFWS] 1974, 1980, 1991), with critical habitats that include portions of the lower Colorado River mainstream (USFWS 1994).

The largest known populations of bonytail and razorback sucker occupy Lake Mohave (Marsh and Minckley 1992, Marsh 1994), a mainstream reservoir impounded across the Arizona-Nevada border. Much smaller populations live in lakes Havasu and Mead.

1 Populations of humpback chub and flannelmouth sucker persist in the mainstream and major tributaries in Grand Canyon (Douglas and Marsh 1996, in press), and flannelmouth sucker also occupies the Virgin River, tributary to Lake Mead. Both these fishes, plus Colorado squawfish, still are found in larger streams of the upper basin (Carlson and Muth 1989).

2 Woundfin (Plagopterus argentissimus) now is restricted to the Virgin River (AZ-NV-UT) and desert pupfish (Cyprinodon macularius) is represented in the United States by a few, scattered natural populations. Both of these endangered species are extirpated from the lower Colorado River. Bluehead sucker (Catostomus discobolus), speckled dace (Rhinichthys osculus), and roundtail chub (Gila robusta) also were present, but rare (Minckley 1973), and are not further considered herein.
(Minckley 1983), and scattered individuals are occasionally encountered in downstream river reaches and confluent canals (Marsh and Minckley 1989).

The U.S. Bureau of Reclamation (USBR) and other entities operate a series of dams, control structures, and water intakes or diversions along the lower river (in part, USBR 1996). High dams and their impoundments are Hoover (Boulder Dam, Lake Mead), Davis (Mohave), and Parker (Havasu), and other structures are Headgate Rock, Palo Verde, and Imperial diversion dams, and Laguna Dam (Water and Power Resources Service [WPRS] 1980a). Major water withdrawals from the river include Southern Nevada Water Authority (Las Vegas Valley), Metropolitan Water District (Los Angeles), Central Arizona Project (Granite Reef Aqueduct), Colorado River Indian Tribes (CRIT) Canal, and All American Canal (Imperial and Coachella valleys; in part, WPRS 1980b).

As part of a formal consultation with U.S. Fish and Wildlife Service (USFWS) in accordance with provisions of the Endangered Species Act of 1973 (as amended), USBR completed a biological assessment of impacts associated with its operation of the lower river (USBR 1996). In response, USFWS issued a Biological Opinion (Opinion), which determined, in part, that operation of the river jeopardized continued existence of two endangered fishes, bonytail and razorback sucker (USFWS 1997). The USFWS Opinion included a suite of Reasonable and Prudent Alternatives (RPAs) and Measures (RPMs), implementation or completion of which would have the effect of removing jeopardy. One of these RPAs addressed research funding, as follows (in part):

"RPA #4. Research Funding. Reclamation will provide funds for research into habitat use and habitat preferences of native and non-native fish in the river with the goal of managing to reduce conflicts detrimental to native fish caused by the presence of non-native fish."
This report serves as a necessary step preliminary to implementation of a potentially costly, long-term research program under auspices of RPA#4. Our objective was to assemble a comprehensive database of information on native and non-native fishes, their known habitat uses and preferences, and the potentials for interaction between the two categories.

The fundamental question addressed was whether biotic or biologic factors exerted an over-riding force in determining viability of native fish populations. It is suggested that native fishes can successfully complete their life cycles in virtually any habitat as long as that habitat is devoid of non-native species. It is further suggested that native fishes cannot complete their life cycles in systems occupied by established populations of non-native fishes, regardless of the nature of the shared habitat. Our approach to address these questions was to critically examine available literature and attempt to reach a conclusion as to the probability of success of a lower Colorado River habitat-management program that would enhance native fishes by reducing conflicts with non-native species. Because simple maintenance of native fishes has become a mechanical practice and now routine at a number of locations throughout the Colorado River basin, we herein define as successful only that habitat management which allows native fish species to complete successive life cycle iterations, attain, and maintain stable population structures (abundance, distribution of age classes, and sex ratio) characterized by normal population dynamics (i.e., rates and variation in recruitment, growth, and mortality), without human intervention.

PROBLEM STATEMENT

Can lower Colorado River habitat be managed in ways that enable native and non-native fishes to co-exist, or do interactions between native and non-native species preclude such co-existence independent of habitat? If the former is answered affirmatively, what specific habitat management can be recommended to achieve co-existence between native and non-native fishes?
METHODS

LITERATURE SEARCH -- On-line computer searches were conducted of the three major scientific data bases: Biological Abstracts, Wildlife and Fisheries Review, and Zoological Records. These subsume a number of other powerful databases. Independent searches also were made of the Comprehensive Dissertation Index, which cross-references with Masters Abstracts International, Dissertation Abstracts International, and American Doctoral Dissertations data bases. We also used the Fish and Wildlife Reference Service (Bethesda MD) web site at www.fws.com, which selectively covers published and unpublished reports resulting from Federal Aid in Fish and Wildlife Restoration, Anadromous Sport Fish Conservation, Endangered Species Grants programs, and the Cooperative Fish and Wildlife Research Units, and contacted the U.S. Fish and Wildlife reference library in Fort Collins CO. All searches were comprehensive of the international literature and incorporated information on target species of the lower Colorado River regardless of where (geographically) the information was generated.

Data-base searches were driven by three categories of key words: fish names, words and phrases, and authors (APPENDIX I). Fish names included Latin (scientific) and common names, including variations, synonyms, and permutations of 11 native and 28 non-native species known from the lower Colorado River. Words and phrases included a suite of descriptive terms associated with fish habitat, behavior, and species interactions. Authors were selected among those making substantial theoretical or pragmatic contributions to the general understanding of aquatic ecology, with emphasis on fish-habitat relationships, mechanisms of community structuring, and species associations and interactions. Coverage included both published and grey literature, and was comprehensive from at least 1980 to 1996. Period-of-record varied among data bases from 1861 to date to 1980 to date.
All citations identified by our searches (summarized in APPENDIX II) were examined for potential relevance to the Problem Statement. Those which clearly did not apply, for example, biochemical, genetic, physiological, systematic, or taxonomic studies, were not further considered. A second level of distillation involved identifying those remaining materials for relevance to our specific problem statement, and acquiring copies from a variety of sources (ASU libraries, interlibrary loans, colleagues, or investigator's private collections). Materials were assembled categorically (see below) and the type of study designated (i.e., field vs. laboratory, and by habitat, see Table 2 in REFERENCES USED), abstracts examined critically, and those works considered germane scrutinized for qual- and quantitative information that could be usefully analyses or otherwise interpreted to shed light on our basic questions.

PRESENTATION OF DATA -- Qual- and quantitative data derived from literature were categorically assembled into a series of 2 x 2 matrices that allowed ready recognition of potential overlap in resource use. Resources included physical and chemical features of aquatic habitat, and life history features of target species. Resource use was presented and examined separately for major life stages (i.e., larva, juvenile, and adult). Larvae are defined as young fish from time of hatch to development of a full complement of rayed-fins, and generally included stages referred to in non-specific, lay terms as "fry." Juveniles were non-reproductive, post-larval stages, including those generally termed "fingerlings." Adults were defined as sexually mature individuals, including both reproductive and post-reproductive stages. Fish referred to as "young of year" generally were assigned to the juvenile category. We did not find that term used for species whose life history would result in "young of year" including two (or all) of the larval, juvenile, and/or adult stages (for example, many short-lived fishes like the shiners [genus Cyprinella] and poeciliids [genera Gambusia and Poecilia], among others) that mature sexually in less than a year.
Many investigators combined bonyn tail and roundtail chubs in their studies, and in such cases we used combined data for the two. Humpback chub data were independent of those for other Gila. We also note that Cichlid fishes now in the lower Colorado River may represent various hybrids and back-crosses, and parentage of many of cannot reliably be determined. A number of species have been introduced to the system (see Barrett 1983), enjoyed a period of abundance or even dominance in the community (Minckley 1979, Marsh and Minckley 1985), then dwindled or been subsumed into the hybrid swarm. Included were blue (Oreochromis [Tilapia] aurea), Mozambique (O. [T.] mossambica), and redbelly (Zill's, T. zilli) tilapia.

We include several sections literature with this report to enhance utility of the document and make it easier for the reader to locate and identify specific information. A LITERATURE CITED follows the body of the paper, which provides references for all literature cited in the text. It is followed by a companion REFERENCES USED, which includes the following sections: (1) fish code list, (2) classification list, (3) numbered tables that match those in text and provide supporting referrals to cited literature, and (4) numerically identified (A) and alphabetic (B) lists of all references selected for use in constructing tabulations and matrices. APPENDIX III (Case Studies) has it's own literature cited. APPENDIX IV is a comprehensive, abbreviated bibliography of all literature examined. Finally, APPENDIX V includes a reference list of important works on meta-analysis (below). Although we have attempted to avoid duplication, in some instances it was necessary for clarity and completeness to include the same references in one or more of these sections.

ANALYTICAL PROCESS -- Each section of an individual study, book chapter or report was critically reviewed, particularly tables and figures. Recorded data was primarily qualitative except for juvenile length at initial piscivory, and habitat and spawning temperatures. Other data (e.g., preferred depths, water quality parameters) were disregarded due to their quantitative nature and specificity. However, many reviewed
studies contained quantitative results specifically concerning fish interactions such as piscivory, competition, predation, and aggression between and among fish species represented in the lower Colorado River. We did not perform statistical analyses or tabulate any statistical summaries.

In the future, meta-analysis may be a useful tool in summarizing the findings of this literature review, minimizing funding needs for impending and possibly futile studies. Meta-analysis is a quantitative method of comparing studies with similar hypotheses, independent of outcomes and generating statistically meaningful results; it is the "analysis of analyses" (Wachter 1988, Wolf 1986). As few as two studies may be used, or as in the meta-analysis that led to conclusive evidence as to aspirin's benefits for heart attack prevention, information from 22,000 U.S. doctors was collected (Mann 1990). Primarily used in social sciences, meta-analysis is beginning to enter into biological sciences (Arnqvist and Wooster 1995, Fernandez-Duque and Vareggia 1994). We performed an additional literature search (using the same three major scientific data bases as cited above; approximate time-frame 1980 to present) to generate studies, articles and books concerning the methodology of this analysis, particularly its pros and cons relative to validity (APPENDIX V).

RESULTS

DATABASE SEARCH OUTCOMES -- There were 95,447 keyword "hits" among our searches, and more than 8500 of these were selected for further examination (APPENDIX II Tables 1, 2 and 3). Biological Abstracts yielded 26,682 hits from which 2514 were selected, Wildlife and Fisheries Review gave 42,485 hits (3151 selected), and Zoological Records produced 26,161 matches (2723 selected). The US FWS web-based site (US Fish and Wildlife Reference Service Database at www.fws.com) provided 59 hits on native and non-native species names (all selected, APPENDIX II Table 2), and our search of academic works through Comprehensive Dissertation
Index, Dissertation Index Abstracts International, Masters Abstracts International, and American Doctoral Dissertations provided 52 graduate degree documents based on native fish species names (all selected, APPENDIX II Table 3). Our final reference list comprised 416 citations published over a four-decade period, 1957 through 1997.

HABITATS IN THE LOWER COLORADO RIVER -- Aquatic habitats of the lower Colorado River have been altered dramatically by human development of water resources (Fradkin 1981). Most striking among changes are those associated with construction and operation of high dams: creation of large lentic habitats represented by impoundments, and perennially clear, cold tailwaters in downstream river reaches. Also associated with dams and other river control structures are altered hydrologic (magnitude and timing of flows) and sediment transport (volume and source) regimes. These last parameters also have been profoundly influenced by land uses of tributary watersheds, such as domestic livestock grazing, groundwater withdrawal, mining, timber harvest, and urban development. Because of the over-riding effects of these by-products of human occupation, there are essentially no natural segments remaining along the mainstream lower Colorado River.

The following discussion is generalized and intended to provide only an overview of the present-day lower Colorado River and its habitats. Although there are abundant anecdotal and narrative accounts of the lower river, there have been few quantitative studies of habitat per se, and fewer yet of habitat in context of fishes (see Minckley 1979, Hiebert and Grabowski 1985, 1887, and Marsh and Minckley 1985, 1987 as important exceptions). Additional detail also can be found in Anderson and Prichard 1951, Jonez and Sumner 1954, Hoffman and Jonez 1973, USBR 1976 and 1996, Priscu 1978, Paulson et al. 1980, Brown 1983, and USFWS 1997, and literature cited therein.
Dams and Reservoirs -- There are three major impoundments on the lower Colorado River: lakes Mead, Mohave, and Havasu. These differ fundamentally in morphology and limnological characteristics (summarized in Table 1).

Hoover (Boulder) Dam and Lake Mead were created primarily to provide flood control and storage of irrigation water. The dam also generates hydroelectric power. Primary inflows to Lake Mead are the Colorado River at the outflow of Grand Canyon and Virgin River. The Virgin River is largely unregulated, although there are several diversion dams, which under some conditions result in severe flow depletions. Lake Mead also receives treated urban wastewater from the city of Las Vegas, which adds substantial quantities of inorganic nutrients to the system. It is morphologically complex with several basins separated by narrow, deep channels. As a result, different parts of the reservoir exhibit unique limnological characters. In one study the Upper Basin (at the Colorado River inflow) was oligotrophic, Boulder Basin was oligo-mesotrophic, and Las Vegas Bay was mesotrophic (Paulson et al. 1980). Overall, the lake is characterized as “mildly-mesotrophic” (LaBounty and Horn 1997). Outflow of Lake Mead is a hypolimnetic discharge at Hoover Dam in Black Canyon.

Davis Dam and Lake Mohave were created primarily to re-regulate fluctuating discharge from Hoover Dam. Hydroelectric power also is generated at Davis Dam. Lake Mohave is best described as a “run of the river” impoundment. An upper reach below Hoover dam flows for about 40 km through a steep, narrow canyon which empties into a modestly-wider “Little Basin.” Next is the relatively wide (6 km) Cottonwood Basin, which narrows at its downstream end to form another canyon reach

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3 The Colorado River through Grand Canyon now is regulated by Glen Canyon Dam on the mainstream about 16 km above Lees Ferry. The dam releases cold, clear hypolimnetic water year around, with discharge regime determined largely by demands for generation. Sediment inputs to the Colorado River in this reach are almost exclusively via tributary streams, the two largest of which are Paria and Little Colorado rivers, and the mainstream runs clear unless these other rivers are in flood.
immediately above Davis Dam. Inflow is almost exclusively discharge from Hoover Dam. Inputs from desert-wash flooding is infrequent, sporadic, and a minor contribution. Thus, Lake Mohave generally is clear year-around. Inflowing water from deep within Lake Mead is relatively rich in nitrogen and phosphorus, and as a result the upper reach of Lake Mohave is highly productive, especially where cold, nutrient-rich and warm, surface water mix. This mixing zone migrates several kilometers up- and down-lake seasonally and with changes in discharge at Hoover Dam.

Lake Havasu is impounded by Parker Dam, closed in 1938. The dam and lake were created primarily to provide a sedimentation basin for the California Aqueduct (see below). The impoundment is separated from Davis Dam by a riverine reach about 85 km long. The reservoir itself (downstream of Blankenship Bend) is approximately 50 km long and nearly 5 km across at its widest point. It is relatively shallow, averaging about 5 m overall and approaching 15 m only in vicinity of the dam. Shorelines are complex, formed of submerged desert washes that create myriad embayments of varying size separated by spits or points. Inflow hypolimnetic discharge from Davis Dam delivered via the river reach through Topock Gorge (below). The Bill Williams River (regulated upstream by Alamo Dam and Reservoir) empties into Lake Havasu from the east a few km upstream from Parker Dam.

Passage of Colorado River water through Parker Dam is via epilimnetic penstocks located near the surface, and is used in generate electricity. Major withdrawals from Lake Havasu are the Granite Reef Aqueduct (Central Arizona Project, AZ) located downstream of the Bill Williams River, and the California Aqueduct (Metropolitan Water District, CA) about 3 km upstream from Parker Dam. Temperature of cold, hypolimnetic water entering Lake Havasu already has been ameliorated while traveling downstream from Davis Dam. This factor combines with relatively shallow depth and susceptibility to strong, prevailing winds to make Lake Havasu warm and often isothermal in summer. Influent water also is nutrient-rich, thus the lake is highly productive, bordering on eutrophy in summer.
Other structures downstream from Parker Dam mostly were constructed as points of
diversion to accommodate agricultural uses along the floodplain and adjacent uplands. Included are Headgate Rock (Squaw) Diversion Dam (River Kilometer [RK] 285, measured upstream from the Southerly International Boundary of United States and Mexico), Palo Verde Irrigation Diversion (RK 214), Imperial Dam (RK 78), Laguna Dam (RK 70) and Morelos Dam (RK 35). Headgate Rock diverts water into Colorado River Indian Tribes (CRIT) canals, and backs up a short (less than a kilometer), shallow area known as Moovalya Lake. Palo Verde Dam diverts water to California agriculture in the Blythe area. Imperial Dam serves as intake point for the Gila Gravity Main Canal, which waters Arizona agriculture in the Yuma area, and for the All American Canal, which serves the Coachella and Imperial valleys of California. Imperial Reservoir is shallow and only a few kilometers long, and acts as a sediment settling basin for canal intakes. Laguna Dam, built in 1906 as the first structure to interdict the lower Colorado River, is no longer in service. Finally, Morelos Dam distributes water into Mexican canals in an amount determined by Treaty Agreements. Except in wet years, the discharge is nil in the Colorado River below Morelos Dam and sometimes no water passes over the river delta to its mouth at the Gulf of California (Sea of Cortez).

River Reaches -- River reaches along the lower Colorado River all are tailwaters below dams and free-flowing streams above impoundments. Inflows to these reaches are the river itself, augmented seasonally by irrigation returns and sporadically by runoff from adjacent watersheds during heavy precipitation. The Gila River, which drains a substantial proportion of central Arizona and part of southwestern New Mexico, enters the Colorado River near RK 54 at Yuma. The Gila itself is highly regulated, and except during floods, flow in its lower reaches is comprised of irrigation returns, or absent. Withdrawals of Colorado River water from riverine reaches mostly are minor to irrigate local agriculture or supply domestic needs.
Among the first modifications of the lower river was construction in the late 1800s and early 1900s of levees to constrain flows and structures to provide bank or floodplain protection, activities that continue today. Minckley (1979) estimated more than 50% of the riverbank downstream from Davis Dam had been modified by riprap or other armoring, or inundation. Imposition of Boulder (=Hoover) Dam on the main river in 1935 ended catastrophic flooding but also virtually eliminated sediment inputs from the entire upper basin. These factors combined with impacts of other structures to dramatically alter the character of the river, which responded by degrading its channel in places where it historically aggraded and depositing sediments elsewhere. For example, downcutting in the river reach below Hoover Dam from the mid-1930s to about 1950 provided materials that settled in the Topock area, and today is represented by the remnant Topock Marsh. Similar scenarios unfolded below other dams, and these new river dynamics were countered by extensive programs to dredge river and constrain it with dikes, which continue in some places today.

Channelized and physically constrained sections of the lower Colorado River average about 150 m wide. Widths may be 60-500 m in non-impounded areas upstream of Imperial Dam where the channel is not constrained. Some highly modified, de-watered reaches in the Yuma area are as narrow as 10-15 m. Stream depths are greatest (about 8 m) in least modified sections, and average between 1 and 3 meters elsewhere. Shallowest portions occur in wide, depositional reaches at the head of impoundments, where bars may be alternately exposed and watered to depths of a meter or less depending upon river flow.

Hiebert and Grabowski (1985, 1987) quantified 10 shoreline and aquatic habitat types along 71.3 km of the lower river (Table 2) through the operational reach designated by USBR as Parker Division, which extends downstream from Headgate Rock Diversion Dam to Palo Verde Diversion Dam near Blythe CA. They considered the upper 1/3 of the reach (Parker I) as highly modified, while the lower 2/3 (Parker II) had not been
extensively developed. Indeed, in the former they estimated 40% of banks in the upper reach was comprised of riprap, while only about 3% was so modified in the lower. There was more than twice as much natural riparian and cattail habitat in the relatively unmodified section. Their data cannot be directly extrapolated to other river reaches of the lower Colorado River, but nonetheless provide a useful indication of the range of conditions available along the lower river (see also Minckley 1979). Habitat types vary, and except for those dictated by fixed structures, their location and extent both are variable through time and in response to discharge changes (see Marsh and Minckely 1985, 1987). There are only a few reaches of the river that persist undredged and without structural modification. Eldorado Canyon, a steep-walled chasm immediately below Hoover Dam, remains intact, although the bottom has been scoured and armored, and thermal and discharge regimes are unlike the natural condition. Likewise, but less spectacular, are short reaches below Davis and Parker dams, which otherwise have been subjected to extensive shoreline development for housing and recreation.

Off-Channel Habitats -- Some aquatic habitats adjacent to the lower river are remnants of old river features such as oxbows and floodplain lakes, but these largely are discontinuous with the present-day mainstream, or connected only at highest river stages. Exceptions include Topock Marsh, created by sediment accrual following closure of Davis Dam and filling of Lake Mohave, fitted with intake and outlet structures to maintain desired water levels; several large backwaters in the reach downstream from Blythe, CA; Palo Verde Oxbow and Cibola lakes, and extensive backwaters and off-channel sites in the reach above Imperial Dam, that represent a small fraction of those present historically.

Substrates -- Substrates of the lower Colorado River are unremarkable. Bedrock, boulder and gravel predominate in armored reaches below major dams and in Topock Gorge, while sand is the typical bottom material in channelized segments. Depositional
environments upstream of dams and diversions or in quiet, off-channel areas have soft, silt-dominated bottoms. Much of the bottom of Lake Havasu is cluttered with vegetative debris, remnants of the extensive riparian forest and desert scrub that existed and was not cleared at the time the reservoir was created. The same is less true of lakes Mead and Mohave, which are much deeper, and where the original riparian zone was narrower.

Discharge and Currents -- Discharge of the lower Colorado River is controlled at every major structure beginning at Glen Canyon Dam upstream of Grand Canyon. That facility has capability to release up to a maximum of 256,000 cfs (combined powerplants, river outlet works, and spillway releases; USBR 1995); however, recent typical flows have varied from about 5,000 to 31,500 cfs with daily fluctuations of 12,000 (October) to 16,000 cfs (August and January). Withdrawals (and evaporative losses) occur along the river course to Morelos Dam where, in many years, all remaining water is diverted and the downstream channel is wetted only by seepage and irrigation returns.

Currents are similarly varied, and in part are determinants of sediment character. Below dams, current velocity may exceed a meter per second at high discharge. Channelized reaches of river have currents of 0.5-1 m/s, while water movement in lentic habitats (reservoirs and backwaters) may be undetectable at the surface. However, substantial underflow may exist in reservoirs when both in- and out-put discharges are occurring. For example, sub-surface currents measured by Langhorst and Marsh (1986) in Lake Mohave ranged upward to 0.25 m/s at 5-15 m depth.

Water Chemistry -- Nowhere in the lower Colorado River mainstream, except in extreme instances such as toxic chemical spills, is water chemistry inhospitable to aquatic life. Dissolved oxygen varies widely, seasonally and with location, but almost always exceeds 50% saturation. Lowest levels occur in quiet habitats with dense
stands of aquatic vegetation at night in warmer times of year. Conductivity in the mainstream varies little through the lower river, from about 900-1200 us/cm² above Yuma, with elevated levels below (Minckley 1979). Tributary streams or irrigation return flows may range above 15,000 us/cm² conductivity, but values typically are lower and effects generally are local. Hydrogen-ion concentration (pH) varies from slightly below neutral (about 6.5) to maxima in the mid-9s, in a pattern similar to that of dissolved oxygen, lowest in reducing environments and highest where primary producers are abundant. Primary inorganic nutrients (phosphate-phosphorous and nitrate-nitrogen) are nowhere limiting to photosynthesis in the lower Colorado River, with concentrations of both ions ranging from about 0.05 to 0.20 mg/L. Highest values typically are associated with inputs of irrigation returns or other sources of enrichment (e.g., municipal effluents), while lowest concentrations are found where local depletions occur as a result of uptake by primary producers.

OVERVIEW OF AQUATIC BIOTA — Aquatic macrophytes generally are absent from the lower Colorado River, although high densities occur locally in suitable habitats. Extensive stands of emergent cattail (Typha domingensis) occupy the Colorado River deltas at lakes Mead, Havasu, and Imperial Reservoir, and the Bill Williams delta on Havasu, but otherwise uncommon along the mainstream. Other emergents, notably giant bulrush or tule (Scirpus californicus), giant reed or carrizo (Arundo donax), and phragmites (Phragmites australis) line the river channel in some reaches and substantially alter shoreline habitat. Submerged macrophytes including sago pondweed (Potamogeton pectinatus) and spiny naiad (Najas marina) are abundant in coves of all major reservoirs and in some river reaches and off-channel habitats, and watermilfoil and parrot feather (Myriophyllum spicatum and M. brasiliense) also are present but less abundant in the same kinds of places. A number of other taxa also are known from the river but generally are too sparse to be significant contributors to physical habitat. Woody riparian vegetation including seepwillow (Baccharis salicifolia) and exotic tamarisk or saltcedar (Tamarix spp.) grows abundantly in places along both
river and reservoir shorelines, and provides temporary fish habitat when flooded. Cottonwood-willow (Populus-Salix) stands and extensive mesquite (Prosopis) forests that once lined parts of the floodplain, are now largely gone.

Other biota may contribute little to physical habitat but may constitute important food resources or play functional roles critical to ecosystem function. Such biota includes algae, zooplankton, and macroinvertebrates. An important exception is the filamentous green alga Cladophera glomerata which forms dense beds in tailwaters and riffle-like areas of the river, and provide home to a suite of benthic animals and epiphytes. Diatoms of great variety are found throughout the stream on virtually all stable substrates, including plants, and are the most common alga. Bluegreens of several genera are found in quiet peripheral areas, forming benthic mats that may alternately float (daytime) and sink (nighttime) in response to changes in buoyance attributable to bubbles of oxygen produced during periods of intense photosynthesis.

Phytoplankters are generally uncommon except in lentic habitats, although mainstream reaches at times may support diversity and abundance comparable to reservoirs. System-wide there are dozens of genera representing well more than a hundred species. Diversity and abundance vary seasonally and geographically in all habitats, and with flow in river reaches. The most common taxa include chlorophytes (e.g., Chlorella vulgaris and Lagerheimia), chrysophytes (e.g., Cyclotella and Stephanodiscus), cyanophytes (e.g., Dactylococcopsis and Anabaenopsis raciborskii) and cryptophytes (e.g., Rhodomonas minuta).

Zooplankton diversity and abundance appear similar for lentic and lotic portions of the lower Colorado River, although few data are available for the latter. Succession is seasonal in reservoirs, where it is closely related to water temperature, and abundance in flowing reaches downstream from major dams is inversely proportional to flow. Predominant kinds include rotifers (e.g., Collotheca, Keratella, and Polyarthra),
cladocerans (e.g., *Daphnia galeata*, *D. pulex*, and *Bosmina longirostris*), and copepods (e.g., *Diaptomus siciloides*, *D. reighardi*, *Cyclops bicuspidatus*, and *C. vernalis*).

Benthic invertebrate communities of the lower Colorado River are most diverse and abundant and diverse on and among stable substrates below major dams and in riffle-like areas within riverine reaches. The benthic fauna is depauperate in most other areas, and especially-so where substrate is shifting sand.

Distributions, numerical abundances and biomass of primary taxa are patchy and subject to wide seasonal as well as geographic variations. Ubiquitous forms (except on unstable bottoms) include oligochaete worms and chironomid larvae, which can attain densities of 10,000 to more than 100,000 per m² in soft bottoms of reservoirs and quiet, off-channel habitats. Dragon- and damselflies also become abundant in shallow lentic places, the latter especially where aquatic vegetation is present. Exotic Asiatic clam (*Corbicula fluminea*) is locally one of the most abundant animals in flowing reaches, where it tends to occur in isolated beds. Tailwater substrates are occupied by a suite of filter/detritus feeders and grazers, including hydropsychids caddisflies, simuliid and tipulid flies, and baetid and heptageniid mayflies. Flatworms, and a few genera of beetles and snails are found sporadically. Exotic crayfish (*Procambarus clarki*) and freshwater shrimp (*Paleomonetes paludosus*) may be locally abundant, the latter especially-so in vegetated areas of the lowermost reaches.

**NATIVE AND NON-NATIVE FISHES OF THE LOWER COLORADO RIVER**

The lower Colorado River main stream historically was occupied by a depauperate assemblage of only 10 fish species (Table 3A; Minckley 1973, 1978). The fauna was predominated by cypriniforms, represented by five cyprinids (humpback, bonytail and roundtail chubs, woundfin, and Colorado squawfish) and two catostomids (flannelmouth and razorback suckers). Two species were primary saltwater invaders, Pacific
tenpounder or machete (*Elops affinis*), which scarcely penetrated upstream beyond the delta, and striped mullet (*Mugil cephalus*), which consistently moved into freshwater upstream to present-day Yuma, AZ. Desert pupfish (*Cyprinodontidae*) was associated with peripheral habitats and likely was in the main river only when dispersing or washed there during flood. Colorado squawfish was the only piscivore within the native fauna.

Non-native (introduced) fishes first began to arrive in the lower Colorado before the end of the 1800s with arrival of common carp (*Cyprinus carpio*) and bullhead catfish (genus *Ameiurus*). Others have been added since to fulfill perceived needs for human food, recreational angling, forage for sport fishes, as biological control agents, or by accident, and 29 species now are established (Table 3B). A majority of these are predators as adults (all salmonids and ictalurids, striped bass [*Morone saxatilis*], and centrarchids), and all are capable of feeding on fish eggs or larvae. Flathead catfish (*Pylodictus olivaris*) and striped bass stand out among predators as obligate piscivores, and others including channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) also feed heavily upon fish. Many of the introduced species are territorial, aggressively pugnacious, or protective of their young. Further, these non-native kinds evolved as parts of species-rich faunas very unlike the natural Colorado River assemblage, and as a result must have developed predator recognition or avoidance mechanisms in their young; capabilities thought not to be developed in native Colorado River fishes (see Johnson et al. 1993, Johnson and Hines, MS).

While native and non-native fishes in the lower Colorado River may have unique evolutionary histories, behaviors, and life histories, they nonetheless must live today in the same physical space and utilize similar or the same resources, and their paths thus intersect. An historical record of observation, research, and case study demonstrates that interposition of these two distinctive categories of fishes on one another usually results in extirpation of the natives and replacement by the non-natives. While the
mechanism(s) mediating this process has yet to be elucidated for all cases, there are convincing examples that predation is a major factor. It thus is instructive and directly relevant to the problem at hand to examine the habitats and trophic biology of fishes that inhabit the lower Colorado River, with special attention paid to overlap in resource use.

PHYSICAL HABITATS OF NATIVE AND NON-NATIVE FISHES -- Larval life stages -- Larvae of native marine species occupy salt water or coastal, tidal inlets, potentially shared only with striped bass among introduced fishes of the lower Colorado River (striped bass are anadromous in their natural range, but also are capable of reproduction in freshwater). All other fishes in the system are primary freshwater species.

Essentially nothing is known of physical habitat use by larval bonytail. There are no field observations and records even are wanting for artificial situations (e.g., hatchery ponds) where they might be observed. Larvae presumably are in open water (Table 4). Colorado squawfish larvae in rivers are pelagic or associated with low velocity shorelines, embayments, or backwaters over mud, sand, gravel, or cobble bottoms. An even broader array of physical habitat features are used by razorback sucker larvae, which have been found in rivers, lakes, reservoirs and canals (Table 4). Early, post-hatch larvae remain in or on coarse substrates until swim-up, then typically are associated with warm, shallow, quiet, near-shore areas. Flannelmouth sucker likely are similar. Desert pupfish larvae are benthic in shallow water or littoral, and often associated with vegetation or other cover.

There are few generalizations as regards habitat use by larvae of non-native fishes in the lower Colorado River. Clupeid young are pelagic and loosely aggregated, and cyprinid larvae may school and associate with shoreline cover. Salmonids generally are solitary and associated with streams substrates in shallow water. Channel,
flathead, and bullhead catfishes remain within the immediate area where produced, under protective parental custody, until moving into the surrounding habitat at large when flathead and young channel catfish go into riffles and bullhead catfishes into pools. Poeciliid larvae inhabit areas with dense algal or macrophyte beds in shallows along stream or pond margins, mostly at or near the surface. Larval centrarchids also may be protected by the male parent and remain within the nest area, then moving into habitat often low-flow or lentic in nature, shallow, and with abundant cover provided by vegetation or other structure. Similar habitat use, parental care, and early larval behavior is characteristic of the various nest-building and mouth-brooding cichlids. Fertilized striped bass eggs are semi-buoyant and larvae hatch while drifting in currents, then assume an open water existence.

Juvenile life stage -- As young fish of a given species develop from larval to juvenile stage they generally move from their natal habitats to occupy a broader variety of environments (Table 5). Juvenile elopids and mullets live and school in brackish estuaries, along shorelines, or lower reaches of freshwater rivers. Bonytail young are found in a diversity of lotic micro-habitats, including shallow shorelines, runs and riffles, below rapids, quiet water of eddies and backwaters, and associated with coarse substrates in currents or finer bottom materials in depositional environments. Humpback chub young frequent the same kinds of places, with a greater tendency toward eddies, runs, and rocky areas. Colorado squawfish in an even greater array of stream habitats than chubs, but most often are in shallow, warm, low-to-no-flow peripheral areas such as backwaters and embayments. Most places have silty bottoms. There likely is no such thing as “typical” habitats used by juvenile razorback sucker since they survive and grow in such varied places, from rivers to stock ponds. In natural settings, their habitat use likely is parallel that of Colorado squawfish in warm, shallow backwaters, pools and bays, or tributary mouths. Juvenile desert pupfish live in the same places as larval and adult life stages.
Juvenile threadfin shad (*Dorosoma petenense*) are pelagic and school in lakes, and in rivers essentially are restricted to backwaters and shorelines where substrates are soft debris or silt and vegetation may be abundant. Cyprinid juveniles often are quiet, peripheral habitats, often associated with cover, but also in shallow, slow-to-modest current in flowing reaches. Riffles and runs are occupied by young channel and flathead catfishes. Bullhead catfish juveniles typically occupy shallow pools, or other low-flow micro-habitats within streams. Salmonid young in streams are at mid-water-column in shallow-to-moderate depths in low-flow reaches, riffles, or in pools. Young trouts typically are in or near cover, either organic or inorganic. Centrarchid juveniles as a group are associated with limnetic shoreline habitats, typically in warm, shallow water over fine substrates, and often associated with cover provided by vegetation or debris. These habitats in streams are represented by pools, backwaters, and peripheral areas. Similar habitats are occupied by juvenile cichlids; which also tend to school in large groups. Striped bass juveniles may be in pelagic schools in larger water bodies, or shoreline-oriented in rivers and lakes and associated with coarse, rocky substrates.

Adult life stages -- Pacific tenpounder adults live primarily in marine or estuarine environs, but occasionally occupy delta areas and enter lower river, freshwater reaches. Specific habitat-use data are not available for this species. Striped mullet also lives in saltwater, but enters rivers and lakes. In rivers it is pelagic in deep water channels adjacent to eddies, along shorelines, or in quiet, low-flow backwaters and marshes.

All native freshwater fishes of the lower Colorado River are thought to historically have occupied large, turbulent streams of the system. Adult bonytail likely lived in modest, mid-channel currents of sandy, valley and flat-water canyon reaches. Or, like humpback chub, it was associated with large structure in currents, below rapids, or with backwaters and eddies. In modern reservoirs and smaller lentic habitats the species is
pelagic except during reproductive periods when it moves into shallow, rocky shoreline areas (see below). Habitat use by adult humpback chub is similar, although there is little information on habitats used in reservoirs where the species is rare. Most large humpback in the Little Colorado River are in eddying currents below travertine dams, in deep flowing pools, and along undercut banks lined with *Phragmites*. Woundfin is typical of turbid rivers and streams, most often in open channels over sandy substrate. Colorado squawfish is found in a variety of depths in the main channels of larger, turbid rivers and tributaries, generally over coarse substrates and often associated with cover. It also uses low-to-moderate flow pools, eddies and riffles, and deeper, peripheral habitats such as tributary mouths, backwaters.

Razorback suckers in turbid rivers often are found near bottom in open channel currents over sandy substrates in relatively shallow water. They also use undercut banks, eddies, pools and backwaters. In clear reservoirs, the species is pelagic at varying depths, except during the spawning season, when it moves inshore (see below). Flannelmouth sucker habitat use is relatively understudied, but the species seems associated with eddies over softer bottoms of whitewater canyons, cut banks and turbulent areas below rapids and dams, and in lower ends tributaries during reproductive periods.

Adult desert pupfish occupy much the same physical habitats as used by earlier life stages. These include quiet, peripheral areas of rivers (backwaters, oxbows, sloughs and marshes), small ponds and creeks, springs. In larger habitats the species is littoral in shallower water. Pupfish often are associated with cover provide by aquatic macrophytes or algae.

The suite of non-native fishes established in the lower Colorado River today occupies as adults a bewildering array of physical habitat types. Most species do especially well in lentic portions of the system, although many species seem equally at home in rivers,
reservoirs, and peripheral areas, and there are few generalizations to be derived. For these reasons, rather than attempt to summarize species-by-species habitat use by non-native fishes in the narrative, the reader is referred to Table 6, general works such as Calhoun 1966, Minckley 1973, Moyle 1985, and APPENDIX IV.

Examination of Table 6 shows extensive overlap in physical habitats used by adult native and non-native fishes of the lower Colorado River. This is well illustrated by the fact that only 7 of 133 habitat descriptors distilled from those used in the literature (Table 6), were associated exclusively with native fish species. And, these terms could scarcely be considered exclusive (i.e., below rapids [bonytail], eddies [humpback chub], creek mouth [Colorado squawfish], midchannel sand bar, shallow run, and glide [razorback sucker], and lateral habitat [desert pupfish]). About one-third of habitat types nonetheless were exclusive to non-native fishes. Thus, nearly two-thirds of the habitat types and features described in the literature were shared by native and non-native lower Colorado River fishes, at all hierarchical levels from micro- to macro scales. All non-native species are associated with rivers (as are all natives), all except Mexican molly (Poecilia mexicana) are associated with reservoirs or lakes, and all save the last and blue tilapia are associated with streams. About half (13 of 29) the species in Table 6 live in deep water (including channel and flathead catfishes, trouts, and several sunfishes [genus Lepomis]) and 17 in shallow water (representatives of the minnows, bullheads, trouts and centrarchids), including 9 known to occupy both categories of depth.

All introduced cyprinids, mosquitofish (Gambusia affinis), warmouth (Lepomis gulosus), green sunfish (L. cyanellus), and striped bass may be associated with turbid habitats, as are most native cypriniform species. Three-fourths of the non-natives use river channels, as do several native fishes. However, only 8 non-natives compared with 6 natives (all the cypriniformes) are associated with lotic systems. This is reflected in flow characteristics of occupied habitats: all non-natives are associated with low-to-no
flow or stagnant conditions, and all except sailfin molly (*Poecilia latipinna*) and striped bass are associated with pools. All non-native fishes of the lower Colorado River make use of some kind of cover, primarily aquatic macrophytes. Native species, on the other hand, make little use of this kind of cover, although they may use overhanging or undercut banks, or inorganic instream cover (see above). Substrate associations are complex and terminology diverse. Most non-natives occur over soft unconsolidated bottoms of sand, silt, or muck. Native Colorado River fishes also are mostly associated with sand or mud bottoms. Seventeen non-native species are associated gravel substrates, and 14 with rock or boulder bottoms. Bedrock, cobble, debris, and peaty bottoms are used less often by non-natives.

TEMPERATURE RELATIONS -- There is a paucity of published data on temperature relations of native Colorado River fishes, especially for early life stages. In contrast, the literature contains an abundance of temperature data on non-native fishes, and we did not attempt to retrieve and evaluate all available information. Rather, we acquired information that bracketed likely preferenda and extreme tolerances of representative species in the lower Colorado River. There generally was broad overlap in temperature relations of native and non-native species, special thermal requirements of cold-water fishes aside.

Larval life stage -- There has been some experimental work on embryo survival relative to incubation temperatures for some native Colorado River fishes (Marsh 1985), but none on larval thermal tolerances or preferenda. Presumably, temperature regimes suitable for larvae would be similar to those that were optimal for development of hatch, which was near 20°C for bonytail, humpback chub, Colorado squawfish, and razorback sucker. However, collections of razorback sucker larvae from the wild have been made over a much wider range of temperatures from about 12°C to near 20°C (personal observation, see also Mueller 1989), suggesting a broad thermal tolerance.
The few available data on thermal criteria for non-native fish larvae (Table 7) show overlap with those presumed for native species. Maximum tolerances for five non-native fishes were >18°C and 21-26°C (two brook trout [Salvelinus fontinalis] studies), 24°C (striped bass), 34°C (bluegill [Lepomis macrochirus]), 38°C (carp), and 39°C (black bullhead [Ameiurus melas]). Minimum tolerance data are available for carp (<7°C), brown trout (Salmo trutta, <4°C) and bluegill (<11°C). Preferred (or optimal) temperature ranges have been determined for carp (27-30°C in two studies), brook trout (9-15°C in three studies), bluegill (25-32°C in two studies) striped bass (13-24°C in five studies). Black crappie (Pomoxis nigromaculatus) larvae have been observed in the wild over a temperature range of 15-30°C (Table 7). These species represent five of the fish families that have a significant presence in the lower Colorado River.

Juvenile life stage -- Except for juvenile desert pupfish, which has a thermal preference/optimum of 30°C (Table 8), there are no data on thermal relations of juvenile life stages of lower Colorado River fishes. This is because of a general paucity of thermal studies on these species, and to rarity in the wild of juveniles of most. It is certain, however, that juvenile thermal tolerances and preferenda are within the range of criteria defined for larval and adult life stages. Further, tolerances can be inferred from thermal data for natural and artificial habitats in which juveniles of each species are found, which likely range from near freezing at latitudinal and elevational extremes of their distributions (e.g., Wyoming for several species, and elevations >1500 m) to more than 30°C in shallow pools and other habitats in the lowermost river during hottest times of summer days, and perhaps even greater than 30°C in thermal springs. Thus, we expect the temperature tolerance range is quite wide for juveniles of native Colorado River fishes.

Temperature tolerance data are available for juveniles of several non-native species from five major families (trouts, minnows, catfishes, sunfishes, and temperate basses), as summarized in Table 8. Maximum tolerance for six species ranged from 25°C
(striped bass) to 39°C (channel catfish), and minimum tolerances were 0°C (brook trout) and 18°C (striped bass). Preferred/optimum values were as low as 8°C (to 19-20°C) for rainbow trout (Oncorhynchus mykiss) and brown trout, to 32-34°C for flathead catfish juveniles. Field observations of temperature where juveniles were present ranged from a low of 7°C for cutthroat trout (Oncorhynchus clarki) to 30°C for flathead catfish. Although comparable data are wanting for most other non-native fish species, and for native Colorado River fishes as a whole, there must certainly be a broad overlap in temperatures tolerated by juveniles of both.

Adult life stage -- Adult fishes generally enjoy a broader tolerance of extreme temperatures than earlier life stages, and this is reflected in thermal data for adult native and non-native fishes of the lower Colorado River (Table 9). Maximum temperatures of native fishes range to an extreme 45°C for desert pupfish, which is approached only by stripers bass (43°C) and goldfish (Carassius auratus, 42°C); thermal maximum of other species all are <39°C. Critical thermal maximum of razorback sucker was 27-32°C, and other native fishes presumably have similar tolerance.

Coldwater salmonids have the lowest tolerance of high temperature, but also tolerate the coldest minima (near 0°C for most species). Critical thermal minima for razorback sucker was 8-15°C, and likely is similar for other native species. Thermal minima tolerated by adults of other non-native fishes are 1°C (threadfin shad), 0°C (goldfish), <4°C (mosquitofish), <5°C (largemouth bass), 3°C (bluegill), 7°C (redear sunfish, Lepomis microlophus), 5°C (Mozambique tilapia), 8°C (redbelly tilapia), and 18°C (striped bass, but perhaps an unrealistically high estimate).

Thermal optima/preferenda of native fish adults were 24°C (bonytail and humpback chub), 23-25°C (razorback sucker), 25°C (Colorado squawfish), and 22-26°C (desert pupfish). Reported optima for non-native fish adults ranged from extremes of 4-34°C
for common carp to 42°C for mosquitofish; most species fell within the range of 10 to 30°C (Table 9). Field temperature at sites where native and non-native were observed had a modestly narrower range: 10-18°C for razorback sucker, 39°C for desert pupfish, and 4-34°C for bluegill, 40°C for red shiner (Cyprinella lutrensis). Broad overlap between native and non-native kinds is indicated.

**FOODS AND FEEDING HABITATS** -- Larval life stage -- Larval fishes are small animals, ranging in length from a few mm at hatch to at most a few cm at transition to juvenile, and once nutrition of the yolk sac has been exhausted, their feeding depends upon exogenous sources. Small larvae consume small food particles, and these invariably include a substantial proportion of microscopic zoo- and phyto-plankton and broad overlap among fish taxa (Table 10). Among all records for lower Colorado River fishes we found only two references to piscivory among larval fishes. Tyus (1991) anecdotally reported larval Colorado squawfish consuming unspecified fish as prey, and Northern squawfish (Ptychocheilus oregonensis) is documented to eat common carp larvae. Calhoun (1966) reported cannibalism among larvae of common carp (Table 11). We found no records of predation by non-native fish larvae upon native fish larvae.

We also examined temporal and spatial aspects of feeding by larval fishes (Table 12) and found no overlap among native and non-native fishes. However, our search turned up relevant information for only a few species: one native (razorback sucker) and eight non-native (golden shiner [Notemogonus crysoleucus], channel catfish, black bullhead, rainbow trout, brook trout, sailfin molly, bluegill, and black crappie).

Juvenile life stage -- Juvenile fishes eat a greater diversity of foods than larvae, items tend to be larger in size, and there is broad overlap in food types between native and non-native fish species (Table 13). Fish larvae are recorded as consumed by juveniles of at least one native (Colorado squawfish) and by a dozen non-native kinds. Aquatic
insects, including ephemeroptera and chironomid immatures, are consumed by native bonytail, and also by at least 14 kinds of introduced fishes. Native razorback sucker eat small aquatic invertebrates and diatoms (Brooks and Marsh, unpublished data), and likely other microplankton and benthos, which resource use is in common with non-native mosquitofish and Mozambique mouthbrooder.

Direct predation (Table 14) on native razorback sucker by non-native juvenile channel catfish flathead catfish has been documented (Marsh and Brooks 1989). Colorado squawfish are known to be cannibalistic as juveniles (Minckley 1979), and to also prey upon larval razorback sucker (Karp and Tyus 1990). Juvenile largemouth bass and striped bass consume an array of other non-natives fishes but there are no published reports of either species eating native fishes. However, there have been direct observations of both these predators and channel catfish, eating juvenile bonytail and razorback suckers repatriated to Lake Mohave (Marsh unpublished; T.E. Burke personal communication; see also Appendix III).

There are few records of temporo-spatial overlap between juvenile native and non-native fishes (Table 15). Juvenile bonytail feed near surface (as do non-native golden shiner and bluegill) in backwaters and along shoreline margins. Brook trout use similar areas but co-occurrences with bonytail are rare, so interaction is unlikely. Razorback sucker juveniles feed in on the bottom, a space resource shared with juveniles of at least nine non-native fishes.

Adult life stage -- The relatively large, adult life stage of most freshwater fishes is more readily captured during sampling, easier to work with from a logistic perspective, usually represents the target stage for resource use (as food or sport), and has greater longevity than earlier life stages. As a result, there is a substantially larger body of published information on adults, including coverage of more species, compared with larvae and juveniles. Unfortunately, for several reasons this is not necessarily the case
for native fishes of the lower Colorado River. At time of their discovery they generally were disregarded other than as scientific oddities. Although several species were important food sources for aboriginal inhabitants and early European settlers, most do not have culinary characteristics desired by modern humans (some are bony, others are oily, and some do not grow acceptably large). By the mid-1930s and into the late 1960s, many native fishes were regarded as little more than forage opportunities for introduced sport fish, an attitude that persists today. By the time their perilous status was recognized and the scientific and conservation communities began to take an interest in their biology, there had been extirpation on a dramatic scale and many species had become too rare to sample effectively. Finally, state protections and federal listing as threatened or endangered impose necessary sanctions on acquisition of specimens except for the most critical of research or management activities. A general paucity of basic life history data is the result.

Although most species are associated with a particular functional feeding group (e.g., phytophagy, detritivory, piscivory), these descriptors are only generally useful and with a few notable exceptions most fishes tend toward opportunistic omnivory. This implies that most fish will use the same food resources, which indeed is the case. This is reflected in Minckley's (1982) examination of food habits of 18 lower Colorado River fishes, all introduced, and his conclusion that food webs were relatively simple and based on autochthonous detritus, algae, and macrophytes, all of which are abundant, and the comparably abundant biota that consumes these basic food sources. Our review supports and expands upon that general conclusion (see Table 16). As a result, there are few opportunities to demonstrate competitive food/feeding interaction between native and non-native fishes — while there is quantitative overlap in foods, there are no suggestions of resource limitation.

Adult bonytail chub eat a variety of immature, pupal and adult aquatic insects, drifting or floating terrestrial arthropods, zooplanktonic crustaceans, filamentous green algae,
30

plant matter, and detritus. These foods also are consumed by virtually all non-native fishes inhabiting the lower Colorado River, although the greatest overlap appears with adult red shiner and sunfishes (Table 16). Bonytail adults also are capable of eating small fishes, and under some conditions are cannibalistic (personal observation).

Woundfin are predaceous on a diversity of invertebrates, especially aquatic and semi-aquatic insects (Greger and Deacon 1988). This resource use overlaps broadly with that by introduced trouts, red shiner, channel catfish, the bullhead catfishes, and centrarchid sunfishes (Table 16).

Colorado squawfish is the only primarily piscivorous, predatory native species in the system. The species and other members of the genus are documented to eat small mammals and birds in addition to a variety of fishes. Non-native predators whose diet includes a substantial portion of fishes are channel catfish, flathead catfish, smallmouth bass, largemouth bass, and striped bass (Table 16), and all except channel catfish and smallmouth bass likely are specialized piscivores.

Adult razorback sucker are planktonic filter feeders on microcrustaceans and algae (Marsh 1987), although other items such as benthic aquatic animals, green algae, macrophyte fragments, and detrital debris are consumed in lesser amounts (Table 16). Striped mullet also is a facultative planktivore, but among adults of introduced fishes, only threadfin shad and blue tilapia have feeding habits similar to these native species. Blue tilapia in its native range consumes phyto- and zooplankton, although detritus was a substantial proportion of foods of fish in the lower Colorado River (Marsh and Minckley 1987).

Flannelmouth suckers are benthic omnivores and consume a variety of bottom materials including attached algae, detritus, and macroinvertebrates (Greger and Deacon 1988). These food resources are shared with many of the non-native fishes,
including red shiner, the poeciliids, and sunfishes (Table 16), however, only common carp, goldfish, and Mozambique mouthbrooder have a bottom feeding mode similar to that of flannelmouth sucker.

Desert pupfish is omnivorous, eating an array of microcrustaceans, aquatic insects, molluscs, algae, and organic detritus. Similar foods are utilized by most non-native cyprinids, salmonids, poeciliids, and centrarchids (Table 16) in the lower Colorado River. Desert pupfish also is cannibalistic on its own eggs and young (Schoenherr 1981, 1985).

Piscivory and cannibalism -- We examined piscivory in greater detail, and identified documented predation on native fishes by 14 non-native species (Table 17). Most fishes become piscivorous long before attaining adult size. For example, native Colorado squawfish initially become piscivorous at about 10 cm total length, and size at which 12 non-native fishes for which we have records begin to eat fish range 2 cm for largemouth bass to more than 40 cm for cutthroat trout (Table 18). It is notoriously difficult to determine by conventional visual technique that small fishes, especially early life stages, have been consumed by a predator. This is because soft tissues are destroyed by mastication or otherwise become unrecognizable soon after ingestion. If this constraint could be removed, if seems certain that piscivory on early life stages of native fishes would be virtually universal among non-native fishes now in the lower Colorado River.

Adult carp are reported to consume humpback chub eggs, and both eggs and larvae of razorback sucker. Red shiner eats larval razorback sucker and undetermined catostomidae. Fathead minnow (*Pimpephales promelas*) also eat razorback sucker larvae. Flathead catfish are documented to eat larval and juvenile razorback sucker, plus undetermined catostomidae, and channel catfish prey upon humpback chub, Colorado squawfish, and razorback sucker. Black bullhead eat early life stages of
Colorado squawfish, and desert pupfish of all sizes, and yellow bullhead (*Ameiurus natalis*) consume juvenile Colorado squawfish. Rainbow and brown trouts both eat humpback chub and undetermined catostomidae. Largemouth bass eat larval and juvenile Colorado squawfish, and have been observed eating juvenile bonytail and razorback sucker. Green sunfish are reported to consume larvae and juveniles of both Colorado squawfish and razorback sucker. Redear sunfish are documented to feed on early life stages of desert pupfish, and black crappie consume young Colorado squawfish. Adult striped bass are reported to prey upon juvenile razorback sucker. None of these results is remarkable. We expect non-native predatory fishes all will consume native fishes if opportunity is available.

Cannibalism represents a special case of piscivory (Table 19). Among native fishes both Colorado squawfish and desert pupfish consume their own young, and we have anecdotal evidence plus personal observation that bonytail and razorback sucker also are cannibalistic. Non-native cannibals in the lower Colorado River include common carp, brown trout, mosquitofish, largemouth bass, green sunfish, Mozambique mouthbrooder, and striped bass. As for the case of piscivory in general, however, we expect that adults of all non-native species would consume at least early life stages of their own kind.

Adult Feeding Areas -- Adult bonytail chub feed near surface in limnetic zone, eddies, and open water pools (Table 20). Non-native surface feeders include golden shiner, channel catfish, cutthroat and brown trouts, mosquitofish, and bluegill, while black bullhead, largemouth bass, bluegill, black crappie, and Mozambique tilapia are reported to feed limnetically. Humpback chub adults feed in mid-water and shoreline eddies. Red shiner, and non-native trouts also are mid-water drift feeders. Colorado squawfish have a roving capture behavior, similar to that of non-native largemouth bass. Colorado squawfish use eddies, shorelines, and pools as feeding sites, which also are used by flathead catfish and brown trout adults. Razorback sucker feed at
night throughout the water column and on/near bottom. A suite of non-native fishes feed after sunset in the same areas (Table 20).

TERRITORIALITY -- Some fishes occupy and defend specific micro-habitats during breeding periods, when feeding, or as a matter of course. Among native fishes of the lower Colorado River, only desert pupfish has demonstrated territorial behavior. Both males and females exhibit of the species this behavior during courtship and breeding. In contrast, some type of territoriality has been attributed to most (19 of 22 species) non-native fishes in the lower Colorado River (Table 21). Adult male red shiner, ictalurid catfishes, all of the centrarchids, and several Cichlids defend areas, nests, and/or young during courtship, breeding and rearing periods, and some are pugnaciously aggressive at these times. Females of some species, including black and yellow bullheads, mosquitofish, and redbelly tilapia also are territorial when breeding. Feeding territoriality is exhibited by red shiner (which have a generally aggressive nature), fathead minnow, and introduced trouts, which occupy spatially delimited territories in pools. Adult flathead catfish not only defend living and feeding places, but if hungry they will attempt to eat virtually any invading fish if the size is suitable.

SPAWNING REQUIREMENTS -- Timing of reproduction -- Spawning by fishes in the lower Colorado River can occur during virtually any season or month (Tables 22 and 23). Although each species has a more-or-less well-defined spawning period, the exact timing is determined of many factors, including photoperiod, hydrologic cues, temperature, and in some cases availability of suitable sites, that vary temporally, latitudinally and elevationally, within the system. For at least one introduced species (Mozambique mouthbrooder), spawning in its native range is cure by onset of the rainy season.

There is broad overlap in timing of reproduction for native and non-native warmwater fishes in the lower Colorado River. Based on our experience, only razorback sucker
spawns at a time of year (winter) when no other warm-water species in the system is in reproductive mode.

Native bonytail spawn in late spring to early summer, and humpback chub reproduce during spring. Colorado squawfish staging in the lower river may have occurred on the delta during winter, and after movement to suitable upstream sites, reproduction in whitewater canyons may have begun in early spring and extend into late summer (Minckley 1991). Recent observations all are from the upper basin, where spawning occurs in summer (Tyus 1991). Razorback sucker typically spawns in late winter into early spring, although reproduction may begin as early as mid-autumn and last to early summer. Striped mullet spawns at sea, anytime during autumn or winter.

Most warmwater, non-native fishes reproduce only during warmer months of early spring through late summer (Tables 22 and 23). Exceptions are threadfin shad, bluegill, and redear sunfish, which also may spawn during autumn. All coldwater trouts reproduce during autumn and/or winter, although rainbow and cutthroat trouts also may breed in springtime if water temperature and other factors are favorable.

Spawning temperature -- The range of water temperatures at which native and non-native fishes will spawn are consistent with their individual seasonalities (above). Thus, bonytail spawn near 18°C, Colorado squawfish from 14-28°C, razorback sucker from 10-24°C, and desert pupfish from 13-48°C (Table 24). Warmwater non-natives reproduce at temperatures as low as 10°C (striped bass) and ranging into the low 30s °C (red shiner, green sunfish). Coldwater trouts all spawn at temperatures of 11°C or less, and rainbow trout may reproduce in water as cold as 1°C.

Spawning areas -- There are few common elements to define or discriminate staging or spawning areas utilized by the suite of fishes that now live in the lower Colorado River, and while some show capability to reproduce in a diversity of habitat types, others
exhibit greater specificity (Tables 25A and 25B). An assumption that native "large river" fishes spawned in riverine habitats must be tempered with recent discovery that bonytail and razorback sucker, at least, are capable of reproducing and completing their life cycle in earthen stock tanks or hatchery ponds that bear little resemblance to their presumed historical homes. Pacific tenpounder and striped mullet both reproduce in the sea, and are not further considered.

There are few observations of natural spawning by bonytail, and none from flowing waters. What was described as a spawning aggregation of perhaps 500 fish was reported by Jones and Sumner (1954), who described a loose school comprised of females each accompanied by 3-5 males, which presumably broadcast gametes over a gravel shelf in up to 9 m of water in Lake Mohave during May. Similar observations were made in springtime of bonytail in hatchery ponds at Dexter NM by W.L. Minckley and in artificial rearing ponds at Cibola National Wildlife Refuge AZ by C.O. Minckley. Despite intensive investigations, there are no direct observations of humpback chub spawning in any habitat. Nonetheless, based upon inference and it seems likely the species spawns in relatively deep water among boulder-size substrates of flowing pools in major streams and tributaries (PCM, personal observation). Timing of bonytail (and humpback chub) reproduction in rivers has been inferred from presence of gravid females and appearance of young (e.g., Vanicek and Kramer 1969, Douglas and Marsh 1996, Gorman et al. 1996, Valdez and Ryel 1996).

Colorado squawfish spawning has been documented only in lotic habitats, where the species aggregates in spring and reproduces at the upstream ends of shallow, gravel bars in riffle or run habitats (Tyus 1990, 1991). Although water depth, turbulence and turbidity prevent direct observations, presence of gravid individuals and appearance of young suggest place and time of spawning.
Nothing is reported that describes the spawning areas used by woundfin. The species occupies swift parts of silty streams and rarely frequents lentic areas represented by backwaters and pools (Minckley 1973). However, successful reproduction likely depends in part on availability of cleaner, coarser, more stable substrates that would protect fertilized ova and newly-hatched larvae. A broadcast spawning behavior seems likely.

Razorback suckers spawn in rivers, reservoirs, and artificial lakes although the "act" has been directly witnessed only in lentic habitats (with an exception of the Hoover Dam tailrace [Mueller 1989], which has unique characteristics). The behavior in these diverse places presumably is consistent with that described by Minckley (1983) and Minckley et al. (1991), involving one or two females joined near bottom by two-to-many males, and a convulsive mutual expression of gametes that incidentally results in excavation of a substantial depression often inappropriately referred to as a "nest" or "redd." Place and timing of spawning in rivers has been inferred from presence of ripe adults and appearance of larvae (see Tyus 1987, Minckley et al. 1991).

Flannelmouth sucker, unlike razorback sucker, has not persisted in lentic areas. Spawning is in late-spring and summer (March to May) in main stream rivers and tributaries mouths. In Grand Canyon, the species reproduces primarily in warmwater tributaries, especially the Paria River. In upper basin rivers, ripe adults are present from April through July and spawning presumably takes place in swift, shallow water over cobble bars, must as for razorback sucker.

Spawning by desert pupfish takes place in quiet areas of springs, marshes, and peripheral areas of lotic systems where females contact territorial males and gametes are placed a few at a time in typically-soft bottoms in shallow water. Their complex reproductive behavior has been described (Cowles 1934, Barlow 1961).
Cold- and warm water non-native fishes have distinctive spawning habitat requirements (Table 25B). Cold water salmonids all spawn preferentially in shallow water over stream riffles, or in thermally-suitable tailwaters below major dams, although lake-shore spawning is reported in some species. Most other non-natives spawn in near shore shallows of lakes or reservoirs, or quiet peripheral areas of larger rivers. Smallmouth bass (*Micropterus dolomieui*), green sunfish, and striped bass also spawn in riverine habitats.

Mode of reproduction — All native freshwater fishes of the lower Colorado River except desert pupfish are broadcast spawners (Table 26); none has direct parental care of embryos or young. Pre-reproductive staging for days-weeks-to-months prior to and during actual spawning is typical in places proximate to spawning habitats.

In contrast, among introduced fishes only introduced the cyprinids and striped bass are broadcast spawners; more than half the non-native species in the system construct some kind of nest prior to spawning (Table 26). Moreover, members of several major groups including the catfishes, centrarchids and cichlids guard their nests and aggressively protect embryos and newly hatched young (Table 26). This life-history strategy imparts a distinct early-life stage survival advantage to the introduced fauna in communities of mixed reproductive modes.

OVERLAP IN RESOURCE USE

It is abundantly clear from the foregoing that native and non-native fishes in the lower Colorado River overlap broadly in their use of environmental resources for essentially all life stages and functions. Although several distinct evolutionary histories are involved, most fishes of the system are opportunistic generalists that can be successful in the variety of physically altered and hydrologically regulated aquatic habitats offered by the lower Colorado River of today. Many of the warm-water non-natives are well
adapted to lakes and reservoirs, and these also thrive in quiet peripheral habitats adjacent to flowing reaches. Others make use of cold tail-waters below high dams. Most of the remainder is at home in the monotonous channels with shifting sand bottoms that comprise much of the rest of the stream. A basic distinction between cold-water trouts and warm-water species was evident, but that did not exclude opportunity for interplay between these two types.

Our literature review identified resource use overlap within and among larval, juvenile and adult life stages of native and non-native fishes. Overlap was evident in 3-dimensional space, at micro- through macro-scales, and in time. Fishes generally occupied the same physical habitat, utilized similar foods, and had common modes of food acquisition. Piscivory and territoriality were more common among adults of non-native species. Temporal, spatial and thermal aspects of spawning were generally similar among native and introduced faunas, coldwater species requirements notwithstanding.

The most distinctive life-strategy difference between native and non-native fishes was in mode of reproduction. As noted above, all but one of the native fishes that occupied the lower Colorado River are broadcast spawners that show no parental care of young. In contrast, only five introduced species, the cyprinids and striped bass, are broadcast spawners. A majority of non-native fishes construct or utilize some kind of nest for spawning, and provide varying levels of protection for embryos and newly hatched young.

**ROLES OF BIOTIC AND ABIOTIC FACTORS**

One of the pressing questions in defining the ultimate reasons for decline of native fish faunas of arid western regions has been discriminating between biotic and abiotic as causative factors. This questions has been only mildly debated in the instant case of
the Colorado River, and has not been resolved to the collective satisfaction of scientists, resource managers, and politicians. Nor is it likely ever to be. We believe that the literature assembled for this report are inadequate to reliably identify unique physical habitat uses, occurrences, or preferences of native and non-native fishes. We further are unable to indict any particular physical habitat alteration, other than desiccation, as solely responsible for the demise of native fishes in the system.

There is a substantial and growing body of evidence that supports an hypothesis that non-native fishes themselves are responsible for the current plight of the imperiled native fauna (in part, APPENDIX III). The mechanism of this interaction may be debatable, but it remains as indisputable fact that non-natives fishes displace or replace native species where the two kinds co-occur, while in the absence of non-native fishes the natives consistently survive, grow, and demonstrate an ability to fulfill all life history functions including reproduction and recruitment. It is not possible in these cases to attribute a primary role to physical habitat, and we are unable to envision habitats with physical characteristics that somehow would allow persistence of mixed native and non-native faunas consisting of self-maintaining species' populations.

MANAGEMENT RECOMMENDATIONS

It is indisputable that the Colorado River has been irreversibly altered and hydrologically controlled to meet human needs. Historical habitats have been mostly destroyed and replaced by reservoirs, tailwaters, and modified river reaches that are subject to unnatural, regulated flows. Superimposed upon these perturbations have been additions of non-native species to the fauna, which themselves constitute major alterations to the system. Introduced fishes predominate the fish fauna of the entire region, and in many places are the only fishes present. There are no populations of native fish species anywhere in the lower Colorado River channel or its reservoirs that are isolated and insulated from non-natives fishes.
The historical fish fauna of the lower Colorado River comprised only ten freshwater species. In the mainstream below Grand Canyon, all these fishes now are either extirpated, endangered, or represented by re-introduced populations. None is self-sustaining. The imperiled status and continued decline of the entire indigenous fauna is attributed to a combination of physical alteration and biological pollution of the system by non-native species.

Native and non-native fishes that occupy the lower Colorado River are superimposed in time and space, and we were unable as a result of this review to identify specific habitat use parameters that separate the two kinds. Habitat use by native and non-native fishes is broadly overlapping, in part because most species of both categories are facultative generalists capable of successfully occupying most or all of the array of physical habitats presented by the lower Colorado River. Both kinds of fishes have similar thermal requirements, and both utilize similar food resources acquired in similar ways. These similarities are evident across all life stages from larva through adult.

There are, however, several important distinctions between the native and non-native fishes of the lower Colorado River. The latter category includes a substantially greater number and proportion of piscivorous predators than the former, and as a result there is a much greater predator load at the community level today than historically (among adults, only Colorado squawfish was a piscivore). And, non-native fishes evolved predator avoidance and other behaviors that allow perpetuation of mixed communities of fishes of diverse feeding modes. These mechanisms are thought not to be shared with native species of the Colorado River, which puts the indigenous fauna at a severe disadvantage, so severe that predation by non-native fishes is considered the single most important factor in the lack of recruitment to native fish populations.

Another advantage to the non-native fauna is that many of these fishes are nest builders that also provide protection to their offspring. In contrast, with exception of
one species, all native fishes of the lower Colorado River are broadcast spawners that
give no parental care. The reproductive strategies of non-native fishes combined with
predator avoidance adaptations increase their early life stage survival relative to that of
native species. Thus, populations of non-natives thrive while their predation pressure
on early life stages precludes recruitment by native fishes.

These compelling arguments support our primary recommendation for the lower
Colorado River that successful management of native fishes requires their physical
segregation from non-native fishes. There is ample evidence that the natives can
complete their life cycles in a variety of habitats in absence of non-natives, while
examples of co-existence of the two kinds through multiple generations are unknown.

We advocate a conceptual plan developed by W.L. Minckley (unpublished and
personal communication) for construction (or reclamation) of substantial areas of off-
channel aquatic habitat that are set aside strictly for native fishes (although compatible
uses should not necessarily be precluded), and are vigorously protected from incursion
of non-natives. Habitat sizes should be variable from a few to perhaps several hundred
hectares, and provided in multiple replicates so that loss of any one or few would not
compromise an overall program, and to offer opportunities for experimental treatments.
Native fishes should be managed as communities of compatible species, with stocks
derived from appropriate, genetically defined wild populations. Self-sustaining
populations in these off-channel habitats could contribute to stocks in the mainstem to
provide a complimentary long-term, genetic repository (Minckley and Fagan,
unpublished), and opportunities to further understand their ecology.

Responsible management entities are urged to move immediately to develop and
implement a protocol to put this recommendation into practice. Status of native fishes
of the lower Colorado River continues to worsen measurably, and on-going programs,
although showing some promise, are not designed and do not appear sufficient to
perpetuate the indigenous fish community.
LITERATURE CITED


Brown, L.R. and A.M. Brasher. 1995. Effect of predation by Sacramento squawfish (Ptychocheilus grandis) on habitat choice of California roach (Lavinia symmetricus) and rainbow trout (Oncorhynchus mykiss) in artificial streams. Canadian Journal of Fisheries and Aquatic Sciences 52: 1639-1646.


