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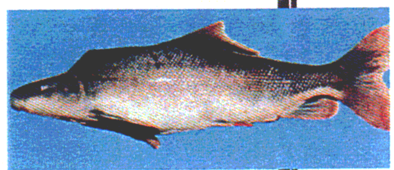
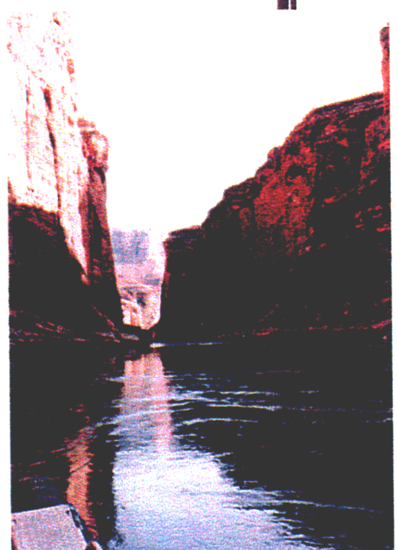
THE AQUATIC ECOSYSTEM OF THE COLORADO RIVER IN GRAND CANYON



Grand Canyon Data Integration Project Synthesis Report

Prepared for

THE BUREAU OF RECLAMATION
Upper Colorado Region
125 South State Street, Room 7217
Salt Lake City, Utah 84138



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Final

THE AQUATIC ECOSYSTEM OF THE COLORADO RIVER IN GRAND CANYON

Grand Canyon Data Integration Project
Synthesis Report

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July 1, 1998

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PREFACE

This report is being submitted to the Bureau of Reclamation, Upper Colorado Region, in partial fulfillment of contract No. 1425-6-CS-40-19040. Initially, the Grand Canyon Data Integration Project was administered by Ms. Christine Karas out of Reclamation's Upper Colorado Regional office in Salt Lake City, with Mr. Michael Yard of the former Glen Canyon Environmental Studies serving as Contracting Office Representative. When the Department of the Interior's Grand Canyon Monitoring and Research Center replaced GCES as the agency responsible for scientific investigations related to Glen Canyon Dam operations, Dr. Barry Gold, Associate Chief of GCMRC, became our federal liaison for this project. We want to acknowledge the important roles these three individuals played in bringing the Grand Canyon Data Integration Project to a successful conclusion, and thank them for their assistance.

We would also like to acknowledge the contributions of the fishery biologists who participated in the *Workshop on Endangered and Other Native Fishes of Glen and Grand Canyons* held in Flagstaff, Arizona, on February 27 and 28, 1997. Their names and affiliations are provided in Appendix A of this report.

Special thanks are due the eight peer reviewers, all anonymous, who, on the behest of GCMRC, meticulously reviewed the preliminary draft and draft versions of this document. Their extensive and thoughtful comments were invaluable.

EXECUTIVE SUMMARY

BACKGROUND

The U.S. Fish and Wildlife Service's 1995 Biological Opinion on the operation of Glen Canyon Dam found that current and proposed dam operations continue to jeopardize two endangered species within Grand Canyon: razorback sucker and humpback chub. Existing data on the population status of these two species indicate that the razorback sucker is virtually extinct in Grand Canyon, and the humpback chub— although reproducing in the Little Colorado River—has been declining in numbers over a 35-year period of record.

In their Biological Opinion, the U.S. Fish and Wildlife Service identified a "Reasonable and Prudent Alternative" to the preferred alternative of the Environmental Impact Statement on the operation of Glen Canyon Dam. The preferred alternative was a regime of modified low fluctuating flows (MLFF). The Reasonable and Prudent Alternative recommends a seasonally adjusted steady flow experiment within the context of the MLFF and undertaken through the Adaptive Management Program.

The steady flow experiment would consist of sustained high releases during the period of April–May, followed by low steady releases during June–October. The high releases would be designed to pond tributary inflows and provide warm nursery habitats for young native fish descending from tributaries. The low releases would be designed to enhance habitat conditions for native fishes by stabilizing and warming mainstem and nearshore habitats, including backwaters (i.e., eddy return-current channels). Experimental steady flows would be released only during low-release years (i.e., ≤8.23 million acre feet) over "a sufficient period of time to allow for experimental design, biological processes to function and for variability inherent in riverine ecosystems to be expressed. The number of years is, therefore, indeterminate" (FWS 1994a). As a preliminary step toward the design of such an experiment, SWCA, Inc. Environmental Consultants was retained by the Bureau of Reclamation to summarize and evaluate known information about native and non-native fishes in Glen and Grand Canyons with the following objectives:

1. Summarize known information that would help predict responses by endangered and other native fishes to steady flows,

2. Identify information that is still needed to understand the relationship of fish and dam release patterns (data gaps), and

3. Frame testable hypotheses for research designed to acquire the needed information.

To this end, we have reviewed the existing knowledge on aquatic ecosystems in Glen and Grand Canyons and synthesized that information so the following questions could be addressed:

- Do sufficient baseline data exist to evaluate the influence of the steady flow experiment described in the RPA?

- Do existing data indicate that the steady flow experiment will likely have an overall positive influence on endangered and other native fishes in Grand Canyon?

METHODS

A two-phased approach was used to complete this study. First, SWCA assembled information from over 400 publications and reports on aquatic resources of Glen and Grand Canyons. This information was evaluated, summarized, and integrated into a preliminary draft of this report. Second, in order to obtain feedback from a broad spectrum of experts, the draft was distributed to 25 aquatic biologists who have worked in the Upper and/or Lower Colorado River Basins in recent years. These specialists were asked to conduct a critical review of the report and to participate in a 2-day workshop. The overriding objective of the workshop, which was held in Flagstaff, Arizona, on February 27-28, 1997, was to obtain as much insight as possible among the biologists on the two questions driving this study. Finally, the report was reviewed by six independent reviewers through two drafts to ensure that the project approach and report were scientifically valid.

RESULTS

The best available scientific information indicates that primary and secondary production have been highest under short-term steady or low fluctuating flows, and lowest under high fluctuating releases. However, drift of algae and macroinvertebrates, a major food source of fishes, has generally been higher during fluctuating flows than during short-term steady flows. Data also indicate higher water clarity and warming during short-term steady flows, but the effect of long-term steady flows on drift, water clarity, and temperature, such as proposed in the experiment, have not been evaluated or modeled. Available data also indicate that, although cold mainstem temperatures and fluctuating flows have limited reproduction and perhaps survival of endangered and other native fishes, these flow variables have also limited invasion and proliferation of warm-water non-native competing and predaceous fishes. Cold mainstem water temperatures have also limited the spread of recently introduced parasites, particularly the potentially lethal Asian tapeworm (*Bothriocephalus acheilognathi*), which has become prevalent in cyprinid fishes of the Little Colorado River.

Except for temperature and possibly turbidity, water quality parameters currently found in the Colorado River in Grand Canyon are not limiting to native fishes. Availability of suitable food for each life stage of fish has been considered a potentially important limiting factor; however, clear evidence of food limitations in Grand Canyon is lacking. Most studies of fish diet report few empty stomachs, and potential food supplies appear to be fairly abundant from drift and benthic macroinvertebrate studies. Nonetheless, a few observations have been made of possible food shortages for specific life stages of some species. Because of cold mainstem temperatures, the only known spawning habitats of native fishes in Grand Canyon are tributaries or warm springs. We believe that most larval flannelmouth suckers, bluehead suckers, and humpback chub descending from warm natal tributaries into the cold mainstem die of thermal shock or from predation elicited by erratic swimming behavior. For those fish old enough to survive the transition, swimming ability may be reduced by as much as 98% by cold mainstem temperatures. This reduced swimming ability, combined with reduced turbidity for cover, greatly advantage cold-water sight predators, such as rainbow trout and brown trout. Juvenile native

11. Timing and degree of drift by native larval fishes at tributary inflows, including those of the Paria River, LCR, Bright Angel Creek, Shinumo Creek, and Kanab Creek.

12. Flows for maintenance of the 30-mile aggregation of humpback chub, as well as the genetic significance of the fish as possible relicts of historic mainstem stocks.

13. Relationship of mainstem flows to nearshore habitats and channel geomorphology.

14. A complete Grand Canyon Aquatic Resources Database that is accessible to researchers and interested parties.

CONCLUSIONS

It is clearly recognized by all biologists consulted, including the authors of this report, that a steady flow experiment would be valuable for testing response hypotheses. However, consistent with the findings of the literature review, workshop biologists concluded that sufficient baseline data to fully evaluate the steady flow experiment, *a priori*, do not currently exist. They agreed that a steady flow experiment is likely to have a positive effect on native fishes by warming and stabilizing nearshore habitats, including backwaters and tributary mouths, and enhancing reproduction, growth, and survival. However, a steady flow would simultaneously benefit warm-water non-native fishes, possibly reduce drifting food availability, and would likely increase the incidence of fish parasites. Many biologists believe that positive effects of steady flows to non-native predators and competitors could offset many of the beneficial effects to native fishes. Existing data reported in the literature (and summarized in Chapter 7) on native/non-native fish interactions consistently indicate that non-native species invade and dominate native species in regulated, warm-water habitats.

The workshop biologists and the findings of our literature review support modifying the steady flow hydrograph to maximize benefits to native fishes, but we caution that implementing an experimental steady flow may constitute an ecological risk due to potential responses by non-native fishes, food resources, and parasites. The authors of this report recommend that a non-native fish control strategy be initiated before beginning experimental steady flows.

fishes along sheltered shoreline habitats are often forced to move to alternative locations by changing river stage, increasing exposure to predators and needless energy expenditure.

The degree to which non-native fish species have negatively affected native fish populations in Grand Canyon through predation and competition has not been clearly demonstrated. Non-native fishes do prey on native fishes in Grand Canyon. Brown trout, channel catfish, rainbow trout, and black bullheads are the principal predators of native fish. The extent of this predation is not known, but predator-prey models suggest it is substantial. Competition between native fishes and non-native fishes is implied by extensive overlap in diet and sympatry in many habitats for all life stages; however, data on abundances, distribution, and habitat use by non-native species in Grand Canyon is patchy because life history studies of these fishes have not been conducted in the canyon.

Without knowing more about native/non-native interactions under existing flow conditions (i.e., low fluctuating flows), it is difficult to predict which, if either, group of fishes would benefit more from steady flows. We cannot predict the outcome for endangered and other native fishes if, indeed, non-native predators and competitors increase in abundance, but all available evidence suggests a detrimental effect on native species unless these species receive substantially disproportionate benefits from the flows. By their nature, non-native fishes have a more variable range of life history requirements that tends to make them more tolerant and resilient to disturbances than the native fishes in Grand Canyon. Hence, flow modifications, even if they resemble historic regimes, may directly benefit native fishes, but may also benefit non-native forms. This could result in overall, long-term negative effects on the natives species.

INFORMATION NEEDS AND DATA GAPS

The 11 most significant information needs identified during this project are as follows:

4. A temperature model that will predict longitudinal downstream warming of the mainstem, as well as warming of shoreline and backwater habitats.

5. Bathymetry and temperature isopleths for inflows of the Paria River, LCR, Shinumo Creek, Bright Angel Creek, and Kanab Creek to determine the extent of ponding and thermal warming at various flows.

6. Primary and secondary productivity rates and levels for different flows longitudinally down the mainstem, in backwaters, and along shorelines.

7. Factors that limit survival of young humpback chub in the mainstem and recruitment to adulthood.

8. Biotic interactions of native/non-native fishes.

9. Rates of algal and macroinvertebrate drift for various flows.

10. Incidence and rates of infection by the fish parasites *Lernaea cyprinacea* and Asian tapeworm as well as risk of increased infection associated with warming mainstem and shoreline habitats.

Chapter 1
INTRODUCTION:
EVOLUTION OF THE EXPERIMENTAL STEADY FLOW

This report identifies and synthesizes information gathered during previous research projects on endangered and other native fishes in Glen and Grand Canyons in the State of Arizona. Emphasis is on ecological requirements and factors that limit reproduction, development, recruitment, and survival of these fishes within the context of water release patterns from Glen Canyon Dam. The reasons for assembling this information stem from requirements of the Reasonable and Prudent Alternative (RPA) of the U.S. Fish and Wildlife Service's (FWS) 1995 Biological Opinion on the operation of Glen Canyon Dam (FWS 1994a). This Biological Opinion specifically addresses the Modified Low Fluctuating Flow alternative (preferred alternative) of the Glen Canyon Dam Environmental Impact Statement (GCDEIS). The RPA calls for the U.S. Bureau of Reclamation (Reclamation) to release experimental steady flows from the dam to study the effects of such flows on endangered and other native fishes downstream. Before embarking on the experiment, Reclamation is both laying the groundwork for an effective experimental design and assessing the potential of steady flows to negatively affect native fish.

Specific objectives in this report are to summarize known information that would help predict responses by endangered and other native fishes to steady flows; identify information that is still needed to understand the relationship of fish and dam release patterns (data gaps); and frame testable hypotheses for research designed to acquire the needed information. To this end, we have reviewed the existing knowledge on aquatic ecosystems in Glen and Grand Canyons and synthesized that information so as to address the following questions:

- Do sufficient baseline data exist to evaluate the influence of the steady flow experiment described in the RPA?
- Do existing data indicate that the steady flow experiment will likely have an overall positive influence on endangered and other native fishes in Grand Canyon?

BACKGROUND

The focus of this document is on the Colorado River fish assemblage in Glen and Grand Canyons in northwestern Arizona (Figure 1). The Glen Canyon reach winds about 25 km downstream from the base of Glen Canyon Dam to the Paria River near Lees Ferry. The upper 450 km of Glen Canyon, the reaches above the dam, are inundated by Lake Powell. Grand Canyon heads at the Paria River and extends some 445 km to its mouth at the Grand Wash Cliffs. Because Lees Ferry roughly marks the political division between the Upper and Lower Colorado River Basins, the Glen Canyon reach officially lies in the Upper Basin, while the Grand Canyon reach occupies the Lower Basin. This distinction between basins in the project area will not be observed in this report.

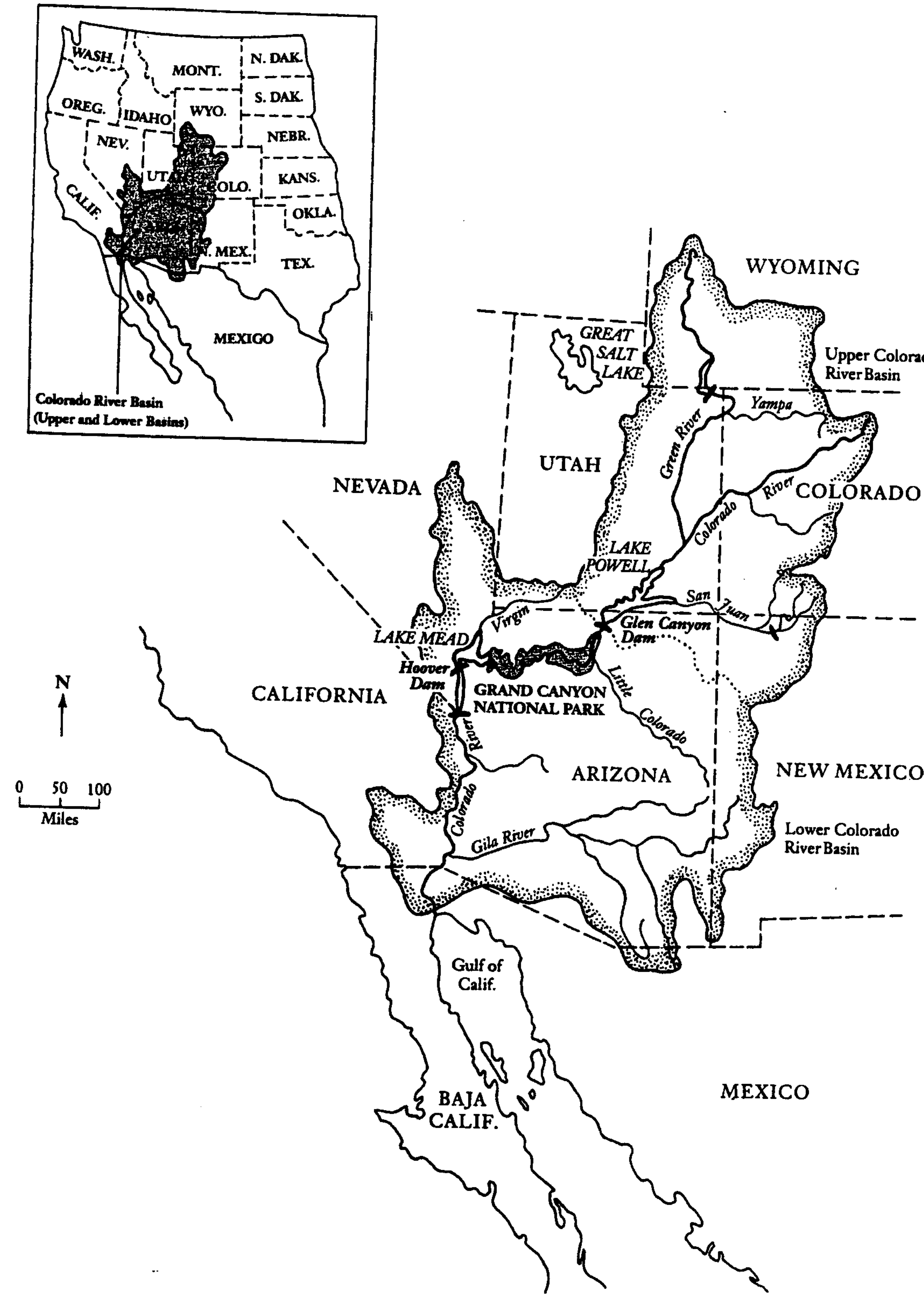

Figure 1. Location map of the Colorado River Basin, showing the project area between Glen Canyon Dam upstream and Lake Mead downstream. The dotted line marks the division between the Upper and Lower Colorado River Basins. (Source: Carothers and Brown 1991)

The project area lies between Glen Canyon Dam (upstream) and the inflow to Lake Mead, the reservoir behind Hoover Dam (downstream; Figure 2). The dams were completed in 1963 and 1935, respectively. From the tailwaters of Glen Canyon Dam to the slack headwaters of Lake Mead, the Colorado River flows freely—although changed from its natural state by dam regulation—for 470 km. Within this reach of river, five species of native fish share the aquatic ecosystem with two dozen species of non-native fish.

The native species are humpback chub, razorback sucker, flannelmouth sucker, bluehead sucker, and speckled dace (Figure 3).[1] Two of these species, humpback chub and razorback sucker, are federally listed as endangered, with combined designated critical habitat that includes the Colorado River from the Paria River confluence to Hoover Dam[2] (FWS 1994b). Three additional species native to the Colorado River, bonytail, roundtail chub, and Colorado squawfish, are extirpated from Glen and Grand Canyons (Minckley and Deacon 1991).

Throughout the arid Southwest, including Grand Canyon, biologists have been documenting declining populations of native fishes for more than 60 years (Minckley and Deacon 1991). This decline probably began with early Euro-American settlement of the region, when farming and ranching practices, small-scale water impoundments and diversions, groundwater pumping, and contaminants began to degrade fish habitat in local permanent water sources (Fradkin 1981, Weatherford and Brown 1986, Reisner 1996; see also Chapters 3, 4, and 6, this document). To their further detriment, native fish were assaulted by unfamiliar competitors and predators after settlers released fish species foreign to the area into streams and ponds, rivers and lakes—initially as potential food sources and later for sportfishing.

Impacts of early Euro-American settlement pale, however, when compared to riverine ecosystem changes that resulted from the Reclamation Act of 1902 and subsequent reclamation legislation. The Reclamation Act, which initiated federal involvement in funding and building irrigation projects for arid lands, was followed over the years by several pieces of legislation specific to the Colorado River drainage. Such laws included the Boulder Canyon Project Act of 1928, which authorized Hoover Dam, and the Colorado River Storage Project Act of 1956, which authorized Glen Canyon Dam. The story of how agriculture boomed in California and Arizona, and how most major urban centers in California, Arizona, and Nevada expanded to their present burgeoning populations, is related to large-scale federal water development and hydropower projects (Reisner 1996). Today, thirteen mainstem dams control the flow of the Colorado River from Wyoming to California, and hundreds of smaller dams and diversions regulate most streams in both the Upper and Lower Colorado River Basins (Fradkin 1981).

Massive alterations of aquatic habitats resulting from these projects, combined with the proliferation of introduced fish species, have devastated native fish populations (Minckley 1991, Minckley and Deacon 1991). Today, in Arizona alone, 81% of native fish species are classified or proposed as threatened or endangered. In New Mexico, 42% of native species are threatened or endangered, and fishes of most other western states are faring no better. The long-term prognosis for survival of southwestern native fish species is not good (Rolston 1991, Minckley and Deacon 1991).

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[1] Scientific names of all species mentioned in the text are listed in Appendix B at the end of this report.

[2] Critical habitat for the razorback sucker extends the full length of this reach, while critical habitat for the humpback chub is contained within Grand Canyon, extending from Nautiloid Canyon, a side canyon at River Mile (RM) 34 to Granite Park at RM 208, and the lower 12.9 km of the Little Colorado River.

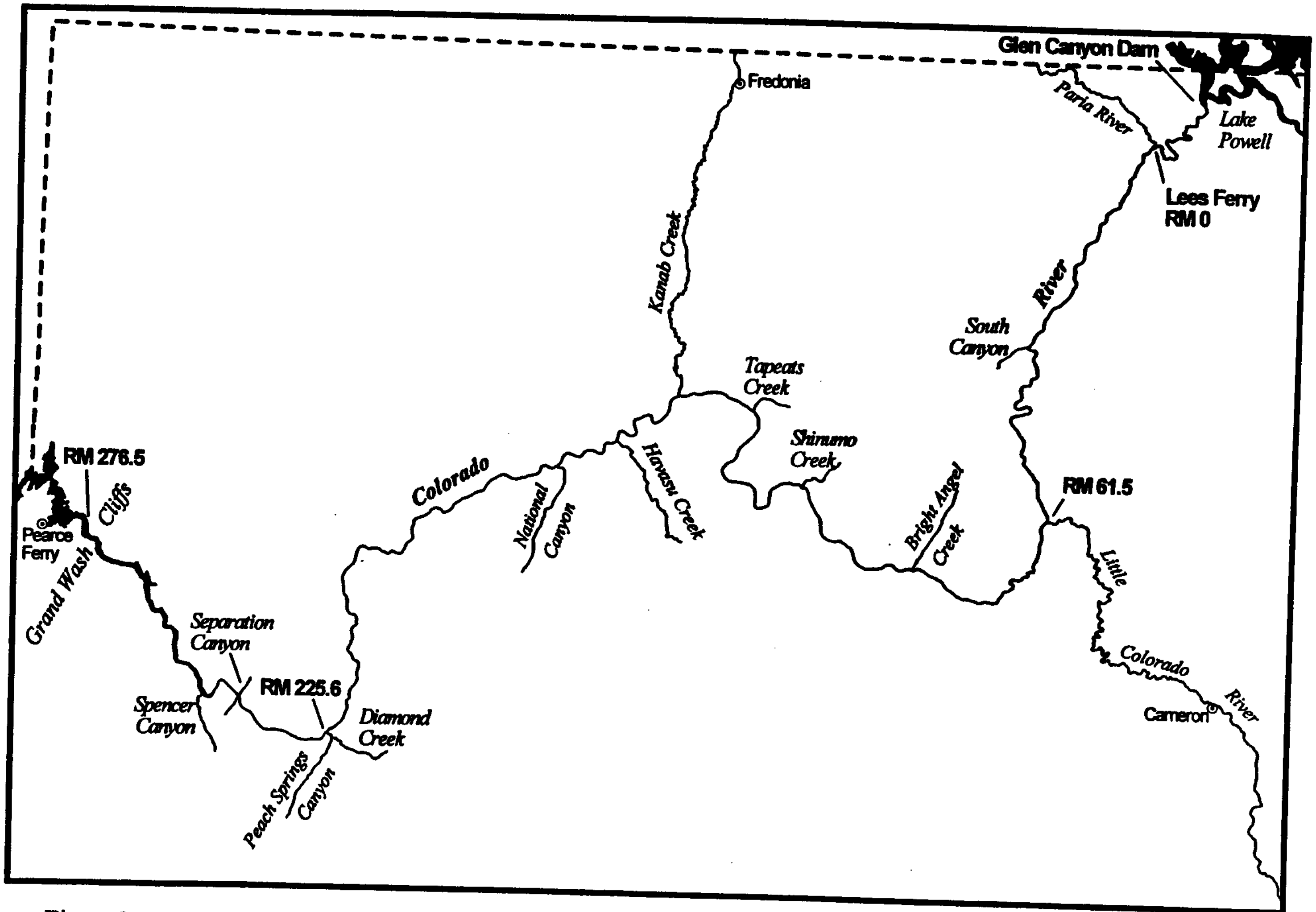


Figure 2. Detail of the project area, which encompasses the Colorado River in Glen Canyon (from Glen Canyon Dam to Lees Ferry) and Grand Canyon (from Lees Ferry to the Grand Wash Cliffs)

Glen Canyon Environmental Studies (GCES Phases I and II)

Since passage of the National Environmental Policy Act of 1969 (NEPA) and the Endangered Species Act of 1973 (ESA), declining populations of native fish species have prompted a growing amount of federally funded research on the impacts of water and hydropower projects. A significant portion of this work has focused on the Colorado River between Glen Canyon Dam and Lake Mead. Reclamation has expended more than $50 million for multidisciplinary studies in the region, pursuing answers to questions important to the preservation of native fishes and other natural resources (National Research Council 1996). This research began as a documentation of dam-caused changes to specific aquatic and riparian resources below Glen Canyon Dam (Carothers and Minckley 1981). It has evolved into an ecosystem-wide approach to understanding cause-and-effect relationships between dam discharge, sediment distribution, geomorphology, water quality parameters, food base, and fish species population dynamics. The focus of fish studies has been on humpback chub and razorback sucker because of their endangered status (Reclamation 1990, 1995).

Most of the research was conducted under Reclamation's Glen Canyon Environmental Studies (GCES), which operated from April 1983 to October 1996. GCES was a special program established by Reclamation to evaluate changes to elements of Glen Canyon Dam's peaking power system in the late 1970s (Reclamation 1989). Public response to the potential impacts of changing dam operations and the lack of adequate scientific information about the downstream ecosystem focused agency attention on the pattern and magnitude of dam releases. To gather the scientific data needed to make informed decisions about future operations, particularly about the effects of operations on endangered species, Reclamation launched 33 multidisciplinary studies conducted 1983–1987 to investigate the relationship between dam operations (high fluctuating flows) and downstream resources (Reclamation 1989). These studies, known as GCES Phase I, were conducted from 1983 through 1987. Research findings indicated that dam releases were negatively affecting canyon resources, but the mechanisms and interrelationships were unclear. A review conducted by the National Research Council (1987) of the National Academy of Sciences determined that sufficient data were not yet available to support changing operations at the dam. The Council recommended more studies.

In 1988, Reclamation initiated GCES Phase II. The Draft Integrated Research Plan (DIRP) for Phase II (Reclamation 1990) described the primary study components necessary to establish the relationship between discharge and impacts, and provided a series of hypotheses for addressing specific questions about specific resources. Initially, this phase of GCES focused on ecosystem responses through 4 to 5 years of additional scientific investigations. However, the research schedule was accelerated when the Secretary of the Interior announced on July 27, 1989, that an Environmental Impact Statement would be prepared on the operation of Glen Canyon Dam (GCDEIS) to meet NEPA compliance requirements (Reclamation 1995). Preliminary research findings from GCES Phase II contributed heavily to the GCDEIS, but some elements of the research, including critical fishery and related aquatic studies, were not completed in time for inclusion in either the GCDEIS or the subsequent Biological Opinion. Much of the voluminous data acquired during these studies have yet to be fully analyzed and compared.

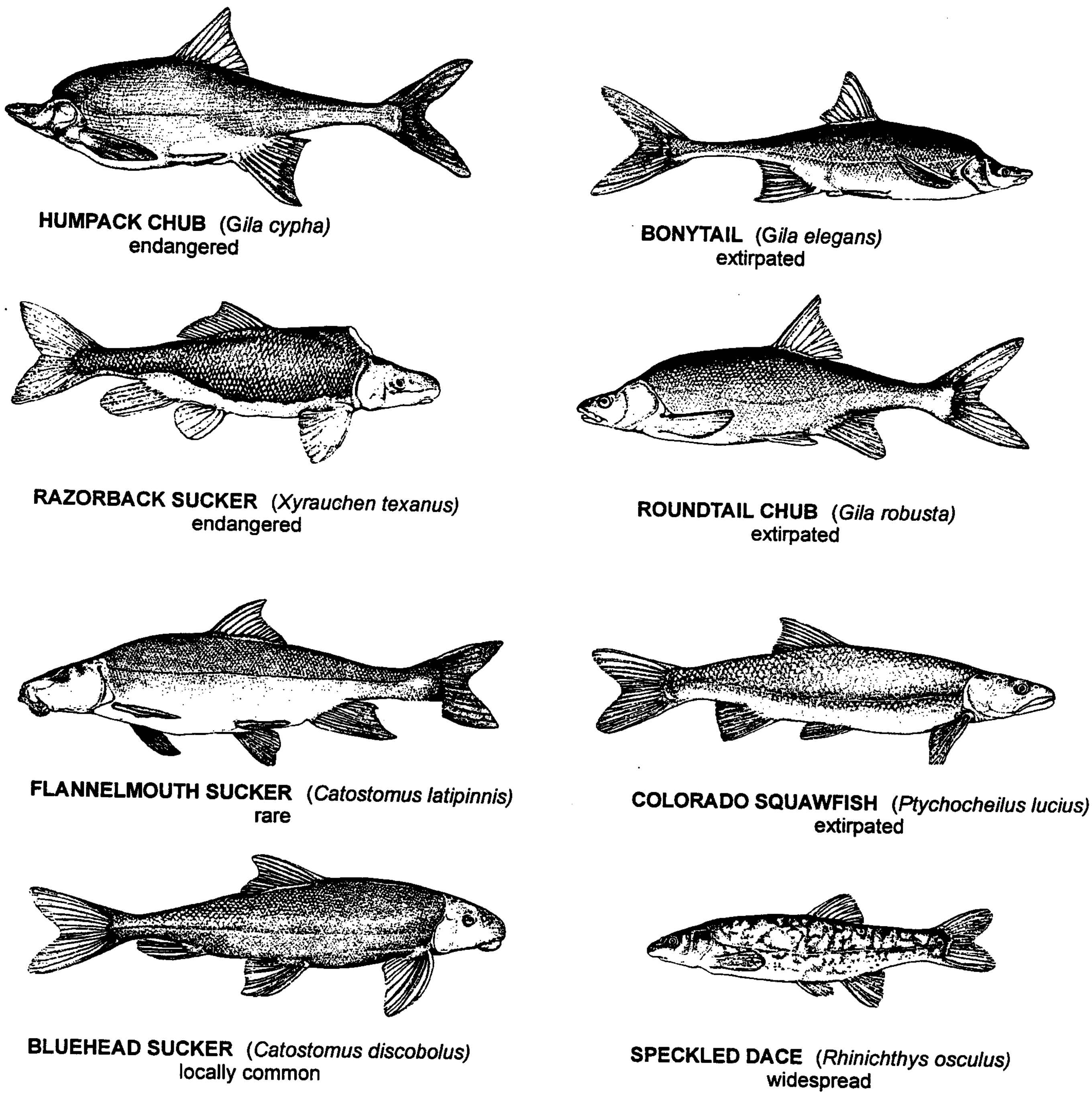


Figure 3. Species and status of native fish in Grand Canyon (Source: Grand Canyon River Guides; Illustrator: M.C. Filbert).

Glen Canyon Dam Environmental Impact Statement

Objectives of the GCDEIS were to analyze an array of reasonable dam operation alternatives and identify an operational mode that would make it possible "to balance and meet statutory responsibilities for protecting downstream resources for future generations and producing hydropower, and to protect affected Native American interests" (Reclamation 1995). These objectives were further refined in 1992 with passage of the Grand Canyon Protection Act, which directed the Secretary of the Interior to develop alternatives "in such a manner as to protect, mitigate adverse impacts to, and improve values for which Grand Canyon National Park and Glen Canyon National Recreation Area were established...."

Reclamation, acting as lead agency, initiated the GCDEIS process by establishing a team made up of representatives from Reclamation and the following 11 cooperating agencies and tribes: National Park Service (NPS), Western Area Power Administration (WAPA), U.S. Fish and Wildlife Service (FWS), Bureau of Indian Affairs (BIA), Arizona Game and Fish Department (AGFD), Hopi Tribe, Hualapai Tribe, Navajo Nation, San Juan Southern Paiute Tribe, Southern Paiute Consortium, and Zuni Pueblo (Reclamation 1995).

The EIS team considered nine alternative dam release scenarios, including No Action, or historic dam operations (see sidebar). The discharge characteristics of these nine alternatives fell into three categories: Unrestricted

The Nine GCDEIS Alternatives

Unrestricted Fluctuating Flows

No Action: Retain historic dam operations; maximum release 31,500 cfs; minimum release 1,000 cfs (fall-winter) 3,000 cfs (spring-summer); maximum daily fluctuation 30,500 cfs (fall-winter) 28,500 cfs (spring-summer).

Maximum Power Plant Capacity: Permit use of full Power plant capacity; maximum release 33,200 cfs; minimum release 1,000 cfs (fall-winter) 3,000 cfs (spring-summer); maximum daily fluctuation 32,200 cfs (fall-winter) 30,200 cfs (spring-summer).

Restricted Fluctuating Flows

High: Slightly reduce daily fluctuations from historic dam operations; maximum release 31,500 cfs; minimum release 3,000, 5,000, or 8,000 cfs depending on monthly volume and market; maximum daily fluctuation 15,000–22,000 cfs.

Moderate: Moderately reduce daily fluctuations from historic operations; maximum release 31,500 cfs; minimum release 5,000; maximum daily fluctuation ±45% of mean flow for month up to ±6,000 cfs.

Modified Low: Substantially reduce daily fluctuations from historic operations; minimum release 8,000 cfs during day, 5,000 cfs at night; maximum release 25,000 cfs; maximum daily fluctuation 5,000, 6,000, or 8,000 cfs for <600,000, 600,000–800,000, or >800,000 ac/ft-months, respectively.

Interim Low: Substantially reduce daily fluctuations from historic operations; minimum release 8,000 cfs during day, 5,000 cfs at night; maximum release 20,000 cfs; maximum daily fluctuation 5,000, 6,000, or 8,000 cfs for <600,000, 600,000–800,000, or >800,000 ac/ft-months, respectively.

Steady Flows

Existing Monthly Volume: Release steady flows on a monthly basis (existing monthly volumes prorated); minimum release 8,000 cfs; maximum release 20,000 cfs; maximum daily fluctuation ± 1,000 cfs.

Seasonally Adjusted: Release steady flows on a seasonal or monthly basis; minimum release varies seasonally 8,000–18,000 cfs; maximum release 18,000 cfs; maximum daily fluctuation ± 1,000 cfs.

Year-Round: Release steady flows throughout the year (yearly volume prorated); maximum daily fluctuation ± 1,000 cfs.

Common Elements in GCDEIS Restricted Fluctuating and Steady Flow Alternatives

Adaptive Management - Reclamation will establish a research/management program whereby the effects of dam operations on downstream environmental elements may be accurately assessed. This program will form the basis for future changes in dam operations.

Monitoring and Protecting Cultural Resources - Reclamation will consult with the Native American groups with whom it has a programmatic agreement about long-term monitoring and protection of cultural resources downstream of the dam.

Flood Frequency Reduction Measures - Reclamation will consider both structural and operational measures to prevent resource-damaging, unscheduled flood releases from the dam.

Beach/Habitat-Building Flows - Reclamation will release, as appropriate, flows designed to reestablish beaches, revitalize backwaters and redistribute nutrients. These flows will, to some extent, mimic elements of the natural hydro-graph eliminated with placement of the dam.

New Population of Humpback Chub - Reclamation will attempt to establish, by reintroduction if necessary, a second repro-ducing population of humpback chub either in the mainstem or in a tributary other than the LCR.

Further Study of Selective Withdrawal - Reclamation will study the operational, economic, and biological feasibility of instal-ling a multilevel intake structure at Glen Canyon Dam to warm mainstem water, and install the intake structure if this action is recommended by the FWS and AGFD.

Fluctuating Flows, Restricted Fluctuating Flows, and Steady Flows. A set of common elements was developed for all restricted fluctuating and steady flow alternatives (see sidebar, next page).

During preparation of the GCDEIS (1990–1995), it became apparent that, despite the efforts directed toward aquatic research, cause-and-effect relationships between the alternative flow scenarios and fish populations remained unclear. The difficulty in assessing the effects of alternative flow scenarios on fishes was (and still is) due to the following:

1) the incomplete state of knowledge on biological, physical, and chemical interactions in the Grand Canyon aquatic ecosystem and how these interactions are influenced by dam discharge patterns;

2) the myriad of habitats involved, changing conditions with increased distance below the dam, and the unpredictable variation in tributary inflows that influence interrelationships between flow and ecosystem components;

3) the dramatic differences between pre- and post-dam river ecosystem characteristics; and

4) the lack of a synthesis and integration of existing data on fish responses to dam releases that clearly articulate what we know and what we do not know.

In January 1993, after 2 years of gathering information and analyzing the potential impacts of the nine flow alternatives, the GCDEIS team met to select a preferred alternative. Final debate focused on the relative merits of the Modified Low Fluctuating Flow alternative (MLFF) and the Seasonally Adjusted Steady Flow alternative (SASF). For purposes of comparison, Table 1 presents the flow characteristics of these two alternatives, along with those of the No Action alternative.

As one of the restricted fluctuating flow alternatives, the MLFF was designed to improve conditions for all downstream natural resources (relative to the No Action alternative), while simultaneously meeting the need for some flexibility in hydropower production.

Compared to No Action, the MLFF is characterized by significant reductions in peak flows, increases in minimum flows, a major reduction in the magnitude of fluctuations allowed each day, and restrictions on the rate of those fluctuations (i.e., cubic feet per second [cfs] per hour change in discharge) (Reclamation 1995).

The SASF alternative was thought to have similar potential benefits as the MLFF for most resources, with two significant differences: SASF was expected to result in 1) lower hydropower production efficiency and higher costs to power users, and 2) greater potential benefits for the aquatic food base and native fishes, including the endangered species (Reclamation 1995, Table II-7; National Research Council 1994). Under the SASF, releases would be constant within defined seasons, with variations between seasons calculated to meet anticipated flow requirements of endangered and other native fishes.

Table 1. Discharge Characteristics of the GCDEIS No Action, MLFF, and SASF Alternatives Reported in Cubic Feet per Second (cfs).

Alternative	Minimum Release (cfs)	Maximum Release (cfs)	Daily Fluctuations (cfs)	Ramp Rate
No Action	1,000 Labor Day to Easter 3,000 Easter to Labor Day	31,5000	30,500 Labor Day to Easter 28,500 Easter to Labor Day	Unrestricted
Modified Low Fluctuating Flow (Preferred Alternative)	8,000 7 a.m. to 7 p.m. 5,000 7 p.m. to 7 a.m.	25,000	5,000; 6,000; or 8,000 depending on monthly release volume	4,000 cfs/hr up 1,500 cfs/hr down
Seasonally Adjusted Steady Flow	8,000 Oct–Nov 8,000 Dec 12,500 Apr 18,000 May–Jun 12,000 Jul 9,000 Aug–Sep	18,000 same same same same same	± 1,000 same same same same same	2,000 cfs/hr when releases are changed between steady flow periods

Source: Reclamation (1995)*

With only one dissenting vote among the 12 cooperating agencies, the MLFF was chosen as the draft GCDEIS preferred alternative (unpublished minutes, GCDEIS Cooperating Agencies meeting, January 27–29, 1993, Reclamation, Colorado River Studies Office, Salt Lake City, Utah). This alternative was thought by its supporters to be the most balanced approach, benefitting the widest range of resources (including the aquatic food base and fish) when compared to historic dam operations. While the MLFF would result in a significant loss of hydropower benefits, compared to historic dam operations, those losses would be less than losses incurred under the SASF. The dissenting vote was cast by the FWS, which felt that the MLFF would not provide sufficient benefit to humpback chub to remove jeopardy (Randle 1993). This decision by the FWS should be viewed within the context of the agency's long-term involvement with listed species in Grand Canyon and the belief that SASF would provide the greatest benefit to the endangered humpback chub, as well as other canyon resources.

The Fish and Wildlife Service's Biological Opinions

The FWS's involvement with Glen Canyon Dam began in 1977 when Reclamation requested consultation under Section 7 of the ESA regarding the effects of dam operations on humpback chub and Colorado squawfish. Both species had been listed as endangered in 1967 (FWS 1978, 32 FR 4001). Bonytail and the razorback sucker, now endangered species, were not included in that consultation because they were not listed until 1980 and 1991, respectively (FWS 1980, 1991). As a result of the consultation, the FWS issued a Biological Opinion, dated May 25, 1978, finding that "past, present and future proposed operations of Glen Canyon Dam...[jeopardize] the continued existence of this species [humpback chub] by limiting its distribution and population size" (FWS 1978). Dam operations were found to limit the recovery of the Colorado squawfish, because downstream flow characteristics and water quality precluded the re-establishment of the species in Grand Canyon.

This Biological Opinion included the following recommendations: 1) determine the potential impact of warming the river water below the dam; 2) identify the ecological needs of the endangered species; 3) develop methods to reduce or eliminate the known constraining factors of low temperature and frequent flow fluctuations; and 4) determine the relationships between mainstem and tributary habitats and their use by endangered species. These recommendations helped to drive and shape the GCES Phase I program (Reclamation 1990).

After completing GCES Phase I in 1987, Reclamation reinitiated Section 7 consultation with the FWS on the operation of the dam (Reclamation 1990, FWS 1994a). This consultation, like the one before, resulted in a jeopardy opinion for the humpback chub, which was issued in draft form on August 25, 1987 (FWS 1994a). The bonytail was listed as endangered by that time, but was not included in the opinion because, like the Colorado squawfish, it was considered extirpated from Grand Canyon. Reclamation then worked with the FWS, AGFD, NPS, and Navajo Nation Natural Heritage Program to develop seven conservation measures that, when successfully implemented, would meet Section 7 consultation requirements (FWS 1990, as cited in FWS 1994a). These conservation measures are as follows:

Conservation Measure 1: Investigate the taxonomic status of the genus *Gila*.

Conservation Measure 2: Maintain hatchery stocks of Grand Canyon humpback chub.

Conservation Measure 3: Ensure that flood releases from Glen Canyon Dam occur with a frequency not greater than 1 in 20 years.

Conservation Measure 4: Develop a management plan for the Little Colorado River.

Conservation Measure 5: Conduct research to identify impacts of Glen Canyon Dam operations on the humpback chub in the mainstem and tributaries.

Conservation Measure 6: Establish a long-term monitoring program to assess the relationship of project operation to the humpback chub (pending completion of research).

Conservation Measure 7: Establish a second spawning population of humpback chub in the Grand Canyon (pending completion of research).

Before the 1987 Biological Opinion could be finalized, the Department of the Interior started the GCDEIS process in 1989. Reclamation and the FWS agreed that the final opinion should wait until the preferred alternative for the GCDEIS was selected. Due to the significance of unanswered questions on aquatic resource issues, it was agreed that research programs associated with the conservation measures could proceed, although it was understood that final results might not be available before the GCDEIS was issued.

On February 5, 1993, Reclamation reinitiated Section 7 consultation with the FWS—this time on the GCDEIS preferred alternative: Modified Low Fluctuation Flows (MLFF) (FWS 1994a). Six species of concern, bald eagle, humpback chub, Kanab ambersnail, peregrine falcon, razorback sucker, and southwestern willow flycatcher, were considered during the consultation. Only two, humpback chub and razorback sucker and their critical habitat (designated in 1994 [FWS 1994b]), were found to be significantly affected by MLFF. In the Final Biological Opinion, dated December 21, 1994, the FWS determined that the proposed operation of Glen Canyon Dam "is likely to jeopardize the continued existence of the humpback chub and razorback sucker and is likely to destroy or adversely modify designated critical habitat" (FWS 1994a).

Thus, in 1994, 16 years after the first Biological Opinion was issued on Glen Canyon Dam operations, 11 years after the GCES research programs were launched, and 5 years after the GCDEIS was mandated, the FWS concluded that the proposed dam operations would continue to jeopardize the humpback chub, as well as the newly listed razorback sucker. The FWS made it clear in the Biological Opinion, as it had throughout GCDEIS deliberations, that, in its judgment, fluctuating releases harm endangered fish. The FWS believed that it had no alternative under provisions of the ESA but to oppose the MLFF alternative. When rendering opinions in the uncertain realm of complex ecological systems, the FWS must take a conservative position on the side of listed species.

The jeopardy opinion has serious potential consequences for dam operations. According to the ESA, to jeopardize the continued existence of a listed species is to engage in an action that may directly or indirectly reduce the likelihood of survival and recovery of that species [16 USC § 1536 (a) (2) (1994)]. The FWS recognized in the Biological Opinion that actions other than *operation* of the dam—for example, initial dam construction and introduction of non-native species (both pre-dating the ESA)—contributed to the decline of humpback chub and razorback sucker in Grand Canyon. But the agency also concluded that current and proposed operations (cold-water releases, daily flow fluctuations, and reduced sediment) further impact the native fish, and as such jeopardize the continued existence of the species.

Reasonable and Prudent Alternative, 1994 Biological Opinion

If the FWS finds that a federal action is likely to jeopardize the continued existence of a listed species, as it has done in this case, it is required under regulations implementing Section 7 of the ESA (50 CFR

§ 402.02) to prepare Reasonable and Prudent Alternatives (RPAs) to that action. Specifically, the FWS must, if possible,

> *define reasonable and prudent alternatives as alternative actions, identified during formal consultation, that (1) can be implemented in a manner consistent with the intended purpose of the action, (2) can be implemented consistent with the scope of the Federal agency's legal authority and jurisdiction, (3) are economically and technologically feasible, and (4) would, the Service believes, avoid the likelihood of jeopardizing the continued existence of listed species or resulting in the destruction or adverse modification of critical habitat* (50 CFR § 402.02).

A multiple-component RPA was included in the Biological Opinion on Modified Low Fluctuating Flows, with the stated objective of attaining "riverine conditions that support all life stages of endangered and native fishes" (FWS 1994a). Although the Biological Opinion expressed concern for all native fishes in the Colorado River, elements of the RPA focused on humpback chub. According to the RPA, the 470 km reach of river downstream of the dam does not appear to provide for survival of all life stages of this species. In particular, this reach does not provide an environment for successful spawning and recruitment of young humpback chub to adult status (FWS 1994a). Regarding the endangered razorback sucker, the Biological Opinion noted that

> *only minimal support for the adult life stage* [of the razorback sucker] *has been identified in the mainstem reach downstream of Glen Canyon Dam....The discussion of effects on razorback sucker is limited due to the now rare occurrence of the species in the Grand Canyon. Very infrequent encounters with razorback suckers by researchers in Grand Canyon have made the task of reporting on status as difficult as reporting on responses of the species to operations. Riverine conditions that support recruiting populations of razorback suckers have not been found throughout the species' range* (FWS 1994a).

The FWS maintains, however, that the stretch of Colorado River through Grand Canyon provides one of the few remaining opportunities for recovering the razorback sucker because of its "length, management direction, and limited number of non-native fish species" and its "connection to Lake Mead." Developing populations in Lake Mead (presumably including the 65-km portion of the reservoir within Grand Canyon) appears to be the FWS's immediate objective for recovering the razorback sucker (FWS 1994a).

In the most critical component of the draft RPA (dated October 13, 1993), the FWS adhered to its long-standing support of steady dam releases by calling for a study in which the "research design and hypotheses to be tested will use the flow pattern of the SASF where applicable...." (FWS 1993). The seasonally adjusted steady flow experiment would be conducted within the context of the MLFF operational criteria. Steady flows would be released only in low-water years (years when releases were equal to or less than 8.23 million acre feet [maf]); and the experiment would begin before or coincident with issuance of the Record of Decision for the GCDEIS. Reclamation responded to this RPA by maintaining that the purported benefits of steady flows for endangered and other native fish were not adequately supported by "the best scientific information" (Reclamation 1994). More importantly, Reclamation was concerned that "steady flows may inadvertently benefit non-native fish species to the detriment of endangered and other native fish species" (Reclamation 1994). Reclamation indicated that, as the agency ultimately responsible for impacts of dam operations on endangered fish and numerous other resources, it was not prepared to release steady flows until 1) an assessment of potential risks to endangered and other native fish had been prepared, 2) research and monitoring designs had been developed, and 3) threshold criteria had been established for adjusting or abandoning the flows if monitoring revealed that native fish were being adversely affected (Reclamation 1994).

The differences of opinion between the FWS and Reclamation, which centered on when and under what conditions a steady flow experiment would be run, were resolved in the final Biological Opinion (dated December 21, 1994) by redefining the experimental flows within the context of the planned Adaptive Management program for dam operations (FWS 1994a). According to RPA 1.A. in that document, scheduling of the experiment would proceed as follows:

> *Design of the experimental flows and associated studies will begin as soon as possible and be targeted for completion by October 1996. Unless the Service determines information provided seriously questions the validity of experimental designs developed or contribution of the resulting data to remove jeopardy to the federally listed aquatic fauna of the Grand Canyon experimental flows will be initiated in April 1997. If sufficient progress and good faith effort is occurring towards initiating experimental flows, implementation of experimental flows may occur later in 1997. If the Service believes there is not sufficient progress Glen Canyon Dam would be operated as SASF flows during spring through fall (April to October) beginning in 1998. If the Service determines a study design can not be developed that is expected to provided* [sic] *information to support removal of jeopardy to the razorback sucker and humpback chub populations in the Grand Canyon and associated tributaries, such will be considered new information and may be grounds for reinitiating formal consultation* (FWS 1994a).

The provision that some sort of experimental steady flows would proceed without a research design if Reclamation had not made sufficient progress toward developing that design by spring 1997 appears to reflect a conviction that seasonally adjusted steady flows present little risk to endangered fishes. As it turned out, experimental flows were not implemented in Spring 1997 or Spring 1998, primarily because the 2 years were forecast as moderate-water years (>8.23 maf), and the experiment can only be conducted in low-water years. Reclamation has not completed the research design as of the writing of this report, but has demonstrated sufficient progress in that regard to satisfy tenets of the Biological Opinion, such as development of this report and convening the associated workshop of aquatic resource specialists.

Low-water years have occurred about 50% of the time since the dam became operational in 1963 (Reclamation 1995). Thus, the experimental flows would be expected only about 50% of the time over the long term, with no control over the sequence of years in which the experiment could be conducted. The final RPA described the duration (number of years) of the experiment as "a sufficient period of time to allow for experimental design, biological processes to function and for variability inherent in riverine ecosystems to be expressed. The number of years is, therefore, indeterminate" (FWS 1994a).

In each year of the proposed experiment, seasonally adjusted steady flows would be released for a period of 7 months (i.e., April through October) in a pattern similar to that of the SASF alternative (Table 2). These flows would be high and steady in the spring and low and steady in the summer/fall (a pattern resembling the pre-dam hydrograph but at a significantly lower maximum discharge and with less variability). During the remaining months, releases would conform to the MLFF pattern.

ADAPTIVE MANAGEMENT

In the RPA, the FWS couched the experimental flows within the framework of the Adaptive Management Program, a common element to all GCDEIS alternatives (see sidebar on page 8). The RPA embraced the adaptive management approach with the following words:

> *We recognize that the aquatic and terrestrial ecosystems below Glen Canyon Dam are still adjusting to impacts from dam operations that will continue into the future. Thus, the need for adaptive management. Actions taken through this approach must be based on an integrated resource approach, and, as discussed by Hilborn (1992), an active rather than a passive learning system that includes deliberate experimental design.* (FWS 1994a)

Table 2. Experimental Flow Scenario (Discharge Reported in Cubic Feet per Second [cfs]).

Release Pattern	Months	Minimum Release (cfs)	Maximum Release (cfs)	Daily Fluctuations (cfs)	Ramp Rate
Steady Flows	Apr	12,500	18,000	± 1,000	2,000 cfs/hr when releases are changed between steady flow periods
	May–Jun	18,000	same	same	
	Jul	12,000	same	same	
	Aug–Sep	9,000	same	same	
	Oct	8,000	same	same	
Fluctuating Flows	Nov–Mar	8,000 7 a.m. to 7 p.m. 5,000 7 p.m. to 7 a.m.	25,000	5,000; 6,000; or 8,000 depending on monthly release volume	4,000 cfs/hr up 1,500 cfs/hr down

Source: FWS 1994a

The Adaptive Management Program for the operation of Glen Canyon Dam is a process that uses scientific methods and information to help formulate, adjust, and improve management strategies (Holling 1978, Lee and Lawrence 1986). The idea is based on applying experimentation to the design and implementation of natural resource and environmental management policies.

Successful applications of adaptive management must be based on sound science and a continuing process of action based on planning, monitoring, evaluation, and adjustment (Forest Ecosystem Management Assessment Team 1993). If properly designed and effectively implemented, adaptive management will enable managers to determine how well their actions achieve their objectives and what steps are needed to improve the program's success. Sound scientific approaches require the use of a deliberate experimental design, suitable controls, and replication that allows sufficient statistical power needed to test hypotheses. A functional adaptive management process demands an understanding of sufficient and adequate baseline information before experimentation.

In the Grand Canyon example addressed in this report, Reclamation has elected to approach the experimental steady flow RPA within an adaptive management structure. Adaptive management requires development of a research design to test the relative impact of MLFF and SASF on endangered and other native fish species. In order to satisfy that requirement, appropriate, testable hypotheses must be developed; adequate baseline information under MLFF must be available; an effective sampling strategy, including sufficient replication, must be developed and implemented for data collection; appropriate data analyses must be conducted; and reliable performance criteria must be developed and applied.

In accordance with the principles of adaptive management and before implementing a steady flow regime, Reclamation is undertaking a process to 1) lay the groundwork for developing a research design for a steady flow experiment and 2) assess the potential of such a regime to negatively affect endangered and other native species. This Grand Canyon Data Integration Project contributes to both steps in this process.

METHODS

Our procedure for assimilating the available information began by assembling a bibliographic database of relevant unpublished technical reports; presented papers; books; and peer-reviewed, published articles. Initially, the database was composed of references from two GCES Scientific Information Management (SIM) databases and one SWCA database, which were combined using Paradox for Windows software. From this list, GCES Phase II aquatic biology reports and associated published papers were selected to serve as baseline references. Information from these references, which are directly pertinent and recent, formed a foundation upon which to build the data compilation.

Eventually the database reached over 1,400 titles, although information was drawn primarily from about 400 of these documents. Consulted documents were chosen by following reference trails through the literature and by conferring with biologists working in each field. Peer-reviewed, published articles were consulted whenever possible, but most information about the native fish assemblage in the Colorado River is contained in technical reports. Of necessity, such reports make up the majority of references cited. Information from both the Upper and Lower Colorado River Basins was included.

In order to make this report as comprehensive and inclusive as possible, Reclamation and SWCA distributed copies of a preliminary draft and an associated workbook to more than 30 aquatic (primarily fisheries) biologists who have in the past or are currently working with the Colorado River ecosystem in either the Upper or Lower Basins. These biologists were invited to comment on the draft, complete a project workbook, and to attend a 2-day workshop held February 27-28, 1997, in Flagstaff, Arizona. Twenty-five scientists participated in the workshop, representing five federal agencies, two state agencies, three universities, and two private consulting firms. See Appendix A for names of participants. In addition, SWCA received completed workbooks and extensive comments from a total of ten individuals. To the best of our ability, we revised the preliminary draft report to reflect these comments and results of the workshop. The Grand Canyon Monitoring and Research Center (GCMRC) then sent the draft report to three independent peer reviewers, and we incorporated our responses to their comments and recommendations into this final document.

Chapter 2
THE CHANGING PHYSICAL ENVIRONMENT
PRE-DAM/POST-DAM

PRE-DAM CONDITIONS

Evolution of the Colorado River Basin

The Colorado River Basin has been developing for more than 30 million years, with earliest evidence of the river's existence in the Upper Basin dating back to the late Oligocene/early Miocene (Hunt 1969, Lucchitta 1990). The drainage evolved in a polyphase fashion, with the ancestral river channel shifting course and configuration in response to episodes of localized uplifting, large-scale faulting, subsidence of the neighboring Basin and Range Province, headward erosion, and stream capture (McKee et al. 1967, Lucchitta 1972, McKee and McKee 1972, Lucchitta 1990). Because of this long and dynamic evolution, portions of the Upper Basin are older than portions of the Lower Basin, apparently by tens of millions of years, and portions of the present drainage were isolated for long periods of time. Although the evolutionary history of the Colorado River is not fully understood, evidence suggests that the river did not follow its present course through Arizona until about 5 million years ago (i.e., late Miocene/early Pliocene; Lucchitta 1990). The last major change in the Colorado River drainage took place only about 0.6 million years ago with capture of the upper Green River system (Minckley 1996).

Researchers have long maintained that the Colorado River Basin must have remained isolated from other drainage basins for a long time for it to have developed a native fish fauna with such a high level of species endemism—74% of the native fish species are found in no other basin on earth (Miller 1959). Extensive isolation is also evidenced by distinctive morphological and physiological adaptations that appear to have been selected for survival in desert streams and rivers (Minckley et al. 1986).

Natural Dams and Climatic Change

The evolution of this distinctive fish fauna is thought to have begun 3–4 million years ago, and Grand Canyon's historic native fish assemblage was likely in place by 1 million years ago (i.e., middle Pleistocene; Minckley et al. 1986, Miller 1959). Even then, these fish had to contend with large dams within their riverine habitat. Geologic evidence in western Grand Canyon shows that at least 12 major lava flows dammed the Colorado River over a period of about 240,000 years (Hamblin 1990). One of these dams (Prospect Dam) was huge even by today's standards, rising more than 732 m from the river channel and backing a lake some 644 km through eastern Grand Canyon, all of Glen Canyon, and into the mouth of Cataract Canyon. Lacustrine terraces possibly dating from that impoundment have been found as far upstream as the mouth of Bullfrog Creek in Utah. It is estimated that the lake behind the dam filled in 22 years, but the dam may have persisted 10,000–20,000 years before being eroded down to bedrock. The influence of these early river channel obstructions on the evolutionary history of the native fish assemblage in Grand Canyon is unknown; however, it may be relevant that contemporary forms have demonstrated the ability to survive in lakes, or lentic, habitats (See Chapter 5).

After the last lava dam eroded, the most significant changes in river characteristics were gradual temperature increases in summer/fall and a reduction in discharge from extremely high base and peak flows during the late Pleistocene to lower base and peak flows in recent times. These changes reflect a warming and drying climatic shift that began some 13,000 years ago, soon after the end of the last glacial episode (Hevly and Karlstrom 1974, Martin 1984). High flows during the late Pleistocene are postulated from the generally wet climatic conditions of the time, as evidenced in pollen studies, and from remnant alluvial deposits found in both the Upper and Lower Basins (Machette and Rosholt 1989). Pleistocene floods, fed by runoff from melting alpine glaciers, deposited widespread sediments. The height of these terraces (at least 24 m above the highest historical floodline; Martin 1984) suggests flows far greater than any recorded in historical times. The last flow of comparable magnitude—about 500,000 cubic feet per second (cfs)—coursed through Grand Canyon during the "Little Ice Age" of the 1600s (Webb 1996, Webb et al. 1991). Since then, climatological evidence, as interpreted from micro- and macro-plant analyses and tree-ring dating, indicates a general, but uneven, pattern of decreasing precipitation and corresponding lower flows in the Colorado River Basin (Martin and Mehringer 1965, Hevly and Karlstrom 1974, Webb et al. 1991).

Within recorded history, the unregulated Colorado River in Glen and Grand Canyons was characterized by dramatically variable seasonal river flows; heavy sediment loads, especially during peak discharges; a wide range of dissolved solids concentrations; and water temperature varying by as much as 30°C between winter and summer (Reclamation 1995). Glen Canyon Dam has significantly altered each of these characteristics.

Discharge

Pre-dam flow variability reflected both differences in annual volume between years and differences in seasonal patterns within years. The total amount of water flowing though the canyon could vary substantially from one year to the next, largely as a function of year-to-year differences in how much winter snowpack accumulated in the upstream mountains. For the period 1922–1962, annual flow volume entering Grand Canyon at Lees Ferry ranged from 4.4 to 19.2 maf (Figure 4) (Reclamation 1989, 1995). The highest measured flow at the U.S. Geological Survey's (USGS) gauge at Lees Ferry was 220,000 cfs on June 18, 1921; the lowest flow was 750 cfs on December 27, 1924 (USGS 1990, cited in Valdez and Ryel 1995; Webb 1996). This high variability in volume caused architects of the Colorado River Compact of 1922[3] to over-allocate the river by estimating average annual flow based on data from a wet period. The signatories divided up a projected annual flow of 16.8 maf, when, in fact, measured annual flows over the subsequent 40 years turned out to average only 11.7 maf (Fradkin 1981).

Before the dam, seasonal flow patterns within years also showed considerable variation. Timing of spring runoff varied greatly according to onset of warming spring temperatures. Late winter warming events and summer thunderstorms compounded variability by adding large volumes of water over short time periods, causing flow spates, or sharp spikes, in the hydrograph, as happened in water years 1929 and 1940 (Figure 5). Once the snowpack began to melt, the entire Colorado River Basin would experience high spring and early summer flows, followed by low late summer, fall, and winter flows.

[3] Agreement by which the waters of the Colorado River were allocated among the seven basin states: Colorado, Wyoming, Utah, New Mexico, Arizona, Nevada, and California.

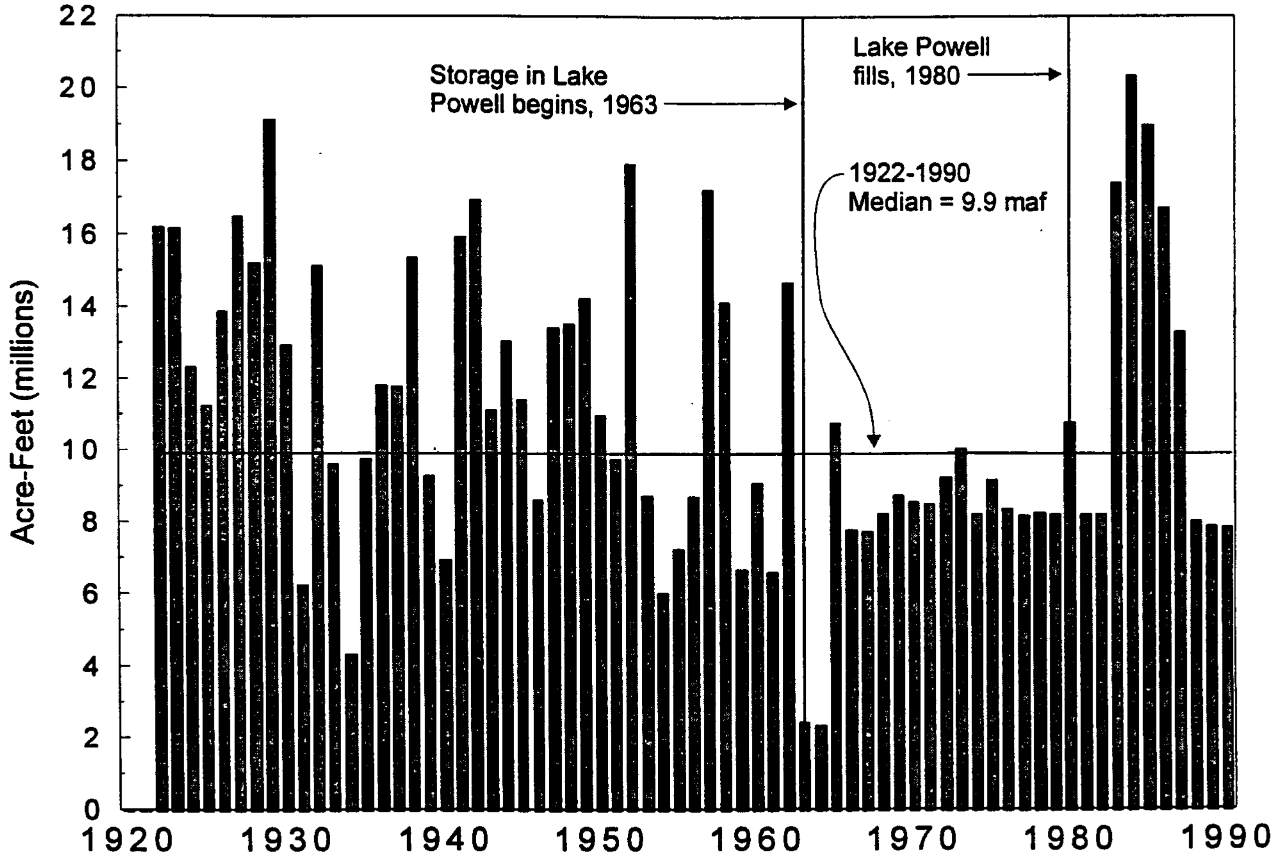


Figure 4. Annual flows at Lees Ferry from 1922-1990. From the GCDEIS (Reclamation 1995).

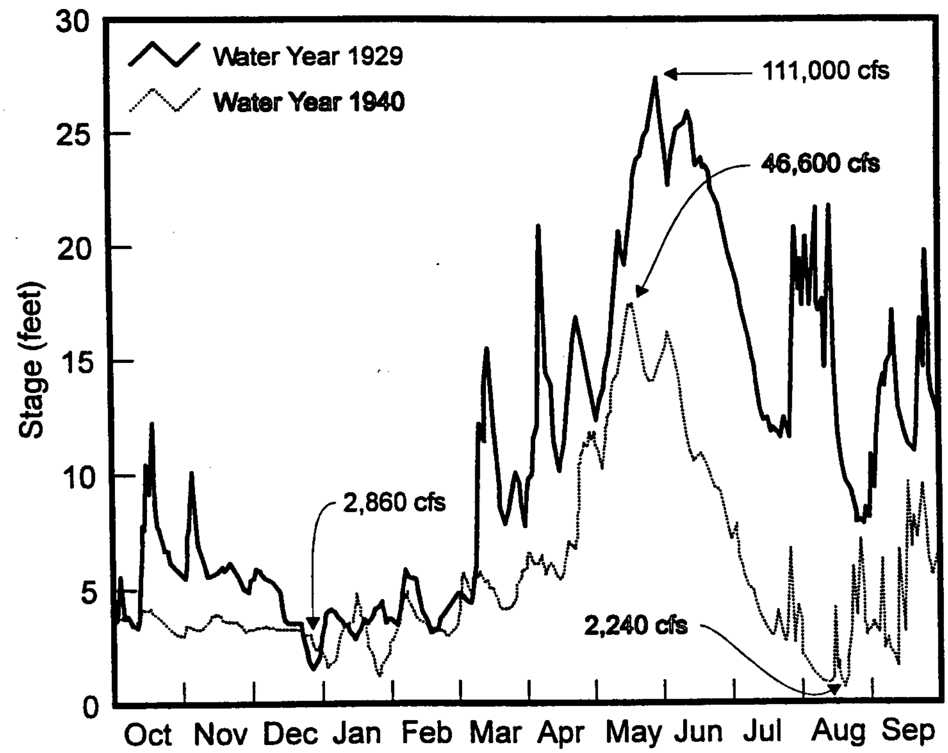


Figure 5. Superimposed stage hydrographs from Phantom Ranch for two pre-dam water years, 1929 and 1940. From the GCDEIS (Reclamation 1995).

Typically, the river in Grand Canyon would begin to rise in March, peak in early May and June, then decline rapidly to a base flow from August to the following March. Historical base flow averaged 5,000–10,000 cfs (Reclamation 1995, Valdez and Ryel 1995).

Nearly 115 years ago, on July 7, 1884, the Colorado River reached a peak flow estimated at 300,000 cfs. This was exceptional. Recorded annual peak discharges usually ranged between 85,000 cfs (Dolan et al. 1974) and 95,000 cfs (Carothers and Brown 1991, Valdez and Ryel 1995, Webb 1996). Mean annual peak flow from 1921 to 1962 was 93,400 cfs (Schmidt and Graf 1990). Spring flows often exhibited double peaks, and, on an average of about every 10 years, a flood of at least 120,000 cfs would rage through the canyon. These high annual flows scoured the channel margin, destroying any vegetation below the high-water line that might have taken root the preceding summer.

In 1953, a typical low-water year (8.79 maf), flow was above 31,500 cfs from late May until the end of June, with a peak of about 70,000 cfs (Reclamation 1989). For most of the rest of the year, flow was very low—typically in the range of 3,000–8,000 cfs. In 1957, a typical high-water year (17.3 maf), flow was above 31,500 cfs from the beginning of May until early August, with a peak of 126,000 cfs. Except for short periods of tributary flooding, flow was in the range of 5,000–10,000 cfs for the rest of the year (Reclamation 1989).

While river flows during the pre-dam era could vary widely by season or year, change in discharge during any given day was usually small. Large daily fluctuations in flow did occur, however. These fluctuations were frequently superimposed on the seasonal pattern by late summer rainstorms (Reclamation 1995, Phillips 1994). Heavy, local downpours in tributaries with large drainage basins like the Paria River and Little Colorado River (LCR) produced floods that would result in substantial stage increases in mainstem flows, sometimes lasting several days. Smaller flash floods down hundreds of otherwise dry side canyons would also affect daily discharge in the mainstem.

Sediment

For millions of years the Colorado River and its tributaries cycled heavy loads of sediment through Grand Canyon in a complex pattern of erosion and deposition. In the pre-dam environment, sediment gave the river its character. Heavy sediments driven along the riverbed by flood flows cut the river's deep canyons; moderate-sized sediments deposited along the channel margins formed the river's numerous sand and gravel bars; and fine sediments in suspension produced the river's signature "colorado," or reddish, hue.

Typically, the majority of sediment was transported down the Colorado River by spring runoff during the months of March through June (Figure 6). In late summer, runoff from torrential rainstorms transported large amounts of sediment from the surrounding landscape into tributaries, and into the river. The characteristic color and texture of deposited sediment often pinpointed the geologic formation affected by the storm, even if that formation was located far upstream. From 1941 to 1957, the average annual suspended sediment load (silts, clay, and sand) moving past the USGS gauge near the mouth of Bright Angel Creek was 85.9 million tons (Andrews 1991). In one record-breaking day, more than 27.0 million tons passed the gauge (Carothers and Brown 1991).

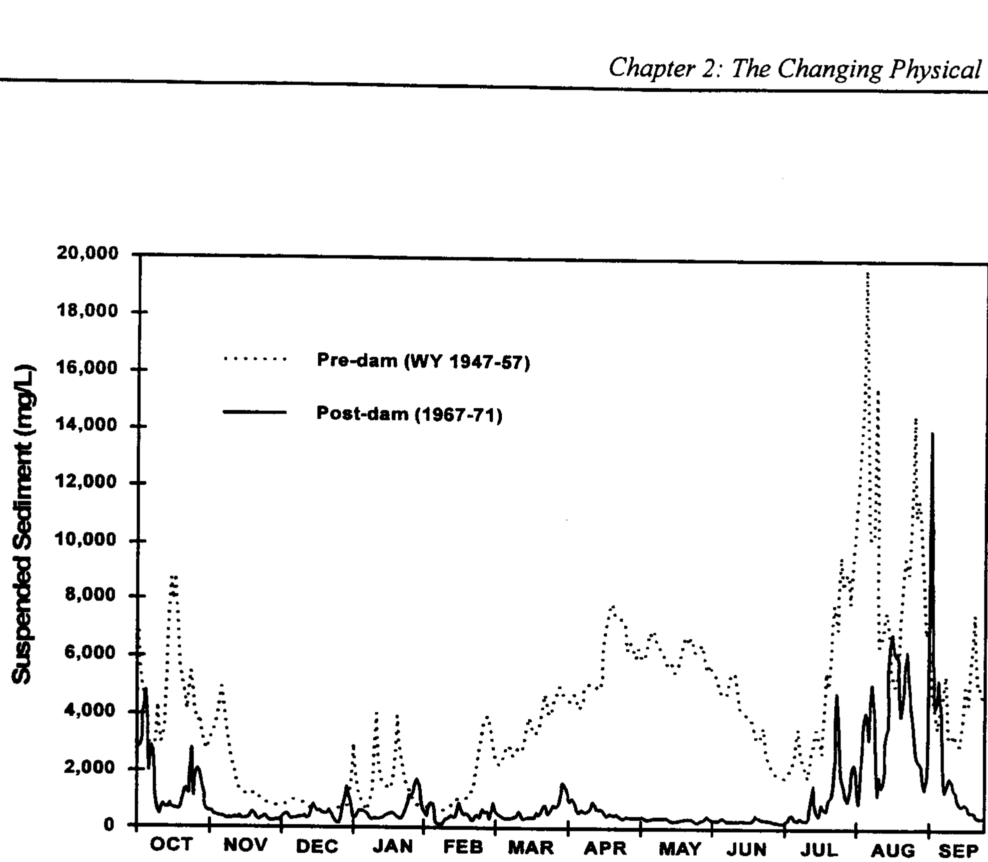


Figure 6. Pre-dam (WY 1947–1957) and post-dam (WY 1967–1971) average daily sediment concentrations (mg/L) at the USGS gauge near Grand Canyon, Arizona (at Phantom Ranch). (Source: Valdez and Ryel 1995)

One of the most important aspects of high sediment concentration in the pre-dam river was its influence on water clarity. Low water clarity typified the pre-dam Colorado River, providing little light penetration for primary productivity (Yard et al. 1993), but offering young-of-year (YOY) and juvenile fishes escape cover from predation (Valdez and Ryel 1995).

In addition to moving large amounts of sediment downstream, annual peak discharges would rework sediment stored on the river bottom, along the channel margins, and in eddy complexes. Sandbars would expand and shrink, in some seasons building, in others, degrading, depending on the sequence and magnitude of high and low flows. Annual peak discharges, particularly exceptionally large floods during high-water years, kept the river free-flowing by forcing a path through debris fans that sporadically constricted the river channel at tributary mouths (Melis and Webb 1993). These massive gravel-boulder deposits (which still form today) result from high-magnitude flood events in tributaries that carry thick slurries of water, mud, rock, and organic material down steep side canyons and into the river (Webb 1996). Debris flows large enough to reach the river constrict its flow, narrowing the channel and raising river bottom elevations to create most of the rapids in Grand Canyon (Leopold 1969, Dolan et al. 1978, Graf 1979, Kieffer 1985). Water moving through the constriction increases in velocity and forms a predictable pattern of waves (Kieffer 1985, Kieffer 1990), while water backed behind the constriction creates a relatively low-velocity pool immediately upstream of the rapid.

Downstream from the rapid (constriction), where the channel widens and river currents slow, large recirculating eddies form in which sand is characteristically deposited (Rubin et al. 1990). Before Glen Canyon Dam, these pools and recirculating eddies would receive large seasonal deposits of fine inorganic materials, including nutrients, from the sediment-rich river. High flows in spring were of sufficient velocity to scour these pools and eddies and redeposit larger substrates such as gravels, pebbles and cobbles. The flooding river also had sufficient energy to transport cobbles and boulders to widen and deepen the channel at points of constriction formed by debris flows (Kieffer 1985, Kieffer 1990).

Temperature

Before the dam, measured extreme mainstem water temperatures ranged from lows near freezing in winter to a daily high slightly in excess of 29.4 °C in late summer. Seasonal water temperature patterns included a warming trend beginning in February, rising gradually to a peak mean monthly temperature of 22.8–26.1 °C in July and August, followed by a relatively rapid decline in September (Figure 7).

We have no pre-dam data on temperature variations in backwater (i.e., eddy return-current channels) or nearshore environments, but they were undoubtedly more extreme. Judging from temperatures in unregulated reaches of river in the Upper Basin, pre-dam water temperatures in Grand Canyon backwaters probably ranged from freezing in winter to over 30 °C in summer.

Riparian Vegetation

One of the consequences of annual spring floods through Grand Canyon was scouring of the shoreline and removal of plants along the water's edge, creating a characteristic high-water zone (Figure 8). Spring floods of 50,000 cfs occurred approximately 80% of the time and floods in excess of 100,000 cfs occurred about 33% of the time (Webb 1996). Only vegetation above a high-water line—a stage reached by about 100,000–120,000 cfs—could endure for more than a few years. The plant community that marked this high-water zone in Grand Canyon was dominated by relatively dense thickets of honey mesquite and catclaw acacia. Upstream in Glen Canyon, netleaf hackberry, redbud, and Apache plume marked the high-water zone. Relatively long-lasting high flows would frequently saturate the substrate under these plants, promoting growth and allowing sporadic reproduction to sustain the community. Most of the time, riverbanks and silty sandbars were barren, except for a few plants and ephemeral grasses in protected places and large piles of driftwood carried from upstream sources by floods (Turner and Karpisack 1980, Carothers and Brown 1991, Webb 1996).

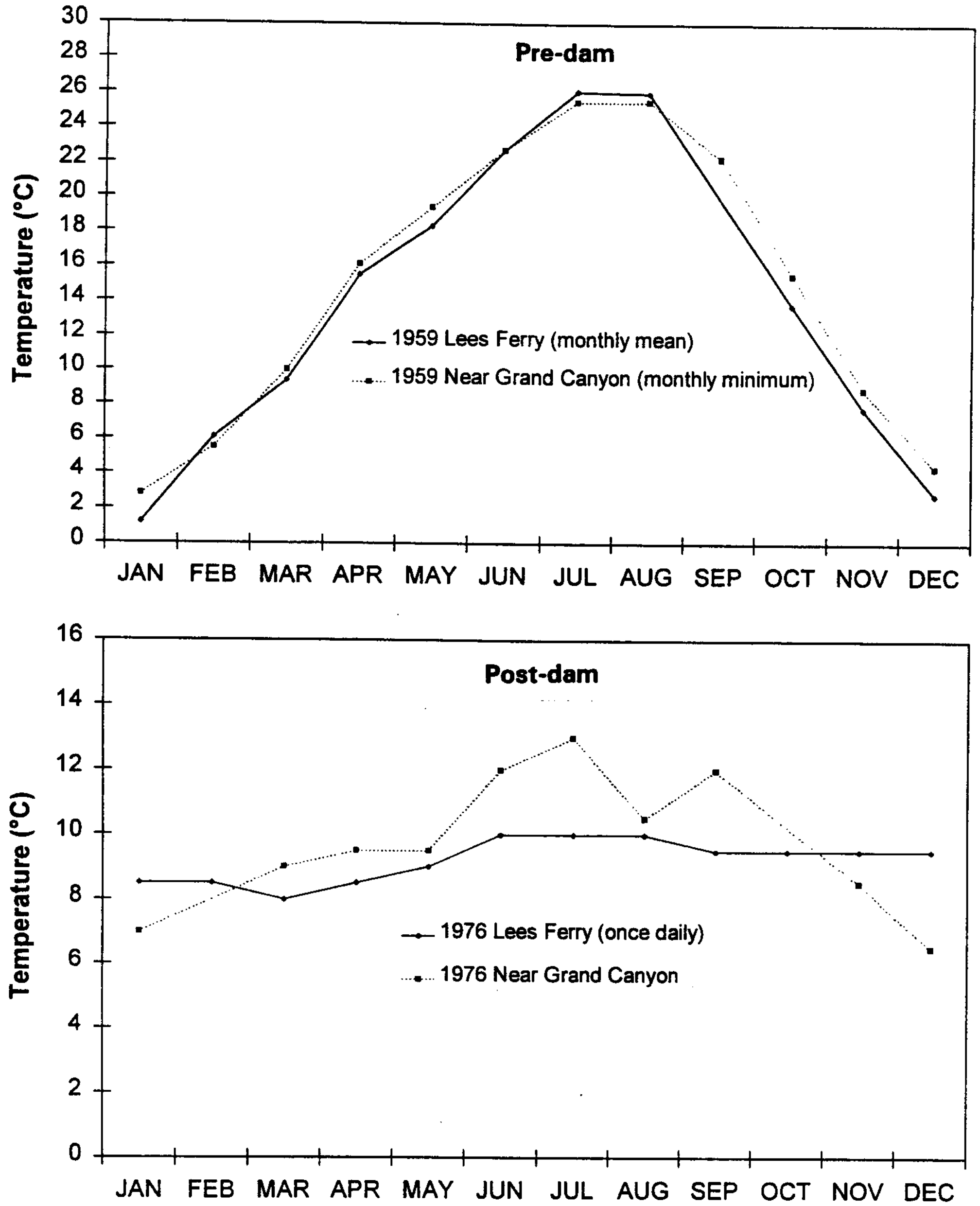


Figure 7. Pre-dam and post-dam annual temperature trends based on monthly means at Lees Ferry and Near Grand Canyon (Mouth of Bright Angel Creek). (Source: Valdez and Ryel 1995)

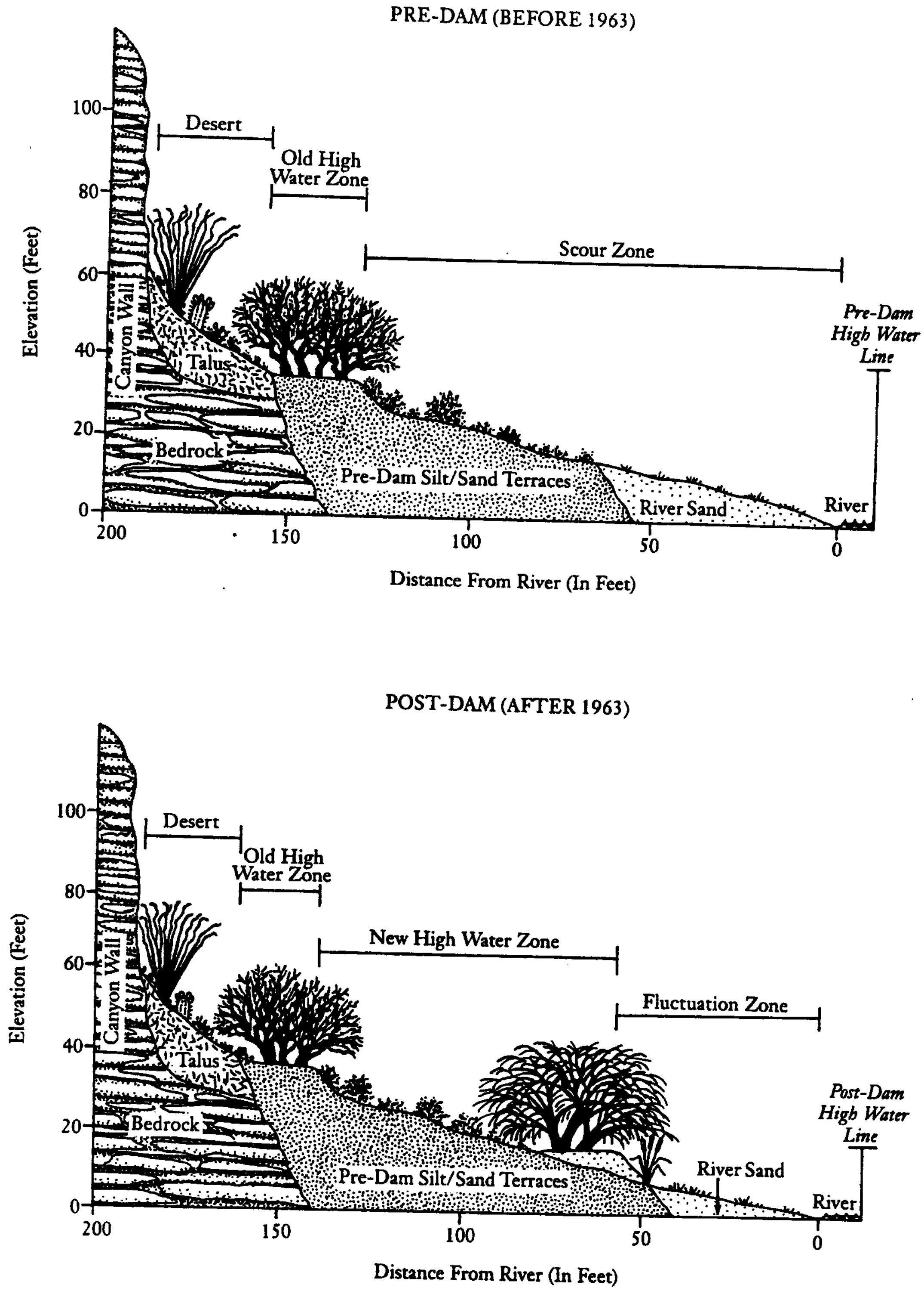


Figure 8. Pre-dam and post-dam cross sections of the shoreline of the Colorado River in Grand Canyon (Source: Carothers and Brown 1991).

POST-DAM/PRESENT CONDITIONS

Discharge

Since closure of Glen Canyon Dam, river discharge in Glen and Grand Canyons has been characterized by large reductions in annual and seasonal variations and by large daily fluctuations (Figure 9). Glen Canyon Dam is operated as a peaking power facility, and hydroelectric power generation has been the dominant influence on operations until interim flows were instituted in August 1991 (Reclamation 1995). The primary function of the dam is water storage, however, and legal constraints require that at least 8.23 maf of water is released into the Lower Basin annually. Since 1965, when sufficient water was first stored behind the dam to operate the power plant (1,064 m above sea level), the minimum annual release from Glen Canyon Dam has been about 8.23 maf in low-water years. The maximum annual release was over 20 maf in 1984 (Reclamation 1995). While the amount of water released each year is mandated by the "Law of the River," flexibility is possible in daily and monthly release schedules (Weatherford and Brown 1986).

Glen Canyon Dam has not been operated in a consistent manner since its completion in 1963. Volume and timing of releases have varied according to power generation, water needs, and annual river volume. Valdez and Ryel (1995) identified six distinct operational scenarios for the period 1963 – 1993 (Figure 10). We have added a seventh scenario to account for operations through 1997. These scenarios are as follows:

1) Initial reservoir filling from March 1963 through water year (WY) 1964.
2) Long-term reservoir filling and operation from WY 1965 to WY 1982.
3) High flood flows (spillway releases) for most of WY 1983 through WY 1986.
4) High fluctuating releases from WY 1987 to June 1, 1990.
5) Research flows from June 1, 1990, through July 29, 1991.
6) Interim flows August 1, 1991, to September 1996.
7) Modified Low Fluctuating Flow Alternative beginning September 1996 to present.

Initial reservoir filling, March 1963 through WY 1964. For a period of 2 years (1963–1964) immediately following closure of Glen Canyon Dam, water releases were extremely low in order to store water in Lake Powell. Less than 2.5 maf passed through the dam, with flows averaging less than 3,000 cfs. A near-record low flow of 700 cfs was released on January 23–24, 1963. These low releases allowed Lake Mead (reservoir immediately downstream of Grand Canyon) water levels to drop below those necessary for hydropower production at Hoover Dam; consequently, in spring of 1965, nearly 11 maf of water was released from Glen Canyon Dam in order to raise the level of Lake Mead for resumption of hydropower production.

Long-term filling and operation, WY 1965 to WY 1982. Flow regulation reduced average annual peak flow from over 90,000 cfs to about 29,000 cfs for the period 1965 to June 1980, when Lake Powell was filling (Reclamation 1989). During minimum-release years (8.23 maf), peak flow remained below power plant capacity of 31,500 cfs. Daily flows were released in response to power demands, fluctuating by as much as 20,000 cfs in a 24-hour period. During this phase of operation, consideration for recreation and fish and wildlife (incidental management objectives to water storage) was limited to minimum summer releases of 3,000 cfs for recreation and minimum winter releases of 1,000 cfs for fish

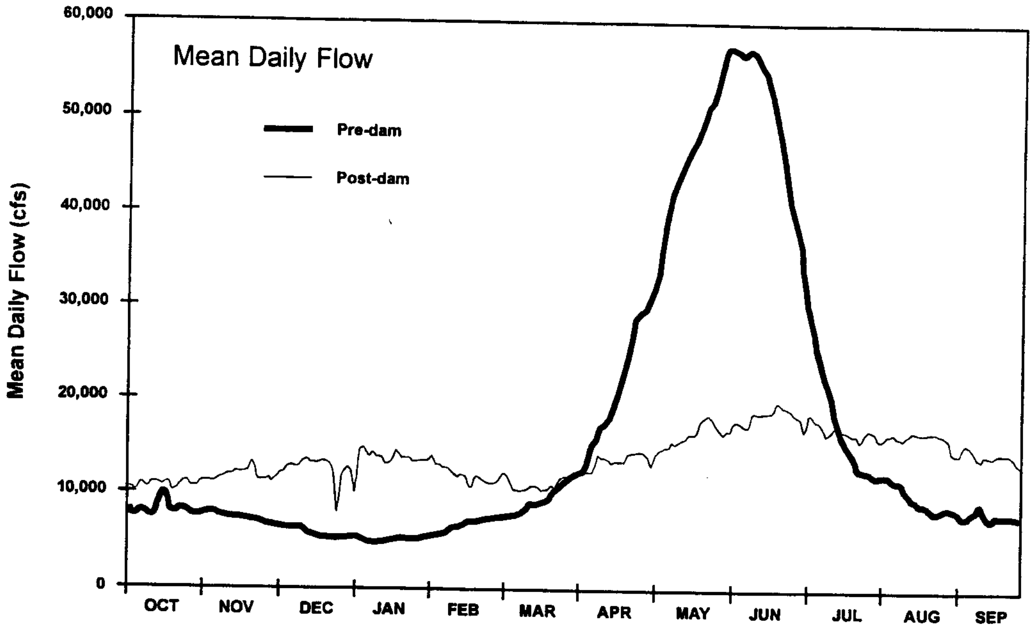


Figure 9. Mean daily pre-dam (WY 1922-1962) and post-dam (1965-1992) flow of the Colorado River at Lees Ferry (Source: Valdez and Ryel 1995).

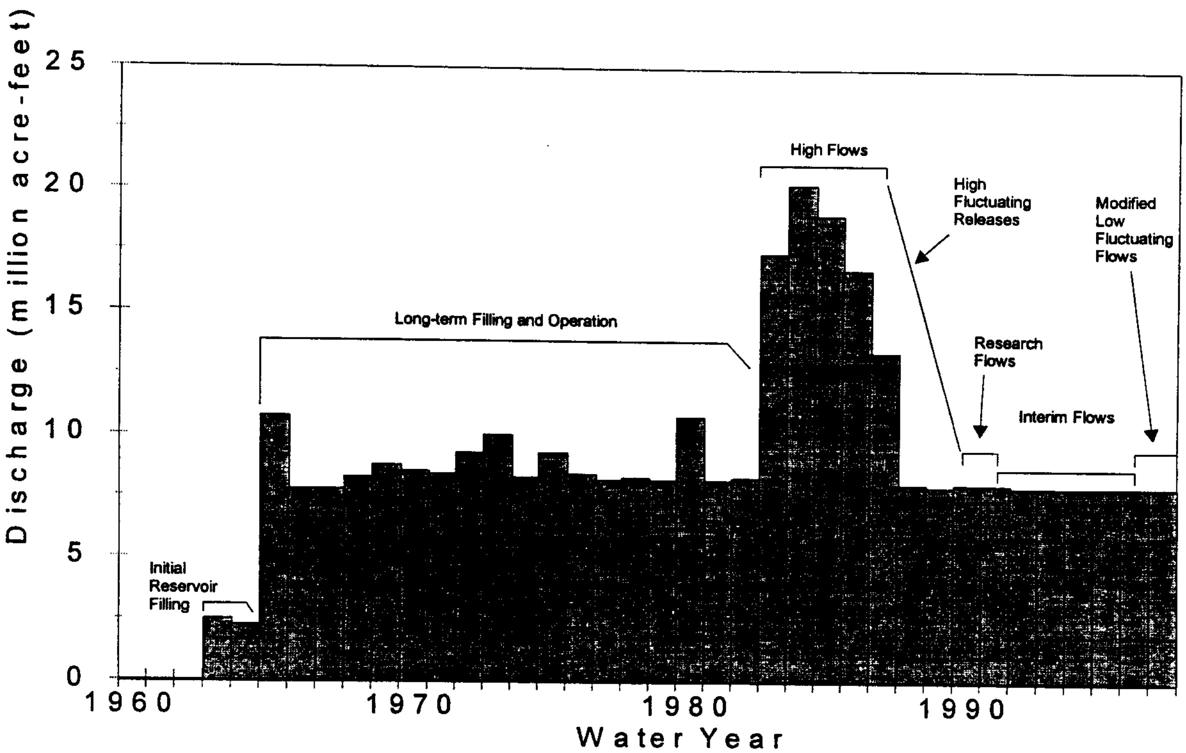


Figure 10. Seven operational scenarios for Glen Canyon Dam for WY 1963-1997, as recorded at the USGS gauge at Lees Ferry, Arizona (Source: Valdez and Ryel 1995).

and wildlife. For a time during this period, special releases were made to enhance habitat for striped bass in Lake Mead. However, these releases were believed to be interfering with water conservation principles and the releases were discontinued (Reclamation 1989).

High flood flows, WY 1983 through WY 1986. The winter of 1982–1983 was characterized by extremely high snowfall throughout the Upper Basin, marking the beginning of a period of very high daily, monthly, and annual releases from Glen Canyon Dam. Lake Powell was nearly full and spring runoff was far greater than predicted. Dam operators were faced with more lake inflow than the dam could discharge through the power plant, and additional water was released through the river outlet works and the spillways. A maximum discharge exceeding 92,000 cfs was released on June 29, 1983. Lake Powell reached maximum capacity of 26,373 maf on July 14, 1983, bringing the lake surface to 1,130 m elevation above mean sea level (USGS 1990).

Hence, in excess of 20 maf of water was discharged in WY 1984 (October 1, 1983, through September 30, 1984). More water flowed through Grand Canyon during this water year than at any time since 1922, when a volume of 22 maf was measured at Lees Ferry. The wet cycle continued from 1983 through WY 1986, and total water volume for water years 1983–1986 averaged 12 maf.

High fluctuating releases, WY 1987 to June 1, 1990. Following the period of high flood flows, annual runoff was relatively low, and annual releases were maintained at the legal minimum of 8.23 maf. In an attempt to store as much water as possible in Lake Powell, daily releases were characterized by high fluctuations. During this period it was not uncommon for daily flows to range from above 20,000 cfs to below 5,000 cfs. Weekends and holidays were characterized by as much as 48 hours of relatively steady low flows of 5,000 cfs or less (Reclamation 1995). Such large fluctuations are possible only in low-water years. During high-water years, the need to release larger amounts of water within power plant capacity precluded low minimum flows and large fluctuations.

Research flows, June 1, 1990, through July 29, 1991. At the request of the GCES research program, a variety of flow scenarios were implemented from June 1990 through July 1991 in an attempt to evaluate effects of fluctuating vs. steady flows. These "research flows" were characterized by fluctuating releases for periods of 10–30 days and constant releases for periods of 3–11 days. Fluctuating releases were made according to the following criteria:

- Minimum daily releases of 1,000 cfs from Labor Day to Easter and 3,000 cfs from Easter to Labor Day.
- Maximum release of 31,500 cfs.
- Daily fluctuations of 30,500 cfs/24 hr from Labor Day to Easter and 28,500 cfs/24 hr from Easter to Labor Day.
- Unrestricted ramping rate (average ramping rate at the USGS gauge above the LCR confluence during research flows was 886 cfs/hr).

Following fluctuating flows, constant releases were made according to the following criteria:

- 5,000 cfs for three days at least once monthly, except for March 1991; and

- 8,000, 11,000, and 15,000 cfs each for 11 days in October and December 1991 and May 1992, respectively.

Interim flows, August 1, 1991, to September 1996. Beginning in August of 1991, and continuing until the GCDEIS Record of Decision (ROD) was signed in September 1996, the dam was operated under "interim operating criteria," or "interim flows." Interim operating criteria were instituted by Reclamation to protect downstream resources in Grand Canyon National Park from the effects of high discharges and high fluctuations while the GCDEIS was being prepared. This regime was characterized by:

- Maximum release of 20,000 cfs.
- Minimum releases of 8,000 cfs daytime and 5,000 cfs nighttime.
- Maximum allowable daily flow variation of 5,000 cfs for low (<600,000 af); 6,000 cfs for medium (600,000–800,000 af); and 8,000 cfs for high (>800,000 af) volume months.
- Maximum allowable increasing flow ramping rate no greater than 2,500 cfs/hr with a maximum of 8,000 cfs change during any 24-hour period.
- Maximum allowable decreasing ramping rate of 1,500 cfs/hr.

Modified Low Fluctuating Flow Alternative, September 1996 to present. The MLFF alternative was the preferred alternative of the GCDEIS and has been in effect since September 1996. This flow regime is essentially the same as interim flows except the maximum release (25,000 cfs) and up-ramp rate (4,000 cfs) are higher. The MLFF also includes the common elements listed in Chapter 1. Hence, research studies evaluating Grand Canyon riverine ecosystems since 1991 have had over 5 years of restricted fluctuating flows to compare with prior operations.

Sediment

Since closure of Glen Canyon Dam in 1963, heavy sediment loads that once characterized the "Rio Colorado" (Spanish for "red river") are trapped in the still waters of Lake Powell (Carothers and Brown 1991). In 1986, these deposits ranged in thickness from 11 m near the base of the dam to 55.5 m near the mouth of Dark Canyon, about 290 km upstream of the dam (Ferrari 1988). The dam, acting as a sediment trap, has resulted in three major changes related to sediment supply in Grand Canyon: 1) total quantity of sediment in transport and storage has been significantly reduced, 2) capacity of the river to move debris from the channel has been reduced, and 3) configuration of riverbed and sandbar deposits has changed.

The reduction in total quantity of sediment transported by the Colorado River is evident when comparing pre-dam and post-dam measurements at USGS gauges in Grand Canyon. At Lees Ferry, upstream of any tributary inputs, the annual suspended sediment load was only 0.4 million tons each in 1982 and 1986, a decrease of about 99.5% from pre-dam loads (Reclamation 1989). At the mouth of Bright Angel Creek, 142 km downstream from Lees Ferry, the annual suspended sediment load now averages 11.0 million tons per year, a decrease of 87% from pre-dam loads. The much larger sediment load at Bright Angel Creek compared to the load at Lees Ferry (a difference of 10.6 million tons/yr) reflects sediment entering the river from tributaries between the two points. About 70% of the river's total load in Grand Canyon comes from the Paria River and the Little Colorado River, both of which join the mainstem between Lees Ferry and Bright Angel Creek (Reclamation 1995). Sediment input now occurs primarily in late summer and early fall when thunderstorms send runoff surging down tributary drainages, sometimes in large amounts. Little sediment is introduced into the system during winter, spring, and early summer (see Figure 6).

The river's ability to transport sediment and debris increases exponentially with flow volume. Because flood magnitudes have greatly decreased, reduced flow volume and reduced sediment input have combined to reduce overall suspended sediment load concentrations. Sediment load at the USGS gauge at Lees Ferry changed from a pre-dam average of 1,500 parts per million (ppm) to a post-dam average of 7 ppm (Howard and Dolan 1981). The modified post-dam hydrology and sediment transport characteristics of the river have resulted in geomorphic adjustments in the river channel. One of these adjustments has been the amount and pattern of sand held in storage in and along the river. Loss of sand from the riverbed and banks is most pronounced in the 25-km reach between the dam and the Paria River, where the substrate is now largely armored with gravels, cobbles, and boulders. Sand continues to be lost from this reach (Pemberton 1976, Howard and Dolan 1981, Angradi et al. 1992). Total sand storage has also decreased in the reach between the Paria River and the LCR, a distance of 97 km. Most of this loss apparently occurred during the flood flow period of 1983–1986 (Reclamation 1995). Downstream of the confluence with the LCR, sand storage in the Colorado River sporadically increases as a result of sediment-laden flood waters from the LCR. The last such event occurred in January 1993.

Geomorphic changes in the river channel have also affected rapids. Reduced flow volume, specifically relative to the very high spring floods that raced through Grand Canyon before the dam, has greatly reduced the ability of the river to forge a path through debris fans that sporadically constrict the river channel at tributary mouths forming rapids (Melis and Webb 1993). Over the long term, the constrictions will grow narrower and the rapids, more severe. This phenomenon has already been seen at Crystal Rapid, where the constriction, created by a debris flow in 1966, remains narrower than other rapids despite flood flows in 1983 that peaked in excess of 92,000 cfs (Kieffer 1985, Kieffer 1990).

Before Glen Canyon Dam, sandbars along the river were aggraded and eroded in a seasonal cycle. In the post-dam environment, before the flood flows of 1983–1986, sandbars above the new high-water line (about 30,000 cfs) demonstrated a consistent pattern of erosion, while sandbars at or below the new high-water line aggraded (Reclamation 1995). During the flood flows of 1983–1986, the general pattern reversed. High elevation sandbars aggraded, while lower elevation bars degraded. With implementation of interim flows in 1991, sandbars and beaches began to erode and aggrade with no discernible pattern of net loss or gain (Beus and Avery 1992, Schmidt and Leschin 1995). These sand beaches are extremely valuable today as substrate for riparian vegetation and as camping beaches for river runners. Associated eddy current-return channels are important habitat for fish.

Temperature

Pre-dam annual temperature extremes of 0.0–29.4°C have been replaced by post-dam annual extremes of only 7.2–10.0°C (i.e., dam releases). Seasonal variation in water temperature decreased gradually from dam closure in 1963 to about 1971, when water began to be drawn from the hypolimnion of Lake Powell (Figure 11). Main-channel temperatures are now relatively isothermal, but warm somewhat longitudinally in summer. Peripheral backwater habitats, partially isolated from main-channel flows, are one of the few aquatic habitats that warm above these levels. Warming occurs seasonally during diel cycles and as a result of combined effects of stage fluctuations and levels of incident solar radiation

(Maddux et al. 1987, Kubly 1990, Angradi et al.1992). In studies conducted between 1991 and 1994, AGFD (1996) recorded backwater temperatures in excess of 25.0°C. Mean monthly temperatures were highest in August (16.75°C) and lowest in February (8.78°C). Backwater temperatures warmed with distance downstream; i.e., highest mean temperature of 16.28°C occurred for backwaters between National Canyon (RM 166.5) and Diamond Creek (RM 226.0).

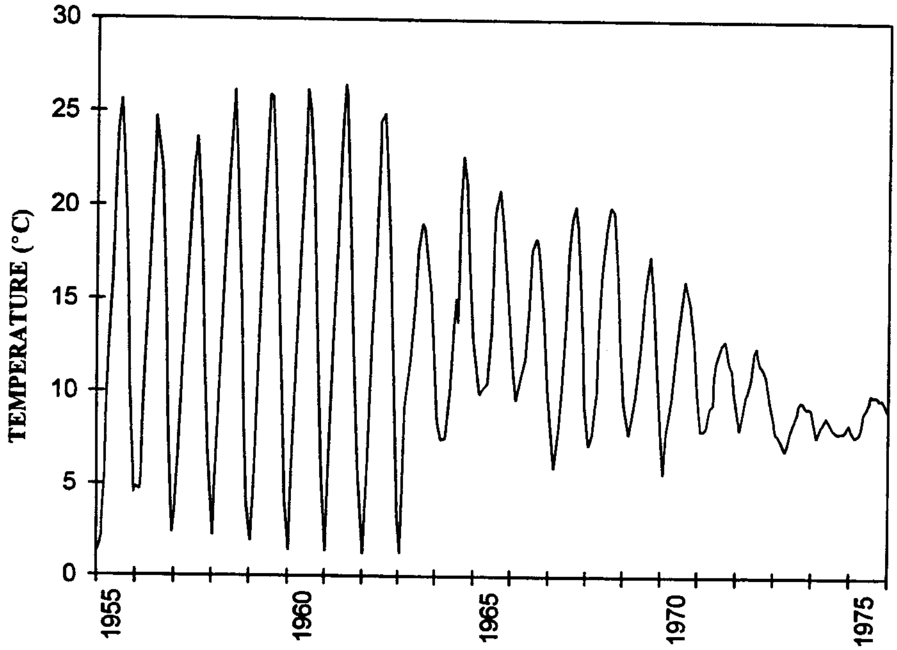


Figure 11. Mean monthly Colorado River temperature at Lees Ferry from 1955 to 1976. (Source: Valdez and Ryel 1995)

In studies conducted from 1991 to 1994, Valdez and Ryel (1995) found that maximum longitudinal warming in summer under interim flows was 1°C/51 km (Figure 11).[4] On average, water left the dam at about 8.0°C and achieved mean daily temperatures of 10.0–11.1°C at the confluence of the LCR; 12.8–13.9°C in Middle Granite Gorge; and 15.0–16.1°C at Diamond Creek (Reclamation 1995). The LCR is located at RM 61.5; Middle Granite Gorge begins at RM 127.0; and Diamond Creek is at RM 226.0. More recent temperature data modeled by the Grand Canyon Monitoring and Research Center (GCMRC) show a maximum longitudinal warming rate in June of 1°C/45 km (Jeanne Korn, GCMRC, per. comm.). Temperatures observed in backwaters in western Grand Canyon exceeded 25.0°C under steady flows while the main channel remained cold (Maddux et al. 1987). Levels of storage in Lake Mead affect distribution of warm water in the lower end of the canyon. The point of influence varies

[4] AGFD (1996) data from 1991-1994 indicated an average downstream warming of 1°C per 77.7 km from Lees Ferry to Diamond Creek. The fasted warming rate they recorded was 1°C per 25.4 km during the month of June.

longitudinally from about Separation Canyon (RM 239.5) during high lake elevations to Pearce Ferry (RM 280.0) at low lake elevations.

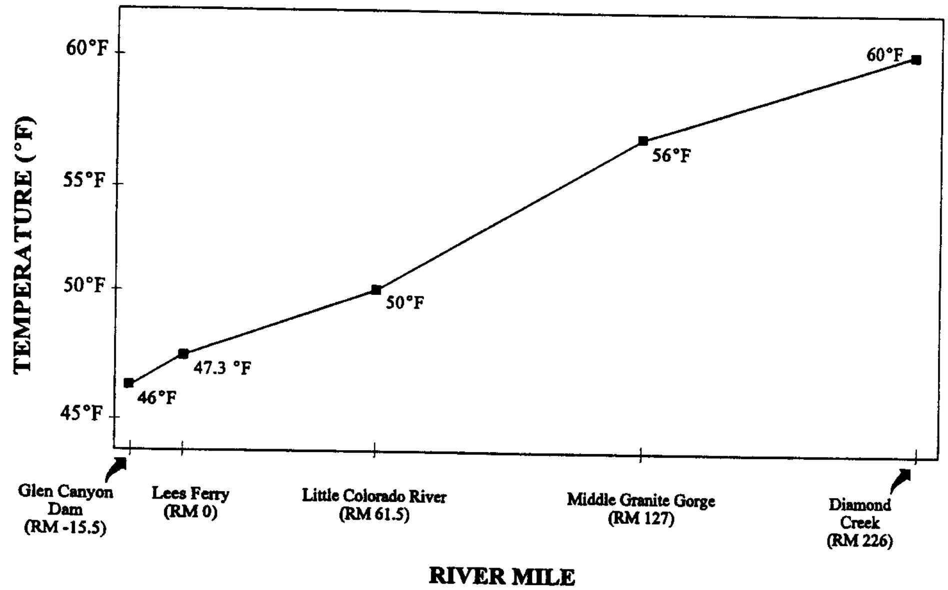


Figure 12. Mean river temperature gradient downstream of Glen Canyon Dam during summer. (Source: Valdez and Ryel 1995)

Riparian Vegetation

Vegetation along the river corridor changed dramatically as a result of regulated discharge and reduced quantities of sediment. Dam-moderated flows have eliminated the pre-dam scour zone created by annual spring floods and produced a new high-water zone of riparian vegetation at a level reached by about 30,000 cfs (Turner and Karpiscak 1980, Carothers and Brown 1991). The old high-water zone still exists, but the vegetation receives little water. Germination of seeds from old high-water trees and shrubs takes place in the new high-water zone, closer to the river. This new zone is dominated by a different community of plants: coyote willow, arrowweed, seep-willow (which are all native plants) and tamarisk (which is non-native). Unlike the pre-dam shoreline, where permanent vegetation was often 30–40 m from the water level at base flow, the post-dam riparian vegetation is often in contact with the water's edge. These new stands of streamside vegetation contribute substantial amounts of organic detritus to the aquatic ecosystem and provide shoreline cover for fish as well as a host of insects that did not exist before the dam (Carothers and Brown 1991, Converse 1996). As a result of dam operations, sediment available for substrate is both diminishing and qualitatively shifting from organic-rich, fine-grained silt to well-sorted, coarse-grained sand with fewer nutrients and less ability to hold water (Stevens and Waring 1988, Webb 1996). These changes are affecting the amount and composition of riparian vegetation along the river, and to some extent, the aquatic environment as well. Since implementation of interim flows and modified low fluctuating flows, wetlands have increasingly encroached into larger, more persistent, backwaters (Stevens et al. In Press).

Chapter 3
FOOD BASE

INTRODUCTION

Abundance and availability of the aquatic food base for fishes of the Colorado River in Grand Canyon have been identified as potential limiting factors directly related to operations of Glen Canyon Dam (Blinn et al. 1992, 1993, 1994; Leibfried 1988; Reclamation 1995; Shannon et al. 1996a, 1996b; Valdez and Ryel 1995). While clear-water discharges from the dam allow far greater primary productivity in the upper reaches, compared to pre-dam conditions (Usher et al. 1987, Leibfried and Blinn 1987, Usher and Blinn 1990, Blinn et al. 1992), turbidity in the lower reaches continues to limit autochthonous aquatic production. Allochthonous terrestrial food sources are greatly reduced compared to pre-dam conditions, and benthic communities have been transformed from a predominantly insect assemblage of primarily filter feeders to an invertebrate assemblage of primarily grazers (Haden et al. 1997). This chapter describes the pre- and post-dam food base with important linkages to fish diet. More detailed information on fish diet is presented in Chapters 5 and 6, as part of the life history of the fishes.

PRE-DAM FOOD BASE

In the turbid waters of the pre-dam Colorado River in Grand Canyon, primary production was low. Low water clarity, shifting substrates, and the scouring effects of sediment-laden flows precluded much growth of algae. Analogous regions of relatively unregulated river in the Upper Basin have relatively low primary production, but support high diversity and standing crop biomass of macroinvertebrates in riffles and cobble bars (Haden et al. 1997), suggesting that the pre-dam river had an abundance of local invertebrate production utilizing large quantities of detritus, characteristic of the historic river. The pre-dam food base for fish was probably a combination of these aquatic resources and the terrestrial foods that reached the river primarily during spring floods and late summer rainstorm spates (Figure 13). The few pre-dam studies of fish diets seem to support this hypothesis. Stomach contents of "bonytail chub" (i.e., roundtail chub, humpback chub, and bonytail) from the upper Green River prior to closure of Flaming Gorge Dam contained aquatic invertebrates and large amounts of terrestrial insects (ants), plants, and seeds (McDonald and Dotson 1960, Vanicek 1967).

Before Glen Canyon Dam, the Colorado River in Grand Canyon contained huge amounts of coarse woody debris and other plant materials carried from upstream sources. Piles of driftwood accumulated along the riverbanks, harboring a great abundance and variety of terrestrial invertebrates. Each spring, this material, along with new debris flushed from riverbanks and tributaries, was swept into the current, along with large numbers of terrestrial invertebrates (Carlson and Muth 1989, Clarkson et al. 1994, Valdez and Ryel 1995). This coarse woody debris was entrained in large recirculating eddies, then stranded as piles of driftwood when flood waters receded, providing renewed cover and food for ants, termites, wasps, and other terrestrial insects (Woodbury 1959). During base flows in summer and fall, local rainstorm events played a major role in redistributing nutrients and introducing additional terrestrial foods, including organic matter, seeds, and insects.

The pre-dam food base was probably supplemented sporadically by insect migrations and emergences. Tyus and Minckley (1988) observed large numbers of humpback chub feeding on migrations of Mormon crickets in the Yampa and Green Rivers of the Upper Basin. Humpback chub and roundtail chub have been observed feeding heavily on grasshopper infestations in Black Rocks and Westwater Canyons of the Upper Colorado River and on large mayfly hatches in Desolation Canyon of the Green River (R. Valdez, SWCA, pers. observ.). These observations suggest that pre-dam fishes in Grand Canyon were also opportunistic feeders and utilized whatever food sources became available.

Opportunistic feeding would have been particularly important in the pre-dam Colorado River because periodic high flows, high turbidity, and unstable substrates limited autochthonous production and periodically buried and/or scoured existing algae and insects (Woodbury 1959, McDonald and Dotson 1960, Clarkson et al. 1994, Reclamation 1995). This was particularly true for the more alluvial regions, such as Glen Canyon, where cobble riffles and bars were less common than in canyon-bound areas. McDonald and Dotson (1960) observed that in Glen Canyon, before completion of Glen Canyon Dam, "The chemical condition of the water appears to be adequate for fish, but the high turbidity, shifting sand bottom and lack of organic material result in relatively low productivity." McDonald and Dotson suggested that, "The dearth of aquatic insects is doubtless one of the factors responsible for the scarcity of fish." Woodbury (1959) made similar observations. He referred to the unproductive Colorado River as an "aquatic desert," and noted that flooding resulted in high turbidity and an unstable streambed, making "bottom conditions so unstable that it is exceedingly difficult for aquatic organisms to find suitable microhabitat conditions." These inventories were primarily of tributary inflows, springs, and seeps, and were not a comprehensive representation of the riverine ecosystem. Woodbury (1959) also observed that, "although the productivity of the river in Glen Canyon is extremely low, there are productive areas at rapids, riffles, whirlpools, or backwaters," as well as at mouths of tributary inflows and side canyons. Rocky riffles, driftwood piles, and sheltered areas of entrainment provided "suitable microhabitat conditions" for aquatic invertebrates. Recent work by Haden (1998) in Cataract Canyon (above Lake Powell) and near the confluence of the Green and Colorado Rivers, revealed invertebrate biomass in riffles and cobble bars comparable to biomass in the highly productive post-dam tailwaters below Glen Canyon Dam.

Some local primary production probably occurred in the pre-dam river during periods of low flow, particularly in the fall, when bottom substrates temporarily stabilized and turbidity decreased, allowing greater light penetration. This production was mostly in the form of benthic algae and diatoms, which were often short-lived because of periodic scouring by silt-laden floods.

Substantially more production took place in tributaries than in the main river channel, primarily because tributaries were generally less turbid with more stable substrates. Large numbers of aquatic insects and dense growths of algae were found in tributaries in summer, only to be scoured by sporadic flash floods that delivered large quantities of organic matter and aquatic insects into the main river (Woodbury 1959, McDonald and Dotson 1960). Woodbury (1959) noted that fish from tributaries and tributary mouths appeared to be better fed during summer than those from the main river; approximately half of fish stomachs examined from the mainstem were empty, while most stomachs of fish from tributaries contained food.

Table 3. Historic and Present Relative Abundance of Fish Species in the Colorado River, Glen Canyon to Separation Canyon. P = present, abundance unknown, A = abundant, C = common, LC = locally common, R = rare, - = not encountered.

Species	Pre-1850[a]	1958-59[b]	1967-68[c]	1968[d]	1967-71[e]	1970-73[f]	1975[g]	1977-78[h]	1980-81[i]	1984-86[j]	1990-93[k]
Family: Clupeidae											
threadfin shad	-	-	-	-	-	R	-	-	-	-	C[l]
Family: Cyprinidae											
red shiner	-	-	C/R	C	-	R	-	-	-	-	A[l]
common carp	-	C	A	C	C	A	C	A	LC	A	A
Utah chub	-	R	-	-	-	-	-	-	-	R	-
humpback chub	P	-	C	R	R	R	R[m]	LC	LC	R	LC
bonytail chub	P	-	-	-	-	-	-	-	-	-	-
roundtail chub	P	R	C	-	-	-	-	-	-	-	-
Virgin spinedace	P	-	-	-	-	R	-	-	-	-	-
golden shiner	-	-	-	-	-	R	-	R	-	R	R[l]
fathead minnow	-	A	-	A	R	C	A	C	A	A	LC
woundfin	P	-	-	-	-	-	-	-	-	-	-
Colorado squawfish	P	R	R	-	-	-	-	-	-	-	-
speckled dace	P	A	-	C	A	A	A	C	C	A	C
redside shiner	-	-	-	-	-	-	-	-	R	-	-
Family: Catostomidae											
bluehead sucker	P	C	C	C	C	C	A	C	C	C	C
flannelmouth sucker	P	C	A	C	C	C	A	C	C	C	C
razorback sucker	P	R	-	-	-	-	-	R	-	R	-
Family: Ictaluridae											
black bullhead	-	C	R	R	-	-	R	-	R	R	R
yellow bullhead	-	-	-	-	-	-	-	-	-	R	-
channel catfish	-	A	A	A	R	C	R	C	LC	R	LC

Family: Salmonidae											
cutthroat trout	-	-	-	-	-	-	-	-	R	R	-
coho salmon	-	-	-	-	-	R	-	-	-	-	-
rainbow trout	-	-	A	C	C	C	C	A	A	A	A
kokanee	-	-	R	-	-	-	-	-	-	-	-
brown trout	-	-	R	-	-	-	-	C	C	C	C
brook trout	-	-	-	-	-	-	-	C	C	C	R
Family: Cyprinodontidae											
plains killifish	-	R	-	-	-	C	C	C	C	R	LC
Family: Poecilidae											
mosquitofish	-	R	-	-	-	R	-	-	-	-	LC
Family: Percichthyidae											
striped bass	-	-	-	-	-	-	-	R	-	R	R
Family: Centrarchidae											
green sunfish	-	C	C	-	-	R	-	R	-	R	R
bluegill	-	R	-	-	-	R	-	R	-	-	R[l]
largemouth bass	-	R	C	-	-	R	-	R	-	R	R[l]
black crappie	-	-	R	-	-	-	-	-	-	-	R[l]
Family: Percidae											
yellow perch	-	R	-	-	-	-	-	-	-	-	-
walleye	-	-	R	-	-	-	-	-	-	-	R
TOTAL NUMBER OF SPECIES	**10**	**17**	**15**	**10**	**8**	**18**	**10**	**21**	**14**	**20**	**22**

Source: Valdez and Ryel 1995

[a]MIller (1959)
[b]McDonald and Dotson (1960)
[c]Stone and Rathbun (1968)
[d]Miller and Smith[k]Valdez and Ryel (1995)
[e]Holden and Stalnaker (1975)
[f]Suttkus et al. (1976)
[g]Minckley and Blinn (1976)
[h]Carothers and Minckley (1981)
[i]Kaeding and Zimmerman (1983)
[j]Maddux et al. (1987)
[l]Valdez (1994), reported only below Diamond Creek
[m]reported as "*Gila elegans*"

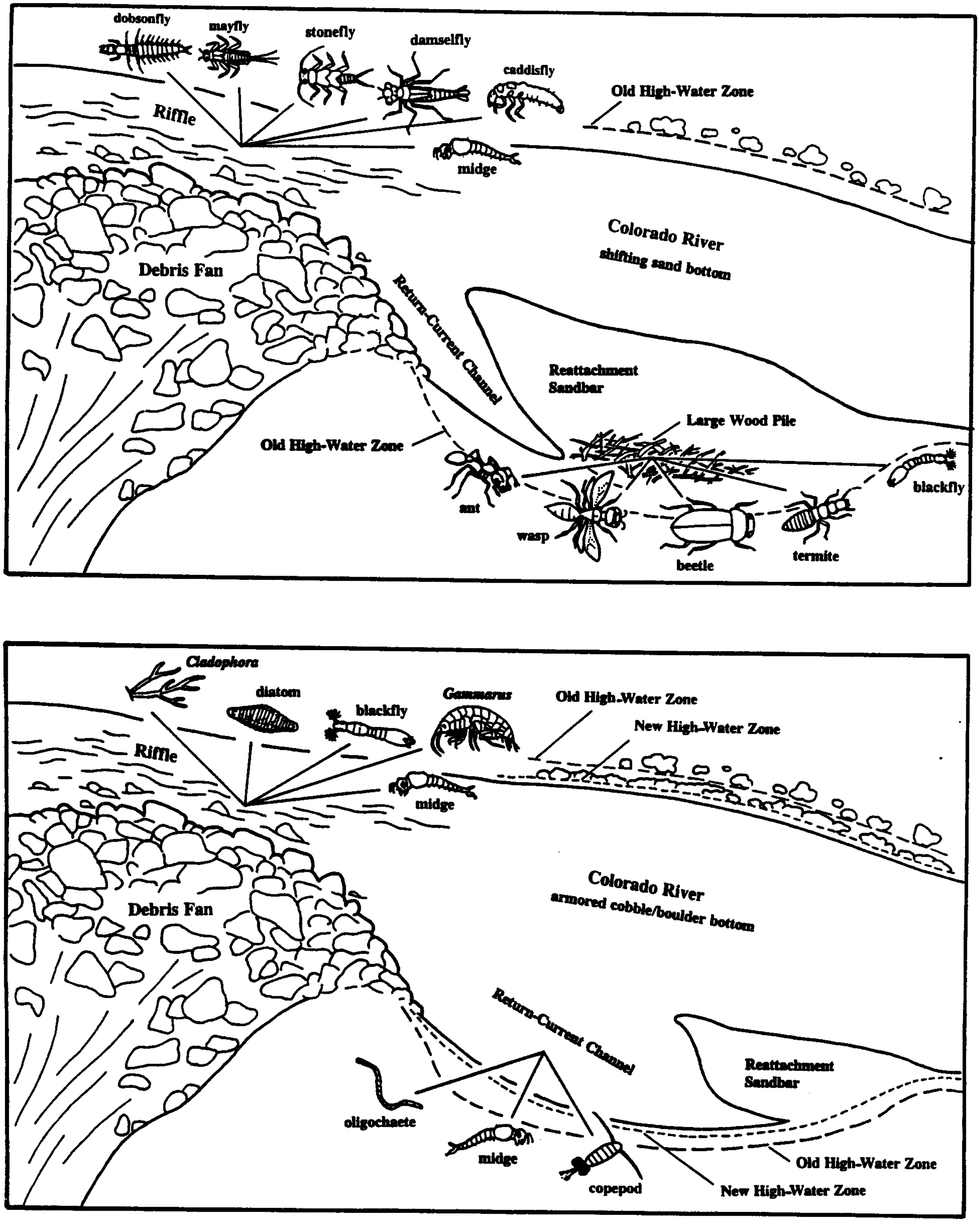


Figure 13. Pre-dam (above) and post-dam (below) aquatic and terrestrial invertebrate communities of the Colorado River corridor in Grand Canyon.

POST-DAM FOOD BASE

Clear releases from Glen Canyon Dam have allowed greater light penetration than during pre-dam flows and significantly increased primary production, especially in the tailwaters immediately below the dam (Usher et al. 1987, Leibfried and Blinn 1987, Usher and Blinn 1990, Blinn et al.1992). As a result, the post-dam food base in the upper reaches of the Colorado River in Grand Canyon is dominated by the green alga *Cladophora*, associated epiphytic diatoms, the amphipod *Gammarus lacustris*, and a variety of chironomids. Hardwick et al. (1992) found nearly 30 species of chironomids in Glen and Grand Canyons. In the lower reaches, below the LCR where turbidity is higher, the food base is dominated by the blue-green alga *Oscillatoria*, its associated epiphytic diatoms, and chironomids and simuliids (midges and blackflies; Figures 13 and 14). The importance of allochthonous terrestrial sources of food for fish varies by reach, depending on the availability of other food, but because of reduced availability, terrestrial foods occur less frequently in fish diets than in the pre-dam river (Valdez and Ryel 1995). The general pattern of aquatic food resources in Grand Canyon, including algae, diatoms, and macroinvertebrates, is high production in the dam tailwaters and decreasing production downstream as a function of distance from nutrient-rich dam releases and increasing turbidity from tributary sediment input (Figure 14; Usher et al. 1987, Leibfried and Blinn 1987, Hardwick et al. 1992). Researchers have found that concentrations of dissolved organic carbon in the Colorado River are also highest immediately below the dam and lowest downstream, but these concentrations vary considerably, apparently in relationship to geomorphology. Unlike production and dissolved organic carbon, drift of suspended material tends to increase downstream.

Prolific growths of green algae (especially *Cladophora glomerata*) in the dam tailwaters were documented as early as 1965, just 2 years after the dam first impounded the river (Stone 1966). Although clear releases increased primary production, macroinvertebrate densities appeared to decrease in the first years after dam completion; numbers were too low to support the new rainbow trout fishery being established in the dam tailwaters (Stone 1964,1965, 1966). Biologists originally attributed the depauperate benthic invertebrate fauna to shifting substrates caused by fluctuating releases from the dam. It is now believed that the loss of thermal cues, previously provided by widely varying seasonal water temperatures, may have prevented many pre-dam invertebrate taxa from completing their life cycles (Ward and Stanford 1979, Blinn et al. 1992). Possibly, the extirpation of the roundtail chub and bonytail from Grand Canyon are related to losses of essential aquatic and terrestrial insect foods, identified by Vanicek (1967) as important pre-dam food items. A similar phenomenon is hypothesized for the loss of these species from regions of the Green River downstream from Flaming Gorge Dam.

Beginning in April 1967, managers of the new rainbow trout fishery attempted to supplement "natural foods" for trout by introducing several species of invertebrates from other stream systems (Stone and Queenan 1967; Stone and Rathbun 1968, 1969). About 10,000 mayfly larvae were released, but did not succeed. Additional introductions included Odonata (dragonflies), Trichoptera (caddisflies), Diptera (true flies, e.g., midges), Hemiptera (true bugs, e.g., water boatmen), Coleoptera (beetles), Decopoda (freshwater shrimp or amphipods), Gastropoda (snails), and Hirudinea (leeches). These introductions were also largely unsuccessful with the exception of midges, snails, and the amphipod *Gammarus lacustris*, which was introduced in 1968 and quickly became established (Stone and Rathbun 1969). *G. lacustris* is tolerant of a wide range of temperatures and soon became a reliable food base that

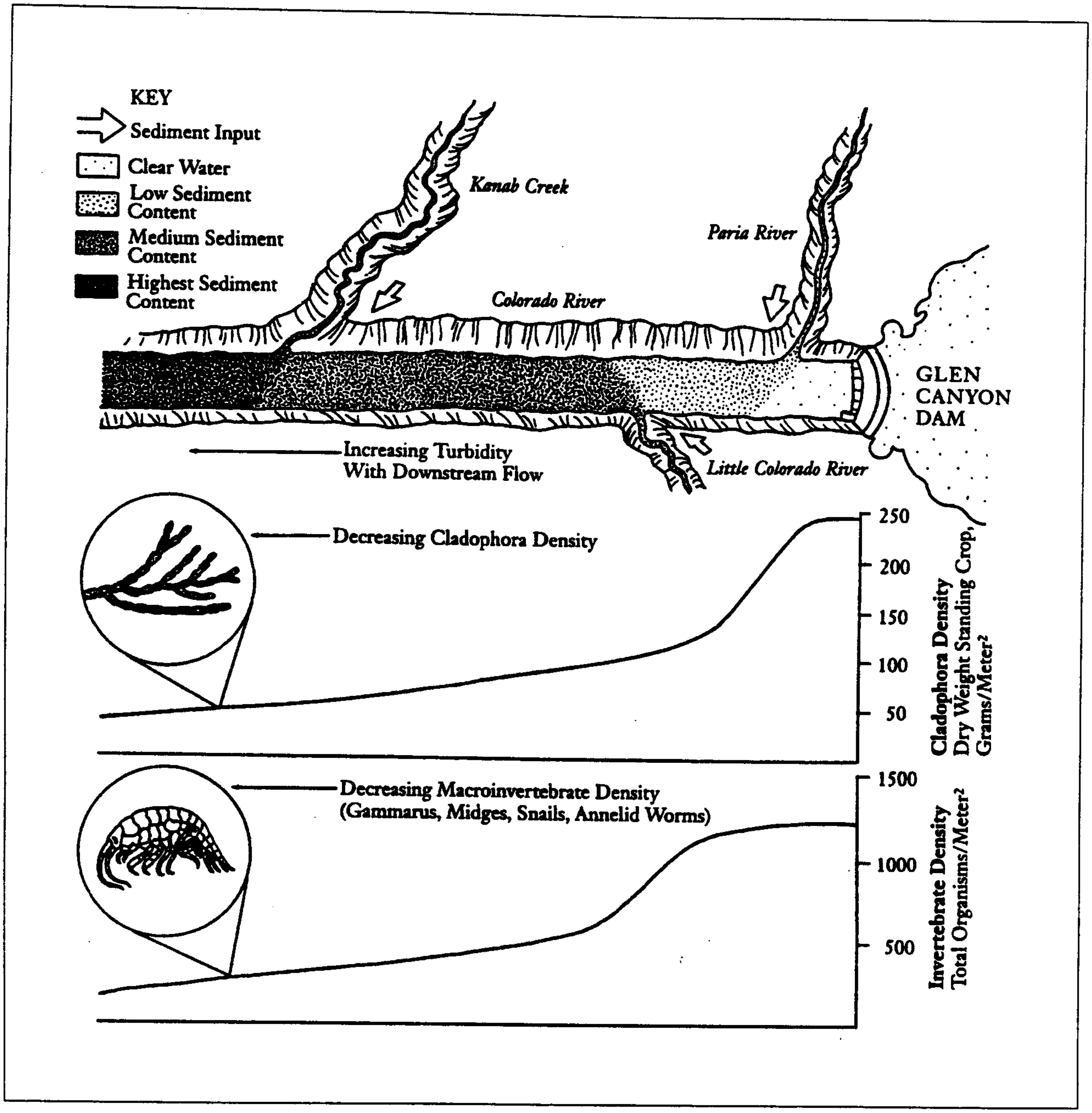


Figure 14. Longitudinal sediment concentration and biomass of *Cladophora* and macroinvertebrates in the Colorado River from Glen Canyon Dam to Diamond Creek (Source: Carothers and Brown 1991).

to the aquatic food base (Stone and Rathbun 1968). By the late 1960s, univoltine midges, able to complete their life cycles in a limited temperature range, also thrived and appeared to be established below the dam (Rathbun 1970). Blackflies (simuliids) became a dominant aquatic macroinvertebrate in some regions of the canyon. By the mid-1970s, the rainbow trout fishery below Glen Canyon Dam had grown to trophy status and was supported by a productive food base (Bancroft and Sylvester 1978). Extensive growths of *Cladophora* had become established in the clear cold tailwaters. Though unknown at the time, an epiphytic diatom assemblage was also flourishing and had likely become an important food resource for invertebrates and rainbow trout (Leibfried 1988, Pinney 1991). By 1972, hypolimnetic releases from the dam were common with water temperatures ranging only from 8.3°C in February to 11.1°C in July (Stone 1972).

The first comprehensive studies of the aquatic food base in Grand Canyon were initiated in 1984 as part of GCES Phase I (Reclamation 1989). These studies were designed to describe the aquatic food base below Glen Canyon Dam and to determine how dam operations affected food resources. Components of the aquatic food base to be studied included primary producers (algae, epiphytic diatoms), zooplankton, and macroinvertebrates. Key study variables included distance from the dam (Usher et al. 1987, Leibfried and Blinn 1987, Haury 1988, and Hardwick et al. 1992), temperature (Blinn et al. 1986, 1989), desiccation (Usher et al. 1987, Usher and Blinn 1990), and flow (Leibfried and Blinn 1987, Hardwick et al. 1992).

GCES Phase II continued studies of the aquatic food base by testing specific hypotheses regarding effects of dam operations on production, trophic interactions, and light availability. The largest body of information came from the reach between Glen Canyon Dam and Lees Ferry and focused on nutrients (Angradi et al. 1992, Ayers and McKinney 1995); organic drift (Angradi et al. 1992; Ayers and McKinney 1995; Angradi and Kubly 1994; Blinn et al. 1992, 1994; Shannon et al. 1996a); primary productivity (Angradi et al. 1992; Angradi and Kubly 1993; Ayers and McKinney 1995; Blinn et al. 1992, 1994; Shannon et al. 1996a); and flow effects on benthic invertebrates (AGFD 1994; Ayers and McKinney 1995, 1996a; Blinn et al. 1995; Shannon et al. 1996a). Additional studies evaluated the relationship between water chemistry and zooplankton in the Lake Powell forebay and downstream tailwater releases (Ayers and McKinney 1996b). Effects of dam operations below Lees Ferry were investigated for benthic and drifting invertebrates in the mainstem (Blinn et al. 1994, Valdez and Ryel 1995, Leibfried and Zimmerman 1996, Hualapai Tribe 1996b) and backwaters (i.e., eddy return-current channels; Angradi et al. 1992, AGFD 1996).

Primary Producers

In the dam tailwaters, production and biomass are dominated by *Cladophora*, which often flourishes in cold, clear waters with high nutrient levels. *Cladophora* effectively assimilates the high concentrations of dissolved nutrients released from reservoirs and provides food and cover for aquatic invertebrates and fish. Downstream from the tailwaters, *Cladophora* abruptly decreases in biomass. Blinn et al. (1992) measured a nearly 15-fold decrease just below the Paria River, the first major contributor of sediment to the river. Downstream from the Paria River, the blue-green alga *Oscillatoria* increases in abundance and, in the reaches below the LCR, dominates over *Cladophora* (Blinn et al. 1992, 1994). This pattern is unexplained, but *Oscillatoria* appears to have a greater tolerance than *Cladophora* for low light levels and more atmospheric exposure, and apparently out-competes *Cladophora* in the more turbid downstream reaches (Blinn et al. 1992). *Oscillatoria* is well adapted to desiccation because it is protected by mucilaginous sheaths and has micro-filaments that can retreat into the damp substrate sediments to remain moist when the alga is dewatered.

The longitudinal changes in these algal species along the river have significant consequences for diatom and macroinvertebrate assemblages and for the fish that feed on them. *Cladophora* has a distinct epiphytic diatom assemblage (Stevenson and Stoermer 1982, Usher et al.1987) that consists primarily of branched, upright, sessile forms (e.g., *Diatoma* spp.) that are more available to grazing invertebrates and small fish than the more tightly attached, adnate forms (e.g., *Cocconeis* spp.) found on *Oscillatoria* (Figure 15). Following the distribution pattern of *Cladophora*, upright forms of diatoms decline in density with distance from the dam and give way to the more adnate forms.

The distribution of diatoms is an important element of the food web in the contemporary Colorado River below Glen Canyon Dam. Diatoms, which contain high energy lipids, are consumed by both fish (Leibfried 1988) and invertebrates (Pinney 1991) in Grand Canyon, and are assimilated into animal tissue as an important source of nutrition. Lipids from diatoms may possibly supply an energy source that spares proteins for additional growth and condition (Watanabe et al. 1979). In the Colorado River, the availability of lipids varies with the type of diatom. The loosely branched structure and high lipid content of the upright forms appear to be more available and desirable than the adnate forms to grazing invertebrates (Pinney 1991) and fish (Leibfried 1988; Blinn et al. 1986, 1989). The preponderance of adnate forms of diatoms in the mainstem below the LCR, combined with lower overall densities of diatoms, limits the ability of invertebrates and fish in lower reaches of the canyon to benefit from the high lipid energy derived from ingesting diatoms.

Zooplankton

Most of the zooplanktonic community of the Colorado River below Glen Canyon Dam has its origins in Lake Powell, and is dominated by copepods. Haury (1986, 1988) reported that the density of zooplankton (primarily copepods) was unchanged in the water column from the dam to Diamond Creek (RM 226.0); however, AGFD (1996) found that total zooplankton densities and densities of individual taxa decreased with distance downstream from Lees Ferry. Haury (1986, 1988) also noted that the proportion of plankton in poor condition increased significantly with distance from the dam, suggesting physical damage to zooplankton during downstream transport. During 1991–1994, AGFD (1996) reported that backwaters contained significantly greater total zooplankton densities than associated main-channel beachfaces—the only other nearshore habitat sampled.

Macroinvertebrates

By the mid-1980s, the aquatic macroinvertebrate assemblage of the Colorado River through Glen Canyon had become quite different from the pre-dam assemblage. Rather than large numbers of taxa and relatively low densities of individuals, the post-dam assemblage was characterized by low taxonomic diversity and high densities of individuals, particularly in the Glen Canyon tailwaters. Leibfried and Blinn (1987) reported only five taxa from the tailwaters, but high densities of individuals, a pattern typical of hypolimnetic tailwaters (Ward 1976).

In the post-dam river, the amphipod *Gammarus lacustris* and larval aquatic Diptera (chironomids and simuliids) are the "keystone resource species for higher aquatic trophic levels in the Colorado River between Glen Canyon Dam and Lake Mead" (Blinn et al. 1992). Leibfried and Blinn (1987) found that *Gammarus* (along with chironomids, oligochaetes, and gastropods) dominated the benthic community in the reach from the dam to the confluence of the Paria River. Biomass of macroinvertebrates was four times greater above the confluence than below, showing a strong positive correlation with *Cladophora* both spatially and seasonally (Blinn et al. 1992, Leibfried and Blinn 1987). *Cladophora* is the substratum for the diatoms that form the major portion of the diet of *Gammarus* and chironomid larvae (Blinn et al. 1992).

Below the confluence with the Paria River, turbidity reduced benthic standing crop (Leibfried and Blinn 1987). *Gammarus* were replaced as the dominant benthic invertebrate by chironomids, and total benthic invertebrate standing crop declined significantly in a downstream direction. Below Bright Angel Creek (RM 88.0), simuliids and ephemeropterans began to appear in benthic samples. Blinn et al. (1992) found that simuliid larvae had largely replaced *Gammarus* below the LCR, in the more turbid reaches dominated by *Oscillatoria*. Blinn et al. (1994) estimated that the amount of caloric energy from macroinvertebrates associated with *Cladophora* was one order of magnitude greater than the caloric energy of macroinvertebrates associated with *Oscillatoria.*

During 1991–1994, AGFD (1996) compared benthic invertebrate assemblages between backwaters and adjacent main-channel beachfaces. They found that oligochaetes, chironomid larvae, other dipterans, nematodes, and ostracods dominated samples from backwaters, while beachfaces were virtually depauperate of invertebrates. AGFD (1996) cautioned that these results should not be interpreted as a comparison of the food base of backwaters versus main-channel habitats, since beachfaces are typically composed of unstable sand, subject to continuous shifting and redeposition (Schmidt and Graf 1990). AGFD (1996) also reported that mean benthic invertebrate densities were higher in spring and summer, before dipterans such as chironomids began emerging, than in fall or winter. As in the main channel, densities of invertebrates were highest in backwaters in the reach between Lees Ferry and the LCR, and decreased significantly with distance downstream. This decline was attributed to high water clarity in backwaters in upper reaches, and increasing turbidity below the Paria River, the LCR, and other tributaries, resulting in decreased production downstream. Mean total densities of benthic invertebrates were higher in 1993 and 1994 than in 1991 and 1992, possibly because flooding in the LCR in 1993 flushed large numbers of benthic invertebrates into the mainstem.

Diets of small native and non-native fishes from these backwaters in 1994 (AGFD 1996) revealed that chironomid larvae were the most common food item by total number and frequency of occurrence. Zooplankton were an important but not dominant part of the diet; cladocerans were the most common zooplankton consumed, although copepods, rotifers, and ostracods were more numerous in the environment. Although oligochaetes dominated the backwater substrate fauna, they were rare in fish stomach contents.

Tributaries, such as the LCR, are a major source of nutrients and aquatic invertebrates for the mainstem river (Hofknecht 1981, Blinn et al. 1994). Grand Canyon tributaries provide more than 25% of the drift in the post-dam Colorado River (Blinn et al 1994) and contribute to macroinvertebrate diversity, especially in areas immediately downstream of tributary inflows. The importance of tributaries in this

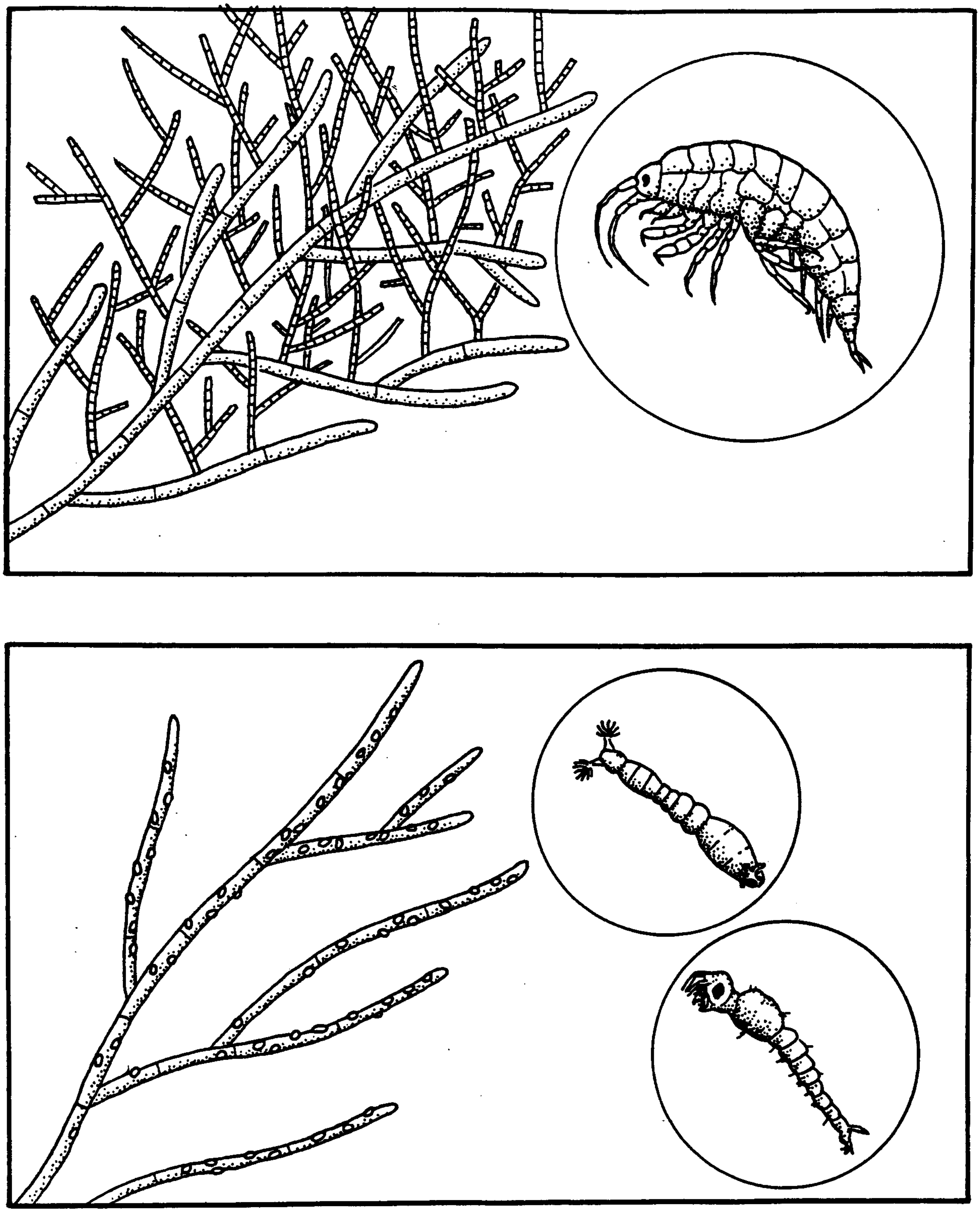


Figure 15. Algal-invertebrate assemblages typical of the Colorado River in Grand Canyon. Upper river reaches (top): *Cladophora* / upright, branched, sessile diatom forms / *Gammarus lacustris*. Lower river reaches (Bottom): *Oscillatoria* / oval, adnate diatom forms / blackflies and midges. (Drawing not to scale.)

regard is illustrated by their relative richness in "miscellaneous invertebrates" compared to the mainstem. Blinn et al. (1992) found that these miscellaneous forms accounted for 47% of tributary biomass, compared to only 5% of main channel biomass. They suggest that the reasons for the paucity of miscellaneous taxa in the mainstem include reduced egg and larval development due to constant cold temperatures, unstable substrates, lack of food, and increased sedimentation of habitats.

Effects of Dam Operations

Researchers have observed a variety of flows and water conditions in Grand Canyon since intensive studies of the aquatic food base began in 1984. The most significant variables have been flow magnitude, flow fluctuation, sediment and turbidity, nutrient input, and water temperature. Daily low and high flows (3,000–31,000 cfs) were found to have a negative effect on primary production by continually resuspending sediments and periodically desiccating large portions of productive shoreline. Ramping to higher flows increased sediments and reduced light penetration, limiting photosynthetic algal production, growth, and survival (Yard et al. 1993, Angradi and Kubly 1993, Leibfried and Blinn 1987, Usher et al. 1987, Blinn et al. 1992, Angradi et al. 1992). Algal beds exposed to atmospheric conditions by low discharges were also less productive. Exposure to air for 12 hours in summer and 3 hours at night in winter was lethal to *Cladophora*, and recovery took many months (Angradi et al. 1992, Angradi and Kubly 1993, Blinn et al.1989, Pinney 1991, Usher et al. 1987). Production of *Cladophora* beds (as indicated by chlorophyl *a*) continually inundated was significantly greater than algal beds exposed to periods of desiccation due to fluctuating flows (Angradi and Kubly 1993). Cobble bars were found to contain the highest biomass of *Cladophora* (Blinn et al. 1992).

Shallow, but consistently inundated substrates also had the highest densities and biomass of invertebrates, compared to zones affected by fluctuating flows (Leibfried and Blinn 1987; Blinn et al. 1992, 1993; Shannon et al. 1996a). Shallow cobble bars had the highest invertebrate densities and were islands, or hot spots, of productivity and food availability, except when they were exposed to periodic desiccation (Blinn et al. 1992, 1993, 1994; Shannon et al. 1996a). Ayers and McKinney (1996a), working in the Lees Ferry reach, reported similar findings, measuring significantly higher densities and biomass of *Gammarus* in habitats not exposed to fluctuations than in inundated habitats. A dramatic example of the effects of desiccation on *Cladophora* and invertebrate communities occurred as a result of the "research flows" of 1990–1991 when a dramatic decline in condition factor of rainbow trout was observed following extended periods of low steady flows (Valdez and Ryel 1995).

Flow magnitude and fluctuation also have significant effects on both algal and invertebrate biomass in drift and hence on availability as food for fish. *Cladophora* can enter drift when stream velocities break filaments weakened from desiccation or senescence (Usher et al. 1987). Leibfried and Blinn (1987), when comparing drift during 3 months of fluctuating flows (3,000–20,000 cfs) versus 5 months of relatively steady flows (18,000–28,000), found no difference in biomass of drifting *Cladophora* in the dam tailwaters. However, when comparing drift between high steady flows (about 42,000 cfs) and lower steady flows (about 25,000 cfs), highest densities of drifting *Cladophora* were reported during the higher flows, suggesting that *Cladophora* filaments were breaking under higher velocities.

Invertebrates can enter drift passively, actively, or catastrophically (Waters 1972). Researchers in Grand Canyon have found that increasing ranges in flow fluctuations significantly increases biomass of invertebrates in drift at Lees Ferry (Blinn et al. 1992, Shannon et al. 1996a). It is unclear if this phenomenon is related to active behavioral drift cues or to passive displacement. Leibfried and Blinn (1987) found that *Gammarus* composed nearly 50% of drifting biomass under fluctuating flows (3,000–20,000 cfs) and only 15% under lower steady flows (about 25,000 cfs), indicating that fluctuations either affected amphipod behavior or dislodged and transported individuals. A consistent pattern of increased invertebrate density during down ramping was observed across seasons and locations, suggesting that river flow affects food resource densities and availability through the entire canyon, although causative factors are unclear. Valdez and Ryel (1995) found a similar relationship farther downstream, near the LCR confluence, where simuliids and chironomids occurred in significantly greater densities during down ramp. However, *Gammarus* were much less abundant in these downstream reaches, and no significant relationship to flow pattern was found for this amphipod.

Interim flows in 1991 reduced flow fluctuations and, consequently, overall densities of drifting macroinvertebrates (Blinn et al. 1994, Valdez and Ryel 1995). Nevertheless, the relationship of increased invertebrate drift density during down ramping was consistent in the dam tailwaters (Blinn et al. 1994) and farther downstream near the LCR (Valdez and Ryel 1995). Valdez and Ryel (1995) also documented lower invertebrate drift densities during short-term (3-day) steady flow conditions compared to interim flows. Hence, the availability of food as drift from upstream reaches is likely to be lower under long-term steady flows than under modified low fluctuating flows, possibly affecting fish populations. Alternatively, a natural drift phenomenon may occur during low fluctuating flows or steady flows that may equal or exceed drift densities under fluctuating flows. Leibfried and Zimmerman (1995) found significantly greater invertebrate drift densities under high steady flows farther downstream at Granite Park (RM 209.0), where fluctuations are ameliorated and aquatic communities are not as dramatically affected by dam operations.

Low fluctuating flows have also resulted in seasonally increased river temperatures in downstream reaches, resulting in increased diversity of benthic invertebrates (Hualapai Tribe 1996b, Shannon et al. 1996a). Starting with interim flows in 1991, ephemeropterans, trichopterans, and other taxa typical of tributaries have been reported in the mainstem (Blinn et al. 1992, 1993; Shannon et al. 1996a; Leibfried and Zimmerman 1995), suggesting that invertebrates descending from tributaries are surviving and reproducing in the mainstem. Most of these invertebrates were collected in western Grand Canyon, where solar radiation has the greatest effect on river warming. Under high fluctuating and interim flows, summer water temperatures increased an average of 1 °C/51 km (Valdez and Ryel 1995), and the temperature of the river at Diamond Creek in summer reached 18.0 °C in the main channel and 20.0 °C in nearshore areas (Blinn et al. 1993, Leibfried and Zimmerman 1995, Valdez and Ryel 1995).[5]

The effects of prolonged periods of steady flows from dam releases have not been studied sufficiently to determine long-term impacts to the aquatic food base. Short-term (3–8 days) experimental releases of steady flows during GCES Phase II were insufficient in duration to determine biological responses or to allow macroinvertebrate assemblages to stabilize. Limited data show increased water temperature and clarity under short-term steady flows in both main channel and nearshore habitats, suggesting the potential for increased photosynthesis, primary production, and greater invertebrate diversity. However, if water temperatures fail to warm sufficiently, new invading insect species may still be unable to complete their life cycles. The importance of steady flows on both drifting and benthic invertebrates

[5] See Footnote 12 for AGFD data from 1991–1995. Their highest main-channel temperature was 18 °C in the lower Grand Canyon during September.

is uncertain, although limited information indicates both beneficial effects (increased benthic standing crop and biomass) and negative effects (less available food in the form of drifting invertebrates) to the food base. A more detailed treatise on the effects of steady flows on the aquatic ecosystem of Grand Canyon is presented in Chapter 8: Impact of Experimental Steady Flows.

Nearshore and backwater habitats can also be dramatically affected by fluctuating flows through stage changes and sediment deposition. These habitats are nurseries and rearing areas for both native and non-native fishes (AGFD 1994; Valdez and Ryel 1995; Blinn et al. 1992, 1993). Periodic desiccation and inundation of nearshore and backwater habitats not only displaces fish, but also results in losses of benthic invertebrates and primary production through desiccation (Clarkson et al. 1994, AGFD 1994), with potentially profound effects on higher trophic levels (Usher and Blinn 1990, Angradi et al. 1992). Sediment deposition buries and suffocates invertebrates and algae (Waters 1995) and resets community succession in backwaters and slack water nearshore areas (Johnstone and Stevens 1996). Abundance of zooplankton in backwaters in the Lower Colorado River was determined by magnitude and rate of flushing and size of backwaters (Holden et al. 1986, Kennedy 1979). Medium to large backwaters that were not well flushed by diurnal river fluctuations exhibited high levels of zooplankton, comparable to those of Lake Mead. Small, highly flushed backwaters had low zooplankton populations, comparable to those of the mainstem river.

Chapter 4
HISTORY AND STATUS OF FISH ASSEMBLAGES

INTRODUCTION

The following overview of the fish assemblage of the Colorado River in Glen and Grand Canyons summarizes historic and current species distributions and relative abundances, and discusses the status of the native fishes. Detailed accounts of life histories of native and non-native fishes are presented in Chapters 5 and 6, respectively. A list of fish species reported for Grand Canyon and covered in the following sections of this chapter is presented in Table 3.

DISTRIBUTION AND ABUNDANCE

Pre-dam (Before 1963)

The historic native fish assemblage (mainstem and tributaries) in the Colorado River Basin consisted of 11 families, 22 genera, and 35 species, with approximately 27% and 74% levels of genus and species endemism, respectively (Miller 1959). The mainstem fish fauna consisted of 2 families (Cyprinidae and Catostomidae), 12 genera, and 23 species, with 50% and 87% levels of genus and species endemism, respectively. In the Grand Canyon reach of the mainstem, the native assemblage was limited to 2 families, 6 genera, and 8 species.

Paleontological and archaeological evidence suggests that the native fishes of the Colorado River Basin evolved in relative isolation, adapting to the system's variable and torrential flows, high turbidity, variable temperature, and high salt concentrations to produce a few, highly specialized forms (Uyeno and Miller 1965, Minckley et al. 1986). By the middle of the Pliocene epoch, about 4 million years ago, fishes ancestral to the living *Ptychocheilus* (squawfish) and *Gila* (chub) species occupied waters of the basin in what is now northeastern Arizona (Uyeno and Miller 1965, Miller 1959, Minckley et al. 1986). Fossils of these fishes—three previously unknown species—were found in the Bidahochi Formation in the LCR drainage, at a level representing mixed fluvial and lacustrine deposits. These fossil species are similar to living forms, suggesting that the ancestral species were adapted to fast flowing rivers and occupied habitats similar to those existing in historical times. Although suckers were not found in the Bidahochi Formation, Uyeno and Miller (1965) reported bones of flannelmouth suckers from an early Pleistocene deposit elsewhere in the LCR drainage, which indicate that members of the family Catostomidae were present in the basin around 2 million years ago.

The earliest evidence of recent fishes in Grand Canyon was unearthed in Stanton's Cave at RM 31.5 (Miller 1955, Miller and Smith 1984). Researchers identified non-fossilized skeletal remains of bonytail, humpback chub, Colorado squawfish, flannelmouth sucker, and bluehead sucker, but none of razorback sucker. The specimens, about 4,000 years old, were probably brought into the cave by otters, pack rats, scavenging birds, or other animals (Miller and Smith 1984, Rea and Hargrave 1984). Farther downstream, about 39 km below Hoover Dam, over 375 bone fragments, most identified as humpback chub, Colorado squawfish, or razorback sucker, were recovered from an archaeological site in Catclaw Cave (Miller 1955). The site, now inundated by Lake Mohave, dated to 750–1100. Jones (1985) also reported bones of *Gila* spp. from an archaeological site of similar age at RM 136.0 in Grand Canyon.

Anecdotal accounts of the historical native fish assemblage in Glen and Grand Canyons appear in John Wesley Powell's report on his explorations of the Colorado River in 1869 and in 1871–1972 (Powell 1875, Dellenbaugh 1908); in Robert B. Stanton's engineering surveys of 1889–1900 (Smith and Crampton 1987); and in the epic filming adventures of the Kolb brothers in 1911–1912 (Kolb and Kolb 1914, Kolb 1914). The first fish surveys of the Colorado River Basin were conducted by Jordan (1891) and Evermann and Rutter (1895). Miller (1944) combined information from these early exploration records and from archaeological findings to determine that the mainstem native fish fauna in Grand Canyon before 1850 consisted of Colorado squawfish, humpback chub, roundtail chub, bonytail, speckled dace, razorback sucker, flannelmouth sucker, and bluehead sucker (Figure 3). Two additional Cyprinidae, Virgin spinedace and the woundfin, were found in tributaries of the Colorado River and occasionally in the mainstem (Minckley and Deacon 1991).

In the 1870s, the newly formed U. S. Fish Commission—precursor to the present-day U.S. Fish and Wildlife Service—began to distribute large numbers of non-native fishes throughout the country, including the Colorado River Basin (Minckley et al. 1991). This program was largely a response to settlers wanting a more diverse selection of fish for food and recreation (Quartarone 1993). Among the species introduced were common carp, channel catfish, smallmouth bass, and largemouth bass. By the late 1880s, anecdotal evidence indicated that carp and catfish had become established throughout the basin (Carothers and Brown 1991), and by the early 1900s, many other non-native species were present as well (Figure 16).

With creation of Grand Canyon National Park in 1919, non-native trout (primarily rainbow trout, brook trout, brown trout, and cutthroat trout) were introduced into the cold-water tributaries of Grand Canyon as sport fish. After Hoover Dam was finished in 1935, state and federal resource agencies made a concerted effort to introduce non-native fishes for sportfishing, forage, and bait into the reservoir forming behind the dam (Miller 1944, Stricklin 1950, Hubbs 1954). As a result of these introductions, fish assemblages of Glen and Grand Canyons had changed dramatically even before completion of Glen Canyon Dam in 1963 (Miller 1961). The first ichthyofaunal surveys in the area were conducted in Glen Canyon as part of pre-impoundment surveys for Glen Canyon Dam. Surveys by Woodbury (1959) during 1957–1958 and by McDonald and Dotson (1960) in 1960 reported the same 17 species of fish, of which 6 were native and 11 non-native (Table 3). Channel catfish represented over 90% of fish captured in the Glen Canyon area. Little work was done farther downstream in Grand Canyon because of logistical difficulties in sampling the area; however, "old timers" (i.e., those who rafted the Colorado River through Grand Canyon before construction of the dam) remember seeing large numbers of carp, rainbow trout, and channel catfish (Webb and Melis 1994).

Post-dam (1963–1998)

Over a period of nearly 40 years (1957–1994), 12 major ichthyological studies and surveys were conducted in the Colorado River in Glen and Grand Canyons (Table 3), with all but two occurring after Glen Canyon Dam was completed in 1963. Of 36 fish species reported collectively by these 12 investigations, only 10 were native to the basin (8 mainstem species and 2 tributary species). Fourteen

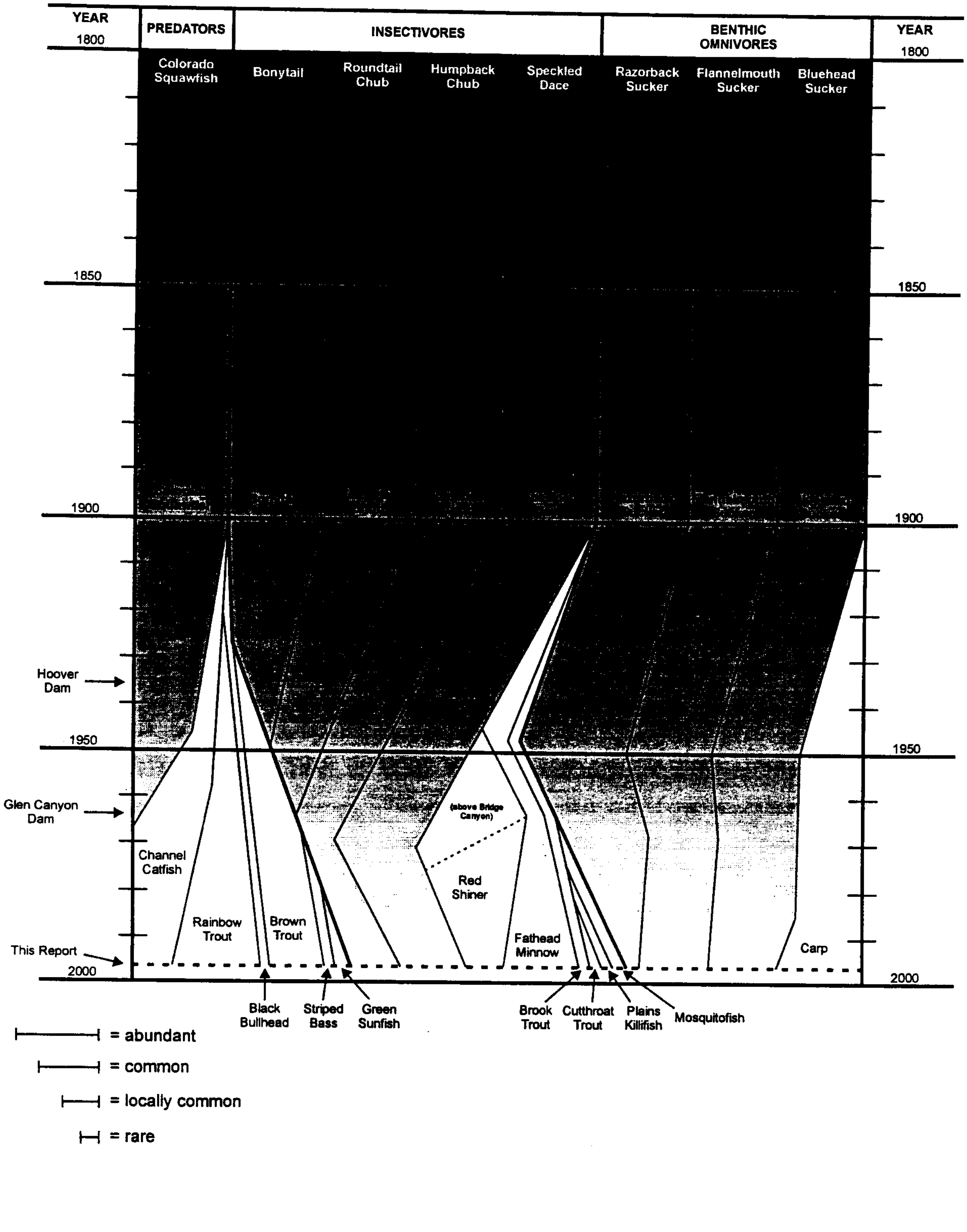


Figure 16. Conceptual chronology of relative abundance of fish species in Grand Canyon from 1800-1997 (Source: Valdez and Ryel 1995).

of the 26 non-native species were already present in the region by 1963. Numbers of fish species and relative abundances reported by these investigations vary, depending on hydrologic conditions, sample gears and techniques, and sample locations and times. For example, humpback chub were classified as rare by some investigators, but as common or locally common by others who encountered the fish in large pre-spawning concentrations at the mouth of the LCR.

Findings of these 12 surveys indicate that relatively few changes have occurred in the ichthyofaunal composition of Grand Canyon since Glen Canyon Dam was completed and Lake Powell became stratified in the early 1970s (Table 4). Four species of native fish—humpback chub, speckled dace, flannelmouth sucker, and bluehead sucker—have been found in every survey since closure of the dam. The more temperature-tolerant species, such as humpback chub, flannelmouth suckers, bluehead suckers, speckled dace, common carp, channel catfish, and fathead minnows, survived in the mainstem and used the tributaries for spawning. The more temperature-sensitive species, such as red shiners and largemouth bass, were nearly extirpated by the cold releases. Colorado squawfish were extirpated from the canyon in the late 1960s—probably as a result of cold-water releases and blockage of migration corridors—and razorback suckers, which were probably never abundant in Grand Canyon, became rare. The most dramatic change in fish assemblages has been proliferation of rainbow trout and brown trout in the dam tailwaters and several tributaries downstream.

Table 4. Relative Stability in Fish Fauna Diversity Since Closure of Glen Canyon Dam.

Date	Investigator	Number of Native Species	Number of Non-Native Species
1967–1968	Stone and Rathbun (1968)	5 [a]	10
1968	Miller and Smith (1972)	4	6
1967–1971	Holden and Stalnaker (1975a)	4	4
1970–1973	Suttkus et al. (1976)	5 [b]	13
1975	Minckley and Blinn (1976)	4	6
1977–1978	Carothers and Minckley (1981)	5 [c]	12
1980–1981	Kaeding and Zimmerman (1983)	4	10
1984–1986	Maddux et al. (1987)	5 [d]	15
1990–1993	Valdez and Ryel (1995)	4	11
1991–1994	AGFD (1996)	4	11

[a] Fifth species was Colorado squawfish
[b] Fifth species was Virgin spinedace
[c] Fifth species was razorback sucker
[d] Fifth species was razorback sucker

The first post-dam survey was conducted in Glen and Grand Canyons in 1967–1968, when Lake Powell was still filling and the river below the dam was still turbid with seasonally variable temperatures. During that survey, Stone and Rathbun (1968) found 15 species of fish, including 5 native and 10 non-native. Of the native species, flannelmouth suckers were abundant; bluehead suckers, humpback chub, and bonytail were common; and Colorado squawfish were rare. Razorback suckers were not found. This survey represents the last documented occurrence of Colorado squawfish in Glen and Grand Canyons. Total catch was dominated by non-natives, including carp, rainbow trout, channel catfish, green sunfish, and largemouth bass, all of which were abundant or common in the tailwater. Speckled dace dominated the tributaries sampled, and red shiners were caught in Diamond and Spencer Creeks. Subsequent surveys in August 1968 reported a similar fish assemblage, but with large numbers of fathead minnows and a dominance of red shiners (Miller and Smith 1972).

As the reservoir filled, a cold, deep, hypolimnion layer formed and dam releases drawing from that layer became colder. In 1967–1971, Holden and Stalnaker (1975a) found that eight species remained common. These were bluehead sucker, flannelmouth sucker, speckled dace, humpback chub, rainbow trout, common carp, channel catfish, and fathead minnow. Red shiners declined in the mainstem, and, in 1971, the last humpback chub were reported from the dam tailwaters. These fish were lost either as a result of persistent cold releases from the hypolimnion or from predation by large rainbow trout, which thrived in the cold tailwaters. Although surveys in 1970–1973 (Suttkus et al. 1976) reported 18 species of fish between Glen Canyon Dam and Pearce Ferry, the same eight species remained common. Plains killifish were also reported as common for the first time. This survey represents the last mainstem record for red shiner between Glen Canyon Dam and the inflow of Lake Mead, until one specimen was captured by the Arizona Game and Fish Department (AGFD 1993) in 1992 at RM 117.4, and three were captured by AGFD in 1995–1996 (Hoffnagle 1997). Minckley and Blinn (1976) reported 10 species of fish in 1975, including the same eight species found by Holden and Stalnaker (1975a) in 1967–1971; only plains killifish and black bullhead were added to the list.

Fish sampling by Carothers and Minckley (1981) in 1977–1979 identified 17 species of fish, including 5 native and 12 non-native. Although species composition was similar to that recorded in previous surveys, Carothers and Minckley reported an increasing dominance by a few species, both native and non-native. Common carp, rainbow trout, speckled dace, flannelmouth sucker, bluehead sucker, and humpback chub collectively composed nearly 100% of the catch. This survey produced the first record of striped bass above the Lake Mead inflow and the first record of razorback suckers (RM 108.0) since before Glen Canyon Dam was closed (McDonald and Dotson 1960).

From 1980 through 1981, the U.S. Fish and Wildlife Service (FWS), as part of the Colorado River Fishery Project, documented 14 species of fish in and around the confluence of the LCR (Kaeding and Zimmerman 1983). This assemblage was dominated by fathead minnows, speckled dace, and plains killifish, all of which were common to abundant along the shorelines. Flannelmouth suckers and bluehead suckers were present downstream of the LCR confluence, and rainbow trout were found throughout the area. Ten redside shiners were reported from RM 61.4 to RM 71.7, the only record of that species from the mainstem Colorado River in the Grand Canyon until one was caught near Lees Ferry in December 1995, and another was caught at RM 63.7 during the post-flood steady flow in April 1996 (Valdez and Cowdell 1996).

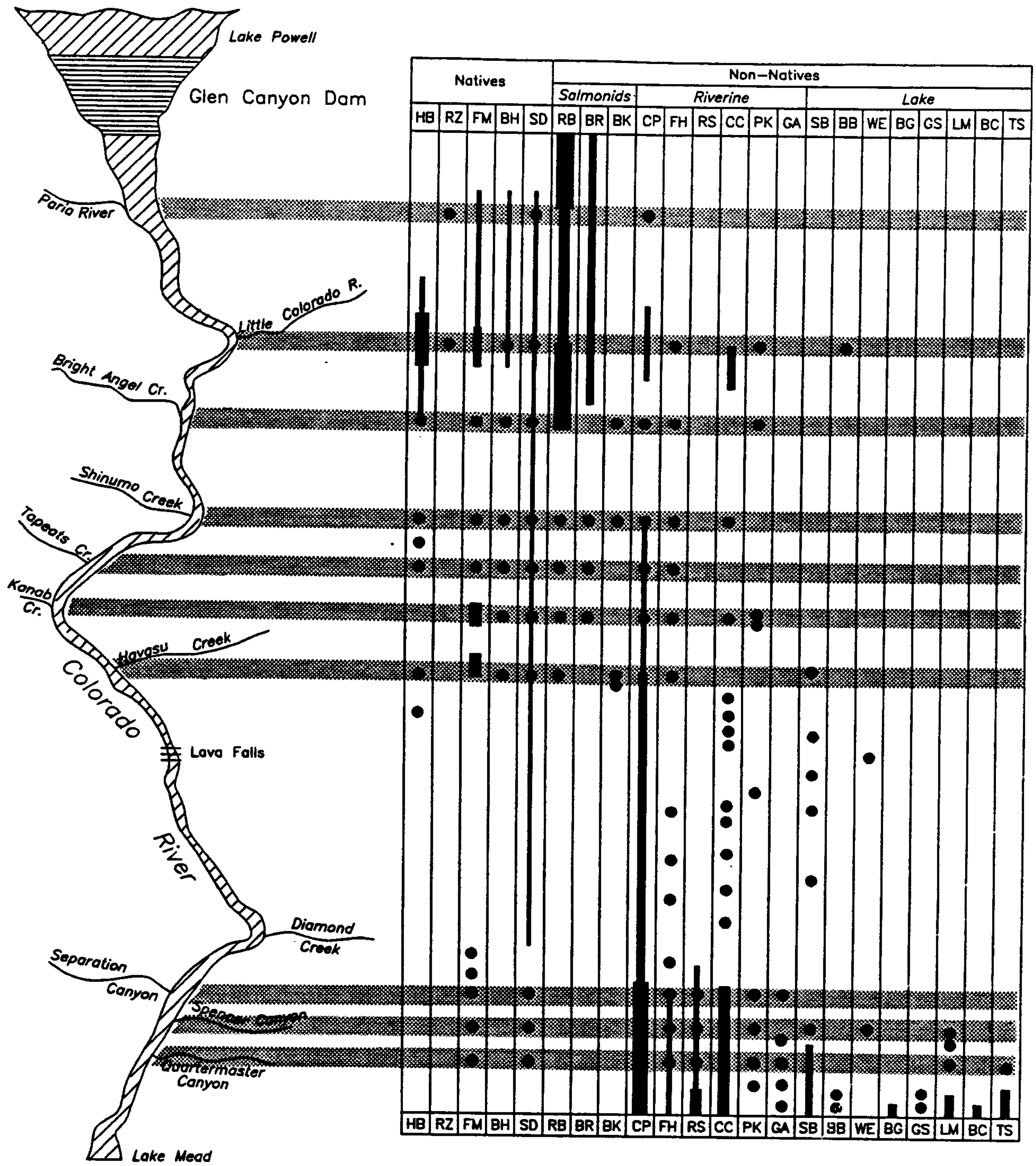
During GCES Phase I, 1984–1986, AGFD reported 20 fish species, 5 native and 15 non-native, from Glen Canyon Dam to Diamond Creek (Maddux et al. 1987). This study was conducted during the highest flows released from the dam since it was completed in 1963 (i.e., average releases in 1984–1986 exceeded 40,000 cfs, with the maximum topping 92,000 cfs in 1983). As a result, some findings may reflect the effects of these unusual hydrologic conditions on sampling and fish behavior. Maddux et al. (1987) were the first to report distributions of fish species throughout Grand Canyon. They concluded that water temperature, water clarity, food abundance, fish stocking, tributary locations, and backwater abundance appeared to be important factors in determining fish distribution. Non-native species dominated the river in summer and the tributaries in winter. Rainbow trout dominated the catch in the dam tailwaters, where temperatures were lowest and water clarity highest. Brown trout were most numerous from below the confluence of the LCR to Bright Angel Creek, reflecting greater tolerance than rainbow trout for warmer temperatures and higher turbidity. In general, non-native warm-water species increased in abundance with increasing distance downstream from the dam to about National Canyon (RM 166.5), where native species increased to a greater relative abundance.

The largest numbers of adult flannelmouth suckers were found in the reach between Glen Canyon Dam and Lees Ferry, and the largest numbers of adult humpback chub were found in the reach from Lees Ferry to Bright Angel Creek (RM 88.0), with most captured in the vicinity of the LCR (RM 61.5). Young-of-year (YOY) and subadult humpback chub were found primarily in the reach from the LCR to Bright Angel Creek and in lower Grand Canyon. Bluehead sucker, speckled dace, and larval and juvenile flannelmouth sucker increased in number in the lower canyon. Maddux et al. (1987) concluded that backwaters (i.e., eddy return-current channels) appeared to be important to fishes from spring through early autumn, when these habitats were often warmer than the main river. In fall and winter, backwaters were about the same temperature as the main channel, and use by native fish decreased. The study also concluded that introduced fishes were generally more abundant than native species in backwaters: non-native fathead minnow and rainbow trout utilized backwaters more than native flannelmouth sucker, bluehead sucker, and humpback chub.

Maddux et al. (1987) also recognized that seasonally warmed tributaries were important spawning and nursery areas for native fish, and at times, for non-native fish. In 3 years of sampling, bluehead sucker, rainbow trout, speckled dace, humpback chub, and flannelmouth sucker dominated tributary collections. Little overlap was observed in use of tributaries by native and non-native species because of seasonal water temperature patterns. Native species dominated tributary catches in spring and summer (89% and 96%, respectively), while trout were more common in winter (68%).

In its review of the GCES Phase I program, the National Research Council (NRC 1987) of the National Academy of Sciences concluded that more information on the effects of Glen Canyon Dam was needed. They recommended that research efforts be integrated through an ecosystem approach to river management, and that more emphasis be placed on hypothesis-based investigations. GCES then developed a Draft Integrated Research Plan (Reclamation 1990) for GCES Phase II to implement the NRC's recommendations. Four groups were contracted to investigate different aspects of fish population ecology in Glen and Grand Canyons. These groups and their areas of study were the Arizona Game and Fish Department (evaluate food base and monitor fish populations); BIO/WEST, Inc. (study life history and ecology of humpback chub in the mainstem); U.S. Fish and Wildlife Service (evaluate habitat in the LCR and other tributaries in Grand Canyon); and Arizona State University (evaluate fish assemblages in the LCR). Following the initial fisheries surveys (1990–1993), the Hualapai Tribe was contracted to quantify fish composition, abundance, and distribution in the Colorado River in lower Grand Canyon, from National Canyon to Pearce Ferry (RM 166.5– RM 280.0).

During GCES Phase II studies, 1990–1994, assemblages of fishes recorded in Grand Canyon remained essentially unchanged from previous surveys. Valdez and Ryel (1995) reported capturing 15 species of fish (4 native, 11 non-native) and 1 hybrid species (flannelmouth sucker x razorback sucker), in the mainstem from the Paria River to Diamond Creek (RM 1.0–RM 226.0; Figure 17). Another seven non-native species were caught in upper Lake Mead (below Diamond Creek). Nine species were captured



KEY TO SPECIES

Native		*Non-native*					
HB	humpback chub	RB	rainbow trout	CC	channel catfish	BG	bluegill
RZ	razorback sucker	BR	brown trout	PK	plains killifish	GS	green sunfish
FM	flannelmouth sucker	BK	brook trout	GA	mosquitofish	LM	largemouth bass
BH	bluehead sucker	CP	common carp	SB	striped bass	BC	black crappie
SD	speckled dace	FH	fathead minnow	BB	black bullhead	TS	threadfin shad
		RS	red shiner	WE	walleye		

Figure 17. Distribution of fishes in Glen and Grand Canyons, 1990–1991 (Source Valdez and Ryel 1995).

consistently and were considered "common" mainstem residents. These were humpback chub, speckled dace, bluehead sucker, flannelmouth sucker, common carp, fathead minnow, channel catfish, rainbow trout, and brown trout. Except for the addition of brown trout, these species were identical to those considered common when Lake Powell first filled and cold-water releases began (Holden and Stalnaker 1975a, 1975b). All four native fish species were found in 9 of the 11 reaches in the study area. No humpback chub were captured in the reach from Lees Ferry to Soap Creek (RM 0.0–RM 11.3), and only flannelmouth suckers were caught in the reach from Soap Creek to North Canyon (RM 11.3–RM 22.6). Of the fishes collected, the number of species increased in a downstream direction from a low of three species in the reach RM 11.3–RM 22.6, to a high of fourteen in the reach RM 159.9–RM 213.9.

AGFD (1996), working during a comparable period (1991–1994) and in the same study area as BIO/WEST, also reported capturing 15 species of fish: 4 native and 11 non-native. Only one species differed between the two studies; Valdez and Ryel (1995) reported capturing one walleye, while AGFD reported capturing one red shiner. Like BIO/WEST, AGFD commonly caught nine species, but, again, one species differed between the two studies. Carp were common in the BIO/WEST study, which sampled a cross section of mainstem habitats, while plains killifish were common in the AGFD study, which focused on sampling mainstem backwaters and beachfaces, as well as tributaries.

GCES Phase II research conducted by Arizona State University resulted in population estimates and information on movement patterns of humpback chub and native suckers in the LCR and its confluence with the Colorado River (Douglas and Marsh 1996a, 1996b, 1996a, 1996a), and research conducted by the FWS provided data on habitats in the LCR and other tributaries (Gorman 1994). Both studies contributed valuable information for understanding the fish assemblages in Grand Canyon, but neither study was designed to evaluate effects of dam operations on those assemblages. While many hypotheses were developed for testing during GCES Phase II, few were tested such that conclusive results are available today for evaluating the influence of an experimental steady flow (see Chapter 8). Since a long-term period of steady dam releases has not occurred in Grand Canyon or other comparable systems, comparative data sets are not available for pre-evaluating such an experiment.

STATUS OF NATIVE FISHES

Of the eight native species historically found in Grand Canyon, four (humpback chub, Colorado squawfish, bonytail, and razorback sucker) are listed as endangered throughout their range. Three of the eight species (Colorado squawfish, bonytail, and roundtail chub) have been extirpated from Grand Canyon, and one (razorback sucker) is exceedingly rare. Only humpback chub, flannelmouth sucker, bluehead sucker, and speckled dace remain.

Decline in native fishes of the Colorado River Basin was documented as early as the 1970s. Miller (1961) noted marked population decreases concurrent with water diversions, dams, land-use practices, and invasion of non-native fishes. Concern over this loss received national attention when the humpback chub and Colorado squawfish were included in the first List of Endangered Species issued by the Office of Endangered Species on March 11, 1967 (32 FR 4001). These fishes were classified as "endangered" and later afforded protection under the Endangered Species Act of 1973, as amended, because of declines in distribution and abundance throughout their range. The bonytail and razorback sucker were also listed as endangered: bonytail on April 23, 1980 (45 FR 27713) and razorback sucker on October 23, 1991 (56 FR 54957). Critical habitat was designated for all four endangered fishes on

March 21, 1994 (50 FR 13374). Razorback sucker critical habitat includes the reach of Colorado River from the Paria River to Hoover Dam; humpback chub critical habitat includes the Colorado River from Nautiloid Canyon (RM 34.0) to Granite Park (RM 208.0), as well as the lower 12.9 km of the LCR.

Humpback Chub

The population of humpback chub in Grand Canyon is the largest of six remaining populations in the Colorado River Basin (Valdez and Claimer 1982). Reasons for the decline of humpback chub are not clearly understood, but it is believed that this species was once distributed through much of Grand Canyon and Cataract Canyon (now inundated by upper Lake Powell). Immediately after closure of Glen Canyon Dam, humpback chub were captured in Glen and Grand Canyons over an area of from the dam to Separation Canyon (Valdez and Ryel 1995). That distribution has since been reduced from 412 km to 293 km (29% reduction), with aggregations found in 1990–1993 from South Canyon (RM 31.5) to Pumpkin Spring (RM 213). One adult humpback chub was captured near Maxson Canyon at RM 253.2 in 1994 (Valdez 1994).

Nine distinct aggregations of humpback chub were recognized in 1990–1993 in the mainstem Colorado River in Grand Canyon and one in the LCR (Figure 18; Valdez and Ryel 1995). Approximately 78% of mainstem individuals occurred in the aggregation near the mouth of the LCR (RM 57.0–RM 65.4), which was the only aggregation known to be self-sustaining. Fish from this aggregation seasonally ascended the LCR for spawning, but the relationship between these mainstem fish and a resident LCR population was unclear. The other eight aggregations lacked reproductive success and seven were located downstream of the LCR, which appeared to be a source of recruitment. One aggregation, located at RM 30.0 (above the LCR), consisted of about 50 large adults that appeared to be pre-dam relicts, since recent exchange of individuals from other aggregations is unlikely (Valdez and Ryel 1995)

During 1990–1993, the mainstem population of humpback chub was estimated at 3,750 adults (>200 mm TL), with about 3,482 adults (95% CI = 2,682–4,281) in the aggregation near the LCR (Valdez and Ryel 1995). This was the first quantitative population estimate for humpback chub in the mainstem Colorado River in Grand Canyon; hence, no other data were available to evaluate trends.

During the same period (1991–1992), Douglas and Marsh (1996a) estimated 4,508 humpback chub (>150 mm TL, no confidence intervals provided for population estimate) within the LCR for the period July 1991 through December 1992 and compared their findings to other population estimates of humpback chub in the LCR (Table 5). The estimated number of humpback chub (>150 mm TL) in the lower 1.2 km of the LCR in May of 1992 was 1,320, which represented a reduction of 27% and 54%, respectively, from Kubly's (1990) estimates of 1,800 and 2,900 individuals (>140 mm TL) in May of 1987 and 1988. The estimate of 4,346 for the entire 14.9-km length of the LCR during May of 1992 (Douglas and Marsh 1996a) was a reduction of about 40% from the estimate of 7,000–8,000 by Kaeding and Zimmerman (1982) and a reduction of 83% from Kubly's (1990) maximum estimate of 25,000 in 1989. Different sampling intensities, techniques, and length partitions make it impossible to determine if the differences in population estimates reflect real population change or anomalies in population estimators. The effects of methodology were illustrated when Douglas and Marsh (1996a) calculated population estimates for their 19-month study period using five models, and got results ranging from 4,508 to 10,444 fish. Different researchers making different assumptions and using different statistical tools might arrive at very different figures. Kubly (1990) and Douglas and Marsh (1996a) noted problems associated with making population estimates in a system lacking geographic and temporal closure, and suggested that the estimates should be viewed with appropriate caution.

Recent evaluation of data collected by Arizona State University, AGFD, FWS, and BIO/WEST (Gorman and Meretsky 1996, Meretsky et al. (In Review) showed a significant linear decline in condition of adult humpback chub (>200 mm TL) in the LCR over the period 1978–1996.

The possible decline in the population of humpback chub in the LCR, as well as in condition factor of individuals—combined with a recent infestation by Asian tapeworm, a potentially lethal parasite (see Chapter 7)—is of concern, particularly since the LCR is the only site for successful reproduction for the species in Grand Canyon. Although the relationship between fish in the mainstem and resident fish in the LCR is unclear, well-being of the humpback chub population in Grand Canyon is clearly linked to the welfare of the fish in the LCR.

Table 5. Population Estimates for Adult Humpback Chub in the Little Colorado River: Confluence Area and Lower 14.9 km (adapted from Douglas and Marsh 1996a).

Year	Month	Method	Estimate	Source
LCR Confluence Area (Lower 1.2 km)				
1987	May	Peterson (all mark-recaptured fish)	5,783	C.O. Minckley (1988)
1987	May	Multiple Census (fish >140 mm TL)	1,800	Kubly (1990)
1988	May	Peterson (all mark-recaptured fish)	7,060	C.O. Minckley (1988)
1988	May	Multiple Census (fish >140 mm TL)	2,900	Kubly (1990)
1992	May	Multiple Census (fish >150 mm TL)	1,320	Douglas and Marsh (1996a)
LCR Lower 14.9 km				
1982	May	Multiple Census (fish >200 mm TL)	7-8,000	Kaeding and Zimmerman (1982)
1989	May	Multiple Census (fish >140 mm TL)	25,000*	Kubly (1990)
1992	May	Multiple Census (fish >150 mm TL)	4,346	Douglas and Marsh (1996a)

* Maximum estimate, dropping to 5,500 by the middle of the sampling period.

Flannelmouth Sucker

In the 1970s, flannelmouth suckers appeared to be reproducing in many reaches of the mainstem and its tributaries in Grand Canyon (Minckley and Blinn 1976, Carothers and Minckley 1981). Fish of all size classes were collected, and the species was considered common or abundant in nine separate surveys from 1957 to 1987. In 1990–1993, flannelmouth suckers were common in the mainstem from Lees Ferry to Diamond Creek, but with declining abundance downstream and evidence of poor

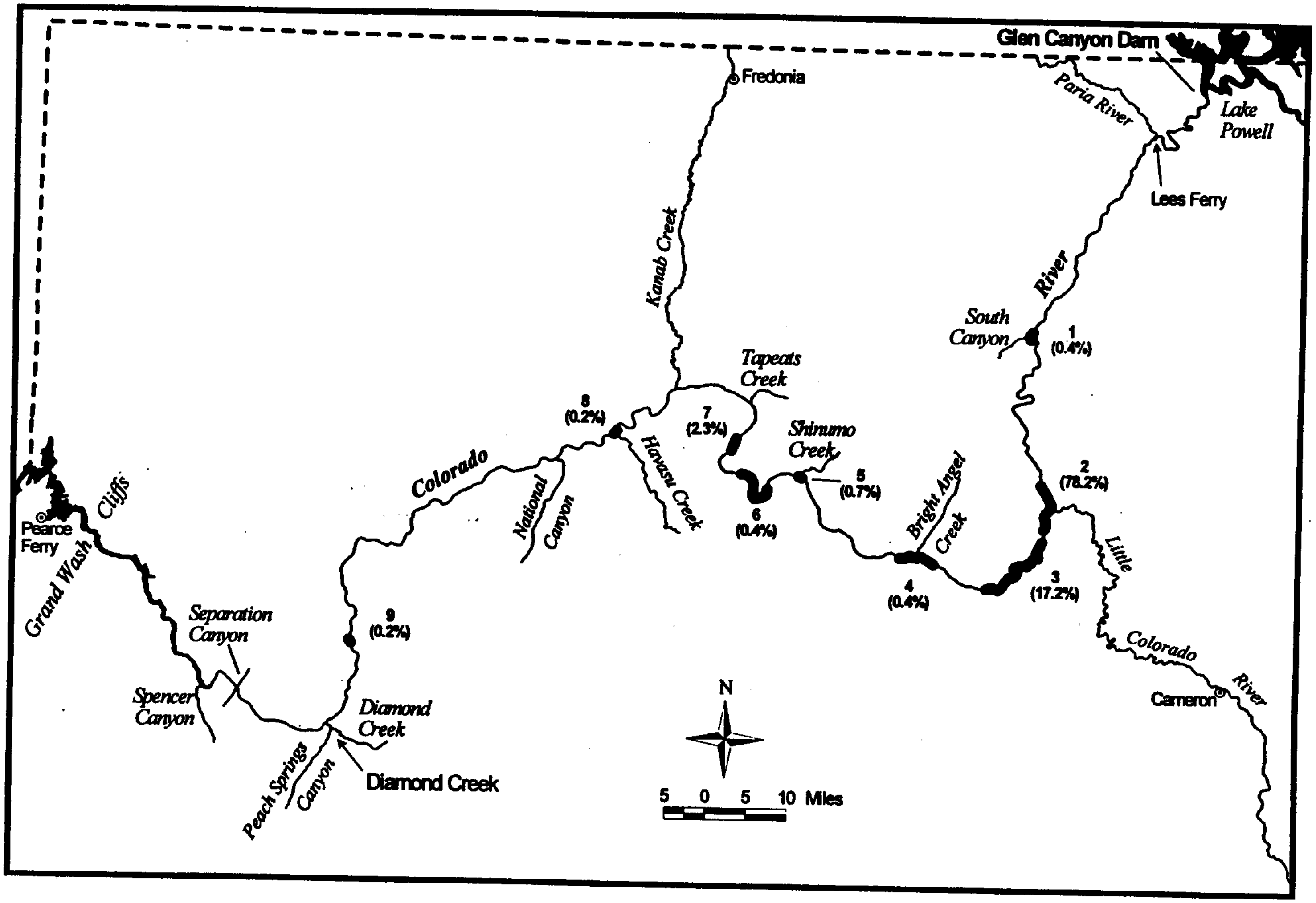


Figure 18. Locations of nine aggregations of humpback chub in the Colorado River through Glen and Grand Canyons. Percentage of total captures are indicated for 1990–1993. (Valdez and Ryel 1995)

recruitment (Valdez and Ryel 1995). Of 2,775 individuals captured, only 578, or 21%, were subadults (183 YOY and 395 juveniles) and 2,197 were adults, indicating poor reproductive success or survival, or both. Highest catch rates were near the LCR and the Paria River inflows, indicating that these seasonally warmed tributaries were principal spawning and nursery areas, but survival of young fish descending from the warm tributaries into the cold mainstem was low.

During surveys conducted 1991–1994, AGFD (1996) found flannelmouth suckers throughout the Colorado River between Lees Ferry and Diamond Creek; 35% were caught in the reach between the LCR and Bright Angel Creek (RM 61.5–RM 88.0) and 48% were caught in the reach from National Canyon to Diamond Creek (RM 166.5–RM 226.0). Most of the larval and juvenile flannelmouth suckers were captured in mainstem backwaters, particularly below National Canyon, but very few were found in tributaries or tributary inflows. None were captured in the mainstem above RM 44.0.

Simultaneous studies in the major tributaries, including the LCR (AGFD 1993, 1994, 1995), Paria River (S.J. Weiss 1993), Bright Angel Creek, Kanab Creek (Otis 1994), and Shinumo Creek (Allan 1993), seemed to support the hypothesis of poor reproductive success by flannelmouth suckers. Large numbers of adult flannelmouth suckers ascended these tributaries in spring, but little or no evidence of successful reproduction was observed. Douglas and Marsh (1996a) estimated a range of 502–7,886 large subadults and adults in the LCR during 1991–1994, indicating movements of large numbers of spawners from the mainstem into that tributary. Robinson et al. (1996) found moderate densities of young flannelmouth suckers drifting in the LCR, but length-frequency analysis indicated low survival.

S.J. Weiss (1993) concluded that the last successful reproduction of flannelmouth suckers in the Paria River had apparently occurred in 1981 (Kaeding and Zimmerman 1983) and 1984 (Maddux et al. 1987), when there were high releases from Glen Canyon Dam. An increase of 53 mm mean length was noted for adult spawners from 1981 to 1993, indicating that a significant portion of the 1993 spawning population was composed of fish from the 1981 and 1984 year classes. Nevertheless, appearance of some small adults into the Paria River spawning population suggested that some recruitment was occurring. S.J. Weiss (1993) also recaptured PIT-tagged flannelmouth suckers in the Paria River that had been previously captured by other investigators as far downstream as Kanab Creek (228 km away), suggesting that this species is highly mobile in Grand Canyon and may use more than one tributary for spawning.

Low survival of young flannelmouth suckers descending from seasonally warmed tributaries into the cold mainstem appeared to be limiting recruitment in the 1980s and 1990s. Possibly hatching success was low, or young were unable to find food in tributaries, succumbed to cold-shock in the mainstem, or were exposed to predation. The few YOY found in the Paria River in 1992 (S.J. Weiss 1993) and 1994 were not recaptured in the mainstem and apparently did not survive (C. McIvor, U of A, pers. comm.). In 1996, relatively large numbers of YOY flannelmouth suckers (576) were collected beginning in May (C. McIvor, U of A, pers. comm.), and by September, these fish ranged from 72 to 111 mm TL. This spawning success and survival was attributed to an absence of floods in the Paria River in 1996, combined with sufficiently high flows in the Colorado River during spring and summer of 1996 to pond the mouth of the Paria River and form a sheltered environment for thermal acclimation

Between 1993 and 1995, abundance of flannelmouth suckers increased between National Canyon and Diamond Creek; catches in trammel nets increased from 2–3 fish/net during 1990–1993 (Valdez and

Ryel 1995) to 6–15 fish/net in 1995 (Leibfried and Zimmerman 1995). Average size of flannelmouth suckers caught in 1995 was 334 mm TL. The estimated age of 4–5 years for these fish corresponds to the implementation of interim flows and greater longitudinal warming that produced water temperatures of up to 18.0°C in lower Grand Canyon. Leibfried and Zimmerman (1995) also captured 335 flannelmouth suckers in 1995 between National Canyon and Diamond Creek, including 141 juveniles and 81 YOY, indicating that greater longitudinal warming had also increased survival of young. The possible beneficial effect of lower flow fluctuations was also seen farther downstream with the capture of post-larval flannelmouth suckers from mainstem cobble riffles near Spencer Creek (RM 246.0; Valdez et al. 1995) and Surprise Creek (RM 248.3; Leibfried and Zimmerman 1996). The farthest downstream capture of flannelmouth suckers in Grand Canyon was near Grand Wash Cliffs (RM 275.1); the species is not found in Lake Mead.

Bluehead Sucker

No information on relative abundance of bluehead suckers or records of distribution is available from the period before Glen Canyon Dam was built, but McDonald and Dotson (1960), during their survey of Glen Canyon in 1958–1959, noted that bluehead suckers were found primarily in tributaries. Bluehead suckers were captured in all surveys after completion of Glen Canyon Dam, but the species was usually less common than flannelmouth suckers (Stone and Rathbun 1968; Miller and Smith 1972; Holden and Stalnaker 1975a; Suttkus et al. 1976; Minckley and Blinn 1976; Carothers and Minckley 1981; Maddux et al. 1987; Valdez and Ryel 1995; AGFD 1993, 1994, 1996). Bluehead suckers have usually been found as residents or spawners in tributaries (Maddux and Kepner 1988) or in the mainstem in close proximity to tributaries (Valdez and Ryel 1995). Like the flannelmouth sucker, bluehead suckers in Grand Canyon appear to have low reproductive success and recruitment. Of 1,040 bluehead suckers captured by Valdez and Ryel (1995) in 1990–1993, only 351 (34%) were subadults. AGFD (1996) found bluehead suckers to be common downstream of the LCR, particularly in the reach from National Canyon to Diamond Creek. Adult fish were captured moving into the mouths of the LCR, Shinumo, Kanab, and Havasu Creeks to spawn; some larvae and few juveniles were found in these tributaries. Young-of-year were collected from mainstem backwaters below Havasu Creek from April through August. Leibfried and Zimmerman (1996) reported low numbers of bluehead suckers from Diamond Creek to Quartermaster Canyon (RM 226.0– RM 259.0), the downstream-most capture location for the species in Grand Canyon. Of 56 individuals captured in this reach, 4 were YOY, 33 were juveniles, and 19 were adults.

Population size has not been estimated for the bluehead sucker in the mainstem Colorado River in Grand Canyon. However, Douglas and Marsh (1996a) reported a "steady and dramatic" decline in numbers of bluehead suckers in the LCR from 1991 to 1995. Estimates of large subadults and adults ranged from 5,143 to 48,415. Estimates began to decease in spring 1993 and declined to the lowest point in April 1995. The initial drop, from 48,415 to 10,532 between April and June of 1993, was attributed to severe flooding in the LCR.

Razorback Sucker

Although razorback suckers were once common or abundant in many regions of the Colorado River Basin (Ellis 1914, Minckley 1973, Bestgen 1990), only ten documented records exist for the species in Grand Canyon (Valdez 1996):

- one adult caught by an angler in Bright Angel Creek in 1944 (Minckley and Carothers 1979);
- one captured by AGFD at the mouth of the Paria River just after closure of Glen Canyon Dam in 1963 (Minckley and Carothers 1979);
- three adults, including a gravid female, from the mouth of the Paria River in June 1978 (Minckley and Carothers 1979);
- one adult from near Lower Bass Camp (RM 108.0) in April 1984 (Maddux et al. 1987);
- one female (555 mm TL, 1,860 gm) from the LCR inflow in May 1989 (C.O. Minckley, FWS, pers. comm.); and
- three adults from the LCR inflow in April 1990, including two males (475 mm TL, 1,211 gm; 476 mm TL, 1,219 gm) and one female (588 mm TL, 2,035 gm) (W. Persons, AGFD, pers. comm.).

All razorback suckers captured in Grand Canyon have been adults, indicating that either this region is not a rearing area for young or that reproduction and recruitment are unsuccessful. The only other report of the species from the area are two "humpback suckers" (common name used for the razorback sucker prior to 1970s), each "about 1½" long," from Glen Canyon (upstream of present Glen Canyon Dam) in July 1958 (McDonald and Dotson 1960). Based on historic captures, Valdez (1996) estimated that fewer than 100 razorback suckers may be left in Grand Canyon.

Several investigators have reported hybrids between razorback suckers and flannelmouth suckers in Grand Canyon (Suttkus et al 1976, Maddux et al. 1987, Valdez and Ryel 1995). These fish have a poorly developed dorsal keel and intermediate morphologic and meristic characteristics, including scale size and lateral line counts, dorsal fin ray counts, size and shape of the head and mouth, and coloration (Hubbs and Miller 1953). Although hybridization between razorback suckers and flannelmouth suckers has been reported for many years (Hubbs and Miller 1953, McAda and Wydoski 1980), the incidence in Grand Canyon appears high relative to the number of razorback suckers present, especially in the LCR where suckers concentrate during spawning. Mainstem collections during 1990–1993 included 2,197 adult flannelmouth suckers, 5 adult hybrids, and no razorback suckers (Valdez and Ryel 1995), while collections in the LCR in 1991–1995 included 25 hybrids (Douglas and Marsh 1996a). Of 12 morphologic hybrids from the LCR in 1994, seven possessed DNA characteristic of razorback suckers and flannelmouth suckers (indicating true genetic hybridization), while five had DNA of primarily flannelmouth sucker, indicating introgressive hybridization (T. Dowling, ASU, pers. comm.).

The paucity of records for razorback suckers in Glen and Grand Canyons may be due to the difficulty of accessing and sampling the deep canyon areas, or perhaps to razorback suckers have always been uncommon inhabitants of turbulent canyon regions (Minckley 1983, Bestgen 1990). Recent surveys of canyon-bound regions in the upper Colorado River Basin (i.e., Cataract Canyon, Westwater Canyon, Desolation Canyon) have yielded few razorback suckers (Valdez 1990). It appears that the species was more common in downstream alluvial regions, as indicated by large numbers of razorback suckers in Lake Mead for about the first 30 years following formation of the reservoir (Minckley et al. 1991). Valdez and Masslich (1989) reported that although razorback suckers inhabited primarily alluvial regions of the upper Green River, some radiotagged adults overwintered in canyon regions.

Douglas and Marsh (1996a) hypothesized that razorback suckers were never abundant in Grand Canyon, suggesting that razorback suckers were not residents of the canyon, but transients, moving between more desirable habitats upstream and downstream. In support of this thesis, they note that razorback sucker remains were not found at Stanton's Cave, where non-fossilized bones of five other native species were discovered, and that razorback suckers were rare in the earliest collections from Grand Canyon. They cite Smith (1959), who reported the species as "...rare, or possibly just difficult to collect in Glen Canyon, since extensive collecting turned up only two immature (i.e., YOY) specimens...." Suttkus et al. (1976) reported three hybrids, but no razorback suckers in 1970–1973, stating that "the razorback has been forced out of existence in the Grand Canyon section of the Colorado River."

Speckled Dace

Although speckled dace were common or abundant in every survey in Grand Canyon, little is known of the life history or population status of this species. Speckled dace have been reported from a variety of habitats in Grand Canyon, including tributaries (Suttkus et al. 1976, Carothers and Minckley 1981, Kaeding and Zimmerman 1983, Maddux et al. 1987); backwaters (AGFD 1996); shallow riffles (Valdez and Ryel 1995); debris fans (AGFD 1996); and thermal springs and inflows (Valdez and Ryel 1995). During 1990–1993, speckled dace occurred in low densities in the mainstem, but at relatively high densities in tributaries and tributary inflows (Valdez and Ryel 1995). This species was common above Bridge Canyon (RM 235.0), but dramatically decreased downstream, where red shiners were abundant (Valdez et al. 1995). AGFD (1996) concluded that, during 1991–1994, speckled dace appeared to be the most common fish species in the Colorado River and in all tributaries sampled (except the LCR) in Grand Canyon. The status of the speckled dace in Grand Canyon is difficult to evaluate because specimens are usually captured incidental to other target fishes and studies have not focused on this species.

Chapter 5
LIFE HISTORY AND ECOLOGY OF NATIVE FISHES

INTRODUCTION

This chapter describes the life history and ecology of the native fishes in Grand Canyon: humpback chub, flannelmouth sucker, bluehead sucker, razorback sucker, and speckled dace. For each species, information from Grand Canyon is presented on distribution and abundance, reproduction, length-weight and condition factor, survival, habitat, movement, diet, and parasites. A summary of this information is presented in Table 6. Also included in this chapter is a discussion of factors that limit the native fish assemblage. Although the endangered razorback sucker is extremely rare in Grand Canyon, it is included in the discussion because the Colorado River downstream of the Paria River to Lake Mead and Hoover Dam is designated critical habitat for this species.

HUMPBACK CHUB

Distribution and Abundance

Humpback chub in Grand Canyon occur as 10 aggregations (i.e., groups of fish, not necessarily reproducing or self-sustaining), including 9 in the mainstem and 1 in the LCR (Table 7; Valdez and Ryel 1995). The upstream-most aggregation, named the 30-Mile aggregation, was located in the proximity of warm springs (the Fence Fault spring complex) from RM 26.9 to RM 32.9, and the downstream-most aggregation was associated with Pumpkin Spring near RM 213.0.

This distribution was similar to that reported by Maddux et al. (1987) 5 years earlier. A single adult was also captured near Maxson Canyon at RM 253.2 in 1993 (Valdez 1994). The aggregation of humpback chub in the LCR appears to be a resident population, with fish restricted to the lower 14.9 km by a series of water falls (Douglas and Marsh 1996a). The total mainstem population of humpback chub in 1990–1993 was about 3,700 adults >200 mm TL (Valdez and Ryel 1995) and the total LCR population was 4,346 fish >150 mm TL (Douglas and Marsh 1996a).

Length-frequency analyses indicate that the 30-Mile aggregation consisted of only adults >325 mm TL, and that the LCR inflow aggregation consisted of all sizes (and presumably all ages) of fish, with a strongly bimodal distribution of sizes, indicating high reproductive success, low survival of young and recruitment, and high survival of adults. The seven other aggregations, all downstream of the LCR, consisted primarily of adults, with some recruitment, presumably from the LCR or possibly from local reproduction.

Table 7. Numbers of Fish Captured in the Nine Aggregations of Humpback Chub in the Grand Canyon (adapted from Valdez and Ryel 1995).

Aggregation Name	RM	Number of Fish Captured, 1991–1995					
		YOY	Juvenile	Adult	Total	Population Estimate	95% Confidence Interval
30-Mile	29.8–31.3	14	0	26	26	52	28–136
LCR Inflow (LCRI)	57.0–65.4	1,830	1,293	1,524	4,647	3,482	2,682–4,281
Lava to Hance	65.7–76.3	778	226	15	1,019	ne*	-
Bright Angel Creek Inflow	83.8–92.2	13	2	9	24	ne*	-
Shinumo Creek Inflow	108.1–108.6	4	13	27	44	57	31–149
Stephen Aisle	114.9–120.1	0	7	17	24	ne*	-
Middle Granite Gorge (MGG)	126.1–129.0	1	4	124	129	98	74–153
Havasu Creek Inflow	155.8–156.7	0	0	7	7	13	5–70
Pumpkin Spring	212.5–213.2	0	0	6	6	5	4–16

ne* = no estimate possible of small number of recapture

Reproduction

Humpback chub are an obligate warm-water species that require relatively warm temperatures for spawning, egg incubation, and survival of larvae. Optimum growth temperature is 16.0–22.0°C (Lechleitner 1992). Successful reproduction in Grand Canyon has been documented only in the LCR, a seasonally warmed tributary, though never directly observed (Kaeding and Zimmerman 1983, Gorman 1994, Douglas and Marsh 1996a). Although adults in the mainstem annually produce viable gametes, water temperatures near the LCR are too cold (i.e., 8-10°C) for egg incubation or larval survival (Kaeding and Zimmerman 1983).

Hatching success under laboratory conditions was 12%, 62%, 84%, and 79% in 12–13°C, 16–17°C, 19–20°C, and 21–22°C, respectively, while survival of larvae was 15%, 91%, 95%, and 99%, at the same respective temperatures (Hamman 1982). Time from fertilization to hatching ranged from 465 hours at 10.0°C to 72 hours at 26.0°C, and time from hatching to swim-up varied from 372 hours at 15.0°C to 72 hours at 21.0–22.0°C. Proportion of abnormal fry varied with temperature, from 33% at 15.0°C to 17% at 25.0°C. Hence, highest hatching success was at 19–20°C with incubation time of 3 days, but highest larval survival was at 21–22°C. Marsh (1985) found similar results.

Humpback chub are broadcast spawners and have a relatively low fecundity rate, compared to cyprinids of similar size (Carlander 1969). Eight humpback chub injected with carp pituitary and stripped in a

Table 6. Life History Parameters for the Native Fishes of the Colorado River in Grand Canyon.

Parameter	Humpback Chub	Flannelmouth Sucker	Bluehead Sucker	Speckled Dace	Razorback Sucker
Population Estimates	Mainstem (1990-93)[a]: 3,750 (>200 mm TL) LCR (1992)[b]: 4,346 (>150 mm TL)	None Available	None Available	None Available	Fewer than 100 adults[q]
Peak Time of Spawning Condition	Mainstem[a] = May-June LCR[b] = Apr-May	Paria River[j] = Mar-Apr	Tribs: mid-Mar-June[n,o]	Mainstem[a]: Apr-Jun	Upper Basin:May-June[l] Lake Mohave: Nov-Mar[r]
Spawning Temp. Range (optimal)	11.5-23°C (16-22°C)[a,b,c]	17-23°C[k]	17-23°C[k] Kanab Cr = 18.2-24.6°C[o]	17-23°C[k,n]	Upper Basin: 6-19[l] Lake Mohave: 10-21[r]
Incubation Temp. Range (optimal)	12-22°C (72 hr @ 19-22°C)[h]	Not Available	Not Available	Not Available	14.4-17.2°C[m]
Larval Survival Temp. (optimal)	12-22°C (21-22°C)[h]	Not Available	Not Available	Not Available	18-20°C[m]
Optimal Growth Temp.	16-22°C[d,f,h,i]	Not Available	Not Available	Not Available	22.9-24.8°C
Eggs/Female Eggs/kg body weight	2,523/female 5,262/kg[h]	4,000/450 mm TL 40,000/500 mm TL[l]	20,227/380-400 mm TL[p]	Not Available	46,740/female 39,600/kg[l]
Egg Diameter	2.6-2.8 mm[h]	3.8-3.9 mm[m]	3.3-3.5 mm[m]	Not Available	2.5-2.8 mm[m]
Size at Hatching	7 mm[d]	10-11 mm[m]	9-11 mm[m]	5-6 mm[m]	7-10 mm[m]
Maximum Size	480 mm TL 1165 g[a]	682 mm TL 2750 g[a]	432 mm TL 986 g[a]	Not Available	Not Available
Maximum Age	22 annular rings [g]	Not Available	Not Available	2-3 years[r]	44 years[l]
Sex Ratio (M:F)	49:51[a]	Not Available	Not Available	Not Available	Not Available
Age at Maturity	males = 3-4 years females = 3-4 years[a]	4-8 years[a]	Not Available	<1 year[r]	2-4 years

Size at maturity (TL)	males = 202 mm females = 200 mm[a]	Not Available	Not Available	Not Available	Not Available
Size at Annulus (TL)	1 = 96 mm 2 = 144 mm 3 = 186 mm[a]	Not Available	Not Available	Not Available	Not Available
Length-weight relationship	log W = -4.564+2.816 log TL, $R^2 = 0.92$[a]	log W = -5.222+3.076 log TL, $R^2 = 0.98$[a]	log W = -5.222+3.090 log TL, $R^2 = 0.97$[a]	Not Available	Not Available
Condition Factor (TL)	Mainstem[a]: males = 0.783-1.023 females = 0.883-1.092	Mainstem[a]: 0.92-1.28	Mainstem[a]: 0.82-1.16	Not Available	Not Available
Growth Rates	LCR[a]: TL = 114.43•$\log_e$(age+1) + 14.921, R^2=0.97 Colorado River[a]: TL = 143.92•$\log_e$(age+1) + 1.0938, R^2=0.99 YOY in Lab[f]: 10.63 mm/30 d @ 20°C 2.30 mm/30 d @ 10°C Scale back-calculations[a] YOY in LCR: 10.30 mm/30 YOY in Mainstem: 3.50-4.00 mm/30 d	Not Available	Not Available	Not Available	150 mm in 1[st] year 70 mm/yr for 1[st] six yr 2.2 mm/yr, 3.1mm/yr as adults
Survival	age 1-3 = 0.01/yr age 3+ = 0.627-0.896, ave. = 0.755[a]	Not Available	Not Available	Not Available	Not Available

[a]Valdez and Ryel (1995)
[b]Douglas and Marsh (1996c)
[c]Kaeding and Zimmerman (1983)
[d]Muth (1990)
[e]Gorman (1994)
[f]Lupher and Clarkson (1994)
[g]Hendrickson (1993)
[h]Hamman (1982)
[i]Marsh (1985)
[j]Weiss (1993)
[k]Lechleitner (1992)
[l]McAda and Wydoski (1978)
[m]Snyder and Muth (1990)
[n]Carothers and Minckley (1981)
[o]Maddux and Kepner (1988)
[p]Smith (1996)
[q]Valdez (1995)
[r]Minckley (1991)
[s]Maddux et al. (1986)

hatchery produced an average of 2,523 eggs/female (355–406 mm TL), or about 5,262 eggs/kg of body weight (Hamman 1982). Egg diameter ranged 2.6–2.8 mm (mean, 2.7 mm). Eleven humpback chub from the LCR yielded 4,831 eggs/female following variable injections of carp pituitary and field stripping (Clarkson 1993). Male to female ratios for mainstem adults captured near the LCR, based on external morphological examination of papillae, ranged from 41:59 to 53:47, for an overall average of 49:51 (Valdez and Ryel 1995).

The LCR has been recognized as the principal spawning area for humpback chub in Grand Canyon since the early 1970s (Miller and Smith 1972, Holden and Stalnaker 1975b, Suttkus et al. 1976), but the extent of use was not investigated until the early 1980s, when it was determined that fish from the mainstem spawned in the LCR simultaneous to a resident population (Kaeding and Zimmerman 1983). It is not clear if the LCR has always been the principal spawning site for humpback chub in Grand Canyon, or if spawning occurred in the mainstem prior to cold releases from Glen Canyon Dam (Valdez 1991). Adults from the other five populations of humpback chub in the Upper Basin are all mainstem spawners (Valdez and Claimer 1982). Possibly, the majority of mainstem spawners in Grand Canyon—except for fish at RM 30.0 and some downstream aggregations—have been extirpated from the system.

Of 227 adult humpback chub in spawning condition (i.e., tubercles, nuptial colors, expressing gametes) at temperatures of 10.0–14°C, 178 were near the LCR inflow, 23 were in Middle Granite Gorge, 7 were at or near a warm spring at RM 30.0, and 5 each were at inflows from Bright Angel Creek, Shinumo Creek, and Havasu Creek (Valdez and Ryel 1995). Fish associated with the LCR inflow were in peak spawning condition about 2 months earlier (i.e., April) than fish from other aggregations (i.e., May, same time as most Upper Basin populations; Valdez and Claimer 1982, Kaeding et al. 1990), indicating that mainstem spawners remain in Grand Canyon, but successful spawning is precluded by cold mainstem temperatures.

Spawning by humpback chub is also suspected in a warm spring at RM 30.0, where about 100 post-larvae were observed in July 1994, in association with an aggregation of about 50 adults (Valdez and Ryel 1995). Tributaries other than the LCR are considered too small, too cold, or too turbid to support substantive spawning by humpback chub. Although Havasu Creek has similar water quality and quantity to the LCR (Gorman 1994), a natural water fall near the mouth is an effective fish barrier. Eggs found at the LCR inflow were believed to have washed down the LCR, and it was surmised that viable eggs in the inflow could not survive because of "daily inundation of the area by cold mainstem fluctuating flows" (Valdez and Ryel 1995).

Humpback chub in Grand Canyon spawn primarily in spring. Valdez and Ryel (1995) described pre-spawning aggregations at the LCR inflow from February through April and ascent of the LCR from March through July. Water quantity and quality were discounted as cues for gonadal development and staging behavior, since flow and temperature of the Colorado River are regulated by Glen Canyon Dam and have no marked seasonal pattern. Conditions of the LCR were also discounted, since fish from upstream and downstream of the LCR staged simultaneously. It was hypothesized that climatic factors, such as photoperiod, cued gonadal development and pre-spawn staging. Once the fish were staged, however, increased water temperature, decreased turbidity, and decreased flow of the LCR were identified as principal cues for ascending fish. Approximately equal numbers of males and females were found staging and ascending the LCR, indicating no sexual segregation during spawning runs.

In the LCR, Gorman and Stone (In Press) found that during 1993–1995, spawning generally commenced in late March, peaked in mid-April, and waned in mid-May. A high proportion of males remained ripe over this period, whereas gravid females were relatively abundant only in April. Ripe males aggregated in areas of complex habitat structure with high angular variation in bottom profiles (matrix of large boulders, travertine masses combined with chutes, runs and eddies, 0.5-2.0 m deep) and were associated with deposits of clear gravel. Gravid females appeared to move to these male aggregations to spawn. Abrasions on anal and lower caudal fins of males and females suggest that spawning involved contact with gravel substrates, although actual spawning sites were not described.

In the LCR, Robinson et al. (1996) found larvae and post-larvae humpback chub at several locations, but were unable to identify specific spawning sites. Observations, supplemented by underwater photography and videography, also failed to provide information on spawning (Gorman 1994). It was concluded that humpback chub might be opportunistic spawners; i.e., they spawn within the range of habitat normally used by adults when environmental cues and physiological conditions are conducive.

During 1990–1993, highest reproductive success for humpback chub in the LCR was for spring 1993 (Valdez and Ryel 1995), following an usually high flood of about 17,000 cfs in January. Gorman (1994) found substantial changes in stream habitat characteristics following the flood. Travertine dams and deep pools were extensively scoured and average channel depth was considerably greater, indicating that the flood had beneficial effects on spawning habitat or egg survival, or both. Peak estimates of juveniles in the mainstem following descent from the LCR were over 3.9 million fish, compared to 738,000 in 1992 and 246,000 in 1991 (Valdez and Ryel 1995).

Unlike other Colorado River fishes (e.g., Colorado squawfish, razorback sucker), larval humpback chub are not prominent in ichthyofaunal drift (Muth 1990). At hatching, larvae have non-functional mouths and small yolk sacs. The larvae swim up about 3 days after hatching but tend to remain close to spawning sites. Robinson et al. (1996) found small numbers of larval humpback chub drifting in the LCR from May through July, primarily at night.

Age and Growth

In work done with humpback chub of the LCR, Hendrickson (1993) reported that the maximum number of annular rings on otoliths (i.e., inner ear bones, lapilli) was 23, showing that the species is long-lived. However, definitive age and growth studies have not been conducted on humpback chub. The cycloid scales are small, and annular and circular rings are severely crowded with increasing age. Peripheral rings often appear to be resorbed or eroded, particularly when the fish reach maturity (Valdez and Ryel 1995). Since the fish is endangered, sacrificing numbers of individuals for otoliths or other bony structures is not practical. Length-frequency analysis distinguish only the first three or four cohorts and slowed growth distorts cohort separation after the fish reach maturity. The only information available on age and growth of humpback chub is from laboratory studies with young fish, mark-recapture data, and scale aging of young individuals.

Humpback chub are approximately 7 mm long at hatching (Muth 1990). In a laboratory, they grew at a rate of 10.63 mm/30 days at a temperature of 20°C (similar temperature to LCR), but only 2.30 mm/30 days at 10°C (similar temperature to mainstem) (Lupher and Clarkson 1994). Valdez and Ryel (1995) found similar growth rates from back-calculations of scale growth rings in juveniles from the

LCR (10.30 mm/30 days) and the mainstem (3.50–4.00 mm/30 days). Higher growth in the mainstem than in the laboratory indicated that young fish periodically occupied warmed shoreline habitats. Average back-calculated growth rates for the first three annular rings were 96, 144, and 186 mm TL. Kaeding and Zimmerman (1983) reported first annulus formation for LCR fish at 100 mm TL, and estimated that fish 250–300 mm TL were 3–4 years old. A growth curve for LCR fish and mainstem fish indicates that 3- to 4-year-old fish are 185–210 mm TL, and that fish 250–300 mm TL are probably 5+ years old (Valdez and Ryel 1995). Average total lengths of humpback chub from Cataract Canyon, based on back-calculations from scale annuli 1-6, were 50, 100, 144, 200, 251, and 355 mm TL, respectively (Valdez 1990). Apparently growth rates of humpback chub vary by population, and growth of fish from the Colorado River in Grand Canyon seems to be higher than other populations studied.

Many humpback chub hatched in the LCR descend into the mainstem in mid to late summer. The proportion of fish that descend and their relationship to mainstem migrating spawners and LCR residents is not known (Valdez and Ryel 1995, Douglas and Marsh 1996a). Valdez and Ryel (1995) used a "transition check" (i.e., discontinuous or crowded circular rings developed when fish moved from about 20°C to 10°C) on scales of young fish (N=78) and back-calculated an average length of 74 mm TL (52–132 mm TL) for young descending from the LCR into the mainstem. Mainstem sampling at the LCR inflow has revealed numerous smaller fish (AGFD 1996, Valdez and Ryel 1995), suggesting low survival from thermal shock by fish smaller than about 52 mm TL. Lupher and Clarkson (1994) reported low survival of humpback chub less than 50 mm TL subjected to temperature changes of greater than about 1–2°C. Researchers have suggested that mainstem flows that pond tributary mouths would allow thermal acclimation by young native fishes and hence, higher survival.

Mark-recapture data reported for the LCR (Minckley 1992) and for the mainstem (Valdez and Ryel 1995) indicate that young humpback chub grow faster in the LCR (about 10 mm/30 days) than in the mainstem (2–4 mm/30 days), but that fish older than about 3 years of age grow faster in the mainstem (mean, 1.36 mm/30 days; range, 0.79–2.79 mm/30 days) than in the LCR (<1–1.4 mm/30 days). Apparently food resources, habitat, and water temperature are more suitable for young fish in the LCR, but habitat and food may be limiting for adults. Abundant habitat, suitable food, and a relatively stable, regulated flow may be favorable for adult growth in the mainstem, despite cold mainstem temperatures. Mark-recapture data for humpback chub from Westwater Canyon, Utah (T. Chart, UDWR, pers. comm.) showed average monthly growth rates of 1.08 mm and 1.35 mm for fish 200–250 mm TL and 250–300 mm TL, respectively, which are similar to the LCR growth rates, but well below Grand Canyon mainstem growth rates.

Length-Weight and Condition Factor

Length-weight relationships for humpback chub for 1990–1991 ($\log W = -5.324 + 3.117 \log TL$, $R^2 = 0.99$), 1992 ($\log W = -5.176 + 3.056 \log TL$, $R^2 = 0.99$), and 1993 ($\log W = -5.034 + 2.986 \log TL$, $R^2 = 0.98$) reveal exponents of 3.117, 3.056, and 2.986, which indicate isometric growth (Valdez and Ryel 1995). An exponent of approximately 3.0 indicates isometric growth or a constant relationship between length and weight (LeCren 1951, Lagler 1956). Although humpback chub change shape dramatically with age (i.e., enlargement of a nuchal hump), length to weight relationship appears constant. Meretsky et al. (In Review) provided length-weight relationships for eight groups of fish from all six populations of humpback chub; exponents ranged from 2.505 to 3.288, indicating different degrees of allometry among populations. Douglas (1993), reported from video image technology that changing body shape of humpback chub affects length to weight relationships, also indicating allometric growth. Douglas (1993) reported no significant difference in sexual dimorphism in adult humpback chub.

Condition factor for adult humpback chub (>200 mm TL) from the mainstem for 1990–1993 ranged from 0.783 to 1.023 for males and from 0.883 to 1.092 for females (Valdez and Ryel 1995). Highest condition was typically seen in February, March, or April, just prior to spawning, and lowest condition was seen in June–September, after spawning. Meretsky et al. (In Review) reported a disconcerting decline in condition factor of adult humpback chub not in immediate spawning condition and captured from the LCR confluence from 1978 to 1996, and hypothesized that the decline could be caused by one or more factors, including an invasion of the Asian tapeworm since in 1990, researcher variation in weighing fish, or natural population variation. This decline is concurrent with an apparent decline of 40–83% in total numbers of adults in the LCR over the same time period (Douglas and Marsh 1996a, 1996a).

Survival

Annual survival rate of subadult humpback chub through their first 3 years of life was estimated at 0.10, based on monthly electrofishing and minnow traps along mainstem shorelines near the LCR (Valdez and Ryel 1995). Larval to adult survival was estimated at 0.001 (i.e., 0.10^3). Survival rates of YOY humpback chub of the 1991 year class, based on monthly electrofishing, were 0.824, 0.312, and 0.097 for 1, 6, and 12 months, respectively. Rates for 1992 were similar with 0.829, 0.326, and 0.106, respectively. However, survival rates for the 1993 year class, following high reproductive success, were much lower at 0.216, $1x10^{-4}$, and $1x10^{-8}$ for 1, 6, and 12 months, respectively. The decrease in density of subadults from September to November 1993 was 95% (521 to 24 fish/10 hours) (Valdez and Ryel 1995), and was comparable to a 98% decrease (2,082 to 58) in total catch of subadults in backwaters (i.e., eddy return-current channels; AGFD 1994). Resultant densities of the 1993 year class were comparable to that of the 1991 and 1992 year classes, suggesting density dependent mortality of first-year humpback chub in the mainstem.

Annual survival rate of mainstem adults, based on mark-recapture data and open population model estimates, was 0.755 (95% C.I. = 0.627–0.896) (Valdez and Ryel 1995). Survival rate between seasons was estimated at 0.932 (95% C.I. = 0.890–0.973). According to these estimates, 204–238 adults are lost seasonally out of a population of 3,000–3,500, and 735–857 are lost annually. Survival rates were not available for humpback chub from the LCR or from other populations in the basin.

Habitat

Humpback chub live in the mainstem and larger tributaries of the Colorado River in canyon-bound regions, characterized by deep, swift currents, and rocky substrates (Valdez and Claimer 1982). Average depths selected by larvae, YOY, juveniles, and adults in the Upper Basin were 1.4, 2.1, 2.3, and 10.3 feet (0.4, 0.6, 0.7, and 3.1 m), respectively (Valdez et al. 1990), while average velocities were <0.1, 0.2, 0.6, and 0.6 feet/sec (0.03, 0.06, 0.18, 0.18 m/sec), respectively. Dominant substrates were silt and sand for YOY, and boulders, sand, and bedrock for juveniles and adults.

In Grand Canyon, highest densities of subadults in the mainstem were from particular shoreline types, indicating a clumped distribution. Vegetation, talus, and debris fans produced highest catch rates

(Valdez and Ryel 1995, Converse 1996). Lowest catch rates were from bedrock, cobble bars, and sand beaches. Availability of vegetation was dependent on river stage. These researchers suggested that vegetated shorelines were used as cover, replacing cover formerly provided by high turbidity. Minimum, average, and maximum velocity selected by YOY (21–74 mm TL) were 0.0, 0.06, and 0.30 m/sec (Figure 19), all at depths <1 m (Valdez and Ryel 1995). Minimum, average, and maximum velocity selected by juveniles (75–259 mm TL) were 0.0, 0.18, and 0.79 m/sec, all at depths <1.5 m. Since vegetation used by these fish is associated with the new high-water zone, contact between the water and the cover of roots, stems, and overhanging branches occurs only at high flows. This vegetative cover is not to be confused with submergent and emergent vegetation associated with encroaching vegetation in backwaters (Stevens et al. 1995).

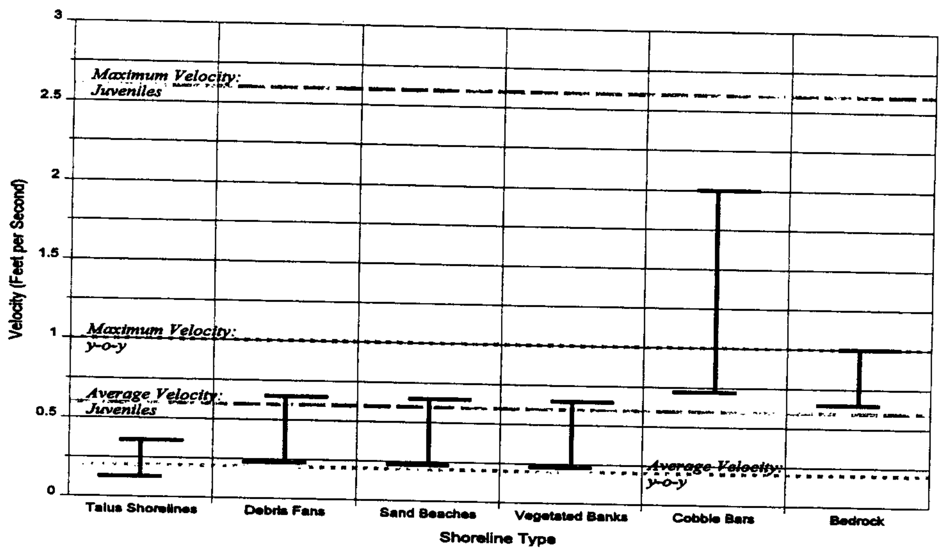


Figure 19. Water velocity ranges in nearshore habitat types and average and maximum velocity preferences of YOY and juvenile humpback chub. (Based on data from Valdez and Ryel 1995)

Velocity ranges of all shoreline habitats, except cobble, appeared suitable for these young fish. However, Bulkley et al. (1982) reported that swimming ability of juvenile humpback chub (73–134 mm TL) in a laboratory swimming tunnel, was positively and significantly related to temperature. Humpback chub forced to swim at a velocity of 0.51 m/sec fatigued after an average of 85 minutes at 20°C, but fatigued after only 2 minutes at 14°C; thus, a decrease of 6°C reduced time to fatigue by 98%. Bulkley et al. (1982) also found that temperature affected burst speed, sustained speed, and cruising speed of juvenile humpback chub. Valdez and Ryel (1995) surmised from these data that YOY (30–100 mm TL) at 14°C (summer mainstem temperature) are capable of burst speeds of 0.40–0.80 m/sec, sustained speeds of 0.20–0.40 m/sec, and cruising speeds of 0.10–0.20 m/sec, while juveniles are capable of burst speeds of 0.80–1.60 m/sec, sustained speeds of 0.40–0.80 m/sec, and cruising speeds of 0.20–0.40 m/sec. Based on these relationships, it was determined that only talus, vegetated banks, debris fans, and sandbars provided suitable velocities, but sandbars were not used due to lack of cover. Assuming that fish occupying shorelines maintain their position under an energy-efficient mode of cruising speed, bedrock and cobble bars were unsuitable for YOY and only marginally suitable for juveniles. At temperatures characteristic of the mainstem (8–12°C), subadults may fatigue rapidly, unable to withstand currents, forage efficiently, or escape predators.

Valdez and Ryel (1995) reported an apparent transition in mainstem habitat use with size and age of humpback chub, such that subadults used primarily shoreline habitats with shallow water and adults used primarily offshore habitats at greater depths. Fish smaller than 100 mm TL were not captured in offshore habitats and fish larger than 100 mm TL were only occasionally captured near shore. Adults in Grand Canyon used primarily large recirculating eddies; 88% of 1,579 adults captured and 74% of 835 radio contacts from 75 radiotagged adults were from eddy complexes that composed only 21% of surface area for the mainstem near the LCR. Smaller percentages of adults were captured or radio contacted in runs (7% and 16%, respectively) that composed 56% of surface area; pools (1% and 3%, respectively) that composed 16% of surface area; and backwaters (4% and 7%, respectively) that composed 0.1% of surface area. Within eddy complexes, fish used shallower areas of main sand platforms and return-current channels (<2 m deep) primarily at dawn, dusk, and night, and remained in deeper areas of sand platforms (2–5 m deep) during the day. Vortices of low-velocity (<0.3 m/s) were selected, in which continuous activity suggested a soaring behavior that enabled the fish to remain in position at low energy expenditure while feeding on drifting food organisms and particles. Association of fish with sand substrate was not considered selection, but coincidental to locations of low-velocity depositional areas created by eddy complexes.

Gorman (1994) also found ontogenic shifts in habitat use by humpback chub in the LCR in which four distinct habitat relationships were associated with four sizes of individuals. Post-larvae (<50 mm TL) used nearshore areas of shallow to moderate depth (<100 cm), low velocity, small substrates, moderate cover and vertical structure, in near-benthic to mid-pelagic position. Young-of-year (50–100 mm TL) used similar habitats of moderate depth (<200 cm), small to large substrates, and moderate to high cover with vertical structure. Juveniles (100–150 mm TL) used near and offshore areas of moderate to deep water (<300 cm, day, <200 cm, night), slow currents, small and large substrates, moderate to high cover and vertical structure, in near benthic position (day) and lower-pelagic position (night). Subadults (150–210 mm TL) used near and offshore areas of moderate to deep water (<300 cm day and night), slow currents, moderate to high cover and vertical structure, in near benthic position (day and night). Post-larvae and YOY were diurnally active, primarily at morning and at night, and juveniles and subadults were nocturnally active.

In summer of 1993, during a year of high reproductive success in the LCR, Gorman (1994) observed adult humpback chub cannibalizing YOY, and hypothesized that the predation was caused by habitat saturation. The extent of this predation and its effects on YOY survival rates is unknown. By August, many YOY humpback chub appeared emaciated and dying, which was interpreted as a consequence of changing food availability, diets, and habitat use. By late summer, densities of YOY humpback chub had declined and habitat use patterns were merging with those of juveniles and adults.

Movement

Humpback chub move substantially less than other native Colorado River fishes (Valdez and Ryel 1995). Mean net movement (distance from first to last radio contact) of 69 radio-tagged adults monitored year-around in the Colorado River in Grand Canyon was 1.49 km (range, 0–6.11 km) over an average monitoring period of 93 days (range, 30–170 days). Of 69 radio-tagged adults, net movement of 35 fish (51%) was less than 1 km and net movement of 58 fish (84%) was less than 3 km. This was comparable to net movement of 1.94 km (range 0–99.8 km) for 188 PIT-tagged fish at large 20–1,065 days (i.e., up to 2.9 years). Only 7 of 188 PIT-tagged fish moved between the nine aggregations; all but one moved downstream short distances. Mark-recapture data from 92 humpback chub marked with Carlin and Floy tags and at large for an average of 2,990 days (range, 304–4,496 days; up to 12.3 years) showed average distance from original capture to recapture of 4.29 km (range, 0.1–14.4 km), revealing remarkable fidelity for specific river locales. This fidelity was observed in other populations of humpback chub; mean net movement of eight radio-tagged adults in Black Rocks, Colorado, was 0.8 km and 1.67 km for PIT-tagged adults (Valdez and Claimer 1982) for 1980–1981; and 0.8 km and 1.4 km, respectively, for 1988–1989 (Kaeding et al. 1990). In contrast, net movement of 43 radio-tagged Colorado squawfish in fall and spring in the Upper Basin was 31.8 km (Archer et al. 1985), and 33.9 km for radio-tagged adult roundtail chub in spring and summer (Kaeding et al. 1990).

In the Colorado River Basin, greatest movement of humpback chub has been reported from Grand Canyon, primarily because adults from the mainstem annually ascend the LCR to spawn. Of 69 radio-tagged adults monitored in the mainstem, 35 (61%) were contacted in the LCR or LCR inflow at least once (Valdez and Ryel 1995). Of 419 PIT-tagged fish marked in the mainstem and recaptured in the LCR, 44% were more than 3 km upstream of the confluence, 36% were more than 5 km upstream, and one fish was captured 14.6 km upstream (fish are blocked from ascending farther than 14.9 km by water falls). Fidelity to specific mainstem locales was striking. Of 60 PIT-tagged fish consecutively captured in the mainstem, LCR, and again in the mainstem, 54 (90%) returned to within 2 km of their original locale; 31 (52%) were recaptured within 0.5 km; and 10 (17%) were recaptured within 0.1 km. No significant differences in movement were noted between male and female humpback chub. Fish moving from the mainstem to the LCR and back to the mainstem, presumably for spawning, tended to be large individuals: 81% were >300 mm TL.

Diet

Carothers and Minckley (1981) observed adult humpback chub actively eating *Cladophora* and organic detritus, and examined digestive tract contents of three juvenile humpback chub that died accidentally, finding benthic insect larvae (chironomids, ceratopogonids, and dolichopodids) and organic detritus. They cited an earlier report (Minckley 1973) of a few specimens caught below Glen Canyon Dam that had been feeding on planktonic crustaceans.

A total of 14 aquatic invertebrate taxonomic groups and 9 terrestrial groups were found in gut contents of 158 mainstem adults treated with a stomach pump (Valdez and Ryel 1995). The most common items were simuliids (blackflies, in 77.8% of fish), chironomids (midges, 57.6%), *Gammarus* (freshwater shrimp, 50.6%), *Cladophora* (green alga, 23.4%), Hymenoptera (wasps, 20.9%), and cladocerans (water fleas, 19.6%). Seeds and human food remains were found in 8 (5.1%) and 7 (4.4%) fish respectively. There were substantial differences in volumetric composition of diets between 128 adults from near the LCR inflow (44.5% *Gammarus*, 40.3% simuliids, 9.4% terrestrial invertebrates, 5.3% chironomids), and 24 adults from Middle Granite Gorge (i.e., 97 km downstream of the LCR; 49.1% simuliids, 29.6% terrestrial invertebrates, 10.4% *Gammarus*, 6.3% other aquatic invertebrates, and 4.6% chironomids). These longitudinal differences indicate that fish at both locations relied heavily on simuliids, but that fish relied more on terrestrial invertebrates in Middle Granite Gorge, where *Gammarus* were less abundant. Seasonal differences were also evident, with *Gammarus* as the primary food item by volume in spring (40.1%), and simuliids in summer (46.4%) and fall (44.7%). Johnson's Electivity Indices (JEIs) (Johnson 1980) showed that terrestrial invertebrates (primarily ants and beetles) were consumed at a disproportionately higher level than their availability in drift, and simuliids, chironomids, and *Gammarus* were consumed at about the same proportion. Diet of humpback chub was not compared with benthic invertebrate densities, although it was acknowledged that the fish probably feed both from pelagic and benthic sources.

Reported diets of humpback chub in Grand Canyon varied among studies by Kaeding and Zimmerman (1983), Kubly (1990), Valdez and Ryel (1995). Larvae of simuliids and chironomids were present in gut contents of humpback chub in all three studies. However, working in the LCR in 1980–1981, Kaeding and Zimmerman (1983) reported that *Gammarus* composed only 1% of gut volume of fish, while Valdez and Ryel (1995), working in the mainstem near the LCR inflow in 1990–1993, reported that *Gammarus* composed approximately 44% of gut volume of chub in that area, and 64% of all guts examined. Valdez and Ryel also reported that *Cladophora* composed approximately 20% of gut volume in humpback chub, while AGFD, working in the LCR inflow 1986–1987, found *Cladophora* composed 77% of gut volume (Kubly 1990). Chironomids and adult terrestrial insects represented 10% of volume. The difference between these study findings may reflect changes in dam operation in 1991 from high fluctuating flows (high *Cladophora* drift) to low fluctuating interim flows (low *Cladophora* drift). Consumption of *Cladophora* may be related to foraging on diatoms or invertebrates associated with the algae. Leibfried (1988) found that epiphytic diatoms on *Cladophora* consumed by rainbow trout were an important source of lipids in the diet. Blinn et al. (1994) found that diatoms and macroinvertebrates associated with *Cladophora* drift packets decreased rapidly downstream due to agitation and pulverization of algae in rapids. This alga was absent from gut contents of 23 humpback chub from Middle Granite Gorge (Valdez and Ryel 1995). Low of use of *Cladophora* by humpback chub in this reach probably reflects less algae present.

The presence of terrestrial invertebrates as an important component of humpback chub diet indicates that humpback chub are opportunistic in their feeding habits, consuming resources that may be only sporadically available. High JEIs indicate that humpback chub selected terrestrial invertebrates relative to their occurrence in the drift. Blinn et al. (1994) found that terrestrial insects were not an important component of stream drift in the Colorado River through Grand Canyon. They suggested that availability may be greatly increased during and after rainstorm events. Disproportionally high use of this food source by humpback chub indicates that these fish are either very adept at foraging on these organisms in drift, or they were able to locate areas where these items are entrained and concentrated, primarily large recirculating eddies. Observations of radio-tagged adults indicated that eddies were used extensively (Valdez and Ryel 1995).

The general condition of adult humpback chub in the mainstem and the small number of fish with empty guts indicate that food was not limiting to adult humpback chub (Valdez and Ryel 1995). However, food may be limiting for subadults, since the smaller fish select shoreline habitats that may have low productivity, particularly in more downstream reaches. Because adults appear to feed primarily in large recirculating eddies and subadults use shallow shorelines, feeding strategies appear to differ. The present aquatic ecosystem in Grand Canyon may not supply adequate food to all ages. Detailed longitudinal studies of subadult feeding habits are needed for humpback chub and other native fishes in Grand Canyon.

Parasites

Two principal parasites—both alien to the Colorado River Basin—have been found on humpback chub in Grand Canyon. The external parasitic copepod *Lernaea cyprinacea* was found on 8 of 6,294 mainstem fish for an infection rate of only 0.13% and an average of 1.25 copepods (range, 1–2) per infected fish (Valdez and Ryel 1995). None of the infected fish showed signs of stress or illness, although open lesions had formed at some anchor points. In the Upper Basin, this parasite was found on 17% and 31% of juveniles and adults, respectively (range, 1–13 copepods/infected fish; Valdez et al. 1982). This parasite was first reported from Grand Canyon in 1979 (Carothers et al. 1981), but has not become problematic because the cold mainstem temperatures fail to reach maturation requirements of 25°C (Valdez and Ryel 1995).

The other principal parasite is the internal Asian tapeworm (*Bothriocephalus acheilognathi*), which was first reported from Grand Canyon in 1990 (Clarkson et al. 1997, Brouder and Hoffnagle 1996). This parasite was found in gut contents of 6 of 168 (3.6%) mainstem adult humpback chub treated with a stomach pump, for an average of 6.7 tapeworms per infected fish (range, 1–28; Valdez and Ryel 1995). Clarkson et al. (1997) found Asian tapeworms in 28% of sacrificed humpback chub examined from the LCR in 1990–1994. They also reported the parasite in speckled dace, common carp, fathead minnows, and plains killifish. Brouder and Hoffnagle (1996) also found Asian tapeworms in humpback chub (22.5%) from the LCR in 1994, as well as plains killifish (10.3%), speckled dace (3.8%), and fathead minnows (2.2%). They reported that nearly all (66.7–100%) of infected fish were captured near the LCR, although the parasite was found as far downstream as Kanab Creek, 132 km downstream of the LCR. Infection of humpback chub by the Asian tapeworm is a concern because of possible stress and death to the host and widespread infestation during periods of stress. This parasite is only able to complete its life cycle in the LCR where the temperature requirement of >20°C is met, but it is apparently able to survive in a fish host in cold mainstem temperatures.

FLANNELMOUTH SUCKER

Distribution and Abundance

Flannelmouth suckers are indigenous to the Colorado River Basin and found in most mainstem regions and large tributaries (Tyus et al. 1982). In Glen and Grand Canyons, they are found from Glen Canyon Dam to the Lake Mead Inflow at Grand Wash Cliffs (RM 276.0; Maddux et al. 1987, Valdez and Ryel 1995, Valdez et al. 1995). Flannelmouth suckers have also been reported from most tributaries, including the Paria River (S.J. Weiss 1993), the LCR (Gorman 1994, Douglas and Marsh 1996a), Bright Angel Creek (Maddux et al. 1987, Otis 1994), Kanab Creek (Maddux et al. 1987, Otis 1994), Shinumo Creek (Allan 1993), and Havasu Creek (Maddux et al. 1987). Tributaries and confluence areas have generally had higher densities of flannelmouth suckers than the mainstream (Maddux et al. 1987, Valdez and Ryel 1995). The canyon-wide distribution of this species does not appear to have changed since completion of Glen Canyon Dam (McDonald and Dotson 1960), although Valdez and Ryel (1995) found declining abundance downstream of the LCR.

Reproduction

Length-frequency analyses of 2,775 flannelmouth suckers from the mainstem in 1990–1993 indicate poor reproductive success and recruitment (Valdez and Ryel 1995). Subadults represented only 21% of total numbers captured (578 of 2,775). Although spawning apparently was occurring at least in the Paria River (S.J. Weiss 1993, AGFD 1996); LCR (Gorman 1994); Shinumo Creek (Otis 1994); Bright Angel Creek (Otis 1994); Kanab Creek (Maddux et al. 1987, AGFD 1996); and Havasu Creek (AGFD 1996), egg or larval survival appeared to be poor.

Studies in the Upper Basin show that flannelmouth suckers were the second most common fish in larval drift with 23–37% of numeric composition (Valdez et al. 1985). Drift occurred primarily at night and fish were typically in the mesolarval stage at 12–18 mm long (Snyder and Muth 1990). S.J. Weiss (1993) reported only five post-larval flannelmouth suckers (22–37 mm TL) in the lower Paria River in spring 1992 and three YOY (42–45 mm TL) at the mouth of the river in June. Thieme (1998) captured 82 YOY (21–36 mm TL) in the Paria River in May 1996, and 576 YOY from May through September 1996; eight of the YOY captured in September were 72–111 mm TL. Robinson et al. (1996) found few larval flannelmouth suckers in the LCR in May through July. These results indicate that either egg survival is low or young are drifting as mesolarvae, undetected by researchers, and probably succumbing to thermal shock in the cold mainstem. Some researchers have suggested that high mainstem flows can be used to pond tributary inflows and provide thermal gradient and habitat refugia for young native fishes descending or drifting into the mainstem (Clarkson et al. 1994, Thieme 1998, C. McIvor, U of A, pers. comm.).

Temperature range for spawning of flannelmouth suckers is 17.0–23 °C (Lechleitner 1992). In the Paria River (S.J. Weiss 1993), adults ascended from the mainstem in late February to early April of 1992 and 1993. Spawning occurred March to early April in shallow, highly turbid water <25 cm deep, over clean gravel (mean size 16–23 mm), and at moderate velocities of 0.3–0.6 m/s. Water temperatures were variable over a 24-hr period. Ripe females were not found in the Paria River until minimum stream temperatures reached 6.0°C, and peak spawning occurred on days when temperatures reached a minimum of 7.0°C and a maximum of 19.0°C. Spawning adults remained within the lower 10 km of stream.

Large numbers of adults (>100) were reported congregated at the mouths of the Paria River, LCR, Kanab Creek, and Havasu Creek each spring, 1990–1993 (Valdez and Ryel 1995, Gorman 1994, Robinson et al. 1996), indicating that at least these tributaries had substantial spawning runs of flannelmouth suckers. Large numbers of adults were observed spawning in Kanab Creek in April 1992 (R. VanHaverbeke, ASU, pers. comm.). Flannelmouth suckers may also be spawning in the mainstem in western Grand Canyon. During 1991–1994, AGFD (1996) reported finding over 3,400 flannelmouth suckers ≤100 mm in length, primarily in April through August and almost exclusively in mainstem backwaters. Highest CPUE (catch per unit effort) tended to occur just downstream of perennial tributaries, notably the LCR, Shinumo Creek, and Havasu Creek, and in the reach of river from RM 180 to RM 205. Post-larval flannelmouth suckers were found just upstream of the Spencer Creek inflow (RM 246.0), as well as in Spencer Creek and in Surprise Creek (RM 248.4; Valdez et al. 1995, Leibfried and Zimmerman 1995).

Fecundity of flannelmouth suckers is highly variable, from 4,000 eggs from a fish 450 mm TL, to

40,000 eggs from a fish 500 mm TL. Water-hardened eggs are demersal, initially adhesive, and 3.8–3.9 mm diameter (Snyder and Muth 1990). Newly hatched larvae are 10–11 mm TL.

Spawning flannelmouth suckers have recently been found at two locations in the Glen Canyon Dam tailwaters, RM -4 (i.e., 4 miles downstream of Glen Canyon Dam) and RM -12 (i.e.,12 miles downstream of Glen Canyon Dam) (Thieme 1997, T. McKinney, AGFD, pers. comm.). These fish appear to be depositing viable eggs in large mainstem cobble bars, but it appears that temperatures are too cold for survival of eggs and larvae.

Age and Growth

Sexual maturity of flannelmouth suckers occurs between 4 and 8 years of age, and maximum age appears to be at least 20 years (McAda and Wydoski 1985); however, age and growth analyses have not been done on flannelmouth suckers.

Length-Weight/Condition Factor

The length-weight relationship for 1,903 flannelmouth suckers from the mainstem during 1990–1993 (Valdez and Ryel 1995) was $\log W = -5.222 + 3.076 \log TL$ (R^2=0.98). The exponent of 3.076 indicates approximate isometric growth. Condition factor ranged from about 0.92 to 1.28. Size range was 27–682 mm TL and maximum weight was about 2,750 g.

Survival

No survival estimates were available for flannelmouth suckers, but length-frequency analyses indicate low survival of young and low recruitment in Grand Canyon (Valdez and Ryel 1995). Of 2,775 specimens captured, only 578 (21%) were subadults (183 YOY, 395 juveniles).

Habitat

Flannelmouth suckers are typically big river fish that inhabit shallow sheltered shorelines as YOY and juveniles, and the lower end of large, mid-channel cobble riffles as subadults and adults (Valdez et al. 1982, Tyus et al. 1982). In the Colorado River in Grand Canyon, YOY and juveniles were found along sheltered shorelines (Maddux et al. 1987) and in backwaters (Maddux et al. 1987, AGFD 1996). Subadults (21–198 mm TL) were found in backwaters and quiet shoreline habitats, with concentrations in the inflows of the LCR, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek (Valdez and Ryel 1995). Young-of-year in the LCR (<130 mm TL) were found in shallow protected shorelines (Gorman 1994). The "overwhelming majority" of YOY flannelmouth suckers from the Paria River were found in a slack water pool about 100 m long, created by steady high flows of 20,000 cfs (C. McIvor, U of A, pers. comm.), indicating that the recently hatched fish descended to low-velocity habitats.

Adults in the mainstem were found in a variety of habitats, including tributary inflows, large recirculating eddies, vegetated shorelines, and in association with large mid-channel cobble bars (Valdez and Ryel 1995). Minckley (1991) described adult flannelmouth suckers as lying in quiet tributary mouths, especially in the Paria River, leaving these inflows in winter when water temperature equilibrated with that of the mainstem. Post-spawning adults remained in flat water or eddies and margins of strong currents, generally in water ≥ 1 m deep. S.J. Weiss (1993) noted that small numbers of flannelmouth suckers remained in the mouth of the Paria River year-round, but were present more consistently at night. In the LCR, adult flannelmouth suckers had an affinity for areas with greater vertical cover and vertical structure during the day and areas with less cover and vertical structure at night (Gorman 1994). S.J. Weiss (1993) found that flannelmouth suckers appeared to shift behavior after dark, using confluence areas periodically in daylight, but consistently at night. Flannelmouth suckers were more likely to be found in shallow slack water, and over fine substrates at night than during the day.

Movement

Adult flannelmouth suckers have been documented to move great distances in the Upper Basin (Chart and Bergerson 1992), as well as in Grand Canyon (S.J. Weiss 1993). Mark-recapture data indicate long-distance movements in relatively short time, usually associated with spawning. Inflated catches of adults at tributary inflows in Grand Canyon in spring (April–May) indicate seasonal spawning congregations. Most adults have been recaptured within 20 km of their original capture location during non-spawning seasons (Carothers and Minckley 1981), but extensive movement is noted during spawning season (Maddux et al. 1987, S.J. Weiss 1993). Of 1,071 adults marked and released in the mainstem, 94% (190 of 202) were recaptured less than 16 km from their original capture locations after periods of up to 790 days (Valdez and Ryel 1995). Some long-distance movements were associated with one or more tributary inflows, e.g., two adults captured near the LCR inflow (RM 61.3) were recaptured near the Havasu Creek inflow (RM 156.6), and one adult was captured near Havasu Creek and recaptured near the LCR. Possibly some fish spawn in one tributary and reside near another, or they alternate spawning tributaries by year. The greatest movement recorded for a flannelmouth sucker in Grand Canyon occurred July 26 to October 13, 1993, but apparently was not related to spawning; the fish moved 247 km upstream from RM 214.0 (near Pumpkin Spring) to RM 60.5 (near LCR inflow) over 79 days. Average downstream movement of 14 PIT-tagged flannelmouth suckers between National Canyon and Pearce Ferry was 46.7 km (range, 35.3–103 km; Leibfried and Zimmerman 1996). The longest upstream movement was from RM 248.0 to RM 225.0. Four fish moved downstream from their original capture locations at Kanab Creek (RM 143.5), and two fish moved from Kanab Creek to the Granite Park area, a distance of 105 km.

S.J. Weiss (1993) also documented substantial movement by adults, although he noted that some flannelmouth suckers remained in the area of the Paria River inflow all year and others moved to and from the area, some from considerable distances. Of 27 fish recaptured in the Paria River, 15 were originally tagged in the LCR (96 km downstream) and one originated in Kanab Creek (228 km downstream). One fish that had been caught several times in the LCR (up to 6 km above the mouth) was recaptured in the Paria River 10 km up from the mouth. Seven fish tagged in the Paria River were recovered by other researchers in or near the LCR, and one fish was recaptured in the LCR 21 days after tagging, while spawning 5 km up the Paria River.

The spawning run in the Paria River appears to be composed of primarily mainstem residents from the Glen Canyon reach, and others from downstream locations, including the LCR (S.J. Weiss 1993). Possibly, flannelmouth suckers disperse from the LCR because of limited, saturated spawning habitat, or they return to their natal stream to reproduce. These long-distance upstream movements may be in response to a downstream gradient in declining biological productivity, based on the presence and abundance of *Cladophora* beds and associated benthic organisms. The presence of large flannelmouth suckers in the vicinity of the Paria River may be a recent phenomenon. Large adults were absent from the 1981 catch data (Bascom 1981, cited in S.J. Weiss 1993); no fish were caught over 510 mm TL and were scarce in the catch records of the 1960s (Stone 1966, 1967; Stone and Queenan 1967).

Diet

Flannelmouth suckers are omnivorous and eat a variety of plant and animal matter in drift, mud sediments, and rock substrates. Their diet has been described as unidentified amorphous material, probably derived from the ooze and algae of muddy bottoms in pools and backwaters (Woodbury 1959), and as omnivorous: feeding heavily on midges, blackflies, scuds, other aquatic and terrestrial invertebrates, organic detritus, seeds of grasses and composites, diatoms, and *Cladophora* (Carothers and Minckley 1981). Seasonal variation in diet was noted, as relative proportions of specific items changed, but gut contents between the mainstem and tributaries were generally similar, with less algae consumed in the latter. S.J. Weiss (1993) observed flannelmouth suckers feeding on sediments in slack water in daylight hours in the Paria River confluence. Epiphytic diatoms were a major component of gut contents of flannelmouth suckers in Grand Canyon (Carothers and Minckley 1981) and the Upper Basin (Carlson et al. 1979, cited in S.J. Weiss 1993). Chironomid larvae and zooplankton, primarily copepods and cladocerans, were consumed by young flannelmouth suckers in Grand Canyon (Maddux et al. 1987), while adults in the LCR fed on aquatic invertebrates (primarily dipterans), organic debris, and sand (an apparent by-product of benthic feeding; Douglas and Marsh 1996a).

Parasites

The parasitic copepod *Lernaea cyprinacea* is common on flannelmouth suckers in the Upper Basin (Flag 1981). It is found on low numbers of flannelmouth suckers in Grand Canyon (R. Valdez, SWCA, pers. observ.). The Asian tapeworm has not been found in flannelmouth suckers.

The fungus *Saprolegnia* spp. was found on small numbers of flannelmouth suckers (Valdez and Ryel 1995). This is a facultative pathogen that attacks necrotic and injured tissue, including abrasions from net capture or wounds from handling and tagging fish. It can also infect apparently uninjured skin. It was not observed on net scars, but was reported from the tail region of adults with abrasions apparently inflicted during spawning.

BLUEHEAD SUCKER

Distribution and Abundance

Bluehead suckers are found throughout the Colorado River Basin in mainstem habitats and large and small tributaries. They are often sympatric with flannelmouth suckers, but occur more abundantly at higher elevations in cooler and clearer waters (Tyus et al. 1982). In Grand Canyon, bluehead suckers have been reported in small numbers throughout the mainstem and more abundant in large and small tributaries and tributary inflows (McDonald and Dotson 1960, Carothers and Minckley 1981, Maddux et al. 1987, Valdez and Ryel 1995). Their distribution appears to have remained the same since the 1970s, but relative abundance may be decreasing. Carothers and Minckley (1981) found bluehead suckers in spring and summer in the Paria River, Buck Farm Creek, LCR, Unkar Creek, Bright Angel Creek, Pipe Creek, Crystal Creek, Elves Chasm Creek, Kanab Creek, and Havasu Creek. In the 1980s, Maddux et al. (1987) found bluehead suckers throughout Grand Canyon, but mostly concentrated in and near tributaries. In 1990–1993, Valdez and Ryel (1995) found bluehead suckers "in smaller numbers and more infrequently than flannelmouth suckers" (1,040 bluehead suckers, 2,775 flannelmouth suckers), with mainstem catch rates "sporadically high at or near major tributary inflows." Like flannelmouth suckers, bluehead suckers were found in decreasing abundance downstream of Lees Ferry. Only 56 bluehead suckers were found between Diamond Creek and Pearce Ferry from June 1992 to January 1995, with no indication of mainstem spawning (Valdez et al. 1995). In 1995, 30 bluehead suckers were found between National Canyon and Pearce Ferry, including ripe and gravid adults with expressible eggs and milt (Leibfried and Zimmerman 1995). Resident populations of bluehead suckers were found in Shinumo Creek and Havasu Creek (Allan 1993), Kanab Creek and Bright Angel Creek (Otis 1994), and the LCR (Gorman 1994, Douglas and Marsh 1996a). Bluehead suckers were rare in the Paria River (S.J. Weiss 1993).

Reproduction

Bluehead suckers in Grand Canyon have been observed spawning in tributaries from mid-March to June, including Shinumo Creek (Carothers and Minckley 1981, Allan 1993), Kanab Creek (Maddux and Kepner 1988, Otis 1994), and the LCR (Douglas and Marsh 1996a, Gorman 1994). Maddux and Kepner (1988) found that spawning adults in Kanab Creek had an affinity for areas with greater cover and vertical structure during the day and areas with less cover and structure at night. Spawning occurred at 18.2–24.6°C over small diameter gravel in 9–29 cm depth and 0.34–0.35 m/sec velocity. Eggs were slightly adhesive (2.4–3.1 mm diameter) and deposited in small depressions, 10–23 cm wide and 21–37 cm long. Each female in the spawning area was accompanied by one to eight males, but only one or two fertilized the eggs. Minckley (1991) described bluehead suckers as spawning over mixed gravel-sand or gravel-cobble in streams with depths from a few centimeters to more than 1 m, and temperatures of 16.0–20.0°C.

Spawning by bluehead suckers has been reported from various studies at temperatures of 17.0–23°C (Lechleitner 1992). Average fecundity of females 380–400 mm TL was 20,227 eggs/female, with one fish 320 mm TL having only 14,720 eggs (Smith 1996). Water-hardened eggs were demersal, initially adhesive, and 3.3–3.5 mm in diameter (Snyder and Muth 1990). Newly hatched larvae were 9–11 mm TL.

Age and Growth

Age and growth analyses have not been done on bluehead suckers.

Length-Weight/Condition Factor

The length-weight relationship for 693 bluehead suckers from the mainstem during 1990–1993 (Valdez and Ryel 1995) was $\log W = -5.222 + 3.090 \log TL$ (R^2=0.97). The exponent of 3.090 indicates approximate isometric growth. Condition factor ranged from about 0.82 to 1.16. Size range was 28–432 mm TL and maximum weight was about 986 g.

Survival

No survival estimates were available for bluehead suckers, but length-frequency analyses indicate low survival of young and low recruitment (Valdez and Ryel 1995). Of 1,040 specimens captured, only 351 (34%) were subadults (101 YOY, 250 juveniles).

Habitat

Bluehead suckers occupy a wide variety of fluvial habitats, ranging from cold, clear trout streams (<20.0°C) to warm, turbid rivers (Lee et al. 1980). In the Colorado River, bluehead suckers are typically mainstem and tributary fish that inhabit riffles (Valdez et al. 1982, Tyus et al. 1982). In Grand Canyon, YOY and juveniles were found in small pools of tributaries and along sheltered mainstem shorelines and in backwaters (Maddux et al. 1987, AGFD 1996). Subadults and adults were found in high gradient, swift tributaries with rocky substrates and in large cobble mainstem riffles (Carothers and Minckley 1981).

Minckley (1991) described bluehead suckers as bottom dwellers that remain in deep pools and eddies in clear water or daytime, and move to shallow riffles to feed at night or in turbid water. Young bluehead suckers were most common in small riffles and along shoreline cobble flats.

Robinson et al. (1996) found larval bluehead suckers drifting primarily at night in the LCR and using shallow shorelines in the day. Bluehead suckers in the LCR changed habitat with size and age, using increasingly higher flow velocities, larger substrates, and habitats farther from shore. Adult bluehead suckers are very adept at maintaining position in swift flows, and have been observed slowly ascending steep waterfalls in Shinumo Creek (R. Valdez, SWCA, pers. observ.).

Movement

Bluehead suckers tend to move less distance than flannelmouth suckers. They typically move only locally from deep pools to cobble riffles to feed at night (Minckley 1991). Greatest movement occurs during spawning when adults ascend nearby tributaries or move short distances within tributaries. In Grand Canyon, bluehead suckers are spring spawners, moving to fast waters in tributaries in April-May to reproduce (Carothers and Minckley 1981). Small pre-spawning congregations of bluehead suckers, usually mixed in large congregations of flannelmouth suckers, have been reported at the mouths of the LCR, Havasu Creek, Kanab Creek, and Shinumo Creek (Maddux et al. 1987, Valdez and Ryel 1995). In the LCR, breeding movements in spring were thought to be restricted to short distances, although a consistent (but statistically nonsignificant) increase in numbers was documented in fall, suggesting increased intra-tributary movement during this season by otherwise sedentary residents (Douglas and Marsh 1996a).

Of 394 adult bluehead suckers marked and released in the mainstem, only 12 were recaptured, including 9 that remained near Havasu Creek, 2 that remained near the LCR, and 2 that moved more than 0.2 km from their original capture location (Valdez and Ryel 1995). The greatest movement was by a fish that moved 47.8 km from Havasu Creek downstream to a site near Whitmore Wash.

Diet

Bluehead suckers develop a hardened cartilaginous radula on the inside of the lower jaw at an early age (Minckley 1973). This radula enables individuals to scrape films of diatoms, algae, and insects from rocks in swift currents (Lee at al. 1980, Minckley 1991). Douglas and Marsh (1996a) described the bluehead sucker as mostly herbivorous, with a mouth adapted for adhering firmly to rocks in torrential streams, and for scraping algae, diatoms and a variety of sessile invertebrates from rock surfaces. Food items of 256 bluehead suckers examined from Grand Canyon included primarily immature dipterans (chironomids and simuliids) and amphipods in the mainstem, and dipterans in tributaries (Carothers and Minckley 1981). Diatoms and organic debris were abundant. Maddux et al. (1987) found that young bluehead suckers consumed chironomid larvae and other immature insects.

Parasites

The parasitic copepod *Lernaea cyprinacea* is common on bluehead suckers in the Upper Basin (Flagg 1981). It is found on low numbers of bluehead suckers in Grand Canyon (R. Valdez, SWCA, pers. observ.). The Asian tapeworm has not been found in bluehead suckers. The fungus *Saprolegnia* spp. was found on small numbers of bluehead suckers (Valdez and Ryel 1995).

RAZORBACK SUCKER

Distribution and Abundance

The razorback sucker is a large river catostomid indigenous to the Colorado River Basin (Ellis 1914, Minckley 1973, Bestgen 1990). Razorback suckers typically inhabit gentle alluvial regions and are uncommon inhabitants of deep, turbulent canyons. Douglas and Marsh (1996a) suggest that razorback suckers were never abundant in Grand Canyon, noting that remains were not found at Stanton's Cave, where non-fossilized bones of five other native species were discovered. They suggest that razorback suckers were not residents of Grand Canyon, but transients, moving between more desirable habitats upstream and downstream.

Only 10 documented razorback suckers have been captured in Grand Canyon (Valdez 1996): one adult caught by an angler in Bright Angel Creek in 1944 (Minckley and Carothers 1979); one captured by AGFD at the mouth of the Paria River just after closure of Glen Canyon Dam in 1963 (Minckley and Carothers 1979); three adults, including a gravid female, from the mouth of the Paria River in June 1978 (Minckley and Carothers 1979); one adult from near Lower Bass Camp (RM 108.0) in April 1984 (Maddux et al. 1987); one female (555 mm TL, 1,860 gm) from the LCR inflow in May 1989 (C.O. Minckley, FWS, pers. comm.); and three adults from the LCR inflow in April 1990, including two males (475 mm TL, 1,211 g; 476 mm TL, 1,219 g) and one female (588 mm TL, 2,035 g) (W. Persons, AGFD, pers. comm.). All of the razorback suckers captured in Grand Canyon were adults, indicating that either this region is not a spawning/rearing area or that reproduction and recruitment are unsuccessful. Valdez (1996) estimated that there are fewer than 100 razorback suckers left in Grand Canyon.

Reproduction

There is no evidence of historic or recent reproduction by razorback suckers in Grand Canyon. Prior to Glen Canyon Dam, in July 1958, two "humpback suckers" (common name used for this fish before the 1970s), each "about 1½" long," were caught in Glen Canyon (McDonald and Dotson 1960), indicating historic reproduction sites or nursery areas upstream of present-day Glen Canyon Dam.

Razorback suckers in the Upper Basin spawn in the Green River in May–June at temperatures of 6–19 °C in velocities <1.0 m/s and depths of <1.0 m, near the upstream end of large gravel-cobble riffles (McAda and Wydoski 1980, Tyus and Karp 1990, Snyder and Muth 1990). Spawning in Lake Mohave (human-made reservoir) occurs in November–March at temperatures of 10–21 °C over coarse gravel bars that are swept free of silt by currents or wave action (Minckley 1991, Schrader 1991, Burke and Mueller 1993). Males congregate over coarse, wave-washed cobble in water 0.5–5 m deep. Several hundred fish may congregate within about 1 m of the bottom, then break into smaller groups and swim along shorelines, each female followed by two or more males. Spawning takes place in small depressions (20 cm deep) in water less than 0.6 m deep. Razorback suckers held at Dexter National Fish Hatchery have successfully spawned in small earthen holding ponds over vegetation (R. Hamman, FWS, pers. comm.).

Natural spawning sites in the Upper Basin are in broad alluvial, flat-water regions with large cobble riffles and large riverside bottomlands as nursery areas immediately downstream (Bestgen 1990; Tyus and Karp 1989, 1990). Adults congregate in deep pools and runs near large cobble bars and spawn in April–May with rising water levels and increasing temperatures. Water temperatures recorded in the upper Green River during spawning were 8.9–17.2°C. Newly hatched larvae drift into highly productive flooded bottomlands, where they remain until the river recedes. The association of spawning during the ascending limb of the spring hydrograph and subsequent transport of newly hatched larvae into flooded bottomlands appears to be a critical relationship to the survival of this species that has been disrupted with regulation of high spring flows.

Razorback suckers may not spawn every year. High reproductive potential and great longevity (e.g., maximum age of 44 years, McCarthy and Minckley 1987) have evolved as strategies for coping with the highly variable Colorado River. Average fecundity of razorback suckers (N=10) was 46,740 eggs/fish (27,614–76,576), or about 39,600 eggs/kg (McAda and Wydoski 1980). Eggs incubated in a hatchery at 14.4–17.2°C had a 95% hatching success, while those incubated at 11.7°C had high mortality (Toney 1974). Water-hardened eggs are 2.5–2.8 mm diameter, and eggs incubated at 18–20 °C hatch in 6–7 days, swim up in 12–13 days, and swim down in 27 days; eggs incubated at 15 °C hatch in 11 days, swim up in 17–21 days, and swim down in 38 days (Snyder and Muth 1990). Newly hatched larvae are 7–10 mm TL.

Several investigators have reported hybrids between razorback suckers and flannelmouth suckers in Grand Canyon (Suttkus et al 1976, Maddux et al. 1987, Valdez and Ryel 1995). These fish have a poorly developed dorsal keel and intermediate morphologic and meristic characteristics, including scale size and lateral line counts, dorsal fin ray counts, size and shape of the head and mouth, and coloration (Hubbs and Miller 1953). Although hybridization between these species has been reported for many years (Hubbs and Miller 1953, McAda and Wydoski 1980), the incidence in Grand Canyon appears high relative to the number of razorback suckers, especially in the LCR where these fish concentrate during spawning. Mainstem collections during 1990–1993 included 2,197 adult flannelmouth suckers, 5 adult hybrids, and no razorback suckers (Valdez and Ryel 1995), while collections in the LCR in 1991–1995 included 25 hybrids (Douglas and Marsh 1996a). Of 12 morphologic hybrids from the LCR in 1994, 7 possessed DNA characteristic of razorback suckers and flannelmouth suckers (indicating true genetic hybridization), while 5 had DNA of primarily flannelmouth sucker, indicating introgressive hybridization (T. Dowling, ASU, pers. comm.).

Age and Growth

Minimum and maximum ages of wild razorback suckers from Lake Mohave (N=70), using growth rings from otoliths, were 24 and 44 years, respectively (McCarthy and Minckley 1987). Growth of razorback suckers is variable, depending on environmental conditions. Razorback suckers reared in hatchery aquaria were 150 mm TL in their first year of life (Valdez et al. 1982; E. Wick, NPS, pers. comm.), but fish reared in outdoor ponds near Vernal, Utah, grew to 127–156 mm TL in 4 months (Bestgen 1990; H. Tyus, FWS, pers. comm.), and fish reared in riverside ponds near Grand Junction, Colorado, grew from an average of 54.8 mm TL to 307 mm TL in 6 months (Osmundson and Kaeding 1989). Scale analyses of razorback suckers from Lake Mohave indicated a growth rate of 70 mm/year for the first 6 years of life (Minckley 1983). Mark-recapture data from wild adults indicate slowed growth with age; Tyus (1987) found average growth of 2.2 mm/year in 39 razorback suckers with 1–8 years between captures.

Length-Weight/Condition Factor

Neither length-weight relationships nor condition factors have been reported for razorback suckers.

Survival

The numbers of this species are extremely low, and no reproduction or recruitment is apparent in the region. Survival of newly hatched larvae appears to be the limiting factor for razorback suckers in the Colorado River Basin (Tyus 1987). Absence of flooding that historically created flooded bottomlands in the Green, Yampa, and Colorado Rivers has limited nursery areas for newly hatched larvae, and the few larvae that are able to find productive, sheltered habitats are often consumed by predators (Bestgen 1990, Tyus and Karp 1990). In Lake Mohave, spawning takes place over coarse gravel bars, but there is little survival of young beyond about 20 mm TL because of predation (Marsh and Langhorst 1988).

Habitat

Razorback suckers use different habitats with season and age (Valdez et al. 1987, Bestgen 1990, Tyus and Karp 1990). Larval razorback suckers, about 2 weeks old, actively enter river drift at night (Paulin et al. 1989), and are transported downstream into large productive flooded bottomlands, where they remain until receding flows carry them back into the main river. Flooded bottomlands have been identified as critical to the survival and growth of these young fish (Tyus 1987). Habitat of juveniles has not been well documented because of small numbers of individuals captured in the wild. Juveniles (59–124 mm TL) have been captured in backwaters, tributary mouths, and flooded bottomlands (Taba et al. 1965, Smith 1959). Adults overwintered in deep runs and pools (0.6–1.4 m deep, 0.03–0.33 m/s) in alluvial and canyon regions of the Green River (Valdez and Masslich 1989), but often move into riverside gravel pits (Valdez et al. 1982) and large flooded bottomlands during spring runoff for feeding and shelter from high mainstem flows (Tyus and Karp 1990). Adults in spring used deep, nearshore runs (0.6–3.4 m deep, 0.3–0.4 m/s), moved to large cobble islands (0.63 m deep, 0.74 m/s) for spawning, and shifted to shallow, slack water near mid-channel sandbars in summer (<2 m deep, 0.5 m/s) (Tyus 1987).

Temperature is an important aspect of habitat for razorback suckers. Thermal preference for adults was 22.9–24.8°C, based on electronic shuttle box studies, and lower avoidance temperature was 8.0–14.7°C and upper avoidance temperature was 27.4–31.6°C (Bulkley and Pimentel 1983). It was concluded from this study that alterations in year-round water temperature outside the range of 12.0–29.0°C should not be allowed if preservation of habitat for razorback suckers is a consideration.

Movement

Razorback suckers can migrate extensively to and from spawning sites in spring, but tend to move very little at other times of the year. Historic reports of large aggregations of adults can probably be attributed to spawning runs and aggregations (Jordan 1891, McAda and Wydoski 1980). As recently as the early 1980s, large numbers of adults were seen congregated at tributary mouths on the Green River (Tyus et al. 1982) and in gravel pits and large flooded bottomlands in the Colorado River (Valdez et al. 1982). Except for spawning migrations, razorback suckers are relatively sedentary, moving only a few kilometers over several months (Tyus 1987, Tyus and Karp 1990). In the Upper Basin, one female adult moved about 21 km from the Green River into the Yampa River for spawning (McAda and Wydoski 1980). Adults that spawned at the southern boundary of Dinosaur National Monument on the Green River overwintered 2 consecutive years in Whirlpool Canyon and Split Mountain Canyon, making round trips of 80 and 38 km, respectively (Valdez and Masslich 1989; H. Tyus, FWS, pers. comm.). Winter movement of 17 radiotagged adults in the Green River was less than 4.8 km (Valdez and Masslich 1989), while annual movement of adults in Lake Mohave was 0.8–1.6 km (Marsh and Minckley 1989).

Diet

Food of larval razorback suckers in fertilized ponds included diatoms, detritus, algae, small rotifers, chironomids, and cladocerans (Papoulias and Minckley 1992). Larvae appeared to select the largest organisms they could consume that were also most abundant, changing diet with size and age. Larvae initially ate sessile diatoms, phytoplankton, and detritus, but by the end of one week, they increasingly ate rotifers, nauplii, cladocerans, eggs, and chironomid larvae. Chironomids and rotifers dominated volumetrically during the second week, and cladocerans became increasingly important by the third week of life. By the fourth week, eggs dominated larval diets in fertilized ponds and cladocerans were eaten even more in unfertilized ponds. Thereafter, cladocerans and chironomids, supplemented by nauplii and ostracods, accounted for most of the diet. This sequence of selected food items corresponds with the phylogeny of zooplankton communities in newly inundated bottomlands (i.e., rotifers → copepods → cladocerans), and the timing of this production with hatching of larvae appears critical to the survival of this species.

Juvenile and adult razorback suckers fed on algae and dipteran larvae in the Lower Colorado River and planktonic crustaceans in Lake Mohave (Minckley 1991). Both adults and larvae ate zooplankton in reservoirs; truly planktonic forms such as *Bosmina* sp. and *Daphnia* sp. were probably consumed from the sediment-water interface where they accumulated after death. Observers of feeding razorback suckers have noted "bouncing" movements by fish near the bottom, actively taking large volumes of sediment into their mouth, manipulating the sediment, and passing it through the opercula while presumably retaining foodstuffs (Minckley 1973). Razorback suckers have been observed to burrow headfirst to depths of 10.0 cm or more (to eye level) and perform this activity for several minutes either at a particular place or with forward movement over distances approaching 1 m.

Marsh (1987) examined digestive tracts of 34 preserved adult razorback suckers from Lake Mohave and found that the combination of planktonic crustaceans, rotifers, diatoms, detritus, and filamentous algae occurred in 44% of digestive tracts. *Bosmina* sp. occurred in all tracts and was the most abundant item. Other cladoceran genera occurred, but only *Daphnia* sp. was common (72% of fish). Rotifers, benthic ostracods, copepods, and chironomid dipteran larvae were found in 53%, 53%, 34%, and 3% of digestive tracts, respectively, but numbers were low, except for rotifers. Diatoms, primarily *Fragillaria crotenensis*, were found in nearly 90% of tracts and filamentous green algae was in 44% of all fish. Detritus and amorphous organic matter occurred in 56% of tracts, and inorganic matter occurred in 16% of tracts.

Parasites

The parasitic copepod *Lernaea cyprinacea* is common on razorback suckers in the Upper Colorado River Basin (Flag 1981). The Asian tapeworm has not been found in razorback suckers. A common pathogen of razorback suckers is the protozoan parasite *Myxobolus* (Flag 1981), which can invade the eye tissue and eventually render the fish blind. This parasite has not been noted in the Grand Canyon.

SPECKLED DACE

Distribution and Abundance

Speckled dace are one of the most widespread fish species in western North America. They occur in small cold streams, large turbid rivers, ponds, lakes, and reservoirs. Speckled dace are distributed throughout the Colorado River Basin from high-elevation streams and lakes to the large, turbid mainstem. They have adapted well to perturbations throughout the basin and appear to have survived where other native species have declined or perished, although no studies of speckled dace have been conducted on the status and trends of populations in the basin.

Speckled dace were not reported in many early accounts of the fishes of the Colorado River in Grand Canyon, probably because they were considered small "minnows" and of little consequence to sport fishing. McDonald and Dotson (1960) reported speckled dace as the most common shoreline inhabitant in 1958–1959. Carothers and Minckley (1981) reported speckled dace from all tributaries examined and from the mainstem, with sporadic variation in seasonal distribution. Minckley (1991) described speckled dace as locally common in the mainstem, especially in tributary mouths and along sandbars. Valdez and Ryel (1995) found speckled dace decreasing in abundance downstream of Glen Canyon Dam, and concentrated in tributary inflows and occasional thermal springs. Below Diamond Creek, speckled dace were low in numbers and declined precipitously at Bridge Canyon (RM 235.0), which marked the upper end of the Lake Mead inflow sediment deposits and where red shiners became very abundant (Valdez et al. 1995). The decline in speckled dace in the Lake Mead inflow appeared to be caused by a combination of habitat alterations from sediment deposits and large numbers of non-native fish species from Lake Mead.

Reproduction

Speckled dace successfully reproduce in the Colorado River in Grand Canyon, as evidenced by large numbers of young along shorelines and in backwaters, tributary inflows, and tributaries. It is not known if speckled dace spawn in the mainstem, or if their spawning activity is restricted to seasonally warmed tributaries and warm springs, as are the other native warm-water fishes. Minckley (1991) differentiated two forms of speckled dace: a mainstem form that moves in and out of tributary mouths and a distinctive tributary form that occurs upstream of barriers (e.g., waterfalls) that ecologically separate the tributary from the mainstem. Speckled dace have been found spawning in tributaries of Grand Canyon at temperatures of 17.0–23.0°C (Carothers and Minckley 1981, Lechleitner 1992), and larvae have been reported from the LCR (Robinson et al. 1996, Gorman 1994).

Age and Growth

No age-growth information is available for speckled dace in Grand Canyon, where it appears that they grow to adulthood in less than 1 year and live 2–3 years (Minckley 1991). Size range of 1,491 speckled dace captured in 1990–1993 in the mainstem was 17–86 mm TL (Valdez and Ryel 1995). Young at hatching are 5–6 mm TL, 5.0–7.0 mm TL as protolarvae, 6.7–11.2 mm TL as mesolarvae, 10.5–19.6 mm TL as metalarvae, and 17.6-50.4 mm TL as juveniles (Snyder 1981).

Length-Weight/Condition Factor

Length-weight information is not available for speckled dace in Grand Canyon.

Survival

Survival information is not available for speckled dace in Grand Canyon.

Habitat

Speckled dace in the mainstem Colorado River in Grand Canyon inhabit a variety of habitats, but have been found primarily in shallow cobble and gravel riffles and runs, especially at tributary inflows (Carothers and Minckley 1981, Maddux et al. 1987, Angradi et al. 1992, Valdez et al. 1992, Valdez and Ryel 1995), as well as in backwaters, along debris fans, and vegetated shorelines. Individuals of all sizes are usually found in water <0.5 m deep (Minckley 1973), with larvae and juveniles in backwaters and sheltered shorelines over gravel or mud substrates, and adults in swift water over gravel and cobble (Maddux et al. 1987). Breeding adults, particularly males, prefer swift water, and in late winter and early spring, both sexes are numerous in swirling waters behind stones or other obstructions in swift riffles (Minckley 1973).

Speckled dace are abundant in many tributaries of Grand Canyon, where they inhabit shallow riffles with gravel or rock substrates (Carothers and Minckley 1981, Maddux et al. 1987). S.J. Weiss (1993) found speckled dace in runs and riffles in the Paria River throughout the year at temperatures of 0.0–34.0°C. Gorman (1994) found that speckled dace in the LCR responded to the array of habitat variables in an apparently random manner, and significant differences between response of YOY and adults were not observed. Robinson et al. (1996) found that YOY speckled dace in the LCR used areas of higher velocity than other native species, and were less likely to be found near cover. At high flows, YOY used shallower water than other native species. Adult speckled dace used deeper water and larger substrates than younger dace and fed higher in the water column.

Minckley (1973, citing John 1964) noted that adult speckled dace appear quite capable of maintaining position in streams during flash floods, but young are carried downstream, often to their deaths in pools that later desiccate. On the other hand, the species persists for long periods of time in intermittent pools, although greatly crowded, diseased, and starving.

Movement

Little is known of movement patterns of speckled dace in Grand Canyon. It appears that populations are localized and individuals move little, except for spawning. Minckley (1991) described spawning movements of speckled dace between tributaries and the mainstem. Adults entered tributaries in March, remained in lower reaches through summer and fall, and moved back to the mainstem in winter, when temperatures in tributaries equilibrated with mainstem temperatures. Their return to the mainstem may be related to thermal changes or to avoid ascent of large spawning aggregations of trout. Observations by other investigators of speckled dace above water falls at Shinumo Creek (Allan 1993) and at Spencer Creek (C.O. Minckley, FWS, pers. comm.) suggest that fish do not leave these streams, but position themselves beneath substrates for cover and remain inactive during winter.

Diet

Speckled dace have been described as omnivorous, feeding on algae, detrital materials, and smaller aquatic invertebrates (Minckley 1973). They often forage on the bottom, but sometimes rise to inspect and devour floating materials in the mid-water column. Lee et al. (1980) stated that speckled dace are typically bottom browsers, feeding on small invertebrates and sometimes on plant material. Carothers and Minckley (1981) found that speckled dace in Grand Canyon consumed mostly benthic invertebrates and organic debris. Ephemeroptera (mayflies), Diptera (true flies), and Trichoptera (caddisflies) were the most common orders of insects, with Chironomidae (midges) and Simuliidae (blackflies) the most common families, except in summer, when *Gammarus* and mayfly nymphs were the major food items. Terrestrial insects were also consumed when available.

Parasites

Speckled dace have been found to be infected by the external parasitic copepod *Lernaea cyprinacea* and the internal Asian tapeworm. The incidence of *L. cyprinacea* has not been documented, but is probably low. Brouder and Hoffnagle (1996) found Asian tapeworms in 3.8% of speckled dace examined from the LCR in 1994, and infected fish were found as far downstream as Kanab Creek, 132 km below the LCR.

LIMITING FACTORS

Various investigators have collectively identified several limiting factors for the native fishes in Grand Canyon, including physical habitat loss, water temperature, water quality, food supply, predation, and parasites and diseases. The following provides a discussion of each of these limiting factors.

Physical Habitat Loss

Completion of Hoover Dam in 1935 and Glen Canyon Dam in 1963 had dramatic effects on habitat of native fishes in Glen and Grand Canyons. These dams and the reservoirs they created fragmented riverine habitats and acted as physical and ecological barriers to fish. Loss of stream passage has been identified as one factor contributing to the decline of the Colorado squawfish, a potomodromous, lotic species that once migrated great distances within the basin for spawning and rearing of young (Tyus 1984). The dams as physical barriers probably also contributed to the decline of the razorback sucker—another highly mobile species that migrated to spawning areas—but this species is able to survive in reservoirs created by the dams, although reproductive success is limited by habitat and predation of young by non-native fishes (Minckley et al. 1991). The last Colorado squawfish in Grand Canyon was reported in 1968 (Stone and Rathbun 1968), and only 10 razorback suckers have been reported since 1944 (Valdez 1996). Colorado squawfish and razorback suckers were probably not common residents of the Colorado River in Grand Canyon, but large numbers may have occurred in spring and early summer as adults migrated to spawning areas, possibly in the canyon or other regions up or downstream. Also, young larvae may have been abundant in the canyon as they drifted downstream to flooded bottomlands (i.e., razorback suckers) or nursery backwaters (i.e., Colorado squawfish) in alluvial reaches (Minckley et al. 1991, Tyus 1991).

Two other native fishes have been extirpated from Grand Canyon: the roundtail chub and bonytail. These were first reported just above the Lake Mead inflow in 1944 (Miller 1944), but have not been reported since. The reasons for their decline and disappearance from the region are unknown.

The Colorado River was confined to about 400 km of flowing, regulated stream by creation of Lake Mead and construction of Glen Canyon Dam. Valdez and Ryel (1995) estimated that these human-made features reduced presumed habitat of humpback chub in the region by 37%. Reduction in high spring flows; increase high summer, fall, and winter flaws; and daily fluctuations for power generation created an environment unlike the historic river below Glen Canyon Dam. These flow regulations destabilized shorelines (Valdez and Ryel 1995, Converse 1996) and modified habitat-forming processes associated with sediment and substrate features (Schmidt and Leschin 1995, AGFD 1996). A major reduction occurred in sediment budget, possibly affecting the formation and persistence of sandbars and associated eddy return-current channels (i.e., backwaters), used as habitat by native fishes.

Clarkson et al. 1994 discussed changes in backwater and shoreline habitats resulting from operation of Glen Canyon Dam. Some habitats are inundated and desiccated on a daily basis as a result of changes in river stage. Such instability precludes the level of biological productivity characteristic of backwaters in the absence of daily changes in stage (Grabowski and Hiebert 1989, Stevens et al. In Press). Young fish in unstable backwaters are forced from these refugia as river stage changes, or they become stranded and subject to potentially lethal temperature, oxygen, or salinity levels in isolated pools. The amount of energy expended to find alternative nurseries and the increased risk of predation are unknown. Historically, the Colorado River in mid-summer was relatively stable, especially in the Upper Basin. In the Lower Basin, late summer monsoonal rainstorms occurred periodically, increasing river stage dramatically over short time periods. These events probably destabilized shoreline habitats used by juvenile humpback chub, but water temperatures in Grand Canyon were nearly twice as warm as they are today; hence, swimming ability of young was not impeded by cold temperatures.

Biologists do not concur on the relative importance of backwaters to native fishes in Grand Canyon. Backwaters are vital to YOY Colorado squawfish as nurseries in the Green and Colorado Rivers of the Upper Basin (Holden and Stalnaker 1975a, Valdez 1990, Tyus 1991). They also support large numbers of larval and post-larval flannelmouth suckers, bluehead suckers, and speckled dace (Grabowski and Hiebert 1989), but these young fish are also abundant along shallow shorelines (Valdez et al. 1982), suggesting lesser dependence on backwaters than Colorado squawfish. In canyon regions in the Upper Basin, such as Westwater Canyon, Cataract Canyon, Desolation Canyon, and Yampa Canyon—where populations of humpback chub persist—numbers of backwaters are small and often inundated by high flows for 1-3 months after the young chubs are hatched and in need of nursery areas (Valdez and Claimer 1982, Karp and Tyus 1990, Valdez 1990). Young humpback chub in these areas inhabit sheltered shorelines and they use backwaters if they are available, but backwaters do not appear to be critical to their survival and recruitment.

In Glen and Grand Canyons, the importance of backwaters has been expressed by various researchers over the last decade and is a driving factor behind dam management proposals, including steady releases. For example, Brouder (1996, citing Maddux et al. 1987, Holden 1978, Valdez and Claimer 1982, Carter et al. 1985, AGFD 1996) stated that "backwaters have become increasingly important as rearing areas for larval and juvenile native fishes in the Colorado River system due to changes in mainstem habitat; primarily decreased water temperature caused by hypolimnial discharge from dams." McGuinn-Robbins (1995) (citing Maddux et al. 1987; Minckley 1991; Angradi et al. 1992; and AGFD 1993, 1994, 1996) contended that "backwaters are important to native fishes in Marble and Grand Canyons as rearing habitat" and "Due to the crucial nature of backwaters as native fish rearing habitat, flows should allow for the greatest number of available backwaters." Maddux et al. (1987) (citing Holden 1977, Valdez and Wick 1981, Archer et al. 1985, and Valdez et al. 1986) maintained that Colorado River backwaters are "important nursery and resting areas for both native and introduced fishes." Maddux et al. (1987) concluded that Colorado River backwaters were important to fishes during spring through early fall, probably because the sun warmed backwaters above ambient river temperature. Percentage of larval seine catches from four mainstem habitats showed that use of backwaters varied by species. Only 6% of young humpback chub were caught in backwaters, but 76%, 67%, and 14% of young flannelmouth suckers, young bluehead suckers, and speckled dace, respectively, were in backwaters. These data showed that young humpback chub were caught mainly in runs (94%) and speckled dace mainly in side channels (62%).

The relative importance of backwaters to humpback chub in Grand Canyon was brought into question by recent studies of mainstem habitat selection (Converse 1996, Valdez and Ryel 1995). Subadult humpback chub utilized nearshore areas more consistently than backwaters. When compared to studies by AGFD (1996), humpback chub were found more consistently along talus slopes, vegetated shorelines, and debris fans than in backwaters. Their use of backwaters seemed strongly correlated to water clarity and temperature: greater numbers of young chubs were found in warm backwaters (>15°C) at moderate to high turbidity (>30 NTU's) primarily in spring, summer, and fall of their first year of life. Few juveniles and adults were found in backwaters. Valdez and Ryel (1995), however, pointed out that "recruitment of these fish to adults is dependent on the presence of large recirculating eddies for food, shelter, and associated proximate spawning sites." Converse (1996) stated that "The few backwaters that are permanent...can have very high densities of young native fish, but fish presence in backwaters depends on high turbidity conditions."

This irregular and inconsistent occurrence of young humpback chub in backwaters, coupled with low dependence of this habitat by chubs in Upper Basin populations, has shed some question on the critical importance of backwaters to native fishes in Grand Canyon. In the Upper Basin, backwaters in alluvial regions are vital habitat for young-of-year Colorado squawfish as sheltered, warm, productive areas, but may not be critical to the humpback chub. In Grand Canyon, however, use of backwaters by young humpback chub may be predicated on the year-around occurrence of these relatively warm, sheltered habitats as refugia from cold mainstem temperatures. Hence, the use of backwaters by young humpback chub in Grand Canyon reported by several surveys appears to be an artifact of a regulated environment. Nevertheless, a significant need for information centers around the compelling question: Should releases from Glen Canyon Dam be focused on maintaining persistent backwaters as vital rearing habitat for humpback chub? More importantly: Would humpback chub survive and thrive in Grand Canyon in the absence of backwater habitats?

Water Temperature

Water temperature is believed to be an overriding constraint for native fish in the Colorado River in Grand Canyon (Reclamation 1995). Minckley (1991) stated that "water temperature too low for reproduction or larval development clearly results in loss of populations and is the culprit excluding natives from Marble/Grand Canyons." Demonstrated or alleged effects of lowered temperatures on native Grand Canyon fishes include reduced growth rates and metabolism (Lupher and Clarkson 1994); decreased survival to sexual maturity (Kaeding and Osmundson 1988); reduced condition, lipid stores, and size that result in elevated overwinter mortality for YOY fishes (Thompson et al. 1991); lowered egg production by adults (McAda and Wydoski 1983); and reduced survival of developing embryos (Marsh 1985, Kaeding and Osmundson 1988). It should also be noted, however, that cold mainstem temperatures have also excluded or reduced numbers of many non-native warm-water fishes in Grand Canyon.

The only known spawning habitats of native fishes in Grand Canyon are tributaries or warm springs. Eggs and larvae transported or drifted into the mainstem probably do not survive because of thermal shock from low temperatures (Bulkley et al. 1982). Angradi et al. (1992) reported measurable drift of native fish eggs and larvae from the LCR into the mainstem, and Robinson et al. (1996) estimated that 377,115 fish drifted from the LCR into the Colorado River from May 11 to June 26, 1993. Eggs have been found in the LCR inflow, but it is believed that daily inundation by cold mainstem temperatures kills the eggs and larvae (Valdez and Ryel 1995).

Temperature shock to eggs and larval fish arriving at the Colorado River is probably lethal (Hamman 1982, Marsh 1985, Maddux et al. 1987, Lupher and Clarkson 1993). Marsh (1985) found total mortality of embryos of humpback chub and other native fishes at 10.0°C and high incidence of deformities at 15.0°C. Under laboratory conditions, eggs of all native fishes failed to hatch at temperatures currently found in the mainstem Colorado River. Hamman (1982) reported only 15% survival for "swim-up fry"

(6.9 mm long) at 12.0–13.0°C. Lupher and Clarkson (1994) reported "cold-shock" in humpback chub 5–7 days old (9 mm TL) and 11–13 days old (11 mm TL) that had been transferred from 20.0°C to 10.0°C. Clarkson and Lupher (1993) found that humpback chub larvae reared for 30 days in 10.0°C, 14.0°C, and 20.0°C, increased in length by 10%, 37%, and 83%, respectively, and increased in weight by 28%, 195%, and 951%, respectively.

Valdez and Ryel (1995) suggested that large numbers of mesolarvae and metalarvae (young less than 2 weeks of age) of all four native species would be expected to drift from tributaries into the mainstem over relatively short time periods, based on observed drift phenomenon in the Upper Colorado River Basin (Valdez et al. 1983). These life stages are highly susceptible to thermal shock (Marsh 1985, Lupher and Clarkson 1994, Bulkley et al. 1982), and the majority probably succumb to changes in temperature during dispersal from warm tributaries to the cold mainstem. Those surviving the transition may exhibit erratic swimming behavior that often elicits predator responses. Hence, the majority of larval fishes reaching the mainstem probably die from either thermal shock or predation. Valdez and Ryel (1995) determined from scale-back calculations that humpback chub able to survive the transition between the LCR and mainstem were an average size of 74 mm TL (52–132 mm TL).

Temperature preferenda for juvenile humpback chub in laboratory tests was 21.0–24.4°C (Bulkley et al. 1982). Maximum river temperature measured in 1990–1993 was only 10–11°C at the LCR confluence (RM 61.5), 13–14°C in Middle Granite Gorge (RM 127.0), and 15–16°C at Diamond Creek (RM 226.0) (Valdez and Ryel 1995). Even maximum downstream temperature was below the preferred temperature of juvenile humpback chub. Survival of eggs was 12%, 62%, 84%, and 79% at 12–13°C, 16–17°C, 19–20°C, and 21–22°C, while survival of larvae was 15%, 91%, 95%, and 99%, respectively (Hamman 1982). Hence, although temperatures are suboptimum for spawning, incubation, and survival of embryos, some success (12% eggs, 15% larvae) is possible from spawning by the Middle Granite Gorge aggregation and others downstream.

Despite the potential negative effects of suboptimal mainstem temperatures on native fishes, some indirect benefits may be associated with these cold temperatures. Since cold hypolimnetic releases began in the early 1970s, the numbers of some warm-water, non-native fishes decreased dramatically; red shiners and largemouth bass were nearly extirpated from the mainstem, and channel catfish became restricted primarily to the warm LCR. Undoubtedly, populations of other warm-water non-native fish, such as common carp, green sunfish, black bullheads, mosquitofish, plains killifish, redside shiners, and golden shiners, were also reduced. Except for carp, these species of fish are now rare or only locally common in Grand Canyon. Hence, the cold mainstem releases may be a key factor limiting invasion and proliferation of certain species of warm-water non-native fishes, which are potential competitors and predators of native species.

The cold mainstem temperatures also appear to be limiting infestations of parasites, especially the parasitic copepod *Lernaea cyprinacea* and the Asian tapeworm. The parasitic copepod uses a fish as the primary and only host, and is unable to complete its life cycle at pH levels <7.0, temperature <15°C, and salinity $\geq 1.8\%$ (Hoffman 1976). The Asian tapeworm uses a cyclopoid copepod as the primary host and a fish as the final host, and requires at least 20°C for completion of its life cycle (Hoffman 1980). Cold mainstem temperature may be keeping these and other unknown parasites in check in Grand Canyon.

Water Quality

Except for temperature and possibly turbidity, water quality parameters currently found in the Colorado River in Grand Canyon are not limiting to native fishes. These parameters include dissolved oxygen, pH, conductivity, and total dissolved solids (TDS). Dissolved oxygen in the mainstem varied from 87 to 100% saturation (8.22–11.03 mg/L) in 1992, and was not considered a problem for fish (Valdez and Ryel 1995). Levels in the LCR during spring runoff in April and May, 1992, were 5.92 and 5.02 mg/L, respectively, but no effect was observed in fish. Stevens et al. (In Press) and AGFD (1996) reported depressed oxygen levels associated with dense vegetation at the back end of backwaters, but these were areas easily avoided by fish. Mean daily pH in 1992 ranged from 7.7 in October to 7.9 in May, with no apparent detrimental effect on fish (Valdez and Ryel 1995). Conductivity of the mainstem at Lees Ferry was 874–981 uS/cm in 1992 and 910–1,010 uS/cm in the LCR. Bulkley et al. (1982) determined that humpback chub have the highest tolerance level for conductivity at 8,500 uS/cm, far above any levels seen anywhere in the Colorado River Basin. Bulkley et al. (1982) also determined that TDS avoidance levels for juvenile humpback chub, bonytail, and Colorado squawfish were about 6,500, 6,000, and 5,500 mg/L, respectively, with preferred ranges of about 1,000–3,500, 4,100–4,700, and 600–1,000 mg/L, respectively. Hence, none of these water quality parameters were found limiting for native fishes in the mainstem or in tributaries (Gorman 1994, AGFD 1996).

Although mainstem temperature has been a dominant influence on native fish species composition, distribution, and abundance in Grand Canyon, water clarity or turbidity have probably also affected distribution, abundance, and possibly health of fish. Valdez and Ryel (1995) determined that activity of adult radiotagged humpback chub was significantly greater at night and during the day when turbidity exceeded 30 NTU's. A similar relationship was noted for subadult humpback chub along shorelines; catch rates were significantly higher at night and during the day in turbid conditions than during the day in clear water. This suggests that humpback chub use turbidity as cover, possibly feeding less in the day time or under clear water conditions. Low turbidity also suggests less cover for escaping sight predators (i.e., brown trout, rainbow trout), which may have a swimming advantage over juvenile humpback chub in the cold mainstem temperatures. Bulkley et al. (1982) determined from laboratory tests that juvenile humpback chub forced to swim at a velocity of 0.51 m/sec fatigued after an average of 85 minutes at 20°C (pre-dam mainstem temperature), but fatigued after only 2 minutes at 14°C (post-dam mainstem temperature): a decrease of 6°C reduced time to fatigue by 98%.

Food Supply

Availability of suitable food for each life stage of fish has been considered a potentially limiting factor. However, clear evidence of food limitations in Grand Canyon is lacking. Most studies of fish diet report few empty stomachs, and potential food supplies appear to be fairly abundant from drift and benthic macroinvertebrate studies (Blinn et al. 1992, 1993, 1994). However, there have been a few observations of possible food shortages for specific life stages of some species. Gorman (1994) noted emaciated and dying YOY humpback chub in the LCR, which he concluded was the result of a recent flood that changed food availability, fish diets, and habitat use. Long-distance movements of some species may be related to food supply. Allan (1993) suggested that movement of flannelmouth suckers to upstream reaches may be in search of better food resources. Stevens et al. (In Press) reported that algal and macroinvertebrate biomass decreased downstream of Glen Canyon Dam in stair-step fashion, as a function of reduced water clarity (and hence, reduced photosynthesis) from incoming tributaries (e.g., Paria River at RM 1.0, LCR at RM 61.5). Limiting food supplies in the mainstem are more likely in the more turbid lower reaches.

A substantial amount of diet overlap was identified between adult humpback chub and rainbow trout, although differences in habitat use and feeding behavior created a degree of spatial segregation (Valdez and Ryel 1995). Both species consumed primarily *Gammarus*, simuliids, chironomids, and *Cladophora*. These items do not appear to be in short supply in upstream reaches (from Glen Canyon Dam to the LCR) since water clarity in this reach is sufficient for photosynthetic production, and supplies of macroinvertebrates are resupplied from upstream sources. Adult humpback chub feed primarily on suspended material that becomes entrained in large recirculating eddies, which are most common from about Saddle Canyon (RM 47.0) to Lava Canyon (RM 65.5), and in Middle Granite Gorge (RM 122.0–RM 130.0; Webb et al. 1991). These two reaches correspond to the largest aggregations of humpback chub in Grand Canyon. However, juvenile humpback chub appear to feed from local shoreline production that appears to decrease dramatically downstream of the LCR, and may be the primary reason for a paucity of young fish in downstream aggregations.

This pattern of decreased productivity seems to end at the Lake Mead inflow, which is marked ecologically by Bridge Canyon (Valdez et al. 1995). Downstream of Bridge Canyon, river currents slow and the channel is filled with sediment deposits and lined with riparian vegetation. Macroinvertebrates are abundant. Increased productivity, however, does not translate to increased abundance of native fish. Native fish are present only in low numbers both upstream and downstream of Bridge Canyon. Upstream they are likely limited by low production and swift habitat; downstream, by an abundance of non-native fish, particularly lacustrine species from Lake Mead that are poorly adapted to the swift, riverine conditions above Bridge Canyon.

Growth and health of adult fish is related to food supply, but condition of fish may vary seasonally with spawning. Valdez and Ryel (1995) calculated monthly relative condition factor (Kn) for adult humpback chub (≥200 mm TL) from October 1990 through November 1993. They found that Kn reflected robustness prior to spawning by the LCRI aggregation, loss of weight during spawning, and regained weight following spawning. Relative condition factors in October and November were higher in 1990 than in 1991, 1992, or 1993, although significantly different only between October 1990 and 1993 (ANOVA, $F=4.32$, $P=0.04$, $df=1.80$; Fishers LSD, $P \leq 0.05$). Higher Kn for October 1990 was attributed to possibly greater availability of drifting food under the variable release regime of research flows. Lower Kn in October 1991, 1992, and 1993 suggests reduced availability of food from lower fluctuations associated with interim flows. The lower Kn found in these years did not indicate that fish were starved or physiologically stressed. The only fish that appeared emaciated were individuals captured at the LCR inflow following a high flood in January 1993. These fish were believed to be LCR residents temporarily transported by high flows into the mainstem.

Predation

The number of known piscivores has increased from one (Colorado squawfish) of eight fish species (13%) in the historic fish assemblage to 10 of 18 (56%) in the contemporary assemblage. Channel catfish, brown trout, rainbow trout, black bullhead, and striped bass all have been documented with remains of all four native fishes in their stomachs (Minckley 1996, Douglas and Marsh 1996b, Valdez and Ryel 1995, Kaeding and Zimmerman 1983). Valdez and Ryel (1995) used predator-prey models to estimate that brown trout, rainbow trout, and channel catfish in the mainstem could consume approximately 250,000 humpback chub annually, or about 4,122 chubs/1,000 predators. Douglas and Marsh (1996b) estimated an annual consumption rate of 3,588 chubs/1,000 predators in the LCR. The total numbers of predators in the mainstem and LCR are not known, but certainly exceed 1,000 individuals (Maddux et al. 1987, Valdez and Ryel 1995), indicating that the potential for predation on native fishes in Grand Canyons is substantial, and could limit survival and recruitment of YOY and juvenile humpback chub, flannelmouth suckers, and bluehead suckers in the mainstem.

The negative effects of predation on native fishes is sympathetic to the effects of cold mainstem temperatures, low turbidity, and unstable shoreline habitats. We believe that most larval flannelmouth suckers, bluehead suckers, and humpback chub descending from warm natal tributaries into the cold mainstem die of thermal shock or from predation elicited by erratic swimming behavior. For those fish old enough to survive the transition, swimming ability may be reduced by as much as 98% by cold mainstem temperatures. Reduced swimming ability, combined with reduced turbidity for cover, greatly advantage cold-water, sight predators such as rainbow trout and brown trout. Juvenile native fishes along sheltered shoreline habitats are often forced to move to alternative locations by changing river stage, increasing exposure to predators and needless energy expenditure.

Parasites and Diseases

Of the two principal parasites found in the native fishes in Grand Canyon—the parasitic copepod *Lernaea cyprinacea* and the Asian tapeworm—the former is of little concern, since it has been known from the same species in the Upper Basin for many years (Flag 1981, Valdez et al. 1982) and in Grand Canyon since 1978 (Carothers and Minckley 1981). Despite infestations (i.e., number of copepods per fish) more severe than any observed in Grand Canyon, *L. cyprinacea* has not been known to cause death in host fish. However, the Asian tapeworm is a recent invader to Grand Canyon, and is of special concern because it can cause substantial stress and eventually death to the host. This tapeworm is specific to Cypriniformes and is particularly dangerous because it takes residence, unattached, in the lower intestine of the host, reaching such abundance and mass as to completely block the intestinal tract. It is considered one of the most dangerous parasites to fish culturists because it spreads rapidly and causes widespread death under crowded, stressful conditions. Aside from physical blockage of the intestinal tract, this tapeworm extracts substantially from the nutrient budget of the food mass in the intestine, and infected fish often appear emaciated with a distended abdomen. A disconcerting decline in condition of adult humpback chub in the LCR may be attributable to the Asian tapeworm (Meretsky et al. In Review). The decline began in 1990, the same year that the parasite was first reported from Grand Canyon.

Chapter 6
LIFE HISTORY AND ECOLOGY OF NON-NATIVE FISHES

INTRODUCTION

This chapter describes the life history and ecology of the non-native fishes in Grand Canyon. Several species of non-native fishes are sympatric with the native species and interact in a variety of ways, sometimes to the detriment of the native species (see Chapter 7). Although 26 species of non-native fishes have been reported from the Grand Canyon area (See Chapter 4), we have chosen to focus on the eight species that are most common and have been determined to be current or potential competitors and/or predators of native fishes. The non-native species discussed below are common carp, channel catfish, fathead minnow, red shiner, plains killifish, striped bass, rainbow trout, and brown trout.

Some of these species are presently uncommon in Grand Canyon (e.g., red shiner), but they were once common in the system and have the capability to become abundant and widespread once again. If conditions become suitable, they could disrupt the life history of native fishes. Species such as black bullhead, yellow bullhead, green sunfish, largemouth bass, smallmouth bass, and walleye are all present in Lakes Powell and Mead and also represent a potential threat if riverine conditions become suitable. Since construction of Glen Canyon Dam, distribution records of non-native fishes from the Grand Canyon area show concentrations around tributary mouths or warm-water plumes of tributary inlets. Some species, such as striped bass and channel catfish and possibly carp, show distinct movements upstream into Grand Canyon from Lake Mead. Others, like red shiners, appear to be limited in their distribution by cold mainstem temperatures and high current velocities.

The most important changes in populations of non-native fishes in Grand Canyon occurred when Glen Canyon Dam was closed. The cooling of river water temperatures initiated a decline in the warm-water non-natives that had become established since the turn of the century (Minckley 1991). The shift from an assemblage dominated by channel catfish and carp to one dominated by cold-water salmonids took several years (Stone 1964, 1965, 1966, 1967; Carothers and Brown 1991). Some warm-water species, including largemouth bass, green sunfish, black bullhead, and red shiner, were extirpated or greatly reduced. The shift in abundance of carp exemplifies the effects of cold-water releases. During the mid-1970s, carp were dominant in the mainstem above the LCR (Carothers and Minckley 1981), but by the mid-1980s rainbow trout dominated the same reach, and the catch of carp had decreased by two-thirds (Maddux et al. 1987). In the 1990s, rainbow trout composed 46-98% of fish biomass between the dam and the LCR, while carp composed only 10-40% (Valdez and Ryel 1995).

Life history studies of non-native fishes have not been conducted in Grand Canyon; little is known about their role in this ecosystem other than what has been reported by early surveys and from incidental catches in sampling for target species (i.e., game fishes such as rainbow trout or endangered fishes). Much of the information presented in this chapter was synthesized from literature outside the Colorado River Basin and from regions in which the particular species is native or indigenous.

COMMON CARP

Distribution and Abundance

Common carp were imported from Europe and actively distributed to many parts of the country by the U.S. Fish Commission in the mid- to late 1800s (Sigler and Sigler 1987, Minckley and Deacon 1991). Carp were first reported in Arizona from ponds in 1885 (Taggart 1885, Rule 1885: both cited in Minckley 1973), and reports of carp in various rivers were common by 1895 (Evermann and Rutter 1895, Gilbert and Scofield 1898: both cited in Minckley 1973). The distribution of carp in Arizona now includes most permanent rivers and lakes below 6,000 ft (1,828 m) elevation (Minckley 1973).

Common carp are believed to have been stocked into the Lower Colorado River around 1890 (Haden 1992). They were reported as one of the dominant species in Glen Canyon before impoundment (Woodbury 1959), and were the most commonly caught species during the 1978–1979 sampling period between Lees Ferry and Separation Canyon at RM 239.5 (Carothers and Minckley 1981). Maddux et al. (1987) reported that, in 1984–1986, carp were the second most common species caught, increasing in abundance gradually downstream, with CPUE for electrofishing ranging from 1.9/100 min in the reach between Glen Canyon Dam and Lees Ferry, to 22.4/100 min between Bright Angel Creek and Diamond Creek. Notable concentrations of carp were observed in tributary inflows. Valdez and Ryel (1995) noted a similar pattern in 1990–1993. Common carp represented 18% of biomass from Lees Ferry to Middle Granite Gorge (beginning at RM 125.5) but over 70% of biomass from Middle Granite Gorge to Diamond Creek. Carp abundance increased not only downstream but at the confluence of warm tributaries such as the LCR (RM 61.5) and at the Fence Fault spring complex (RM 26.9 to 32.9) where the fish apparently sought out warmer temperatures, especially during the spawning season.

Common carp have been observed in Grand Canyon tributaries (Minckley 1979, Carothers and Minckley 1981, Minckley 1990, Angradi et al. 1992, Haden 1992, S.J. Weiss 1993, Gorman 1994, Leibfried and Zimmerman 1995, Valdez et al. 1995, Douglas and Marsh 1996b) but have usually represented a small percentage of the catch. Large numbers of adult carp are usually present in the lower 2 km of the LCR in spring, presumably for spawning. Abundances of carp are greater in tributaries in western Grand Canyon, particularly below Bridge Canyon.

Reproduction

Under optimum conditions, male carp mature in 1 year (Bardach et al. 1972. Under more typical conditions, males mature in 2–4 years with females requiring 3–5 years (Carlander 1969). Spawning occurs at a range of 18.0–26.0°C with an optimum of 23.0°C (Bell 1990, Edwards and Twomey 1982, Swee and McCrimmon 1966). Spawning season for carp varies with temperature throughout its range. Carp spawn from May to June at northern latitudes and from March to June at southern latitudes (McCrimmon 1968). Evidence suggests that carp may spawn for longer periods of time if water temperature is within limits (Carothers and Minckley 1981, Edwards and Twomey 1982). Carp spawning is also variable in that it can be halted if temperatures drop below preference levels and resumed when conditions are favorable (Scott and Crossman 1973).

Carp often spawn in large, conspicuous aggregations in shallow water (Minckley 1973, Scott and Crossman 1973). Carp prefer to spawn nearshore and over vegetation or other objects on which their eggs can adhere. A greater abundance of submerged vegetation will increase reproductive success (Scott and Crossman 1973). In reservoirs and lakes, an increase in water level at appropriate water temperatures is a strong impetus for carp to spawn over newly submerged terrestrial vegetation (Edwards and Twomey 1982). This spawning behavior is exploited by fisheries managers by lowering reservoir levels after a spawning event by carp, thus eradicating a significant number of eggs (Edwards and Twomey 1982).

Reproduction by carp in the Colorado River in Grand Canyon appears to be limited by temperature (Maddux et al. 1987). Spawning occurs in low-gradient tributaries from late winter to early fall (Carothers and Minckley 1981). Juveniles and YOY carp are seldom collected, indicating low reproductive success in upper reaches (Carothers and Minckley 1981, Maddux et al. 1987); however, YOY carp have been collected from the LCR (Minckley 1979) and from the mainstem between RM 60.0 to RM 226.0 (Maddux et al. 1987). Large numbers of adults are often seen in the lower reaches of the LCR, and adhesive eggs are common on submerged vegetation and exposed roots of tamarisk and *Fragmites* (R. Valdez, SWCA, pers. observ.). Most adults in the canyon are thought to be migrants from Lake Mead (Carothers and Minckley 1981), or recruited from the LCR, Kanab Creek, or other warm tributaries. A large spawning run of carp was observed in March 1994 in Spencer Creek (RM 246.0) at water temperatures of 16.0–25.0°C (Valdez 1994). The spawning temperature range of 18.0–26.0°C is seldom, if ever, reached in main-channel habitats.

Fry and juvenile carp utilize shallow (<2 m), warm, low-velocity areas with abundant vegetation (Sigler 1958). Preference for turbidity has also been reported and is thought to provide additional cover from predators (Edwards and Twomey 1982). Optimum temperature for embryo hatching is 21.0°C, with a range of 20.0–25.0°C (Bell 1990, Edwards and Twomey 1982). Carp fry are more tolerant of temperature extremes than eggs.

Habitat

Carp are ubiquitous, but prefer warm, shallow, eutrophic areas of rivers, streams, and lakes with ample cover, warm backwaters, and organically polluted areas (Sigler 1958, Pflieger 1975). Under favorable conditions, carp will use shallow areas with abundant vegetation. Carp have been found to move into deeper habitat when water temperature exceeds their preference range, or dissolved oxygen levels are reduced (Sigler and Sigler 1987).

Carp do not appear to be limited by substrate type. They prefer mud and silt substrates; stirring up turbidity may enhance their ability to compete with other species by (Edwards and Twomey 1982). Tolerance of turbidity by carp is extremely high as long as food resources are abundant. Carp tend to agitate bottom sediments during spawning and feeding such that turbidity over silty substrate may exceed 200 JTU with Secchi depths <8 cm.

Carp are well adapted to a variety of water quality parameters. They are tolerant of low dissolved oxygen (DO) levels that are characteristic of many warm, eutrophic systems, such as shallow lakes, marshes, farm ponds, and sewage lagoons (Pflieger 1975; Sigler 1955, 1958). Adult carp will occasionally feed in the hypolimnion where DO levels may be less than 2 mg/L. Carp can also survive periods of oxygen depletion (DO ≤ 0.5 mg/L) by gulping air at the water's surface (Edwards and Twomey 1982). Lower lethal dissolved oxygen limit for fry is reported as <1.6 mg/L at 21.0–22.0°C.

Juveniles can tolerate slightly less dissolved oxygen at 1.0 mg/L at temperatures less than 20.0°C. Optimum dissolved oxygen levels (>6 mg/L) are similar to those of adults.

Carp are tolerant of gradual increases in salinity (Edwards and Twomey 1982) and may enter brackish waters and estuaries. Growth is slow at 2.0–3.0 parts per thousand (ppt) sodium chloride (NaCl). Death occurs at 7.2 ppt NaCl after 36 days of exposure (average ocean concentration is 35 ppt). Fry and juvenile carp tolerate less variation in salinity than adults. Upper lethal limit is ≥4 ppt for fry and ≥6 ppt for juveniles. A pH lower than 5.0 is detrimental to carp; a pH higher than 10.5 is lethal (Edwards and Twomey 1982).

Water temperature is thought to be the major limiting factor for carp in Grand Canyon. Their temperature tolerance range is 7.0–38.0°C (Lechleitner 1992). The lower lethal limit for carp fry is ≤7.0°C, while the upper lethal limit for both fry and juveniles is near 38.0°C, but these fish can remain active at 36.0° (Edwards and Twomey 1982). Overall preferred temperature for adults is 27.0°C; optimum growth occurs at 30.0°C. Juvenile carp have a varied preferred temperature range of 27.0–33.5°C, while optimum growth is reported at 28.0–30.0°C (Lechleitner 1992).

Use of habitat by common carp in Grand Canyon is similar to use in other large rivers, with some exceptions. As in other rivers, carp select low-velocity areas such as eddies and eddy return-current channels, or backwaters (Maddux et al. 1987, Carothers and Minckley 1981). Selected areas have warmer temperatures than the main channel. Carp are reported to be locally abundant around the Fence Fault spring complex (RM 26.9 to RM 32.9) ,where they congregate in warm spring outflows and are sympatric with a small aggregation of humpback chub (Valdez and Ryel 1995). Large numbers of carp have also been reported in April and May in the LCR, where they occur sympatrically with a population of humpback chub (Minckley 1990). Juvenile carp have been collected at several sites in Grand Canyon. YOY carp have been collected in the LCR (Minckley 1979) and between RM 60.0 and RM 236.0 (Maddux et al. 1987).

Movement

Movement of carp in Grand Canyon has not been described. Adults are known to annually congregate at mouths of seasonally warmed tributaries to spawn, and they appear throughout the mainstem at all times of year; however, lack of tagging studies precludes a better understanding of their movements.

Diet

Carp are omnivorous, their feeding habits allowing them substantial flexibility in utilizing available food resources. Food items are consumed from the surface or from benthic or littoral regions, and may include algae, seeds and other plant matter, and invertebrates (Edwards and Twomey 1982; Sigler and Sigler 1987). Common carp are also known to consume small fish and eggs (Minckley 1973). Aggregations of adults have been observed vacuuming recently deposited eggs of razorback suckers in Lake Mohave (Marsh and Langhorst 1988) and eggs of red shiners in Spencer Creek in western Grand Canyon (Valdez et al. 1995). Carp are known to increase turbidity and destroy aquatic macrophyte beds through their feeding activities, which often include rooting and plowing the bottom (Minckley 1973, Edwards and Twomey 1982).

Carp in Grand Canyon rely heavily on *Cladophora* throughout the year (Carothers and Minckley 1981). Gut samples from 200 carp ranging from 2 to 12 years of age revealed that *Cladophora* constituted 55.1–86.6% of their diet. Detritus and sand composed 8.4–14.7% of gut samples, indicating a benthic feeding mode and perhaps some reliance on detritus. Aquatic invertebrates such as amphipods (*Gammarus*), black fly larvae (*Simuliidae*), aquatic worms (*Annelida*), plant matter, and seeds made up the remainder of the diet. One specimen contained a speckled dace, which indicates predation or opportunistic scavenging of dead fish.

CHANNEL CATFISH

Distribution and Abundance

Channel catfish were first introduced into the Lower Colorado River in the 1890s (Miller and Alcorn 1943). Pre-dam conditions in Glen and Grand Canyons were favorable for this species, and their distribution was extensive. Woodbury et al. (1959) reported that channel catfish were "...found abundantly in all habitat types in the river and larger tributaries and is probably the dominant fish in Glen Canyon." Records from 1968 also report catfish as abundant (Miller and Smith 1968), while data from 1975 reported them as rare to locally abundant (Holden and Stalnaker 1975a), indicating that numbers in the mainstem decreased dramatically following completion of Glen Canyon Dam in 1963 and releases of cold hypolimnetic waters in the early 1970s.

Information on the distribution of channel catfish in Grand Canyon in the 1970s indicated that their numbers were greatest in western Grand Canyon and in and around the LCR (Carothers and Minckley 1981). In the 1980s and 1990s, catch rates indicated a decrease in numbers, with seasonal variation (Maddux et al. 1987, Valdez and Ryel 1995). At present, the upstream distribution of channel catfish in Grand Canyon is from the vicinity of the LCR, where they are still common (Douglas and Marsh 1996b), to Lake Mead, where they are abundant (Haden 1992, Leibfried and Zimmerman 1994, Valdez et al. 1995). Channel catfish are absent from the Glen Canyon tailwaters.

Reproduction

Channel catfish mature at various ages, depending on habitat conditions. Maturity may occur as early as 18 months (Scott and Crossman 1973) and as late as 8 years (Sigler and Sigler 1987). Channel catfish spawn in spring and summer throughout most of their range. Spawning commences at a temperature range of 21.0–29.0°C, with an optimum of 27.0°C (Lechleitner 1992). Lower and upper lethal limits for eggs are 15.5°C and 29.5°C, respectively. Optimum hatching success is reported at 27.0°C (Lechleitner 1992). Males construct or locate suitable nest holes and may defend them aggressively (Minckley 1973, Sigler and Sigler 1987). The male may also stay with the fry for a varied amount of time until they disperse (Scott and Crossman 1973).

Channel catfish reproduction in Grand Canyon has been verified (Carothers and Minckley 1981, Maddux et al. 1987, Valdez and Ryel 1995). Adults in reproductive condition have been documented at the LCR inflow (Carothers and Minckley 1981, Maddux et al. 1987, Valdez and Ryel 1995) and Kanab Creek (Carothers and Minckley 1981). Spawning has been reported from these localities in spring and summer (Carothers and Minckley 1981), but reproductive success and recruitment are thought to be limited (Maddux et al. 1987).

Habitat

Channel catfish prosper in a variety of habitats and are well adapted to stream life. In rivers and large streams, small channel catfish use large rocks or other obstacles as current breaks. Adults prefer the cover of deep pools, undercut banks, log jams, or other quiet retreats (Scott and Crossman 1973). Smaller individuals are commonly associated with riffles (Minckley 1973, Sigler and Sigler 1987). Channel catfish also appear to tolerate a variety of substrates. They are reported as common in sand- or gravel-bottomed rivers (Scott and Crossman 1973), and they can flourish in turbid waters (Sigler and Sigler 1987).

Channel catfish are usually regarded as a warm-water game fish. Temperatures of 36.1–36.4°C have been determined to be the upper lethal limit for adults (Jobling 1981), while fry have an upper lethal limit of 35.0–38.0°C (Allen and Strawn 1968). Optimal growth temperature for adults has been reported differently by researchers and probably varies slightly with dissolved oxygen levels. Growth was optimal at 28.0–30.0°C (Andrews and Stickney 1972, Andrews et al. 1972, Jobling 1981) and at 26.6–29.4°C (Shrable et al. 1969). Growth was slow below 21.0°C (Andrews and Stickney 1972).

This species is also tolerant of poor water quality. Channel catfish are known to enter brackish waters in coastal areas (Scott and Crossman 1973). They tolerate turbidity, as evidenced by their pre-dam distribution in the Colorado, Green, and San Juan Rivers. The lower lethal limits for dissolved oxygen are reported as 0.95, 1.03, and 1.08 ppm at 25.0, 30.0, and 35.0°C, respectively (Scott and Crossman 1973).

In Grand Canyon, adult channel catfish have been captured in eddies, deep pools, and runs, as well as in tributary inflows (Valdez and Ryel 1995). YOY channel catfish have been collected in the LCR and Kanab Creek (Carothers and Minckley 1981). Success of fry and juvenile catfish is probably greater in warmer reaches of the mainstem near Lake Mead (Haden 1992).

Movement

Movements of channel catfish in the mainstem Colorado River in Grand Canyon suggest an upstream passage during warmer months. Catch rates of channel catfish increase in upper sections of the river as main-channel temperatures increase in summer (Valdez and Ryel 1995). This trend is most apparent below Diamond Creek, between RM 226.0 and RM 280.0. Channel catfish represented only 2.4% of the catch in early spring, and 18.0–16.5% in summer and fall (Leibfried and Zimmerman 1994, 1996).

The annual appearance of large adult channel catfish at the inflow of the LCR in spring also signifies movement of fish from the mainstem to this seasonally warmed tributary, presumably to spawn. The occurrence of these large predators at the inflow may be a significant source of mortality for young native fishes descending to the mainstem (Valdez and Ryel 1995).

Diet

Channel catfish are omnivorous scavengers and predators, depending on food availability (Scott and Crossman 1973). Stomach contents have contained aquatic invertebrates, plant matter, sand, *Cladophora*, fish, detritus, and garbage from boaters and campers (Woodbury et al. 1959, Douglas and

Marsh 1996b). Catfish fry depend heavily on aquatic insect larvae until they reach 100 mm TL. From that point, they become omnivorous and are able to consume small fish (Minckley 1973). Both young and adults forage in riffles, particularly at night. Rising water levels often stimulate diurnal feeding (Sigler and Sigler 1987).

Leibfried and Zimmerman (1995) reported that channel catfish taken from National Canyon to Pearce Ferry (RM 166.5–RM 280.0) in Grand Canyon consumed *Cladophora*, detritus, aquatic and terrestrial invertebrates, and fish. In a sample of 58 fish, the relative volume of stomachs contained 45.8% *Cladophora*, 29.7% food scraps from camp refuse, 15.0% detritus, 5.4% invertebrates, 0.3% percent fish, and 3.7% miscellaneous items. Stomachs from channel catfish taken from the LCR contained vegetation, *Gammarus lacustris*, aquatic insect larvae, terrestrial invertebrates, and several species of fish, including humpback chub (Douglas and Marsh 1996b). Piscivorous behavior has been noted from many individuals taken over the years in Glen and Grand Canyons (Woodbury et al. 1959, Carothers and Minckley 1981, Minckley 1990).

FATHEAD MINNOW

Distribution and Abundance

Introductions of fathead minnows began around 1940, reportedly from Lake Mead area bait shops (McCall 1979). This is likely the original source of fathead minnows in Grand Canyon. Currently, fathead minnows are absent or uncommon in the mainstem Colorado River above the LCR (Valdez and Ryel 1995, AGFD 1996) but locally common or abundant in warm tributary outflows, nearshore habitats, and backwaters throughout the rest of the system (Kaeding and Zimmerman 1983, Maddux et al. 1987, Angradi et al. 1992, Valdez and Ryel 1995). During the 1980s, fathead minnows were the second most abundant non-native fish (after rainbow trout) caught throughout the Colorado River system in Grand Canyon (Maddux et al. 1987), and during the 1990s, they were the most abundant non-native fish caught (AGFD 1996). Valdez and Ryel (1995) noted that numbers of fathead minnows captured in the mainstem increased dramatically after 1991, possibly because of more stable shoreline habitats as a result of interim flows starting in August 1991, and to the transport of fish from the LCR by floods in 1992 and 1993. AGFD (1996) reported that the percentage of catch composed of fathead minnows declined in 1992 and 1993 in all reaches below the LCR.

AGFD (1996) commonly found fathead minnows in all tributaries sampled between 1990 and 1994, although the percent composition of catch was small (0.2% in Havasu Creek to 3.2% in the LCR) except in Kanab Creek, where it was 21.2% of the catch. Many researchers have noted the presence of fathead minnows in the LCR (Carothers and Minckley 1981, Maddux et al. 1987, Minckley 1990, Angradi et al. 1992, Gorman 1994, AGFD 1996, Douglas and Marsh 1996b). Only Minckley (1979) and Kaeding and Zimmerman (1983) reported finding them in relatively large numbers. The sudden appearance of fathead minnows in mainstem catches at and below the LCR (compared to upstream reaches) suggests that this tributary is a major source of these fish since reproduction appears to be limited in the mainstem by cold temperatures (Valdez and Ryel 1995).

Reproduction

Fathead minnows have a short life span of 2 years or less and can reach reproductive condition in 4–5 months under favorable conditions (Minckley 1973). Fathead minnows spawn fractionally[6] and may reproduce 16–26 times in one summer at a temperature range of 16.0–30.0°C, with an optimum of 25.0°C (Gale and Buynak 1982). Most spawning takes place between May and August in most of its range (Scott and Crossman 1973, Sigler and Sigler 1987). Females spawn with multiple males and allow a male to guard the nest and fry (Scott and Crossman 1973, Sigler and Sigler 1987). Eggs are attached to the underside of suspended objects in low-velocity areas (Scott and Crossman 1973). Defense of the nest site by the male can be aggressive enough to drive other fishes from the immediate area (Scott and Crossman, Sigler and Sigler 1987). Egg development and hatching occurs at 22.0–30.0°C, with optimum hatching at 26.0°C (Cherry et al. 1977).

In Grand Canyon, successful spawning by fathead minnows is thought to occur only in the Colorado River's warmer backwaters and in seasonally warmed tributaries during summer. Spawning in the main channel is precluded by sub-optimal water temperatures. Males and females in reproductive condition have been collected along main-channel shorelines, but are not believed to achieve reproductive success in those habitats (Valdez and Ryel 1995). Water temperatures are believed to be warm enough for maturation of gametes, but not for successful embryo development and survival. Fluctuating flows in Grand Canyon are thought to lessen reproductive success of fathead minnow by disrupting warm, stable habitats and washing larvae and juveniles into the cold main channel (Maddux et al.1987).

Most small fathead minnows (<25 mm) collected by Maddux et al.(1987) were from lower reaches of the river, with highest CPUE of fathead minnows this size occurring between RM 184.0 and RM 204.0. The only exception to this trend was the area immediately below the LCR. High densities of small fathead minnows in all reaches were generally in or adjacent to backwaters.

Habitat

Fathead minnows tend to occupy low-velocity areas (Scott and Crossman 1973), preferably with submerged vegetation (Haden 1992). The species is a rapid colonizer of new habitat and is very tolerant of conditions found in ephemeral pools (Minckley 1973). Fathead minnows appear to tolerate most substrate types and have a preference for turbidity (Maddux et al. 1987). They do not coexist well with other species and typically reach their greatest numbers when isolated (Minckley 1973).

Upper lethal temperature for adult fathead minnows is 33.2°C (Lechleitner 1992). Temperature for optimal growth is reported as 25.5–26.0°C. Preferred temperature can vary from 19.8°C to 28.9°C.

Fathead minnows are tolerant of low dissolved oxygen levels associated with many habitats. They are one of the most abundant species in saline lakes, with tolerance to salinity reported to be 10,000 ppm (Scott and Crossman 1973).

According to Haden (1992) the majority of fathead minnows captured in Grand Canyon have been from backwaters and other low-velocity areas. Most fathead minnows captured by AGFD (1996) came from backwaters, and fathead minnows were the only species to be commonly found in backwaters during winter. Maddux et al. (1987), however, caught the largest number of fathead minnows in runs with

[6] Fractional spawners may make several deposits of eggs when and where environmental conditions are appropriate.

vegetation, in the deepest water of all fish captured with larval seines. Maddux et al. also found this minnow occupying faster water than all other species except humpback chub. Kaeding and Zimmerman (1982, 1983) reported that fathead minnows were common to abundant along main-channel shorelines, and Valdez and Ryel (1995) found fathead minnows to be common associates with subadult humpback chub in nearshore habitats.

The fathead minnow's reported intolerance of high-velocity flows appears to have been borne out by dramatic decreases in density in the Upper Basin during the high flows of 1983–1986 (Valdez and Ryel 1995). In Grand Canyon, following the beach/habitat-building test flow in spring 1996, when 45,000 cfs was released for seven days, fathead minnow populations were significantly reduced in reaches immediately below the LCR (Hoffnagle et al. 1996)

Maddux et al. (1987) examined the relative abundances of fish in backwaters during steady and fluctuating flows and found that, under steady flow conditions, fathead minnows represented 62.7% of fish caught in backwaters between the LCR and Bright Angel Creek, 55.6% between Bright Angel Creek and National Canyon, and 35.4% between National Canyon and Diamond Creek. Under fluctuating flows, percentages of fathead minnows in backwaters in these three reaches changed to 19.2%, 69.0%, and 38.4%, respectively. During the early 1990s (under reduced fluctuating flows), AGFD (1996) found that the percentages of fathead minnows in backwaters in these reaches were 42%, 22%, and 22%, respectively.

Movement

Movement of fathead minnows in Grand Canyon is not understood, but is probably very local in nature. Movement into the mainstem from seasonally warmed tributaries is attributed to appearance of fathead minnows in mainstem habitats following dramatic flow events, such as the beach/habitat-building flow in spring 1996 (Hoffnagle et al. 1996, Hoffnagle et al. In Review). A concurrent increase in numbers of fathead minnows in downstream reaches following this 1996 flow event indicates that these fish were passively transported downstream by the high flows.

Diet

Fathead minnows are omnivorous and feed mostly on algae, detritus, and small aquatic invertebrates (Minckley 1973, Scott and Crossman 1973). In Grand Canyon, these fish are known to consume black fly and midge larvae, immature black flies and midges, and organic detritus (Carothers and Minckley 1981).

RED SHINER

Distribution and Abundance

Red shiners were introduced into Lake Mead sometime in the 1940s. Use of this minnow as bait is believed to have initiated the red shiner's spread across the southwestern United States (Hubbs 1954), and its range was probably extended by the fish's rapid colonizing habits (Minckley 1973). In the Virgin River, red shiners repeatedly recolonized sections of the river treated with rotenone as part of a major eradication program. Each time, recolonization occurred in a matter of months, demonstrating the rapid, aggressive colonizing ability of this species. Conditions favorable to red shiners are exploited to the fullest, often to the detriment of the native fish fauna.

Red shiners were present from Glen Canyon Dam to Diamond Creek into the mid-1960s, but by 1968, they could only be found in small numbers above Lake Mead (Miller 1968, Stone and Rathbun 1968). From 1970 to 1973, red shiners were reported from only two locations (RM 194.5 and RM 212.5) in Grand Canyon above Diamond Creek (Suttkus et al. 1976). That was the last report of red shiners in any substantial quantity above Diamond Creek for 20 years. Their decline has been attributed to cold fluctuating releases from Glen Canyon Dam (McCall 1979).

Recently, red shiners reappeared in upper Grand Canyon. One was captured in 1992 at RM 117.4 (AGFD 1993), and several more were captured in 1995–1996 (Hoffnagle 1997). Some of these were in the mainstem but most were in the LCR, where they were reported as common in 1996. It is suspected that red shiners were swept into Grand Canyon by flood events in the upper LCR drainage, and have dispersed into the mainstem Colorado River. Reestablishment of this species in the mainstem also coincides with lower fluctuating dam releases started in August 1991 as the interim flow regime and continued since 1996 as the Modified Low Fluctuating Flow (MLFF) regime.

Red shiners have remained common to abundant in the lower reaches of Grand Canyon. Valdez et al. (1995) reported red shiners as "abruptly abundant" just below Bridge Canyon at RM 235.0, where upstream movement was apparently restricted by high water velocities, low availability of sheltered shorelines, and year-around low water temperatures. Downstream of Bridge Canyon, in Spencer, Surprise, Lost, and Quartermaster Creeks, red shiners are the dominant fish species throughout the year and tend to increase in abundance in summer. They have been reported as very abundant in tributaries below Bridge Canyon (Leibfried and Zimmerman 1995) and in Lake Mead (McCall 1979).

Reproduction

In Arizona, red shiners spawn from March through June in backwaters, small riffles, and crevices (Minckley 1973). Spawning takes place over a variety of substrates, including fine gravel, boulders, logs, brush, roots, aquatic vegetation, and even the nests of sunfishes. The temperature range for spawning is 15.0–30.0°C (Scott and Crossman 1973). In Grand Canyon, red shiners are known to spawn in Spencer Creek and may be spawning in other tributaries in Grand Canyon (Valdez et al. 1995).

Habitat

Red shiners are rapid colonizers of newly available and disrupted habitat where anthropogenic alterations have recently caused changes in species composition (Minckley 1973). Red shiners prefer low-gradient, low-velocity areas and are reported as rare in swift, clear streams. They can be very abundant in warm backwaters (Lee et al. 1980), and are one of the most abundant fish species in backwaters and shorelines of the Upper Colorado River Basin (Valdez and Williams 1993).

The upper lethal limit for adult red shiners is 39.0°C (Matthews and Hill 1977). Studies have demonstrated that different populations of red shiners from regulated and unregulated rivers have about a 3.0°C difference in preferred temperature. Populations from regulated rivers appear to prefer lower temperatures than those from unregulated rivers (Matthews et al. 1977).

Movement

Movement of red shiners in Grand Canyon is not understood, but is probably very local in nature. Movement into the mainstem from seasonally warmed tributaries may occur following dramatic flow events, such as the beach/habitat-building releases in spring 1996 (Hoffnagle et al. 1996). Upstream movement from Lake Mead appears to be impeded by high water velocity, low availability of sheltered shorelines and tributary inflows, and year-around low water temperatures (Valdez et al. 1995).

Diet

Red shiners are omnivorous, feeding on planktonic algae and invertebrates and benthic invertebrates (Scott and Crossman 1973). Fish fry have been reported from the stomachs of red shiners (Minckley 1973, Ruppert et al. 1993).

PLAINS KILLIFISH

Distribution and Abundance

Plains killifish were first reported from the LCR basin (the middle part) in 1938 (Miller and Lowe 1967). From the LCR they presumably entered the Colorado River, where they were reported in low numbers below Glen Canyon Dam in 1964 (Stone 1964, 1965). Presently, plains killifish are found in warm, sheltered habitats in Grand Canyon. They occupy warm tributaries, occasionally tributary outflows (Minckley and Blinn 1976), mainstem backwaters (Maddux et al. 1987, AGFD 1996), and were common to abundant along shorelines during surveys in 1990–1993 (Valdez and Ryel 1995). Plains killifish have been reported from tributaries such as the LCR and Crystal, Royal Arch, Deer, Kanab, Spencer, and Surprise Creeks (Carothers and Minckley 1981, Angradi et al. 1992, Valdez et al. 1995, Valdez and Ryel 1995, Leibfried and Zimmerman 1995).

Reproduction

Killifish are a short-lived species that reach maturity in 1 year, with a life span of rarely more than 3 years (Minckley 1973). Killifish generally spawn in late spring and summer (Minckley 1973, Lee et al. 1980), at a temperature of 27.0°C (Haden 1992). Spawning occurs in water less than 15 cm deep over sand or fine gravel (Lee et al. 1980). During spawning, males become aggressive and exclude other fishes from nest sites.

Little information exists on spawning by plains killifish in Grand Canyon. Suttkus et al. (1976) observed many spawning groups of plains killifish at Spencer Creek, and Minckley and Blinn (1976) recorded adults in reproductive condition from the inflows to the LCR and Chuar, Pipe, Royal Arch, Crystal, and Stone Creeks. Juveniles were captured at the inflows to Chuar, Garden, and Crystal Creeks and Parashant Wash.

Habitat

Plains killifish prefer small, shallow, warm streams with varied water velocity (Minckley 1973, Lee et al. 1980, Sigler and Sigler 1987). The species occurs in limited abundance in lakes and reservoirs

(Sigler and Miller 1963, Sigler and Sigler 1987) but does not appear to be highly successful in the Colorado River in Grand Canyon (Carothers and Minckley 1981).

In small streams, plains killifish prefer sandy substrate (Lee et al. 1980, Haden 1992), into which they burrow to avoid predators (Minckley 1973). Plains killifish are tolerant of high salinities and alkalinities (Sigler and Miller 1963). No information exists on the upper and lower lethal limits or preferred temperature of plains killifish.

In Grand Canyon, plains killifish are typically found in tributaries and persistent backwaters with vegetation. They occupy areas of low velocity or shallow riffles with overhanging cover, if available. Plains killifish appear particularly susceptible to high volume flows, and were radically reduced in the upper mainstem by the beach/habitat-building flow spring 1996 (Hoffnagle et al. 1996). Although other species, such as fathead minnows, quickly reinvaded the mainstem following the spring flow, re-invasion by plains killifish was much slower.

Movement

Movement of plains killifish in Grand Canyon is not understood, but is probably very local in nature. Movement out of seasonally warmed tributaries appears to be the principal avenue of invasion into the mainstem.

Diet

Killifish are omnivorous. They prefer aquatic and terrestrial invertebrates (Brouder and Hoffnagle 1996) but will consume algae and plant matter if prey items are not available (Lee et al. 1980). According to Scott and Crossman (1973), killifish feed at all levels of the water column, despite the dorsal position of their mouths. Minckley and Klaasen (1969) reported that plains killifish are primarily benthic feeders, scooping up sand and expelling it to obtain food. Others describe this species as being primarily surface feeders (Sigler and Miller 1963, Sigler and Sigler 1987).

Plains killifish in Grand Canyon use all available invertebrates that are of suitable size (Carothers and Minckley 1981). Stomach samples contained primarily midge larvae (*Chironomidae*) and mayfly nymphs (*Ephemeroptera*) and, to a lesser extent, ostracods, terrestrial insects, and detritus. Copepods have not been observed in gut samples, but infections of Asian tapeworm (which use a cyclopodic copepod as an intermediate host) indicate that copepods must be occasionally ingested (Brouder and Hoffnagle 1996).

STRIPED BASS

Distribution and Abundance

Striped bass were introduced into Lake Mead in 1969 (Allan and Roden 1978, McCall 1979) and quickly became established as a large pelagic predator. Striped bass were stocked into Lake Powell in 1974 and were found to be reproducing 5 years later in the Colorado River inflow and along cobble shoals (Persons et al. 1982; Gustavson et al. 1985, 1990).

At present, striped bass are common in Lakes Mead and Powell and comprise a significant portion of sport fisheries in those reservoirs (Gustavson et al.1990). From Lees Ferry to the LCR, striped bass are reported as rare or incidental (Haden 1992, Carothers and Minckley 1981, Valdez and Ryel 1995). Striped bass captured in that reach are thought to have escaped from Lake Powell through spillway releases from Glen Canyon Dam (Persons et al. 1985, Valdez and Ryel 1995). In September 1983, within 3 months of spillway releases to accommodate unexpected high inflow into Lake Powell, 7 of 10 fish caught by one angler 3.2 km downstream from the dam were striped bass (S. Carothers, SWCA, pers. observ.). Striped bass captured downstream of the LCR, especially in years without spillway releases, are considered to be upstream migrants from Lake Mead. Lone individuals have been caught as far upstream as RM 24.5 and at RM 61.0, near the LCR inflow (Minckley 1990). In Grand Canyon, striped bass have been captured predominantly in late spring and summer between RM 132.0 and RM 280.0 (Leibfried and Zimmerman 1995, Valdez et al.1995, Valdez and Leibfried In Review).

Reproduction

Male striped bass may reach reproductive maturity in 3–5 years. Females take slightly longer to mature at 4–7 years (Minckley 1973). Fecundity of large females can be enormous. An average of 4.5 million eggs were present in a Maryland sample of 14 year-old females that weighed an average of 41.9 pounds (19 kg) (Jackson and Tiller 1952, cited in Minckley 1973).

Natural populations of striped bass are anadromous, living at sea and migrating up coastal rivers in spring to spawn in fresh water (Scott and Crossman 1973). Temperature at which spawning runs are initiated is reported to be 12.0–24.0°C (Hill 1989) and 14.0–20.0°C (Talbot 1966). Landlocked striped bass demonstrate an affinity for "running" up streams and rivers in an attempt to duplicate anadromous spawning behavior (Persons et al.1982). They spawn fractionally, broadcasting their eggs in areas of suitable current during these upstream migrations (Minckley 1973), and have been known occasionally to remain in cold dam tailwaters after spawning (Coutant 1985).

The population of Lake Mead striped bass is strongly suspected of undertaking a limited spawning run upstream into the Colorado River each spring (Valdez and Leibfried In Review). In the lower reaches of the river, striped bass in reproductive condition have been collected from May through July (Carothers and Minckley 1981, Valdez and Ryel 1995). Water temperatures were 12.7–17.0°C, which are within the range of spawning temperatures listed by Hill (1989) and Talbot (1966). It should be noted that the majority of individuals caught displayed few if any expressible gametes. It is not known if striped bass are reproducing successfully in the mainstem in Grand Canyon (Leibfried and Zimmerman 1995, Valdez and Leibfried In Review). An abrupt seasonal abundance of striped bass in the lower canyon has been documented in spring and summer between RM 230.0 and RM 280.0 (Leibfried and Zimmerman 1994, 1996; Valdez et al. 1995). This increase in abundance continues in an upstream direction as summer progresses and main-channel water temperatures approach the spawning range of 12.0–24.0°C.

Habitat

In lacustrine habitats, striped bass tend to occupy pelagic (open water) zones (Scott and Crossman 1973). Striped bass are obviously tolerant of salinity as evidenced by anadromous behavior. In the Colorado River in Grand Canyon, striped bass have usually been caught in large eddies or deep runs.

Movement

Striped bass display an upstream migration pattern in summer that mimics the spawning migration found in anadromous populations. In fall and winter, striped bass are markedly absent from Grand Canyon, but by late May they start to appear in reaches above Lake Mead and are present farther upstream as summer progresses. Lava Falls (RM 179.0) was once thought to be a barrier to upstream passage by non-native fish; however, recent records suggest that the migration generally terminates around RM 132.0 below Dubendorff Rapid (Leibfried and Zimmerman 1995, Valdez et al. 1995), and striped bass have been caught as far upstream as the mouth of the LCR (RM 61.5; Minckley 1996).

Diet

Striped bass are primarily piscivores, but will consume various crustaceans, insects, or other small animals (Lee et al. 1980). Larger individuals are reported to feed in a sporadic manner, especially if prey is abundant. Striped bass will gorge themselves upon prey species, such as threadfin shad, and refrain from feeding again until their stomachs are empty (Minckley 1973, Scott and Crossman 1973, Allan and Roden 1978). Fry and juvenile striped bass are reported to consume crustaceans and insect larvae (Minckley 1973).

Stomachs of striped bass collected from Grand Canyon are often empty, possibly due to fasting during spawning runs (Engeling 1990). A sample of 14 striped bass taken in western Grand Canyon in April, June, and September contained 78.6% fish, 14.3% detritus, midge and black fly larvae, and 7.1% *Cladophora* (Leibfried and Zimmerman 1995). Of 48 striped bass captured above Diamond Creek, 8.3% contained fish remains (Valdez and Ryel 1995).

RAINBOW TROUT

Distribution and Abundance

Rainbow trout were introduced into Grand Canyon at Tapeats Creek in 1923 (Stricklin 1950). Since that time rainbow trout have been the subject of massive stocking campaigns in the Colorado River, its tributaries, and elsewhere in the state of Arizona. Stocking ceased in the tributaries of Grand Canyon in 1972, but the tailwaters of Glen Canyon Dam have been stocked regularly since 1964 (Haden 1992).

The present-day distribution of rainbow trout includes the Colorado River and most tributaries between Glen Canyon Dam and Havasu Creek (Valdez and Ryel 1995). Mainstem abundance is highest in the dam tailwaters and decreases downstream coincident with greater dependence on tributaries and tributary inflows. Downstream distribution appears to be limited by decreased water clarity, which reduces feeding opportunities. Below the LCR, turbidity increases in the mainstem and rainbow trout distribution becomes more closely associated with tributary inflows (AGFD 1996).

Reproduction

Under ideal conditions, male rainbow trout mature in 1 year (Scott and Crossman 1973). Females may take up to 6 years in less favorable circumstances. Average age of maturity in most systems is 3-5 years. Rainbow trout typically spawn in late winter and early spring (Scott and Crossman 1973, Minckley 1973). Spawning occurs at a temperature range of 2.0–20.0°C (Bell 1990, Raleigh et al. 1986), with optimum spawning temperature at 10.0°C. Embryo hatching success varies with temperature and dissolved oxygen levels. Eggs may hatch within a range of 3.0–15.0°C, and optimum egg hatching occurs at 10.0°C (Lechleitner 1992).

Rainbow trout require clean gravel to spawn (Scott and Crossman 1973). Redd sites are often located in riffles at the head of pools. Average size of gravel particles is usually greater than 3.0 mm; gravel smaller than this increases fry mortality via entrapment and asphyxiation. Females may construct and spawn in several redds. Males become aggressive during the spawning season and compete over females.

Rainbow trout in Grand Canyon spawn in cold, high-gradient tributaries, near local springs, and in the upper reaches of the mainstem (Carothers and Minckley 1981, Maddux et al. 1987). Spawning can occur from late fall to early spring depending on water temperatures, but usually peaks in December and January when water temperatures in tributaries are near optimum. Tributary use by rainbow trout is often the inverse of use by native fishes. Trout move into tributaries predominantly in winter and spring, and native fishes use these tributaries primarily in spring, summer, and fall. Natural reproduction by rainbow trout occurs in the tailwaters above Lees Ferry and is important to maintaining the rainbow trout fishery in that area. Trout fry have been collected from the main channel above Lees Ferry and in some downstream areas with no tributary influence (Maddux et al. 1987), indicating some mainstem reproduction.

Habitat

Stocked rainbow trout can occupy a wide range of habitats, ranging from small ponds and streams to large, high-velocity rivers and large lakes (Scott and Crossman 1973, Sigler and Sigler 1987). In addition to anadromous stocks of the Pacific drainage, different populations have evolved in lotic and lacustrine habitats (Lee et al.1980). Behavioral differences occasionally exist between populations in different habitats (Scott and Crossman 1973). Stream dwelling populations often exert territorialism and can be aggressive to other fishes.

Most strains are limited by similar temperature requirements. The lower lethal limit for adult and juvenile rainbow trout is reported as 0.0°C (Bell 1990). Upper lethal limit for adults is 25.0–26.5°C (Cherry et al. 1977, Jobling 1981). Juveniles have an upper lethal limit of 22.4-25.7°C (Black 1953). Optimum growth temperatures for adults has been reported to be 12.0–17.2°C (Bell 1990, Jobling 1981) and 14.8–18.6°C (Hokanson et al. 1977). Trout have a pH tolerance range of 5.8-9.6 and prefer a pH of 7–8 (Sigler and Sigler 1987).

Trout fry undergo several stages of growth in the redd before emerging from the gravel. After emerging, fry seek out low-velocity shore habitat that reduces the risk of downstream displacement (Montgomery and Tinning 1996). Habitat of rainbow trout fry is consistently shallower and of lower velocity than that of adults.

In Grand Canyon, adult rainbow trout have been most abundant in runs over gravel substrate in the reaches upstream of the LCR, and in backwaters near larger rubble and boulders in the reaches downstream (Maddux et al. 1987). Subadult rainbow trout have been most abundant in eddies and runs in the reaches above Bright Angel Creek and in backwaters below. They have been found most often near rubble, boulders, and gravel with vegetation present. Fry have been captured most often in runs and eddies, both with a substrate of sand and very slow currents. Depth averaged 23.6 cm.

Movement

Movements of rainbow trout in Grand Canyon are seasonal in nature and most often associated with reproduction (Maddux et al. 1987). In late fall and winter, adults seek tributaries such as Nankoweap, Bright Angel, Deer, and Shinumo Creeks to spawn (Maddux et al. 1987, Valdez and Ryel 1995). Between National Canyon and Diamond Creek (RM 166.5–RM 226.0), rainbow trout catch rates rise gradually from early winter until spring (Leibfried and Zimmerman 1995), indicating downstream dispersal in response to prolonged cold temperatures.

To determine if rainbow trout from the Lees Ferry fishery disperse downstream, fingerlings stocked at Lees Ferry from October 1983 to April 1986 were marked with oxytetracycline dye (Maddux et al. 1987). In survey trips conducted between April 1984 and June 1986, dye-marked trout represented 61% of the fish collected above Lees Ferry, but only about 7% of those collected between Lees Ferry and the LCR, and a very small percentage downstream of that point, indicating little movement downstream. Angradi et al. (1992) reported that half of the adult rainbow trout followed radiotelemetry studies remained in the general location where they were originally caught. This affinity for a particular area was also demonstrated by the same individuals being repeatedly stranded in the same pools during fluctuating flows. Similar results were found when Arizona Game and Fish Department released 78,000 rainbow trout with coded wire nose tags in 1992 and another 73,000 in 1993 in the tailwaters. Of nearly 8,000 rainbow trout captured downstream of the tailwaters, only three of these fish were recaptured, all within 3.5 miles downstream of the tailwater section (Valdez and Ryel 1995).

Diet

Adult and juvenile rainbow trout rely heavily on aquatic and terrestrial invertebrates (Minckley 1973, Scott and Crossman 1973, Sigler and Sigler 1987). Larger adults develop piscivorous habits, especially in lakes.

In Grand Canyon, the diet of rainbow trout was found to display the greatest variety of food organisms of any fish species sampled (Carothers and Minckley 1981). This diet appeared to be subject to seasonal variability. In spring and summer, rainbow trout guts contained more terrestrial insects than in other seasons. In fall and winter, aquatic invertebrates, especially black fly (Simuliidae) and midge (Chironomidae) larvae, were of greater relative importance. Seasonal variation in diet probably reflected an abundance of these prey items rather than food preference. In all seasons, the filamentous algae *Cladophora* constituted a substantial portion (25–50%) of stomach contents. Maddux et al. (1987) reported that *Cladophora* (>50% of gut contents in most seasons), chironomids, simuliids, the amphipod *Gammarus lacustris*, and detritus occurred in the majority of rainbow trout guts examined from the mainstream and combined tributaries. The percentage of *Cladophora* decreased consistently downstream, while the percentage of immature insects increased, forming 66% of the mean food contents volume in the reach between National Canyon and Diamond Creek. Investigating rainbow trout from the LCR, Douglas and Marsh (1996b) found *Cladophora* (47% of gut contents), vegetation, *Gammarus lacustris*, aquatic insect larvae, terrestrial invertebrates, and fish (including humpback chub) in the guts examined.

A key difference between the diets of Grand Canyon trout and other trout populations is the high percentage of *Cladophora* consumed by Grand Canyon fish (Carothers and Minckley 1981). A possible benefit to Grand Canyon population by the consumption of *Cladophora* is the intake of epiphytic diatoms which are high in lipids. A study by Leibfried (1988) demonstrated significantly lower lipid content associated with *Cladophora* from the lower intestine than prior to consumption. When fed *Cladophora* without the associated diatoms, trout in a laboratory situation lost 0.3% of their body weight per day.

Predation by rainbow trout on other fishes in the Colorado River in Grand Canyon has been reported by at least four studies (Rathbun 1970, Maddux et al. 1987, Valdez and Ryel 1995, Douglas and Marsh 1996b). Rathbun (1970) found an abundance of trout with fish in their stomachs. The prey were threadfin shad that had passed through Glen Canyon Dam. Fish occurred in about 1% of mainstem rainbow trout examined by Maddux et al. (1987), but fish and fish eggs were exceeded only by *Cladophora* in trout from tributaries. Valdez and Ryel (1995) reported finding fish in the guts of 0.6% of rainbow trout examined. Douglas and Marsh (1996b) found humpback chub remains in stomachs of about 1.7% of rainbow trout from the lower LCR.

BROWN TROUT

Distribution and Abundance

Brown trout were first introduced from Europe into the United States in the late 1800s, and were quickly distributed throughout the country as a desirable game and food fish. Brown trout were first introduced into Grand Canyon at Shinumo Creek in 1926. Additional stockings occurred at Garden and Bright Angel Creeks soon after. The last reported stocking took place in 1934 (Stricklin 1950). Brown trout persevered in Grand Canyon before closure of Hoover and Glen Canyon Dams by seeking out the cooler temperatures of tributaries. They may have ventured into the mainstem during colder months (Haden 1992). No estimates have been made of pre-dam brown trout population sizes or the impact of this species on native fishes.

The present population of brown trout is somewhat restricted within Grand Canyon. Cold water temperature and high clarity in the mainstem from Glen Canyon Dam to Lees Ferry make habitats in that reach unsuitable for brown trout Maddux et al. (1995). Brown trout are concentrated between the LCR and RM 150.0, especially near the inflows of Bright Angel and Shinumo Creeks (Valdez and Ryel 1995). Of 1,673 brown trout captured, 1,582, or 95%, were from this reach of river, with over half of these fish associated with Bright Angel and Shinumo Creeks. Brown trout were the second most common fish caught between the LCR and Bright Angel Creek (19% of composition), and the most abundant fish at the mouth of Bright Angel Creek. The most recent population data indicate that brown trout have increased in numbers in Grand Canyon in the last 15 years. Inventories conducted in 1980 near Bright Angel Creek (Carothers and Minckley 1981, Usher et al. 1984) revealed that the ratio of brown trout to rainbow trout was 1:10. In 1992–1993, Otis (1994) reported that brown trout made up a mean percent composition of 80.6% of catch in the lower 14 km of Bright Angel Creek, indicating the ratio of brown trout to rainbow trout had been reversed in the 15-year period.

The Grand Canyon population of brown trout is most commonly associated with tributaries, especially during the spawning season. From November through January, brown trout use Bright Angel, Shinumo, Phantom, and Kanab Creeks for spawning (Carothers and Minckley 1981, Minckley 1978, Maddux et al. 1987; Valdez and Ryel 1995). Brown trout residing in the mainstem are thought to derive from tributary spawning (Maddux et al. 1987). Adequate reproductive success of brown trout requires approximately 5% of the total habitat to be suitable for spawning (Raleigh et al. 1986). Since the Grand Canyon population of brown trout is self sustaining and apparently increasing, it is reasonable to infer that the reproductive and nursery habitat requirements for this species are being met, primarily in tributaries and tributary inflows.

Reproduction

Brown trout are able to reproduce at 1 year of age under optimal conditions (McFadden et al. 1965). Under less favorable conditions, they may not reach maturity until the eighth year of life. Average time to sexual maturity is 3–5 years (Raleigh et al. 1986). Spawning is reported to begin in fall and last into early winter (Scott and Crossman 1973), depending on latitude. The initiation and duration of spawning is correlated with both water temperature and photoperiod. Brown trout are migratory in their breeding habits and tend to utilize streams and tributaries where possible. Homing with a high degree of fidelity has been reported in some streams and rivers (Raleigh et al. 1986). Spawning migrations are initiated at 6.0–7.0°C, often with a corresponding decrease in photoperiod. Spawning occurs at temperatures of 7.0–9.0°C through its range (Raleigh et al. 1986). During the spawning migration, female brown trout show specificity in the selection of redd sites based on temperature and dissolved oxygen levels.

Average depth of redds is 7.62 cm, although depths of 30.5 cm have been reported (Raleigh et al. 1986). Redd width can range from <30 cm to >107 cm, depending on the size of the female. Suitable water depth for redds can vary from 12.2 to 91.4 cm, with optimal depth placed between 24.4 and 45.7 cm. Water velocity has been cited to be more influential than depth in the selection of redd sites (Raleigh et al. 1986). Suitable water velocities for redds range from 15.2 to 91.4 cm/s, with optimal velocities reported as 53.3 to 68.6 cm/s.

Site selection and construction of redds are contingent upon several environmental factors, including temperature and dissolved oxygen. Females have been shown to avoid areas of increased temperature and decreased dissolved oxygen; these factors may adversely affect development of eggs (Raleigh et al. 1986). Substrate composition and heterogeneity also constitute major factors in redd construction. Gravel in the range of 1.0–7.0 cm diameter is used most frequently for spawning substrate. Redds are often constructed at the head of riffles and outflow of pools where the gravel is slightly inclined. This is thought to help preclude the risk of sedimentation of eggs and embryos.

The rate of brown trout egg development varies with water temperature. Optimum temperature for reproductive success has been reported as 7.0–12.0°C and 6.6–12.8°C (Raleigh et al. 1986). At lower water temperatures, embryo development is slower than at higher temperatures. Hatching was determined to take 148 days at 1.9°C and only 34 days at 11.2°C.

Reproduction by brown trout in Grand Canyon has been verified, mostly in Clear Creek and Bright Angel Creek (Maddux et al. 1987, Valdez and Ryel 1995). Brown trout in reproductive condition have also been encountered in Shinumo, Tapeats, Deer, and Kanab Creeks (S. Carothers, SWCA, pers. observ.).

Habitat

Brown trout prefer cover far more than other trout species. Increase in the amount of cover in streams has been correlated to an increase in the number and weight of adult brown trout (Raleigh et al. 1986). A stream providing 35% cover is considered adequate. Brown trout use pools 50–70% of the time and riffle-run habitat 30–50% of the time. These preferred habitats are further characterized by low velocity, rocky substrate, and amply vegetated stream banks with moderate to low gradients. Adult brown trout use different types of habitat in winter than in summer. At around 4.0–8.0°C, adults prefer deeper, lower velocity water (Raleigh et al. 1986).

Juvenile brown trout are reported to select pools with rocky substrates and ample cover (Raleigh et al. 1986). These areas overlap with adult habitat, but fry and juveniles avoid places occupied by older fish. The small fish are often forced into shallow environments with low substrate heterogeneity at the edges of riffles or nearshore habitat. Backwaters are rarely utilized. Brown trout fry survival greatly depends on the presence of cover.

Adult brown trout are more tolerant of higher temperature and lower water quality than other species of salmonids (Allan and Roden 1978); however, streams that approach 27.0°C regularly cannot maintain populations of brown trout. Adult brown trout have an upper and lower lethal limit of 2.0°C (Bell 1990) and 26.4°C, respectively (Cherry et al. 1977, Jobling 1981). Temperatures for optimum growth and survival range between 12.0°C and 19.0°C (Raleigh et al. 1986). Brown trout fry have a temperature tolerance range of 5.0–25.5°C (Raleigh et al. 1986) and grow best at 12.8°C. Thermal constancy is a factor in determining this species' success in streams.

Fry mortality is high during the months following emergence. Intraspecific aggression between juveniles adds a density-dependent mortality factor for brown trout. In winter, fry and small juveniles burrow into gravel to escape harsh conditions. Temperatures of 4.0–8.0°C elicit this winter "avoidance" behavior. Gravel and cobble of 10–40 cm diameter offer adequate refugia for fry and juveniles to overwinter.

Brown trout are not as affected by turbidity as are rainbow trout (Valdez and Ryel 1995). Dissolved oxygen levels of >3 to ≤7 ppm at temperatures ≤ 15.0°C, and >5 to ≤9 ppm at >15.0°C, are recommended for optimal growth of brown trout in hatchery situations or streams considered for stocking (Raleigh et al. 1986). Brown trout fry are thought to have dissolved oxygen requirements of 2.3 ppm at 10.8°C; 14 ppm carbon dioxide has been shown to be lethal to fry. Fluctuations in dissolved oxygen are known to impair growth, reduce fecundity, and terminate spawning behavior.

In Grand Canyon, Carothers and Minckley (1981) and Valdez and Ryel (1995), determined that brown trout did not use backwaters to any measurable extent. This finding is consistent with habitat use reported from other systems. However, between the LCR and Bright Angel Creek, where most brown trout are found, Maddux et al. (1987) caught more adult and subadult brown trout in backwaters than in any other habitat; river flows during this study were unusually high. In other reaches, adults were generally captured in runs, with substrate varying from cliffs to boulders. CPUE was always highest in the presence of vegetation, except along cliffs. For subadults, rubble was the most common substrate selected. Between Lees Ferry and Bright Angel Creek, CPUE for subadults was also highest in vegetation.

Movement

Movements of brown trout in Grand Canyon are like those of rainbow trout: seasonal in nature and most often associated with reproduction (Maddux et al. 1987). In late fall and winter, adults seek tributaries, primarily Bright Angel Creek, to spawn (Maddux et al. 1987, Valdez and Ryel 1995). Increased catch rates of adult brown trout were noted in the vicinity of the LCR inflow during fall and winter (Valdez and Ryel 1995), indicating movement to these areas, perhaps to forage on the abundance of fishes associated with this area, including young humpback chub.

Diet

Fry and juveniles of brown trout are motile after emergence and can feed aggressively (Raleigh et al. 1986). Smaller individuals eat plankton, switching to aquatic and terrestrial insects as they attain greater size (Sigler and Sigler 1987). Prey item selection is size-mediated in smaller trout. Brown trout over 200 mm TL tend to become piscivorous at an earlier age than other trout species (Carlander 1969, Sigler and Sigler 1987). Feeding activity tends to occur at twilight and even at night in adults (Raleigh et al. 1986). Active feeding has also been reported during winter conditions under surface ice. Prey include aquatic and terrestrial invertebrates, crustaceans, mollusks, amphibians, small mammals, and fishes of various size.

In Grand Canyon, feeding by brown trout does not appear to be as affected by turbidity as feeding by rainbow trout, and food habits of brown trout show a higher degree of piscivorous behavior and less reliance on *Cladophora* than rainbow trout (Valdez and Ryel 1995). Brown trout feed primarily on invertebrates and fish (Valdez and Ryel 1995, Douglas and Marsh 1996b), and fish eggs when they are available. Otis (1994) observed groups of brown trout behind spawning suckers in Bright Angel Creek, and found over 100 flannelmouth sucker eggs in the guts of one brown trout. Valdez and Ryel (1995) reported that 18.8% of brown trout caught in the mainstem contained fish, including juvenile humpback chub. Gut samples of brown trout collected in the LCR by Douglas and Marsh (1996b) contained 20% fish and 20% invertebrates. Historically, brown trout have been used to control suckers and chubs in various river basins outside the Colorado River Basin (Walden 1964).

LIMITING FACTORS FOR NON-NATIVE FISHES

Habitat Loss

The Colorado River in Grand Canyon is not highly desirable habitat for most non-native fishes, except rainbow trout in the dam tailwaters. If it were not for the numerous tributaries in the canyon, warm-water non-native fishes would be virtually non-existent in Grand Canyon, primarily because of cold year-around temperatures, daily fluctuating flows, and relatively high water clarity. The Colorado River in Grand Canyon is a swift, canyon-bound region lacking flooded bottomlands and with relatively few persistent, stable backwaters and sheltered shoreline areas. The numerous tributaries are the primary refugia for the various warm-water species, providing suitable spawning and rearing conditions, which are rarely met in the mainstem. These tributaries provide a constant source of fish for reinvasion to the mainstem, particularly after flood events.

Construction of Glen Canyon Dam did not alter physical habitat for non-native fishes as much as it altered water quality. Consistent cold water temperatures and high water clarity were the most dramatic changes to non-native fish habitat below the dam in Glen and Grand Canyons. Increased water clarity has enabled rainbow trout to become successfully established in the dam tailwaters, with localized populations inhabiting (along with brown trout) tributary inflows downstream. Periods of decreased water clarity have affected sight feeders, such as brown trout, rainbow trout, and striped bass. During 1992-1993, rainbow trout numbers and condition factor decreased dramatically below the LCR following a prolonged and persistent period of highly turbid floods from the LCR (Valdez and Ryel 1995). Loss in numbers and condition factor were attributed to the inability of rainbow trout to actively feed at high turbidity levels (i.e., NTU>30). Conversely, Valdez and Ryel (1995) hypothesized that turbidity acts as a form of cover for small native fishes and therefore reduces predation pressure. Near-surface movement by radio-tagged adult humpback chub was significantly greater at high turbidity (i.e., NTU>30) and at night than during daytime under high water clarity.

Fluctuating flows from the dam may limit spawning habitat for mainstem salmonids. Under interim flows and MLFF, the reduced fluctuations have increased spawning success for rainbow trout in the dam tailwaters (AGFD 1993,1994). Brown trout and rainbow trout in downstream reaches rely on tributaries for spawning, and their reproduction is probably not affected by fluctuating mainstem flows.

Water Temperature

Before Glen Canyon Dam closed, the water temperature of the Colorado River in Glen and Grand Canyons varied from near freezing in winter to about 28.0°C in summer (Carothers and Brown 1991). The non-native fishes that were established at the time were primarily warm-water species. The dominant forms were carp and channel catfish, with red shiners, largemouth bass, green sunfish, and black and yellow bullheads present but less abundant. It is apparent from the few pre-dam studies and the immediate post-dam surveys that some of these warm-water species were extirpated when hypolimnetic releases from Glen Canyon Dam decreased the magnitude and range of tailwater temperatures to 8.0–10.0°C.

A review and synthesis of pre-dam and immediate post-dam data by Leibfried and Zimmerman (1994) described the shift from a fish community dominated by warm-water non-native species to one dominated by cold-water non-native species. In 1958, channel catfish comprised 90% of the fish community in Glen Canyon (Woodbury 1959). By 1968, channel catfish decreased to less than 5% of the fish captured in the dam tailwaters, while rainbow trout increased to nearly 30%. By 1972, rainbow trout accounted for over 50% of the fish community in the tailwaters (Stone 1972). The temperature changes caused by the dam not only affected the native fishes, but also changed the non-native fish community that had become established in the preceding 40–50 years.

The effect of temperature on the non-native fishes of the Colorado River is an important limiting factor for all non-native fishes inhabiting Grand Canyon today. Although the present temperature regime favors salmonids, the lack of warmer water prevents invasion and establishment of non-native fishes from Lakes Mead and Powell. For example, red shiners are abundant in the Lake Mead inflow below

Bridge Canyon (RM 235.0) but are absent immediately upstream. It appears that the combined effects of cold mainstem temperatures and high water velocity are preventing re-invasion by this species into Grand Canyon (Valdez et al. 1995).

Striped bass and channel catfish also are limited in their distribution by these colder temperatures. Channel catfish in Grand Canyon are found primarily in the LCR, with few numbers in the mainstem. Striped bass reside in Lakes Mead and Powell and make upstream spawning ascents in early summer from Lake Mead. The number of fish and distance moved upstream into Grand Canyon are probably limited by the persistent cold river temperatures. Seasonal warming of river temperatures during spring and summer in western Grand Canyon coincide with movements upriver from Lake Mead by striped bass and channel catfish (Leibfried and Zimmerman 1994, 1996; Valdez et al. 1995). River temperatures usually peak near 15.0°C by June or early July, after which high releases from Glen Canyon Dam and summer storm cloud cover reduce the ability of the river to warm. The onset of cooler river temperatures and increased turbidity correlate with declining numbers of both species in the lower river.

Food Supply

Reductions in food supply or availability may limit success of non-native fishes in Grand Canyon. The amount of food is directly related to turbidity and flow fluctuations as described in Chapter 3. Condition factors of mainstem trout below the LCR declined dramatically (Maddux et al. 1987), coincidental to a significant decline in food organisms (Leibfried and Blinn 1987; Blinn et al. 1992,1994) and increased turbidity (Valdez and Ryel 1995). Tributary fishes are not as susceptible to food limitations because tributaries are usually clear and more productive than the mainstem. It is hypothesized that low mainstem food resources in the lower canyon are a limiting factor to both native and non-native fishes (Valdez and Ryel 1995, Valdez et al. 1995).

Parasites and Diseases

Some species of non-native fishes in Grand Canyon have been documented with various parasites. Channel catfish in western Grand Canyon were found with the "catfish tapeworm" (*Bothriocephalus claviceps*) (Valdez et al. 1995). *Lernaea cyprinacea* is found on both native and non-native fishes, primarily on those from tributaries where water temperatures are sufficiently high for these parasites to complete their life cycles. At this time neither parasite appears to be limiting the survival of any fish species, but pathogens in general could increase with warmer mainstem temperatures. Several unidentified types of bacteria and fungi have been seen on carp, and it is unknown if these might spread to other fishes with warmer temperatures. No other parasites or diseases were noted that might limit non-native fishes in Grand Canyon.

Chapter 7
NATIVE/NON-NATIVE FISH INTERACTIONS

INTRODUCTION

Among the most pressing issues for native fishes in the Colorado River Basin are the effects of non-native fish species on the health of indigenous populations (Minckley 1991, Tyus and Saunders 1996). Interrelationships have been identified between and among some species, but little is known about long-term impacts on native fish communities (Stanford 1994). Understanding these relationships in Grand Canyon is critical if Glen Canyon Dam is to be operated as an effective tool for managing downstream resources (e.g., sediment redistribution, nutrient recycling, fish habitat improvement; Reclamation 1995). Discharging steady flows from the dam has been proposed as a way to enhance habitat for endangered and other native fishes downstream, but a steady flow scenario also has the potential to enhance conditions for non-native fishes. This biological response could eventually have negative effects on native species (e.g., competition, predation, parasite vectors) that outweigh the beneficial results of the proposed operations.

Fishes of the American Southwest are particularly vulnerable to invasion by non-native fishes. The low diversity of native species has resulted in few strategies for coping with predation and competition (Miller 1961, 1972; Williams et al. 1989). In the last 100 years, 27 of 1,003 fishes native to North America have become extinct, and 265 species are threatened with extinction. A disproportionately large percentage of these imperiled species evolved in the southwestern United States. Destruction of physical habitat has been cited as the most common reason (73% of cases) for the decline, followed by displacement by introduced species (68%) (Wilson 1992). The harmful effects of non-native fishes on native fish communities is a "forgone conclusion" (Taylor et al. (1984), but the problem is complex and must be viewed within the context of specific regional conditions. According to the Aquatic Nuisance Species Task Force (ANSTF 1994):

> *By competing for resources, preying on native fauna, transferring pathogens, or significantly altering habitat, the introduction of a nonindigenous species may work synergistically with other factors, such as water diversions or pollutants, to alter the population and distribution of indigenous species. The factors are often cumulative and/or complementary. For example, habitat degradation may make a species more vulnerable to the introduction of nonindigenous species.*

In isolated ecosystems like the Colorado River Basin, a rigorous physical, chemical, and biological environment provided little opportunity for natural invasion by alien species. However, human intervention, through flow regulation and land management practices, has ameliorated these rigorous conditions and allowed species introduced by humans to thrive (Miller 1961). Controlling and managing these non-native fishes has become one of the most difficult challenges facing scientists and natural resource managers alike in the Colorado River Basin.

Alien fishes are not undesirable from every perspective. Many non-native fishes in reservoirs (e.g., largemouth bass, striped bass, crappies, walleye, channel catfish) and tailwaters (e.g., rainbow trout, trout, cutthroat trout) are highly valued game species, while others (e.g., red shiners, fathead minnows, carp) are considered forage for those game species. Sport fishing has a large and influential constituency among state taxpayers. Public resource managers must heed their concerns, as well as the concerns of water and power interests and biodiversity advocates—all while complying with the requirements of the Endangered Species Act to protect listed species. Even more daunting than clashing political forces are the overwhelming practical problems associated with physically eradicating, or even suppressing, a fish species once it has become entrenched in a large and complex aquatic system.

The combined native/non-native fish assemblage in Grand Canyon now consists of the four native species discussed throughout this report—humpback chub, razorback sucker, flannelmouth sucker, bluehead sucker, speckled dace—and at least two dozen introduced species (see Table 3 in Chapter 4 for a list of all fish species recorded from Grand Canyon). The purpose of this chapter is to review what is known about interactions and relationships between these native fish species and the non-native fish species that share their environment.

THE FISH COMMUNITY

Over the last 120 years, the fish community in the Colorado River Basin shifted from a native fish assemblage to a combined native/non-native assemblage. The native fish assemblage consisted of only 36 species, which is considered relatively depauperate when compared to other basins in North America (Minckley et al. 1986). Then, beginning in the late 1800s, at least 67 non-native fish species were introduced, either actively or passively, into the same environment. Fifty-seven of these species have become established (Tyus et al. 1982, Minckley 1991). In many regions, non-native species now dominate: Valdez (1990) reported that 95% of all fish captured in 193 km of the Green and Colorado Rivers were non-native species.

Most native species have had difficulty coping with environmental changes in the basin and are greatly reduced in numbers and distribution. Some appear to have adapted to substantial habitat changes but are suppressed by the abundance of non-native fishes. For example, hatchery-raised razorback sucker thrive in human-made habitats—such as hatchery ponds, livestock tanks, golf course ponds, and urban recreational lakes—as long as non-native species are absent (Minckley et al. 1991). A large number of wild razorback suckers survive in Lake Mohave, but surveys in the late 1980s showed that the youngest fish were 24 years of age and the population was quickly aging (McCarthy and Minckley 1987). These fish have been observed spawning over shallow cobble terraces (Douglas 1952; Jonez and Summer 1954; Minckley 1983; Muller et al. 1982, 1985), producing large numbers of larvae (Bozek et al. 1984, Langhorst and Marsh 1986, Langhorst 1987, Papoulias 1988) that are being consumed by a vast assemblage of predators (Papoulias 1988; Minckley 1982; Ulmer and Anderson 1985). Carp, rainbow trout, channel catfish, striped bass, smallmouth bass, largemouth bass, bluegill, green sunfish and redear sunfish all inhabit the area and are known to prey upon eggs and/or larvae of razorback suckers (Jonez and Summer 1954, Langhorst 1989, Marsh and Langhorst 1988, Ulmer 1980). The negative impact of non-native predators is further supported by the survival and growth of larval razorback suckers in habitats that are physically isolated from non-natives (Langhorst and Marsh 1986, Marsh and Langhorst 1988). In two of these studies (Langhorst and Marsh 1986, Marsh and Langhorst 1988), adult razorback suckers released in an isolated bay in Lake Mohave following removal of non-native fish spawned successfully, and growth rates of larvae were comparable to those raised in hatchery conditions.

FACTORS INFLUENCING INTRODUCTIONS

The success of fish species moved into foreign environments depends on several factors. Each species has specific life history requirements that have evolved over many years. If sufficient life history needs are met in a new environment, species are likely to survive; if these requirements are not met, species will perish. Species can thrive if their needs are met and limiting factors are absent or reduced. Non-native species have frequently been able to out-compete native species, particularly in altered habitats, which often favor non-natives. Understanding the characteristics of native and non-native fishes in the Colorado River in Grand Canyon is thus important to understanding why certain species have succeeded there and others have not.

Characteristics of Native Fishes

The native fishes of the desert Southwest have high tolerances to extremes in physical and chemical parameters such as flows, water temperatures, turbidity, salinity, and dissolved oxygen, but have little means of defense from invaders (Deacon and Minckley 1974, Deacon 1979). Native fishes within the Colorado River drainage have evolved in relatively long geologic isolation from other drainages, resulting in the highest level of species endemism (74%) of any major river basin in North America (Miller 1959). Such isolated faunas are similar to those of island communities, being relatively depauperate, with specialized niches and unsaturated or "patchy" environments (Crowl et al. 1992). Isolated fish communities tend to be "simple" with low species diversity (Minckley and Deacon 1968). Individuals within the community have little experience coexisting with competitors or predators (McDowall 1968). Such characteristics make these fish faunas extremely vulnerable to introduced, non-native fishes, especially those from more diverse and complex faunas (Deacon and Minckley 1974, Moyle 1986, Pister 1981, Schoenherr 1981, Taylor et al. 1984, Tyus and Karp 1990). As a result of their evolutionary history, the native species of the Colorado River are:

- highly specialized and generally tolerant of variable flow conditions;
- non-aggressive with little tendency for predation;
- ecologically and behaviorally distinct, with few strategies for coping with new forms of predation or competition;
- restricted by few reproductive strategies, therefore ill-adapted for extensive habitat modification; and
- pre-adapted to specific habitat and ecological conditions.

Characteristics of Non-Native Fishes

Fishes that are alien to the Colorado River Basin have varied life history requirements, and include warm-water species (e.g., carp, channel catfish, fathead minnows, red shiners, plains killifish), cold-water species (e.g., rainbow trout, brown trout), and cool-water species (e.g., walleye, smallmouth bass) (Valdez and Ryel 1995). Each has specific life history needs and each has succeeded in Grand Canyon by filling empty or vulnerable niches coincidental with those needs. Many non-native fishes were unsuccessful, despite extensive introductions and stockings, such as coho salmon and brook trout in Grand Canyon and coho salmon in Lakes Mead and Mohave. The sensitivity and vulnerability of even these non-native fishes to environmental changes is evident from changes in fish composition with completion of Glen Canyon Dam and releases of cold hypolimnetic waters. Channel catfish and red shiners, formerly abundant in the pre-dam community, were greatly reduced in number and distribution, while rainbow trout, once restricted to cold tributaries, became common and abundant in the cold, clear dam tailwaters (Maddux et al. 1987).

Introduced, non-native species are considered "invasive" once they establish self-sustaining populations without further human interventions (Usher et al., 1988). Invasiveness depends on compatibility of introduced fishes with the host system, including availability of appropriate food and habitat, presence of few predators and competitors, and existence of suitable environmental conditions (i.e., water temperature, dissolved oxygen, salinity, turbidity; Crowl et al. 1992). Introduced species that become invasive tend to originate from highly diverse faunas with high species diversity and complex interactions with other species (McDowall 1968). Survival in such habitats often depends on evolution of aggressive and adaptable traits. These characteristics give these species a "competitive edge" when they are introduced into less diverse faunas (McDowall 1968), allowing them to penetrate into such systems with relative ease (Haden 1992). Taylor et al. (1984) provided a comprehensive list of characteristics attributed to the viability of successfully introduced, non-native species:

- very hardy, able to survive transport and thrive in disturbed environments;
- very aggressive, eliminating natives through competition or predation;
- ecologically or behaviorally distinct from natives, with highly developed strategies of predation or competition;
- flexible in their reproductive strategies, which seem to confer on them an unusual degree of "fitness"; and
- pre-adapted to distinctive local environmental conditions.

TYPES OF INTERACTIONS

Introduced species generally interact with native forms in a variety of ways, influencing abundance, distribution, condition, and/or reproductive success (McDowall 1968). Although native fishes may use non-natives as forage (e.g., Colorado squawfish consume red shiners [Jacobi and Jacobi 1981]), the majority of reported interactions are negative for native fishes and may include 1) habitat alterations, 2) hybridization, 3) transfer of parasites and diseases, 4) predation, and 5) competition (Taylor et al. 1984). The following discussion presents a perspective on each type of interaction, and documents known or suspected native/non-native interactions for the Colorado River system in Grand Canyon. These interactions are summarized in Table 8.

Habitat Alterations

There is no indication that non-native fishes have altered habitats in the Colorado River Basin (Hawkins and Nesler 1991). However, potential exists for local habitat alteration with the persistence of large numbers of common carp in such confined habitats as the LCR (Minckley 1990). Through their tendency to uproot vegetation during feeding, carp are known to destroy vegetation, disrupt spawning areas, and increase water turbidity in small streams and ponds (Moyle 1976, Taylor et al. 1984). Although such activities do not seem detrimental to native fishes in riverine habitats, they have been related to declines of fish populations in lake habitats. For instance, reduced abundance of Sacramento perch, *Archoplites interruptus*, in Clear Lake, California, was related to the destructive behavior of carp (Miller 1959). Jordan and Gilbert (1894) noted that the Sacramento perch was "Formerly very common, but now becoming scarcer as its spawning grounds are devastated by the carp....The destruction of this valuable fish is one of the most unfortunate results of the ill-advised introduction of the carp into California waters." Carp have been observed "vacuuming" substrates being used for spawning by razorback suckers in Lake Mohave (J. Hanson, FWS, pers. comm.) and by red shiners in Spencer Creek (Valdez et al. 1995).

Table 8. Interactions Between Native and Non-native Fishes in the Colorado River through Grand Canyon. HA=habitat alteration, HY=hybridization, PA=parasites and diseases, PR=predation, CO=competition, ?=suspected or potential.

Non-Native Species	**humpback chub**	**flannelmouth sucker**	**bluehead sucker**	**speckled dace**	**razorback sucker**
red shiner	PR?	PR?	PR?	PR?	PR
carp	PA, PR?	PA, PR?	PA, PR?	HA, PA, PR	PR
golden shiner					
fathead minnow	PR?, CO?	PR?, CO?	PR?, CO?	PR?, CO?	PR?
black bullhead	PR?	PR?	PR?	PR?	
channel catfish	PR	PR?	PR	PR?	
rainbow trout	PR	PR?	PR?	PR?	
brown trout	PR	PR	PR	PR	
brook trout					
plains killifish	CO?	CO?	CO?	CO?	CO?
mosquitofish	CO?	CO?	CO?	CO?	CO?
striped bass	PR?	PR?	PR?	PR?	
green sunfish	PR?	PR?	PR?	PR?	PR?
bluegill	PR?	PR?	PR?	PR?	PR?
largemouth bass	PR?	PR?	PR?	PR?	PR?
black crappie	PR?	PR?	PR?	PR?	PR?
walleye	PR?	PR?	PR?	PR?	PR?
threadfin shad					

Hybridization

Hybridization among fishes is common in nature, but can tend to become elevated when environmental changes—either natural or anthropogenic—reduce or eliminate reproductive isolating mechanisms. Hybridization between native and non-native fishes has not been documented in Glen or Grand Canyons, but it is known to occur in the Upper Basin, where flannelmouth suckers and bluehead suckers hybridize extensively with the introduced white sucker (Wick et al. 1981, 1985, 1986; Valdez et al. 1982).

Hybridization of native Colorado River fishes tends to be more common between native sympatric species than with introduced non-natives. Hybridization between razorback suckers and flannelmouth suckers or bluehead suckers has been reported in many regions of the Colorado River Basin (Hubbs and Miller 1953; McAda and Wydoski 1980; 1983, 1985; Tyus and Karp 1990), including Grand Canyon (Suttkus et al. 1976, Minckley 1991, Valdez and Ryel 1995). The other common occurrence of hybridization in the basin is among the three congeneric species of *Gila*, humpback chub, roundtail chub, and bonytail (Holden and Stalnaker 1970, Valdez and Claimer 1982, Douglas 1993, Douglas et al. 1989). Although this form of hybridization was once thought to be associated with disruption of habitat (Joseph et al. 1977, Valdez and Claimer 1982), it has recently been hypothesized that hybridization among these congeneric species is part of the evolutionary history of these fishes and may be advantageous to their survival (Dowling and DeMaris 1993).

Parasites and Diseases

The two principal forms of alien parasites among fishes of the Colorado River in Grand Canyon, (*Lernaea cyprinacea*) and Asian tapeworm (*Bothriocephalus acheilognathi*), were probably introduced into the canyon by non-native fish: possibly infected fish swept down from the upper LCR by floods (AGFD 1996) or, in the case of *L. cyprinacea*, brought into the canyon by infected bait fish from Lake Mead or by infected trout stocked at Lees Ferry (Carothers and Minckley 1981). The transfer of parasites to native fishes by introduced fish vectors has been documented in other systems (Meffe 1985). Non-native fish species in the Grand Canyon known to serve as vectors for these parasites include fathead minnows and common carp (*L. cyprinacea* and Asian tapeworm), and plains killifish, red shiners, and golden shiners (just Asian tapeworm).

Neither parasite is known to have caused the death of any native fish in the Colorado River Basin but both are detrimental to fish, and infestation by the Asian tape worm can be lethal (Brouder and Hoffnagle 1996). *L. cyprinacea* (also called "anchor worms") attach themselves to the outside of the host fish, causing irritation and local hemorrhaging at the point of attachment (Valdez and Ryel 1995). Secondary infections by bacteria may develop at these anchor points. Asian tapeworm may kill the host fish by blocking its gastrointestinal tract, perforating the intestines, and/or destroying the intestinal mucosa (Brouder and Hoffnagle 1996). Mortality rates as high as 90% have been reported from infestations in common carp. Chronic effects may include weight loss, anemia, reduced growth and reproductive potential, and depressed swimming ability, liabilities that could lead to secondary bacterial infections, susceptibility to predation and stress, loss of competitive advantage, and other threats to survival (Clarkson et al. 1997).

L. cyprinacea was first reported from Grand Canyon in 1978 (Carothers et al. 1981). In 1990–1993, this parasite was found on 8 of 6,294 mainstem humpback chub (<1%) examined by Valdez and Ryel (1995). No evidence of stress or illness was noted on infected fish. The low infection rate was attributed to low mainstem temperature; *L. cyprinacea* is not able to complete its life cycle at temperatures below 15.0°C (Valdez and Ryel 1995, citing Hoffman 1976). In 1993, *L. cyprinacea* was commonly found attached to YOY humpback chub in the LCR and on most fish caught in Kanab Creek (Gorman 1994). Evidently, this parasite is able to complete its life cycle only in seasonally warmed tributaries of the canyon, since cold mainstem temperatures preclude maturation and reproduction and may cause individuals to shed from the host. *L. cyprinacea* has also been reported from flannelmouth suckers, bluehead suckers, speckled dace, common carp, and fathead minnows in Grand Canyon (Kaeding and Zimmerman 1983; AGFD 1993, 1994, 1996; Valdez and Ryel 1995).

Asian tapeworms were first reported in 1990 from the LCR in Grand Canyon, where Angradi et al. (1992) found that 80% of juvenile humpback chub (13–35 mm TL) captured were infested. None had been infested the previous year. During the study period 1990–1994, Clarkson et al. (1997) reported finding Asian tapeworms in 25.5% of juvenile humpback chub (≤100 mm TL, n=411) and 51.3% (>100 mm TL, n=39) of adults examined from the LCR. They also reported the parasite in common carp (25%, n=4). During a 1990–1993 study of mainstem fish, Asian tapeworms were found in gut contents of 6 of 168 (3.6%) adult humpback chub treated with a stomach pump for an average of 6.7 tapeworms per infested fish (range, 1–28; Valdez and Ryel 1995). It was noted that some subadults "appeared emaciated, but the incidence of tapeworms in subadults could not be accurately assessed...." In 1994, AGFD (1996) found Asian tapeworms in 22.5% of humpback chub (12–110 mm TL) caught in the mainstem. The parasite was also found in speckled dace (3.8%), plains killifish (10.3%), and fathead minnows (2.2%). Nearly all (66.7–100%) the infected fish were captured near the LCR, although the parasite was found as far downstream at Kanab Creek, 132 km downstream of the LCR.

The Asian tapeworm is able to complete its life cycle in the LCR because it requires temperatures of >20°C, but it is apparently able to survive in a host in the cold mainstem. The primary host of this tapeworm is one of several species of cyclopoid copepods, and the final host is a fish. Asian tapeworms are reported mostly from minnows and are considered à dangerous parasite to the baitfish industry, where crowded and stressed fish become so heavily infected that the tapeworms clog the intestine of the host (Granath and Esch 1983, Riggs and Esch 1987).

External maladies other than parasites, including fungus, bacterial infections, abrasions, growths, and tumors, were noted on 17 of 6,294 (0.27%) humpback chub (Valdez and Ryel 1995). The fungus appeared to be characteristic of *Saprolegnia* spp., a facultative pathogen that attacks necrotic and injured tissue, including abrasions from net capture or wounds from tagging (Flag 1981). It can also infect apparently uninjured skin. Although not observed on net scars, *Saprolegnia* was noted from the tail region of adult humpback chub and flannelmouth suckers on abrasions apparently inflicted during spawning.

Predation

Predation is probably the most cited interaction between native and non-native fishes in the Colorado River Basin (Tyus and Saunders 1996), possibly because predation is the most easily documented (e.g., with direct evidence from stomachs of non-native predators). Predation may, in fact, be the most common interaction because evolutionary ecology and biology of the native fishes predisposed them to a higher risk of predation under present circumstances (Meffe 1985, Miller 1961, Minckley 1983). Native fish in the Colorado River Basin evolved in relatively predator-limited environments and thus lack "anti-predator traits" (Meffe 1985, Miller 1961). Of 36 fish species native to the Colorado River Basin, only 4 (11%) are known piscivores (Lee et al. 1980). In contrast, at least 26 (46%) of the 57 introduced fishes known to have established in the basin are piscivores, increasing the number of predator species by more than sixfold (Meffe 1985). In Grand Canyon, only 1 (13%) of the 8 native fishes was a known predator—the Colorado squawfish—while 10 (56%) of the 18 non-native fishes are predators (Valdez and Ryel 1995), increasing the number of predator species by tenfold.

Introduction of large numbers and several species of new predators has been blamed, at least in part, for the decline in populations of "naive" native fishes (Meffe 1985, Minckley 1983). It is difficult to confirm predation as the single cause of species reduction or elimination in natural areas (Moyle 1976). In order to observe actual effects of predation on native populations, studies must be conducted soon after initial colonization by the predator (Meffe 1985). However, predation is typically observed after the predator has been established for a period of time and native species have reached an equilibrium with predation pressures (Hawkins and Nesler 1991).

Predators are usually "opportunistic" feeders and will consume any prey made available in large numbers (Hawkins and Nesler 1991). This is especially true when the new food source is disoriented in an unfamiliar habitat. Osmundson (1987) documented predation on newly stocked YOY and juvenile Colorado squawfish by largemouth bass, green sunfish, black crappie, and black bullhead. Largemouth bass switched from their usual prey to feed specifically on the newly introduced squawfish. Similarly, Hendrickson and Brooks (1987) documented predation of Colorado squawfish stocked in the Verde River, Arizona, by yellow bullhead and largemouth bass. Marsh and Brooks (1989) also documented predation of newly stocked razorback suckers by channel catfish and yellow bullheads. The catfish switched from an otherwise omnivorous diets to feed almost exclusively on young suckers. Predation levels by the two catfish species were considered high enough to preclude success of stocking unless introduced razorback suckers were large enough to avoid predation (>300 mm TL).

Several studies in the Upper Basin demonstrate actual and potential predation by piscivorous non-native fishes on native species (Miller and Hubert 1990). Channel catfish consumed Colorado squawfish in the Dolores River (Coon 1965) and in Cataract Canyon (Valdez 1990), as well as speckled dace and bluehead suckers and flannelmouth suckers in the Green and Yampa Rivers (Tyus and Nikirk 1990). Predation on larval Colorado squawfish and razorback suckers by red shiners was demonstrated in the laboratory (Ruppert et al. 1993). Adult fathead minnows and red shiners are suspected of significant predation on young Colorado squawfish in backwaters because these non-natives hatch in spring and become established in nursery habitats used in summer by larval squawfish (Valdez et al. 1982).

Predation by non-native fishes probably occurred prior to Glen Canyon Dam, but the only evidence available is anecdotal. Woodbury (1959) and McDonald and Dotson (1960) reported predation by channel catfish, largemouth bass, and green sunfish within Glen Canyon, but the prey species were not identified. In the first years after the dam was completed, the focus of studies was on rainbow trout in the tailwaters, which were not found to be predaceous, except on threadfin shad escaping through the dam from Lake Powell (Bancroft and Sylvester 1978; Persons 1985; Stone 1964, 1965, 1966; Stone and Queenan 1967; Stone and Rathbun 1968, 1969; Rathbun 1970). Several later studies, however, did document predation on the four remaining native fishes (Carothers and Minckley 1981, Douglas and Marsh 1996b, Minckley 1996, Valdez and Ryel 1995).

Humpback chub. Predation on humpback chub has been documented from the LCR and from the mainstem Colorado River near the LCR. Known predators include channel catfish, brown trout, rainbow trout, and black bullhead. Humpback chub remains were found in approximately 2.5% (Minckley 1996) and 4.0% (Douglas and Marsh 1996b) of channel catfish examined from the LCR, and in 1.5% of channel catfish examined from the mainstem near the LCR (Valdez and Ryel 1995). Channel catfish were the most abundant non-native predator in the LCR (Douglas and Marsh 1996b) and were implicated in attacks on adult humpback chub, as evidenced by crescent-shaped wounds (Kaeding and Zimmerman 1983, Tyus and Karp 1990). These bite marks may represent aggression or unsuccessful predation attempts, since scarred individuals were larger than those normally preyed upon by channel catfish. Many of the wounds were known to have been inflicted when both species were captured in hoop nets (Minckley 1996) and were forced into unnatural proximity to each other.

Predator-prey models (Valdez and Ryel 1995) showed that channel catfish in the mainstem were capable of ingesting humpback chub up to 165 mm TL; larger catfish were observed in the LCR but were not included in this analysis. Remains of humpback chub were also found in stomachs of rainbow trout (A. Leweka, FWS, pers. comm. in Minckley 1996) and black bullheads (Douglas and Marsh 1996b) from the LCR, as well as 10.4% of brown trout from the mainstem (Valdez and Ryel 1995). Predator-prey models (Valdez and Ryel 1995) showed that brown trout in the mainstem were capable of ingesting humpback chub up to 340 mm TL Douglas and Marsh (1996b) also found humpback chub in 2 of 12 (16.8%) black bullhead stomachs examined, indicating that this species was the most significant predator in the LCR, although it occurred in small numbers. Often predators at low densities can impose severe pressures on native fishes in confined environments such as backwaters and tributaries (Hawkins and Nesler 1991, Valdez and Ryel 1995).

Using observed predation rates, Douglas and Marsh (1996b) calculated that channel catfish and rainbow trout in the LCR could potentially consume 3,588 humpback chub per 1,000 predators annually, while Valdez and Ryel (1995) predicted that estimated total populations of brown trout, rainbow trout, and channel catfish in the mainstem could consume approximately 250,000 humpback chub annually (Table 9). By transforming these data into standard weekly consumption rates and setting the number of predators at 1,000, estimated annual potential predation remains at 3,588 in the LCR and readjusts to 4,122 in the mainstem, for a total of 7,710 humpback chub/1,000 predators (i.e., channel catfish, brown trout, rainbow trout). For the principal predators (i.e., channel catfish in the LCR, brown trout in the mainstem), estimated total predation was 8,286 humpback chub/1,000 predators.

These estimates of predation appear to be conservative. Actual numbers of predators in the two systems are difficult to estimate, but are probably well above 1,000 individuals (Valdez and Ryel 1995). In addition, unidentifiable fish remains in stomachs were not considered in the calculations (Douglas and Marsh 1996b, Valdez and Ryel 1995). Laboratory studies demonstrate that fish remains become unidentifiable 4 hours after ingestion (Meffe 1985). Remains of eggs and larvae disintegrated in less time; none were documented in stomachs from non-natives in the LCR area. Furthermore, seasonal variations in predator movement and feeding patterns, which may be linked to water temperature changes in the LCR, were not considered. Marsh and Brooks (1989) demonstrated that channel catfish consumed large quantities of stocked juvenile razorback suckers in spring, but none in winter.

Table 9. Estimates of Humpback Chub Predation in Grand Canyon.

Study	% of Predators	Predator	# Chub Consumed	# Assumed Predators	Annual Predation
Douglas and Marsh (1996b)	3.0%	channel catfish / rainbow trout combined	2.3/week	1,000	**3,588**
Valdez and Ryel (1995)	10.4% 1.5% 1.5%	brown trout, rainbow trout, channel catfish	2.0/day 1.0/day 1.0/day	3,000 5,000 500 8,500	227,760 27,373 2,738 **257,871**
Valdez and Ryel (1995) *transformed*	10.4% 1.5% 1.5%	brown trout, rainbow trout, channel catfish	2.0/week 1.0/week 1.0/week	333 333 333 1,000	3,602 260 260 **4,122**
Douglas and Marsh (1996b) / Valdez and Ryel (1995) *combined*	4.0% 10.4%	channel catfish brown trout	2.75/week 2.0/week	500 500	2,860 5,408 **8,286**

Flannelmouth and bluehead suckers. Reports of non-native predation on flannelmouth and bluehead suckers include remains of "Fingerlings" flannelmouth suckers in stomachs of largemouth bass near Lees Ferry (Stone 1968), remains of a flannelmouth sucker in the stomach of a channel catfish from the mainstem (Carothers and Minckley 1981), and remains of an adult bluehead sucker in the stomach of a brown trout from the confluence of Kanab Creek (Otis 1994). Remains of a bluehead sucker (Carothers and Minckley 1981) and a bluehead sucker and a flannelmouth sucker (Douglas and Marsh 1996b) were identified in stomachs of channel catfish from the LCR. Also, remains of two bluehead suckers, one in the stomach of a brown trout and the other from a channel catfish, were found in the mainstem near the LCR (Valdez and Ryel 1995). These reports suggest that channel catfish and brown trout are the principal predators of native suckers.

Speckled dace. Predation by non-native fishes on speckled dace has been reported from the LCR. Douglas and Marsh (1996b) identified an average of 1.0 speckled dace in 1.2% of rainbow trout stomachs, an average of 1.2 in 2.5% of channel catfish stomachs, and an average of 1.0 in 10% of brown trout stomachs. Neither Valdez and Ryel (1995) nor Carothers and Minckley (1981) found identifiable remains of speckled dace in stomachs of non-native fishes in or around the LCR.

Speckled dace were also found in stomachs of non-native species in the Colorado River outside the LCR. Remains of speckled dace were found in stomachs of rainbow trout, brown trout, channel catfish, and carp from the mainstem between Lees Ferry and Separation Canyon in the 1970s (Carothers and Minckley 1981). They were also found in gut contents of rainbow trout, brown trout, striped bass, and channel catfish in western Grand Canyon, from National Canyon to Lake Mead, in the 1990s (Leibfried and Zimmerman 1994, 1995, 1996). Channel catfish in the latter study were from Spencer Creek (RM 246.0), while the other predators were from the mainstem between RM 169.0 and RM 234.0.

Rainbow and brown trout as predators. Rainbow trout are the most common non-native fish species in Grand Canyon and brown trout are among the largest (Valdez and Ryel 1995). Rainbow trout have been implicated in the decline or elimination of native species in small streams where they were introduced as a game fish (Miller 1968). Decline of the Little Colorado River spinedace in the upper LCR drainage (Blinn and Run 1990) and extirpation of speckled dace in Tapeats Creek (Miller 1968) are attributed to the introduction of rainbow trout.

Although rainbow trout are usually considered "opportunistic omnivorous" (Haden 1992), some strains (e.g., Kamloops) are primarily piscivorous. This is of particular concern in Grand Canyon because of the large population of rainbow trout in the dam tailwaters that is supplemented by hatchery stocks from a variety of strains. Also, local populations of rainbow trout occur at several tributaries and warm springs, such as Vasey's Paradise, Nankoweap Creek, the LCR, Clear Creek, Bright Angel Creek, Shinumo Creek, Deer Creek, Tapeats Creek, and Havasu Creek. Of an estimated 151,000 juvenile rainbow trout with coded wire tags released in the dam tailwaters by AGFD in 1992–1993, only three were recaptured below Lees Ferry, all within 5.6 km downstream (Valdez and Ryel 1995). These mark-recapture results, as well as sampling throughout the canyon, show that there is little downstream dispersal of rainbow trout from the dam tailwaters and little movement elsewhere in Grand Canyon. Hence, predation by rainbow trout on native fishes is probably from fish of local resident populations.

Of 11,121 rainbow trout captured below Lees Ferry in 1990–1993 (Valdez and Ryel 1995), maximum size was 708 mm (28 inches) and 6,641 g (14.6 lbs.). Although large rainbow trout in Grand Canyon are not abundant, it is well known that these fish become increasingly piscivorous with size (Carlander 1969). Fish remains were not found in rainbow trout stomachs during the first few years of stocking at Lees Ferry (Stone 1964, 1965, 1966); however, fish of unknown identity (0.4–0.6% of stomach contents) were found after the trout became established (Stone and Queenan 1967, Stone 1968, Stone and Rathbun 1969). In 1969–1970, fish remains (primary threadfin shad) made up 25.0% of diets of rainbow trout, second only to the "typical" major food source: algae (Rathbun 1970). This increase in piscivory was attributed to the escape of threadfin shad through Glen Canyon Dam following stockings in Lake Powell. The diet of rainbow trout changed dramatically from algae, plankton, insects, and moss in July–January, to 66% fish and 34% algae and insects in February, and 79% fish and 21% algae and insects in March. Before establishment of threadfin shad in Lake Mead in 1954, rainbow trout fed primarily on algae and zooplankton (Jonez and Summer 1954), but shifted to threadfin shad when they became available (McCall 1983).

These results demonstrate the opportunistic and selective nature of rainbow trout for an available source of soft-rayed prey species. This behavior may account for large numbers of humpback chub in stomachs of rainbow trout at the LCR inflow during the mid- to late summer descent of young chubs (Douglas and Marsh 1996b), and the absence of fish in trout diets the rest of the year (Valdez and Ryel 1995). Young humpback chub are particularly susceptible to predation as a result of "thermal shock" during the transition from warm LCR water (20°C) to the cold mainstem (8–10°C), unless water clarity is sufficiently low to preclude trout predation (Valdez and Ryel 1995). Radiotelemetry and diel sampling suggest that humpback chub use turbidity as cover, with greatest activity at about 30 NTUs (Valdez and Ryel 1995), which is the level above which rainbow trout significantly reduce foraging efforts (Barrett et al. 1992). Despite being a cold-water, sight-predator, rainbow trout apparently are still effective predators in marginally warm and turbid waters. Rainbow trout (N=1) taken immediately after a high experimental release from Glen Canyon Dam contained two speckled dace, nine fathead minnow, and one unidentified cyprinid (Hualapai Tribe 1996a).

Brown trout are also significant predators of native fishes in Grand Canyon, but they move greater distances and occupy warmer and more turbid waters than rainbow trout. Although the major population of brown trout appears to be located in and around Bright Angel Creek, large individuals were captured preying on juvenile humpback chub near the LCR inflow (Valdez and Ryel 1995). Of 1,673 brown trout captured in 1990–1993, maximum size was 730 mm TL and 4,423 g (9.7 lbs). According to predator-prey models, a fish of this size is capable of ingesting a humpback chub 340 mm TL. Brown trout apparently move extensively to feed before spawning in late fall and winter (Carlander 1969), and may pose the greatest threat to native fishes at that time.

Brown trout have been implicated in the decline of speckled dace in Bright Angel Creek, although direct evidence of predation has not been reported. Between 1978 and 1992, the number of speckled dace in the creek plummeted, from an estimated density of 2,800 fish/hectare in 1978 (Carothers and Minckley 1981) to only 13 fish caught in more than 1,000 trap-hours in 1992–1993 (Otis 1994). Over the same period (1980–1992), the abundance of brown trout in the lower 3.0 km of Bright Angel Creek increased dramatically, from 4.7% of the creel census in winter 1980 (Usher et al. 1984) to 66.3% of the catch in winter 1992 (Otis 1994). The supposition that predation by brown trout was responsible for the decline of speckled dace in Bright Angel Creek is supported by reports of similar reductions in non-game fish from other systems where brown trout have been introduced (McDowall 1984, Otis 1994).

Competition

Competition has been defined as "the demand, typically at the same time, of more than one organism for the same resources" (Larkin 1956). The resources must be shared and limiting in order for competition to exist. Furthermore, the overlapping resource use must negatively affect one of the two competing species (Li 1979). Competition is difficult to demonstrate because biological responses are often delayed and complex. The most common forms of competition are trophic (for food) or spatial (for habitat, feeding station, or spawning space). Fishes that utilize and rely on the same food resource demonstrate "dietary overlap." If non-native species are better able to utilize a limited food resource, then quality and quantity of food becomes reduced for native species, resulting in decreased condition, fecundity, and survival. Competition for space can manifest similar detrimental effects on native species if introduced species are more aggressive or better suited to conditions. Figure 20 compares spatial fidelity, feeding strategy, and temperature preferences for eight native and eleven non-native fish species of the Colorado River in Grand Canyon.

Non-native fishes overlap native fishes in Grand Canyon with regard to feeding and temperature preferences, but it is unknown if this overlap constitutes competition and negatively affects one or more species. Spawning, egg hatching, and growth temperatures (Figures 21, 22, and 23) are similar for the native fishes and four common non-native species (i.e., red shiners, common carp, fathead minnows, and channel catfish).

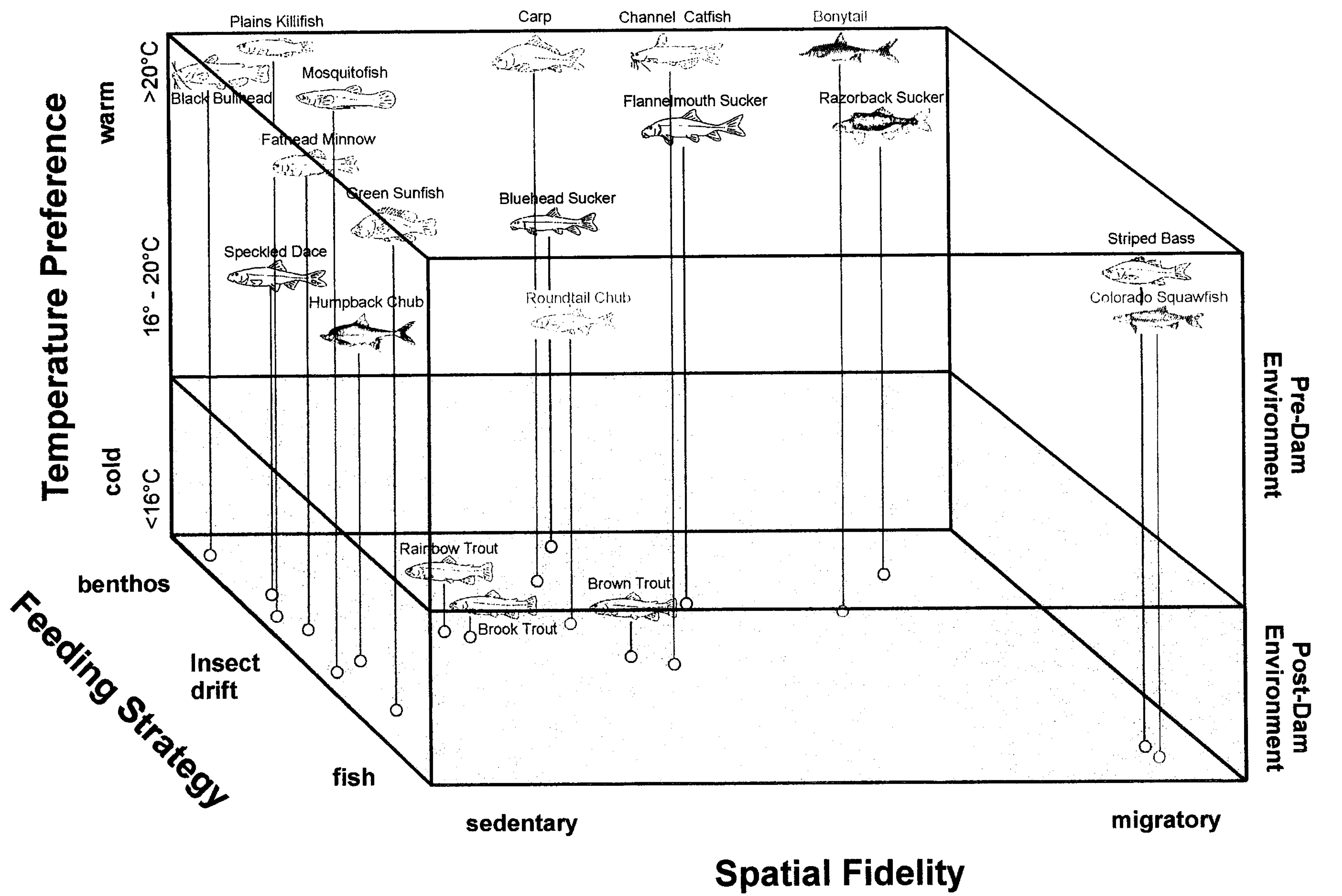


Figure 20. Graph showing guild box with respect to spatial fidelity, feeding strategy, and temperature preference for the 8 native fish species and 11 principal non-native fishes of the Colorado River in Grand Canyon. Extirpated species are shown in red, endangered species are shown in blue, and non-native species are shown in green.

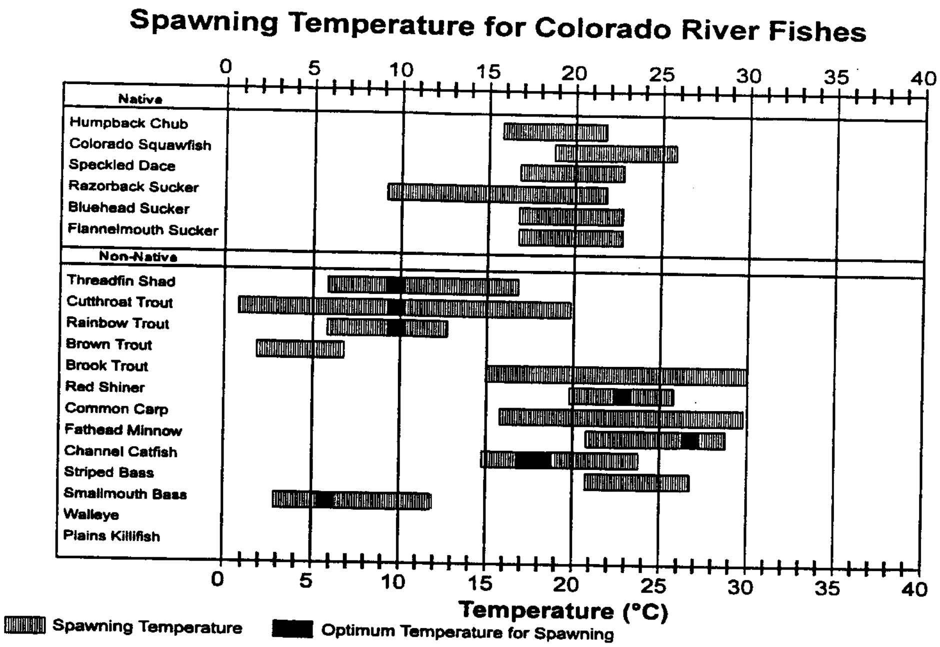


Figure 21. Spawning temperature for Colorado River fishes. (From Valdez and Ryel 1995 and Lechleitner 1992)

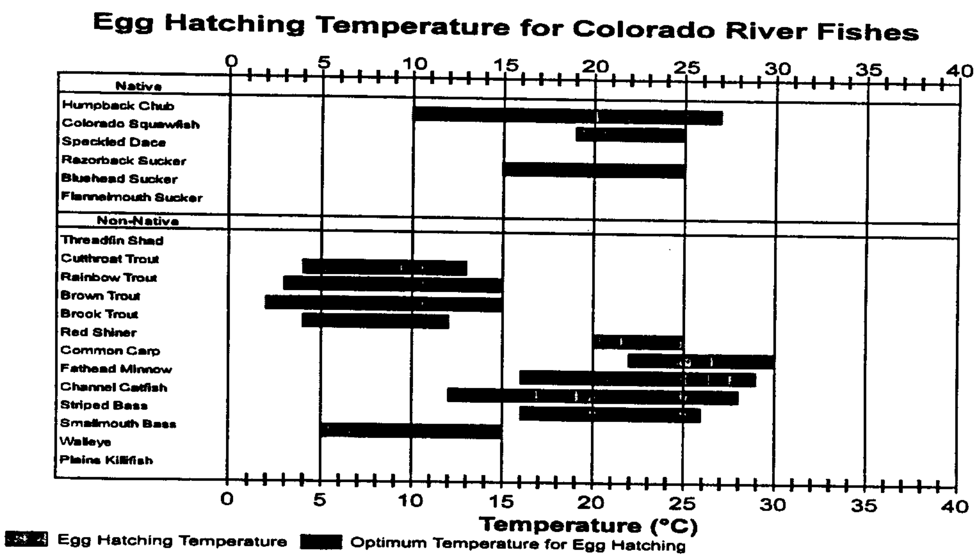


Figure 22. Egg-hatching temperature for Colorado River fishes. (From Valdez and Ryel 1995 and Lechleitner 1992)

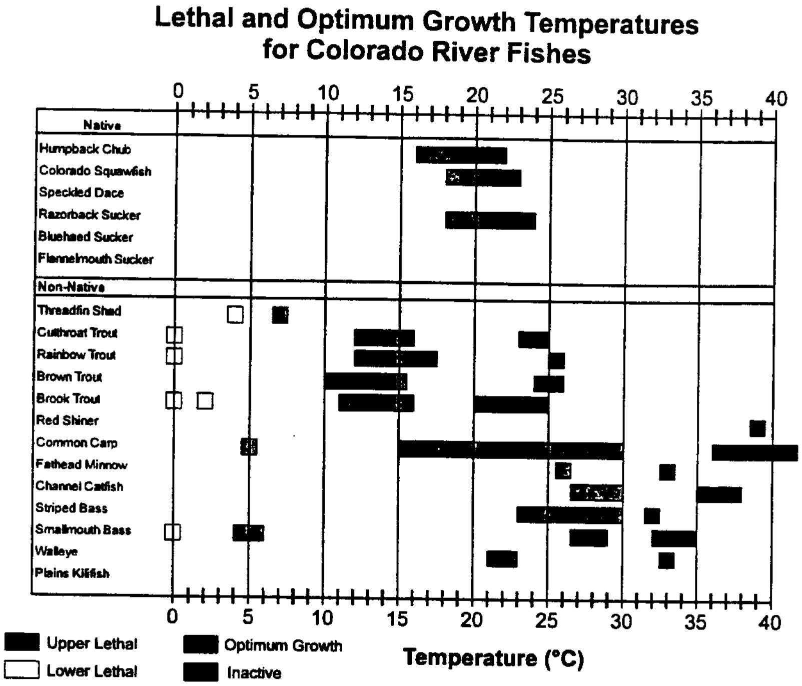


Figure 23. Lethal and optimum growth temperature for Colorado River fishes. (From Valdez and Ryel 1995 and Lechleitner 1992)

Competition for food. Competition for food is implicated between native and non-native fishes in the Colorado River of Glen and Grand Canyons. Carp have been implicated as competitors with native suckers since before construction of Glen Canyon Dam. Woodbury (1959) noted that:

> *The contents of four stomachs of the native flannelmouth sucker and five stomachs of the introduced carp were much alike, containing mainly unidentified amorphous material, probably derived from the ooze and algae of muddy bottoms in pools and backwaters of the river which are their principal home areas. This suggests the idea that there may be considerable competition between the two species and that this may have reduced the native sucker's populations in proportion.*

Diet and habitat overlap were also documented for rainbow trout and humpback chub in Grand Canyon during 1990–1993 (Valdez and Ryel 1995). Although condition of humpback chub was relatively high and stable throughout the study, condition of rainbow trout was lower and more variable, indicating that during periods of high fluctuation and turbidity, feeding opportunities for rainbow trout decreased, while food and feeding opportunities for humpback chub were constant or increased. The extent to which this diet overlap implies competition is unknown.

Competition for food and space is further implicated by the overwhelming biomass attributed to non-native fishes in Grand Canyon (Figure 24). Valdez and Ryel (1995) found that non-native fish

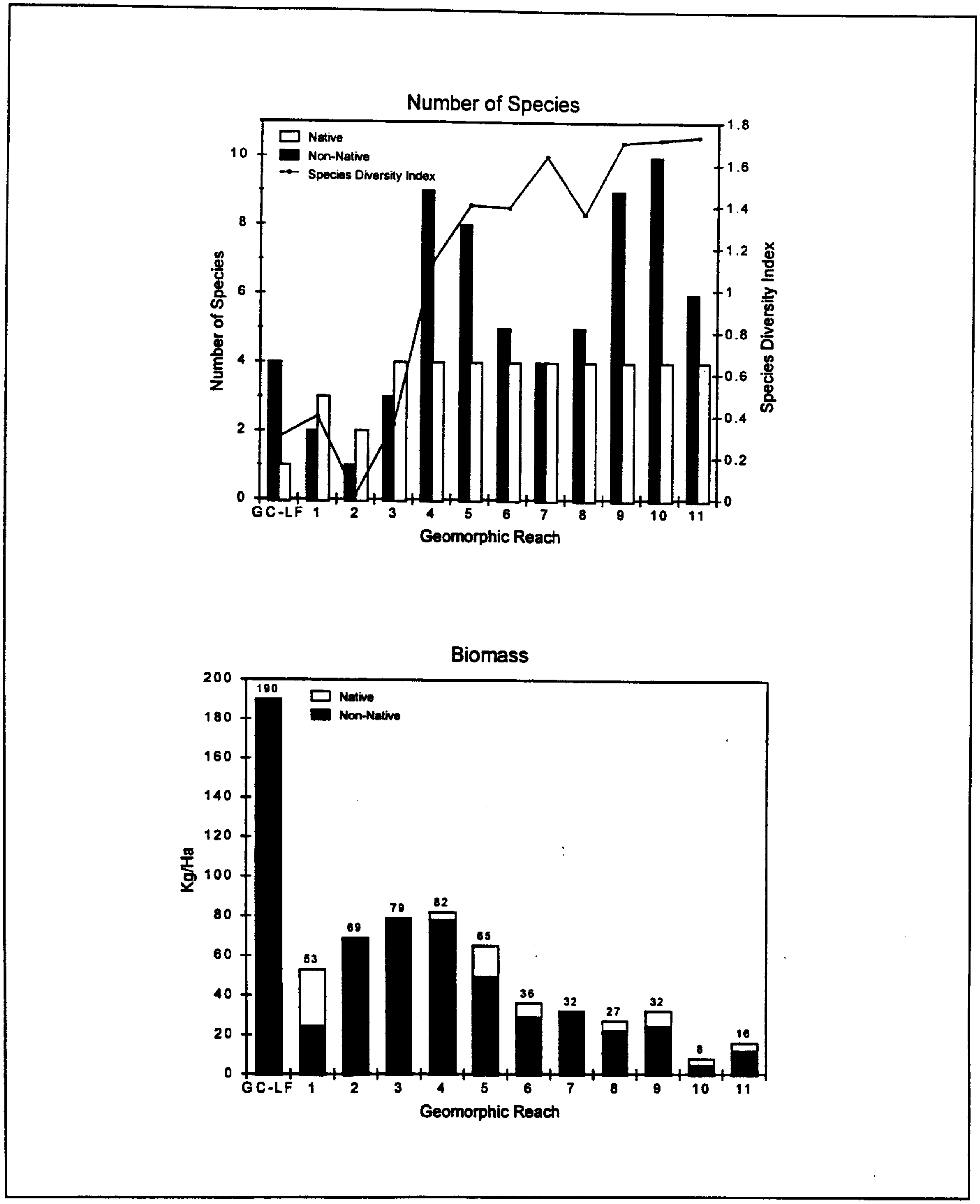


Figure 24. Number of species, species diversity, and biomass of native and non-native fish species by geomorphic reach from Lees Ferry to Diamond Creek. (Source: Valdez and Ryel 1995).

composed over 90% of fish biomass, suggesting that alien fish were utilizing most of the available food supplies. Fish biomass was highest in the tailwaters from Glen Canyon Dam to Lees Ferry (190 kg/ha, primarily rainbow trout) and lowest in the downstream-most reaches (8 kg/ha, trout). Highest biomass, other than in the tailwaters, was associated with the reaches around the LCR, where biomass was dominated by carp and rainbow trout. The two reaches with greatest native fish biomass reflected aggregations of flannelmouth suckers (RM 0–RM 11.3) and humpback chub (RM 61.5–RM 77.4).

In the Upper Basin, various life stages of non-native species (channel catfish, fathead minnows, red shiners, sand shiners, and plains killifish) have diets similar to those of native species (bluehead suckers, flannelmouth suckers, humpback chub and speckled dace; Jacobi and Jacobi 1981). Dietary overlap has also been documented between Colorado squawfish and black bullheads, channel catfish, common carp, and green sunfish (Grabowski and Hiebert 1989), and between juvenile Colorado squawfish and channel catfish and red shiners (McAda and Tyus 1984).

The effects of dietary competition are rarely documented. Osmundson and Berry (1986) demonstrated that juvenile Colorado squawfish had higher growth rate in ponds with sufficient forage fish in the absence of non-native competitors (centrarchids) than in ponds with competitors. Behnke and Benson (1983) suggested that non-native species caused the decline in roundtail chub—the historical food of Colorado squawfish—and thus indirectly contributed to the decline of the squawfish. However, Colorado squawfish seemed to have shifted to red shiners as their primary forage fish (Jacobi and Jacobi 1981), and are known to consume channel catfish (McAda 1983).

Competition for Space. Habitat overlap between native and non-native fishes appears common throughout the Colorado River Basin, particularly in backwaters that are used as nurseries by native species (Miller and Hubert 1990). Adult channel catfish and northern pike were reported in the same habitats as adult Colorado squawfish in the Yampa and Green Rivers (Tyus and Karp 1989, Valdez and Masslich 1989); red shiners and fathead minnows were sympatric with YOY Colorado squawfish (Holden 1977, McAda and Tyus 1984); channel catfish, common carp, and red shiners were found in the same habitat as humpback chub (Behnke and Benson 1983, Holden 1977, Valdez 1990); and channel catfish, green sunfish, largemouth bass, red shiners, and redside shiners overlapped spatially with juvenile chubs (Joseph et al. 1977).

In Glen and Grand Canyons, young humpback chub, flannelmouth suckers, bluehead suckers, and speckled dace use the same backwaters and sheltered shorelines as fathead minnows, red shiners, and plains killifish (Maddux et al. 1987, AGFD 1996, Valdez and Ryel 1995). Significant spatial overlap also exists between adult native fishes and adult carp, channel catfish, and rainbow trout. Habitat overlap may also occur during spawning in tributaries such as the LCR, where large numbers of carp and channel catfish spawn simultaneously with humpback chub, flannelmouth suckers, bluehead suckers, and speckled dace. Although this spatial overlap implies competition, evidence of negative effects has not been documented.

SUMMARY OF NATIVE/NON-NATIVE FISH INTERACTIONS

Native fish populations do not appear to have been negatively affected by alterations in habitat resulting from activities of non-native fishes, except, perhaps, by local disturbance of spawning areas from carp stirring up bottom sediments in the LCR and other warm-water tributaries. The extent of this disturbance and its impact on the reproduction of native fishes, particularly the endangered humpback chub, is unknown. Hybridization between native and non-native fish species has not been documented in Grand Canyon.

Non-native species have probably introduced two notable parasites, *Lernaea cyprinacea* and Asian tapeworm, that currently infect native species in Grand Canyon; however, the negative effects of this transfer of pathogens on native populations is unclear. Although, *L. cyprinacea* is a common ectoparasite on Colorado River fishes, this infestation is not expected to have significant negative effects. The Asian tapeworm, however, has only recently been discovered in fishes of Grand Canyon and poses a serious threat to humpback chub under stressful conditions. The potential for non-native fish to spread these parasites to presently unaffected aggregations of native fish exists but has not been studied. Non-native fishes could introduce additional pathogens into Colorado River ecosystem in Grand Canyon, but the nature and extent of this threat is unknown.

The degree to which non-native fish species have negatively affected native fish populations in Grand Canyon through predation and competition has not been clearly demonstrated. Non-native fishes do prey on native fishes in Grand Canyon. Brown trout, channel catfish, and rainbow trout are the principal predators of humpback chub, flannelmouth suckers, bluehead suckers, and speckled dace. The extent of this predation is not known, but predator-prey models suggest it is substantial (Valdez and Ryel 1995, Douglas and Marsh 1996b). Additional investigations are needed to better define the degree of predation and its effect on native fish populations.

Competition between native fishes and non-native fishes is implied by extensive overlap in diet and sympatry in many habitats for all life stages; however, data on abundances, distribution, and habitat use by non-native species in Grand Canyon is patchy because life history studies of these fishes have not been conducted in the canyon. Little is known about their role in this ecosystem other than what has been reported by early surveys and from incidental catches in sampling for target species (i.e., game fishes such as rainbow trout or endangered fishes). Our knowledge of resource limitations in specific habitats, particularly those in the LCR and along the mainstem shoreline, is also inadequate to accurately assess the nature and extent of competition between species.

Without knowing more about native/non-native interactions under existing flow conditions (i.e., low fluctuating flows), it is difficult to predict which, if either, group of fishes would benefit more from steady flows. We cannot predict the outcome for endangered and other native fishes if, indeed, non-native predators and competitors increase in abundance, but all available evidence suggests a detrimental effect on native species unless these species receive substantially disproportionate benefits from the flows. By their nature, non-native fishes have a more variable range of life history requirements that tends to make them more tolerant and resilient to disturbances than the native fishes in Grand Canyon. Hence, flow modifications, even if they resemble historic regimes, may directly benefit native fishes, but also benefit non-native forms that could result in overall, long-term negative effects on the natives species.

Chapter 8
EFFECTS OF EXPERIMENTAL STEADY FLOWS

INTRODUCTION

Background

As described in the FWS Biological Opinion (FWS 1994a), releases from Glen Canyon Dam for the steady flow experiment are patterned after the Seasonally Adjusted Steady Flow (SASF) alternative in the Environment Impact Statement for the Operation of Glen Canyon Dam (GCDEIS), except that steady flows would be released for only part of each year (April–October), with Modified Low Fluctuating Flows released the rest of the year, and the experiment would be run only in low-volume release years ($\leq$8.23 maf/yr). The SASF alternative was designed to mimic historical seasonal patterns, and is characterized by high, steady flows in May–June, and low, steady flows in summer/fall.

The literature on southwestern river systems is replete with references demonstrating benefits of a natural hydrograph to native fishes, including re-creating historic interactions among hydrology, aquatic habitats and native fish life histories, while disrupting life histories of non-native species (Clarkson et al. 1994, Minckley and Meffe 1987, FWS 1994a and references therein). However, steady flow experiments of the proposed magnitude have not been conducted on a river the size of the Colorado River in Grand Canyon. Some expected or postulated effects are supported by data, but many effects cannot be anticipated because ecological relationships are poorly understood and responses are likely to be complex and long-term. A well-designed experimental steady flow with appropriate monitoring programs would shed light on many aspects of these ecological relationships.

Postulated Effects

The experimental steady flow proposed by FWS in the 1994 Biological Opinion consists of two major hydrologic phases: 1) sustained high spring flows, and 2) low, steady summer/fall flows. We reviewed and evaluated changes likely to occur under these phases to the physical, chemical, and biological aspects of aquatic habitat. Current operations (i.e., Interim Flows, 1991–1996; MLFF, 1996–present) were used as baseline. We then evaluated, in light of our current state of knowledge, possible responses to these changes by each native fish species and important non-native fish species in the system.

Sustained high spring flows are expected to result in high, turbid main-channel flow; ponded tributary mouths; and rebuilt backwater habitats. Low, steady summer/fall flows are expected to result in stable and warm shorelines and backwaters, warm main-channel flow, and a stable main-channel flow with less turbidity. These driving variables, independently and sympathetically, affect aquatic resources throughout the canyon. A composite of postulated effects of these variables on fish is presented in Table 10. This list was assimilated from the review of information presented in this document, as well as from FWS (1994), Reclamation (1995), Valdez and Ryel (1995), and Clarkson et al. (1994).

Table 10. Driving Variables and Postulated Effects of Experimental Steady Flows on Fish.

Low, Steady Summer/Fall Flows

Variable: Stable shorelines and backwaters
- Effect: Increased nursery/rearing habitat
  - Increased holding/feeding habitat for adults
  - Decreased energy expenditures from forced movements
  - Decreased movement-related predation
  - Suppressed dissolved oxygen concentrations in confined backwaters
  - Long-term sedimentation and filling of backwaters

Variable: Warm shorelines and backwaters
- Effect: Increased nursery/rearing habitat for warm-water fishes
  - Increase backwater production
  - Increase incidence of parasitic infestations and pathogenic infections

Variable: Warm main channel
- Effect: Increase spawning opportunities
  - More suitable temperatures for warm-water fish species
  - Increased primary and secondary production
  - Increased opportunity for parasite maturation and proliferation
  - Reduced effects of thermal shock
  - Decreased energy expenditure

Variable: Stable main-channel flow and less turbidity
- Effect: Increased shoreline primary and secondary production
  - Increased risk of predation from sight predators
  - Reduced daytime feeding activity
  - Reduced macroinvertebrate drift as food for fish

Sustained High Spring Flows (i.e., habitat maintenance, habitat/beach building)

Variable: Inundated backwaters and shoreline habitats
- Effect: Unavailability of backwaters for young fish
  - Change in stage elevation of shoreline habitats
  - Availability of flooded shoreline vegetation
  - Ponding of dry canyon mouths

Variable: High, turbid main-channel flow
- Effect: Surge of increased macroinvertebrate drift as food for fish
  - Increased feeding opportunities for non-sight feeders, including native fishes
  - Increased density of terrestrial invertebrates (as food for fish) washed from shorelines
  - Displacement of fish in high sediment depositional zones of recirculating eddies
  - Reinforced spawning cues for spring-spawning fish
  - Unsuitable conditions for non-native fishes

Variable: Ponded tributary mouths
- Effect: Increased nursery habitat and thermal acclimation for YOY descending from tributaries
  - Increased access to tributaries for spawning adults
  - Concentrations of predators at tributary inflows

Variable: Rebuilt backwater habitats
- Effect: Increased nursery/rearing habitat following high flows
  - Increased adult feeding/holding habitat
  - Increased primary and secondary production in backwaters following redistribution of organics

For example, past studies and observations consistently show that steady flows result in a warmer main-channel flow. The degree of warming, longitudinally down the river and laterally to shoreline habitats, is not well known, but is important information for anticipating responses by different life stages of various aquatic resources.

The following sections provide a discussion of postulated effects of low, steady summer/fall flows and sustained high spring flows. For each of these flow phases, variables and associated effects have been identified. Each effect is described as the most likely scenario, based on existing data and information.

POSTULATED EFFECTS - LOW, STEADY SUMMER/FALL FLOWS

Stable Shorelines and Backwaters

Increased Suitable Nursery/Rearing Habitat. Backwaters are sheltered, productive habitats used by a variety of fish species throughout the Colorado River Basin (Holden and Stalnaker 1975a, 1975b; Tyus et al. 1982; Valdez et al. 1982). In the post-dam river in Grand Canyon, stable, persistent backwaters (i.e., eddy return-current channels), warmed by solar radiation, may be highly desirable as refugia for warm-water fishes from cold mainstem temperatures (AGFD 1996, Stevens et al. In Press). Backwaters; shallow, sheltered shorelines; tributary inflows; and occasional thermal springs are the only mainstem habitats available for nursing and rearing of warm-water native species in this confined canyon region of the Colorado River. Hence, flow releases that maximize the number of reliable backwaters could be desirable and beneficial for native fishes (FWS 1994a, Clarkson et al. 1994, Valdez and Ryel 1995, Reclamation 1995).

The relationship of higher numbers of backwaters at low, steady mainstem flows has been described by several investigators (Anderson et al. 1986, J. Weiss 1993, McGuinn-Robbins 1995, Brouder 1996). Flows between 5,000 and 10,000 cfs were established in the GCDEIS as the basis for producing significantly more backwaters than flows greater than 10,000 cfs (Reclamation 1995). This supposition is based primarily on work by J. Weiss (1993) and McGuinn-Robbins (1994). J. Weiss (1993) compared backwaters with a surface area over 100 m^2 at steady flows of 15,000 cfs and 5,000 cfs, and found an increase of 46 to 114 backwaters and more than twice the area at the lower flow. McGuinn-Robbins (1994) also found significantly more backwaters (42 vs. 21) at a low, steady flow of 5,000 cfs than at a higher steady flow of 8,000 cfs.

Although a correlation exists between lower discharges and greater numbers of backwaters, precise numbers and persistence of specific backwaters could not be reliably predicted. McGuinn-Robbins (1994) counted backwaters from Lees Ferry to Diamond Creek for 4 years (1990, 1992, 1993, and 1994) at constant steady flows of 8,000 cfs (released annually during Easter weekend for aerial photographic documentation), and found that the total number of backwaters varied substantially: 146 in 1990, 70 in 1992, 113 in 1993, and 89 in 1994. Variation was attributed to changes in mainstem sediment load and different eddy return-current channel elevations as a result of different antecedent flows.

The importance of shoreline habitats to native fishes in Grand Canyon has been known for some time, but the focus of studies has been limited to backwaters (Maddux et al. 1987; AGFD 1993, 1994, 1995). In 1990–1993, Valdez and Ryel (1995) and Converse (1997) discovered extensive use of other shoreline habitat (talus, debris fans, vegetation) by juvenile humpback chub. These studies, in coordination with studies by AGFD, revealed that juvenile humpback chub consistently used shorelines with abundant cover at higher densities of individuals than in backwaters. Valdez and Ryel (1995) and Converse (1997) also discovered that these shorelines can undergo considerable changes with change in river stage as a result of dam operations. They hypothesized that the magnitude and rate of these changes contribute to low juvenile survival and recruitment seen for the species in Grand Canyon.

It can be assumed that experimental steady flows will stabilize backwaters and other mainstem rearing habitats, but the sequence of flow discharges necessary to optimize the amount of rearing habitat is unknown. It is also unknown how any given sequence of flows affects the availability of backwaters and specific types of shorelines longitudinally through the canyon (Schmidt and Graf 1990, Rubin et al. 1990, Melis and Webb 1993). Even if these physical relationships are defined and understood, the relative importance of backwater habitats for native fishes in Grand Canyon is likely to remain a point of debate by researchers (See discussion on habitat of humpback chub in Chapter 5).

Increased Holding/Feeding Habitat for Adults. Radiotelemetry with adult humpback chub (Valdez and Ryel 1995), sonic telemetry with adult flannelmouth suckers (Thieme 1997), and widespread sampling (Carothers and Minckley 1981, Maddux et al. 1987, Valdez and Ryel 1995) have shown that the majority of fishes in Grand Canyon use all but the central third of the river channel. Young fish prefer habitats in shallow, sheltered areas, while adults tend to use deeper eddies, runs, or pools, although adults frequent shorelines at night to forage under the security of darkness. Enhanced stability of shorelines is likely to benefit adults of all species by providing nocturnal holding and feeding areas. This requirement is probably not critical to adults of large mainstem species, since these fish are capable of holding and feeding in a variety of habitats. However, stable shorelines are vital to survival of small species, such as speckled dace, fathead minnows, red shiners, and plains killifish. During the habitat/beach-building flows (i.e., 45,000 cfs) of spring 1996, only native speckled dace used alternative habitats, while juvenile humpback chub remained along talus slopes and debris fans (Hoffnagle et al. 1996). The inability of small non-native species to seek and find alternative habitats may be a factor in attempting to control these species through high releases.

Decreased Energy Expenditures from Forced Movements. The amount of energy expended by fish forced to leave habitats is unknown. In radiotelemetry studies of adult Colorado squawfish and razorback suckers in the Green River, Valdez and Masslich (1986) determined that fluctuating flows from Flaming Gorge Dam caused stage changes and ice floes that forced fish near the dam to move significantly more than fish located far downstream and away from effects of dam operations. This additional energy expenditure was identified as a possible detriment to the fish, but could not be quantified as loss of weight, condition, or spawning readiness. Radiotelemetry studies of adult humpback chub have shown little movement by individuals, even during the high (45,000 cfs) release of spring 1996. However, shoreline inhabitants, such as juvenile humpback chub, forced to abandon preferred habitats during changes in river stage, are likely to expend additional energy, but the effects of that expenditure are unknown.

Decreased Movement-Related Predation. It is surmised that since non-native fish became residents in Grand Canyon, the number of piscivorous fish species in Grand Canyon has increased tenfold, from one to ten (Valdez and Ryel 1995). Experimental steady flows are expected to allow young fishes to remain along sheltered shorelines and in persistent backwaters, reducing the risk of predation that would otherwise occur if these habitats were regularly inundated and desiccated by fluctuating flows. Risk of predation along shorelines and in backwaters is also a function of water clarity and depth. Predation by sight-feeders, such as rainbow trout and brown trout, would be expected to be higher in clear water. Predation by nocturnal predators, such as channel catfish, would probably occur regardless of turbidity, assuming that water was sufficiently deep for large predators to access prey species.

Suppressed Dissolved Oxygen Concentrations in Confined Backwaters. Low dissolved oxygen can be a problem for fish in backwaters lacking sufficient circulation (J. Weiss 1993, Kennedy 1979, Vanderford 1980, Holland et al. 1983, Gutreuter 1980), but is not expected to be a problem with fish in Grand Canyon. Oxygen in slack water environments like backwaters is controlled by chemical and biological oxygen demand, temperature, water circulation, and bottom substrate (Doudoroff and Shumway 1967). Steady flows in Grand Canyon allow backwaters to stabilize and accumulate sand and silt, with increased algal and macrophytic growth (Johnstone and Stevens 1996). High water temperatures and dense growths of aquatic plants and algae can cause "oxygen sags" as a result of oxidation of organic matter and nocturnal respiration by plants. These conditions often limit certain species of fishes and invertebrates (Kennedy 1979).

AGFD (1996) and Hoffnagle (1997) reported that mean dissolved oxygen levels in a backwater in Grand Canyon were lower (10.04 mg/L) under short-term steady flows (8,000 cfs) than under fluctuating flows (10.80 mg/L). The mean minimum concentration under steady flows was 8.89 mg/L, compared to 10.11 mg/L under fluctuating flows. These differences were attributed to alternating photosynthetic and respiratory activity by algae (AGFD 1996). Fluctuating flows infuse fresh river water that moderates oxygen sags, but steady flows stagnate warm, oxygen-deficient water. Short-term steady flows did not produce detrimental oxygen levels for fish, and, although the effects of steady flows of longer duration are not known, detrimental effects are not expected as a result of an experimental steady flow.

Long-term Sedimentation and Filling of Backwaters. Steady flows in Grand Canyon will allow backwaters to stabilize and accumulate sand and silt, with increased algal and macrophytic growth. Sediment deposition buries and suffocates invertebrates and algae (Waters 1995) and resets community succession in backwaters and slack water nearshore areas (Johnstone and Stevens 1996). Backwaters would be expected to fill faster under sustained steady flows than under current operations (Reclamation 1995); however, such effects would be limited under experimental steady flows because these releases are proposed for only 7 months (April–October) of the year, and only in low-volume years (i.e., <8.23 maf). Habitat/beach-building flows designed to reform eddy return-current channels would be released under current operations but not under the experimental flows because the habitat/beach-building flows can only be released during high-volume years, and the experimental steady flows only during low-volume years. Stevens et al. (1995) present data indicating that releases of 50,000–60,000 cfs may be necessary to reform backwaters.

Warm Shorelines and Backwaters

Increased Nursery/Rearing Habitat for Warm-Water Fishes. Temperature has been identified by many investigators as a principal limiting factor to reproduction, survival, growth, and recruitment of warm-water fishes in Glen and Grand Canyons. Hence, dam operations that produce and enhance warm-water habitats will tend to favor warm-water fish communities. Shallow backwaters warm by solar radiation, particularly with hot summer temperatures, if they are not periodically flushed by cold mainstem waters (Maddux et al. 1987, Angradi et al. 1992). Valdez and Ryel (1995), during high fluctuating flows and interim flows, measured a summertime daily average of 1 °C/51 km longitudinal warming, from 8 °C at the dam to 15.5 °C at Diamond Creek, 389 km downstream. A temperature model by GCMRC (Jeanne Korn, GCMRC, per. comm.) predicts maximum warming of 1 °C/45 km under interim flows and MLFF. Depending on the temperature of the water released from the dam, main-channel temperatures at Diamond Creek reach about 20 °C under current operations, when release temperatures are at a maximum of 12 °C. Longitudinal warming is expected to be greater under experimental steady flows. AGFD (1996) reported that the mean temperature of selected backwaters was 14.53 °C under short-duration steady flows and only 11.97 °C under fluctuating flows. It can be surmised that potential maximum backwater temperatures under long-term steady flows, assuming little or no circulation, should be comparable to Upper Basin maximum backwater temperatures: about 25–30 °C (Tyus et al. 1982, Valdez et al. 1982). Maddux et al. (1987) found that some backwaters in Grand Canyon warmed to daytime highs of nearly 25.0 °C during short-term, low, steady flows in summer, while main-channel temperatures remained about 10.0 °C.

Experimental steady flows will also stabilize tributary inflows and warm springs. Valdez and Ryel (1995) reported that perennial tributaries warmed to temperatures higher than mainstem levels from about April through September, and provided warm plumes of up to 200 m extending into the mainstem. Maximum summer temperatures in tributaries often exceed those of the mainstream by 10.0 °C (Maddux et al. 1987), with warmer tributaries, like the Paria River and Kanab Creek, at temperatures of up to 33.9 °C and 35.0 °C, respectively (S.J. Weiss 1993, Valdez and Ryel 1995). Cooler tributaries, like Bright Angel Creek, have been measured at temperatures of up to 23.9 °C (Maddux et al. 1987). Steady flows could result in more persistently warm tributary inflows, depending on inflow geomorphology.

Riverside and in-channel warm springs create thermal plumes that attract large numbers of fish in Glen and Grand Canyons. Two of the nine mainstem aggregations of humpback chub are associated with warm springs, and other thermal areas support large numbers of fish of various species. Experimental steady flows will probably enhance the value of these springs, depending on spring elevation and local hydraulic patterns, by enabling fish to remain in place, and by enhancing survival of eggs and young hatched in these areas. In July 1993, about 100 YOY humpback chub were found in a warm spring at RM 30.0, but these fish were not present 1 month later, following a period of fluctuating flows (Valdez and Masslich In Review).

Increase Backwater Production. Areas of slower current (backwaters, eddies, wide canyon reaches) are considered important for production of algae and aquatic invertebrates because they trap organic material and may be warmer than mainstem waters. Daily fluctuation in flow rate causes temporal instability in backwaters that reduces the level of biological productivity (Clarkson et al. 1994). The transitory nature of nearshore habitats in Grand Canyon has rendered them largely unsuitable for colonization by desiccant-intolerant algae and invertebrates (Usher and Blinn 1990, Angradi et al. 1992). The length of time a backwater would have to remain stable to result in increased productivity cannot be predicted.

Increase Incidence of Parasite Infestations and Pathogenic Infections. Increased temperatures in backwaters could allow Asian tapeworms (*Bothriocephalus acheilognathi*) to mature (>20 °C is required) and shed eggs into the water to be consumed by copepods (its primary host), which, in turn, would be ingested by fish (its final host). This parasite, which tends to select cyprinid species, can kill the host fish by blocking its gastrointestinal tract and damaging intestines (Brouder and Hoffnagle 1996). Chronic debilitating effects indirectly threaten host survival (Clarkson et al. 1997). In Grand Canyon, Asian tapeworms have been documented in humpback chub, speckled dace, common carp, fathead minnows, and plains killifish (Clarkson et al. 1997, AGFD 1996). Infection rates appear to be high in the LCR, probably because high water temperatures there allow the Asian tapeworm to complete its life cycle, but relatively low in the mainstem, where low water temperatures largely preclude its maturation (Valdez and Ryel 1995). Warmer, more stable backwaters could provide additional habitats for this parasite to propagate and for host copepods to substantially increase in abundance, resulting in the spread of the Asian tapeworm infestation along the mainstem and into additional warm-water tributaries. Such an occurrence could seriously threaten the humpback chub population, and possibly speckled dace populations, in Grand Canyon.

Increased temperatures and stability in backwaters could also promote the spread of the parasitic copepod *Lernaea cyprinacea* throughout the fish assemblage. Although this parasite, which lacks host specificity, rarely causes death to the host fish, it can contribute to stress under less than optimal environmental conditions.

No other pathogens are expected to be problematic for fishes in Grand Canyon, although many opportunistic, facultative organisms generally increase in incidence at warmer temperatures. Increasing temperatures of backwaters could lead to increased incidence of fungal and bacterial infections, coincidental to injuries or from abrasions sustained during spawning activity.

Warm Main Channel

Increase Spawning Opportunities. Mainstem spawning by warm-water fishes has not been documented in Grand Canyon since Glen Canyon Dam began releasing cold hypolimnetic waters in the early 1970s. Nevertheless, ripe and gravid flannelmouth suckers have been found attempting to spawn in the dam tailwaters (Thieme 1997; T. McKinney, AGFD, pers. comm.), near the Paria River (S.J. Weiss 1993), and in various other locations throughout the canyon (Carothers and Minckley 1981, Maddux et al. 1987, Valdez and Ryel 1995, Leibfried and Zimmerman 1995, Valdez et al. 1995). Ripe and gravid humpback chub have also been found in several mainstem locations, and YOY were found in a warm spring at RM 30.0 (Valdez and Masslich In Review). These observations suggest that warm-water fishes would spawn in the mainstem given suitable temperatures, 14–22°C for most species. The experimental steady flows are expected to warm the mainstem and may provide these suitable spawning temperatures, especially in the lower canyon. Degree of warming and longitudinal rate of warming are critical information in predicting response by various fish species. Timing and duration of warming are also critical. Suitable temperatures would have to occur when fish reach peak gonadal maturation, and temperatures would have to persist long enough for young fish to sufficiently deal with resumed cold mainstem temperatures and fluctuating flows.

More Suitable Temperatures for Warm-Water Fish Species. Maximum longitudinal warming of the Colorado River has been recorded at between 1°C/45 km and 1°C/51 km, depending on dam operations and water volume. This has resulted in an increase in water temperature from about 8.0°C at the dam to about 16.0–20.0°C at Diamond Creek, about 389 km downstream. Under steady summer/fall flows, longitudinal warming would be expected to increase at a higher rate. Valdez and

Ryel (1995) found that the mainstem temperature at Diamond Creek (RM 226.0) increased by 3.0°C as result of a short-term change in operations (from fluctuating flows to steady flows of 5,000 cfs) after only 3 days. Hence, low, steady flows of comparable magnitude would be expected to produce mainstem temperatures of well over 20°C near Diamond Creek.

Increased Primary and Secondary Production. Warmer water temperatures are likely to support a greater diversity and biomass of macroinvertebrates than do present mainstem temperatures. These conditions would allow for greater survival and reproduction by zooplankton (i.e., rotifers, copepods, cladocerans) passing through Glen Canyon Dam from Lake Powell. Blinn et al. (1995) found a greater diversity of macroinvertebrates in downstream reaches of Grand Canyon as a result of longitudinal warming from interim flows and MLFF. Drifting invertebrates from tributaries can quickly colonize mainstem habitats, given suitable temperature and water quality. It is not known, however, if the duration of the experimental steady flows (i.e., 7 months) is sufficient to establish thermal regimes suitable for completion of insect life cycles.

A potentially negative effect of warm mainstem temperatures would be a shift in epiphytic diatom communities. Laboratory experiments by Blinn et al. (1989) showed that epiphytic diatom communities from dam tailwaters changed from large, upright forms to small, more adnate forms with an increase in water temperature from 12.2°C to 17.8°C. Adnate forms of diatoms may be more difficult for invertebrates and fish to consume, resulting in a loss of high-lipid energy gained by ingesting diatoms (Leibfried 1988).

Increased Opportunity for Parasite Maturation and Proliferation. Mainstem temperatures in excess of 15°C would allow maturation of *Lernaea cyprinacea*, and temperatures in excess of 20°C would allow maturation of *Bothriocephalus acheilognathi*. Proliferation of these parasites might be possible in very sheltered shoreline environments if these areas consisted of warm quiet water, silt beds, and an abundance of cyclopoid copepods. Although few mainstem habitats would meet these requirements, warm mainstem temperatures would allow these parasites to mature, which would increase the risk of transmission to other fish when the hosts entered backwaters or tributaries.

Reduced Effects of Thermal Shock. Thermal shock from cold mainstem temperatures has been recognized as a possible cause of mortality for young fish leaving seasonally warmed tributaries (Lupher and Clarkson 1993, 1994; Valdez and Ryel 1995; Thieme 1997). Young fish, particularly newly hatched larvae of native species, drift from natal tributaries into the mainstem (Robinson et al. 1996, S.J. Weiss 1993, Thieme 1997), making a transition from water temperatures of about 20°C to temperatures of about 10°C. The extent of drift (i.e., numbers of young) of a given species, the timing of drift, and the tributaries from which these fish drift are not known. However, the phenomenon of drift is common with flannelmouth suckers, bluehead suckers, and speckled dace in Upper Basin populations (Muth and Snyder 1995, Valdez et al. 1985). Laboratory studies clearly show "cold shock," stress, slowed growth, and mortality of larval fish exposed to sudden temperature change. Cold shock can also illicit predator responses. Experimental steady flows could enhance survival of young fish by warming the mainstem and reducing the magnitude of temperature change.

As with other temperature-related effects, the patterns of warming from steady flows would need to be known to determine if the effects are beneficial to fish. Laboratory tests showed total mortality of embryos of humpback chub and other native fishes at 10.0°C and high incidence of deformities at 15.0°C (Marsh 1985). Only 15% of humpback chub "swim-up fry" (6.9 mm long) survived at 12.0–13.0°C (Hamman 1982), and chubs 5–7 days old (9 mm TL) and 11–13 days old (11 mm TL) experienced "cold shock"when transferred from 20.0°C to 10.0°C (Lupher and Clarkson 1994). Survival of humpback chub eggs was 12%, 62%, 84%, and 79% at 12–13°C, 16–17°C, 19–20°C, and 21–22°C, respectively, while survival of larvae was 15%, 91%, 95%, and 99%, respectively (Hamman 1982). Knowing the extent of longitudinal warming in the mainstem is critical to predicting the effect of steady flows on native and non-native fishes.

Decreased Energy Expenditure. Native fish in the mainstem do not appear to move much in response to various flow regimes. Except for local activity in response to changes in microhabitat depth or velocity, most movement seems related to spawning events. Radiotelemetry studies of adult humpback chub showed movement to and from the LCR for spawning but little movement otherwise, even during the high, 45,000 cfs release during spring 1996 (Valdez and Cowdell 1996, Valdez and Hoffnagle In Review). Sonic tracking revealed considerably more movement of adult flannelmouth suckers than of humpback chub, but most seemed to be related to spawning events and not to changes in river stage (Thieme 1998). Steady flows are likely to require less movement by individual fish, but the effect of the energy saved is unknown with regard to survival, growth, reproduction, or general health. Although experimental steady flows may not benefit mainstem inhabitants, juvenile fishes along shallow shoreline habitats are likely to benefit from energy savings.

Stable Main Channel Flow and Less Turbidity

Increased Shoreline Primary and Secondary Production. Light penetration and attenuation, which determine primary and secondary productivity in mainstem habitats, are a function of water depth and clarity. Yard et al. (1993) found that, at 5,000 cfs, light penetration reached the bottom of the river throughout the canyon, but at 15,000 cfs, light penetration was prevented by depth and turbidity and failed to reach the bottom in some reaches below RM 150.0. All observations of steady flows, in the absence of local turbid tributary floods, have shown increased water clarity, which would be expected to result in increased algal growth and increased densities of diatoms and possibly macroinvertebrates (Kennedy 1979, AGFD 1996, FWS 1994a). Extreme fluctuations in nearshore habitats have rendered cobble flats largely unsuitable for colonization by desiccant-intolerant algae and invertebrates (Usher and Blinn 1990, Angradi et al. 1992). The green alga *Cladophora glomerata* dies after 12 hours or less of exposure to air (Leibfried and Blinn 1987, Usher et al. 1988, Blinn et al. 1992, Angradi et al. 1992, Angradi and Kubly 1993), and recovery can be protracted, if it occurs at all (Pinney 1991, Angradi et al. 1992). Gross primary productivity of *Cladophora* was 10 times greater when permanently inundated than when subjected to daily fluctuations.

Increased Risk of Predation from Sight Predators. Few sight predators in the mainstem are capable of consuming adult humpback chub, flannelmouth suckers, or bluehead suckers. Although length-frequency analyses showed that 30% of brown trout in Grand Canyon are capable of ingesting adults (>200 mm TL), predator-prey models (Valdez and Ryel 1995) showed that most rainbow trout and brown trout are capable of ingesting only subadult native fish (<200 mm TL). The incidence of predation in offshore habitats is probably not high. Most predation probably occurs in nearshore habitats. It is expected that experimental steady flows will increase water clarity downstream of Glen Canyon Dam and increase risk of predation by sight-feeders, primarily along shorelines.

Reduced Daytime Feeding Activity. Radiotagged adult humpback chub were found to be significantly less active in the daytime when the main channel was clear than when turbidity exceeded 30 NTU's (Valdez and Ryel 1995). Similar activity was noted for juveniles, as indicated by electrofishing and minnow trap catch rates. These observations indicate that humpback chub use turbidity as cover, to escape predators, and to feed in the mid-water column in large recirculating eddies. Experimental steady flows are expected to reduce mainstem turbidity and possibly reduce daytime feeding activity by these fish. Nighttime feeding in clear water may expose these fish to increased risk of predation by sight-predators (e.g., rainbow trout, brown trout) and nocturnal predators (e.g., channel catfish).

Reduced Macroinvertebrate Drift as Food for Fish. The absence of changes in water velocity and river stage associated with daily flow fluctuations are likely to reduce the amount of algae (*Cladophora*) and macroinvertebrate drift (Angradi et al. 1992, Reclamation 1995, Leibfried and Blinn 1987, Blinn et al. 1992). Fluctuating flows alternately wet and dry portions of the nearshore "intertidal" zone, dislodging algae and invertebrates, and flushing terrestrial insects, arthropods, spiders, and other potential fish food items into the river (Leibfried et al. 1987). Experimental steady flows would largely negate this effect and reduce available macroinvertebrates in drift. Leibfried and Blinn (1987) reported a positive correlation between increasing range of discharges and drift of *Gammarus* during transition from steady flows to fluctuating flows, although *Cladophora* and chironomid larvae did not respond similarly. Valdez et al. (1992) observed the highest density of macroinvertebrate drift during the down-ramp of fluctuating flows. Hence, the majority of studies show a strong relationship between steady flows and reduced macroinvertebrate and algal drift. However, steady flows of longer duration may invoke behavioral traits (e.g., insect emergence) or growth cycles (*Cladophora* sloughing) not observed during steady flows of shorter duration. Leibfried and Zimmerman (1996) measured an increase in invertebrate drift under steady flows during one sample period at Granite Park (RM 209.0), an area far enough away from the dam that fluctuating flows are normally modulated. Little information exists on the effects of steady flows on planktonic drift (i.e., rotifers, copepods, cladocerans), an important source of food for YOY and juveniles, including humpback chub, flannelmouth suckers, and bluehead suckers (Haury 1988, Maddux et al. 1987)

POSTULATED EFFECTS - SUSTAINED HIGH SPRING FLOWS

Inundated Backwaters and Shoreline Habitats

Unavailability of Backwaters for Young Fish. Backwaters in Grand Canyon are typically inundated by moderate and high flows and are no longer available to young fish as nurseries and rearing areas. This effect can be damaging to a year class of fish if inundation occurs in late spring and summer when young are in backwaters. Researchers in Grand Canyon have found backwater numbers and surface areas highest at lower discharges when comparing 5,000 and 15,000 cfs (J. Weiss 1993); 5,000 and 8,000 cfs (McGuinn-Robbins 1994); and 8,000 cfs (Brouder 1996). Carothers and Dolan (1982) suggested that flows of 40,000 cfs would inundate most backwater humpback chub habitat under widely fluctuating flows (3,000–31,500 cfs). AGFD (1996) noted that under interim flows, backwaters would be inundated at about 20,000 cfs. Backwaters during the beach/habitat-building flow in spring 1996 were completely inundated at about 30,000 cfs, but many reattachment bars were topped and eddy return-current channels were flooded at about 25,000 cfs (R. Valdez, SWCA, pers. observ.). The general conclusion is that most backwaters in Grand Canyon are available at lower flows (i.e., <15,000 cfs), but that the relationship between backwater formation and flow stage is variable. Since most backwaters in Grand Canyon are formed by eddy return-current channels associated with reattachment bars (Rubin et al. 1990), the elevation at which these channels form or become inundated depends on the magnitude and duration of antecedent flows, as well as on local channel geomorphology. These relationships are not fully understood; therefore, it is not currently possible to identify a specific range of sustained high flows and low steady flows that would maximize backwater habitats.

Change in Stage Elevation of Shoreline Habitats. Change in volume of dam releases from MLFF to high sustained flows can dramatically alter the character of shoreline habitats, and negatively affect native fishes, particularly at earliest life stages. Shoreline habitats, particularly talus, debris fans, and vegetation, are important for speckled dace and young humpback chub (Valdez and Ryel 1995, Converse 1996). Large vertical changes in river stage can dramatically change the character of a given shoreline from a talus slope to a sandbar or a cliff face. These changes can significantly alter depth and velocity characteristics of the narrow 1- to 2 m-wide strip along the shoreline used most frequently by these fish. Change in operation from MLFF to high sustained flows are likely to significantly alter these shoreline habitats, possibly forcing fish to seek alternative sites.

Availability of Flooded Shoreline Vegetation. The new high-water zone along the Colorado River in Grand Canyon places willows, tamarisk, and other plants in close proximity to the high-water line of current operations (i.e., 20,000-25,000 cfs). High discharges associated with experimental steady flows will inundate this vegetation, creating potential habitat for fish. Inundated shoreline vegetation was substantial during the beach/habitat-building flow in spring 1996, but fish use of the newly created habitat was not as extensive as expected (Valdez and Cowdell 1996, Hoffnagle et al.1996). Non-native fathead minnows did use these areas, but the majority of humpback chub remained in shorelines classified as talus or debris fan, and speckled dace switched from mid-channel riffles to debris fans.

Ponding of Dry Canyon Mouths. The Colorado River through much of Glen and Grand Canyons is strongly confined by steep slopes, cliffs, and canyon walls. Dry side canyons occur frequently along the shoreline. During high flows, water backs into these side canyons and ponds, creating shoreline embayments of low-velocity currents that attract fish. This phenomenon was observed during the spring 1996 beach/habitat building flows.

High, Turbid Main-Channel Flow

Surge of Increased Macroinvertebrate Drift as Food for Fish. Several investigators have identified a relationship between fluctuating flows and increased algal and macroinvertebrate drift (Angradi et al. 1992, Reclamation 1995, Leibfried and Blinn 1987, Blinn et al. 1992, Valdez and Ryel 1995). These increased food supplies are utilized by at least humpback chub and rainbow trout (Valdez and Ryel 1995), and the phenomenon of periodic drift may be important to many fishes as a source of food. Reduced macroinvertebrate and algal drift has been observed during steady flows of short duration, but the drift phenomenon during sustained high flows is not known. Current information suggests that sustained high flows will initially dislodge and flush large volumes of algae and invertebrates into the current. This drift would be expected to decrease as available supplies are depleted.

Increased Feeding Opportunities for Non-sight Feeders, Including Native Fishes. The four species of native fish remaining in Glen and Grand Canyons have developed strategies for feeding in a turbid river, including highly sensitized neuromast systems (sensory organs) and a highly developed lateral line. These fish are capable of detecting struggling insects many meters away (B. Muth, FWS, pers. comm.). Radiotelemetry studies of adult humpback chub (Valdez and Ryel 1995) and numerous mainstem sampling efforts (Carothers and Minckley 1981, Maddux et al. 1987) show that adults and large juveniles feed on entrained material in large recirculating eddies. This relationship of adult distribution to debris fan-eddy complexes appears to partly explain longitudinal occurrence of aggregations of fish in the canyon (Valdez and Ryel 1995). Sustained high releases will initially dislodge large amounts of algae and associated benthic macroinvertebrates, as well as flush terrestrial invertebrates from shoreline vegetation and woody debris. This phenomenon was observed during the beach/habitat-building flow of spring 1996 (Valdez and Cowdell 1996, Hoffnagle et al. 1996). However, the duration of the phenomenon will depend on the supply of insects and material available in the system.

Increased Density of Terrestrial Invertebrates Washed from Shorelines, as Food for Fish. Gut analyses of humpback chub and flannelmouth suckers captured before Glen Canyon Dam and from unregulated river reaches show a high percentage of terrestrial invertebrates in the diet of these fish (Woodbury 1959, Valdez 1990, Vanicek 1967). The high proportion of terrestrial invertebrates in diets of native fish during local rainstorm spates (Tyus and Minckley 1988, Carothers and Minckley 1981, Maddux et al. 1987, Valdez and Ryel 1995) indicates that this is a highly sought food source, despite their apparent lack of abundance in river drift (Blinn et al. 1994, Shannon et al. 1996b). Sustained high flows are expected to flush large numbers of terrestrial invertebrates from shoreline vegetation, woody debris, and rock piles. This source of food resources is expected to be high during the first part of the high release, then subside with diminished supplies.

High Sediment Depositional Zones in Recirculating Eddies Displace Fish. During the beach-habitat/building flow of spring 1996, Valdez and Cowdell (1996) reported that adult radiotagged humpback chub used low-velocity regions of secondary deposition within large recirculating eddies during the high flows. In one case, fish were forced to move from this region because of a shift in sediment budget in the eddy that caused substantial redeposition. These movements were observed concurrently with mapping of channel bathymetry, which confirmed that the sediment budget in these eddy complexes had exceeded capacity, causing large zones of sediment shifts and deposition. Although this was interpreted as displacement, the fish quickly found alternative eddies for holding during the high flows, and the movement was not interpreted as detrimental to the fish. This phenomenon is not expected to be common or detrimental to adult humpback chub during a high sustained flow.

Reinforced Spawning Cues for Spring-Spawning Fish. Spawning cues are important for many species of riverine fishes, and include, at least, water temperature, flow, and photoperiod (Hynes 1970). Spawning cues for the native fishes in Grand Canyon are poorly understood, but appear to be related to the same environmental factors as spawning cues for Colorado squawfish (Tyus 1991), razorback suckers (Tyus 1991), and humpback chub (Valdez and Claimer 1982) in the Upper Basin. Increased flow is a key spawning cue for many fishes, along with increased water temperature.

It has been conjectured that sustained high spring flows will provide environmental cues for gonadal maturation in native fish of Grand Canyon, where flow is regulated and temperature is relatively isothermal (Clarkson et al. 1994, FWS 1994a). However, many investigators have found fish in spawning condition in the mainstem and tributaries despite regulated flow and constant mainstem temperatures. Kaeding and Zimmerman (1983) stated that gonadal maturation occurred in mainstem humpback chub, but temperatures were too cold for egg and larval survival. Valdez and Ryel (1995) hypothesized that staging by humpback chub at the mouth of the LCR appeared to be independent of flow or temperature, and was probably related to photoperiod. Ascent of the LCR, however, was closely linked to conditions in the LCR: decreasing flows, increasing water temperature, and decreasing turbidity. Valdez and Claimer (1982) and Kaeding et al. (1990) reported annual mainstem spawning by humpback chub in an Upper Basin population at considerably different flows and temperatures. Spawning aggregations of flannelmouth suckers and bluehead suckers at tributary mouths in Grand Canyon also suggest that spawning cues for these native fish species are independent of river flow and temperature. No compelling evidence exists indicating that, since cold releases began in the early 1970s, native fishes in Grand Canyon have failed to reach spawning readiness, and no evidence exists that sustained high flows are needed as spawning cues.

Unsuitable Conditions for Non-native Fishes. It has also been suggested that high, steady spring flows reduce the populations of mainstem non-native fishes through downstream displacement, disruption of reproduction, and lowered survivorship of early life stages (Clarkson et al. 1994). Minckley and Meffe (1987) suggested that high discharges one order of magnitude above average stream flow are needed to significantly displace non-native fishes, and approximately two orders of magnitude are needed to eliminate non-native species from small and medium stream ecosystems in arid, canyon-bound habitats. For the Colorado River in Grand Canyon, one and two orders of magnitude above average flow are about 120,000 cfs and 1.2 million cfs, respectively. One order of magnitude from average flow may be possible in Grand Canyon, but two orders of magnitude—or nearly five times the combined discharge capacity of Glen Canyon Dam—are unlikely.

Studies in the Upper Basin have documented positive correlations between low flows and high abundance of non-natives fishes, as well as decreased abundance of non-natives following high flows (Osmundson and Kaeding 1989, McAda and Kaeding 1989, Valdez 1990). The most dramatic decrease in non-native fishes occurred as a result of high flows in excess of 100,000 cfs in Cataract Canyon in 1983–1984. However, catch rates of red shiners and fathead minnows nearly doubled 2 years after these high flows, demonstrating the high resilience of some of these non-native fishes (Valdez 1990).

In Grand Canyon, high releases in 1983–1984 peaked at more than 92,000 cfs, but did not appear to significantly reduce abundances of non-native or native fishes (Carothers and Minckley 1981, Maddux et al. 1987). The 7-day experimental beach/habitat-building flow of 45,000 cfs in spring 1996 temporarily reduced catch rates of plains killifish and fathead minnows, but these fish recovered within 8 months by re-invading from tributary streams and natural reproduction (Hoffnagle et al.1996, Hualapai Tribe 1996a, Valdez and Cowdell 1996). These decreases were temporary and it was determined that "floods of a different magnitude and/or duration will be required to significantly diminish exotic fish populations" (Hoffnagle et al.1996).

Ponded Tributary Mouths

Increased Nursery Habitat and Thermal Acclimation for YOY Descending from Tributaries. Clarkson et al. (1994) advocated releasing sustained high flows in spring sufficient to pond tributary inflows for rearing habitat, and recommended sustained releases of 30,000 cfs or higher in May or June.

Wegner and Protiva (in preparation) mapped the LCR inflow at three discharge ranges: 9,200–9,600 cfs, 12,130–12,809 cfs, and 17,470–17,798 cfs, as shown in Figures 25, 26, and 27, respectively. At a base LCR flow of 230 cfs, the greatest area of low-velocity, shallow, warm-water habitat occurred at mainstem discharges of 12,130–12,809 cfs (Figure 25). This range is consistent with the discharge proposed for the month of July in the experimental steady flow regime (i.e., 12,500 cfs). At roughly this discharge, Wegner and Protiva (in preparation) found that the LCR plume flowed through the secondary channel at temperatures of 20.0–24.0°C. At mainstem flows approaching 18,000 cfs, the highest discharge proposed for the experimental steady flows (May–June), the LCR inflow area was inundated by mainstem water of 10.0–12.0°C, effectively reducing the area of ponding. At most tributaries, maximum benefit from ponding depends on the inflow geomorphology of the tributary, and may vary seasonally and from year to year. Thieme (1998) found significant sand deposits in the Paria River inflow that changed the characteristics of ponding from one year to the next. These studies and observations indicate that the degree of ponding at a given tributary is related not only to mainstem flows, but to tributary flows and inflow geomorphology as well.

Increased Access to Tributaries for Spawning Adults. Access to tributaries by mainstem fish has not been identified as a problem since minimum dam releases increased from 1,000 cfs to 8,000 cfs starting with interim flows on August 1, 1991. Bathymetric and temperature maps of the LCR inflow showed no restriction to access by adult humpback chub at base LCR flows of 230 cfs and mainstem flows of 5,000 cfs and higher, assuming a minimum water depth of 1.5 times body depth of the largest fish (Valdez and Ryel 1995). Access to other tributaries has not been evaluated, but observations indicate no problems with access to any tributaries. Water falls that occur in many perennial tributaries within Grand Canyon (i.e., Shinumo Creek and Havasu Creek) are considered fish barriers independent of river operations.

Concentrations of Predators at Tributary Inflows. Several investigators in Grand Canyon have reported increased numbers of non-native fishes in tributary inflows during high releases (Maddux et al. 1987, Valdez and Cowdell 1996, Hoffnagle et al. 1996). Sustained high flows create high, turbulent, and turbid conditions in the mainstem that may be unsuitable for many species of fish, particularly non-natives. Tributaries and tributary inflows provide a temporary refuge from rigorous mainstem conditions during high releases. Concentrations of young fish at these inflows tend to attract large predators seeking refuge and feeding opportunities. The effect on native fishes is unknown, but ponded tributary mouths in late spring and early summer could hold large numbers of post-larval native fishes descending from natal streams, increasing risk of predation by other species.

Rebuilt Backwater Habitats

Increased Nursery/Rearing Habitat Following High Flows. Creation of backwater habitats, although cited as an advantage of sustained high spring flows on the order of 30,000 cfs (Clarkson et al. 1994), is not an issue when comparing effects of experimental steady flows against those of current dam operations. Both scenarios include the common element of a periodic beach/habitat-building flow in excess of power plant capacity (which is about 33,200 cfs). Discharges of this magnitude are necessary to move sediment from the riverbed to the channel margin and to rebuild reattachment bars in eddy complexes (Reclamation 1995).

Maximum Pool Area
(Left Channel Warm)

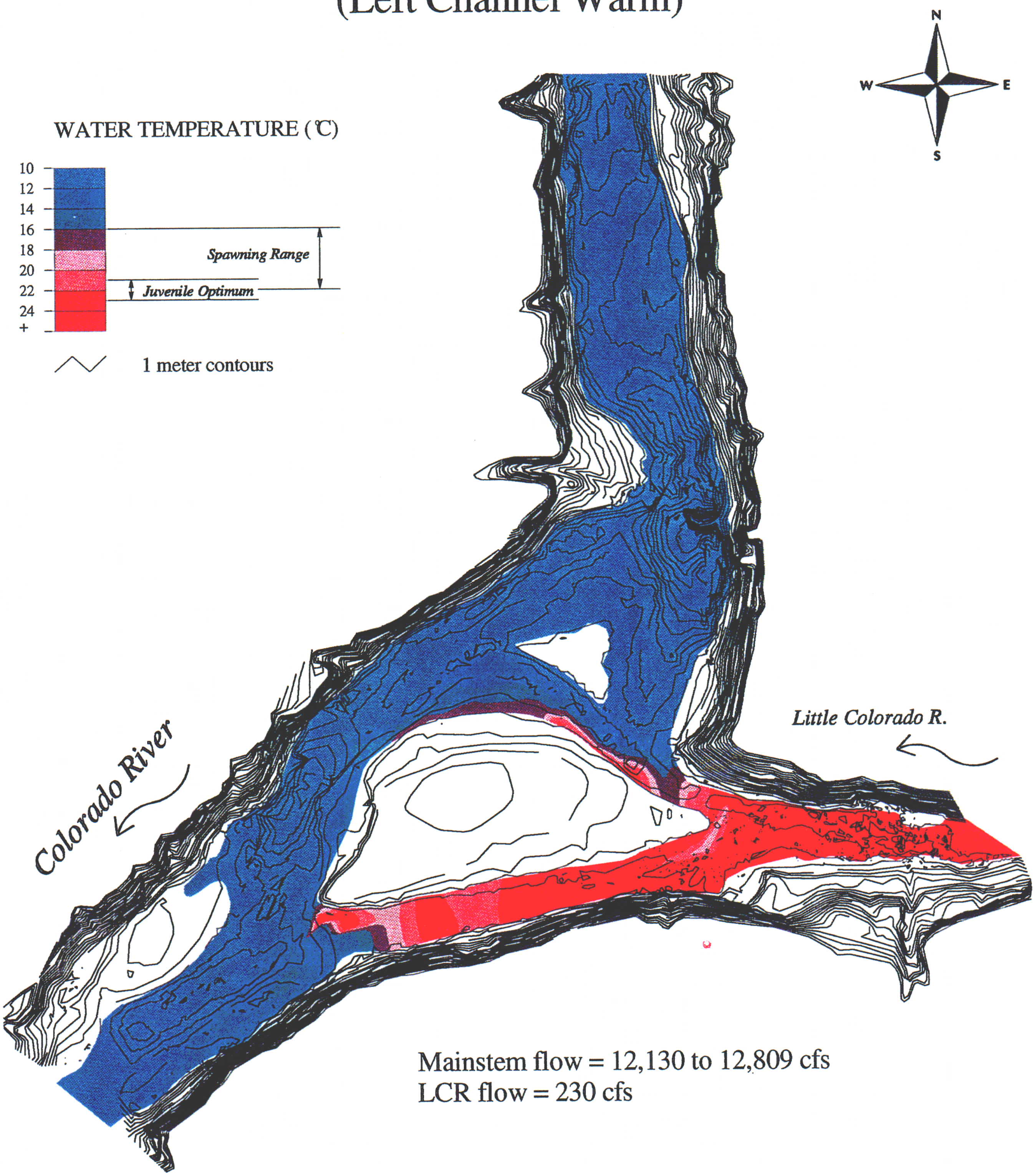


Figure 26. LCR inflow at 12,130 to 12,809 cfs mainstem discharge. LCR flow diverted to secondary channel.

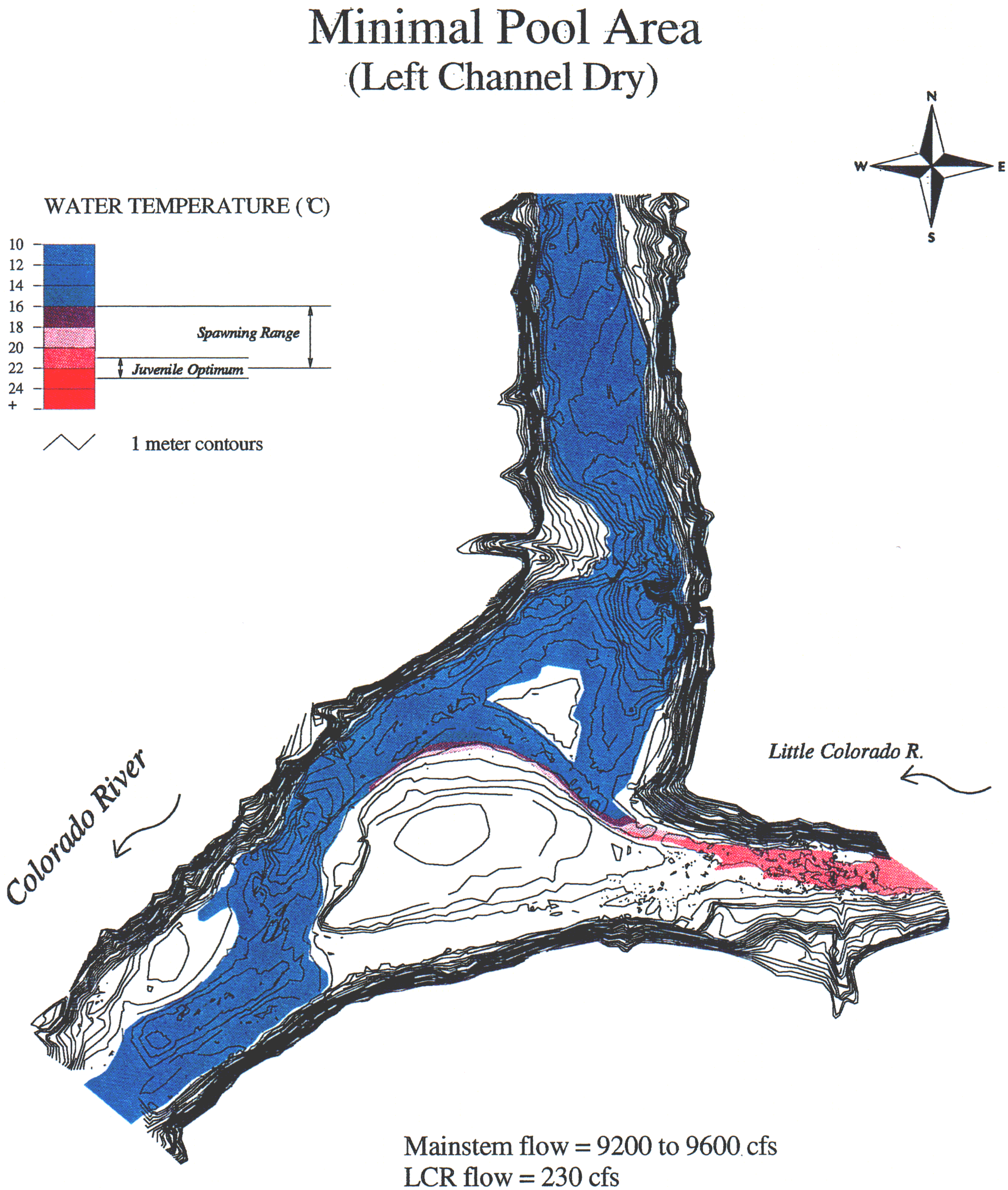


Figure 25. LCR inflow at 9,200 to 9,600 cfs mainstem discharge. Secondary channel dry.

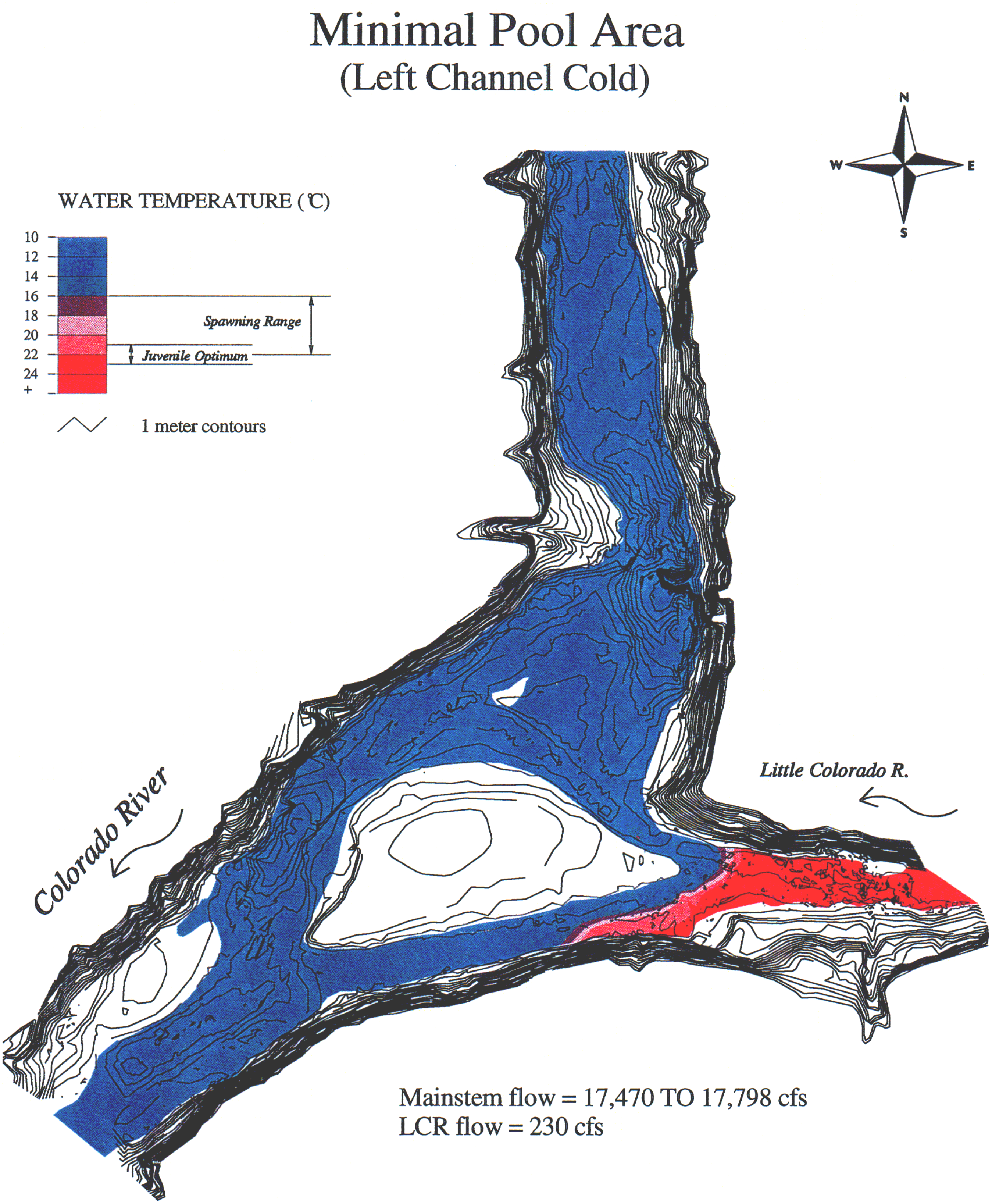


Figure 27. LCR inflow at 17,470 to 17,798 cfs mainstem discharge. Secondary channel flooded by mainstem.

Increased Adult Feeding/Holding Habitat. Backwaters are not typically used by adults of large fish species, except for occasionally feeding at night on highly productive benthos or on small fishes. These backwaters, however, may be important feeding and holding areas for adults of small riverine forms, such as speckled dace, fathead minnows, and red shiners. Newly formed backwaters following high rebuilding flows are likely to be highly productive during their first few months of existence (Johnstone and Stevens 1996, Stevens et al. In Press). This high productivity attracts many fishes for feeding on primary and secondary production, and these fish, in turn, attract predators. Small, shallow backwaters, although more productive from high solar penetration, are less valuable to adults than large deep backwaters. Hence, sustained high flows that form large deep backwaters provide greater access and habitat for adults, whereas flows that form small, shallow backwaters provide habitat for young and small fishes.

Increased Primary and Secondary Production in Backwaters Following Redistribution of Organics. Sustained high releases that exceed pre-existing highs are likely to flush large amounts of dead and dying vegetation and coarse and fine particulate organic matter from shorelines. This phenomenon was observed for the 45,000 cfs beach/habitat-building flow of spring 1996, the highest flow in the Colorado River in Grand Canyon since 1987. Copious amounts of organic matter were entrained in large recirculating eddies and deposited in the reattachment bars of these eddies. This influx of organic matter was buried in sand and sediment deposits, then slowly released into the system with erosion of retaining sandbars (Johnstone and Stevens 1996).

Chapter 9
INFORMATION NEEDS, DATA GAPS, AND RESEARCH HYPOTHESES

INTRODUCTION

Background

In previous chapters, we reviewed existing knowledge of aquatic resources in the Colorado River through Glen and Grand Canyons, and postulated effects of the experimental steady flow proposed by the FWS in the Biological Opinion on the Glen Canyon Dam Environmental Impact Statement (FWS 1994, Reclamation 1995). In this chapter, we identify information needs, data gaps, and research hypotheses needed to better evaluate those effects. While the information needs on fish assemblages in the Colorado River are extensive (as they are in most ecosystems), we are able to reduce the scope of this effort by focusing on those issues that are related to discharges from Glen Canyon Dam. We have identified data gaps and hypotheses specific to native fishes in Grand Canyon and to the evaluation of an experimental steady flow. We recognize that the data gaps and hypotheses identified in this chapter are not all-encompassing, and refinement will have to be an ongoing process.

Overview of Aquatic Resource Studies in Grand Canyon

Resource inventories and life history studies of selected species make up the majority of scientific information collected to date in Grand Canyon. Specific studies associated with GCES Phase I and Phase II focused on 1) inventory of species, 2) quantification of population levels, 3) documentation of life history characteristics, and 4) initial studies of population dynamics. Some of these studies described immediate physical, chemical, and biological linkages, and some scientists developed frameworks for interrelationships of connecting variables (Patten 1991; L. Stevens, GCMRC, pers. comm.), but greater integration and synthesis across resource disciplines is needed.

Native and endangered fish populations in Grand Canyon exist amid wide variability in environmental conditions, many of which have been induced by human activities. Key questions remain to better understanding long-term preservation and recovery of these species, including the role of dam-controlled releases, water quality, native/non-native fish interactions, habitat availability, pathogens, and influence of variable conditions in tributary watersheds. To move beyond traditional approaches, and advance our understanding of critical ecosystem processes and fish species interactions, it is necessary to implement specific hypothesis-driven studies that link ecosystem processes to native fish population responses. Our understanding of how these interrelationships affect fish population trends will undoubtedly increase through time, as more is learned, and we refine the list of information and data gaps as well as driving hypotheses. The best vehicle for promoting this scientific environment is adaptive management. Adaptive management theoretically provides linkages among scientists and feedback mechanisms between scientists and managers in order to fine tune studies vital to better understanding dam management in concert with aquatic resources.

INFORMATION NEEDS AND DATA GAPS

Information Needs

During this project, a total of 33 information needs were identified from reports and literature reviewed. We organized these needs into nine general categories (food base, demographics, survivorship, movement, habitat requirements and use, interactions between native and non-native fish species, parasites and diseases, effects of flow, and information management). Additional research questions were identified, but we have attempted to highlight only those specific to evaluating effects of an experimental steady flow on the Grand Canyon aquatic ecosystem.

A project workshop was held February 27–28, 1997, to solicit opinions and responses of 25 biologists on the experimental steady flows. Before the workshop, biologists were sent a workbook and asked to prioritize the identified information needs. Six returned a complete set of responses. The results of this prioritization are presented in Table 12 at the end of this chapter. In this table, each information need has a reference number (e.g., A.1, A.2, etc.) corresponding to the text descriptions provided in the following list, a priority ranking (1, 2, 3, etc.), and a weighted score based on the opinions of the biologists. Information needs with similar weighted scores were assigned the same rank. Weighted scores reflect the sums of weighted factors (low = 1, medium = 2, high = 3), as a percentage of the highest possible score; i.e., 100% means that all respondents ranked a given need as highest priority. The 33 information needs are listed below as excerpted from cited reports. Portions of excerpts may be italicized to emphasize salient points.

A. <u>Food Base</u>

1) Relationship of Drift and Benthos

"The relationship between drift (algae, detritus, macroinvertebrates) and benthos is not clear as a longitudinal sequence from the dam to Lake Mead. The work by Blinn et al. (1993, 1994) indicates a stair step effect for production. *The short distance in which macroinvertebrates abandon algal clumps and in which pulverization of these clumps occurs suggests that food resources for fish probably originate from local sources*, except during large tributary floods that wash great quantities of terrestrial detritus and macroinvertebrates into the river. Understanding this longitudinal relationship in primary and secondary production is important in testing the hypothesis that food resources are limited downstream of Havasu Creek. Understanding food availability in the lower canyon may partly explain the low numbers of fish in these lower reaches in otherwise favorable habitat. *Determining the relationship of drift and benthos should be done with a focus on the effect of interim flows on shoreline production.*" (Valdez and Ryel 1995)

2) Interrelationships of Flow Regimes, Sediment Augmentation, and Temperature on Primary and Secondary Productivity

"Primary and especially secondary production in the historic river was probably distributed in clumped fashion with islands of high densities of macroinvertebrates associated with debris fans, talus slopes, or woody debris. Existence and location of these biological "hot spots" may help to explain fish distributions and habitat uses, and identify particular habitats that need to be conserved under dam operations. Examples of these habitats are backwaters (i.e., eddy return-current channels), debris fans, vegetated banks, and accumulations of woody debris. The interrelationships of flow regimes, sediment augmentation, and temperature on primary and secondary productivity need to be better understood." (Valdez and Ryel 1995)

3) Relationship Between Flushing of Backwaters and Productivity on the Colorado River in Grand Canyon

"The relationship between flushing of backwaters and productivity on the Colorado River in Grand Canyon is not known, but backwaters on the Lower Colorado (below Lake Mead) need to be flushed, preferably with a slow current, to maximize aquatic productivity. Too much flushing results in a riverine environment, too little results in stagnation and water quality problems. This finding was noted for the Lower Colorado River backwaters by Kennedy (1979) and Arizona Coop Fish Unit (1976), and for Mississippi River backwaters by Vanderford (1980), Holland et al. (1983) and Gutreuter (1980), and others." (J. Weiss 1992)

B. Demographics

4) Genetics of Humpback Chub Aggregations in Grand Canyon (30-Mile, LCR, Middle Granite Gorge)

"Fish need to be captured for obtaining muscle tissue to determine if genetic differences exist [between aggregations of] mainstem fish. Special techniques, such as DNA fingerprinting (Gross et al. 1994) may need to be employed to distinguish subtle differences." (Valdez and Ryel 1995)

5) Relationships Between the LCR and Mainstem Components of the Humpback Chub Population

"The relationships between the LCR and mainstem components of the humpback chub population remain unclear. Understanding these relationships is essential in understanding the relative importance of the two systems to the species. Many demographic attributes are not easily attained from field studies or laboratory experiments, but existing data should provide approximations that can be used in empirical models. These models are needed to determine the trajectory of the population under existing conditions, as well as to predict effects of proposed elements such as selective withdrawal and steady summer releases. Population models may also be important in interpreting monitoring data. This population modeling project has been initiated by Ryel and Valdez (1995) with development of a preliminary conceptual model. The results of this report have been incorporated into that modeling effort to began to identify important parameters and state variables (Supplement No. V)." (Valdez and Ryel 1995)

C. *Survivorship*

6) Causative Factors for Mortality of Young Humpback Chub

"Factors that contributed to decreased densities of subadults include downstream dispersal and mortality (i.e., predation, thermal shock, diseases and parasites, starvation). These were offset by dispersal from the LCR. This effect was minimized by performing analyses during periods with few LCR floods. The effects of each of these factors were not determined and remain the subject of needed research to fully understand causative factors for mortality of young humpback chub." (Valdez and Ryel 1995)

7) Swimming Performance of YOY and Juvenile Humpback Chub at Different Temperatures

"We hypothesize that densities of subadult humpback chub near the LCR inflow are reduced by destabilization of shorelines caused by cold fluctuating flows that force fish to leave these otherwise sheltered habitats. Laboratory swimming performance tests are needed for YOY (range, 50–100 mm TL) and juveniles (range, 100–200 mm TL) at 10.0, 12.0, 15.0, and 20.0°C. Acclimation temperature should be comparable to warm LCR waters (e.g., 20.0°C) to simulate young fish descending from the LCR to the mainstem. These experiments also need to be conducted on adults (>200 mm TL) to test the hypothesis that low-velocity habitat is limited for adults, and partly explain their disproportionately high use of low-velocity areas in large recirculating eddies. Cold temperatures significantly reduced swimming ability of subadult humpback chub; laboratory tests showed 90% reduction in time to fatigue in 0.51 mps velocity at 20.0°C compared to 14.0°C (Bulkley et al. 1982)." (Valdez and Ryel 1995)

D. <u>Movement</u>

8) Dispersal of Young Fish to Mainstem

"Dispersal of subadults from the LCR to the mainstem appeared to be related to habitat suitability and possibly to food resources, but long-range downstream movement or transport in the mainstem was not fully explained. Absence of large numbers of young downstream of canyons occupied by populations in the Upper Colorado River Basin suggests little or no downstream dispersal. Yet this investigation and a previous study by Maddux et al. (1987) found subadults distributed over 250 km downstream of the LCR, the only presumed source of substantial numbers of subadults. There is no evidence that these fish return to the LCRI aggregation as subadults or adults, and annual reduction in numbers of subadults in all mainstem areas indicates that their survival is low. This effect is believed to be related to cold-water releases and fluctuating flows from Glen Canyon Dam that displace fish downstream., and perhaps food limitations. Survival in downstream areas is apparently limited by lack of sheltered shoreline habitat, large numbers of predators, and possibly food shortage. These hypotheses need to be more fully investigated in future studies." (Valdez and Ryel 1995)

E. <u>Habitat Requirements and Use</u>

9) Relationship of Flow Regimes to Morphology and Longevity of Backwaters

"The relationship between flow and backwaters is not known, but may play a vital role in backwater formation and longevity. A coordinated research project should be conducted on backwaters with the involvement of both sediment researchers and biologists. The morphology of backwater formation and longevity, and how backwater formation relates to different flow regimes needs to be investigated." (J. Weiss 1992)

10) Relationships Between Mainstem Water Temperature and Flow Regulation

"Relationships between mainstem water temperature and flow regulation are indicated by this investigation, and suggest that *the river is likely to warm and clear under constant low releases.* These relationships need to be better defined temporally and spatially to identify possible temperature modification through flow regulation. (*A reach-based temperature model is needed).*" (Valdez and Ryel 1995)

11) Relationships Between Flow, Channel Geomorphology, and Fish Habitat

"The linkages between fish habitat and geomorphology are unclear and need to be better defined, and related to availability of food resources and effects of temperature on swimming performance of various life stages. The historic aspects of channel geomorphology (i.e., changes since the dam) need to be described in order to distinguish effects of dam construction from effects of operations on distribution and abundance of fish. Integrating these disciplines is vital to understanding the underlying principles that drive habitat distribution and use in the Colorado River....[and] to understanding habitat availability for humpback chub, and possibly other native fishes at cold temperatures. This information is needed to further test the hypothesis that fish habitat is limited by the effect of cold temperatures on swimming performance of the fish." (Valdez and Ryel 1995)

12) Relationships Between Reattachment Bars and Eddy Return-Current Channel Elevations, as Affected by Antecedent Flows, for All Presumed Nursery Reaches in Grand Canyon

"The level at which to stabilize this flow may be difficult to determine because the elevation of the reattachment sandbars and associated eddy return channels is determined by antecedent flows. Hence, the level that produces the greatest number of backwaters is likely to vary by year. Also, channel geomorphic characteristics differ longitudinally and greatly influence sandbar formation and elevation, such that steady flows may maximize backwater habitat in some reaches of the canyon, but not in others." (Valdez and Ryel 1995)

13) Association of Cover to Water Depth and Velocity along Channel Margins

"In this study, selection for cover appears to override any association with water depth or velocity in channel margins. Although undetected in this study, I suspect that the presence of cover affects local conditions of water depth and velocity in channel margins. I chose 2.5 m as the channel margin width that was influenced by shoreline structure. It is possible that this distance is too broad to detect associations of fish with conditions of depth and velocity; small fish may be responding only to conditions within 0.5 to 1 m of the waters edge. An unperceived association between fish and depth or velocity may have been masked by main channel hydraulic conditions. A better approach would be to analyze the physical conditions only within the channel margin area that subadult humpback chub use, which may vary among shoreline types, rather than a specific distance from shore." (Converse 1996)

14) Mainstem Habitats of Adult and Juvenile Humpback Chub

"Microhabitats of adult and juvenile humpback chub in the Colorado River mainstem have not been satisfactorily determined." (Reclamation 1995)

15) Non-backwater Habitats for Larval and Juvenile Fishes

"Other habitats (other than backwaters) that may be important to larval and juvenile fishes are channel margins and cobble riffles. These other habitats have not been quantified to date, but are worthy of investigation." (McGuinn-Robbins 1995)

16) Flow Requirements for Humpback Chub / Quantitative Information on Water Depth, Velocity, Substrate, and Cover Requirements

"Development of...HSI curves [for humpback chub] revealed a lack of quantitative information on water depth, velocity, substrate, and cover, that hindered defining flow requirements for the species. Lack of data was attributed primarily to the difficulty of accessing and sampling canyon regions in which the species occurs. Areas inhabited by humpback chub are typically deep, swift, and turbid, precluding direct observation of individuals and making accurate parameterization of habitat difficult. Habitat utilization data derived from past investigations of humpback chub have attempted to describe *microhabitat site selection (i.e., depth, velocity, substrate, cover), but associated channel features (e.g., debris fans, eddy complexes, shoreline types) and habitat diversity have not been described and may be of greater importance* (Osmundson et al. 1995)." (Valdez and Ryel 1995)

17) Magnitude of Effects of Thermal Shock on the Humpback Chub Population

"Daily fluctuations destabilized the flow and temperature of the LCR inflow and probably precluded staging and thermal acclimation by YOY and juveniles descending to the colder mainstem. This hypothesis was partly addressed with laboratory tests of thermal acclimation and tolerance by YOY (Lupher and Clarkson 1994), confirming the likelihood of thermal shock which is likely to result in either direct mortality or erratic behavior resulting in intensified predator response. The magnitude of this effect on the population has not been evaluated, and is an important aspect in determining the need for high spring releases to impound tributary inflows." (Valdez and Ryel 1995)

18) Mainstem Flow Needs for the 30-Mile Aggregation

"Relationships between mainstem flow and elevations of warm springs, stable thermal plumes, and spawning and nursery cover are important in understanding how to enhance successful spawning by humpback chub in the 30-Mile aggregation. Areas around the eight Fence Fault springs should be surveyed for elevations of spring sources and crevices used for egg deposition and as cover by larval fish. Flows that provide optimal conditions need to be identified to determine if existing flows are suitable for spawning, egg incubation, larval survival and escape from predators." (Valdez and Ryel 1995)

F. Interactions Between Native and Non-native Fish Species

19) Levels of Predation on Native Fishes by Non-native Brown Trout and Striped Bass

"Further studies...documenting [and evaluating] predation of native fishes should be included in future monitoring of the Colorado River in Grand Canyon. The piscivorous habits of brown trout and their apparent expansion in abundance is worthy of further investigation. The likelihood of predation on humpback chub [by striped bass] in Grand Canyon is unknown, and needs to be further investigated in light of its highly piscivorous diet (Engeling 1990)." (Valdez and Ryel 1995)

"Major predators such as large rainbow trout, brown trout, channel catfish, striped bass, and green sunfish need to be captured and their viscera examined for native fishes. The focus of this investigation should be the Colorado River from RM 30.0 to RM 90.0; this area has the highest degree of sympatry between these predators and subadult humpback chub. Nonlethal stomach pumping techniques are available, or non-native fish in this region can be sacrificed with little effect to any major fishery. Buchal diameters need to be determined for all sizes of each major predator and related to body size. Also, body depth to total length relationships are needed for subadult humpback chub (>200 mm TL). Stomach contents of predators need to be carefully examined for scales, bones, pharyngeal teeth, etc. in case digestion has distorted the identity of the prey. The percentage of native fishes by species in the diet of each predator species needs to be determined, and total numbers of predators estimated to approximate the total potential predation on native fishes. These predator-prey models are important in understanding the different sources of mortality on native fishes." (Valdez and Ryel 1995)

20) Predatory or Competitive Interactions Between Specific Species under Variable Field Conditions (e.g., Temperature, Substrate, Current Velocity, Turbidity, Cover, Prey and Predator Density, Alternate Prey Choices) (Hawkins and Nesler 1991)

21) Effects of Predation on Early Life Stages of Humpback Chub and Long-Term Population Viability

"Humpback chub is represented in several areas by seemingly sustaining populations, but assessment of the effects of predation on early life stages...on long-term population viability cannot be made until suitable methods to quantify this predation are worked out." (Douglas and Marsh 1996b)

22) Impacts of Small-Bodied Forms of Introduced Fishes to Reproductive Success and Survival of YOY Native Fish (Hawkins and Nesler 1991)

23) Cause-Effect Relationship Between Reproductive Success, Spawning, or Other Life History Activities of Small-Bodied Introduced Species with Major Flow Regime Events (Hawkins and Nesler 1991)

24) Evaluation of Possible Non-native Fish Control Methods

"A plan needs to be developed for evaluating control measures for rainbow trout, brown trout, and channel catfish in Grand Canyon. Methods need to be investigated for controlling the numbers of these predators to reduce mortality of native fishes, and to evaluate the likelihood of success.

Primary population centers of target fish should be identified, and sensitive areas such as the tailwater blue ribbon trout fishery and the Nankoweap Creek trout population addressed. Information from all investigations should be assimilated to determine the distribution and relative abundances of these species. This plan should be reviewed and agreed to by all the resource management agencies in Grand Canyon in order to minimize potential resource conflicts, e.g., reducing numbers of rainbow trout at Nankoweap Creek would reduce a valuable food source for migrating bald eagles." (Valdez and Ryel 1995)

G. Parasites and Diseases

25) The Degree of Infestation by Asian Tapeworms and Parasitic Copepods in Humpback Chub, Other Native Fishes, and Non-native Fishes (Lechleitner 1992)

26) Incidence of Tapeworms in Subadult Humpback Chub (Valdez and Ryel 1995)

27) The Effects of Temperature on Asian Tapeworms in Grand Canyon (Lechleitner 1992)

28) Extent of Infestation of Asian Tapeworms in Kanab Creek

"Of particular concern is the speckled dace captured in Kanab Creek. Water temperatures of Kanab Creek are warm enough to allow for reproduction by Asian tape worms, with mean temperatures exceeding 20°C in May, July, and August, and reaching as high as 34°C (AGFD 1996). Whether this occurrence of an infected speckled dace is indicative of a separate, reproducing population of Asian tapeworm or just an infected fish that had emigrated downstream from the LCR is not clear. This fish was caught in the lower section (<500 m from the mouth) of Kanab Creek, so either alternative is possible. In any event, since speckled dace and fathead minnow are resident and humpback chub are occasionally found in Kanab Creek (AGFD 1996), the potential exists for this parasite to become established in this tributary. Therefore, although the cold water temperature of the mainstem Colorado River seems to be limiting the distribution of this parasite, there is an indication that it may have colonized Kanab Creek. Further examination of this is warranted and planned." (Brouder and Hoffnagle 1996)

H. Effects of Flow

29) The Effects of Steady Flow Conditions on Plankton and Aquatic Invertebrates

"The effects of steady flow conditions on plankton and aquatic invertebrates was not tested but could be extensive." (AGFD 1996b)

30) Response by Fish in Backwaters to Steady Flows over Time

"The effects of steady flows and changing river and backwater conditions on fishes is inconclusive, but could...be considerable. Response by fish to steady flows is expected to be longer than the three days monitored in this study. This response will be measured by changes in growth, survival, recruitment, and reproduction in each species. Extended periods of steady flow will be required for fish populations and growth rates to be altered. At a minimum, backwater usage under steady flows by larval and juvenile fish probably won't increase until food (zooplankton and benthic invertebrates) availability increases." (AGFD 1996)

31) Effects of a High Spring Release on Shoreline Vegetation and Hence Survival and Recruitment of Subadult Native Fishes

"This flow...could also transport young natives as well, depending on ramping rate, temperature of the release, and the age of fish in the area; i.e., swimming ability of younger warm-water species is significantly reduced at colder temperatures. Sufficiently low ramping rates may reduce the risk of transporting young chub downstream by allowing them to find alternative habitat areas as flows rise. The major benefit of this high release would be in reshaping habitat and reducing non-native species."

"A high spring release prior to June 10 would transport the least numbers of young humpback chub, since most recently-hatched fish would still be in the LCR. Individuals of the previous year class would be sufficiently large to better withstand higher volumes of water and faster velocities. The effects of a high spring release on shoreline vegetation and hence survival and recruitment of subadults are not fully understood." (Valdez and Ryel 1995)

I. Information Management

32) General Habitat Classification System

"While a common assemblage of terms continues to be used by various investigators in the Colorado River (Valdez and Wick 1983, Tyus 1984, Kaeding and Osmundson 1988, Tyus and Karp 1990, Harvey et al. 1993, Stanford 1994), a general habitat classification system is needed to establish a standard frame of reference to facilitate communications among researchers and managers (Hawkins et al. 1993), and to provide integrative and comparative data analyses." (Valdez and Ryel 1995)

33) Integration of Existing Information

"Elements of the EIS, such as selective withdrawal, high spring releases, and steady summer flows, cannot be fully evaluated without the benefit of an integration of existing information. This information is vital to developing benefit/risk analyses of these elements. Risk analyses are recommended for evaluating selective withdrawal and flow management (i.e., high spring release, steady summer flows)." (Valdez and Ryel 1995)

Data Gaps

The following is a list of the 11 most significant data gaps identified from the previously described information needs. They were prioritized by workshop participants during the give and take of open discussion. This ranking is based on technical information needs for evaluating an experimental steady flow and does not consider budgetary or logistical constraints.

1) A temperature model that will predict longitudinal downstream warming of the mainstem, as well as warming of shoreline and backwater habitats.

2) Bathymetry and temperature isopleths for inflows of the Paria River, LCR, Shinumo Creek, Bright Angel Creek, and Kanab Creek to determine the extent of ponding and thermal warming at various flows.

3) Primary and secondary productivity rates and levels for different flows longitudinally down the mainstem, in backwaters, and along shorelines.

4) Factors that limit survival of young humpback chub in the mainstem and recruitment to adulthood.

5) Biotic interactions of native/non-native fishes.

6) Rates of algal and macroinvertebrate drift for various flows.

7) Incidence and rates of infection by fish parasites, *Lernaea cyprinacea* and Asian tapeworm, as well as risk of increased infection associated with warming mainstem and shoreline habitats.

8) Timing and degree of drift by native larval fishes at tributary inflows, including the Paria River, LCR, Bright Angel Creek, Shinumo Creek, and Kanab Creek.

9) Flows for maintenance of the 30-mile aggregation of humpback chub, as well as the genetic significance of the fish as possible relicts of historic mainstem stocks.

10) Relationship of mainstem flows to nearshore habitats and channel geomorphology.

11) A complete Grand Canyon Aquatic Resources Database that is accessible to researchers and interested parties.

RESEARCH HYPOTHESES

Statement and Evaluation of Primary Hypotheses

The following nine primary hypotheses were developed following an evaluation of postulated effects (Chapter 8), information needs, and data gaps associated with evaluating an experimental steady flow. These hypotheses were first presented as "assumptions" to Project Workshop participants, who were asked to agree or disagree with each statement. All participants agreed that these assumptions were central to evaluating the effects of an experimental steady flow on aquatic resources of Grand Canyon, but most felt that not enough was known about ecological interrelationships to definitively accept or reject a given assumption. We, therefore, established each assumption as a "primary hypothesis," which became the framework for organizing a list of more specific and detailed "secondary hypotheses." Secondary hypotheses were developed from our literature review and from input of workshop participants. The primary hypotheses are narrative and deal with basic ecological principles essential to understanding effects of an experimental steady flow. The secondary hypotheses (SHo) provide statements on more specific issues.

Primary Hypothesis 1: Sustained high steady flows of the appropriate magnitude and timing will impound tributary inflows, increasing the area of relatively warm, low velocity current.

Primary Hypothesis 2: Low steady flows will stabilize nearshore, backwater, and tributary inflow habitats and increase the area and numbers of reliably available backwaters.

Primary Hypothesis 3: Low steady flows will increase water clarity throughout the mainstem river.

Primary Hypothesis 4. Mainstem water temperatures will increase during low steady summer/fall flows.

Primary Hypothesis 5: Backwaters and tributary inflows will warm during low steady summer/fall flows.

Primary Hypothesis 6: Low steady flows will reduce dissolved oxygen levels in some backwater habitats.

Primary Hypothesis 7: Primary and secondary productivity of the mainstem river, backwaters, and nearshore habitats will increase with low steady flows.

Primary Hypothesis 8: Drifting macroinvertebrates and algae will decrease with low steady flows.

Primary Hypothesis 9: The likelihood of *Lernaea cyprinacea* and Asian tapeworms parasitizing fish will increase with warming of the mainstem river and associated backwater habitats.

Biologists at the Project Workshop were asked to opine on expected responses by various fish species to the nine primary hypotheses. These views are summarized in a matrix presented as Table 11. The matrix presents the nine hypotheses and the expected response of each of the five native species (humpback chub, flannelmouth sucker, bluehead sucker, speckled dace, razorback sucker), as well as the eight most common or threatening (known to prey on or compete with native species) non-native species (carp, channel catfish, fathead minnow, red shiner, plains killifish, striped bass, rainbow trout, brown trout). Selection of these species was based on the information presented in Chapters 5 and 6. Fish response was depicted in terms of eventual change (or lack of change) in species population, according to the opinions of the biologists. Matrix categories of expected responses to changes in flows are:

"0" means no expected change;
(↓) means potential for population decrease;
(↑) means potential for population increase; and
(?) means data gaps and/or response unknown.

Each category was evaluated independently, regardless of compounded or symbiotic effects, and no attempt was made to differentially weight effects of expected responses to overall effects of an experimental flow. The biologists overwhelmingly expressed reservation about making determinations contained in the matrix because of information and data gaps in resource variables and interrelationships.

The resource matrix provides an expected tendency or pattern in single species response, rather than an integrated resource response. The matrix indicates if steady flows would be expected to favor one fish or group of fishes over another. In many cases, baseline data are lacking or minimal, but most biologists agreed to the expected response for a given fish species. We note that the hypotheses presented in the resource matrix are descriptive hypotheses. These were not tested for acceptance or rejection, but were used as a focal point for discussion of the most pertinent likely effects of an experimental steady flow on the fishes of Glen and Grand Canyons.

The resource matrix indicates that both native and non-native fishes would benefit directly from an experimental steady flow. The primary benefits are expected from ponding of tributary inflows, increased nearshore and backwater habitat stability, increased backwater and mainstem temperatures, and increased shoreline production. Adverse effects are expected from depressed dissolved oxygen concentrations in backwaters and from increased rates of copepod and tapeworm parasitism. Direct benefits to native and non-native warm-water fishes would come from increased water temperature that should increase survival and growth of young, as well as local food production. Direct benefits to rainbow trout and brown trout would come from stable flows and increased water clarity. Populations of trout in the dam tailwaters would not be affected by temperature since no change is expected near the dam, but populations in lower Grand Canyon could be detrimentally affected because of warmer mainstem temperatures. Warming is not expected to be great enough, however, to do significant harm. The brown trout population in the Bright Angel Creek area could benefit from warmer and more optimal growth temperatures, as well as increased water clarity.

Many indirect effects are expected from an experimental steady flow that are not reflected in the resource matrix. Positive responses by non-native fishes could result in negative effects to native fishes through competition and predation. The greatest potential for this effect would be in nearshore and backwater habitats, where species like fathead minnows, red shiners, plains killifish, black bullheads, and green sunfish could reproduce and rapidly increase in abundance. Studies in the Upper Colorado River Basin show that fathead minnows and red shiners can produce up to two broods annually and dramatically increase their numbers in backwater habitats during a single summer.

Other indirect detrimental effects to native fishes are a possible increase in pathogens as a result of warmer mainstem and nearshore temperatures, possible reduction in drifting food resources, and increased risk of predation. Although the parasitic copepod *Lernaea cyprinacea* is not considered a serious threat to native fishes, little is known about the effects of Asian tapeworms in the Colorado River native fishes. This parasite has only been reported in Colorado squawfish, humpback chub, and speckled dace in the last 10 years and the effects on populations are unknown. Asian tapeworms are known to cause massive deaths to fish in crowded and stressed conditions. The reduction in drifting food resources could be offset by increases in shoreline production from clear, stable flows, and from normal behavioral drift of macroinvertebrates. Greater water clarity may also increase the risk of predation for native fishes, particularly from sight feeders like trout, but warmer temperatures may enhance swimming ability of young fish, providing a greater ability to escape predators.

Table 11. Matrix Showing Expected Responses of Native and Non-native Fish Species to Hypothesized Effects of Experimental Steady Flows.

Species		Hypotheses									
		1	2		3	4	5	6	7	8	9
		Ponded Tributary Inflows	Enhanced Shoreline Stability		Increased Water Clarity (Predation)	Increased Mainstem Water Temperature	Increased Backwater Temperature	Depressed O_2 in Backwaters	Increased Shoreline & Backwater Production	Decreased Drift Rate	Increased Rate of Parasitism
			Nearshore	Backwater							
Native Species	Humpback chub	↑	?	↑	O	↑	↑	↓	↑	↓	↓
	Razorback Sucker	↑	?	↑	O	↑	↑	O ?	↑	↓	↓
	Flannelmouth sucker	↑	?	↑	O	↑	↑	↓	↑	O	↓
	Bluehead sucker	↑	?	↑	O	↑	↑	↓	↑	O	↓
	Speckled dace	↑	?	↑	O	↑	↑	↓	↑	O	↓
Non-Native Species	Carp	↑	?	↑	O	↑	↑	O↑	↑	↓	↓
	Channel Catfish	↑	O	O	O	↑	↑	O↑	O	O	↓
	Fathead Minnow	?	?	↑	O	↑	↑	↓ ?	↑	O	↓
	Red Shiner	?	?	↑	O	↑	↑	↓	↑	O	↓
	Plains Killifish	?	O	↑	O	↑	↑	↓	↑	O	↓
	Striped Bass	↑	?	O	O	↑	↑	O	O	O	↓
	Rainbow Trout	↑	?	↑	O	↑	↑	O	O	↓	↓
	Brown Trout	↑	?	↑	↑	↑	↑	O	O	↓	↓

The effects of enhanced shoreline stability on most fish species were not clearly understood, and are indicated with a question mark (?) in the resource matrix. Biologists felt that baseline data are lacking which clearly describe river stage to habitat relationships for nearshore habitats. Some species (e.g., channel catfish) are not shoreline inhabitants and would not be expected to be affected.

Evaluation and Prioritization of Secondary Hypotheses

The following is a list and evaluation of hypotheses developed as a result of reviewing all available literature on aquatic resources in Grand Canyon and from opinions expressed by biologists at the Project Workshop. We recognize that this list is probably not inclusive of all hypothesized effects, but these hypotheses represent the major concerns expressed by researchers in literature and by biologists at the workshop. Evaluations of each hypothesis are brief and without references in order to focus on associated critical points and issues.

A total of 23 secondary hypotheses were evaluated prior to and at the Project Workshop. Before the workshop, biologists were sent a workbook and asked if these hypotheses should be pursued from a purely scientific standpoint (Yes, No, Yes/With Modification) and to prioritize each as high (H), medium (M), or low (L). The results of this prioritization are presented in Table 13. For each hypothesis, there is an overall priority ranking, based on weighted scores. Hypotheses with similar weighted scores were assigned the same rank. Weighted scores reflect the sums of weighted factors (low = 1, medium = 2, high = 3), as a percentage of the highest possible score; i.e., 100% would mean that all respondents ranked a given hypothesis as high priority.

Primary Hypothesis 1. Sustained high steady flows of the appropriate magnitude and timing will impound tributary inflows, significantly increasing the area of relatively warm, low-velocity current.

Detailed surveys of depth and temperature have been done only at the LCR inflow, and some depth and temperature measurements have been made in the Paria River inflow. Maximum ponding with the LCR at base flow of 230 cfs (6.5 m^3/s) was at mainstem flows of 12,130–12,809 cfs, and substantial ponding was observed and measured at the Paria River inflow at mainstem flows of 20,000 cfs. Clearly, additional surveys of bathymetry and temperature need to be done at different flows for key tributaries used by native fishes for spawning (i.e., Paria River, LCR, Shinumo Creek, Kanab Creek, Bright Angel Creek). Mainstem flows needed to impound each of these tributary inflow areas may not be the same.

SHo 1a: High sustained flows will impound tributary mouths and significantly improve reproductive success and abundance of mainstem native fishes.

Downstream transport of larval native fishes is a common phenomenon in the Upper Basin; flannelmouth suckers, bluehead suckers, and speckled dace are prominent in drift, while humpback chub are uncommon in drift. In-depth studies of larval drift have not been conducted in any tributaries in Grand Canyon to determine if active or passive transport by larvae and YOY is a significant aspect of the life history of the native fishes. Estimates of escapement are also valuable for determining survival, habitat availability, predation, and food supplies. Ponding relatively warm tributary inflows (i.e., decreasing velocity and raising stage) by high mainstem spring flows should reduce the transport of early life stages of native fishes from tributaries into cold mainstem waters, where they are exposed to temperatures that can cold-shock or kill young (<50 mm) humpback chub. Researchers have identified spawning activity by native fishes in the Paria River, LCR, Bright Angel Creek, Shinumo Creek, Kanab Creek, and. Havasu Creek, as well as several tributaries in western Grand Canyon.

SHo 1b: Significant numbers of larval and YOY native fishes die of thermal shock and predation as they descend from natal tributaries into the mainstem.

Laboratories studies show low survival and low growth by humpback chub exposed to cold temperatures, similar to those of the mainstem. Similar studies are needed for flannelmouth suckers, bluehead suckers, and speckled dace. In addition to these laboratory studies, field tests should be conducted to confirm laboratory results.

SHo 1c: Significant numbers of young native fishes will be transported downstream by sustained high cold releases.

Historically, high flows occurred in the Colorado River from mid-April to late June, at temperatures of >15°C. Temperatures from sustained high releases at the dam during March–May would be expected to be 8–10°C, which is considerably colder than historic temperatures during spring runoff. Warm-water fishes, particularly young native fishes, are particularly susceptible to cold-shock and reduce swimming ability from cold temperatures. A high surge of cold water could displace fish from habitats or force fish to move downstream in search of alternative habitats.

Sho 1d: Significant numbers of young rainbow trout from the dam tailwaters will be transported downstream by sustained high cold releases.

It is estimated that 10% of juvenile rainbow trout were lost to downstream transport by the spring 1996 flood of 45,000 cfs. Depending on timing and magnitude, a comparable loss would be expected with future high sustained releases. It was also estimated that reproductive success replaced this loss of fish, and no long-term detrimental effect occurred to the tailwater trout population. Overall effect to a given fish species would depend on the life stage present during a high flow; earlier life stages would be more susceptible to transport.

SHo 1e: Experimental steady flows will significantly alter life histories of native fishes.

A flow scenario of high, steady, spring releases and low, steady, summer releases is different from any scenario the Colorado River and the fish assemblages have ever experienced. These flows may alter reproductive success, survival, growth, food habits, and possibly distribution and abundance. The purpose behind an experimental steady flow is to enhance life histories of native fishes in a beneficial way.

Primary Hypothesis 2. Low steady flows will stabilize nearshore, backwater, and tributary habitats and significantly increase the area and number of reliably available backwaters.

Low, steady, summer flows are expected to stabilize and warm nearshore and backwater habitats, increasing the availability of suitable nursery and rearing areas for native fishes. Warming patterns of nearshore environments need to be determined in order to predict responses by algae, diatoms, macroinvertebrates, fishes, and fish parasites to experimental steady flows. Nearshore habitats are important as nurseries and rearing areas to young native fishes, but are also important habitat for non-native species that may compete with or prey on native fishes.

SHo 2a: Densities of humpback chub near the LCR inflow will be significantly reduced by destabilization of shorelines caused by cold fluctuating flows that force fish to leave otherwise sheltered habitats.

Recent studies report dramatic overwinter declines in densities of subadult humpback chub along shoreline habitats in Grand Canyon, including talus, debris fans, vegetation, and backwaters. The causes for this decline are not understood, but may be related to changing river stages from daily fluctuations and transition from low to high-volume release months. These habitat changes may be gradually displacing fish downstream and exposing them to greater risk of predation by non-native species, and transporting them into areas of marginal habitat (e.g., Inner Gorge).

SHo 2b: Experimental flows will significantly reduce negative effects of mainstem hydrology on number of nearshore habitats and use by native fishes.

High fluctuating flows have been identified as detrimental to native fishes primarily because of the destabilizing effects on shoreline habitats. Low steady flows are expected to stabilize shorelines and make nearshore habitats more suitable. The flow levels at which this effect are maximized is unknown.

SHo 2c: Experimental flows will benefit native fishes by significantly reducing interactions with non-native fishes, especially in nearshore habitats.

A high steady flow in spring could make conditions unsuitable for non-native fishes. The spring 1996 beach/habitat-building flow of 45,000 cfs reduced numbers of some non-native fishes, but these recovered to former densities within 8 months, primarily from instream reproduction and invasion from tributaries. A low steady flow following a high steady flow could provide ideal conditions for non-native fish to reproduce and increase in numbers and distribution.

One of the major concerns of experimental steady flows is the potential for an increase in distribution and abundance of non-native fishes as a result of stabilized and warmed shorelines and backwaters. These concerns warrant considerable attention in determining magnitude and duration of the experiment. Reliable predictions of thermal warming patterns, backwater development and persistence, and responses by native fish species to these hydrologic and physical changes are needed for evaluating the risk posed by potentially increasing numbers of non-native fishes. A steady flow release during the summer months (i.e., June–September) that consistently produces over 18 °C in backwaters would allow species like red shiners, fathead minnows, carp, green sunfish, plains killifish, and black bullheads to spawn and rear their young. These fish can be large enough to cope with mainstem conditions within 4 months, and most reach sexual maturity in less than 1 year. A steady release of only one summer could allow these and other warm-water species to gain access to nearshore habitats and tributary inflows and gain a competitive advantage over native species.

SHo 2d: Young humpback chub are not widespread in the mainstem because high base flows and cold temperatures produce marginal conditions.

Humpback chub are mainstem inhabitants and spawners in all Upper Basin populations, with young fish extensively using shoreline habitats (not necessarily backwaters). In Grand Canyon, greatest numbers of chubs inhabit the LCR, probably to avoid high base flows and cold temperatures in the mainstem.

SHo 2e: Elevations and longitudinal locations of sandbars and associated eddy return-current channels (i.e., backwaters) depend on channel geomorphology and antecedent flows that suspend and redeposit sediments..

Studies of sandbar formation in the Upper Basin and in Grand Canyon strongly suggest that backwater elevations are a function of antecedent flows. Antecedent flows needed to form and rebuild sandbars and associated backwaters may differ in magnitude, depending on several variables (e.g., sand stored upstream in the river channel), such that flows needed to flood and maintain backwaters in different reaches of the river are likely to vary from one year to the next.

Studies of sandbar formations longitudinally down the Green River and the Colorado River through Grand Canyon strongly suggest that different channel geomorphologies result in different elevations of sandbars. Hence, flows that may maximize backwater formation in one reach may inundate or dewater backwaters in another reach, providing little fish habitat.

Primary Hypothesis 3. Low steady flows will significantly increase water clarity throughout the mainstem.

Observations and measurements during the research flows of 1990–1991 and during short-term steady flows of 5,000 and 8,000 cfs have shown significant increases in water clarity in the mainstem. This is believed to result from the absence of fluctuating flows and lack of high velocities that continually resuspend and transport even small amounts of sediment. Short-term low steady flows appear to produce greater water clarity than high steady flows because of greater velocities, but this relationship may not hold true over time. The beach/habitat-building flow of spring 1996 was held at 45,000 cfs for about 7 days, and water clarity was low, particularly during the first 3 days of the high release. This was primarily because of resuspension of sediments by higher velocities in the river channel. These sediments were soon redeposited in large eddies and along channel margins. The pattern of water clarity for a long-term high or low steady release is not known, but less turbidity would be expected after the first few days, in the absence of turbid flows from tributaries.

SHo 3a: Increased water clarity will significantly improve feeding conditions for sight-feeders, such as rainbow trout and reduce feeding opportunities for native fishes, such as humpback chub.

Studies in 1990–1993 showed that consistently decreased water clarity in the mainstem below the LCR caused a decline in abundance and condition of rainbow trout. Conversely, higher clarity increased condition, indicating that cold-water sight feeders, like rainbow trout and brown trout, could benefit from increased feeding opportunities from steady flows. Conversely, feeding opportunities for native fishes like humpback chub may be decreased; studies have shown significantly reduced movement at turbidity levels <30 NTUs.

SHo 3b: Local movements of native fishes are significantly influenced by water clarity, time of day, season, flow regime, flow level, ramping rates, and flow magnitude.

Behavior of native fishes in the mainstem is not well understood, especially as that behavior is affected by dam operations. Recent studies found that spring spawning season outweighed other variables in determining movement of adult humpback chub. Movement was also significantly greater under changing flow regimes and fluctuations. Movement of fish and behavior have not been evaluated for long-term steady flows, particularly at low-magnitude releases.

SHo 3c: Research flows of 1990–1991 maintained high fluctuations that enhanced drift and sediment and kept water clarity low, reducing condition of rainbow trout but keeping condition of humpback chub high.

During research flows in 1990–1991, operations varied between periods of high fluctuations and steady flows. These dam operations tended to maintain turbidity in the river and reduce water clarity. Since rainbow trout are sight feeders, feeding activity was likely reduced despite increased availability of food, while native humpback chub were able to maintain feeding activity under the cover of turbidity.

Primary Hypothesis 4. Mainstem water temperatures will increase significantly during low steady summer/fall flows.

Researchers have determined that short-term steady releases from Glen Canyon Dam in summer result in increasingly greater water temperature progressively downstream, presumably because of a relatively smaller, constant water mass that is warmed by solar radiation. Observations and measurements of short-term steady flows (5,000 cfs) showed higher mainstem temperatures of about 3 °C at Diamond Creek after only 3 days. Precise longitudinal warming patterns and rates are unknown, but periodic summer measurements show a warming rate of 1 °C/51 km of distance from the dam under fluctuating flows and interim operations, and 1 °C/45 km under interim flows and MLFF. Steady flows are expected to produce warmer mainstem temperatures. Precise warming rates and patterns are important information for predicting biological responses by algae, diatoms, macroinvertebrates, fishes, and fish parasites.

SHo 4a: Experimental flows will alter water temperatures, which will significantly improve reproductive success, growth, and survival of native fishes.

One of the principal limiting factors for the warm-water native fishes in Grand Canyon is the effect of cold temperatures on reproduction, growth, and survival. Numerous surveys have failed to locate reproduction of native fishes in the mainstem Colorado River, and all successful reproduction is thought to occur in seasonally warmed tributaries. Successful reproduction by humpback chub is suspected in warm mainstem springs, and spawning by flannelmouth suckers occurs in the dam tailwaters and is suspected in the downstream-most reaches of western Grand Canyon. Although river temperatures in the upper reaches would probably continue to be sub-optimal for spawning, a prolonged steady flow may warm the main channel sufficiently for reproduction, improved growth, and higher survival. This hypothesis assumes that mainstem reproduction prevailed in pre-dam conditions, as it currently does in other populations of humpback chub. Historic records in Grand Canyon are inadequate to definitely identify spawning locations.

SHo 4b: Numbers and survival of fish in downstream reaches are significantly limited by cold temperatures, lack of suitable habitat, low shoreline production, and low food resources.

Some investigators have reported low densities of fish in the downstream reaches of Grand Canyon, suggesting that the combination of cold temperatures and constant turbidity limit primary production and historic macroinvertebrate communities. Densities of warm-water fishes in otherwise suitable habitats are significantly lower than in upstream reaches, indicating that food may be a limiting factor.

SHo 4c: Fish habitat is limited by the effect of cold temperatures on swimming performance of fish.

Laboratory tests have demonstrated that juvenile humpback chub fatigue significantly faster at colder temperatures (i.e., 14°C) than at warmer temperatures (i.e., 20°C). Mainstem temperatures in the areas occupied by the nine mainstem aggregations of humpback chub rarely reach 14°C in summer. It is thought that these cold temperatures reduce swimming ability of young warm-water native fishes for escaping predation. Warmer temperatures from steady releases may enhance swimming performance by native fishes and increase survival of young and recruitment to adulthood.

Primary Hypothesis 5. Backwaters and tributary inflows will warm during low steady summer/fall flows.

Recent studies have demonstrated that during low steady flows, backwaters warm substantially, especially in late summer. Temperatures of mainstem backwater and nearshore habitats have a direct effect on the ability of warm-water native and non-native fishes to successfully spawn and survive as eggs and young. While the steady flow experiment will not affect the temperature of water released from the dam, stabilized flows will allow for a certain amount of longitudinal warming, especially in low-velocity shoreline habitats where the water has greater exposure to solar radiation.

SHo 5a: Backwaters will warm sufficiently under steady flows for reproduction by non-native fishes.

Small non-native species, like fathead minnows, red shiners, carp, green sunfish, black bullheads, and plains killifish can spawn successfully in backwaters and may be able to reproduce during a low steady summer release. The four native fish species in Grand Canyon, except perhaps for speckled dace, are not known to spawn in backwaters. Low, steady summer releases may enable non-native fishes to successfully rear a strong cohort of young that would survive subsequent dam operations and persist as larger, more widespread populations than at present. Many researchers feel that although cold mainstem temperatures preclude spawning by native fishes, these suboptimal temperatures also keep warm-water non-native fishes in check by minimizing reproduction, survival, and recruitment. It is unknown if the benefits of warming the system for native species would be outweighed by increased distribution and abundance of non-native fishes.

Primary Hypothesis 6. Low steady flows will significantly reduce dissolved oxygen levels in some backwater habitats

Low dissolved oxygen concentrations in backwaters are not expected to be a widespread problem for aquatic life. Depressed oxygen levels would be expected during steady flows in backwaters with dense growths of vegetation and accumulations of organics. These conditions could produce localized oxygen sags, in which nighttime respiration by plants reduces dissolved oxygen produced in the daytime by photosynthesis. Decomposition of organics could impose a constant oxygen depression.

SHo 6a: Low dissolved oxygen conditions in backwaters will significantly stress fish and reduce macroinvertebrate diversity.

Most fish would be expected to avoid these conditions, and the effect of low oxygen levels should be minimal on fish populations. Dissolved oxygen thresholds are 3–5 mg/L, depending on the species and life stage. Cold-water fishes, such as trout, are less tolerant, and become stressed at about 5 mg/L. Carp and fathead minnows can tolerate less than 3 mg/L, often resorting to gulping air at the water's surface. Dissolved oxygen thresholds for the native fishes are not known, but are expected to be 3–5 mg/L.

Low dissolved oxygen levels can also alter invertebrate assemblages. Coupled with a predominance of silt and sand in backwaters, the invertebrate fauna may become less diverse. Only those species adapted to these substrates and chemical condition will survive. Chironomids and tubificids that live in sand and silt may become dominant. These insects live in bottom substrates and may be less available as food to fishes.

Primary Hypothesis 7. Primary and secondary productivity of the mainstem river, backwaters, and nearshore habitats will increase significantly with stabilization and warming of the mainstem river and associated backwater habitats

Clear, warm conditions expected to result from steady flows would be expected to increase photosynthetic processes in shallow mainstem riffles, nearshore habitats, and backwaters, resulting in increased algal production and associated diatom and macroinvertebrate assemblages.

SHo 7a: Experimental flows will alter energy pathways of food resources and nutrients to significantly improve production of native fish.

Sustained high flows are expected to redistribute organics and nutrients held in bottom sediments and riverside sand deposits and vegetation. These nutrients will be made available for photosynthetic primary production and direct consumption by detrital feeders. Subsequent steady summer flows will provide warm, stable mainstem and nearshore conditions that could enhance photosynthetic activity and macroinvertebrate production, a principal food source of fish. An increase in productivity will increase food availability through the food chain for all fish. This in turn should increase growth and survivorship in both native and non-native species.

SHo 7b: Food is limiting fish density in otherwise suitable habitat in western Grand Canyon.

Primary and secondary production is thought to be low in western (lower) Grand Canyon because the combination of cold mainstem temperatures and moderate to low water clarity precludes substantial photosynthesis in shallow riffles, along shorelines, and in backwaters. Fish numbers are greatly reduced in western Grand Canyon, despite seemingly suitable habitat. This relationship of decreased production in western Grand Canyon and suppressed fish populations should be investigated more thoroughly. Presently, adult humpback chub seem to survive where large recirculating eddies entrain food materials delivered from upstream. Subadult humpback chub are dependent on shoreline food resources, which appear to limit densities of young fish where primary and secondary production are low.

SHo 7c: Removal of woody debris has greatly altered organic carbon budgets of the river and significantly depleted shoreline sources of terrestrial insects as fish food.

Regulation of the Colorado River has significantly reduced the amount of woody debris that was historically carried and deposited by the river during spring runoff and during late summer monsoonal spates. It is believed that removal of this high organic carbon has detrimentally affected food supplies for fish. High steady releases are likely to exceed normal dam operations and inundate shorelines where woody debris had accumulated from local vegetation and flooding. Woody debris can be a valuable, though short-term, source of terrestrial insects as food for fish.

Primary Hypothesis 8: Drifting macroinvertebrates and algae will significantly decrease with low steady flows.

Drifting macroinvertebrates and algae are important food sources for fish in the Colorado River in Grand Canyon. Drifting algal packets and dislodged macroinvertebrates are consumed by trout in the dam tailwaters as well as by native fishes farther downstream. The relationship of drift to extended low steady flow periods is unknown.

SHo 8a: Food availability will be significantly reduced for fish by low steady flows.

Algae and macroinvertebrates have usually declined in drift during short-term steady flows. Their presence in drift is thought to be a function of fluctuating releases dislodging materials from the shoreline and river bottom. Drift patterns for long-term steady flows are unknown, since the Colorado River in Grand Canyon has not experienced a relatively steady flow of more than about 7 days since Glen Canyon Dam was constructed in 1963. Drifting patterns of algae over long-term steady flows may become a function of dying and sloughing of algal mats, and drift patterns of macroinvertebrates may be related to behavior as they are in unregulated rivers.

Primary Hypothesis 9. The likelihood of* Lernaea cyprinacea *and the Asian tapeworm parasitizing fish will increase significantly with warming of the mainstem river and associated backwater habitats.

The two most common and invasive pathogens in fishes of Grand Canyon are the parasitic copepod *Lernaea cyprinacea* and the Asian tapeworm. These parasites are alien to the Colorado River Basin, having been introduced with non-native fish species. *Lernaea* are not host-specific and have been found on virtually every species of fish in the Colorado River, while Asian tapeworm are typically host-specific to Cypriniformes (minnow-like fishes). These parasites are warm-water organisms.

SHo 9a: Experimental flows will cause significant increases in parasites and diseases in native fish.

The parasitic copepod *Lernaea cyprinacea* requires 15°C (15–32°C optimal) to complete its life cycle of shedding eggs into the water, hatching, transforming through several immature stages, and attacking and attaching to a host fish. This life cycle usually occurs in quiet, warm habitats, such as backwaters. Increased infection of fishes would be expected under steady summer flows, but this parasite would not be expected to detrimentally affect any fish species in Grand Canyon. *Lernaea cyprinacea* has been commonly found in fishes of the Upper Basin, but is not considered a cause of death. This parasite is shed from the host at temperatures of less than about 14°C, and usually does not persist at cold mainstem temperatures.

The Asian tapeworm requires 20°C and a free-living host cyclopoid copepod (not *L. cyprinacea*) to complete its life cycle of shedding segments into the water, releasing eggs, and hatching. Suitable cyclopoid copepods apparently exist in Grand Canyon, probably in seasonally warmed tributaries such as the LCR, and could inhabit persistent mainstem backwaters. Increased infection of Asian tapeworm would be expected under steady flows, and could remain in the population for a long time because this parasite can survive in host fishes in cold mainstem temperatures, even though it cannot mature. Increased infection of Asian tapeworm is considered to be a potential major detrimental effect on native fishes, since this tapeworm causes intestinal blockage and can be lethal to stressed fish.

Hypotheses Not Directly Related To Evaluating Steady Flows

The following is a list of hypotheses not directly related to evaluating an experimental steady flow. Many of these hypotheses were presented by biologists at the Project Workshop. These are presented in this document to provide the reader with a perspective of additional issues of concern in Grand Canyon.

Hypothesis 1: *Channel geomorphology determines hydraulic patterns that form fish habitat and drive selection by humpback chub for canyon regions and reaches.*

Hypothesis 2: *Predominant shoreline geology and channel geomorphology change longitudinally, forming co-dependant relationships among cover, substrate, depth, and velocity of fish habitat.*

Hypothesis 3: *Two behaviorally distinct stocks of humpback chub occur in Grand Canyon: 1) fish that historically spawned in the LCR and continue to do so, and (2) relicts of mainstem stocks; e.g., 30-Mile aggregation.*

Hypothesis 4: *Recruitment to the adult population of humpback chub is primarily by small adults from the LCR.*

Hypothesis 5: *Numbers of young humpback chub remaining in the LCR are determined by available habitat and food, suggesting density dependence.*

Hypothesis 6: *Eddies are selected habitats in Grand Canyon because they provide low-velocity feeding and resting habitats that entrain drifting food materials.*

Hypothesis 7: *Low-velocity habitat is limited for humpback chub in Grand Canyon.*

Hypothesis 8: *Mainstem adult humpback chub spawning in the LCR appear to respond to photoperiod for gonadal maturation, but spawn with warm LCR temperatures; other mainstem humpback chub peak gonadal maturation 2 months later.*

Hypothesis 9: *Survival of fish in downstream areas is limited by food shortage, lack of habitat, large numbers of predators.*

Hypothesis 10: *Vegetated shorelines may be the most productive shoreline habitat available to fish.*

Table 12. Information needs for aquatic resources of the Colorado River in Grand Canyon, as prioritized at the Project Workshop. Reference numbers in parentheses (e.g., D.8) refer to text descriptions. Information needs with no reference numbers were identified as additional needs by workshop participants (N=25).

Data Gap (Reference Number To Text Description)	Priority Ranking	Weighted Score
Dispersal of young fish to mainstem (D.8)	1	83%
Integration of existing information (I.33)	2	79%
Evaluation of possible non-native fish control methods (F.24)	2	79%
Causative factors for mortality of young humpback chub (C.6)	3	75%
Magnitude of effects of thermal shock on the humpback chub population (G.17)	3	75%
Swimming performance of YOY and juvenile humpback chub at different temperatures (C.7)	4	71%
Relationships between the LCR and mainstem components of the humpback chub population (B.5)	5	67%
Mainstem habitats of adult and juvenile humpback chub (E.14)	5	67%
Predatory or competitive interactions between specific species under variable field conditions (F.20)	5	67%
Effects of predation on early life stages of humpback chub and long-term population viability (F.21)	5	67%
Relationship between mainstem water temperature and flow regulation (D.10)	6	63%
Relationship between flow, channel geomorphology, and fish habitat (D.11)	6	63%
Non-backwater habitats of adult and juvenile humpback chub (E.15)	6	63%
Levels of predation on native fishes by non-native brown trout and striped bass (F.19)	6	63%
Relationship between flushing of backwaters and productivity of the Colorado River in Grand Canyon (A.3)	7	58%
Relationship between reattachment bars and eddy return-current channel elevations, as affected by antecedent flows, for all presumed nursery reaches in Grand Canyon (E.12)	7	58%
Association of cover to water depth and velocity along channel margins (E.13)	7	58%
Flow requirements of humpback chub/quantitative information on water depth, velocity, substrate, and cover requirements (E.16)	7	58%
Effects of steady flow conditions on plankton and aquatic invertebrates (H.29)	7	58%
Response by fish in backwaters to steady flows over time (H.30)	7	58%
Effects of high spring release on shoreline vegetation and hence survival and recruitment of subadult native fishes (H.31)	7	58%
General habitat classification system (I.32)	7	58%

Table 12. Continued.

Data Gap (Reference Number To Text Description)	Priority Ranking	Weighted Score
Interrelationships of flow regimes, sediment augmentation, and temperature on primary and secondary productivity (A.2)	8	54%
Relationship of flow regimes to morphology and longevity of backwaters (E.9)	8	54%
Impacts of small-bodied forms of introduced fishes to reproductive success and survival of YOY native fish (F.22)	8	54%
The degree of infestation by Asian tapeworms and parasitic copepods in humpback chub, other native fishes, and non-native fishes (G.25)	8	54%
Incidence of Asian tapeworms in subadult humpback chub (G.26)	8	54%
Survival rates of parasitized immature native fish	8	54%
Relationship of drift and benthos (A.1)	9	50%
Mainstem flow needs for 30-Mile aggregation of humpback chub (E.18)	9	50%
The effects of temperature on Asian tapeworms in Grand Canyon (G.27)	9	50%
Genetics of humpback chub aggregations in Grand Canyon (30-Mile, LCR, Middle Granite Gorge) (B.4)	10	46%
Cause-effect relationship between reproductive success, spawning, or other life history aspects of small-bodied introduced species with major flow regime events (F.23)	10	46%
Extent of infestation of Asian tapeworms in Kanab Creek (G.28)	10	46%

Table13. Research hypotheses for aquatic resources of the Colorado River in Grand Canyon, as prioritized by Project Workshop biologists (N=6). Reference numbers in parentheses (e.g., SHo 4a) refer to text descriptions. SHo = secondary hypotheses related to experimental steady flow, NHo = hypotheses not related to experimental steady flow.

Research Hypotheses for Experimental Flows (EF)	Is Hypothesis Worth Pursuing?	Priority	Overall Priority Rank
EF will alter water temperatures, which will significantly improve reproductive success, growth, and survival of native fishes (SHo 4a)	Y - 100%	H - 75%	1 - 93%
High sustained flows will impound tributary mouths and significantly improve reproductive success and abundance of mainstem native fishes (SHo 1a)	Y - 100%	M - 76%	2 - 88%
Densities of humpback chub near the LCR inflow will be significantly reduced by destabilization of shorelines caused by cold fluctuating flows that force fish to leave otherwise sheltered habitats (SHo 2a)	Y - 95%	H - 81%	2 - 88%
Numbers and survival of fish in downstream reaches are significantly limited by cold temperatures, lack of suitable habitat, low shoreline production, low food resources (SHo 4b)	Y - 95%	M - 76%	3 - 86%
EF will significantly reduce negative effects of mainstem hydrology on number of nearshore habitats and use by native fishes (SHo 2b)	Y - 100%	M - 67%	4 -83%
EF will benefit native fishes by significantly reducing interactions with non-native fishes, especially in nearshore habitats (SHo 2c)	Y - 90%	M - 71%	5 - 81%
Two behaviorally distinct stocks of humpback chub occur in Grand Canyon: 1) fish that historically and presently continue to spawn in LCR, 2) relicts of mainstem stocks; e.g., 30-Mile aggregation (NHo 3)	Y - 90%	M - 67%	6 - 79%
Numbers of young humpback chub remaining in the LCR are determined by available habitat and food, suggesting density dependence (NHo 5)	Y - 95%	M - 62%	6 - 79%
Young humpback chub are not widespread in the mainstem because high base flows and cold temperatures produce marginal conditions (SHo 2d)	Y - 95%	M - 81%	2 - 88%
Fish habitat is limited by the effect of cold temperatures on swimming performance of fish (SHo 4c)	Y - 95%	M - 62%	6 - 79%
Mainstem humpback chub that spawn in the LCR respond to photoperiod for gonadal maturation, but spawn with warm LCR temperatures; other mainstem chubs peak gonadal maturation 2 months later (NHo 8)	Y - 95%	M - 62%	6 - 79%
Survival of fish in downstream areas is limited by food shortage, lack of habitat, and large numbers of predators (NHo 9)	Y - 85%	M - 71%	6 - 79%

Table 13. Continued.

Research Hypotheses for Experimental Flows (EF)	Is Hypothesis Worth Pursuing?	Priority	Overall Priority Rank
Predominant shoreline geology and channel geomorphology change longitudinally, forming co-dependent relationships among cover, substrate, depth, and velocity as fish habitat (NHo 2)	Y - 95%	M - 57%	7 - 76%
Eddies are selected habitats in Grand Canyon because they provide low-velocity feeding and resting habitat that entrain drifting food materials (NHo 6)	Y -95%	M - 57%	7 - 76%
EF will alter energy pathways of food resources and nutrients to significantly improve production of native fish (SHo 7a)	Y - 86%	L - 52%	8 - 69%
EF will cause significant increases in parasites and diseases in native fish (SHo 9a)	Y - 86%	L - 52%	8 - 69%
Recruitment to the adult population of humpback chub is primarily by small LCR adults (NHo 4)	Y/M - 76%	M - 57%	9 - 67%
Local movements of native fishes are significantly influenced by time of day, season, flow regime, flow level, ramping rates, and flow magnitude (SHo 3b)	Y - 86%	L - 48%	9 - 67%
Food is limiting fish density in otherwise suitable habitat in western Grand Canyon (SHo 7b)	Y - 81%	L - 48%	10 - 64%
Channel geomorphology determines hydraulic patterns that form fish habitat and drive selection by humpback chub for canyon regions and reaches (NHo 1)	Y - 86%	L - 38%	11 - 62%
Vegetated shorelines may be most productive shoreline habitat available to fish (NHo 10)	Y/M - 71%	L - 52%	11 - 62%
EF will significantly alter life histories of native fishes (SHo 1e)	Y/M - 76%	L - 43%	12 - 60%
Low velocity habitat is limited for humpback chub (NHo 7)	Y/M - 62%	L - 38%	13 - 50%
Research flows of 1990–1991 maintained high fluctuations that enhanced drift and sediment and kept water clarity low, reducing condition of rainbow trout but keeping condition of humpback chub high (SHo 3c)	Y/M - 57%	L - 43%	13 - 50%

Chapter 10
CONCLUSIONS, STRATEGIES, AND RECOMMENDATIONS

INTRODUCTION

The primary purpose of this project was to synthesize and integrate the available information on aquatic resources in Glen and Grand Canyons to address the two central questions introduced in Chapter 1:

1) Do sufficient data exist to reliably predict the effects of an experimental steady flow, presented as a "Reasonable and Prudent Alternative" (RPA) in the Biological Opinion (FWS 1994) of the final GCDEIS?

2) If so, do these data indicate positive effects on endangered and other native fishes in Glen and Grand Canyons?

A two-phased approach was used to complete this study. First, SWCA assembled information from over 400 publications and reports on aquatic resources of Glen and Grand Canyons. This information was evaluated, summarized, and integrated into a preliminary draft of this report. Second, in order to obtain feedback from a broad spectrum of experts, the draft was distributed to 25 aquatic biologists who have worked in the Upper and/or Lower Colorado River Basins in recent years. These specialists were asked to conduct a critical review of the report and to participate in a 2-day workshop. The overriding objective of the workshop, which was held in Flagstaff, Arizona, on February 27–28, 1997, was to obtain as much insight as possible from the biologists on the two questions driving this study. In addition to a copy of the draft report, each participant received a workbook requesting input on expected biological responses, data gaps, and research hypotheses. Throughout the workshop, opinions were freely expressed and duly recorded, but at no time did participating biologists vote on issues. They did mutually define the most important data gaps (listed in Chapter 9 and here under the heading "Strategies for Evaluating an Experimental Steady Flow") and reach a measure of consensus on prioritizing those gaps. As a result of this overall process, we are confident that the conclusions presented in this chapter reflect the perspective of a large segment of the scientific community working in the Colorado River Basin.

In addition to these conclusions, this chapter presents strategies for evaluating a steady flow experiment, as well as recommendations on how to comply with the requirement to conduct such an experiment as a Reasonable and Prudent Alternative to the Modified Low Fluctuating Flow (MLFF) regime.

CONCLUSIONS

The effectiveness of the prescribed steady flow experiment relies on many factors, but two in particular must be addressed before proceeding further with research design. First, researchers conducting the experiment must have sufficient baseline data to quantitatively measure the effects the experiment.

Second, researchers and managers must have a very high level of confidence based on scientifically collected and analyzed data that the experimental flows will not further harm the target species (endangered and other native species). After reviewing the pertinent literature and discussing these issues with colleagues at the Project Workshop, our responses to the questions central to this study are as follows:

12) Do sufficient baseline data exist to evaluate the influence of the steady flow experiment described in the RPA?

    No. Sufficient baseline data do not exist to evaluate the effect of a steady flow experiment on aquatic resources in Glen and Grand Canyons. Additional studies need to be conducted in the field (e.g., temperature model, native/non-native fish interactions) and in the laboratory (e.g., magnitude of thermal shock) before implementing the experimental steady flows. These studies are described in the following section on strategies for evaluating an experimental steady flow. Even with additional baseline information, fully evaluating the effects of a steady flow *a priori* is not possible, and a well designed sampling program is necessary to evaluate effects that are possible only through the experiment.

13) Do existing data indicate that the steady flow experiment will likely have an overall positive effect on endangered and other native fishes in Grand Canyon?

    Inconclusive. The answer to this question cannot be given as a simple "yes" or "no." In the absence of non-native predators and competitors, a steady flow scenario in Grand Canyon would most likely substantially benefit the endangered and other native fishes of the system. But non-native predators and competitors are present in the system, and existing data indicate that a properly designed steady flow experiment will benefit both native and non-native species. Stable flows and warmer mainstem and nearshore habitats would probably enhance reproduction, survival, and growth of both groups. Designing a steady flow experiment that would be advantageous for native fishes but disadvantageous for non-native warm-water fishes would be very difficult, if not impossible, because of great similarities in life history strategies. The major concern and overriding issue is a possible disproportionate increase in non-natives and the resultant elevated competition and predation pressures on native species. It is the opinion of the authors of this report that the overall and long-term benefits of an experimental steady flow can only be realized if populations of non-native fishes are reduced in targeted areas within the system before steady flows are implemented.

STRATEGIES FOR EVALUATING AN EXPERIMENTAL STEADY FLOW

As a result of this project, 11 significant data gaps were identified and prioritized. Strategies for filling these gaps are vital elements of an overall research design to evaluate experimental steady flows. These elements are listed here in order of priority starting with the most important. Workshop participants strongly agreed on the need for a Grand Canyon Aquatic Resources Database that would centralize data collected by all investigators and include a common database of pit tag numbers and associated physical, chemical, and biological data.

River Temperature Model

The effect of an experimental steady flow on river temperature is vital information for predicting positive or negative responses by aquatic resources. A model is needed to predict water temperature from Glen Canyon Dam downstream to the Lake Mead inflow on a spatial and temporal basis. The most important aspects of the model would be to predict water temperatures at any point downstream of the dam in the central channel, as well as along nearshore habitats, including backwaters. The model should be effective for every month of the year and for flow release volumes of 8,000–45,000 cfs. The model should also be able to predict daily warming and cooling.

Output from this model would provide scientists with a tool for predicting biological responses by fish and other components of the aquatic ecosystem in Grand Canyon. The model would provide resulting water temperatures from steady flows that, combined with knowledge of life histories, would enable scientists to predict such responses as mainstem spawning by native and non-native fishes, increases or decreases in food resources, changes in aquatic community species composition, and increases in pathogen infestations. Understanding potential and likely biological responses would enable biologists to provide a risk assessment of given flow management scenarios (not necessarily restricted to steady flows), and facilitate development of accurate and meaningful monitoring programs.

Relationship of High Mainstem Flows to Ponding of Tributary Inflows

Many scientists believe that ponding tributary mouths could provide large, warm, sheltered habitats for larvae and YOY fish descending from warm natal streams into the cold mainstem. Ponding is believed to be a beneficial effect because an expanded thermal gradient in tributary mouths would provide greater opportunity for young native fish to acclimate to cold mainstem temperatures. This reduces the effects of cold shock, which can lead to death or increased risk of predation associated with aberrant swimming behavior.

The extent of ponding is likely to differ for a given mainstem flow because inflow geomorphology differs for each tributary. Hence, key natal tributaries need to be identified and inflow areas mapped in order to determine mainstem flows at which maximum ponding occurs. Also, inflows of some tributaries with high sediment loads, such as the Paria River and Kanab Creek, can vary geomorphologically, depending on recent tributary floods.

Temperature pattern is an equally important variable to geomorphology of ponded tributary inflows. Most seasonally warmed tributaries are 16-24°C in spring and summer when native fish are descending into the cold mainstem, which is 8–12°C. Many young warm-water fish are unable to tolerate a sudden change in temperature and may become cold-shocked or eaten by other fishes because of slowed and erratic swimming behavior. Mapping temperature patterns for given mainstem and tributary flows is vital information for predicting effects on young fish in tributary mouths. A model exists for the LCR for mainstem flows of 9,200–17,798 cfs. Data are needed to expand this model and to develop models for other tributaries at flows of 8,000–45,000 cfs.

Biologists also recognized the importance of understanding the timing and degree of drift by native larval fishes at tributary inflows, including the Paria River, LCR, Shinumo Creek, Kanab Creek, and Bright Angel Creek. Very little information is available on larval drift within and from tributaries. The extent and timing of drift by native fishes is important for timing mainstem ponding flows. Equally important is information on drift of non-native fishes into the mainstem, since ponding will also benefit non-native species. Flow management could be used to thermally shock young non-natives descending at different times than natives.

Estimates of Primary and Secondary Production

Cold, clear mainstem releases, since completion of Glen Canyon Dam, have increased primary production in the tailwaters and altered macroinvertebrate community composition throughout Glen and Grand Canyons. Generally, algal communities are dominated by *Cladophora glomerata* in the tailwaters and *Oscillatoria* sp. further downstream. Macroinvertebrate species diversity is higher in the *Cladophora*-dominated reach above the mouth of the Paria, and lower downstream. Steady releases are likely to warm the mainstem nearshore environment, possibly increasing primary and secondary production and species diversity. However, warm temperatures may also lead to a change in diatom species composition, from the larger, more upright forms to smaller, more adnate forms, which are relatively unavailable to invertebrate grazers. The effect of a steady flow on primary and secondary production is vital information to prevent loss or possible collapse of the food base for trout and native fish.

Causative Mortality Factors for YOY Humpback Chub

Survival of juvenile humpback chub in the mainstem is believed to be low, limiting mainstem stocks. Factors contributing to this low survival need to be identified and mitigated in order to enhance recruitment and species recovery. Possible causative factors include instability of nearshore habitats from fluctuating flows, large changes in flow magnitude, predation, competition, food shortage, parasites, cold mainstem temperatures that limit swimming ability, or any combination of these factors. Survival appears to be lowest in the first year of life after young descend or are flushed from the LCR into the mainstem. Verifying and quantifying causative mortality factors will enable scientists and managers to plan and manage releases (e.g., steady flows, beach/habitat-building flows, habitat maintenance flows) with a better understanding of biological consequences. If, in fact, recruitment from young mainstem fish is insignificant, identifying and mitigating causes of mortality could be a key factor in recovering the humpback chub in Grand Canyon.

Of equal importance to assessing mortality of young humpback chub in the mainstem is determining the primary sources of recruitment to mainstem fish stocks. Recent studies have suggested little or no survival by young humpback chub hatched in the LCR and descending to the mainstem as YOY, but recruitment does appear to be occurring from subadult and small adults that originated in the LCR.

Biotic Interactions of Native/Non-Native Fishes

One of the primary concerns for an experimental steady flow is a possible positive response by non-native fishes that are predators and competitors of native fishes. Some biotic interactions are known, such as predation of humpback chub by brown trout, channel catfish, and rainbow trout. The magnitude of this effect on populations of native fish is not quantified, but is potentially a significant limiting factor. Other interactions, such as competition for food and space, as well as vectors for pathogens, are not well understood for Grand Canyon fishes.

Understanding biotic interactions of native and non-native fishes is vital information for evaluating the possible long-term effects of an experimental steady flow, and identifying long-term fishery management opportunities with respect to flow modification. If warmed nearshore and backwater habitats enable non-native fishes to successfully spawn, populations of species such as red shiners, fathead minnows, channel catfish, carp, black bullheads, and green sunfish could increase dramatically. Controlling and reducing these populations could be difficult once these species become established and abundant. Evidently, these species were abundant in the Colorado River through Glen and Grand Canyons prior to completion of Glen Canyon Dam but declined dramatically because of cold fluctuating flows. Reappearance of red shiners and increased numbers of fathead minnows have occurred since implementation of interim flows and MLFF, suggesting that flow variability (i.e., extreme fluctuating flows from power production) may be a controlling factor for these non-native fishes.

Rates of Algal and Macroinvertebrate Drift

Past studies indicate a decrease in algal and macroinvertebrate drift during short-term steady flows (i.e., 5,000 or 8,000 cfs for <72 hrs). Apparently fluctuating dam releases dislodge algae and benthic macroinvertebrates, making food resources available to fish in drift. The relationship of drift to long-term steady flows, however, is unknown, and is an important information gap for evaluating an experimental steady flow, since drift is an important food source for native fishes.

Effects on Parasites

Two principal species of parasites are most common in native fishes of Glen and Grand Canyons: the Asian tapeworm and a parasitic copepod (*Lernaea cyprinacea*). These alien parasites are warm-water species that require 20°C and 15°C, respectively, to complete their life cycles. Understanding how these parasites will respond to increased mainstem, nearshore, and backwater temperatures is important for predicting possible effects on fish populations. An experimental steady flow may provide warm temperatures of sufficient magnitude and duration to enable these parasites to complete their life cycles and spread through native fish populations. Information for predicting possible effects may need to be obtained in a laboratory setting.

Magnitude of Thermal Shock on Early Life Stages of Native Fishes

Laboratory tests show that larval and immediate post-larval native fishes are susceptible to cold shock when transferred from warm to cold waters, as happens during descent from natal tributaries. Pre-dam mainstem temperatures were warmer and closer to those of seasonally warmed tributaries during emergence and drift of these young fish. The magnitude of this post-dam effect to each year class of humpback chub, flannelmouth suckers, bluehead suckers, and speckled dace is unknown, but could be a significant limiting factor to native fish populations. If mortality is substantial, one possible mitigative action would be to pond tributary inflows, as described above. Laboratory testing will be required to determine the magnitude of tolerable temperature change and minimal amount of acclimation required by each species of fish from larvae to juvenile.

Genetic Significance of 30-Mile Aggregation of Humpback Chub and Effects of Mainstem Flow

Approximately 50 adults form the largest aggregation of humpback chub between Glen Canyon Dam and the LCR. The fish are all large adults, suggesting little if any reproductive success or recruitment. Aging of humpback chub with otoliths indicates that the fish probably reach 25–30 years of age, which could place these fish near maximum longevity if they hatched in about 1970—the last year in which mainstem temperatures were sufficiently warm for reproduction in Grand Canyon. These fish may constitute the last remaining recognizable mainstem stock of humpback chub left in Grand Canyon. Banking genetic material from these fish using cryopreservation, or taking individuals to hatchery facilities for culture may be an important action for preserving the genetic integrity of the humpback chub in Grand Canyon.

These mainstem aggregations may be important stocks for a second population of humpback chub in Grand Canyon. The 30-Mile aggregation may be too far upstream to benefit from longitudinal warming of steady flow, but stable water levels could promote reproduction and survival of eggs and larvae in the warm spring inhabited by these fish. Natural reproduction is suspected from the discovery in July 1994 of 100 post-larval humpback chub in the spring, which is located too far from known spawning areas, such as the LCR (50 km downstream), for the young fish to have originated in those areas. Another aggregation at Middle Granite Gorge is located about 220 km downstream of Glen Canyon Dam, and could benefit from longitudinal warming. Under current operations, mainstem temperature in summer reaches 14°C at this aggregation, and steady flows would be expected to be even warmer. Although limited reproductive success can occur at 14°C, optimal temperature for spawning by humpback chub is 16–22°C.

Relationship of Mainstem Flows to Nearshore Habitats and Channel Geomorphology

Shoreline habitats are believed to be more unstable since Glen Canyon Dam was built because of daily fluctuations from power generation. Implementation of steady flows in summer could provide stable, warm, nearshore and backwater habitats that could increase survival and recruitment of native fishes. Recent mainstem data suggest that the importance of nearshore habitats to young native fishes in Grand Canyon may have been underestimated, and the importance of backwaters overestimated (Valdez and Ryel 1995). Understanding these relationships is important for determining possible effects on native fishes in nearshore habitats and for weighing possible benefits to native fishes by warming and stabilizing backwaters.

It will also be necessary to understand the relationship of backwater elevation to channel geomorphology, antecedent flows, and existing flows, if formation, maintenance, and persistence of backwaters continues to be a primary objective of flow management. These relationships need to be understood for recognized nursery areas (e.g., Colorado River near the LCR), and should be tested longitudinally to determine if given flows maximize backwater numbers and areas in all regions of the canyon.

Grand Canyon Aquatic Resources Database

A consistent, accessible database is needed for aquatic resources in Grand Canyon. This database should be maintained and kept current through ongoing contractual agreements with researchers conducting the work and collecting the data. Constraints need to be in place to prevent use of data and publication of information without prior written consent of principal investigators.

ALTERNATIVE HYDROGRAPH DESIGNS

Workshop biologists concurred on the need to conduct some form of steady flow experiment to test important hypotheses regarding flow and resource response—but most, if not all, advocated using a different hydrograph from the one implied in the Biological Opinion RPA. One dissenting opinion questioned the need for an experimental steady flow in light of other more direct actions that could provide immediate benefit to native fishes (e.g., non-native fish control).

Biologists focused part of the workshop proceedings on developing a steady flow hydrograph that would, in their opinion, provide the greatest benefit to aquatic resources. The discussion began with a review of the logic and perspective of the GCDEIS's SASF alternative. It was widely recognized that this flow alternative was developed on the basis of information available in 1994, with the chief purpose of protecting the endangered and native fish populations. The SASF alternative was designed with the following release patterns and objectives:

- High spring flows to simulate a natural spring peak with cues for spawning, to pond tributary inflows for YOY native fish, and to flush non-natives.
- Stepped reductions in late spring to simulate a natural, or pre-dam, pattern.
- Low summer steady flows to allow for warming of backwaters.

The following points were made in the workshop as to why the SASF alternative was not consistent with the overall goal of protection and enhancement of habitat for endangered and other native fish:

- Humpback chub in the Grand Canyon do not need a spring discharge peak in the mainstem as a spawning cue. Their reproductive activities appear to be keyed to day length and temperature.
- Most tributaries will not be impounded at 18,000 cfs (the peak of the experimental steady flows prescribed in the RPA), and young humpback chub need ponding at the LCR inflow to keep them from entering the mainstem until they are large enough to withstand the cold water temperatures.
- The peak flow of 18,000 cfs is not high enough to displace non-native fish; much greater flows are needed.
- Most backwaters form below the lowest flows in the SASF hydrograph.

Three alternative steady flow regimes (Figure 28) were developed by the workshop participants. Each alternative is predicated on running a habitat maintenance flow (i.e., 33,200 cfs) immediately before any experimental steady flow. The reduction in flow from 33,200 cfs to the experimental flow level should occur as quickly as possible. Several participants advocated developing non-native fish control strategies before implementing the experimental flow/response studies. We endorse such a strategy and believe it should include studies targeting potentially harmful non-native species. The objectives of these investigations would include learning more about their abundance and distribution in the system; their habitat use, especially as it overlaps use by different life stages of native fish; diet overlap with native fishes; the possibility of competition with native fishes for limited food resources; and the extent of predation pressure on native species. Ways to control populations of problematic non-native species should be explored and implemented if judged practical. The objective of this program would be to reduce potential adverse impacts from non-native fish benefitting disproportionately over native fish from steady flows.

The three proposed alternative hydrographs are listed below with the anticipated benefits and negative effects cited at the workshop. Each alternative would be expected to warm mainstem water, but the degree and pattern of warming would differ. Each alternative has the potential to result in net benefits for native fishes or disproportionate benefits for non-native species.

<u>Hydrograph Alternative One</u> - Steady 12,500 cfs Year-Round Experimental Flow (except for habitat maintenance flow in spring)

Benefits

- This alternative could provide maximum stability and clearest water conditions: optimal conditions for evaluating survival of YOY humpback chub, humpback chub in the 30-Mile population, and other native and non-native fishes.
- Primary and secondary productivity would benefit from a year-round stable wetted perimeter; stable backwaters; and low turbidity, allowing greater light penetration.

Negatives

- Shoreline velocities under a year-round, 12,500 cfs experimental flow may be high, disrupting rearing habitat for juvenile native fish for the duration of the flow.
- Backwaters would fill with silt and vegetation faster than under other alternatives, reducing habitat for young native fish.
- Higher water clarity may increase predation on native fish by sight feeders.
- Non-native fish may benefit disproportionately because they are better adapted to stable flows.
- Steady flows would enhance reproductive and growth potential in rainbow and brown trout.[7]
- A steady, year-round flow does not mimic the natural hydrograph and therefore may not provide the benefits associated with a more natural hydrograph to native fish.

<u>Hydrograph Alternative Two</u> - Stepped Experimental Flow: habitat maintenance flow of 33,200 cfs for March and April; 12,500 cfs for May and June; and approximately 10,000 cfs for July through February.

Benefits

- Lower water levels in the summer should allow the water to warm more than under Alternative One but not as much as under Alternative Two. Warmer water should increase primary productivity and benefit native fishes.
- The Habitat Maintenance Flow concept could be tested over a longer period.

Negatives

- Wetted perimeter would decrease in the summer compared to Alternative One.

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[7] Some initial discussion revealed that several biologists felt that 12,500 cfs flows would benefit rainbow and brown trout, and should therefore be considered a positive effect of the experiment. However, given the recent data (see Valdez and Ryel 1995, Douglas and Marsh 1996b) on introduced fish predation on humpback chub, and the positive effect on trout is considered here to be a negative factor in implementing the RPA.

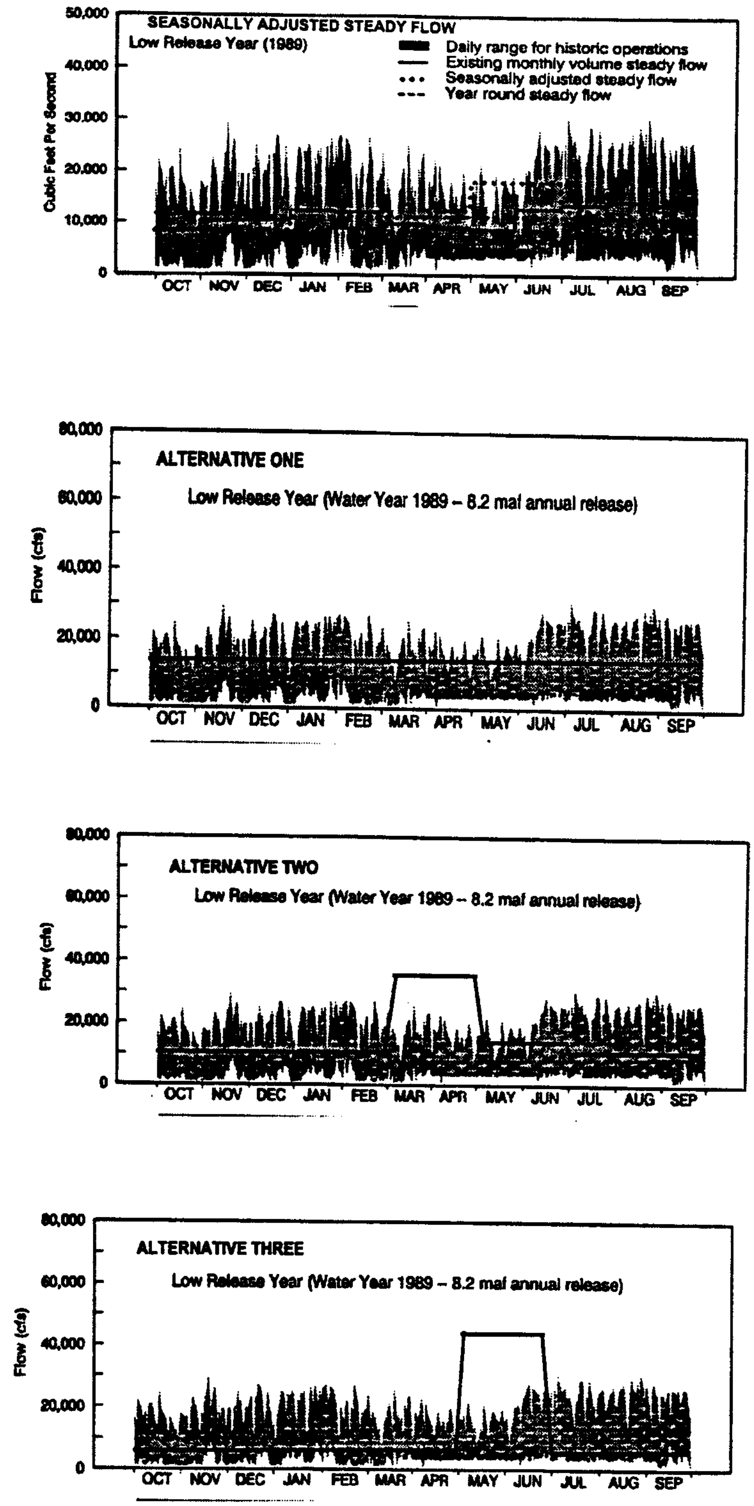

Figure 28. Three flow alternatives developed by Project Workshop participants, compared to the Seasonally Adjusted Steady Flow alternative (SASF), which served as the model for experimental steady flow recommended by FWS in the GCDEIS Biological Opinion.

- The long duration of high spring flows could erode sand out of the system.

Hydrograph Alternative Three - High Spring Experimental Flow: 42,000 cfs May and June; 5,000 cfs July through October; and then balance the low flow over the rest of the year to meet the 8.23 maf/yr requirement.

Benefits

- High spring flows should most effectively pond the mouth of the Little Colorado River, providing shelter for larvae and YOY native fish, particularly humpback chub.
- High spring flow may disrupt the life cycles of non-native fishes.
- Low, steady flows in summer should allow the mainstem to become warmer than under the other two altenatives, which should increase primary productivity and benefit native fishes.
- This alternative most closely resembles the natural hydrograph, which is assumed to be advantageous to native fishes.

Negatives

- High spring flows will likely erode sandbars retaining eddy return-current channels (i.e., backwaters).
- Backwaters may be lost over the summer at flows below 8,000 cfs.
- Wetted perimeter would decrease in the summer the most of any alternative.
- Warmer water in summer should benefit non-native fishes.

For the first time, a fisheries workshop brought together researchers and scientists from both the Upper and Lower Colorado River Basins in an attempt to achieve consensus on issues related to experimental steady flows as described in the FWS RPA and their influence on the native and non-native fishes in the Colorado River through Grand Canyon National Park. From this initial meeting, it is clear that communication and coordination among scientists is critical so that information and data can be shared and discussed among peers.

RECOMMENDATIONS

It is important to restate that an experimental steady flow is a key element in the FWS Biological Opinion on the operation of Glen Canyon Dam, and that the primary purpose of this steady flow is to improve conditions for greater survival and growth of native fishes in Grand Canyon. In the context of recovering the endangered humpback chub, a steady flow experiment is considered a Reasonable and Prudent Alternative to dam operations that otherwise jeopardize the continued existence of the species. At this time, an experimental steady flow release is prescribed as a condition of compliance with the Endangered Species Act.

Given the legal requirement to provide a steady flow experiment in the appropriate low-release year ($\leq$8.23 maf), and the findings of this report on prevailing scientific evidence of potential consequences to native and non-native fish species, the authors of this report offer the following recommendations:

1) Develop a hydrograph for the experimental steady flow, using the RPA in the GCDEIS

Biological Opinion as a departure point, that will likely benefit native fish and the aquatic ecosystem in general.

Workshop participants recommended the experimental hydrograph be restructured by biologists experienced with Grand Canyon and, if possible, with flow management in other regions of the Colorado River Basin. Most researchers supported a sustained high spring flow sometime during the period April–May, followed by a moderate to low steady flow during the period of June–October. The purpose of the sustained high flow is to rebuild backwater habitats, pond tributary mouths, and redistribute organic matter and nutrients. The purpose of the moderate-to-low steady summer flow is to stabilize and warm the mainstem and nearshore habitats, including backwaters. The magnitude and duration of the sustained high flow was not determined, but will in all likelihood be within the present operating range (MLFF; <20,000 cfs), since a low steady summer flow could only be held on a low-release year, precluding a release in excess of existing dam operations. The low steady flow will need to be determined from field measurements of reattachment bar and eddy return-current channel elevations, if establishment and maintenance of backwaters is to be a primary objective. Some researchers advocate power plant fluctuations under the MLFF operation following the low steady flow November–March) to minimize optimal habitat conditions for non-native fishes.

2) Evaluate non-native fish control measures to reduce the risk of negative secondary effects from increased abundances and distributions of competitive and predaceous species.

Substantial scientific evidence suggests that a steady flow during summer and fall (e.g., June through October) would benefit native fishes by stabilizing and warming nearshore nursery and rearing habitats. There is also compelling evidence that non-native fishes would benefit as well, possibly increasing risk of competition and predation on native species. Our review of the data and discussions with colleagues at the workshop have led us to conclude that insufficient baseline data are available to evaluate this relationship and other ecological risks associated with the steady flow experiment as described in the RPA. Although many ecological interactions are poorly understood, the negative effects of increased abundance of warm-water non-native fishes appears to be a significant risk that may outweigh the benefits of increased growth and survival of native fishes. The magnitude of this potential should be evaluated based on data scientifically gathered for this purpose. We advise that experimental steady flows not be implemented without a strategy for controlling non-native fish in Grand Canyon.

3) Conduct the steady flow release as an experiment from April through October, including appropriate control of non-native fishes and procurement of an adequate baseline for measuring biological response to the experiment.

Substantial data from Glen and Grand Canyons indicate that prolonged periods of steady flow could have direct and short-term beneficial effects to aquatic resources. However, the potential of an indirect and long-term negative effect from increased abundance and distribution of non-native fishes, increased incidence of parasites, and reduced availability of drift food resources, may outweigh the benefits of the steady flow. We recommended that the proposed low, steady summer flow be followed by fluctuating flows to offset or dampen increases of non-natives. It also appears necessary to moderate flow volume changes in order to minimize dramatic stage changes along shoreline habitats.

Based on literature review and opinions of biologists, it appears that the goals of an experimental steady flow (i.e., improve conditions for survival and growth of young native fishes) are more likely to be met if non-native fish control measures are implemented first. Conducting an experimental steady flow without non-native fish control risks a biological response by non-native fishes that could have long-term detrimental effects on native species.

4) Design and implement a monitoring program to establish a baseline of aquatic resources (algae, macroinvertebrates, fish) in order to measure a biological response.

Workshop participants agreed that the baseline database for evaluating a steady flow experiment is inadequate. Many of the information needs identified in this document need to be fulfilled before an adequate evaluation is possible. Studies should be initiated at least 2 years in advance of a steady flow experiment in order to collect sufficient baseline data to render an evaluation of effects. A monitoring program should be established for testing the appropriate hypotheses presented in this report. The program needs to be initiated at least 2 years prior to the experiment, conducted through the experiment, and continued for at least 2 years following the experiment.

LITERATURE CITED

Allan, N.L. 1993. Distribution and abundance of fishes in Shinumo Creek in the Grand Canyon. M.S. thesis, University of Arizona, Tucson.

Allan, R.C., and D.L. Roden. 1978. Fish of Lake Mead and Lake Mohave. Nevada Department of Wildlife. Biological Bulletin No. 7. 103 pp.

Allen, K.O., and K. Strawn. 1968. Heat Tolerance of channel catfish, *Ictalurus punctatus*. Proceedings of the Southeastern Association of Game and Fish Commissions 21:399-411.

Anderson, L.S., L.M. Lucas, M. McGee, M. Yard, and G.A. Ruffner. 1986. Aquatic habitat analysis for low and high flows of the Colorado River in Grand Canyon. Glen Canyon Environmental Studies, Flagstaff, Arizona.

Andrews, E.D. 1991. Sediment transport in the Colorado River Basin. Pages 54–74 in Colorado River ecology and dam management, Proceedings of a symposium, May 24-25, 1990, Santa Fe, New Mexico, edited by a committee of the National Research Council. National Academy Press, Washington, D.C.

Andrews, J.W, and R.R. Stickney. 1972. Interactions of feeding rates and environmental temperature on growth, foos conversion, and body composition of channel catfish. *Transactions of the American Fisheries Society* 101:94-99.

Andrews, J.W., L.H. Knight, and T. Murai. 1972. Temperature requirements for high density rearing of channel catfish from fingerling to market size. *Progressive fish-Culturist* 34:240-241.

Angradi, J.D., and D.M. Kubly. 1993. Effects of atmospheric exposure on *Chlorophyll a,* biomass and productivity of the epilithon of a tailwater river. *Regulated Rivers: Research and Management* 8: 345–358.

Angradi, T.R., and D.M. Kubly. 1994. Concentration and transport of particulate organic matter below Glen Canyon dam on the Colorado River, Arizona. *Journal of the Arizona - Nevada Academy of Science* 1/2(28):12–22.

Angradi, J.D., R.W. Clarkson, D.A. Kingsolver, D.M. Kubly, and S.A. Morgensen. 1992. Glen Canyon Dam and the Colorado River: responses of the aquatic biota to dam operations. Prepared for the Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, Arizona. Cooperative Agreement No. 9FC-40-07940. Arizona Game and Fish Department, Phoenix, Arizona.

ANSTF. 1994. Findings, conclusions, and recommendations of the intentional introductions policy review: Report to Congress. Aquatic Nuisance Species Task Force, U.S. Fish and Wildlife Service, Washington, DC. 53 pp.

Archer, D.L., L.R. Kaeding, B.D. Burdock, and C.W. McAda. 1985. A study of the endangered fishes of the upper Colorado River. U.S. Fish and Wildlife Service, Colorado River Fishery Project, Grand Junction, Colorado.

Arizona Cooperative Fishery Research Unit. 1976. An ecological analysis of backwaters of the lower Colorado River with special emphasis on Deer Island Lake. U. of Arizona, Tucson. 240 pages.

Arizona Game and Fish Department. 1993. Glen Canyon Environmental Studies Phase II, 1992 draft annual report. Prepared for the Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, Arizona. Cooperative Agreement No. 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Arizona Game and Fish Department. 1994. Glen Canyon Environmental Studies Phase II, 1993 draft annual report. Prepared for the Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, Arizona. Cooperative Agreement No. 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Arizona Game and Fish Department. 1996. Ecology of Grand Canyon Backwaters. [Prepared for the Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Cooperative Agreement No. 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Ayers, A.D., and T. McKinney. 1995. Effects of different flow regimes on periphyton standing crop and organic matter and nutrient loading rates for the Glen Canyon Dam tailwater to Lee's Ferry, draft final report. [Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Cooperative Agreement # 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Ayers, A.D., and T. McKinney. 1996a. Effects of Glen Canyon Dam operations on *Gammarus lacustris* in the Glen Canyon Dam tailwater, draft report. Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona. Cooperative Agreement # 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Ayers, A.D., and T. McKinney. 1996b. Water chemistry and zooplankton in the Lake Powell forebay, Glen Canyon Dam discharge and tailwater, draft final report. [Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Cooperative Agreement # 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Bancroft, D.C., and K. Sylvester. 1978. The Colorado River Glen Canyon tailwater fishery, annual report. Arizona Game and Fish Department, July 1977–June 1978.

Bardach, J.E., J.H. Ryther, and W.O. McLarney. 1972. Aquaculture: the farming and husbandry of freshwater and marine organisms. Wiley Interscience, New York.

Barrett, J.C., G.D. Grossman, and J. Rosenfeld. 1992. Turbidity-induced changes in reactive distance of rainbow trout. *Transactions of the American Fisheries Society* 121:437-443.

Baucom, F. 1981. Raw Data. United States Fish and Wildlife Service. Phoenix, Arizona.

Behnke, R.J., and D.E. Benson. 1983. Endangered and threatened fishes of the Upper Colorado River Basin. Colorado State University Cooperative Extension Service Bulletin 503A:1–38.

Bell, M.C. 1990. Fisheries Handbook of Engineering Requirements and Biological Criteria. Chapter 11. Fish Passage Development and Evaluation Program. U.S. Army Corps of Engineers, North Pacific Division, Portland, Oregon.

Bestgen, K.R. 1990. Status review of the razorback sucker, *Xyrauchen texanus*. Larval Fish Laboratory Report #44. Colorado State University, Ft. Collins.

Beus, S.S., and C.C. Avery, eds. 1992. The influence of variable discharge regimes on Colorado River sand bars below Glen Canyon Dam. Northern Arizona University, Flagstaff.

Black, E.C. 1953. Upper lethal temperatures of some British Columbia freshwater fishes. *Journal of the Fisheries Research Board of Canada* 10(4):196–210.

Blinn, D.W., and C. Runck. 1990. Importance of predation, diet and habitat on the distribution of *Lepidomeda vittata*: a federally listed species of fish. Coconino National Forest, Flagstaff, Arizona.

Blinn, D.W., C. Pinney, R. Truitt, and A. Pickart. 1986. The influence of elevated water temperatures on epiphytic diatom species in the tailwaters of Glen Canyon Dam and the importance of these epiphytic diatoms in the diet of *Gammarus lacustris*. Submitted to Bureau of Reclamation. Glen Canyon Environmental Studies, Flagstaff. Arizona Northern Arizona University, Flagstaff.

Blinn, D.W., C. Runck, D.A. Clark, and J.N. Rinne. 1993. Effects of rainbow trout predation on Little Colorado spinedace. *Transactions of the American Fisheries Society* 122:139–143.

Blinn, D.W., L.E. Stevens, and J.P. Shannon. 1994. Interim flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Glen Canyon Environmental Studies Program and National Park Service. Cooperative study agreement CA 8024-8-0002.

Blinn, D.W., J.P. Shannon, L.E. Stevens, and J.P. Carter. 1995. Consequences of fluctuating discharge for lotic communities. *Journal of the North American Benthological Society* 14:233–248.

Blinn, D.W., L.E. Stevens, and J.P. Shannon. 1992. The effects of Glen Canyon Dam on the aquatic foodbase in the Colorado River corridor in Grand Canyon, Arizona. Glen Canyon Environmental Studies Technical Report. Northern Arizona University, Flagstaff.

Blinn, D.W., L.E. Stevens, and J. P. Shannon. 1993. Interim flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Glen Canyon Environmental Studies Program and National Park Service. Cooperative study agreement CA8024-8-0002.

Blinn, D.W., L.E. Stevens, and J. P. Shannon. 1994. Interim flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Glen Canyon Environmental Studies Program and National Park Service. Cooperative study agreement CA8024-8-0002.

Blinn, D.W., R. Truitt, and A. Pickart. 1989. Responses of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. *Regulated Rivers: Research & Management* 4:91-96.

Boussu, M.F. 1954. Relationship between trout populations and cover on a small stream. *Journal of Wildlife Management* 18(2):229–239.

Bozek, M.A., L.J. Paulson, and J.E. Deacon. 1984. Factors affecting reproductive success of bonytail chubs and razorback suckers in Lake Mohave. Technical Report number 12. Lake Mead Limnological Research Center, Department of Biological Sciences, University of Nevada, Las Vegas.

Brouder, M.J. 1996. Number and area of backwaters. Chapter 4 in The effects of an experimental flood on the aquatic biota and their habitats in the Colorado River, Grand Canyon, Arizona, draft final report. [Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Arizona Game and Fish Department, Phoenix.

Brouder, M.J., and T.L. Hoffnagle. 1996. Distribution and prevalence of the Asian fish tapeworm, *Bothriocephalus acheilognathi*, in the Colorado River and tributaries, Grand Canyon, Arizona. Draft [report. Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Arizona Game and Fish Department, Flagstaff, Arizona.

Bulkley, R.V., and R. Pimentel. 1983. Temperature preference and avoidance by adult razorback suckers. *Transactions of the American Fisheries Society* 112:601–607.

Bulkley, R.V., C.R. Berry, R. Pimentel, and T. Black. 1982. Tolerance and preferences of Colorado River endangered fishes to selected habitat parameters. Pages 185–241 in Colorado River Fishery Project, final report, Part 3: Contracted studies. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.

Burke, T., and G. Mueller. 1993. Native Fish Work Group, 1992 annual report. U.S. Bureau of Reclamation, Boulder City, Nevada.

Carlander, K.D. 1969. Handbook of freshwater fishery biology, Vol. 1. Iowa State University Press, Ames.

Carlson, C.A., and R.T. Muth. 1989. The Colorado River: lifeline of the American Southwest. Pages 220–239 in Proceedings of the International Large River Symposium, edited by D.P. Dodge. Canadian Special Publication, Fisheries and Aquatic Sciences, 106.

Carlson, C.A., C.G. Prewitt, D.E. Snyder, E.J. Wick, E.L. Ames, and W.D. Front. 1979. Fish and macroinvertebrates of the White and Yampa rivers, Colorado. U.S. Bureau of Land Management, Biological Sciences Series 1, Denver.

Carothers, S.W., and B.T. Brown. 1991. The Colorado River through Grand Canyon; natural history and human change. University of Arizona Press, Tucson.

Carothers, S.W., and R. Dolan. 1982. Dam changes on the Colorado River. *Natural History* 91(1):74-83.

Carothers, S.W., and C.O. Minckley. 1981. A Survey of the fishes, aquatic invertebrates and aquatic plants of the Colorado River and selected tributaries from Lees Ferry to Separation Rapids. Final report for U.S. Bureau of Reclamation Contract 7-07030-C0026. Museum of Northern Arizona, Flagstaff.

Carothers, S.W., J.W. Jordan, C.O. Minckley, and H.D. Usher. 1981. Infestation of the copepod parasite *Lernaea cyprinaceae* in native fishes of the Grand Canyon. Pages 452-460 in Proceedings of the Second Conference on Scientific Research in the National Parks. National Park Service Transactions and Proceedings Series, Vol. 8.

Carter, J.G., R.A. Valdez, and R.J. Ryel. 1985. Fisheries habitat dynamics in the upper Colorado River. *Journal of Freshwater Ecology* 3(2):249–264.

Chart, T.E., and E.P. Bergersen. 1992. Impact of mainstream impoundment on the distribution and movements of the resident flannelmouth sucker (Catostomidae: *Catostomus latipinnis*) population in the White River, Colorado. *Southwestern Naturalist* 37(1):9–15.

Cherry, D.S., K.L. Dickson, J. Carins, Jr., and J.R. Stauffer. 1977. Preferred, avoided and lethal temperatures of fish at during rising temperature conditions. *Journal of the Fisheries Research Board of Canada* 34:239-246.

Clarkson, R.W. 1993. Unpublished data with the Arizona Game and Fish Department.

Clarkson, R.W., A.T. Robinson, and T.L. Hoffnagle. 1997. Asian tapeworm (*Bothriocephalus acheilognathi*) in native fishes from the Little Colorado River, Grand Canyon, Arizona. *Great Basin Naturalist* 57(1):66-69.

Clarkson, R.W., O.T. Gorman, D.M. Kubly, P.C. Marsh, and R.A. Valdez. 1994. Management of discharge, temperature, and sediment in Grand Canyon for native fishes. Issue Paper. Glen Canyon Environmental Studies, Flagstaff, Arizona.

Converse, Y.K. 1996. A geomorphic assessment of subadult humpback chub habitat in the Colorado River through Grand Canyon. M.S. Thesis, Utah State University, Logan.

Coon, K.L., Jr. 1965. Some biological observations on the channel catfish, *Ictalurus punctatus* (Rafinesque), in a polluted western river. M.S. thesis, Utah State University, Logan.

Coutant, C.C. 1977. Compilation of temperature preference data. *Journal of the Fisheries Research Board of Canada* 34(5):739–745.

Coutant, C.C. 1985. Striped bass, temperature and dissolved oxygen: a speculative hypothesis for environmental risk. *Transactions of the American Fisheries Society* 114(1):31–61.

Crowl, T.A., C.R. Townsend, and A.R. McIntosh. 1992. The impact of introduced brown and rainbow trout on native fish: the case of Australasia. *Reviews in Fish Biology and Fisheries* 2:217–241.

Deacon, J.E. 1979. Endangered and threatened fishes of the West. *Great Basin Naturalist Memoirs* 3:41–64.

Deacon, J.E., and W.L. Minckley. 1974. Desert fishes. Pages 385–488 in Desert biology II, edited by G.W. Brown. Academic Press, New York.

Dellenbaugh, F.S. 1908. A canyon voyage. University of Arizona Press, Tucson.

Dill, W.A. 1944. The fishery of the Lower Colorado River. *California Fish and Game* 30:109–211.

Dolan, R., A. Howard, and A. Gallenson. 1974. Man's impact on the Colorado River in the Grand Canyon. *American Scientist* 62:392–401

Dolan, R., A. Howard, and D. Trimble. 1978. Structural control of the rapids and the pools of the Colorado River in the Grand Canyon. *Science* 202:629–631.

Doudoroff, P., and D.L. Shumway. 1970. Dissolved oxygen requirements of freshwater fishes. FAO Fisheries Technical Paper 86.

Douglas, M.E. 1993. Analysis of sexual dimorphism in an endangered cyprinid fish (*Gila cypha*) using video image technology. *Copeia* 1993(2):334-343.

Douglas, M.E., and P.C. Marsh. 1996a. Catostomidae of the Grand Canyon Region of Arizona: population estimates, movements and survivability. Section 3 in Ecology and conservation biology of humpback chub (*Gila cypha*) in the Little Colorado River. Draft final report. [Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Contract number 1-FC-40-10490. [Arizona State University, Tempe.]

Douglas, M.E., and P.C. Marsh. 1996b. Endangered humpback chub (*Gila cypha*) as prey of introduced fishes in the Little Colorado River, Arizona. Section 2 in Ecology and conservation biology of humpback chub (*Gila cypha*) in the Little Colorado River. Draft final report. [Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Contract number 1-FC-40-10490. [Arizona State University, Tempe.]

Douglas, M.E., and P.C. Marsh. 1996c. Population estimates/population movements of *Gila Cypha*, an endangered Cyprinid fish in the Grand Canyon region of Arizona. *Copeia* 1996 (1):15–28.

Douglas, M.E., and P.C. Marsh. 1996d. Survivability of an endangered species (*gila cypha*) in the grand canyon region of Arizona: results of a five-year mark/recapture study. Section 4 in Ecology and conservation biology of humpback chub (*Gila cypha*) in the Little Colorado River. Draft final report. Contract number 1-FC-40-10490 [for] Bureau of Reclamation, Salt Lake City, Utah.

Douglas, M.E., W.L. Minckley, and H.M. Tyus. 1989. Qualitative characters, identification of Colorado River chubs (Cyprinidae: Genus *Gila*) and the "art of seeing well." *Copeia* 1989:653–662.

Douglas, P.A. 1952. Notes on the spawning of the humpback sucker, *Xyrauchen texanus* (Abbott). *California Fish and Game* 38:149–155.

Dowling, T.E., and B.D. DeMarais. 1993. Evolutionary significance of introgressive hybridization in cyprinid fishes. *Nature* 362:444–446.

Edward, E.A., and K. Twomey. 1982 Habitat suitability index models: common carp. U.S. Fish and Wildlife Service.

Ellis, M.M. 1914. Fishes of Colorado. University of Colorado Studies 11:1-136.

Embody, G.C. 1934. Relation of temperature to the incubation periods of eggs of four species of trout. *Transactions of the American Fisheries Society* 64:281–291.

Engeling, N.T. 1990. Winter feeding and gastric evacuation of striped bass (*Morone saxatilis*). Master of Science Thesis, Southwest Texas State University, San Marcos, TX. 32 pp.

Everest, F.H. 1969. Habitat selection and spatial interaction of juvenile chinook salmon and steelhead trout in two Idaho streams. Ph.D. Dissertation, University of Idaho, Moscow.

Everhart, W.H., and W.D. Youngs. 1981. Principles of fisheries science, 2nd edition. Comstock Publishing Associates, Ithaca, NY. 107 pp.

Ferrari, R.L. 1988. 1986 Lake Powell survey. Bureau of Reclamation, Report no. REC-ERC-88-6.

Flagg, R. 1981. Disease survey of the Colorado River fishes. Pages 177–184 in Colorado River Fishery Project, final report, Part 3: Contracted studies. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.

Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: an ecological, economic, and social assessment, report of the Forest Ecosystem Management Assessment Team. VIII-17 to VIII-27.

Fradkin, P.L. 1981. A river no more: the Colorado River and the West. University of Arizona Press, Tucson, Arizona.

Gale, W.F. and G.L. Buynak. 1982. Fecundity and spawning frequency of the fathead minnow: a fractional spawner. *Transactions of the American Fisheries Society* 111:35-40.

Gilbert, C.H., and N.B. Scofield. 1898. Notes on a collection of fishes from the Colorado Basin in Arizona. *Proceedings of the U.S. National Museum* 20:487–499.

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.

Gorman, O.T., and V.J. Meretsky. 1996. Condition factor changes for humpback chub. Unpublished data. U.S. Fish and Wildlife Service, Flagstaff, Arizona.

Gorman, O.T., and D.M. Stone. In Press. Ecology of spawning humpback chub, Gila cypha, in the Little Colorado River near Grand Canyon, Arizona. *Environmental Biology of Fishes.*

Grabowski, S.J., and S.D. Hiebert. 1989. Some aspects of trophic interactions in selected backwaters and the main channel of the Green River, Utah, 1987–1988. Bureau of Reclamation, Salt Lake City, Utah.

Granath, W.O., Jr. and G.W. Esch. 1983. Seasonal dynamics of *Bothriocephalus acheilognathi* in ambient and thermally altered areas of a North Carolina cooling reservoir. *Proceedings of the Helminthological Society of Washington* 50:205-218.

Gross, M.L., A.R. Kapuscinski, and A.J. Faras. 1994. Nest-Specific DNA Fingerprints of smallmouth bass in Lake Opeongo, Ontario. *Transactions of the American Fisheries Society* 123(4):449-459.

Graf, W.L. 1979 . Rapids in canyon rivers. *Journal of Geology* 87:533–551.

Grand Canyon River Guides. 1993. Native fishes of Grand Canyon. Written by R.A. Valdez, Illustrated by M.C. Filbert. Flagstaff, Arizona.

Griffith, J.S. 1978. Effects of low temperature on the survival and behavior of threadfin shad, *Dorosoma petenense*. *Transactions of the American Fisheries Society* 107:63-70.

Gustaveson, A.W., B.L. Bonebrake, S.J. Scott, and J.E. Johnson. 1985. Lake Powell Fisheries Investigation. Five-year completion and 1984 (Segment 13) annual performance report for Colorado River drainage and tailwaters. Utah Department of Natural Resource, Division of Wildlife Resources.

Gustaveson, A.W., H.R. Maddux, and B. Bonebrake. 1990. Lake Powell fisheries investigations: annual performance report and completion report.

Gutreuter, S. 1980. Factors affecting fish community structure and habitat preference in Mississippi backwaters. M.S. Thesis, University of Missouri, Columbia.

Haden, A. 1992. Nonnative fishes of the Grand Canyon, a review with regards to their effects on native fishes. Glen Canyon Environmental Studies, Flagstaff, Arizona.

Haden, A. 1998. Benthic ecology of the Colorado River system through Canyonlands National Park. M.S. Thesis, Northern Arizona University, Flagstaff.

Haden, A., D.W. Blinn, J.P. Shannon, C. O'Brien, and K.P. Wilson. 1997. Benthic ecology of the Colorado River System through the Colorado Plateau Region of the southwestern United States. Final Report to Glen Canyon Environmental Studies, Bureau of Reclamation. Northern Arizona University Department of Biological Sciences.

Hamblin, W.K. 1990. Late Cenozoic lava dams in the western Grand Canyon. Pages 385–433 in Grand Canyon geology, edited by S.S. Beus and M. Morales. Oxford University Press, New York; Museum of Northern Arizona, Flagstaff.

Hamman, R.L. 1982. Spawning and culture of humpback chub. *The Progressive Fish-Culturist* 44:213–216.

Hanson, W.R. 1985. Drainage development of the Green River Basin in southwestern Wyoming and its bearing on fish biogeography, plate tectonics, and paleoclimates. *Mountain Geologist* 22:192–254.

Hardwick, G., D.W. Blinn, and H.D. Usher. 1992. Epiphytic diatoms on *Cladophora glomerata* in the Colorado River, Arizona: longitudinal and vertical distribution in a regulated river. *Southwestern Naturalist* 37:148–156.

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.

Haury, LR. 1986. Zooplankton of the Colorado River from Glen Canyon Dam to Diamond Creek. Glen Canyon Environmental Studies Technical Report. GCES Rep. No. B-10. Bureau of Reclamation, Salt Lake City, Utah.

Haury, L.R. 1988. Zooplankton of the Colorado River, Glen Canyon Dam to Diamond Creek. Pages 205–215 in Glen Canyon Environmental Studies Executive Summaries of Technical Reports. Bureau of Reclamation, Salt Lake City, Utah.

Hawkins, J.A., and T.P. Nesler. 1991. Nonnative fishes of the Upper Colorado River Basin: an issue paper. Final report to U.S. Fish and Wildlife Service.

Hendrickson, D.A. 1993. Progress Report on study of the utility of data obtainable from otoliths to management of humpback chub (*Gila cypha*) in the Grand Canyon. Progress report submitted to AGFD. 1-42 pp.

Hendrickson, D.A., and J.E. Brooks. 1987. Colorado squawfish introduction studies. *Proceedings of the Desert Fishes Society* 18:207 (abstract).

Hevly, R.H., and T.N.V. Karlstrom. 1974. Southwest paleoclimate and continental correlations. Pages 257–294 in Geology of northern Arizona, with notes on archaeology and paleoclimate, edited by T.N.V. Karlstrom, G.A. Swan, and R.L. Eastwood. Geological Society of America, Rocky Mountain Section, Guidebook 27, Pt.1, Regional Studies.

Hilborn, R. 1992. Can fisheries agencies learn from experience? *Fisheries* 17(4):6–14.

Hill, J., J.W. Evansand and M.J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) - Striped Bass. Biological Report 82(11.118). U.S. Fish and Wildlife Service, Washington, D.C.

Hoffman, G.L. 1976. The Asian tapeworm, *Bothriocephalus gowkongensis,* in the United States, and research needs in fish parasitology. Proceedings of the 1976 Fish Farming Conference and Annual Convention of Catfish Farmers of Texas, Texas A and M University, College Station, Texas.

Hoffman, G.L. 1980. The Asian tapeworm, *Bothriocephalus acheilognathi,* Yamaguti, 1934, in North America. *Fisch und Umwelt* 8:69–75.

Hoffnagle, T.L. 1997. Letter dated March 3, 1997, to Dorothy House, SWCA, Inc., Environmental Consultants.

Hoffnagle, T.L.; M.J. Brouder; T.J. Dresser, Jr; and D.W. Speas. 1996. The effects of an experimental flood on the aquatic biota and their habitats in the Colorado River, Grand Canyon, Arizona. Draft final report. [Submitted to Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona.] Arizona Game and Fish Department, Phoenix.

Hoffnagle, T.L., R.A. Valdez, and D.W. Speas. In Review. The effect of a controlled flood on fish populations, distribution and habitat use in the Colorado River, Grand Canyon, in Floods and River Management: The 1996 Controlled Flood in Grand Canyon, edited by R.H. Webb, J.C. Schmidt, G.R. Marzolf, and R.A. Valdez.

Hofknecht, G.W. 1981. Seasonal community of aquatic invertebrates in the Colorado River and its tributaries within Grand Canyon, Arizona. M.S. thesis, Northern Arizona University, Flagstaff.

Hokanson, K.E.F., C.F. Kleiner, and T.W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* 34:639-648.

Holden, P.B. 1977. Habitat requirements of juvenile Colorado squawfish. Western Energy and Land Use Team, Office of Biological Services, U.S. Fish and Wildlife Service, Fort Collins, Colorado.

Holden. P.B. 1978. A study of the habitat use and movement of the rare fishes in the Green River, Utah. *Transactions of the Bonneville Chapter of the American Fisheries Society* 1978:64–89.

Holden, P.B., and C.B. Stalnaker. 1970. Systematic studies of the cyprinid genus *Gila* in the Upper Colorado River Basin. *Copeia* 1970:409–420.

Holden, P.B., and C.B. Stalnaker. 1975a. Distribution and abundance of mainstream fishes of the middle and upper Colorado River Basin, 1967–1973. *Transactions of the American Fisheries Society* 104(2):217–231.

Holden, P.B., and C.B. Stalnaker. 1975b. Distribution of fishes in the Dolores and Yampa River systems of the Upper Colorado River Basin. *Southwestern Naturalist* 19:403–412.

Holden, P.B., R.D. Hugie, L. Christ, S.B. Chanson, and W. J. Masslich. 1986. Development of a fish and wildlife classification system for backwaters along the Lower Colorado River. For the Bureau of Reclamation. BIO/WEST, Logan, Utah.

Holland, L., C. Bryan, and J. Newman, Jr. 1983. Water quality and the rotifer populations in the Atchafalaya River Basin, Louisiana. *Hydrobiologia* 98(1):55-70.

Holling, C.S. (ed.) 1978. Adaptive environmental assessment and management. John Wiley and Sons, New York.

Howard, A.D., and R. Dolan. 1981. Geomorphology of the Colorado River in the Grand Canyon. *Journal of Geology* 89(3):269–297.

Hualapai Tribe. 1996a. Effects of a controlled flood on aquatic and riparian resources in lower Grand Canyon, Arizona. Draft report submitted to Bureau of Reclamation Grand Canyon Area Office and Glen Canyon Environmental Studies. Hualapai Department of Natural Resources, Peach Springs, Arizona.

Hualapai Tribe. 1996b. Effects of high, steady Colorado River flows and rising Lake Mead levels on aquatic and riparian resources in lower Grand Canyon and upper Lake Mead, Arizona. Draft report submitted to Bureau of Reclamation Grand Canyon Area Office. Hualapai Department of Natural Resources, Peach Springs, Arizona.

Hubbs, C.L. 1954. Establishment of a Forage Fish, the Red Shiner. *(Notropis lutrensis)* in the Lower Colorado River System. California Fish and Game 40:287-294.

Hubbs, C.L., and G.P. Cooper. 1935. Age and growth of the long-eared and green sunfishes in Michigan. *Papers of the Michigan Academy of Science, Arts and Letters* 20:669–696.

Hubbs, C.L., and R.R. Miller. 1953. Hybridization in nature between the fish genera *Catostomus* and *Xyrauchen.* *Papers of the Michigan Academy of Arts, Science and Letters* 38:207–233.

Hunt, C.B. 1969. Geologic history of the Colorado River. Pages 59–130 in The Colorado River region and John Wesley Powell. U.S. Geological Survey Professional Paper 669-C.

Hynes, H.B.N. 1970. The ecology of Running Waters. University of Toronto Press. 555 pp.

Jackson, H.W., and R.E. Tiller. 1952. Preliminary observations on spawning potential in striped bass (*Roccus saxatilis* [Walbaum]). Report of the Maryland Department of Research and Education, 93.

Jacobi, G.Z., and M.D. Jacobi. 1981. Fish stomach content analysis. Pages 285–324 in Colorado River Fishery Project, final report, Part 3: Contracted studies. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.

Jobling, M. 1981. Temperature tolerance and the final preferendum-rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology* 19:439-455.

John, K.R. 1964. Survival of fish in intermittent streams in the Chiricahua Mountains, Arizona. *Ecology* 41:112–119.

Johnstone, H.C., and L.E. Stevens. 1996. Physical and biological development of a large Colorado River backwater in Grand Canyon, Arizona. Desert Fishes Council Symposium, November 1996, La Paz, Baja California Sur.

Jones, A.T. 1985. A cross section of Grand Canyon archaeology: excavations at five sites along the Colorado River. Western Archaeological and Conservation Center Publication in Anthropology Number 28.

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, final report. Federal Aid Wildlife Restoration (Dingell-Johnson) Project F-l-R, Nevada Game and Fish Commission, Carson City.

Jordan, D.S. 1891. Report of explorations in Utah and Colorado during the summer of 1889, with an account-of the fishes found in each of the river basins examined. Bulletin of the U.S. Fish Commissioner 9, 1–40.

Jordan, D.S., and C.H. Gilbert. 1894. List of the fishes inhabiting Clear Lake, California. Bulletin of the U.S. Fisheries Commission 14 (1895):139–140.

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 system. U.S. Fish and Wildlife Service, Office of Biological Services 77/62, Fort Collins, Colorado.

Kaeding, L.R., and D.B. Osmundson. 1988. Interactions of slow growth and increased early life mortality: a hypothesis on the decline of Colorado squawfish in the upstream regions of its historic range. *Environmental Biology of Fishes* 22:287–298.

Kaeding, L.R., and M.A. Zimmerman. 1982. Life history and population ecology of the humpback chub in the Little Colorado River of the Grand Canyon, Arizona. Pages 281–321 in Colorado River Fishery Project Final Report Part 2, Field Investigations. U.S. Fish and Wildlife Service, Grand Junction, Colorado.

Kaeding, L.R., and M.A. Zimmerman. 1983. Life history and ecology of the humpback chub in the Little Colorado and Colorado Rivers of Grand Canyon. *Transactions of the American Fisheries Society* 112:577–594.

Kaeding, L.R., B.D. Burdock, P.A. Schrader, 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.

Karp, C.A., and H.M. Tyus. 1990. Behavioral interactions between young Colorado squawfish and six fish species. *Copeia* 1990:25–34.

Kennedy, D.M. 1979. Ecological investigations of backwaters along the Lower Colorado River. Ph.D. dissertation, University of Arizona, Tucson.

Kieffer, S.W. 1985. The 1983 hydraulic jump in Crystal Rapid: implications for river-running and geomorphic evolution in the Grand Canyon. *Journal of Geology* 93(4):385–406.

Kieffer, S.W. 1990. Hydraulics and geomorphology of the Colorado River in the Grand Canyon. Pages 333–384 in Grand Canyon geology, edited by S.S. Beus and M. Morales. Oxford University Press, New York; Museum of Northern Arizona, Flagstaff.

Kolb, E.L. 1914. Through the Grand Canyon from Wyoming to Mexico. MacMillan Co., New York. Reprinted, 1990, University of Arizona Press, Tucson.

Kolb, E.L., and E. Kolb. 1914. Experience in the Grand Canyon. *National Geographic Magazine* 26(2):99–184.

Kubly, D.M. 1990. The endangered humpback chub (*Gila cypha*) in Arizona: a review of past and suggestions for future research, draft report. Arizona Game and Fish Department.

Lagler, K.F. 1956. Freshwater Fishery Biology. 2nd Edition. W.M.C. Brown Company publishers. Dubuque, IA. 421 pp.

Langhorst, D.R. 1987. Larval razorback sucker, *Xyrauchen texanus*, in Lake Mohave, Arizona-Nevada. *Proceedings of the Desert Fishes Council* 17 (1985):164–165 (Abstract).

Langhorst, D.R. 1989. A monitoring study of razorback sucker, *Xyrauchen texanus*, reintroduced into the Lower Colorado River in 1988. Final Report for California Department of Fish and Game [Blythe], Contract FG-7494.

Langhorst, D.R., and P.C. Marsh. 1986. Early life history of razorback sucker in Lake Mohave. Final Report to U.S. Bureau of Reclamation, Lower Colorado River Region, Order No. 5-PG-30-06440.

Larkin, P.A. 1956. Interspecific competition and population control in freshwater fish. *Journal of the Fisheries Research Board of Canada* 13:327–342.

Lechleitner, R.A. 1992. Literature review of the thermal requirements and tolerances of organisms below Glen Canyon Dam. Draft document submitted to Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona.

LeCren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch *Perca fluviatilis*. *Journal of Animal Ecology* 20:201-219.

Lee, D.S., C.R. Carter, C.H. Hocutt, R.E. Jenkins, D.E. McAllister, and J.R. Stauffer. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History.

Lee, K.N., and J. Lawrence. 1986. Adaptive management: learning from the Columbia River Basin Fish and Wildlife Program. *Environmental Law* 16:431–60

Leibfried, W.C. 1988. The utilization of *Cladophora glomerata* and epiphytic diatoms as a food resource by rainbow trout in the Colorado River below Glen Canyon Dam, Arizona. M.S. Thesis, Northern Arizona University, Flagstaff.

Leibfried, W.C., and D.W. Blinn. 1987. The effects of steady versus fluctuating flows on aquatic macroinvertebrates in the Colorado River below Glen Canyon Dam, Arizona. Final Report [for] Arizona Game and Fish Department, Phoenix, Contract No. 6400042.

Leibfried, W.C., and B.H. Zimmerman. 1994. Non-native fish interactions in the Colorado River, Grand Canyon: what will the future hold? American Fisheries Society Annual Meetings, Western Division: Flagstaff, Arizona.

Leibfried, W.C., and B.H. Zimmerman. 1995. Hualapai aquatic resources study: transition monitoring of Glen Canyon Dam interim operations on aquatic resources between National Canyon and Pearce Ferry. Draft report submitted to Bureau of Reclamation, Glen Canyon Environmental Studies. Hualapai Department of Natural Resources, Peach Springs, Arizona.

Leibfried, W.C., and B.H. Zimmerman. 1996. Hualapai aquatic resources study: transition monitoring of Glen Canyon Dam interim operations on aquatic resources between National Canyon and Pearce Ferry. Draft report submitted to Bureau of Reclamation, Glen Canyon Environmental Studies. Hualapai Department of Natural Resources, Peach Springs, Arizona.

Leopold, L.B. 1969. The rapids and the pools—Grand Canyon. U.S. Geological Survey Professional Paper 669-D.

Li, H. 1979. Competition and coexistence in stream fish. Pages 19–30 in Symposium on Trout/non-gamefish Relationships in Streams, edited by P.B. Moyle and D. Koch. Miscellaneous Report Number 17, Desert Research Institute. University of Nevada, Reno.

Luchitta, I. 1972. History of the Colorado River in the Basin and Range Province. *Geological Society of America Bulletin* 83:1933–1948.

Luchitta, I. 1990. History of the Grand Canyon and of the Colorado River in Arizona. Pages 311–332 in Grand Canyon geology, edited by S.S. Beus and M. Morales. Oxford University Press, New York; Museum of Northern Arizona, Flagstaff.

Lupher, M.L., and R.W. Clarkson. 1993. Temperature tolerance of humpback chub (*Gila Cypha*) and Colorado squawfish (*Ptychocheilus Lucius*), with a description of culture methods for humpback chub. [Draft final report to Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona. Arizona Game and Fish Department, Flagstaff, Arizona.]

Lupher, M.L., and R.W. Clarkson. 1994. Temperature tolerance of humpback chub (*Gila cypha*) and Colorado squawfish (*Ptychocheilus lucius*), with a description of culture methods for humpback chub. In Glen Canyon Environmental Studies Phase II, 1993 annual report. [Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.] Cooperative agreement 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Machette, M.N., and J.N. Rosholt. 1989. Quaternary terraces in Marble Canyon and eastern Grand Canyon, Arizona. Pages 205–211 in Geology of Grand Canyon, northern Arizona (with Colorado River guides), edited by D.P. Elston, G.H. Billingsley, and R.A. Young. 28th International Geological Congress, Fieldtrip Guidebook T115/315. American Geophysical Union, Washington D.C.

Maddux, H.R., and W.G. Kepner. 1988. Spawning of bluehead sucker in Kanab Creek, Arizona (Pisces: Catostomidae). *Southwestern Naturalist* 33:364–365.

Maddux, H.R., D.M. Kubly, J.C. deVos, W.R. Persons, R. Staedicke, and R.L. Wright. 1987. Evaluation of varied flow regimes on aquatic resources of Glen and Grand Canyon, final report. [Prepared for Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona.] Contract # 4-AG-40-01810. Arizona Game and Fish Department, Phoenix.

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

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

Marsh, P.C., and D.R. Langhorst. 1988. Feeding and fate of wild larval razorback sucker. *Environmental Biology of Fishes* 21:59–67.

Martin, P.S., and Mehringer. 1965. Pleistocene pollen analysis and biogeography of the Southwest. Pages 433–451 in The Quaternary of the United States, edited by H.E. Wright Jr. and D.G. Frey. Princeton University Press, Princeton, New Jersey.

Marsh, P.C. 1987. Digestive tract contents of adult razorback suckers in Lake Mohave, Arizona-Nevada. *Transactions American Fisheries Society* 116:117–119.

Marsh, P.C., 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.

Martin, P.S. 1984. Stanton's Cave during and after the last Ice Age. Pages 133–137 in The archaeology, geology, and paleobiology of Stanton's Cave, edited by R.C. Euler. Grand Canyon Natural History Association Monograph No. 6. Grand Canyon, Arizona.

Matthews, W.J., and L.G. Hill. 1977. Tolerance of the red shiner, *Notropis lutrensis* (Cyprinidae) to environmental parameters. *Southwestern Naturalist* 22:89-98.

Matthews, W. J., and J.D. Maness. 1979. Critical thermal maxima, oxygen tolerances and success of cyprinid fishes in a southwester river. *American Midland Naturalist* 102:374-377.

McAda, C.W. 1983. Colorado squawfish, *Ptychocheilus lucius* (Cyprinidae), with a channel catfish, *Ictalurus punctatus* (Ictaluridae), lodged in its throat. *Southwestern Naturalist* 28(1):119–120.

McAda, C.W., and L.R. Kaeding. 1989. Relations between maximum annual discharge and the 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.

McAda, C.W., and H.M. Tyus. 1984. Resource overlap of age-0 Colorado squawfish with other fish species in the Green River, fall, 1980. *Proceedings of the Bonneville Chapter, American Fisheries Society* 1984:14–54.

McAda, C.W., and Wydoski, R.S. 1980. The razorback sucker, *Xyrauchen texanus*, in the Upper Colorado River Basin, 1974-76. Technical Papers of the U.S. Fish and Wildlife Service 99. U.S. Fish and Wildlife Service, Washington, D.C.

McAda, C.W., and R.S. Wydowski. 1983. Maturity and fecundity of the bluehead sucker, *Catostomus discobolus* (Catostomidae), in the Upper Colorado River Basin, 1975–1976. *Southwestern Naturalist* 28:120–123.

McAda, C.W., and Wydoski, R.S. 1985. Growth and reproduction of the flannelmouth sucker, *Catostomus latipinnis*, in the Upper Colorado River Basin, 1975–76. *Great Basin Naturalist* 45(2):282–286.

McCall, T.C. 1979. Fishery Investigation of Lake Mead, Arizona-Nevada, from Separation Rapids to Boulder Canyon, 1978–79. Final report to USDI Water and Power Resources Service, Contract No. 8-07-30-X0025. Arizona Game and Fish Department, Kingman.

McCall, T.C. 1983. Lee's Ferry Fishery Investigation. Arizona Game and Fish Department - Research Branch. Federal Aid in Restoration Program. Project F-14-R-15.

McCarthy, M.S., and W.L. Minckley. 1987. Age estimation for razorback sucker (Pisces: Catostomidae) from Lake Mohave, Arizona and Nevada. *Journal of the Arizona-Nevada Academy of Science* 21:87–97.

McDonald, D.B., and P.A. Dotson. 1960. Pre-impoundment investigation of the Green River and Colorado River developments. In Federal Aid In Fish Restoration Investigations of Specific Problems in Utah's Fishery. Federal Aid Project No. F-4-R-6, Departmental Information Bulletin No. 60-3. State of Utah, Department of Fish and Game, Salt Lake City.

McDonald, D.B., and P.A. Dobson. 1960. Investigations of specific problems in Utah's fishery: Job No. V Pre-Impoundment investigations of the Green and Colorado River developments. Federal Aid Project No. F-4-R-6. Utah Department of Fish and Game, Salt Lake City, Utah.

McDowall, R.M. 1968. Interactions of the native and alien faunas of New Zealand and the problem of fish introductions. *Transactions American Fisheries Society* 97:1–14.

McDowall, R.M. 1984. Exotic fishes - the New Zealand experience. Pages 177-199 in Distribution, Biology, and Management of Exotic Fishes, edited by W.R. Courtenay, Jr., and J.R. Stauffer, Jr. The Johns Hopkins University Press, Baltimore, Maryland.

McFadden, J.T., E.L. Cooper, and J.K. Anderson. 1965. Some effects of environment on egg production in brown trout (Salmo trutta). *Transactions of the American Fisheries Society* 10(1):88–95.

McGuinn-Robbins, D.K. 1995. Comparison of the number and area of backwaters associated with the Colorado River in Glen, Marble, and Grand Canyons, Arizona, draft final report. [Submitted to Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona.] Contract #9-FC-40-07940, Arizona Game and Fish Department, Flagstaff, Arizona.

McKee, E.D., and E.H. McKee. 1972. Pliocene uplift of the Grand Canyon region: time of drainage adjustment. *Geological Society of America Bulletin* 83:1923–1932.

McKee, E.D., R.F. Wilson, W.J. Breed, and C.S. Breed. 1967. Evolution of the Colorado River in Arizona. Museum of Northern Arizona Bulletin 44. Museum of Northern Arizona, Flagstaff.

Meffe, G.K. 1985. Predation and species replacement in American southwestern fishes: a case study. *Southwestern Naturalist* 30:173–187.

Melis, T.S., and R.H. Webb 1993. Debris flows in Grand Canyon National Park, Arizona: magnitude, frequency and effects on the Colorado River. Pages 1290–1295 in Hydraulic Engineering '93, edited by H.W. Shen. Hydraulics Division of the American Society of Civil Engineers, Vol. 2.

Meretsky, V.J., R.A. Valdez, M.J. Brouder, M.E. Douglas, O.T. Gorman, and P.C. Marsh. In Review. Temporal and spatial variability in length-weight relations of adult humpback chub. *Transactions of the American Fisheries Society.*

Miller, R.R. 1944 [Unpubl. Manuscript. Letter dated 28, August 1944, pertaining to a list of fishes occurring in Grand Canyon National Park] preliminary checklist.

Miller, R.R. 1955. Fish remains from archaeological sites in the Lower Colorado River Basin, Arizona. *Papers of the Michigan Academy of Science, Arts, and Letters* 40:125–136.

Miller, R.R. 1959. Origin and affinities of the freshwater fish fauna of western North America. Pages 187–222 in Zoogeography, edited by C.L. Hubbs. American Association for the Advancement of Science Publication 51. Washington, D.C.

Miller, R.R., 1961. Man and the changing fish fauna of the American Southwest. *Michigan Academy of Science, Arts, and Letters Paper* 46:365–404.

Miller, R.R. 1968. [Unpublished field notes] 1968 Arizona collecting expedition. On file in the Fish Division, University of Michigan Museum of Zoology, Ann Arbor, Mich.

Miller, R.R. 1972. Threatened freshwater fishes of the United States. *Transactions of the American Fisheries Society* 101 :239-252.

Miller, R.R., and C.H. Lowe. 1967. Fishes of Arizona. Part 2 of The vertebrates of Arizona, edited by Charles H. Lowe. University of Arizona Press, Tucson.

Miller, R.R., and J.R. Alcorn. 1946. The introduced fishes of Nevada, with a history of their introduction. *Transactions of the American Fisheries Society* 73:173–193.

Miller, A.S., and W.A. Hubert. 1990. Compendium of existing knowledge for use in making habitat management recommendations for the Upper Colorado River Basin. US. Fish and Wildlife Service, Denver, Colorado.

Miller, R.R., and G.R. Smith. 1968. Report on fishes of the Colorado River drainage between Lee's Ferry and Pierce's Ferry. MS., collecting report.

Miller, R.R., and G.R. Smith. 1972. Fishes collected on Grand Canyon survey, Lees Ferry to Diamond Creek, August 1968. Unpubl. Manuscript.

Miller, R.R., and G.R. Smith. 1984. Fish remains from Stanton's Cave, Grand Canyon of the Colorado, Arizona, with notes on the taxonomy of *G. cypha*. Pages 61-65 in The archeology, geology and paleobiology of Stanton's Cave, in Grand Canyon National Park, Arizona, edited by R.C. Euler. Grand Canyon National History Association Monograph 6. Grand Canyon, Arizona.

Miller, A.S., and W.A. Hubert. 1990. Compendium of existing knowledge for use in making habitat management recommendations for the Upper Colorado River Basin. US. Fish and Wildlife Service, Denver, Colorado.

Minckley, C.O. 1979. Research conducted on the Little Colorado population of the humpback chub during May, 1989. Final report to Arizona Game and Fish Department, Phoenix.

Minckley, C.O. 1990. Final report on research conducted on the Little Colorado River population of the humpback chub. During April-May, 1990. Arizona Game and Fish Department.

Minckley, C.O. 1992. Observed growth and movement in individuals of the Little Colorado population of the humpback chub *(Gila cypha)*. Proceedings of the Desert Fishes Council; 22:35-36. English and Spanish abstracts only. FR 38(1).

Minckley, C.O. 1996. Observations on the biology of the humpback chub in the Colorado River Basin, 1908–1990. Ph.D. Dissertation. Northern Arizona University, Flagstaff.

Minckley, C.O., and H.E. Klassen. 1969. Life history of the plains killifish, *Fundulus kanase* (Garman), in the Smoky Hill River, Kansas. *Transactions of the American Fisheries Society* 98: 460-465.

Minckley, C.O., and D.W. Blinn. 1976. Summer distribution and reproductive status of fish of the Colorado River and its tributaries in Grand Canyon National Park and vicinity, 1975. Final Report to the National Park Service. Contribution No. 42.

Minckley, C.O., and S.W. Carothers. 1979. Recent collections of the Colorado squawfish and razorback sucker from the San Juan and Colorado Rivers in New Mexico and Arizona. *Southwestern Naturalist* 24:686–687.

Minckley, W.L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix.

Minckley. W.L. 1982. Trophic interrelations among introduced fishes in the lower Colorado River, southwestern United States. *California Fish and Game* 68(2):78–79.

Minckley, W.L. 1983. Status of the razorback sucker, *Xyrauchen texanus* (Abbott) in the Lower Colorado River Basin. *Southwestern Naturalist* 28:165–187.

Minckley, W.L. 1991. Native fishes of the Grand Canyon Region: an obituary? Pages 124–177 in Colorado River ecology and dam management, Proceedings of a symposium, May 24-25, 1990, Santa Fe, New Mexico, edited by a committee of the National Research Council. National Academy Press, Washington, D.C.

Minckley, W.L., And J.E. Deacon. 1968. Southwestern fishes and the enigma of "endangered species." *Science* 159:1424–1432.

Minckley, W.L., and J.E. Deacon. 1991. Battle against extinction, native fish management in the American West. The University of Arizona Press, Tucson.

Minckley, W.L., and G. K. Meffe. 1987. Differential selection by flooding in stream-fish communities of the arid American Southwest. Pages 93–104 in Community and evolutionary ecology of North American stream fishes, edited by W.J. Matthews and D.C. Heines. University of Oklahoma Press, Norman.

Minckley, W.L., D.A. Hendrickson, and C.E. Bond. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. Pages 519–613 in The zoogeography of North American freshwater fishes, edited by C.H. Hocutt and E.O. Wiley. Wiley-Interscience, New York.

Minckley, W.L., 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 Battle against extinction, edited by W.L. Minckley and J.E. Deacon. University of Arizona Press, Tucson.

Montgomery, W.L., and K. Tining. 1996. Impact of fluctuating water levels on early life history of rainbow trout. Draft report to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona.

Moyle, P.B. 1976. Inland fishes of California. University of California Press, Berkeley.

Moyle, P.B. 1986. Fish introductions in North America: patterns and ecological impact. Pages 27–43 in Ecology of biological invasions of North America and Hawaii, edited by H.A. Mooney and J.A. Drake. Springer-Verlag, New York.

Mueller, G., W. Rinne, T. Burke, and M. Delamore. 1982. Habitat selection of spawning razorback suckers observed in Arizona Bay, Lake Mohave, Arizona-Nevada. U.S. Bureau of Reclamation, Lower Colorado River Region, Boulder City, Nevada.

Mueller, G., W. Rinne, T. Burke, and M. Delamore. 1985. Habitat selection of spawning razorback suckers observed in Arizona Bay, Lake Mohave, Arizona-Nevada. *Proceedings of the Desert Fishes Council* 14 (1982):157 (abstract).

Muth, R.T., and D.E. Snyder. 1995. Diets of young Colorado squawfish and other small fish in backwaters of the Green River, Colorado, and Utah. *Great Basin Naturalist* 55:95-104.

Muth, R. 1990. Ontogeny and taxonomy of humpback chub, bonytail, and roundtail chub larvae and early juveniles. Dissertation. Colorado State University, Fort Collins, Colorado. 1-262 pp.

National Research Council. 1987. River and dam management: a review of the Bureau of Reclamation's Glen Canyon Environmental Studies, committee to review the Glen Canyon Environmental Studies. National Academy Press, Washington, D.C.

National Research Council. 1994. Review of the Draft Environmental Impact Statement on Operation of Glen Canyon Dam. National Academy Press, Washington, D.C.

National Research Council. 1996. River resource management in the Grand Canyon. [Prepared by the] Committee to Review the Glen Canyon Dam Environmental Studies. National Academy Press, Washington, D.C.

Osmundson, D.B. 1987. Growth and survival of Colorado squawfish *(Ptychocheilus lucius)* stocked in riverside ponds, with reference to largemouth bass *(Micropterus salmoides)* predation. M.S. Thesis, Utah State University, Logan.

Osmundson, D.B., and C.R. Berry, Jr. 1986. Largemouth bass predation on stocked Colorado squawfish. Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissions 65:146 (abstract).

Osmundson, D.B., 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 the Green Mountain and Ruedi Reservoir water sales, final report. U.S. Fish and Wildlife Service, Colorado River Fisheries Project. Grand Junction, Colorado.

Osmundson, D.B., P. Nelson, and D. 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. 127 pp + 82 pp appendices.

Otis, E.O. 1994. Distribution, abundance, and composition of fishes in Bright Angel and Kanab Creeks, Grand Canyon National Park, Arizona. M.S. Thesis, University of Arizona, Tucson.

Papoulias, D. 1988. Survival and growth of larval razorback sucker, *Xyrauchen texanus*. M.S. thesis, Arizona State University, Tempe.

Papoulias, D., and Minckley, W.L. 1992. Effects of food availability on survival and growth of larval razorback suckers in ponds. *Transactions of the American Fisheries Society* 121:340–355.

Pearson, W.D. 1967. Distribution of macroinvertebrates in the Green River below Flaming Gorge Dam, 1963-1965. Master of Science Thesis, Utah State University, Logan, UT. 105pp.

Pemberton, E.L. 1976. Channel changes in the Colorado River below Glen Canyon Dam. Pages 5-61 to 5-73 in Proceedings of the Third Federal Interagency Sedimentation Conference, Denver, Colorado, March 22–25, 1976. Water Resources Council.

Persons, W.R., K. McCormack, and T. McCall. 1985. Fishery investigations of the Colorado River from Glen Canyon Dam to the confluence of the Paria River: assessment of the impact of fluctuating flows on the Lee's Ferry fishery. Federal Aid in Sport Fish Restoration Dingell Johnson Project F-14-R-14. Arizona Game and Fish Department, Phoenix.

Pflieger, W.L. 1975. The fishes of Missouri. Missouri Department of Conservation, Jefferson City.

Phillips, C. 1994. Memorandum to Gordon Lind, [Reclamation] GCDEIS Manager, from Craig Phillips [Reclamation], August 2, 1994.

Pinney, C.A. 1991. The response of *Cladophora glomerata* and associated epiphytic diatoms to regulated flow, and the diet of *Gammarus lacustris*, in the tailwaters of Glen Canyon Dam. M.S. Thesis, Northern Arizona University, Flagstaff.

Pister, E.P. 1981. The conservation of desert fishes. Pages 411–446 in Fishes in North American deserts, edited by R.J. Naiman and D.L. Soltz. John Wiley and Sons, New York.

Powell, J.W. 1875. Exploration of the Colorado River and its tributaries, explored in 1869, 1870, 1871, and 1872. U.S. Government Printing Office. Washington, D.C.

Privolnev, T.I. 1954. Physiological adaptations of fishes to new conditions of existence. *Trudy Soveshch. Ikhtiol. Kom.* 3:40-49.

Quartarone, F. 1993. Historical accounts of upper Colorado River Basin endangered fish. U.S. Fish and Wildlife Service. Recovery and Implementation Program for Endangered Fish of the Upper Colorado River Basin.

Raleigh, R.F., L.D. Zuckerman, and P.C. Nelson. 1986. Habitat suitability index models and instream flow suitability curves: brown trout. Revised [edition]. U.S. Fish and Wildlife Service, Biological Report 82 (10.124).

Randle, T. 1993. EIS update. [Bureau of Reclamation] *Colorado River Studies Office Newsletter* Spring 1993.

Rathbun, N.L. 1970. Reservoir fisheries investigations: creel census and plankton studies, in Glen Canyon Unit, Colorado River Storage Project, Job Progress Report F-17-R. Arizona Game and Fish Department, Phoenix.

Rea, A.M, and L.L. Hargrave. 1984. The bird bones. Pages 77–93 in The archeology, geology and paleobiology of Stanton's Cave, in Grand Canyon National Park, Arizona, edited by R.C. Euler. Grand Canyon National History Association Monograph 6. Grand Canyon, Arizona.

Rehder, D.D. 1959. Some aspects of the life history of the carp, Cyprinus carpio, in the Des Moines River, Boon County, Iowa. *Iowa Journal of Science* 34(1):11-26.

Reisner, M. 1996. Cadillac desert. Revised and updated ed. Penguin Books, New York.

Riggs, M.R., and G.W. Esch. 1987. The suprapopulation dynamics of *Bothriocephalus acheilognathi* in North Carolina reservoir: abundance, dispersion, and prevalence. *Journal of Parasitology* 73:877-892.

Robinson, A.T., D.M. Kubly, and R.W. Clarkson. 1996. Limnology and the distributions of native fishes in the Little Colorado River, Grand Canyon, Arizona, final report. [Submitted to the Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, Arizona]. Cooperative Agreement # 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Rolston, H. 1991. Fishes in the desert: paradox and responsibility. Pages 43–54 in Battle against extinction: native fish management in the American West, edited by W.L. Minckley and J.E. Deacon. University of Arizona Press, Tucson.

Rubin, D.M, J.C. Schmidt, and J.N. Moore. 1990. Origin, structure, and evolution of a reattachment bar, Colorado River, Grand Canyon, Arizona. *Journal of Sedimentary Petrology* 60:982–991.

Ruppert, J.B., R.T. Muth, and T.P. Nesler. 1993. Predation on fish larvae by adult red shiner, Yampa and Green Rivers, Colorado. *Southwestern Naturalist* 38(4): 397-399

Rule, R. 1885. Southern region. Pages 10–15 in Annual report, Arizona Fish Commission, 1883–1884, to Governor of the Territory of Arizona, edited by J.H. Taggart.

Schmidt, J.C., and J.B. Graf. 1990. Aggradation and degradation of alluvial sand deposits, 1965 to 1986, Colorado River, Grand Canyon National Park, Arizona. U.S. Geological Survey Professional Paper No. 1439. Salt Lake City, Utah.

Schmidt, J.C., and M.F. Leschin. 1995. Geomorphology of post-Glen Canyon Dam fine-grained alluvial deposits of the Colorado River in the Point Hansborough and Little Colorado River confluence reaches in Grand Canyon National Park, Arizona. Prepared in cooperation with and funded by U.S. Bureau of Reclamation, Glen Canyon Environmental Studies. Utah State University, Logan.

Schoenherr, A.A. 1981. The role of competition in the replacement of native species by introduced species. Pages 173–203 in Fishes in North American deserts, edited R.J. Naiman and D.L. Soltz. John Wiley and Sons, New York.

Schrader, P.A. 1991. Endangered and threatened wildlife and plants: the razorback sucker (*Xyrauchen texanus*) determined to be an endangered species. *Federal Register* 56:54957–54967.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bulletin 184, Fisheries Research Board of Canada, Ottawa.

Shannon, J.P., D.W. Blinn, P.L. Benenati, and K.P. Wilson. 1966a. Organic drift in a regulated desert river. *Canadian Journal of Fisheries and Aquatic Sciences*.

Shannon, J.P., D.W. Blinn, K.P. Wilson, P.L. Benenati, and G. Oberlin. 1966b. Interim flows and beach building spike flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Draft annual report to Glen Canyon Environmental Studies. Northern Arizona University, Flagstaff.

Shrable, J.B., O.W. Tiemeier, and C.W. Deyoe. 1969. Effects of temperature on the rate of digestion by channel catfish. *Progressive Fish-Culturist* 31:131–137.

Sigler, W.F. 1955. An ecological approach to understanding Utah's carp populations. *Utah Academy of Science, Arts, and Letters* 32:95–104.

Sigler, W.F. 1958. The ecology and use of carp in Utah. Utah State University Agricultural Experiment Station Bulletin 405.

Sigler, W.F., and R.R. Miller. 1963. Fishes of Utah. Utah Department of Fish and Game, Salt Lake City.

Sigler, W.F., and J.W. Sigler. 1987. Fishes of the Great Basin. University of Nevada Press, Reno.

Smith, D.L., and C.G. Crampton, eds. 1987. The Colorado River Survey: Robert B. Stanton and the Denver, Colorado Canyon & Pacific Railroad. Howe Brothers, Salt Lake City, Utah.

Smith, G.R. 1959. Annotated check list of fishes of Glen Canyon. *In*, Ecol. studies of the flora and fauna in Glen Canyon. Univ. Utah Anthrop. Pap., 40, B: 195-199.

Snyder, D.E. 1981. Contribution to a guide to the cypriniform fish larvae of the upper Colorado River System in Colorado. U.S. Bureau of Land Management, Biological Sciences Series 3, Denver.

Snyder, D.E., and R.T. Muth. 1990. Descriptions and identification of razorback, flannelmouth, white, Utah, bluehead, and mountain sucker larvae and early juveniles. Contribution 38 of the Larval Fish Laboratory, Colorado State University, Fort Collins. Technical Publication No. 38, Colorado Division of Wildlife.

Stanford, J. A. 1994. Instream flows to assist the recovery of endangered fishes of the upper Colorado River Basin. Biological Report 24. U.S. Department of the Interior. National Biological Survey. Washington, D.C.

Stevens, L.E., and G.L. Waring. 1988. Effects of post-dam flooding on riparian substrate, vegetation, and invertebrate populations in the Colorado River corridor in Grand Canyon. Pages 257–270 in Glen Canyon Environmental Studies Executive Summaries of Technical Reports. Bureau of Reclamation, Salt Lake City, Utah.

Stevens, L.E., J.P. Shannon, and D.W. Blinn. 1997. Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary, and geomorphic influences. *Regulated Rivers: Research & Management* 13:129–149.

Stone, J.L. 1964. Limnological study of Glen Canyon tailwater area of the Colorado River. Colorado River Storage Project, Public Law 485, Section 8, annual report. Bureau of Reclamation, Salt Lake City, Utah.

Stone, J.L. 1965. Limnological study of Glen Canyon tailrace area of Colorado River, July 1, 1964, to June 30, 1965. Colorado River Storage Project, Public Law 485, Section 8, annual report. Bureau of Reclamation, Salt Lake City, Utah.

Stone, J.L. 1966. Tailwater fisheries investigations creel census and limnological study of the Colorado River below Glen Canyon Dam July 1, 1965–June 30, 1966. Arizona Game and Fish Department, Phoenix.

Stone, J.L. 1967. Tailwater fisheries investigations creel census and limnological study of the Colorado River below Glen Canyon Dam July 1, 1966–June 30, 1967. Arizona Game and Fish Department, Phoenix.

Stone, J.L. 1968. Tailwater fisheries investigations creel census and limnological study of the Colorado River below Glen Canyon Dam July 1, 1967–June 30, 1968. Arizona Game and Fish Department, Phoenix.

Stone, J.L. 1972. Tailwater fisheries investigations creel census and limnological study of the Colorado River below Glen Canyon Dam July 1, 1971–June 30, 1972. Arizona Game and Fish Department, Phoenix.

Stone, J.L., and J.R. Bruce. 1971. Tailwater fisheries investigations creel census and limnological study of the Colorado River below Glen Canyon Dam July 1, 1970–June 30, 1971. Arizona Game and Fish Department, Phoenix.

Stone, J.L., and A.B. Queenan. 1967. Tailwater fisheries investigations: creel census and limnological study of the Colorado River below Glen Canyon Dam. Colorado River Storage Project, Public Law 485, Section 8, annual report. Bureau of Reclamation, Salt Lake City, Utah.

Stone, J.L., and N.L. Rathbun. 1968. Tailwater fisheries investigations: creel census and limnological study of the Colorado River below Glen Canyon Dam.. Arizona Game and Fish Department, Phoenix.

Stone, J.L., and N.L. Rathbun. 1969. Tailwater fisheries investigations: creel census and limnological study of the Colorado River below Glen Canyon Dam. Arizona Game and Fish Department, Phoenix.

Stricklin, H.B. 1950. Letter to superintendent, Grand Canyon National Park describing Bright Angel Creek fish plant. 4 pp.

Suttkus, R.D., G.H. Clemmer, C. Jones, and C. Shoop. 1976. Survey of the fishes, mammals and herpetofauna of the Colorado River in Grand Canyon. Colorado River Research Series Contribution 34. Grand Canyon National Park, Grand Canyon, Arizona.

Swee, U. B., and H. R. McCrimmon. 1966. Reproductive biology of the carp, *Cyprinus carpio* L., in Lake St. Lawrence, Ontario. *Transactions of the American Fisheries Society* 95(4):372–380.

Taba, S.S., J.R. Murphey, and H.H. Frost. 1965. Notes on the fishes of the Colorado River near Moab, Utah. Utah Academy Proceedings 42:280-283 pp.

Taggart, J.H. 1885. Annual Report of Arizona Fish Commission, 183-1884, to Frederick A. Tritle, Governor of the Territory of Arizona, 15 pp.

Talbot, G.B. 1966. Estuarine and environmental requirements for striped bass. pp. 37-42 in R.F. Smith, A.H. Swartz, and W.H. Massmann, eds. A symposium on Estuarine Fishes. American Fisheries Society Special Publication 3.

Taylor, J.N., W.R. Courtenay, Jr., and J.A. McMann. 1984. Known impacts of exotic fish introductions in the continental United States. Pages 322–373 in Distribution, biology, and management of exotic fishes. Edited by W.R. Courtenay, Jr. and J.R. Stauffer, Jr. John Hopkins University Press. Baltimore, Maryland.

Thieme, M. 1996. Flannelmouth Sucker Project, quarterly report, October 1996. University of Arizona, Tucson.

Thieme, M. 1998. Movement and recruitment of flannelmouth sucker in the Paria and Colorado Rivers, Arizona. M.S. Thesis. University of Arizona, Tucson.

Thompson, J.M., E.P. Bergersen, C.A. Carlson, and L.R.Kaeding. 1991. Role of size, condition and lipid content in the overwinter survival of age-0 Colorado squawfish. *Transactions of the American Fisheries Society* 120:346–351.

Toney, D.P. 1974. Observations on the propagation and rearing of two endangered fish species in a hatchery environment. Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissions, 54:252–259.

Turner, R.M., and M.M. Karpiscak. 1980. Recent vegetation along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. U.S. Geological Survey Professional Paper 1132.

Tyus, H.M. 1991. Movements and habitat use of young Colorado squawfish. Pages 379-402 in Battle Against Extinction: Native fish management in the American West, edited by W.L. Minckley and J.E. Deacon. University of Arizona Press, Tucson, AZ.

Tyus, H.M. 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.

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. Thome Ecological Institute Technical Publication No. 14. Boulder, CO.

Tyus, H.M., 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). Vernal, Utah.

Tyus, H.M., and C.A. Karp. 1990. Spawning and movements of razorback sucker, *Xyrauchen texanus*, in the Green River Basin of Colorado and Utah. *Southwestern Naturalist* 35:427–433.

Tyus, H.M., and W.L. Minckley. 1988. Migrating Mormon crickets, *Anabrus simplex* (*Orthoptera:-tettigoniidae*), as food for stream fishes. *Great Basin Naturalist* 48(1):25–30.

Tyus, H.M., and N.J. Nikirk. 1990. Abundance, growth, and diet of channel catfish, *Ictalurus punctatus*, in the Green and Yampa rivers, Colorado and Utah. *Southwestern Naturalist* 35:188–198.

Tyus, H.M., and J.F. Saunders, III. 1996. Nonnative fishes in natural ecosystems and a strategic plan for control of nonnatives in the Upper Colorado River Basin, draft report. Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin.

Tyus, H.M., B.D. Burdock, 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 Fishes of the Upper Colorado River system: present and future, edited by W.H. Miller, H.M. Tyus, and C.A. Carlson. Western Division, American Fisheries Society.

Ulmer, L. 1980. Movement and reproduction of the razorback sucker *(Xyrauchen texanus)* inhabiting Senator Wash Reservoir, Imperial county California. Proc. Desert Fishes Council Vol. 12:106. (abstract)

Ulmer, L., and K.R. Anderson. 1985. Management plan for the razorback sucker (*Xyrauchen texanus*) in California. California Department of Fish and Game, Region 5 Information Bulletin 0013-10-1985.

U.S. Bureau of Reclamation. 1989. Glen Canyon Environmental Studies final report. January 1988, revised and reprinted May 1989. Upper Colorado Regional Office, Salt Lake City, Utah.

U.S. Bureau of Reclamation. 1990. Glen Canyon Environmental Studies draft integrated research plan. Glen Canyon Environmental Studies, Flagstaff, Arizona.

U.S. Bureau of Reclamation. 1994. Comments on the October 13, 1993, Draft biological opinion on the Preferred Alternative for the operation of Glen Canyon Dam (DBO), Consultation No. 2-21-93-F-167. Memorandum from Charles A. Calhoun, Acting Regional Director, Upper Colorado Regional Office, to Regional Director, U.S. Fish and Wildlife Service, Albuquerque, New Mexico. Salt Lake City, Utah.

U.S. Bureau of Reclamation. 1995. Operation of Glen Canyon Dam, environmental impact statement. Colorado River Studies Office, U.S. Bureau of Reclamation, Salt Lake City, Utah.

U.S. Fish and Wildlife Service. 1978. Biological opinion of the effects of Glen Canyon Dam on the Colorado River as it affects endangered species. Memorandum from Regional Director, U.S. Fish and Wildlife Service, Albuquerque, New Mexico, to Acting Regional Director Harl Noble, Bureau of Reclamation, Salt Lake City, Utah.

U.S. Fish and Wildlife Service. 1980. Determination that the bonytail chub *(Gila elegans)* is an endangered species, Final Rule, April 23. *Federal Register* 45(80):27710–27713.

U.S. Fish and Wildlife Service. 1990. Operation of Glen Canyon Dam (BR-AZ) - section 7 consultation and related Environmental Impact Statement (EIS). Memorandum from Acting Field Supervisor, Ecological Services, to Regional Director, Bureau of Reclamation, Salt Lake City. Phoenix, Arizona.

U.S. Fish and Wildlife Service. 1991. Endangered and threatened wildlife and plants; the razorback sucker *(Xyrauchen texanus)* determined to be an endangered species, 50 CFR Part 17, Final Rule, October 23, 1991. *Federal Register* 56(205):54957–54967.

U.S. Fish and Wildlife Service. 1993. Draft biological opinion, operation of Glen Canyon Dam as the Modified Low Fluctuating Flow Alternative of the final Environmental impact statement operation of Glen Canyon Dam. Phoenix, Arizona.

U.S. Fish and Wildlife Service. 1994a. Final biological opinion, operation of Glen Canyon Dam as the Modified Low Fluctuating Flow Alternative of the final Environmental impact statement operation of Glen Canyon Dam. Phoenix, Arizona.

U.S. Fish and Wildlife Service. 1994b. Endangered and threatened wildlife and plants; proposed determination of critical habitat for the Colorado River fishes: razorback sucker, Colorado squawfish, humpback chub, and bonytail chub, 50 CFR Part 17, Final Rule, March 21, 1994. *Federal Register* 59(18):6578–6597.

U.S. Geological Survey. 1990. Water resources data Arizona, Water Year 1990. U.S. Geological Survey Water-Data Report AZ-90-1.

Usher, H.D., and D.W. Blinn. 1990. Influence of various exposure periods on the biomass and chlorophyll a of *Cladophora glomerata* (Chlorophyta). *Journal of Phycology* 26:244–249.

Usher, H.D., W.C. Leibfried, D.W. Blinn, and S.W. Carothers. 1984. A survey of present and future impacts of water depletions and additions on the aquatic and terrestrial habitats of Roaring Springs, Brightangel, Garden, and Pipe Creeks, Grand Canyon National Park. Final Report to Western Region, National Park Service. Museum of Northern Arizona, Flagstaff, Arizona.

Usher, H.D., D.W. Blinn, G.C. Hardwick, and W.C. Leibfried. 1987. *Cladophora glomerata* and its diatom epiphytes in the Colorado River through Glen and Grand Canyons: distribution and desiccation tolerance. Glen Canyon Environmental Studies, GCES Report number B-8. Submitted to Arizona Game and Fish Department, Phoenix, AZ.

Usher, M.B., F.J. Kruger, L.A.W. MacDonald, L.L. Loope, and R.F. Brockie. 1988. The ecology of biological invasions into nature reserves: an introduction. *Biological Conservation* 44:1–8.

Uyeno, T., and Miller, R.R. 1965. Middle Pliocene fishes from the Bidahochi Formation, Arizona. *Copeia* 1965(1):28–41.

Valdez, R.A. 1990. The endangered fish of Cataract Canyon. Final report prepared for the Bureau of Reclamation, Salt Lake City, Utah, Contract No. 6-CS-40-03980, Fisheries Biology and Rafting. BIO/WEST Report No. 134–3. BIO/WEST, Inc., Logan, Utah.

Valdez, R.A. 1991. Characterization of the life history and ecology of the humpback chub (Gila cypha) in the Grand Canyon. Annual Report - 1990 to Bureau of Reclamation, Contract No. 0-CS-40-09110 BIO/WEST Report No. TR-250-02. 74pp.

Valdez, R.A. 1994. Effects of interim flows from Glen Canyon Dam on the aquatic resources of the lower Colorado River from Diamond Creek to Lake Mead. Annual Report - 1993 to Hualapai Wildlife Management Department and Glen Canyon Environmental Studies. BIO/WEST Report No. TR-354-01. 52 pp + appendix.

Valdez, R.A. 1996. Synopsis of the razorback sucker in Grand Canyon. Paper presented at the Razorback Sucker Workshop, January 11–12, 1996, Laughlin, Nevada.

Valdez, R.A., and G.C. Clemmer. 1982. Life history and prospects for recovery of the humpback and bonytail chub. Pages 109–119 in Fishes of the upper Colorado River system: present and future, edited by W.H. Miller, H.M Tyus and C.A. Carlson. Western Division, American Fisheries Society, Bethesda, Maryland.

Valdez, R.A., and B.R. Cowdell. 1996. Effect of Glen Canyon Dam beach/habitat-building flows on fish assemblages in Glen and Grand Canyons, Arizona. Project Completion Report, submitted to Arizona Game and Fish Department and Glen Canyon Environmental Studies. BIO/WEST, Inc., Logan Utah.

Valdez, R.A., and T.L. Hoffnagle. In Review. Movement, habitat use, and diet of adult humpback chub during the 1996 controlled flood in Grand Canyon, in Floods and River Management: The 1996 Controlled Flood in Grand Canyon, edited by R.H. Webb, J.C. Schmidt, G.R. Marzolf, and R.A. Valdez.

Valdez, R.A., and W.C. Leibfried. In Review. Captures of striped bass in the Colorado River in Grand Canyon, Arizona. *Southwestern Naturalist.*

Valdez, R.A., and W.J. Masslich. 1989. Winter habitat study of endangered fish - Green River: wintertime movement and habitat of adult Colorado squawfish and razorback suckers. Report to U.S. Bureau of Reclamation, Salt Lake City, Utah. BIO/WEST Report No. 136-2. BIO/WEST, Inc., Logan, Utah.

Valdez, R.A., and W.J. Masslich. In Review. Evidence of reproduction by humpback chub in a warm spring of the Colorado River in Grand Canyon, Arizona. *Southwestern Naturalist.*

Valdez, R.A., and R.J. Ryel. 1995. Life history and ecology of the humpback chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona. Final report to the Bureau of Reclamation, Salt Lake City, Utah, Contract No. 0-CS-40-09110. BIO/WEST Report No. TR-250-08. BIO/WEST, Inc., Logan, Utah.

Valdez, R.A., and E.J. Wick. 1981. Natural vs. manmade backwaters as native fish habitat. Pages 519–536 in Aquatic resources management of the Colorado River ecosystem, edited by V.D. Adams and V.A. Lamarra. Ann Arbor Science Publishers, Ann Arbor , Michigan.

Valdez, R.A., and E.J. Wick. 1983. Natural vs. manmade backwaters as native fish habitat. Pages 519-536 in Aquatic Resources Management of the Colorado River ecosystem, edited by V.D. Adams and V.A. Lamarra. Ann Arbor Science, Ann Arbor, Michigan.

Valdez, R.A., and R.D. Williams. 1993. Ichthyofauna of the Colorado and Green Rivers in Canyonlands National Park. Utah, Pages 2-22 In P.G. Rowlands, C. van Riper III, and M.K. Sogge (editors) Proceedings of the First Biennial Conference on Research in Colorado Plateau National Parks. Transactions and Proceedings Series NPS/NRNAU/NRTP-93/10, National Park Service, Denver, Colorado.

Valdez, R.A., J.G. Carter, and R.J.Ryel. 1985. Drift of larval fishes in the upper Colorado River. Proceedings of the Western Association of Fish and Wildlife Agencies: 171–185, Snowmass, Colorado.

Valdez, R.A., B.R. Cowdell, and E.E. Prats. 1995. Effects of interim flows from Glen Canyon Dam on the aquatic resources of the lower Colorado River from Diamond Creek to Lake Mead. Phase II report. Submitted to Hualapai Natural Resources Department and Glen Canyon Environmental Studies. BIO/WEST, Inc. Logan, Utah.

Valdez, R.A., P.B. Holden, and T.B. Hardy. 1990. Habitat suitability index curves for humpback chub of the Upper Colorado River Basin. *Rivers* 1:31–42.

Valdez, R.A., P.G. Magnan, R. Smith, and B. Nilson. 1982. Upper Colorado River investigations (Rifle, Colorado, to Lake Powell, Utah). Pages 100–279 in Colorado River Fishery Project, final report, Part 2: Field investigations. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.

Valdez, R.A., W.J. Masslich, W.C. Leibfried. 1992. Characterization of the life history and ecology of the humpback chub (*Gila cypha*) in the Grand Canyon. Annual report to the Bureau of Reclamation, Contract No. 0-CS-40-09110. BIO/WEST Report No. TR-250-04. BIO/WEST, Inc., Logan, Utah.

Valdez, R.A., R.J. Ryel, and B. Williams. 1986. The importance of the Colorado River above Lake Powell to the Colorado squawfish, humpback chub, and bonytail. Report to the Bureau of Reclamation, Contract No. 5-CS-40-02820.

Vanderford, M. 1980. Fish and wildlife work group I. Final Report to the Great River Environmental Action Team I. Volume 5, Great I. Study of the upper Mississippi River.

Vanicek, C.D. 1967. Ecological Studies of Native Green River Fishes below Flaming Gorge Dam, 1964-1966.

Walden, H.T. 1964. Familiar freshwater fishes of America. Harper and Row, New York, NY. 324 pp.

Ward, J.V. 1976. Effects of flow patterns below large dams on stream benthos: a review. Pages 235–252 in Instream flow needs, Volume 2, edited by Osborn and Allman. American Fisheries Society.

Ward, J.V., and J.A. Stanford. 1979. Ecological factors controlling zoobenthos with emphasis on thermal modification of regulated rivers. In Ecology of regulated streams. Plenum Press, New York.

Watanabe, T, T. Takeuchi, and C. Ogino. 1979. Studies on the sparing effects of lipids on dietary protein in rainbow trout (*Salmo gairdneri*). In Proc. World Symposium on Finfish Nutrition and Fishfeed Technology. Berlin Heeneman.

Waters, T.F. 1972. The drift of stream insects. *Annual Review of Entomology* 17:253–272.

Waters, T. F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph 7. American Fisheries Society, Bethesda, Maryland.

Weatherford, G.D., and F.L. Brown, eds. 1986. New courses for the Colorado River: major issues for the next century. University of New Mexico Press, Albuquerque.

Webb, R.H. 1996. Grand Canyon, a century of change: rephotography of the 1889–1890 Stanton expedition. University of Arizona Press, Tucson.

Webb R.H., and T.S. Melis. 1994. Observations of environmental change in Grand Canyon: a report on the old timers trip. U.S. Geological Survey, Tucson, Arizona.

Webb, R.H., P.T. Pringle, and G.R. Rink. 1991. Debris flows from tributaries of the Colorado River, Grand Canyon National Park, Arizona. U.S. Geological Survey Professional Paper 1492.

Weiss, J. 1992. The relationship between flow and backwater fish habitat of the Colorado River in Grand Canyon. Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona.

Weiss, J. 1993. The relationship between flow and backwater fish habitat of the Colorado River in Grand Canyon, draft report. Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona.

Weiss, S.J. 1993. Spawning, movement and population structure of flannelmouth sucker in the Paria River. M.S. thesis. University of Arizona, Tucson.

Wick, E. J., J. A. Hawkins, and C.A. Carlson. 1985. Colorado squawfish and humpback chub population and habitat monitoring, 1983–1984. Endangered wildlife investigations, final report SE 3-7. Colorado Division of Wildlife, Denver.

Wick, E.J., J.A. Hawkins, and C.A. Carlson. 1986. Colorado squawfish population and habitat monitoring, 1985. Endangered wildlife investigations, final report SE 3-8. Colorado Division of Wildlife, Denver.

Wick, E.J., T.A. Lytle, and C. M. Haynes. 1981. Colorado squawfish and humpback chub population and habitat monitoring, 1979–1980. Endangered wildlife investigations, SE-3-3, Colorado Division of Wildlife, Denver.

Williams, J.D., J.E. Johnson, and D.A. Hendrickson, S. Contreras-Balderas, J.D. Williams, M. Navarro-Medoza, D.E. McAllister, and J.E., Deacon. 1989. Fishes of North America endangered, threatened, or of special concern. *Fisheries* 14:(6):2-19. Bethesda, Maryland.

Wilson, E.O. 1992. The diversity of life. W.W. Norton Company, New York, NY. 442 pp.

Woodbury, A.M. 1959. Ecological studies of flora and fauna in Glen Canyon. University of Utah Anthropological Papers, No. 40. University of Utah, Salt Lake City.

Yard, M.D., G.A. Haden, and W.S. Vernieu. 1993. Photosynthetically available radiation (PAR) in the Colorado River: Glen and Grand Canyons. Glen Canyon Environmental Studies Technical Report. Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, Arizona.

APPENDIX A

Participants in Workshop on Endangered and Other Native Fishes of Glen and Grand Canyons February, 27–28, 1997, Flagstaff, Arizona

Participants

Mr. Mark Brouder	Arizona Game and Fish Department
Dr. Steven Carothers	SWCA
Mr. Robert Clarkson	U.S. Bureau of Reclamation, Lower Colorado Region
Mr. Lawrence Crist	U.S. Bureau of Reclamation, Upper Colorado Region
Dr. Barry Gold	Grand Canyon Monitoring and Research Center
Dr. Owen Gorman	U.S. Fish and Wildlife Service
Dr. Tim Hoffnagle	Arizona Game and Fish Department
Ms. Helene Johnstone	University of Arizona
Mr. William Leibfried	SWCA
Dr. Vicky Meretsky	Indiana University
Dr. Linn Montgomery	Northern Arizona University
Mr. William Persons	Arizona Game and Fish Department
Mr. Frank Pfeifer	U.S. Fish and Wildlife Service
Dr. David Propst	New Mexico Game and Fish Department
Mr. Joseph Shannon	Northern Arizona University
Dr. Larry Stevens	Grand Canyon Monitoring and Research Center
Ms. Michele Thieme	University of Arizona
Mr. David Trueman	U.S. Bureau of Reclamation
Dr. Richard Valdez	BIO/WEST
Mr. Dave Wegner	Ecosystem Management International
Mr. Robert Williams	U.S. Fish and Wildlife Service
Dr. Robert Winfree	National Park Service, Grand Canyon National Park
Mr. Mike Yard	Grand Canyon Monitoring and Research Center

Observers

Mr. Ron Borkan	SWCA
Ms. Dorothy House	SWCA
Ms. Elizabeth Taylor	Sheehan and Sheehan

APPENDIX B

Scientific Names of Species Referred to By Common Name in this Report

Native Fish

bluehead sucker (*Catostomus discobolus*)
bonytail (*Gila elegans*)
Colorado squawfish (*Ptychocheilus lucius*)
flannelmouth sucker (*Catostomus latipinnis*)
humpback chub (*Gila cypha*)
razorback sucker (*Xyrauchen texanus*)
roundtail Chub (*Gila robusta*)
speckled Dace (*Rhinichthys osculus*)
Virgin River Chub (*Gila seminuda*)
Virgin spinedace (*Lepidomeda mollispinis*)
woundfin (*Plagopterus argentissimus*)

Non-Native Fish

black bullhead (*Ameiurus melas*)
black Crappie (*Pomoxis nigromaculatus*)
bluegill (*Lepomis macrochirus*)
brook trout (*Salvelinus fontinalis*)
brown trout (*Salmo trutta)*
channel catfish (*Ictalurus punctatus*)
coho Salmon (*Oncorhynchus kisutch*)
common carp (*Cyprinus carpio*)
cutthroat trout (*Oncorhynchus clarki*)
fathead minnow (*Pimephales promelas*)
golden Shiner (*Notemigonus crysoleucas*)
green sunfish (*Lepomis cyanellus*)
June sucker (*Chasmistes liorus*)
Kokanee (*Oncorhynchus nerka kennerlii*)
largemouth bass (*Micropterus salmoides*)
mosquitofish (*Gambusia affinis*)
plains killifish (*Fundulus zebrinus*)
rainbow trout (*Oncorhynchus mykiss*)
red shiner (*Cyprinella lutrensis*)
smallmouth bass (*Micropterus dolomieui*)
striped bass (*Morone saxatilis*)
threadfin Shad (*Dorosoma petenense*)
Utah sucker (*Catostomus ardens*)
white sucker (*Catostomus commersonii*)
yellow Perch (*Perca flavescens*)
yellow Bullhead (*Ameiurus natalis*)

Parasites

Asian tapeworm (*Bothriocephalus achielognathi*)
catfish tapeworm (*Bothriocephalus claviceps*)

Other Invertebrates

Kanab ambersnail (*Oxyloma haydeni kanabensis*)
mayfly (*Ephemeroptera* sp.)
Mormon crickets (*Anabrus simplex*)

Birds

bald eagle (*Haliaeetus leucocephalus*)
peregrine falcon (*Falco peregrinus*)
southwestern willow flycatcher (*Empidonax traillii extremis*)

Terrestrial Plants

Apache plume (*Filago parabola*)
arrowweed (*Tessaria sericea*)
catclaw acacia (*Acacia greggii*)
coyote willow (*Salix exigua*)
honey mesquite (*Prosopis glandulosa*)
netleaf hackberry (*Celtis reticulata*)
redbud (*Cercis occidentalis*)
seep-willow (*Baccharis glutinosa*)
tamarisk (*Tamarix chinensis*)

ABBREVIATIONS USED IN REPORT

AGFD	Arizona Game and Fish Department
ANSTF	Aquatic Nuisance Species Task Force
BIA	Bureau of Indian Affairs
CFR	Code of Federal Regulations
cfs	cubic centimeters per second
DIRP	Draft Integrated Research Plan
DNA	Deoxyribonucleic acid
ESA	Endangered Species Act
FR	Federal Register
FWS	U.S. Fish and Wildlife Service
GCDEIS	Operation of Glen Canyon Dam Environmental Impact Statement
GCES	Glen Canyon Environmental Studies
JEI	Johnson Electivity Index
km	kilometers
Kn	condition factor
LCR	Little Colorado River
LCRI	Little Colorado River inflow
m	meters
maf	million acre-feet
MLFF	Modified Low Fluctuating Flow alternative
NEPA	National Environmental Policy Act
NPS	National Park Service
NTU	Nephelometric turbidity unit
PIT	Passive Integrated Transponder
ppm	parts per million
Reclamation	U.S. Bureau of Reclamation
RM	river mile
ROD	Record of Decision
RPA	Reasonable and Prudent Alternative
SASF	Seasonally Adjusted Steady Flow alternative
SIM	Scientific Information Management
SWCA	SWCA, Inc., Environmental Consultants
TDS	total dissolved solids
TL	total length
UDWR	Utah Division of Wildlife Resources
USC	United States Code
USGS	United States Geological Survey
WAPA	Western Area Power Administration
WY	water year
YOY	young-of-year

GLOSSARY

Adaptation - Evolutionary process of a plant or organism adjusting to the ongoing environmental conditions of its surroundings.

Adaptive Management - A process that uses scientific methods and information to help formulate, adjust, and improve management strategies.

Adnate - Joined or attached.

Allochthonous - Originating from outside a system.

Allometry - Relative growth of a part in relation to an entire organism or to a standard; disproportional change in weight relative to length.

Alluvial - Deposits of sand or gravel laid down by rivers.

Alluvial fan - Sand, gravel, cobbles, and/or boulders deposited at the mouth of a side canyon or tributary stream, primarily during a flood event. Also called a debris fan.

Anthropogenic - Of, relating to, or resulting from the influence of human beings.

Aquatic - Of or relating to water environments.

Attenuation - Reduction in observed correlation or oscillation.

Autochthonous - Originating from within a system.

Beachface - The river side of a reattachment bar, usually consisting of a sand beach.

Benthic organism - An organism that lives on the bed of a water body or river.

Bimodal distribution - A statistical pattern in which the frequencies of values in a sample have two distinct peaks, even though parts of the distribution may overlap.

Biomass - The total mass or weight of organisms in a given environment or at a certain trophic level.

Broadcast spawner - A fish that scatters its eggs in the absence of building a nest or redd; the eggs either float in the water column (pelagic) or sink to the bottom (demersal) onto gravel, cobble, vegetation, or other substrates. Aggregations of broadcast spawners typically consist of many fish of both genders of a single species.

Carlin tag - A sequentially-numbered, colored, plastic tag affixed externally to a fish to provide a unique identification.

Chironomid - Common name for insects known as the non-biting midges, belonging to the family Chironomidae.

Community - A naturally occurring group of plants and/or organisms of different species that live together and interact as a self-contained unit, relatively independent of inputs and outputs from adjacent communities.

Confluence - A coming or flowing together of two streams.

Congeneric species - Species of the same genus.

Copepod - Any minute crustacean of the subclass Copepoda.

Cryopreservation - Preservation (as of cells) by subjection to extremely low temperatures.

Cycloid scale - A type of fish scale, typically of cyprinids (minnows), catastomids (suckers), and salmonids (trout) that tends to be round or oblong with circular growth rings radiating from a centrum.

Demersal - Living on or near the bottom in deep waters.

Depauperate - Impoverished.

Detritus - Any organic debris.

Dewatering - The process of diverting or withdrawing water from a stream course.

Diatom - A single-celled or colonial algae of the family Bacillariophycea, with an external skeleton of silica. Diatoms can be free-living or attached and compose a significant part of plankton and benthos.

Diurnal - Of or referring to daytime.

Ecosystem - A collection of plants and animals interacting with each other and with their physical and chemical surrounding.

Emergence - To come out or appear, as in an immature insect leaving a body of water to mature on land.

Endemic - Occurring or restricted to a particular region or locale, i.e., a specific river basin. Synonym: indigenous.

Entrain - To draw, trap, and hold by the movement of water.

Epiphytic - Living on the surface of plants.

Exotic - Not native to the place where found. Exotic fish originate in a different continent.

Fauna - The grouping of animals present in a place and time in geologic history.

Fecundity - The potential reproductive capacity of a fish measured as numbers of eggs produced per female.

Fish barrier - A physical or chemical impediment to fish movement, typically waterfalls, a series of cascades, or low oxygen/high carbon dioxide.

Flow fluctuation - Change in the amount of water released from a dam.

Flow magnitude - The size, extent, or force of a water flow.

Floy tag - An elongated, tubular, external tag inscribed with a unique number and generally attached near the base of the dorsal fin of a fish.

Fluvial - Of, relating to, or living in a stream or river.

Gamete - A germ cell possessing the haploid number of chromosomes; especially a mature sperm or egg cell capable of participation in fertilization.

Gravid - The condition of a female fish with mature or maturing eggs prior to spawning.

Host - The organism on or in which a parasite lives. Synonym: vector.

Hybrid species - Offspring of a cross between two genetically unlike individuals.

Hydrograph - The flow of a river or stream for a given period of time, depicted as volume (e.g., cubic meters per second) over time.

Hypolimnetic - Of or relating to the hypolimnion or lower stratum of a lake, lying below the mesolimnion (thermocline), and characterized by cold temperatures and low oxygen.

Icthyofauna - The assemblage of fish species.

Indigenous - Born or originating in a particular locale. Synonym: endemic.

Introgressive hybridization - The spread of genes of one species into the germ plasma of another species as a result of hybridization.

Invertebrate - Animals that do not possess a vertebral column (backbone).

Isometric growth - Relative growth of a part in relation to an entire organism or to a standard; proportional change in weight relative to length.

Lacustrine - Of or pertaining to a lake; living or growing in a lake.

Larvae - The life stage of some fish species, from hatching to full development of fins.

Lateral line system - A system of sense organs located in a pale line extending from head to tail along the sides of most aquatic vertebrates.

Lipid - A biological compound containing carbon, hydrogen, and oxygen together with other elements such as nitrogen and phosphorous. Lipids are structural components of cell membranes and nervous tissue.

Lotic - Of or relating to an aquatic environment with flowing water.

Mainstem - The primary channel in a river system.

Meristic - Proportions or relationships of body parts or morphology for use in distinguishing species or other taxa.

Microhabitat - Characteristics of the immediate surroundings of a fish, typically water depth, velocity, substrate, cover.

Miocene - A division of the Tertiary period, lasting from 26 million to 7 million years ago.

Morphology - Shape and general appearance or form of an organism or its parts.

Neuromast - A sensory projection (papilla) of the lateral line system of fish and other lower vertebrates that registers vibrations and pressure.

Nuchal hump - The swollen fleshy back of the humpback chub, most pronounced immediately behind the head and tapering toward the tail.

Oligocene - A division of the Tertiary period occurring between 38 and 26 million years ago.

Otolith - A granule (or several associated granules) of calcareous material associated with the ear of vertebrates, aiding in the assessment of their position with respect to gravity. One of three pairs of inner ear bones of fish, often used for determining age from growth rings.

Parasite - An organism that lives with, and at the expense, of another organism.

Pathogen - Any organism that causes disease.

Pelagic - Of or relating to open water, as in an ocean or lake.

Photoperiod - Interval in a 24-hour period in which an organism is exposed to sunlight.

Piscivorous - Fish-eating.

Plankton - The collection of organisms inhabiting the water column.

Pleistocene - A division of the Quaternary period lasting from 2 million years ago to 10,000 years ago.

Potomodromous - Fish that migrate extensively within a river system for spawning and rearing, but do not enter the ocean.

Ramping rate - The rate of change in flow measured in cubic feet per second for a period of one hour.

Reach - A length of stream channel that is relatively uniform with respect to geomorphic characteristics.

Reattachment Bar - A sandbar deposited by recirculating flows in an eddy complex, typically extending outward from, and parallel to, the shoreline at the lower end of the recirculation zone.

Recruitment - Replacement of adults through growth and maturity of young individuals.

Riverine - Relating to, formed by, or resembling a river.

Scale annuli - Radiating growth rings on scales of fish, each usually signifying one year of growth.

Senescence - The process of growing old, a slowing of metabolism.

Sessile - Remaining sedentary or attached.

Sexual dimorphism - Morphologic distinction between sexes of the same species.

Staging area - Habitat at or near a tributary inflow used by fish to rest prior to ascent, usually for spawning.

Subadult - Immature fish, including young-of-year and juveniles.

Sub-reach - Portion on stream channel within a reach.

Substrate - Medium on which an organism can grow, usually referring to a stream or lake bottom, composed of silt, sand, gravel, cobble, boulder, and/or bedrock.

Symbiosis - The intimate association of two dissimilar organisms from which each organism benefits.

Sympatric - Occupying in the same or overlapping geographic area without interbreeding.

Taxonomic - Rank of an organism within a hierarchical classification.

Terrestrial - Of the land as opposed to air or water.

Thermal cues - An innate threshold response by fish to water temperature that usually induces gonadal maturation, spawning, or other physiological responses.

Thermal plume - A warm flow of water emanating from a spring or tributary that becomes diluted by a cold, larger body of water such as a lake or river. Thermal plumes are characterized by a temperature gradient from source to receiving water.

Thermal shock - The physiological effect of an organism moving between temperature extremes, such as a fish moving from warm to cold waters. The effect may be manifest as lethargy, erratic swimming behavior, disorientation, or eventual death.

Trammel net - Entanglement net for catching fish, composed of two outer panels of small mesh and one inner panel of large mesh.

Travertine - A buff-colored porous mineral formed in streams by deposition of calcium carbonate.

Tributary - A stream feeding a larger stream or lake.

Trophic - Of or relating to nutrition.

Trophic level - Any of the feeding levels that energy passes through as it precedes through the ecosystem.

Turbidity - The condition of lowered water clarity caused by suspended sediments, organic matter, and color.

Univoltine - Able to complete one life cycle per year.

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