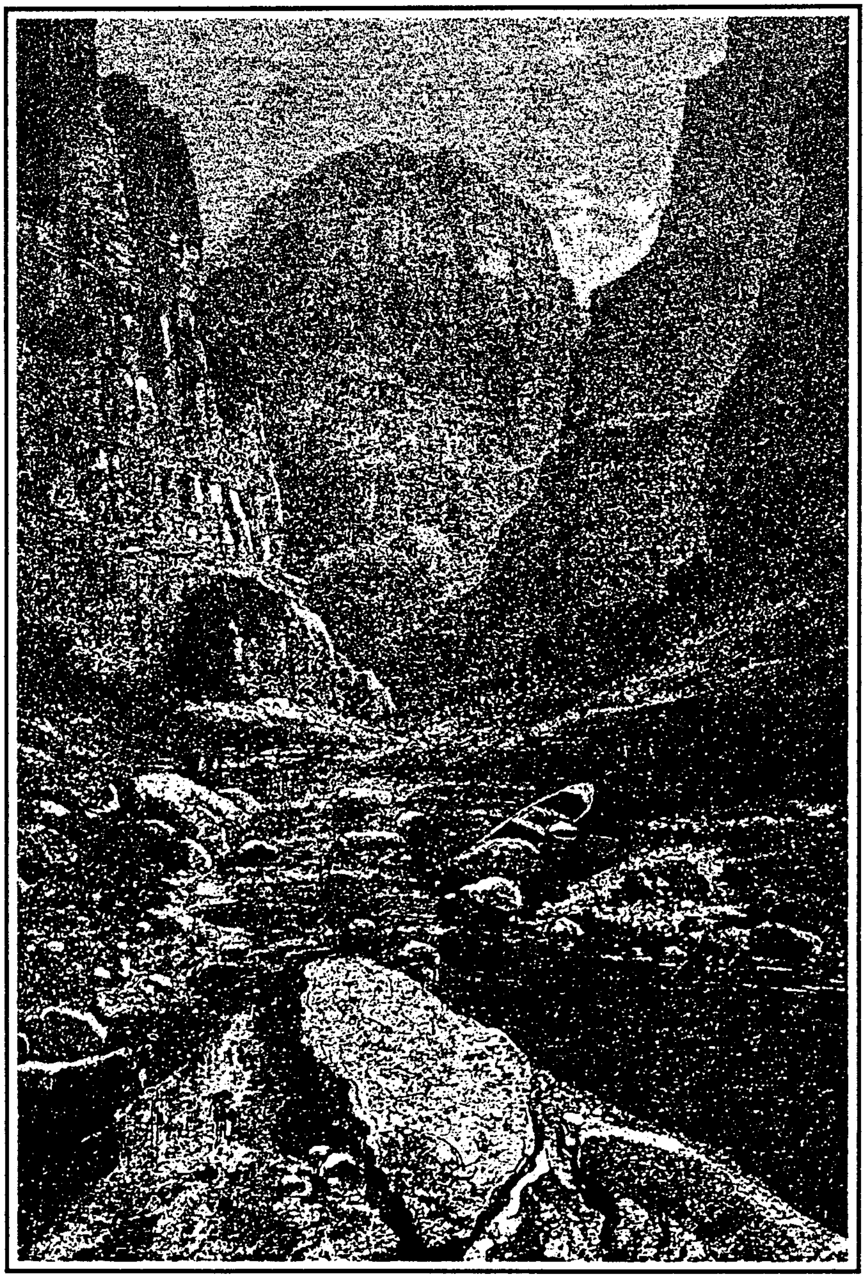
Life History and Ecology of the Humpback Chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona

Final Report



Bureau of Reclamation

U.S. DEPARTMENT OF THE INTERIOR
BUREAU OF RECLAMATION

BIO/WEST, Inc.

Glen Canyon Environmental Studies

GLEN CANYON ENVIRONMENTAL STUDIES

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Cover drawing from Powell (1875)

Life History and Ecology of the Humpback Chub (Gila cypha) in the Colorado River, Grand Canyon, Arizona

Final Report

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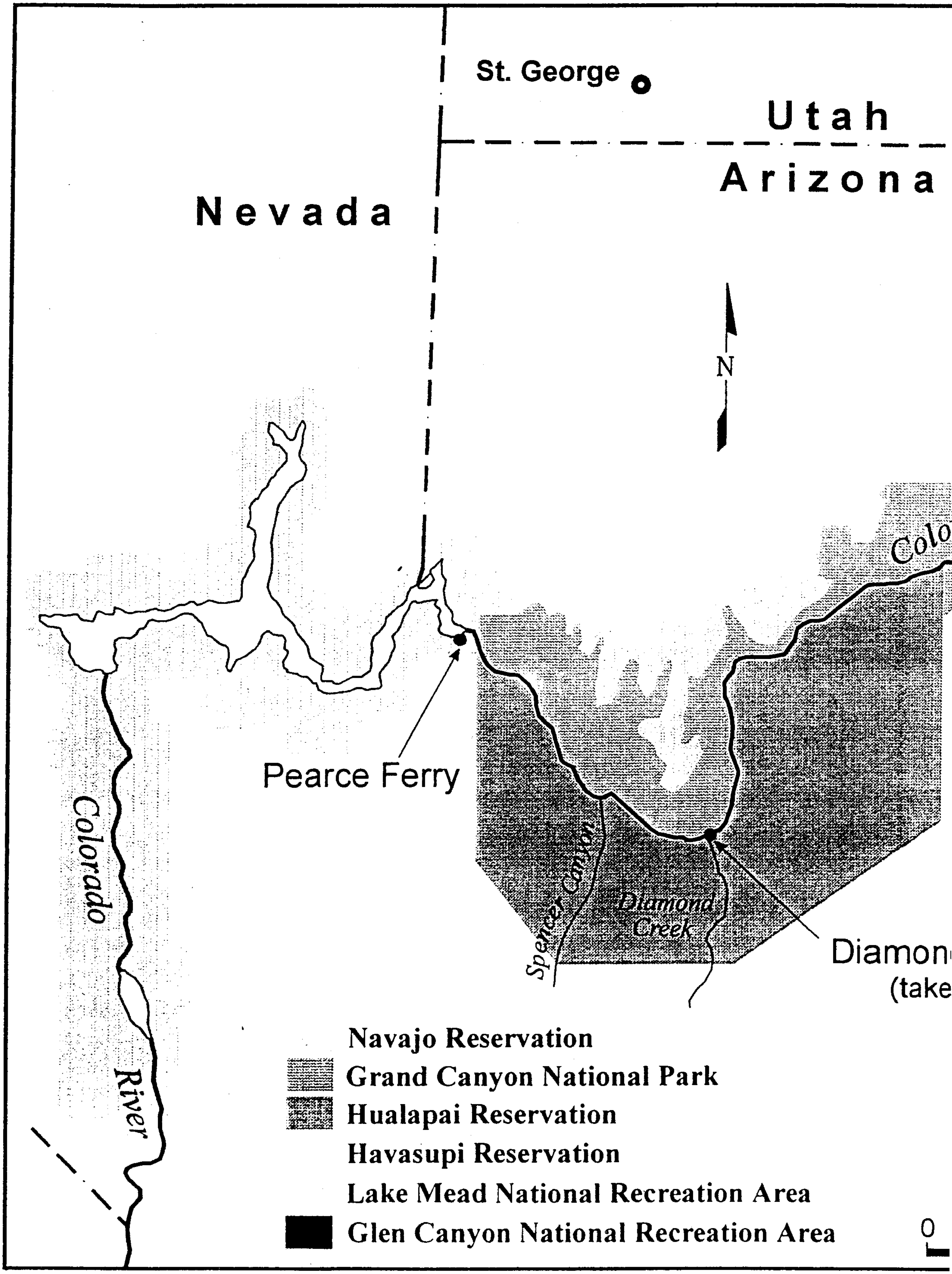
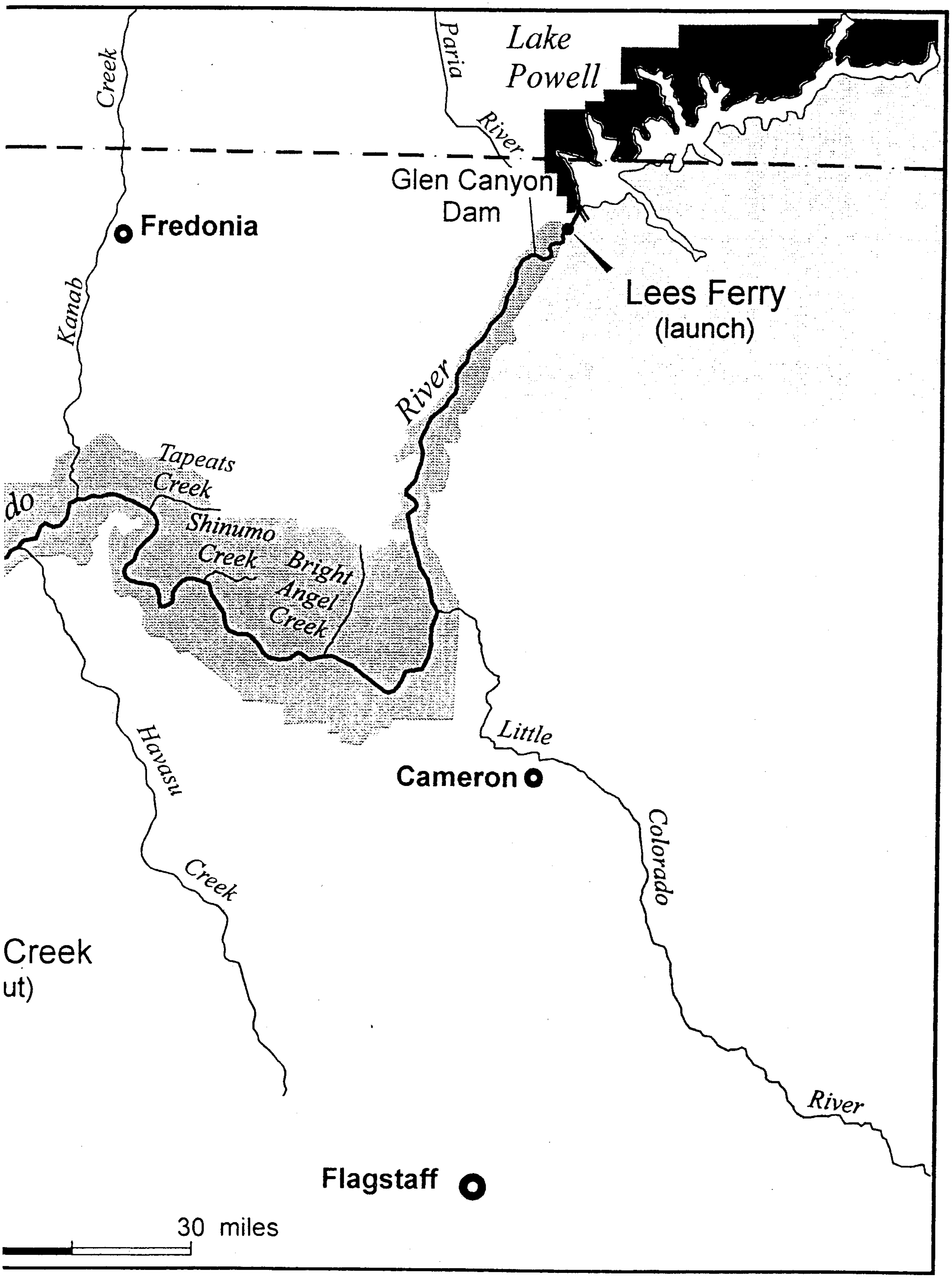
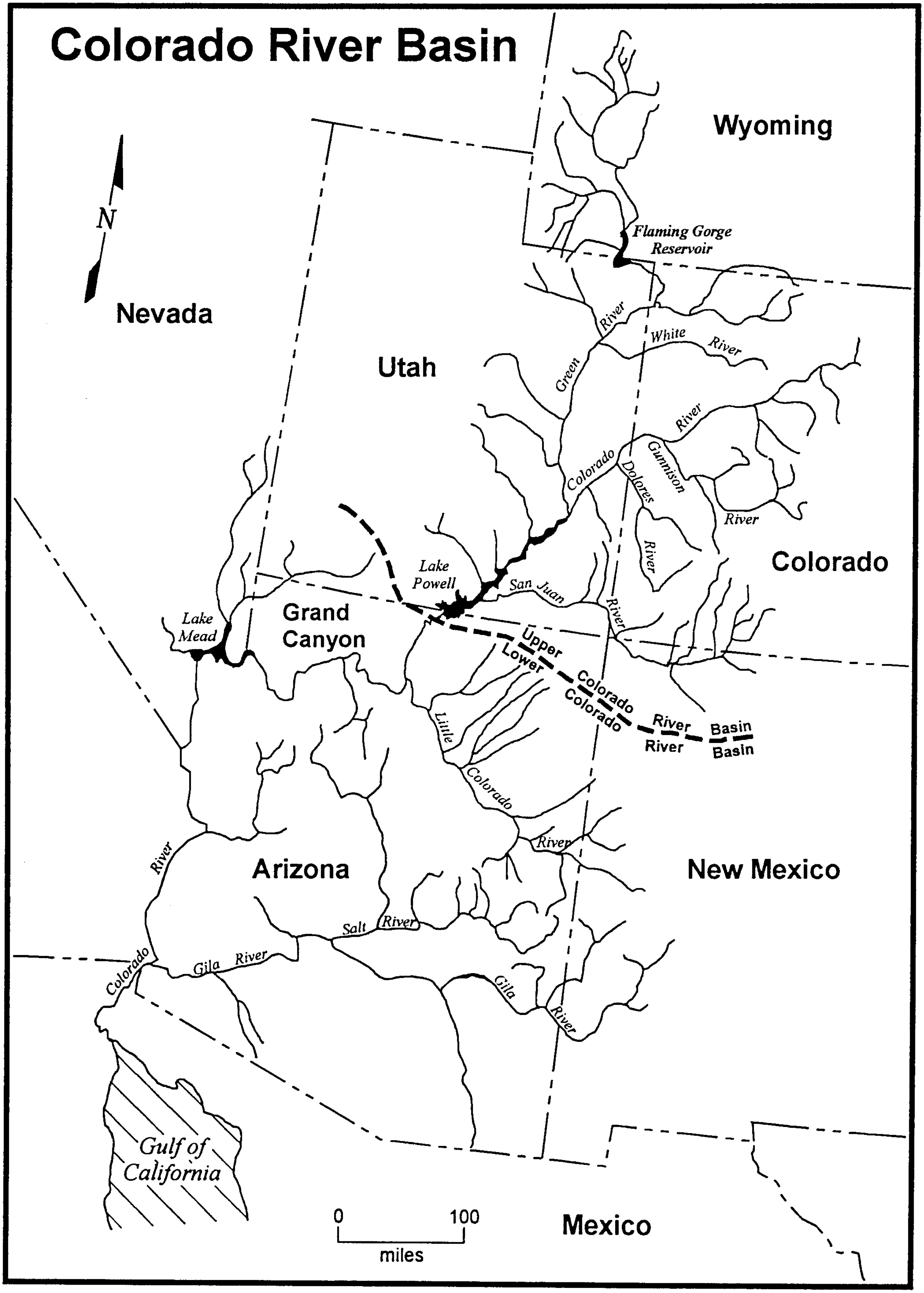
September 1995



General area map of the Grand Canyon.



Lake Powell
Paria River
Creek
Kanab
Glen Canyon Dam
Fredonia
Lees Ferry (launch)
River
Tapeats Creek
do
Shinumo Creek
Bright Angel Creek
Little
Cameron
Colorado
River
Havasu Creek
Creek
ut)
Flagstaff
30 miles


Colorado River Basin
N
Wyoming
Flaming Gorge Reservoir
Nevada
Utah
Green River
White River
Colorado River
Gunnison River
Dolores River
Colorado
Lake Powell
San Juan River
Lake Mead
Grand Canyon
Upper Colorado River Basin
Lower Colorado River Basin
Little Colorado River
Arizona
New Mexico
Salt River
Gila River
Colorado River
Gulf of California
0 100 miles
Mexico

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PREFACE

Nearly one million people a year visit Grand Canyon National Park. Most come to peer into the depths of the canyon to catch a glimpse of the thin watery ribbon of the Colorado River nearly 1 mile below the canyon rim. And many, over 20,000 people annually, come to raft the world-renowned whitewater marked by 160 recognized rapids in 225 miles of largely inaccessible wilderness. Despite the many people who visit or know of the Grand Canyon, few recognize or understand the fishes that live in this ancient desert river.

The Colorado River and surrounding arid landscape hardly seem a fitting place for fish. Yet, the very nature of this violent, muddy, and saline river has given rise over nearly 3 million years to one of the most unique and highly indigenous fish assemblages in North America. Of 35 fish species native to the Colorado River Basin, 26 (74%) are endemic, or found in no other basin on earth. Until recently, when the names of these fishes began appearing in news articles and environmental reports, the fishes of the Colorado River and Grand Canyon were known primarily to ichthyologists, and their role and importance in the ecosystem were not well understood.

Native Americans and early explorers used the fishes of the Colorado River as a food source, but the inaccessible and treacherous river made widespread use of the fish impractical. More recently, anglers considered them "trash fish", and they were poisoned by resource agencies to make room for introduced trout and other game fishes. Federal protection for these fish (i.e., Endangered Species Act of 1973) brought to the attention of the public the decline of these unique life forms and the plight of this ancient and overused western river. Protection for the bonytail, roundtail chub, and Colorado squawfish--largest of North American minnows at 100 pounds!--came too late in Grand Canyon, where the species were extirpated by the early 1970s. It may also be too late for the razorback sucker, a species that is now very rare in the region. Declining numbers of flannelmouth suckers and bluehead suckers also warn of impending and persistent threats to these native species. Only the speckled dace seems to be widespread, although its numbers may also be declining.

Many people think of the Colorado River fishes as channel catfish in muddy waters or rainbow trout in cold, clear tailwaters below dams. While these introduced species are valuable game fishes, they often compete with or prey upon the native forms. Hence, the dozen or so alien species that inhabit the river are also an important aspect of the present aquatic ecosystem, and these species are important considerations in achieving a balanced approach to river management.

While the emphasis of this report is on the humpback chub, the decline of all the Colorado River native fishes serves as a reminder of the connectivity between all life forms and the need to protect ecosystems. Aldo Leopold (1949) best described the relationship:

"The outstanding scientific discovery of the twentieth century is not television, or radio, but rather the complexity of the land organism. Only those who know the most about it can appreciate how little is known about it. The last word in ignorance is the man who says of an animal or plant: 'What good is it?' If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering."

The aquatic ecosystem of the Colorado River has been dramatically altered since the late 1800s. Many aspects of the historic structure and function of the system have been modified or eliminated. While recovery of the pre-1800s condition is not possible, preservation of some historic structure and function is possible and essential to preservation of native fishes and maintenance of a balance native/non-native fish assemblage.

Although this report focuses on the humpback chub, we advocate development of a fish management plan that considers the existing native fish assemblage (humpback chub, razorback sucker, flannelmouth sucker, bluehead sucker, speckled dace), extirpated native species (Colorado squawfish, bonytail, roundtail chub), and numerous non-native species. This multispecies approach, balanced with the needs of other resources, will provide a meaningful approach to managing the Grand Canyon ecosystem.

While this report presents new and valuable information on the humpback chub in Grand Canyon, it is naive to assume that one study can provide "all there is to know" about this population, let alone give a full understanding of the aquatic ecosystem in the canyon. While such complete information would be valuable in fully assessing effects of dam operations, a complete ecological study would require time and thorough planning (Marzolf 1991). Instead, the research process of this study focused on specific aspects of life-history and ecology which were deemed important for the population and which may be affected by dam operations. This study was constrained by available research techniques (some of which were developed during this project), modified dam operations, concerns for personal safety, time, and money. Despite these constraints, valuable information was gathered and we feel that this report provides a reasonable characterization of the species as we know it today.

The study design, purpose, and objectives of this study were developed to integrate with other investigations. Parallel and simultaneous studies of the life-history and ecology of the species in the Little Colorado River were conducted by other researchers. The various research activities now need to be integrated to produce a broad and more comprehensive picture of humpback chub ecology in the Grand Canyon, and to more fully assess the effects of Glen Canyon Dam. Such integration must extend to other disciplines, where they affect the species, including geomorphology, climatology, water quality, and other biological components of the ecosystem. In addition, a more complete understanding of humpback chub, both in terms of ecology and population viability, will require integrating information from populations throughout the basin. This integration will provide a basis for designing more broad-based ecological studies for fishes within the entire Colorado River Basin.

Specific recommendations for management of Glen Canyon Dam are not included in this report. Instead, the effects of various operational components on humpback chub were assessed in order to provide the information to Reclamation and other cooperators of dam operations. We recognize that recommendations for dam operations are beyond the scope of this work, and perhaps premature until the integration process is completed. Assessing economic effects of dam operations designed to minimize impacts to humpback chub is also beyond the scope of this work, but we recognize the importance of cost in evaluating any management scheme. Researchers should strive to develop a consolidated and integrated information base by which managers and administrators can make informed decisions on dam management.

This report is intended as a scientific document for agency administrators and the scientific community. We endeavored to present our findings in a manner that is readable and understandable to a wide audience. We did this to make the document informative and useful, and as a tribute to the unique fishes that live in Grand Canyon. Consistent with this effort, we have provided English and metric units of measure, either jointly for ease of conversion or individually in commonly used terms. For example, river flow is presented as cubic feet per second instead of cubic meters per second and locations are referenced in river miles instead of kilometers. Scientific and common names are consistent with nomenclature of the American Fisheries Society List of Common and Scientific Names of the United States and Canada. The editorial style of the North American Journal of Fisheries Management was used except where abbreviations and scientific notation were awkward (e.g., cubic feet per second was abbreviated 'cfs' instead of ft^3/s). A glossary and list of abbreviations are provided to facilitate understanding of scientific terms used in the text of this report.

This report is presented as ten chapters. Following the Introduction (Chapter 1) and Study Design (Chapter 2) are a characterization of Hydrology (Chapter 3) and Water Quality (Chapter 4). The next four chapters describe life history aspects of humpback chub, including Distribution and Abundance (Chapter 5), Demographics (Chapter 6), Habitat (Chapter 7), Movement (Chapter 8), and Food Habits (Chapter 9). The last chapter is an Integration (Chapter 10) of information and a discussion of effects of dam operations on the humpback chub in Grand Canyon. An Executive

Summary and an Appendix of detailed tables and figures are companion documents to this report. Also, six supplements were produced to provide more detail on data collection, evaluation of sampling, a photographic record of humpback chub, a population model, and a flow routing model.

The Grand Canyon leaves an inescapable impression on all who experience its scenic beauty. But having the opportunity to study the fish that inhabit its depths has been especially rewarding and exciting. We thoroughly enjoyed working in this great wonder of the world, and we sincerely hope that our involvement and scientific contribution will help to provide a balance between the integrity of this unique ecosystem and the needs of society.

R.A. Valdez
R.J. Ryel

PROLOGUE

Gila Complex of the Colorado River

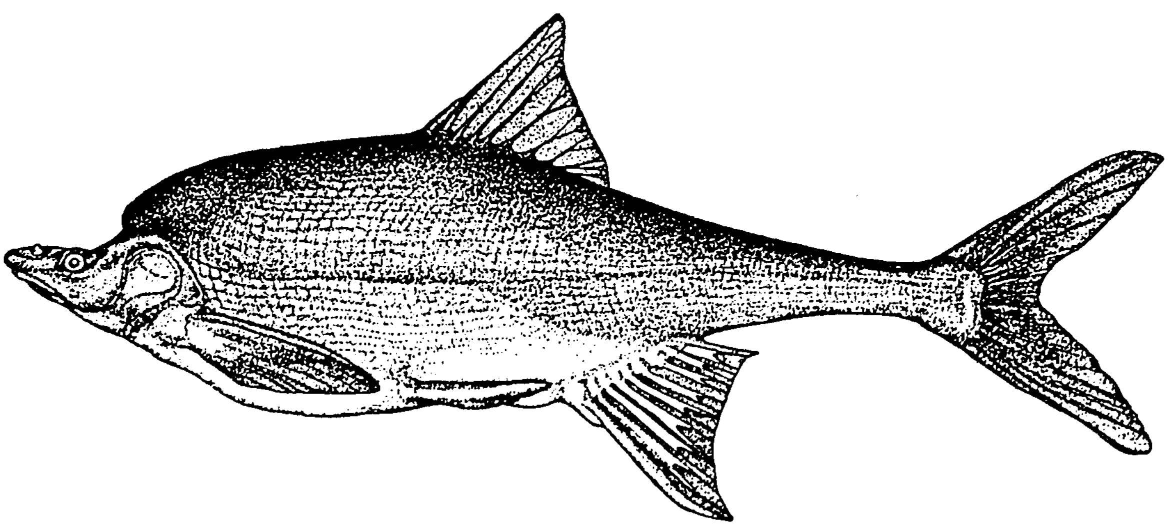
Three fish species of the genus Gila inhabit the mainstem Colorado River, including the humpback chub (G. cypha Miller, 1945), bonytail (G. elegans Baird and Girard, 1853), and roundtail chub (G. robusta Baird and Girard, 1853). These species are considered part of a morphologically diverse group or complex of western minnows that includes several congeneric species outside of the Colorado River Basin, with a pervasive influence of hybridization throughout their evolutionary histories (Dowling and DeMarais 1993). This apparent introgressive hybridization has resulted in high phenotypic plasticity with morphologic integrades present in all sympatric populations of Colorado River Gila (Holden and Stalnaker 1970, Valdez and Clemmer 1982, Kaeding et al. 1990). Gila cypha and G. elegans appear to be specialized derivatives of the G. robusta complex, and may have arisen in response to special conditions in large erosive Colorado River habitats (Smith et al. 1979, Minckley et al. 1989), an hypothesis that is being supported by recent allozyme and mitochondrial DNA analyses (Dowling and DeMarais 1993, Starnes 1995).

These three chub species belong to the Class Osteichthyes (bony fishes), Order Cypriniformes, and Family Cyprinidae (carps and minnows), which is the most diverse and widespread family of fishes in North America with over 240 recognized species (American Fisheries Society 1991). These chub species are part of the Gila complex and represent half of six recognized species or subspecies inhabiting the Colorado River basin, including the humpback chub (G. cypha), bonytail (G. elegans), roundtail chub (G. robusta), Virgin River chub (G. robusta seminuda), Pahranagat roundtail chub (G. r. jordani), and Gila chub (G. intermedia). The other three taxa, Virgin River chub, Pahranagut roundtail chub, and Gila chub, are isolates and primarily tributary inhabitants, although historic hybridization with other forms of Gila is evident.

Humpback chub (Gila cypha)

The humpback chub was described in 1945 by R.R. Miller (1946) from specimens taken in Grand Canyon. It was included in the first List of Endangered Species issued by the Office of Endangered Species on March 11, 1967 (32 FR 4001). The humpback chub was classified as "endangered" because of declines in distribution and abundance throughout its range. It was afforded full protection under the Endangered Species Act of 1973, as amended.

It is surmised that the humpback chub speciated from a G. elegans-like form in canyons of Northern Arizona (i.e., Grand Canyon) about 3-5 million years ago (Miller 1946, Holden 1968, Minckley et al. 1986), during the mid-Pliocene and early Pleistocene epochs. During this time, the Colorado River was cutting through the Kaibab upwarp of the Colorado Plateau to join the ancient upper basin with the lower Hualapai Drainage System (McKee



Humpback chub

et al. 1967). The humpback chub is a relatively large North American minnow reaching a maximum total length of 480 mm and a weight of 1,165 g (this study).

Humpback chub have a laterally-compressed and tapering fusiform body, short narrow caudal peduncle with deeply forked tail fin, and large falcate paired fins. Adults have a narrow flattened head, with small eyes and a long fleshy snout and inferior subterminal mouth. Subadults are olivaceous above with silvery sides fading to a creamy white belly, while adults are light olivaceous and slate-gray dorsally and laterally, with a white belly tinged with light orange and yellow.

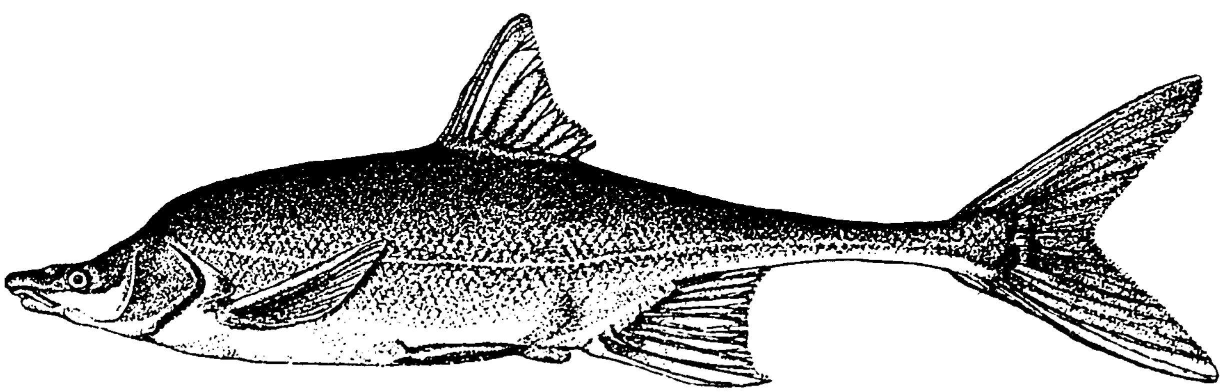
Dorsal and anal fins typically have 9 and 10 principal rays, respectively; caudal peduncle length divided by head length is typically less than 1.0, and head length divided by caudal peduncle depth is usually less than 5.0. Scales are deeply embedded, isolated dorsally and imbricated laterally and ventrally, with the head and nuchal hump naked. The pharyngeal arch is small with a short lower ramus and deciduous teeth in a typical pattern of 2,5-4,2. Spawning adults during March-June are tinged with rosy red on the gill coverings, paired fins, and belly, and pimple-like nuptual tubercles develop on the head and paired fins. The head is narrow and flattened and may be dorsally concave. The eyes are small and the snout is long and fleshy with an inferior subterminal mouth. The paired fins (pectoral and pelvic) are large and falcate.

Critical habitat for the humpback chub and three other mainstem species (Colorado squawfish, bonytail, razorback sucker) was designated on March 21, 1994 (50 FR 13374). For the humpback chub, critical habitat includes 610 km (379 mi) in seven reaches of the Colorado River Basin representing about 28% of historic habitat. Critical habitat for humpback chub in Grand Canyon includes 280 km of the Colorado River from Nautaloid Canyon (RM 35) to Granite Park (RM 209) and the lower 12.9 km (8 mi) of the Little Colorado River (LCR).

In addition to Grand Canyon in the lower Colorado River basin, humpback chub remain in five canyon regions in the upper Colorado River basin (Black Rocks, Westwater Canyon, Cataract Canyon, Desolation/Gray canyons, Yampa Canyon). Specimens and historic records (Gaufin et al. 1960, Hagen and Banks 1963, Holden and Stalnaker 1975) indicate that the species was extirpated from at least seven additional canyon regions in the upper basin (Flaming Gorge, Lodore Canyon, Whirlpool Canyon, Split Mountain Canyon, Moab Canyon, Debeque Canyon, Narrow Canyon). Reasons for decline and major threats faced by the species today include inundation of habitat behind mainstem dams, coldwater releases below dams, modified habitat from channel geomorphic changes, altered flow regimes, altered food bases, invasion by non-native fishes, alien parasites and diseases, and introgressive hybridization with native congeneric species (Valdez and Clemmer 1982).

Bonytail (Gila elegans)

The bonytail is the rarest of the big river fishes of the Colorado River. Fewer than 10 individuals have been caught in the upper basin in the last decade and small numbers of adults persist in Lake Mohave, Nevada-Arizona (Kaeding et al. 1986, Minckley et al. 1989, Valdez et al 1995). It was listed as an



Bonytail

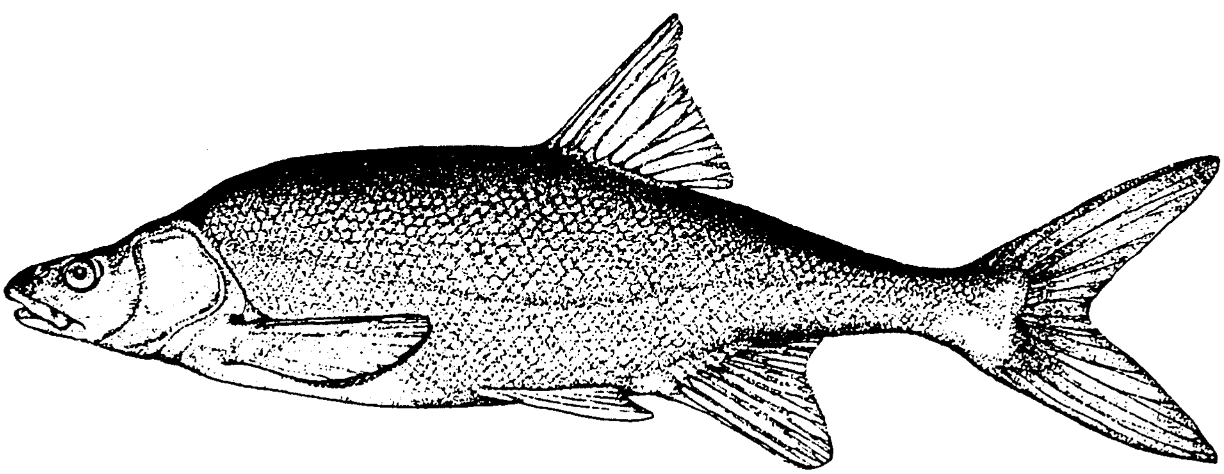
endangered species in 1980. The occurrence of this species in Grand Canyon is based on 16 specimens reported by R.R. Miller in the 1940s (M. Douglas, ASU, pers. comm.)

Bonytail have an elongated fusiform body, small flattened head with small eyes, subterminal mouth, long slender caudal peduncle, and large deeply forked tail fin. Subadults are olivaceous above with silvery sides fading to a creamy white belly, while adults are greenish to gray dorsally and laterally, with a white belly and irregular black lateral spots. Dorsal and anal fins typically have 10 principal rays each; caudal peduncle length divided by head length is typically greater than 1.0, and head length divided by caudal peduncle depth is usually greater than 5.0. Scales are small dorsally and ventrally, larger laterally, and embedded throughout with 75-88 scales along the lateral line. The pharyngeal arch is small with a short lower ramus and deciduous teeth in a typical pattern of 2,4-5,2.

Roundtail Chub (Gila robusta)

The roundtail chub is locally common in middle to upper elevations of the mainstem and tributaries of the Colorado River. It is not federally protected, but is of special concern in all seven basin states. Its occurrence in Grand Canyon is based on reports by McDonald and Dotson (1960) and Stone and Rathbun (1968). Although roundtail chub have not been reported from the Colorado River in Grand Canyon since 1968, the species was recently reported from Chevlon Creek, a tributary of the LCR in Arizona (R. Clarkson, AGF, pers. comm.)

Roundtail chub have a cylindrical body and head, with small eyes, and a terminal mouth, short thickened caudal peduncle, and rounded tail fin and paired fins. Subadults are olivaceous above with silvery sides fading to a creamy white belly, while adults are olivaceous dorsally and laterally, with a white belly and irregular black lateral blotches. Dorsal and anal fins typically have 9 and 9 principal rays, respectively; caudal peduncle length divided by head length is typically less than 1.0, and head length divided by caudal peduncle depth is usually less than 4.0. Scales are small dorsally and ventrally, larger laterally, and imbricated throughout with 75-96 along the lateral line. The pharyngeal arch is small with a short lower ramus and deciduous teeth in a typical pattern of 2,4-5,2.



Roundtail chub

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ADMINISTRATIVE ASSISTANCE AND TECHNICAL SUPPORT

We are indebted to many people who helped bring this project to a successful completion, and we appreciate the assistance of those too numerous to mention at this time. Bob Williams of Bureau of Reclamation had the vision and foresight to implement a comprehensive ecological investigation of fishes in Grand Canyon, and Larry Crist, Chris Karas, Rick Gold, and Lee McQuivey continued support of the program. Dave Wegner, Program Manager for Glen Canyon Environmental Studies, and his staff Michael Yard, Allen Haden, Bill Vernieu, Dr. Richard Lechleitner, Judy Weiss, Jeannie Korn, Frank Protiva, Mark Gonzales, Chris Brode, Karel Malloy, and LeAnn Skrzynski provided untiring logistical support, field assistance, and project coordination. Many members of the BIO/WEST staff assisted in project administration, including John Littell, Jennifer Rose, Jeff Steinitz, and Maggie Bowler. Special thanks to Drs. Paul Holden and Tom Twedt, principals at BIO/WEST, for their continuing support.

We thank many agency and university people who patiently helped with collecting permits, logistical coordination, and sharing of ideas, data, and personnel. These include Bruce Taubert, Jim DeVos, Dennis Kubly, Bill Persons, Tim Hoffnagle, Rob Clarkson, Alan Kinsolving, Mark Seversen, and Brian Bagley of Arizona Game and Fish Department; Frank Baucom, Jim Hansen, Dr. Owen Gorman, Stuart Leon, C.O. Minckley, Don Metz, Kathleen Linder, John Seals, Vickie Meretsky, and Deborah Bills of U.S. Fish and Wildlife Service; George Neusaenger, Johnny Ray, Mark Law, Sue Cherry, Tom Workman, and Dave Derossier of the National Park Service; Drs. Duncan Patten, Paul Marsh, Michael Douglas, and W.L. Minckley of Arizona State University; Mike Tremble, Jeff Cole, Pat Ryan, and Carol Yazzie of the Navajo Natural Heritage Program; Mike Yates, Jane Bremner and Ron Morgan of the Hopi Tribe; Dr. Wayne Starnes of the Smithsonian Institute; and the late Dr. Merec Kalizewski of Brigham Young University. Thanks also to Doug Young, Jim Sartoris, Jerry Miller, Mike Pucherelli, and Patrick Wright of Bureau of Reclamation for sharing ideas and providing field support.

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We thank the river guides for sharing their knowledge of Grand Canyon; their immeasurable whitewater expertise was a key to the safety and success of this study. The Grand Canyon River Guides helped to promote continuation of sound scientific investigations of Glen Canyon Dam operations and they continually challenged and improved many aspects of our study. Mike Walker of OARS coordinated river logistics and provided specially-designed boats to accommodate our research needs. We also express our deepest gratitude to the volunteers who unselfishly dontated their time.

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Ann Zwinger

KEY PROJECT PERSONNEL

The following individuals were the key personnel on this project and their job titles. Most remained with the project throughout its duration and others for shorter periods, but each was a valuable asset to the overall success of the program.

PRINCIPAL INVESTIGATOR .... Dr. Richard A. Valdez
PROJECT LEADERS .... William J. Masslich, William C. Leibfried, Larry Crist
SENIOR BIOLOGIST .... Anthony Wasowicz, Bryan R. Cowdell
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BIOLOGIST/DATA ANALYST .... Leslie Brown
BIOLOGIST/DATABASE MANAGER .... Lydia 'Penny' Trinca
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ASSISTANT BIOLOGISTS .... Paula Trater, Tom McKay, Chris Carrier
ASSISTANT BIOLOGISTS .... Peggy Wood, John Kleinfelter, Kirsten Tinning
RIVER GUIDE/EQUIPMENT COORDINATOR .... Peter Weiss
RIVER GUIDE/LOGISTICS SUPPORT .... Brian Dierker, Teresa Yates
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GIS COORDINATOR .... Todd Hougaard
STATISTICIAN .... Dr. Ronald J. Ryel

CONTRIBUTORS AND REVIEWERS OF THIS FINAL REPORT

This Final Report is a synthesis of the efforts and ideas of many individuals. These ideas were integrated into 10 chapters, each dealing with a specific aspect of the life history and ecology of the humpback chub and management of Glen Canyon Dam. The report was written in a scientific format in response to the National Research Council (1987) review of the GCES Phase I reports. That review concluded that while much new and valuable information had been gathered during Phase I, "...the production of unpublishable results is testimony to the inadequacy of the work and of the planning that led to it." The review further concluded that a shortfall of the GCES program was "Uncertain conversion of the research results into management options." Hence, the study design of this project was hypothesis-driven, and the report was written as an integrative document to provide Bureau of Reclamation with scientifically-defensible information by which to make management decisions on the operation of Glen Canyon Dam. This report was also written in a journal-like style to facilitate extraction of publishable information, and key personnel were encouraged to publish various aspects of the results of this study.

This Final Report was developed through a process in which data and ideas of many people were assimilated through a series of trip reports, annual reports, workshops, and campfire discussions involving field personnel and administrative staff. This interaction and exchange of information led to the development, by key project personnel, of preliminary chapters that provided detailed data summaries and preliminary analyses on specific aspects of the life history of the humpback chub. These preliminary chapters became the basis for this Final Report in which data were further analyzed, and ideas and hypotheses were refined.

The preliminary chapters were written by the project leaders and senior biologists who were responsible for certain aspects of the work throughout the project. Workshops and coordination meetings were held regularly to collaborate efforts and ensure consistency among contributors. Bill Masslich was principal field coordinator and project leader who coordinated all remote and mobile radiotelemetry instrumentation, surveillance, and monitoring, and together with Bryan Cowdell, performed the initial data analysis and wrote the preliminary chapter on Movement. Helen Yard served as principal surgeon for implanting radio-transmitters in humpback chub. Bill Leibfried coordinated all the drift studies and fish diet data and developed the preliminary chapter on Food Habits. Tony Wasowicz coordinated development of a stomach pump and gut analyses of fish in the field and wrote the preliminary chapter on Distribution and Abundance. Penny (Lydia) Trinca and Leslie Brown served as Database Manager and Data Analyst, respectively, and together with Erika Prats, developed the preliminary chapter on Demographics. Yvette Converse wrote part of the preliminary report on habitat as part of her Master's Thesis. Gloria Hardwick coordinated procurement of water quality data, ensured that field instruments were calibrated before and after each trip, and developed the preliminary chapter on Water Quality. Craig Goodwin, staff hydrologist, developed a flow routing model and wrote the preliminary chapter on Hydrology. Copies of these preliminary chapters are available from BIO/WEST upon request.

From these preliminary reports, an internal review draft of the Final Report was developed and circulated for review by the BIO/WEST staff to ensure accuracy and consistency in data presentation and interpretation. Comments were integrated and an Agency Review Draft was sent to interested agencies and the BIO/WEST staff. A Draft Final Report was developed and sent for external review that led to this Final Report. The preliminary chapters were modified and refined to reflect the purpose and objectives of the project and to address the concerns expressed by the National Research Council (1987) in their review of the Phase I reports.

Denise and Kurt Pruhs played a vital role in the development of this Final Report. Denise was administrative assistant and coordinated all project activity schedules, travel arrangements, and collating, editing, and issuance of all reports. She was pivital in assimilating this Final Report by integrating editorial comments and graphics, and working closely with the printers to ensure a quality product. Kurt Pruhs created all the computer graphics and cover and chapter separations for this report, demonstrating new and innovative techniques for effective visual representation of results.

The following individuals reviewed the Final Report and provided written or oral comments: Dave Wegner, Mike Yard, Larry Crist, Larry Stevens, Ted Melis, Dr. Robert Muth, Dr. Todd Crowl, Dr. Jack Schmidt, Dr. Richard Marzolf, Doug Osmundson, Gordon Lind, Bill Masslich, Bill Leibfried, Bryan Cowdell, Leslie Brown, Erika Prats, Lydia (Penny) Trinca, and Yvette Converse.

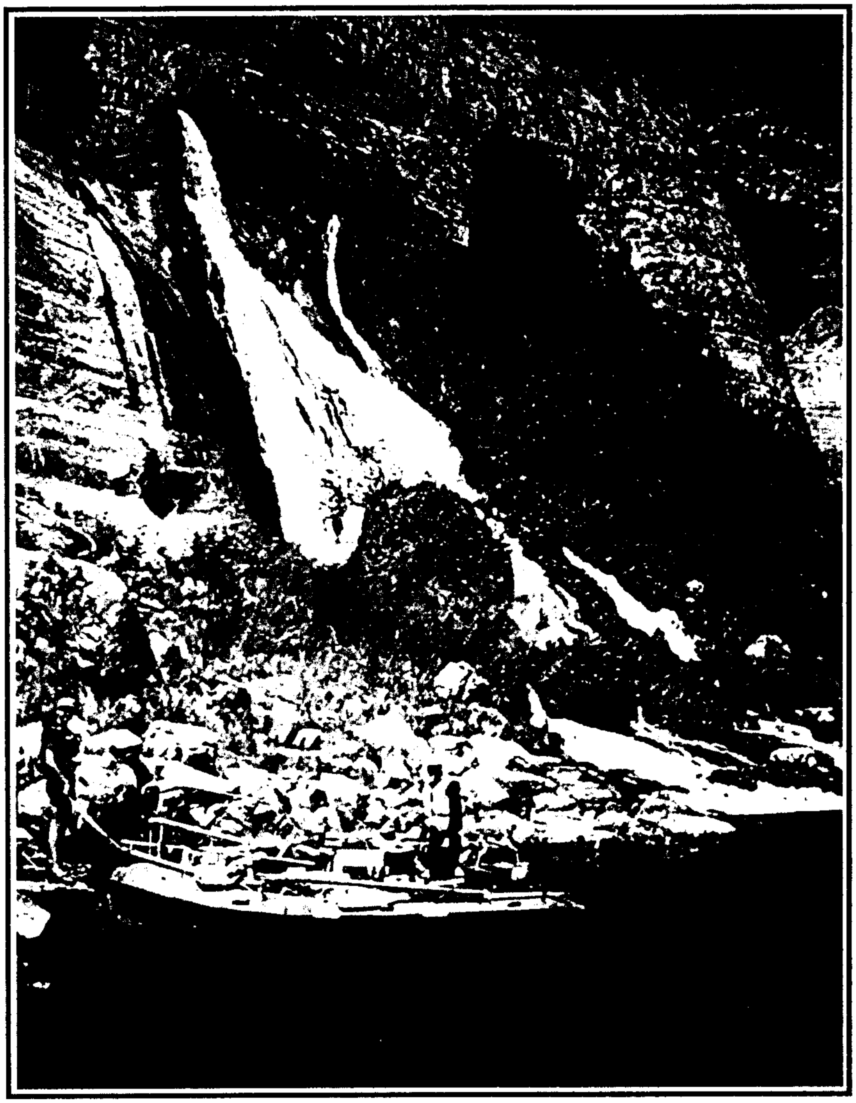
Drawings of the fish presented in this report were done by Marianne Filbert. We are indebted to Marianne for her time and care in ensuring realism and accuracy in every aspect of the fish.

The trips through Grand Canyon and the process of writing this report were sometimes long and arduous and took many people away from families and loved ones for long periods of time. We acknowledge and thank families and friends for their patience and understanding. Special thanks to Becky and Corinne.

The time and effort expended in analyzing the data and assimilating this report was necessary to meet the project objectives, to describe as best as possible the information gathered, and to give justice to a tremendous overall effort by many people. Otherwise, that effort would be for naught and the sacrifices by many a waste.

Introduction

Chapter 1



Chapter 1 - Table of Contents

CHAPTER 1 - INTRODUCTION

This Final Report was submitted to Bureau of Reclamation (Reclamation) by BIO/WEST, Inc. (B/W) in partial fulfillment of Reclamation Contract No. 0-CS-40-09110 entitled Characterization of the Life History and Ecology of the Humpback Chub in the Grand Canyon. The report presents findings of a fisheries investigation as part of Reclamation's evaluation of Glen Canyon Dam operations. Information contained in this report was collected in 36 monthly trips through Grand Canyon from October 1990 through November 1993 and is summarized in Trip Reports and Annual Reports for 1990 (Valdez 1991), 1991 (Valdez et al. 1992), and 1992 (Valdez and Hugentobler 1993). An Executive Summary and an Appendix were issued as companion documents to this Final Report and an electronic database is available from B/W or Reclamation for data collected during this investigation. Six supplemental reports were produced in response to specific tasks or amendments of the contract:

- Supplement No. I: Data Collection Plan
- Supplement No. II: Evaluation of Sampling Design
- Supplement No. III: Photographic Record of Humpback Chub
- Supplement No. IV: Grand Canyon Fisheries Integrated (GCFIN) Database
- Supplement No. V: Development of a Population Model for Humpback Chub (Gila cypha) in Grand Canyon.
- Supplement No. VI: Flow Routing Model

A complete list of reports and publications produced during this investigation is included in Appendix A. The reader is referred to the Executive Summary and to Chapter 10 - INTEGRATION for a synopsis of findings.

BACKGROUND

This investigation was conducted as part of the Native and Endangered Fish (NEF) Studies (Fig. 1-1) of the Phase II Draft Integrated Research Plan (DIRP, U.S. Department of Interior 1990) of the Glen Canyon Environmental Studies (GCES) (See Box 1-1). The DIRP was developed as a roadmap to provide overall research direction and logic, as well as technical information transfer to GCES researchers, the scientific community, and the interested public. The objective of the NEF Studies

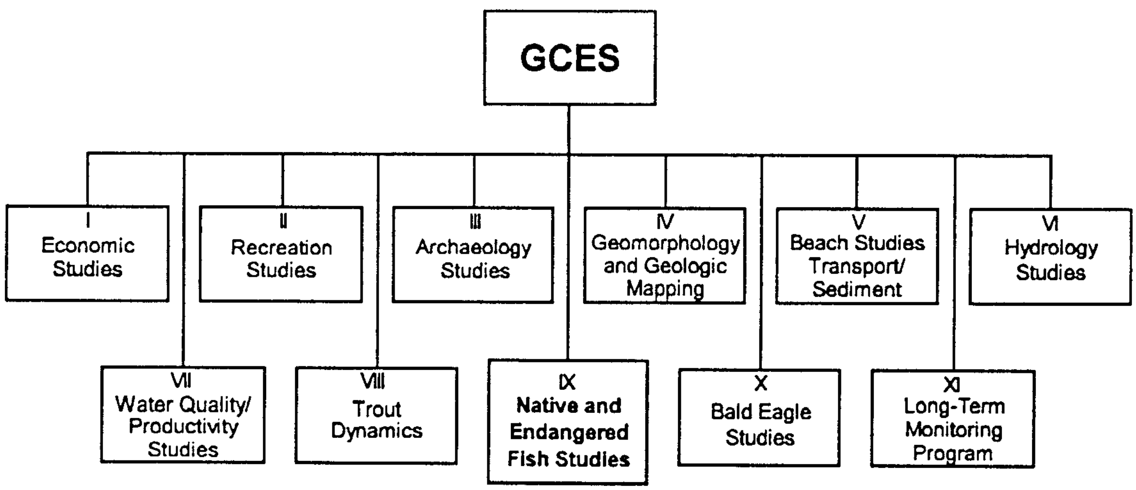


Fig 1-1. Components of the Glen Canyon Environmental Studies (GCES) Phase II Draft Integrated Research Plan.

Box 1-1. Glen Canyon Environmental Studies

Glen Canyon Environmental Studies was formed on April 15, 1983 in response to public concern over the effects of Glen Canyon Dam operations on Grand Canyon resources. Reclamation Commissioner, Robert M. Broadbent, instructed Regional Director, Clifford Barrett (letter dated December 6, 1982), to determine the effect of present (1982) flow patterns on the canyon environment. In 1988, GCES submitted a Phase I Report (U.S. Department of Interior 1988), which determined that flood releases and fluctuating flows had substantial adverse effects on downstream resources. A review by the National Research Council (1987) of the National Academy of Sciences recommended further investigations to identify the causes of these effects.

On June 19, 1988, the U.S. Department of Interior directed Reclamation to continue GCES with the recognition that sufficient data had not been collected or analyzed under Phase I to make operational decisions on Glen Canyon Dam. The Phase II program was designed to assess the relationship of low and fluctuating flows on specific resources in Grand Canyon and the potential economic impact of operational modification. The Phase II DIRP identified ten primary study components and one monitoring components to assess impacts of operations on specific resources (Fig. 1-1). A series of hypotheses was developed by the GCES Senior Scientific Advisor, GCES researchers, interested groups, and the National Academy of Sciences to address specific questions for each resource (GCES 1990).

was to understand the population ecology of the fish and identify responses to the operation of Glen Canyon Dam. These studies were a cooperative effort among Arizona Game and Fish Department (AGF), U.S. Fish and Wildlife Service (Service), National Park Service (NPS), Arizona State University (ASU), Reclamation, and the Navajo Nation, Hopi Tribe, and Hualapai Tribe. These entities comprised the Aquatic Coordination Team (ACT), a group of researchers that worked jointly and cooperatively to ensure an integrated research approach and provided guidance to a Senior Scientific Advisor and the GCES Program Manager.

The NEF Studies consisted of Native Fish Studies in the mainstem Colorado River, Little Colorado River (LCR), and other tributaries. The Endangered Fish Studies consisted of eight study plans (Fig. 1-2). BIO/WEST was contracted by Reclamation to assist with study plan B-7 (ecological studies of Gila) by conducting investigations in the mainstem Colorado River. These studies include the elements of early life history, adult movement, adult and juvenile demographics and habitat (Table 1-1). Results of these studies were provided to aid Reclamation in its mandated responsibility under Section 7(a)(1) of the Endangered Species Act of 1973, as amended, to *"...utilize their authorities in furtherance of the purposes of this Act by carrying out programs for the conservation of endangered species and threatened species..."*.

The Endangered Fish Studies of the Phase II DIRP were formulated in response to a 1978 Biological Opinion (Opinion) which determined that the operation of Glen Canyon Dam *"...is likely to jeopardize the continued existence of the humpback chub..."* (U.S. Fish and Wildlife Service 1978). This determination was considered in developing the GCES Phase I Studies and, at their conclusion, the Service reinitiated consultation with the new information collected. The reconsultation resulted in seven conservation measures developed jointly by AGF, NPS, the Service, the Navajo Nation, and Reclamation:

Conservation Measure 1: Taxonomic status of the genus Gila.

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

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

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

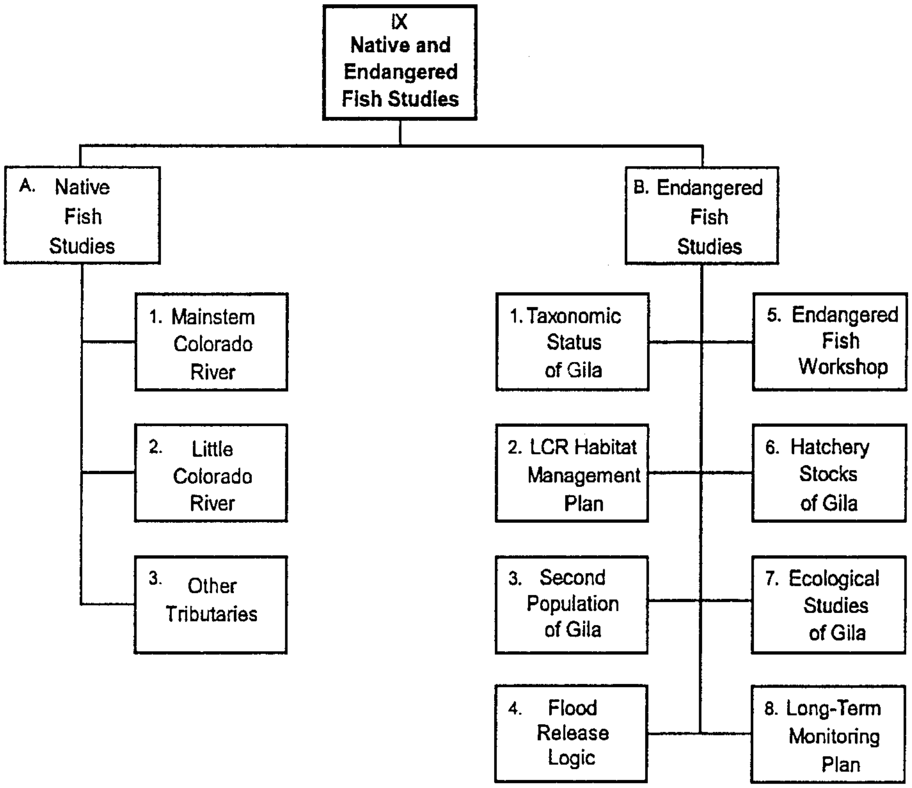


Fig. 1-2. Technical study plans for the Native and Endangered Fish Studies component of the GCES Phase II Draft Integrated Research Plan.

Table 1-1. Life stages of humpback chub studied by various investigators.

Life Stage	Investigator
	Mainstem Colorado River (Lees Ferry to Diamond Creek)
Larvae, YOY, Juveniles	Arizona Game and Fish Department (backwaters and beach faces)
	BIO/WEST (all habitats except backwaters)
	Hualapai Tribe (National Canyon to Pearce Ferry)
Adults and Juveniles	BIO/WEST
	Little Colorado River
Larvae, YOY, Juveniles	Arizona Game and Fish Department
Adult and Juveniles	Arizona State University
Adult and Juvenile Habitat	U.S. Fish and Wildlife Service
	Other Tributaries
All Life Stages	University of Arizona
	U.S. Fish and Wildlife Service

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 operations to the humpback chub.

Conservation Measure 7: Establish a second spawning population of humpback chub in the Grand Canyon.

Conservation measures 5 and 7 provided the framework for the purpose and objectives of the B/W investigation, as detailed in the following section. These measures also guided study designs of other investigations as part of the Phase II DIRP.

On July 27, 1989 Secretary of Interior, Manuel Lujan, directed the initiation of an Environmental Impact Statement (EIS) on the Operation of Glen Canyon Dam. Passage of the Grand Canyon Protection Act of 1992 (PL 102-575) on October 30, 1992 mandated completion of a Final EIS no later than 2 years after the date of enactment (Sec. 1804). Most of the NEF Studies identified in Fig. 1-2 were not completed in time for the Draft EIS, and only preliminary findings and results were provided from this B/W investigation to the EIS Team.

PURPOSE AND OBJECTIVES

The purpose of this investigation, as stated in Reclamation Contract No. 0-CS-40-09110 to B/W, was to:

"Evaluate the ecological and limiting factors of all life stages of humpback chub in the mainstem Colorado River, Grand Canyon, and the effects of Glen Canyon Dam operations."

This investigation was designed to describe physical, chemical, and biological components of the Grand Canyon aquatic ecosystem and to identify principal factors limiting the survival and proliferation of the endangered humpback chub. This investigation addressed only certain aspects of these components and was designed to share roles and responsibilities with other investigations, as outlined in Table 1-1.

The study objectives for B/W were to determine the following attributes for humpback chub in the mainstem Colorado River in Grand Canyon:

- Distribution, abundance and movement.
- Survivorship of early life stages.
- Reproductive capacity and success.
- Resource availability and use (i.e., habitat, food).
- Important biotic interactions with other species for all life stages.
- The life history schedule.

These objectives were developed by Reclamation as part of the NEF Studies to address Conservation Measures 5 and 7 and to provide insight into Question 6 and Hypotheses Ho-6.1, Ho-6.1a, and Ho-6.1b of the Phase II DIRP (Volume 1, pages 10-11). Question 6 and the associated DIRP hypotheses are addressed in Chapter 10 - INTEGRATION of this report.

Question 6: "How do discharge fluctuations and rates of change in fluctuating discharges affect other fish, especially native fish species? Do the USFWS (Service) Conservation Measures adequately address this question?"

Ho-6.1: "There is no significant relationship between the population dynamics (including short-term abundance of early life stages and potential predation relationships) of native (especially the humpback chub) and introduced fish species in the mainstem Colorado, including mainstem backwaters and the confluence of the Little Colorado, and the magnitude of fluctuations, minimum discharges and rates of change of fluctuating discharges."

Ho-6.1a: "There is no significant relationship between population dynamics of native and introduced fish species in the mainstem Colorado, including backwaters and tributaries, and the magnitude of discharge fluctuations."

Ho-6.1b: "There is no significant relationship between population dynamics of native and introduced fish species in the mainstem Colorado, including backwaters and tributaries, and the magnitude of minimum discharges."

SCOPE OF WORK

The scope of work for this investigation was based on a sampling program that provided an understanding of the life history and ecology of the humpback chub and simultaneously addressed hypotheses on effects of Glen Canyon Dam operations. The nature of the study objectives required an integrated approach to link humpback chub life history requirements with physical, chemical, and biological components of the environment that are potentially affected by dam operations. A comprehensive understanding of life history requirements was required to evaluate limiting factors.

Although the humpback chub was described in 1945 (Miller 1946) and periodically studied since the late 1960s, only general life history information and schedules are known. While the population in Grand Canyon is the most intensively studied, the focus of investigations has been on the LCR rather than on the mainstem Colorado River. The lack of information on the humpback chub required parallel and sometimes simultaneous assimilation of life history information and hypothesis development and testing (Fig. 1-3). Limiting factors were identified and explained through a process of life history descriptions leading to multiple sequential hypotheses and multiple parallel hypotheses (Schumm 1991). Hypotheses were developed as ideas or propositions to provide a foundation for explaining certain phenomena. This approach was used to focus the study design on an evaluation of effects with a dedicated data collection protocol.

Flow characteristics of the Colorado River in Grand Canyon varied during this investigation and have varied dramatically since Glen Canyon Dam began impounding water on March 13, 1963 (See Chapter 3 - HYDROLOGY). Hence, the scope of work for this investigation focused on operational components (i.e., magnitude of fluctuations, minimum and maximum discharges, and rates of change in fluctuating discharges) rather than operational regimes because of the varied flow characteristics. Operational regimes during this investigation included "research flows" (June 1, 1990 through July 29, 1991) and "interim flows" (August 1, 1991 through completion of this field investigation). The short duration of each of these flow scenarios precluded identifying, isolating, and

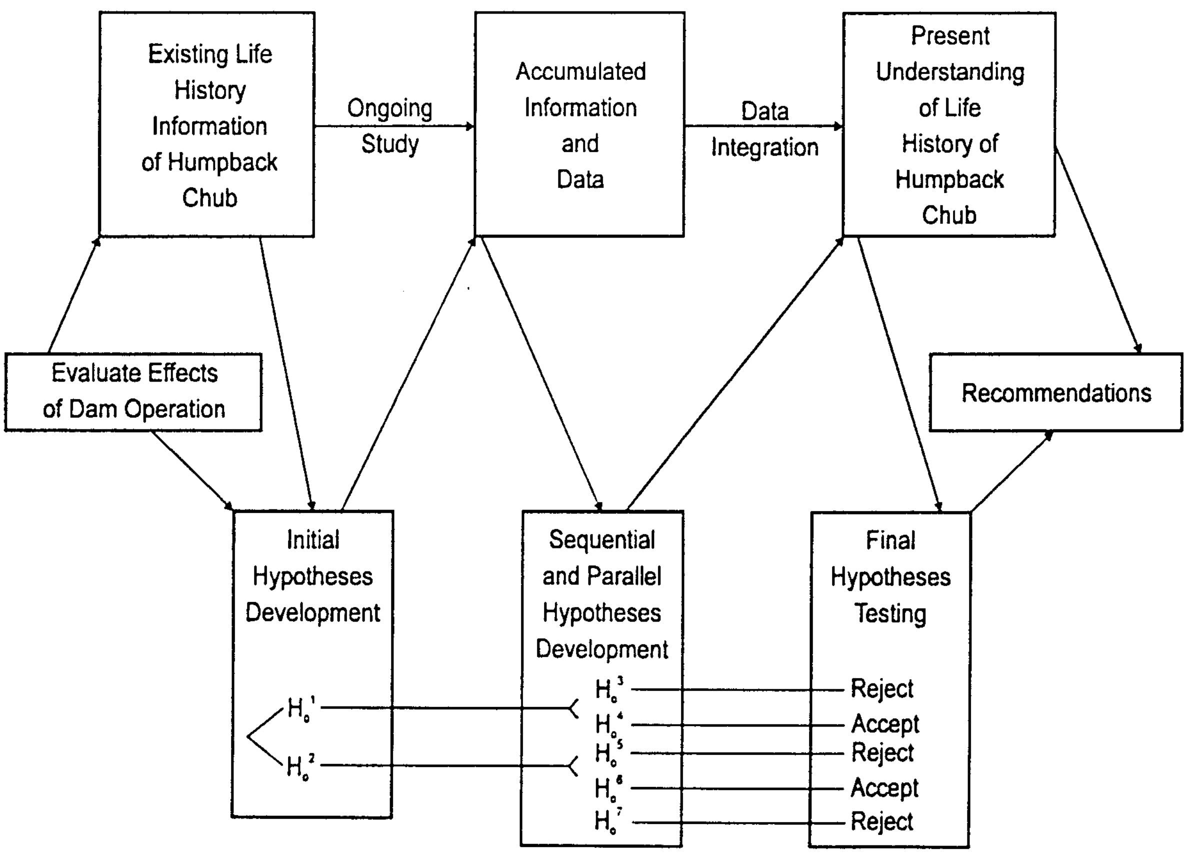


Fig. 1-3. Relationship of assimilation of life history information and hypothesis development and testing.

tracking important physical, chemical, and biological variables and measures of biological responses.

Changes in operational regimes during this study limited opportunities for inducing and observing long-term biological responses. Rigorous testing of hypotheses was not possible, because the system under investigation was not experimentally manipulated for ichthyofaunal responses, and replicate systems were not identified and simultaneously studied. Cause-effect relationships were first identified through systematic sampling, and hypotheses were developed from inferences of these relationships. These hypotheses provided valuable insight into ecological limitations of humpback chub and helped to identify mechanisms and causes of effects from dam operations.

Inferences that identified possible effects of dam operations on humpback chub were based on literature and available data collected from this and other investigations. Few inferences were made for operational effects on other trophic levels, because data collected in parallel studies by other researchers were preliminary and largely unavailable. Integration with tributary studies, particularly in the LCR, was also minimal, since information from these investigations was not available.

Selected physical, chemical, and biological components were described and quantified, where possible, to provide an integrated understanding of those elements of the ecosystem that most likely affect and limit humpback chub in Grand Canyon. Data were systematically collected in this study, or in cooperation with other studies, to minimize overlap with other research efforts and provide a comprehensive database to GCES for development of an integrated report.

STUDY AREA

The Colorado River through Grand Canyon flows for about 470 km (293 mi) from Glen Canyon Dam to the Lake Mead Inflow at Grand Wash Cliffs (Fig.1-4, Table 1-2). The river in this area is controlled entirely by Glen Canyon Dam, except for periodic floods from tributaries that otherwise insignificantly affect flow volume. The study area began at Lees Ferry (RM 0.0), 25.4 km (15.8 mi) downstream of the dam and extended 364 km (226 mi) to Diamond Creek (RM 226.0). For the purposes of this report, the area between Glen Canyon Dam and Grand Wash Cliffs (RM 277.0) is referred to as the Grand Canyon. This area includes the lower 25.8 km of Glen Canyon (dam to Paria River), 97.2 km of Marble Canyon (Paria River to LCR), and 347.0 km of Grand Canyon (LCR to Grand Wash Cliffs).

This study area was divided into four study regions to partition sampling effort by major longitudinal areas. The four regions were further divided into 11 geomorphic reaches (Schmidt and Graf 1990) as sampling units (See Chapter 2 - STUDY DESIGN). The four study regions included: (1) Region 0--Lees Ferry to Kwagunt Rapid, (2) Region I--Kwagunt Rapid to Hance Rapid, (3) Region II--Hance Rapid to below Havasu Creek, and (4) Region III--below Havasu Creek to Diamond Creek. Regions I, II, and III were sampled from October 1990 through November 1993. Region 0 was added to extend the investigation upstream in January 1993. A fifth region--Region IV (Diamond Creek, RM 226.0, to Pearce Ferry, RM 280.0)--was investigated as part of an aquatic resources study for the Hualapai Indian Tribe and GCES (Valdez 1993, 1994, 1995).

Reference landmarks along the river corridor were located to the nearest tenth (0.1) of a river mile (i.e., distance downstream from Lees Ferry along the center of the river) according to Belknap and Evans (1989), and sample sites were entered in the database to the nearest twentieth (0.05) of a river mile. It should be noted that Lees Ferry is 15.8 river miles downstream of Glen Canyon Dam, and river miles cited in this report are in reference to Lees Ferry and not Glen Canyon Dam, unless otherwise specified. A list of sites commonly referenced in this report is provided in Table 1-2 with river miles, river kilometers, and miles and kilometers downstream from Glen Canyon Dam. The following is a description of the four study regions (O-III). This description and Fig. 1-5 are provided to familiarize the reader with the physical character and lithology of the study area, and to develop a foundation for later discussion of fish habitat availability and use. (See Chapter 7 - HABITAT). Detailed descriptions of Grand Canyon geology were presented by Hamblin and Rigby (1968, 1969) and Howard and Dolan (1981).

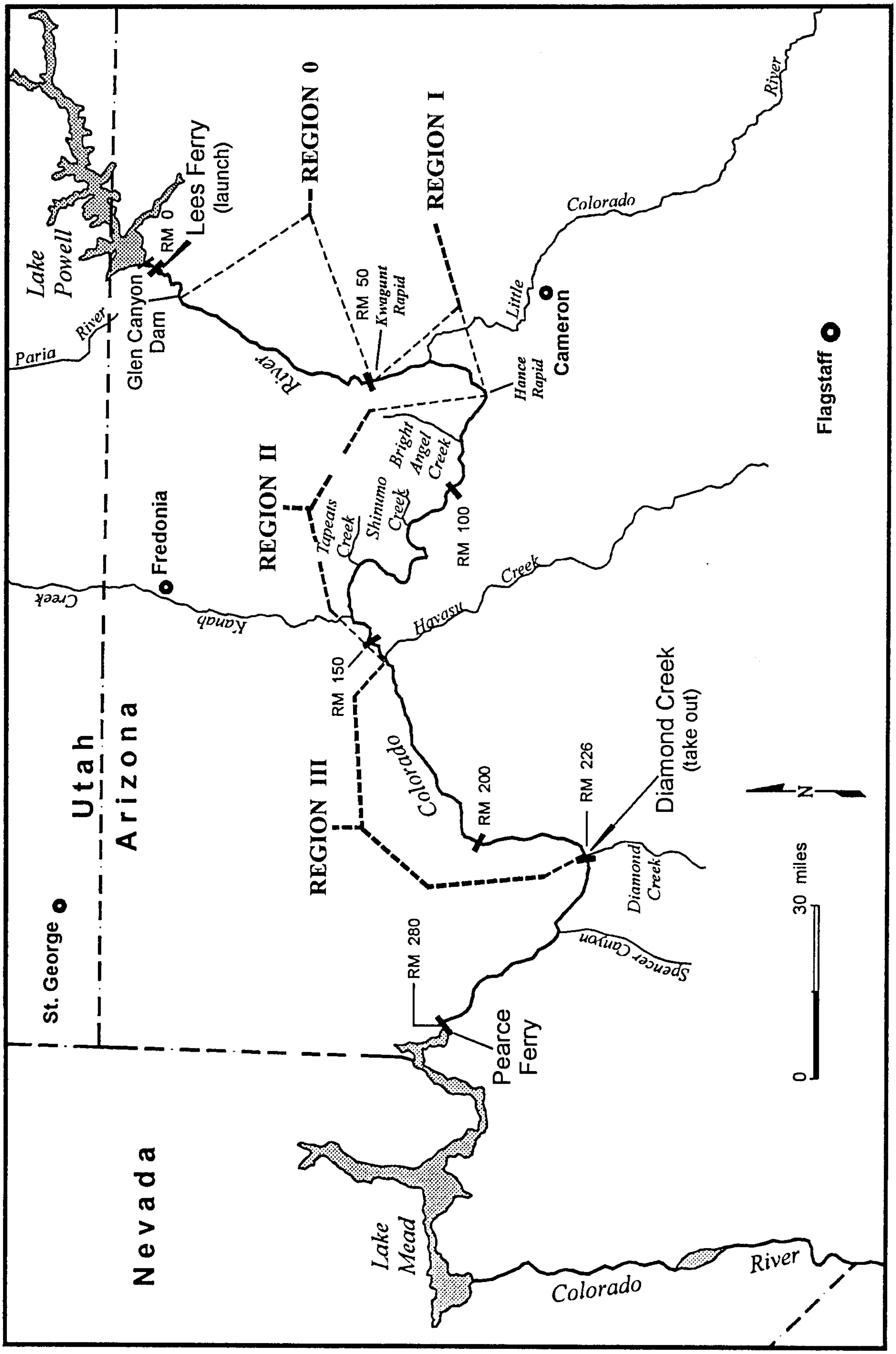


Fig. 1-4. BIO/WEST study area in Grand Canyon and four sample regions.

Table 1-2. Sites commonly referenced in this report by river mile and river kilometer downstream from Lees Ferry, and as miles and kilometers from Glen Canyon Dam. Sites upstream from Lees Ferry are preceded by '-'.[a]

	Distance from Lees Ferry		Distance from Glen Canyon Dam	
Site	River Mile	River Kilometers	River Mile	River Kilometer
Glen Canyon Dam	-15.8	-25.4	0	0
Lees Ferry	0	0	15.8	25.4
Lees Ferry - USGS gage	0.1	0.2	15.91	25.6
Paria River	0.9	1.4	16.7	26.9
Shinumo Wash	29.3	47.1	45.1	72.5
South Canyon	31.6	50.6	47.4	76.3
Vasey's Paradise	31.8	51.2	47.6	76.6
Nankoweap Canyon	52. 2	84.0	68.0	109.4
Kwagunt Rapid	55.9	90.0	71.7	115.4
Malagosa Canyon	57.6	92.7	73.4	118.1
Awatubi Canyon	58.3	93.8	74.1	119.2
Little Colorado River	61.3	98.7	77.1	124.1
Carbon Creek	64.7	104.1	80.5	129.5
Lava Canyon (Chuar)	65.4	105.2	81.2	130.7
Tanner Canyon	68.5	110.2	84.3	135.7
Cardenas Creek	71.1	114.4	86.9	139.8
Papago Creek	75.8	122.0	91.6	147.4
Hance Rapid	76.6	123.3	92.4	148.7
Clear Creek	84.1	135.3	99.9	160.8
Cremation Creek	85.7	137.9	101.5	163.3
Bright Angel Creek	87.7	141.1	103.5	166.6
Crystal Creek	98.1	157.9	113.9	183.3
Shinumo Creek	108.6	174.8	124.4	200.2
Elves Chasm	116.6	187.6	132.4	213.1
Stephen Aisle	117-119	188.3-191.5	132.8-134.8	213.7-216.9
Blacktail Canyon	119.9	193.0	135.7	218.4
Fossil Canyon	124.9	201.0	140.7	226.4
127-Mile Creek	126.8	204.1	142.6	229.5
Middle Granite Gorge	127-135	204.4-217.3	142.8-150.8	229.8-242.7
Tapeats Creek	133.7	215.2	149.5	240.6
Deer Creek	136.3	219.3	152.1	244.8
Kanab Creek	143.5	230.9	159.3	256.4
Havasu Creek	156.7	252.2	172.5	277.6
National Canyon	166.3	267.6	182.1	293.1
Lava Falls Rapid	179.4	288.7	195.2	314.1
Whitmore Wash	188.0	302.5	203.8	328.0
Pumpkin Spring	212.8	342.5	228.6	367.9
220-Mile Canyon	219.8	353.7	235.6	379.2
Granite Spring Canyon	220.5	354.8	236.3	380.2
Diamond Creek	225.7	363.2	241.5	388.6
Separation Canyon	239.5	385.4	255.3	410.8
Grand Wash Cliffs	276.0	444.2	291.8	469.6

[a]River Miles from Belknap and Evans (1989).

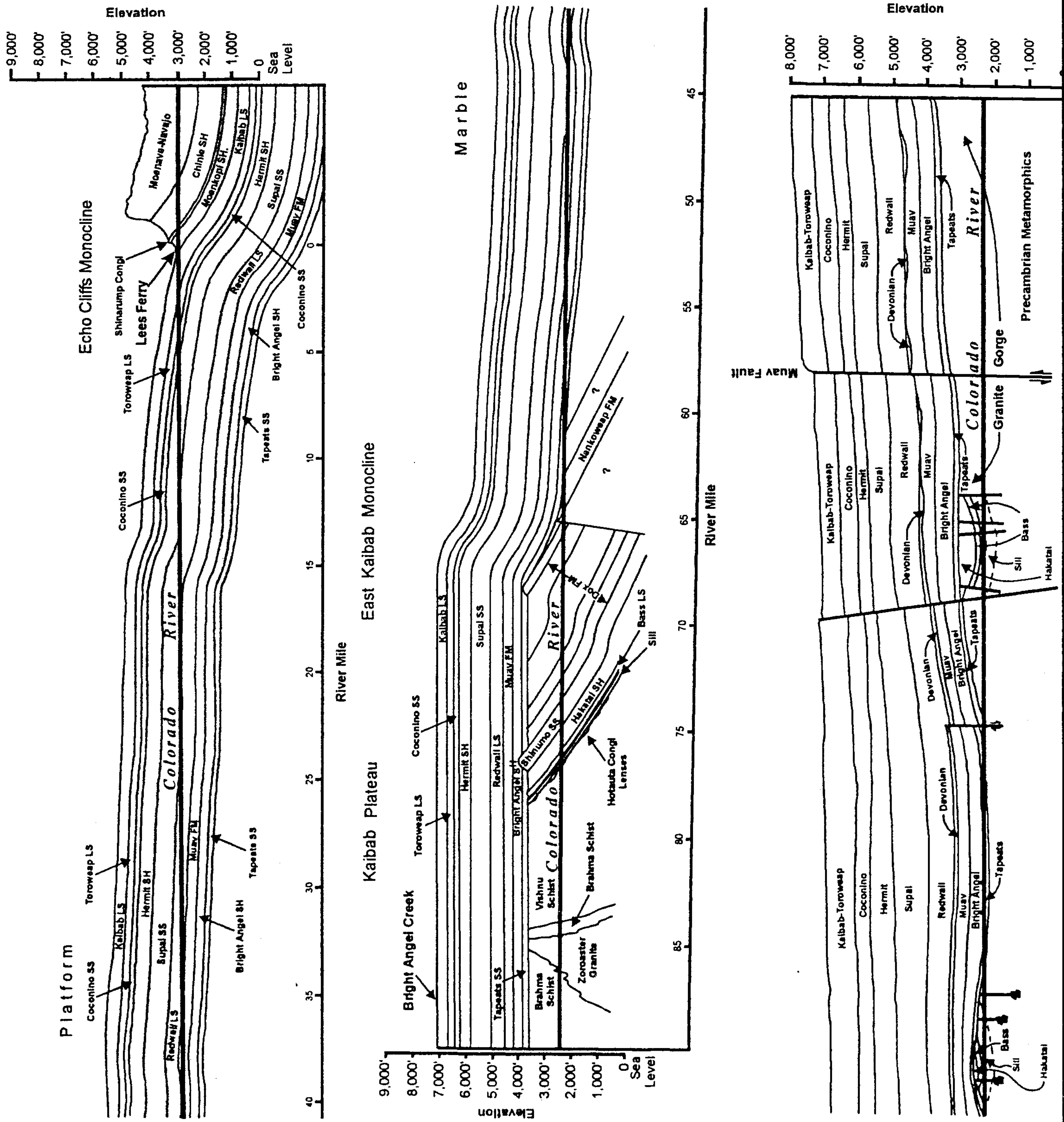
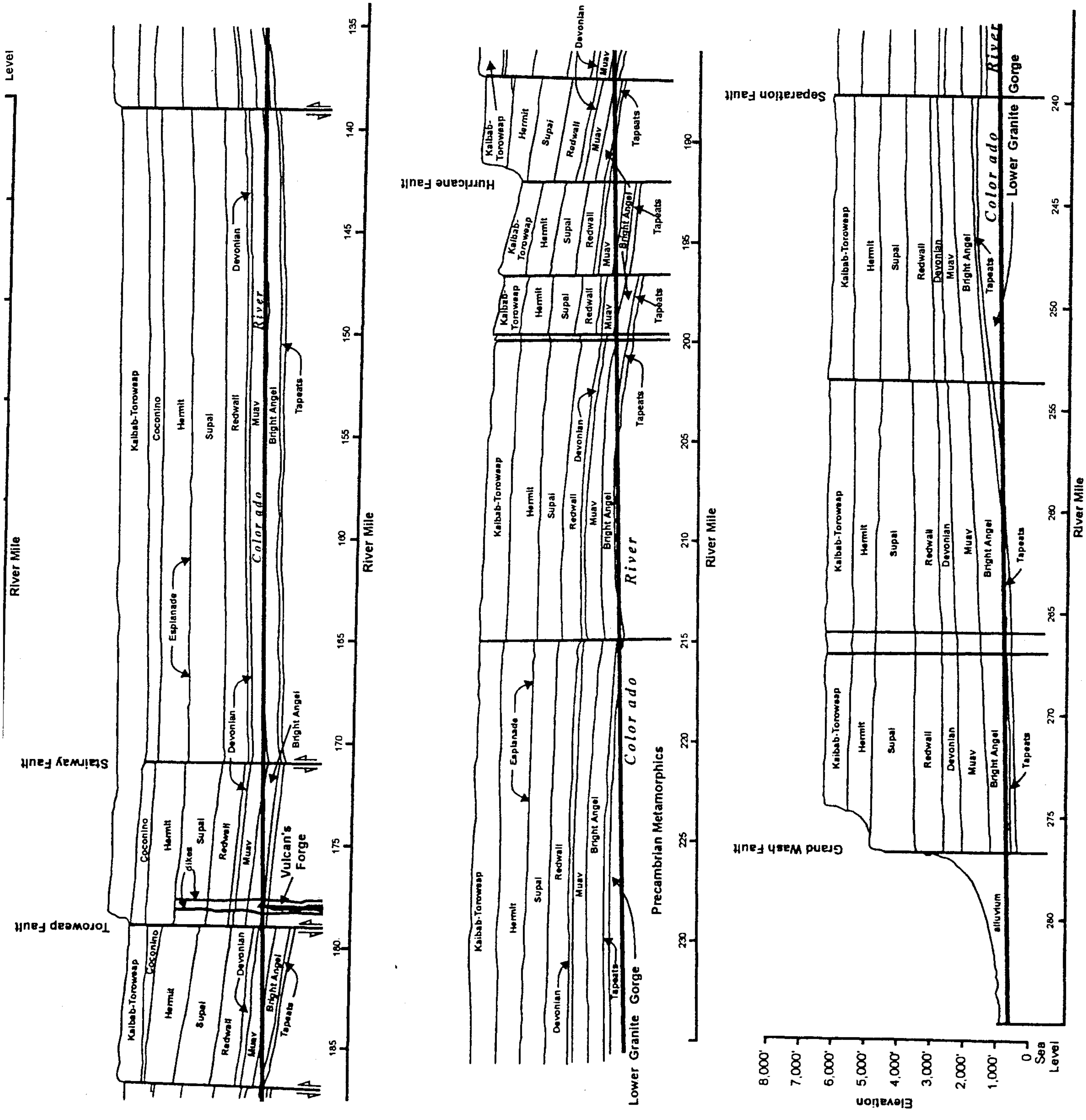


Fig. 1-5. Longitudinal cross section of the rock sequence along the Colorado River from Lees Ferry (RM 0) to Lake Mead (RM 2
Rigby (1968, 1969).



From Hamblin and

Region 0 (Lees Ferry to Kwagunt Rapid)

This region was 90.1 km (56.0 mi) long from Lees Ferry to Kwagunt Rapid (RM 0.0-56.0) and was characterized by four geomorphic reaches--Permian Section, Supai Gorge, Redwall Gorge, and the upper portion of Lower Marble Canyon (Table 1-3). Average channel widths in the four reaches were 79, 64, 67, and 107 m (280, 210, 220, and 350 ft), respectively, and channel slope was low to moderate (Schmidt and Graf 1990). Substrate was composed of 36-81% bedrock and boulders, and the shoreline was typically talus with intermittent tributary alluvial fans, sand bars, or earthen banks with vegetation.

Shoreline features in Region 0 (Fig. 1-5) are formed primarily by the Toroweap Formation and Coconino Sandstone (RM 2.0-5.0); Hermit Shale (RM 5.0-11.3); the Supai Group, including Esplanade Sandstone (RM 11.3-15.0); Wescogame, Manakacha, Watahomigi, and Surprise Canyon Formations (RM 15.0-23.0); Red Wall Limestone (RM 22.6-35.9); and Muav Limestone (RM 37.0-56.0).

The Paria River (RM 1.0) and Nankoweap Creek (RM 52.2) are the only perennial tributaries in this region. Several local drainages flow intermittently during rain spates in June, July, and August, introducing large amounts of sediment into the river. The largest contributor of sediment to this upper portion of the study area is the Paria River. Large alluvial fans at tributary inflows in this region constrict the channel and form 12 minor and 6 major rapids (Badger Creek, Soap Creek, House Rock, North Canyon, 21-Mile, Nankoweap).

Region I (Kwagunt Rapid to Hance Rapid)

Region I was 34.4 km (21.4 mi) long from Kwagunt Rapid to Hance Rapid (RM 56.0-77.4) and was characterized by two geomorphic reaches--Lower Marble Canyon and Furnace Flats (Table 1-3). The river channel in these reaches averaged 107 and 119 m (350 and 390 ft) in width, respectively, and channel slope was low to moderate at 0.10 and 0.21 %, respectively. Substrate was composed of 30-36 % bedrock and boulders, and shoreline was typically talus, ledges, or vertical cliffs with intermittent tributary alluvial fans, sand bars, or earthen banks with vegetation.

Shoreline features in Region I are formed primarily by Bright Angel Shale (RM 47.0-58.0), Tapeats Sandstone (RM 58.0-63.0), and the Unkar Group (RM 63.0-77.4) of the Great Unconformity. Soft shales and sandstones of Bright Angel Shale and Tapeats Sandstone create characteristic ledges and shorelines with fractured and collapsed rock fragments.

The Precambrian sedimentary series first appears in the Nankoweap Formation as an angular unconformity at RM 63.0 and, from that point to RM 65.5, the shoreline is characterized by steep vertical walls and talus with large angular blocks. Cardenas Basalt and Dox Sandstone of the Unkar Group are angularly juxtaposed downstream of the Palisades Fault so that from Lava Canyon (RM 65.5) to Escalante Creek (RM 75.0), the channel is wider and the shoreline is composed of boulders and cobble, with intermittent talus and occasional vertical walls.

The only perennial tributary in Region I is the LCR (RM 61.3), which is the largest tributary in Grand Canyon and the largest contributor of sediment to the Colorado River in Grand Canyon. Large alluvial fans form 9 minor and 6 major rapids (Kwagunt, 60-Mile, Lava Canyon, Tanner, Unkar, Nevills) in this region.

Region II (Hance Rapid to below Havasu Creek)

Region II was 132.7 km (82.5 mi) long, and extended from Hance Rapid to below Havasu Creek (RM 77.4-159.9). This region was composed of four geomorphic reaches, including Upper Granite Gorge, Aisles, Middle Granite Gorge, and Muav Gorge (Table 1-3). Upper Granite Gorge (RM 77.4-117.8) had the lowest average ratio of top canyon width to mean depth (7), the second narrowest average channel width (60 m, 190 ft), and the steepest channel slope (0.23%) of any geomorphic reach in Grand Canyon. The river in Upper Granite Gorge flows primarily through Vishnu Schist (black), Zoroaster Granite (pink), and Hotauta Conglomerate. These are resistant Precambrian formations about 1.8 billion years old

Table 1-3. Characteristics of geomorphic reaches[a] within the four study regions of the Colorado River in Grand Canyon.

Study Region	Geomorphic Reach	Extent of Reach (river miles)	Name of Geomorphic Reach	Major Geologic Units at River Level[b]	Description of Reach Width	Average Ratio of Top Width to Mean Depth	Average Channel Width (feet)	Channel Slope	Percentage of Bed Composed of Bedrock and Boulders
0	1	0-11.3	Permian Section	Kaibab Limestone Toroweap Formation Coconino Sandstone Hermit Shale	Wide	11.7	280	.00099	42
	2	11.3-22.6	Supai Gorge	Supai Group	Narrow	7.7	210	0.0014	81
	3	22.6-35.9	Redwall Gorge	Redwall Limestone	Narrow	9.0	220	0.0015	72
I	4	35.9-61.5[c]	Lower Marble Canyon	Muav Limestone Bright Angel Shale Tapeats Sandstone	Wide	19.1	350	0.0010	36
	5	61.5-77.4	Furnace Flats	Tapeats Sandstone Unkar Group	Wide	26.6	390	0.0021	30
II	6	77.4-117.8	Upper Granite Gorge	Zoroaster Plutonic Complex Trinity and Elves Chasm Gneisses Vishnu Schist	Narrow	7	190	0.0023	62
	7	117.8-125.5	Aisles	Tapeats Sandstone Vishnu Schist	Narrow	11	230	0.0017	48
	8	125.5-139.9	Middle Granite Gorge	Tapeats Sandstone Unkar Group Vishnu Schist	Narrow	8.2	210	0.0020	68
	9	139.9-159.9	Muav Gorge	Muav Limestone	Narrow	7.9	180	0.0012	78
III	10	159.9-213.9	Lower Canyon	Basalt Muav Limestone Bright Angel Shale	Wide	16.1	310	0.0013	32
	11	213.9-226.0	Lower Granite Gorge	Vishmu Schist	Narrow	8.1	240	0.0016	58

[a]Adopted from Schmidt and Graf (1988, 1990), with slight variation in river miles (0.1 mi) for Middle Granite Gorge, Muav Gorge, and Lower Canyon; Lower Granite Gorge was adjusted to 226.0 to correspond to the study area designation; features identified at 24,000 cfs.
[b]From Hamblin and Rigby (1969).
[c]Regions 0 and I divide at RM 56.0; See Table 2-1.

that form steep canyon walls and smooth scoured shorelines with little talus.

The Aisles (RM 117.8-125.5) include Stephen Aisle and Conquistador Aisle which are characterized by the reappearance of Tapeats Sandstone (RM 120.0-130.0) also found in Lower Marble Canyon. Average channel width was 70 m (230 ft) and 48% of the river bed was composed of bedrock and boulders.

The river in Middle Granite Gorge (RM 125.5-139.9) flows through a combination of Precambrian sedimentary rock and volcanic and metamorphic rock consisting of amphibolitic schist, limestones, diabase intrusives, and granitic plutons. These relatively resistant materials constrict the river to its narrowest point in Grand Canyon--23 m (76 ft) at RM 135.0. Average channel width in this reach is 64 m (210 ft), and the bed is composed of 68% bedrock and boulders.

The river in Muav Gorge (RM 139.9-159.9) flows through resistant Precambrian vishnu schist and zoroaster granite, which constrict the channel to the narrowest average width of any geomorphic reach in Grand Canyon--55 m (180 ft). The river bed in this area has the highest percentage of bedrock and boulders (78%).

Eight perennial tributaries flow into the Colorado River in Region II. These include Clear Creek (RM 84.1), Bright Angel Creek (RM 87.7), Crystal Creek (RM 98.1), Shinumo Creek (RM 108.6), Tapeats Creek (RM 133.7), Deer Creek (RM 136.3), Kanab Creek (RM 143.5), and Havasu Creek (RM 156.7). These streams typically have low base flows, which have little effect on mainstem flows and only local effects on water chemistry. Occasionally floods from spring snowmelt or summer thunderstorms produce high tributary flows which have short-term effects on mainstem water quantity and quality.

Region II has 36 major rapids (Hance, Sockdolager, Grapevine, 83-Mile, Zoroaster, Pipe Springs, Horn Creek, Salt Creek, Granite Creek, Hermit, Boucher, Crystal, Tuna Creek, Sapphire, Turquoise, 104-Mile, Ruby, Serpentine, Bass, Shinumo, 110-Mile, Waltenberg, Forster, Fossil, 128-Mile, Specter, Bedrock, Dubendorff, Tapeats, 135-Mile, Fishtail, Kanab, Matkatamiba, Upset, Sinyala, and Havasu).

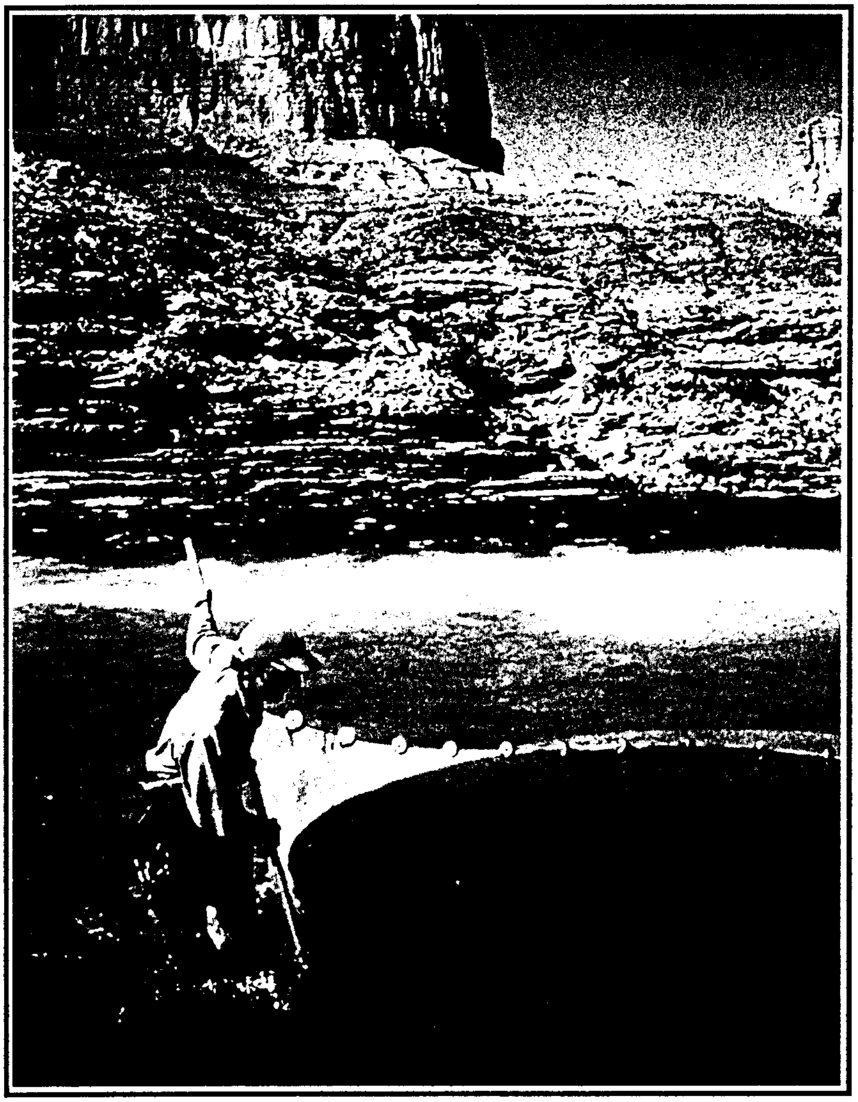
Region III (Below Havasu Creek to Diamond Creek)

Region III was 104.8 km (65.1 mi) long from below Havasu Creek to Diamond Creek (RM 159.9-226.0) and was divided into two geomorphic reaches--Lower Canyon and Lower Granite Gorge (Table 1-3). Lower Canyon (RM 159.9-213.9) had an average channel width of 94 m (310 ft), a moderate slope (0.13%), and a bed composition of only 32% bedrock and boulders. Lower Granite Gorge (RM 213.9-226.0) had an average channel width of 73 m (240 ft), a moderate slope of 0.16%, and a bed composed of 58% bedrock and boulders. The river in Lower Canyon flows through sedimentary deposits consisting primarily of Bright Angel Shale, and the shoreline is characterized by talus with intermittent alluvial fans. Tertiary lava flows downstream of RM 180.0 shape much of the shoreline with emergent boulders and cliffs formed by columnar basalt. The river in Lower Granite Gorge flows through metamorphic and sedimentary features similar to those in the lower portion of Upper Granite Gorge. The geologic formations consist primarily of granitic and granodioritic rock of the Zoroaster Granite Complex intermixed with Tapeats Sandstone.

This region has 11 major rapids (164-Mile, Fern Glen, Gateway, Lava Falls, 185-Mile, Whitmore, 205-Mile, 209-Mile, 217-Mile, Granite Spring, and 224-Mile) formed mostly by alluvial fans. No significant perennial tributaries exist in Region III.

Study Design

Chapter 2



Chapter 2 - Table of Contents

CHAPTER 2 - STUDY DESIGN

This chapter describes the study design elements common to the overall sampling program, including project schedule, sampling design, fish sampling, methods, and fish handling methods. More detailed methods are presented in respective chapters, such as techniques to gather hydrology data (Chapter 3), and water quality data (Chapter 4), or unique methods and calculations to determine distribution and abundance (Chapter 5), demographics (Chapter 6), habitat use (Chapter 7), movement (Chapter 8), and food habits (Chapter 9).

PROJECT SCHEDULE

This study was initiated by BIO/WEST (B/W) in September 1990 and completed with this report in September 1995 (Fig. 2-1). Project workshops were held in December of 1990, 1991, 1992, 1993, and 1994 to provide ongoing staff coordination, identify and resolve problems, update the data collection protocol, and provide progress reports to Bureau of Reclamation (Reclamation) and Glen Canyon Environmental Studies (GCES). A Data Collection Plan (Plan), issued as Supplement No. I to this Final Report, was drafted early in the project as a field handbook and updated periodically to standardize techniques and establish protocols for consistency in data collection and compatibility with other GCES investigations. This Plan provides detailed descriptions of field sampling methods, care and handling of fish, and database management that were too lengthy to include in this report. An Evaluation of Sampling Design (Supplement No. II) provides details on the efficiency of sampling techniques.

Field Trips

A total of 36 monthly field trips were conducted on the Colorado River in Grand Canyon from Lees Ferry to Diamond Creek (RM 0.0-226.0) starting in October 1990 and ending in November 1993 (Fig. 2-1). Trips were held monthly, except for December 1991 and 1992. From October 1990 through November 1992, trip length alternated between 12 and 20 days; hence, in 1991 and 1992, five 12-day trips (February, April, June, August, October) and six 20-day trips (January, March, May, July, September, November) were conducted. The schedule was modified in 1993 to eight 16-day trips (January, February, March, April, June, August, October, November), and three 20-day trips (May, July, September). Launch dates and sampling locations were coordinated with Arizona Game and Fish Department (AGF), when possible, to provide concurrent sampling and complementary datasets.

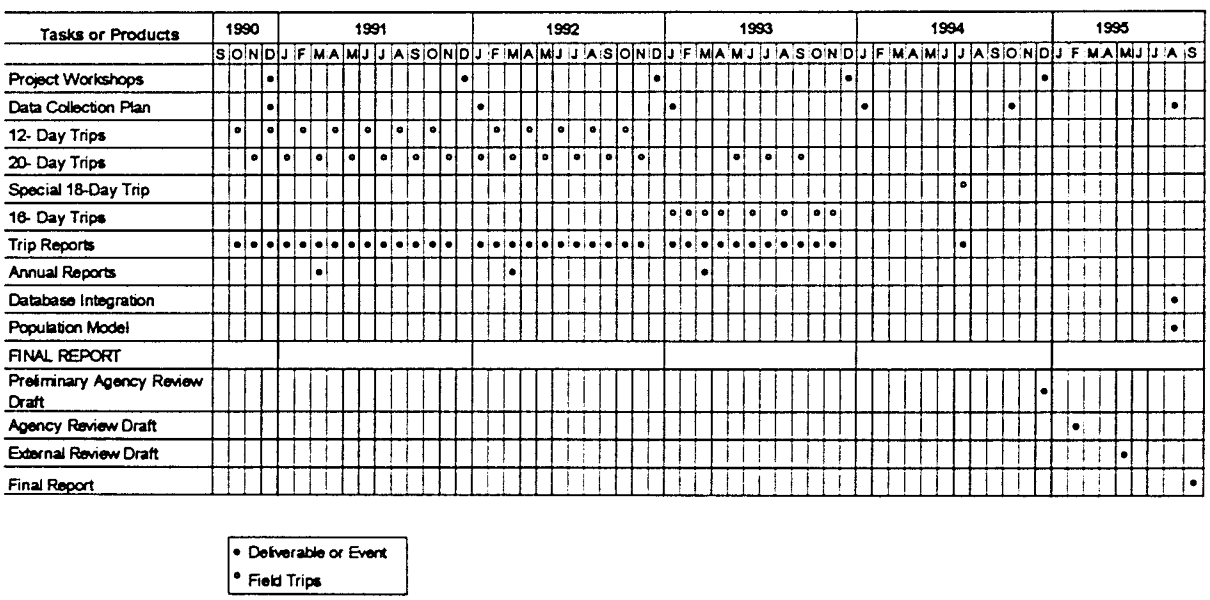


Fig. 2-1. BIO/WEST project schedule

Twenty-day trips were conducted to assess composition and distribution of fish, monitor habitat availability and use, determine important biotic interactions between humpback chub and other fish species, and capture humpback chub for implanting radio transmitters. These trips included two field crews. Crew one consisted of six B/W biologists and one Aquatic Coordination Team (ACT) biologist sampling in Region I. Crew two consisted of four B/W biologists and one ACT biologist sampling in Region II. The two crews jointly sampled Region III during the last 5 days of the trip, so that each of the three study regions was sampled with equal effort of about 10 crew-days.

Twelve-day trips were conducted primarily to recontact previously radio-tagged adult humpback chub and to monitor their movement and habitat use in Region I. These trips involved one field crew with six B/W and two ACT biologists. Fish were usually equipped with radio transmitters during 20-day trips, and they were tracked and monitored during 12-day trips from October 1990 through November 1992.

Sixteen-day trips were conducted from January through November 1993 after radiotelemetry was discontinued in Region I and implemented in Region II. The 16-day schedule allowed crews to allocate more time to tracking fish in Region II, while maintaining sampling frequency and intensity throughout the study area. The number of crews on 16-day trips alternated between one crew (February, April, June, August, October) and two crews (January, March, May, July, September, November) with numbers of personnel as described for 12-day and 20-day trips, respectively.

Reports

Trip reports were completed and submitted within 10 days of the completion of each of the 36 field trips, and annual reports were completed at the end of 1990, 1991, and 1992. These reports were submitted to Reclamation and GCES, and distributed to cooperating agencies and interested individuals. A list of reports and publications produced from this investigation is included as Appendix A of this Final Report. This Final Report was written by the B/W Grand Canyon Staff and reviewed by GCES, Reclamation, the Senior Scientist, several independent reviewers, and the National Research Council of the National Academy of Sciences.

SAMPLING DESIGN

A stratified sampling design was implemented to distribute sampling effort in time and space (Schreck and Moyle 1990). The four study regions (0-III) were longitudinally divided into 11 geomorphic reaches previously described by Schmidt and Graff (1988, 1990), each with distinct channel and shoreline characteristics (See Chapter 1 - INTRODUCTION, Table 1-3). The 11 geomorphic reaches were subdivided into 34 sample strata that ranged from 3.2 to 19.5 km (2.0 to 12.1 mi) in length (Table 2-1). These strata were the primary spatial sampling units and were considered representative of the geomorphic reaches in which they occurred (Fig. 2-2). Eight to 16 strata were randomly selected for sampling during each monthly trip. Selected strata were not eliminated from consideration for selection on subsequent trips, i.e.,sample with replacement. The five major tributary inflows in Region II (Bright Angel Creek,

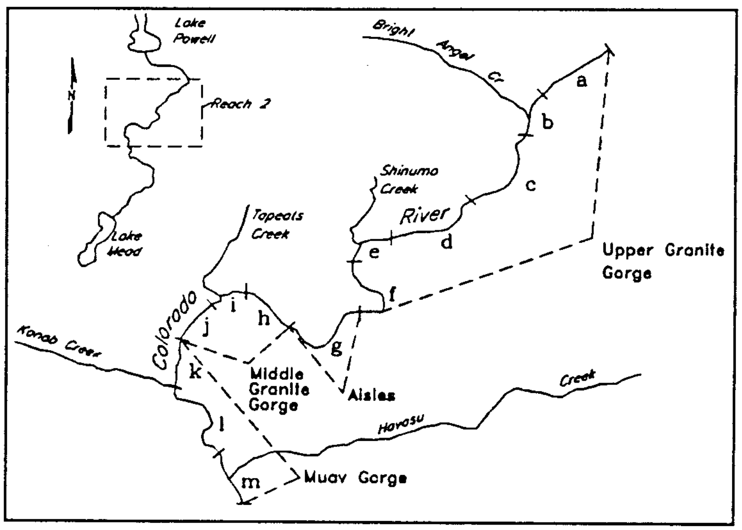


Fig. 2-2. Spatial stratified sampling design for Region II; a through m are sampling strata within geomorphic reaches, Upper Granite Gorge, Aisles, Middle Granite Gorge, and Muav Gorge.

Table 2-1. Lengths of sample strata within the 11 geomorphic reaches.

Study Region	Geomorphic Reach	Sample Strata	River Miles	Length km(mi)
0	1 - Permian Section	a. Paria - Badger Creek	1.0-8.0	11 .3 (7.0)
		b. Badger Creek - Soap Creek	8.0-11.3	5.3 (3.3)
	2 - Supai Gorge	c. Soap Creek - Sheer Wall	11.3-14.5	5.1 (3.2)
		d. Sheer Wall - House Rock	14.5-17.0	4.0 (2.5)
		e. House Rock - North Canyon	17.0-22.6	9.0 (5.6)
	3 - Redwall Gorge	f. North Canyon - Tiger Wash	22.6-26.5	6.3 (3.9)
		g. Tiger Wash - Vasey's	26.5-35.9	15.1 (9.4)
	4 - Lower Marble Canyon	h. Vasey's - President Harding Rapid	35.9-43.7	12.6 (7.8)
		I. President Harding Rapid - Nankoweep	43.7-52.0	13.4 (8.3)
		j. Nankoweep - Kwagunt	52.0-56.0	6.4 (4.0)
I	4 - Lower Marble Canyon	a. Kwagunt - LCR	56.0-61.5	8.9 (5.5)
	5 - Furnace Flats	b. LCR - Chuar Rapid	61.5-65.5	6.4 (4.0)
		c. Chuar Rapid - Unkar Rapid	65.5-72.5	11.3 (7.0)
		d. Unkar Rapid - RM 77.4	72.5-77.4	7.9 (4.9)
II	6 - Upper Granite Gorge	a. Hance Rapid - Cremation Canyon	77.4-86.5	14.6 (9.1)
		b[a]. Bright Angel Creek	86.5-89.0	4.0 (2.5)
		c. Pipe Creek - Crystal Rapid	89.0-98.0	14.5 (9.0)
		d. Crystal Rapid - Bass Rapid	98.0-107.8	15.8 (9.8)
		e[a]. Shinumo Creek	107.8-109.8	3.2 (2.0)
		f. 110-mile Rapid - RM 117.8	109.8-117.8	12.9 (8.0)
	7 - Aisles	g. Aisles	117.8-125.5	12.4 (7.7)
	8 - Middle Granite Gorge	h. RM 125.5 - Dubendorf SSR	125.5-131.7	9.8 (6.2)
		i[a]. Tapeats Creek	131.7-134.5	4.5 (2.8)
		j. 134 Mile Rapid - RM 140.0	134.5-139.9	8.7 (5.4)
	9 - Muav Gorge	k[a]. Kanab Creek	139.9-143.8	6.3 (3.9)
		l. Kanab Rapid - Sinyala Rapid	143.8-153.5	15.6 (9.7)
		m[a]. Havasu Creek	153.5-159.9	10.3 (6.4)
III	10 - Lower Canyon	a. RM 160.0 - RM 169.9	159.9-169.9	15.8 (9.8)
		b. RM 169.9 - Lava Falls	169.9-179.4	15.3 (9.5)
		c. Lava Falls - RM 189.1	179.4-189.1	15.6 (9.7)
		d. RM 189.1 - RM 200.0	189.1-200.0	17.5 (10.9)
		e. RM 200.0 - 209-Mile Rapid	200.0-208.9	14.3 (8.9)
		f. 209-Mile Rapid - 214 Mile Cr	208.9-213.9	8.0 (5.0)
	11 - Lower Granite Gorge	g. 214-Mile Cr - Diamond Creek	213.9-226.0	19.6 (12.1)

[a]Tributary strata

Shinumo Creek, Tapeats Creek, Kanab Creek, and Havasu Creek) were each treated as unique strata; these were selected and sampled at least once seasonally to insure adequate temporal characterization of areas.

The length of each sampling stratum was determined primarily by the distance of river between large rapids that was repeatedly accessible by research boats (See Box 2-1.), and by the location of temporary riverside camps for setting and retrieving sampling gear and tracking radio-tagged fish. Whitewater rapids too large or swift to ascend with small motorized research boats prevented repeated access to sample sites and frequently delineated stratum boundaries.

Sampling was conducted monthly and at different times of the day and night to account for seasonal and daily variation (Fig. 2-3). Sample effort was partitioned by season to represent winter (December-February), spring (March-May),

Box 2-1a. Electrofishing Boat

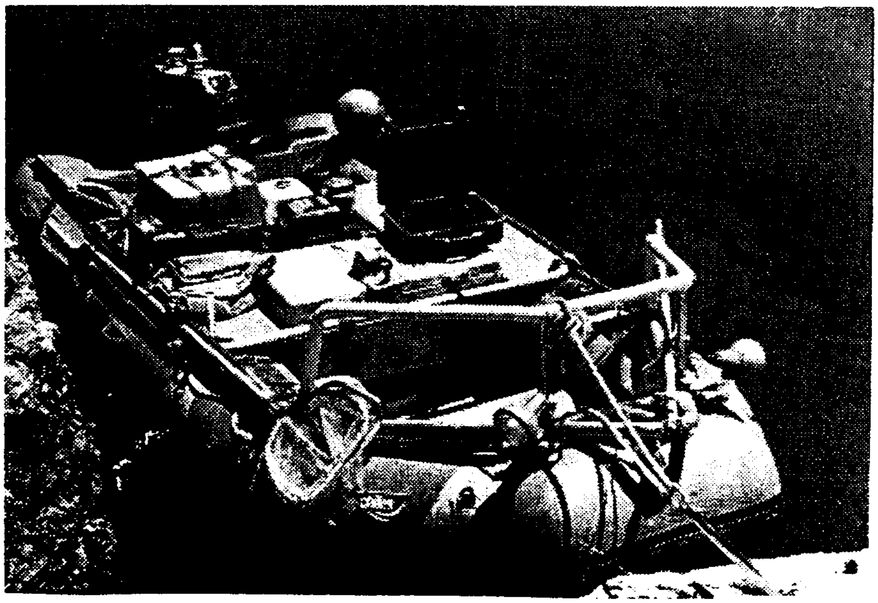
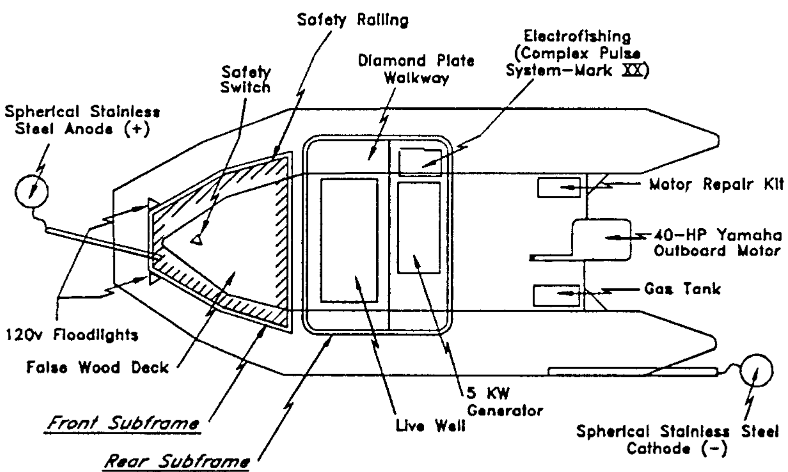


Photo of SU - 16

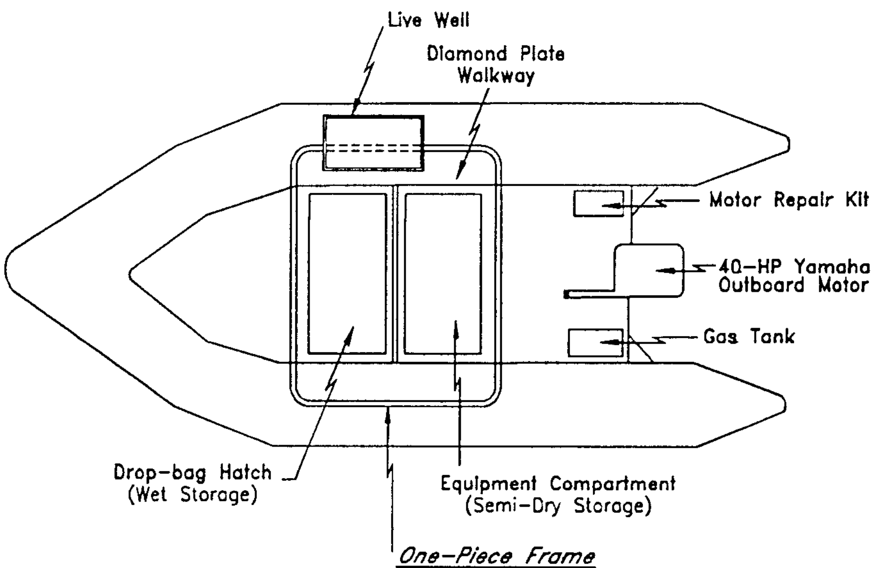


Frame Design for SU - 16

An Achilles sport utility boat (Achilles Corp., Tokyo, Japan), model SU-16 was used for electrofishing. The inflatable hypalon boat was 4.9 m long, was powered by a 40-hp Yamaha outboard motor, and had a removable sectional aluminum floor and fixed wooden transom. Welded tubular aluminum frames were specially designed to accommodate netters, a generator, voltage regulator, live well, and safety equipment.

Box 2-1b. Netting and Radio-Tracking Boat

Photo of SH - 170



Frame Design for SH - 170

An Achilles sport heavy duty boat (Achilles Corp., Tokyo, Japan) model SH-170 was used for netting and radio-tracking. The inflatable hypalon boat was 5.2 m long, was powered by a 40-hp Yamaha outboard motor, and had a removable sectional aluminum floor and fixed wooden transom. Welded tubular aluminum frames were specially designed to accommodate nets, live well, and safety equipment.

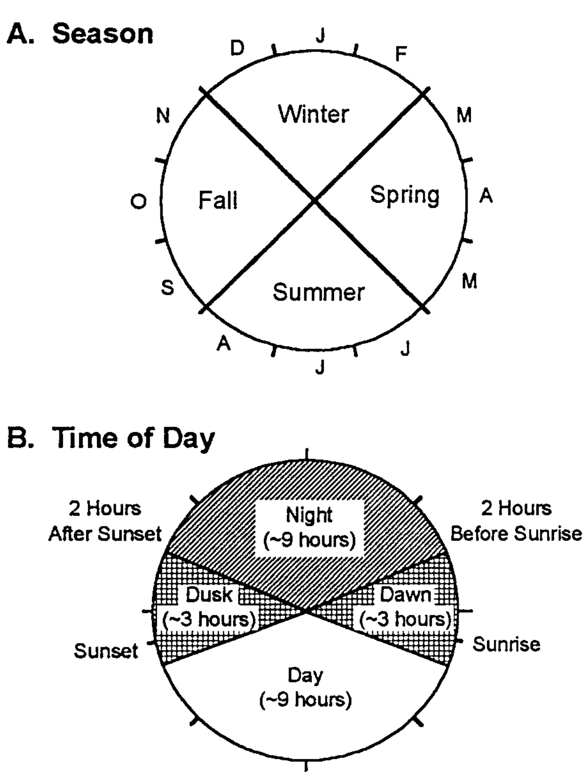


Fig. 2-3. Temporal stratified sampling design for seasons (A) and time of day (B).

summer (June-August), and fall (September-November), and by time of day to represent night, dawn, day, and dusk. Since day length and photoperiod varied with season, a computer program (Sun and Moon Events Worksheet, Heizer Software, Inc., Palo Alto, CA) was used to appropriately adjust diel time blocks.

FISH SAMPLING METHODS

Twenty-four different gear types or methods were used to sample fish. Descriptions and codes for each type or method are presented in Table 2-2.

Gill and Trammel Nets

Gill and trammel nets were the primary gear used to sample assemblages of large fish in deep habitats and to capture adult humpback chub for implanting radio transmitters. Nets were used to collect fish for comparing distribution and abundance by area and time, as well as to characterize general adult fish habitat to supplement radiotelemetry data. These types of nets are commonly used to survey and monitor other populations of humpback chub in the Upper Colorado River Basin (Valdez and Clemmer 1982, U.S. Fish and Wildlife Service 1987, McAda et al. 1994).

Gill nets were 30.5 m long and 1.8 m deep with 3.8 or 5.1-cm square mesh (100 ft x 6 ft deep, 1.5 or 2-in mesh). Experimental gill nets were also used with four sections of 1.3, 2.5, 3.8, 5.1-cm mesh (0.5, 1, 1.5, and 2-in). Trammel nets were 22.9 m long and 1.8 m deep (75 ft x 6 ft) with three panels of netting--two outer walls of 30.5-cm (12-in) mesh and one inner panel of 1.3, 2.5, or 3.8-cm mesh (0.5, 1, or 1.5-in). Gill and trammel nets were made of double knotted #139 multifilament twine with 1.3-cm (0.5-in) diameter braided polyfoamcore float line and 0.8-cm (5/16-in) leadcore line.

Gill and trammel nets were typically tied to shore, and stretched along the channel bed with net weights anchoring each end of the leadline (Fig. 2-4). Polypropylene mesh bags were filled with rocks and used as net weights. White mooring buoys were tied to the distal end of each net line as marker floats to facilitate relocation and retrieval of nets, and to alert boaters of submerged nets. Nets were also suspended in the water column to sample midwater habitat. Nets were checked at intervals of about 2 hr to minimize stress and reduce mortality of entangled fish. Nets clogged with algae (Cladophora glomerata) or debris were replaced and cleaned regularly.

Hoop Nets

Hoop nets were used in various shoreline habitats. Three sizes of hoop nets used included 0.6 m x 3.0 m x 1.3-cm (2 ft x 10 ft x 0.5-in), 0.9 m x 4.0 m x 2.5-cm (3 ft x 13 ft x 1-in), and 1.2 m x 4.9 m x 1.3-cm (4 ft x 16 ft x 1-in) (diameter x length x square mesh). Two 7.6-m (25-ft) wings with 2.5-cm (1-in) mesh were attached to the opening of the hoop nets. Hoop nets were set by anchoring the rear of the net with a length of rebar and orienting the throat in a downstream direction to capture fish moving upstream (Fig. 2-5). Hoop nets were checked at least every 8 hr to minimize stress and mortality to fish.

Table 2-2. Description of fish sample gear types or methods used in the Colorado River in Grand Canyon, October 1990 - November 1993.

Sample Gear Code-Description	Total No. Samples	Total Effort
Gill Nets		(Hours)
GP - 100'x6'x1.5" gill net	1,321	2,751
GM - 100'x6'x2" gill net	932	1,945
GX - Experimental gill net (100'x6'x0.5, 1, 1.5, 2")	509	1,061
Trammel Nets		
TL - 75'x6'x1.5"x12" trammel net	3,235	6,774
TK - 75'x6'x1"x12" trammel net	3,229	6,734
TM - 50'x6'x1"x12" trammel net	747	1,550
TN - 50'x6'x1.5"x12" trammel net	767	1,599
TW - 75'x6'x0.5"x10" trammel net	22	43
TY - Floating TK	6	11
TZ - Floating TL	3	5
Hoop Nets		
HL - Large hoop net (4'x16'x1")	63	910
HM - Medium hoop net (3'x13'x1")	17	270
HS - Small hoop net (2'x10'x0.5")	86	1,369
Minnow Traps		
MT - Commercial minnow trap (17.5"x9")	4,562	85,111
Electrofishing		
EL - 220-V DC	2,886	784
Seines		(m^2)
SA - 10'x3'x0.125" seine	113	15,672
SB - 30'x4'x0.25" seine	83	10,562
SG - 30'x5'x0.25" seine	328	59,057
GF - Floated gill net	6	1,350
TF - Floated trammel net	2	22,500
Misc. qualitative seine hauls	83	-
Angling[a]		
AN - standard gear	2	-
AL - standard gear, lures	4	-
Total	**19,006**	-

[a]no effort recorded

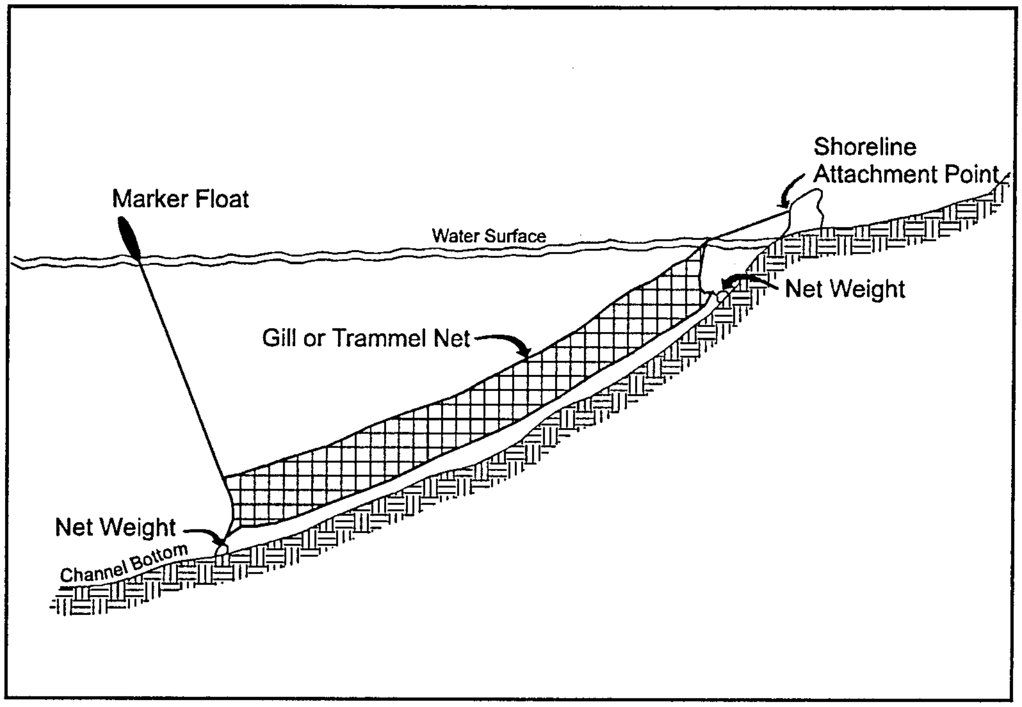


Fig. 2-4. Typical gill and trammel net set.

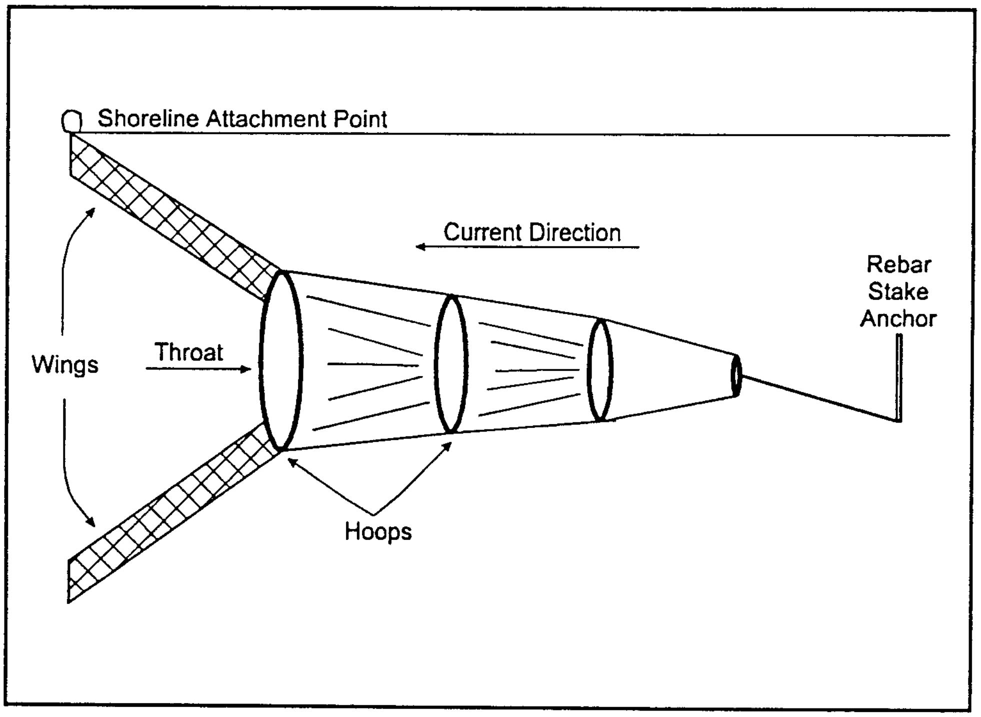


Fig. 2-5. Typical hoop net set.

Minnow Traps

Unbaited minnow traps were used to sample small fish in shoreline habitats. Commercial Gee minnow traps were used that were 44.5 cm (17.5 in) long, 22.9 cm (9 in) diameter, and constructed of galvanized wire and steel. Funneled openings were located at each end of the trap. Traps were placed on the bottom or suspended in the water column depending on conditions. Traps were also set in pods of five as sample repetitions for habitat types. Each trap was tethered to a secure anchor point and discretely flagged for easy relocation. Traps were checked at intervals of no longer than 12 hr to minimize stress and mortality to fish, and to minimize escapement by fish.

Seines

Seines were used to sample assemblages of small fish in relatively shallow habitats (up to about 1.5 m in depth). Three sizes of seines were used, including 9.1 m x 1.2 m x 0.6-cm (30 ft x 4 ft x 0.25-in), 9.1 m x 1.5 m x 0.6-cm (30 ft x 5 ft x 0.25-in), and 3.0 m x 0.9 m x 0.3-cm (10 ft x 3 ft x 0.125-in) (length x height x square mesh). The float line was constructed of 0.8-cm (0.32-in) braided polypropylene with hard foam floats at 45-cm (18-in) intervals. The bottom line was made of braided polypropylene line with lead sinkers at 15-cm (6-in) intervals.

Length and width of each seine haul were measured and three water depths were recorded at each sample site; one at the deepest point of the haul, one midway between the deepest point and the nearest shore, and one between the deepest point and distal end of the seine haul. Length and width of the habitat sampled were also recorded.

Electrofishing

Electrofishing was used to sample fishes along shorelines and to capture adult humpback chub for implanting radio transmitters. Each electrofishing effort was conducted within a distinct geomorphic shoreline type (i.e., debris fan, bedrock cliff, cobble bar, sand bar, talus, vegetation) to evaluate habitat use and reduce variability in comparing catch rates between habitats and reaches, as well as between flow levels and over time. Electrofishing was conducted along shallow shorelines and partitioned by day, night, and crepuscular periods.

Electrofishing was conducted from an Achilles SU-16 research boat capable of ascending small and medium-sized rapids for increased access to sample areas (See Box 2-1a.). Each boat was designed to meet Occupational Safety and Health Administration (OSHA) safety standards with specialized features such as pressure-sensitive safety switches, insulated railing, separate line-channeling for circuits and lights, and complete system grounding. Rubber gloves, rubber boots, and fiberglass-lined dip nets were provided for netters and boat handlers. The system was powered by a 5,000-W Yamaha industrial grade generator (Model YG-500-D) or a Honda 5,000-W generator (Model EB 5,000X) and routed through a Mark XX Complex Pulse System (CPS) developed by Coffelt Manufacturing (Flagstaff, AZ). Stainless steel spheres were used as electrodes with the anode (positive electrode) suspended on a cable from a fiberglass boom projecting from the bow, and the cathode (negative electrode) was suspended from a cable from the stern. Anode and cathode were exchanged every 45-60 min of electrofishing to allow for cleaning of the cathode surface by reversing the electroplating process.

During 1990-91, CPS output ranged from 15 to 20 A and 300 to 350 V, as recommended by Coffelt Manufacturing for electrofishing in the Colorado River below Glen Canyon Dam (N. Sharber, Coffelt Manufacturing, pers. comm.). In 1992, output was reduced to a range of 8 to 10 A and 200 to 250 V after bruise marks were observed on trout under the higher settings. The electrofishing system and the fish captured were continually monitored to minimize injury to fish as reported by Sharber and Carothers (1988), Sharber et al. (1994), and McMichael (1993)..

Angling

Angling has been used as an effective method for capturing humpback chub in the Upper Colorado River Basin, in Black Rocks and Westwater Canyon (Valdez et al. 1982) and in Yampa Canyon (Tyus and Karp 1989). Cheese balls, commercial salmon eggs, stink bait, grasshoppers, Mormon crickets (Tyus and Minckley 1988), and artificial flies have been used with varying success. Angling was not used extensively in this Grand Canyon study because of the time necessary to catch this species by angling, and because other sampling gears were more efficient with little perceptible injury to the fish. However, angling was used to catch actively-feeding rainbow trout for stomach analysis to assess predation on young-of-year (YOY) and juvenile humpback chub in the vicinity of the LCR inflow.

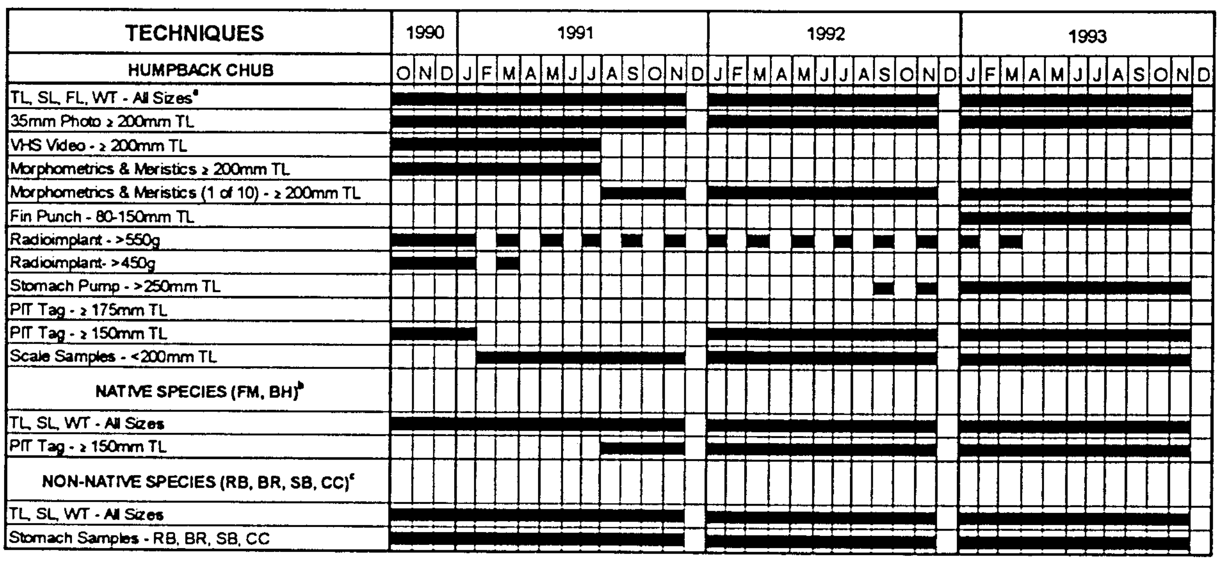
FISH HANDLING METHODS

Care and Processing

Fish were placed in live wells to minimize stress and to enhance their recovery from handling. Live wells consisted of 127-L insulated coolers located on each netting and electrofishing boat, 13-L bail buckets carried by seining crews, and 1.2 m x 1.8 m x 1.3-cm mesh (4 ft x 6 ft, 0.5-in) holding pens placed in the river. Fresh river water was used in all live wells and water was changed frequently when holding time was prolonged or when large numbers of fish were being held. Fish showing signs of stress (e.g., increased or irregular gill movements, loss of equilibrium, dramatic color change, reddened fins, excessive slime) were isolated in fresh water, carefully monitored, and treated with a 5% salt solution to minimize electrolytic losses (Hattingh et al. 1975, Bulkley et al. 1981). Fish with extended lethargy or obvious injuries were appropriately treated (e.g., Betadine™ was applied to wounds) and released upon recovery. Dead fish were preserved in an appropriately labeled container and transferred to the ichthyology collection at Arizona State University. Incidental mortality of humpback chub from this investigation did not exceed 10 per year, which was the number allowed under B/W's federal collecting permit.

From October 1990 through July 1991, all humpback chub captured were transported to a central processing station near each camp and returned to their respective capture locations for release--a one-way distance of up to 6.4 km (4 mi). This protocol prolonged holding time and unnecessarily stressed the fish. It was modified in August 1991 so that humpback chub were processed and released near their capture location, and only adults destined for radio-implant were transported to a central processing station.

A number of fish processing procedures were used during the course of this investigation. Some were initiated by the original study design and modified or discontinued, while others were implemented as a result of specific data needs or at the request of the ACT (Fig. 2-6). Humpback chub were measured for total length (TL), standard length (SL), and fork length (FL) in millimeters, weighed wet in grams, and gender was determined for each fish. From October 1990 through July 1991, the left side of every humpback chub 200 mm TL or longer was photographed (35-mm color slide and VHS video) on a white plasticized board; the board was marked with a 1-cm grid to provide a spatial reference scale



[a] TL= total length, SL= standard length, FL= forked length, WT= weight
[b] FM= flannelmouth sucker, BH= bluehead sucker
[c] RB= rainbow trout, BR= brown trout, SB= striped bass, CC= channel catfish

Fig. 2-6. Schedule of fish processing procedures conducted by BIO/WEST.

for morphometric measurements from photographs. Primary rays of dorsal and anal fins were counted, and ten morphometric dimensions were measured (± 0.01mm) with venier calipers; i.e., depth of nuchal hump, head length, snout length, distance between insertion of pelvic and pectoral fins, maximum body depth, caudal peduncle length, maximum caudal peduncle depth, minimum caudal peduncle depth, length of anal fin base, and length of dorsal fin base (Fig. 2-7). Starting in August 1991, 35-mm photographs, ray counts, and morphometrics were taken of every tenth adult captured (excluding recaptures), and videography was discontinued.

Adult humpback chub weighing more than 550 g were selected and surgically equipped with 11-g radio transmitters from October 1990 through January 1991 and alternate months through March 1993. An effort was made to maintain ten fish with active transmitters during the radiotelemetry phase of the study, and efforts to capture fish and implant radio-transmitters were scheduled according to anticipated extinction times of active transmitters.

Other techniques included stomach pumping of adults and scale collection from juveniles. A nonlethal stomach pumping technique was implemented in September 1992 following an evaluation of the technique (Wasowicz and Valdez 1994). Scales were taken from humpback chub less than 200 mm TL to determine age and size at transition from the LCR to the mainstem

Other native species including flannelmouth sucker, bluehead sucker, and speckled dace were measured for total length and standard length and weighed. Non-native species were also measured for total and standard length, weighed, examined for reproductive condition and gender, and released. Channel catfish, striped bass, and selected rainbow trout and brown trout were sacrificed for removal of stomachs. Stomachs were preserved in ethanol, placed in labeled whirl-packs, and transported to Leibfried Environmental Services in Flagstaff, Arizona for identification and quantification of food items (See Chapter 9 - FOOD HABITS).

All fish were examined for anomalous characteristics such as previous marks (e.g., fin punches, fin clips, external fish tags), parasites, wounds, or deformities. Anomalies were recorded in detail on appropriate data sheets and photographed if relevant to effects of sampling gear or radio-implant procedures.

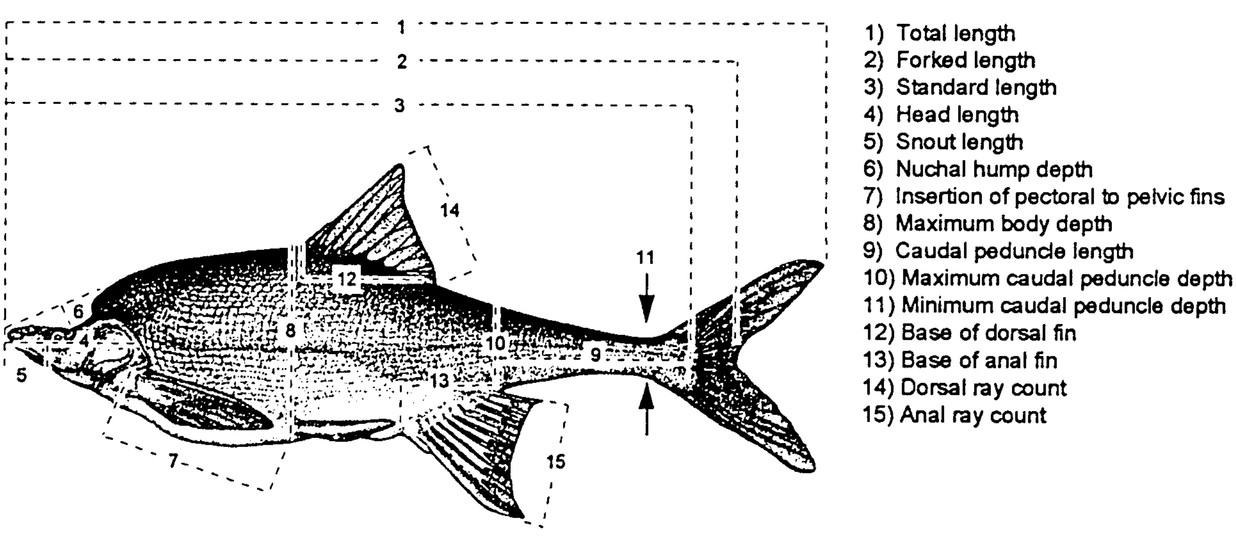


Fig. 2-7. Morphometrics and meristics recorded for adult humpback chub ≥200 mm total length.

Marks

A Passive Integrated Transponder (PIT) tag was injected into the intra-parietal cavity (Fig. 2-8) of each humpback chub 175 mm TL and longer. Starting in February 1991, minimum size of tagging was reduced to 150 mm TL. External tags (i.e., Carlin or Floy tags) placed by previous investigators were removed from native fish and replaced with PIT tags with both tag numbers recorded. These old tags were replaced at the request of the ACT because PIT tags were considered more reliable; i.e., less chance of tag loss and greater capacity and facility for information retrieval (Burdick and Hamman 1993). PIT tags were also injected into other native species (i.e., flannelmouth suckers, bluehead suckers) 150 mm TL or greater starting August 1, 1991.

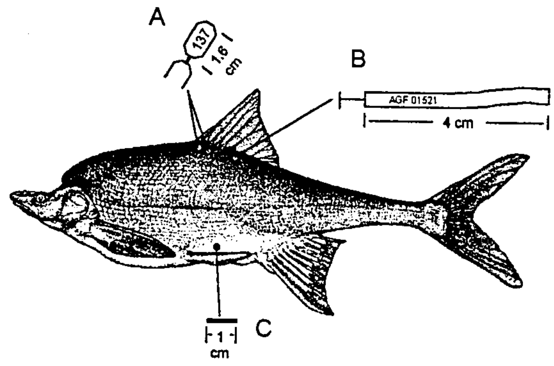


Fig. 2-8. Attachment sites for Carlin dangler tag (A) and Floy anchor tag (B) by previous investigators, and injection site for PIT tag (C) by this investigation. Approximate fish length = 400 mm TL.

Beginning in January 1993, juvenile humpback chub (range, 60-150 mm TL) were marked with temporary fin punches (Fig. 2-9) to track longitudinal dispersal. A 3-mm diameter biopsy needle was used to punch various fin combinations specific to river subreaches (Wydoski and Emery 1983). Various fin punch combinations were used by B/W and AGF for juveniles captured and released within respective subreaches of the mainstem Colorado River (Table 2-3). Also fin clip combinations were used by ASU for juveniles captured and released at respective reaches of the LCR.

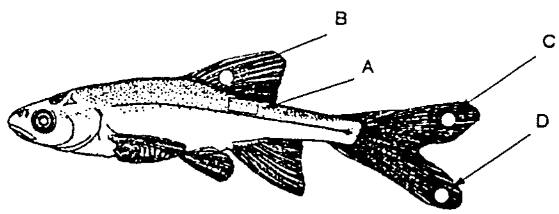


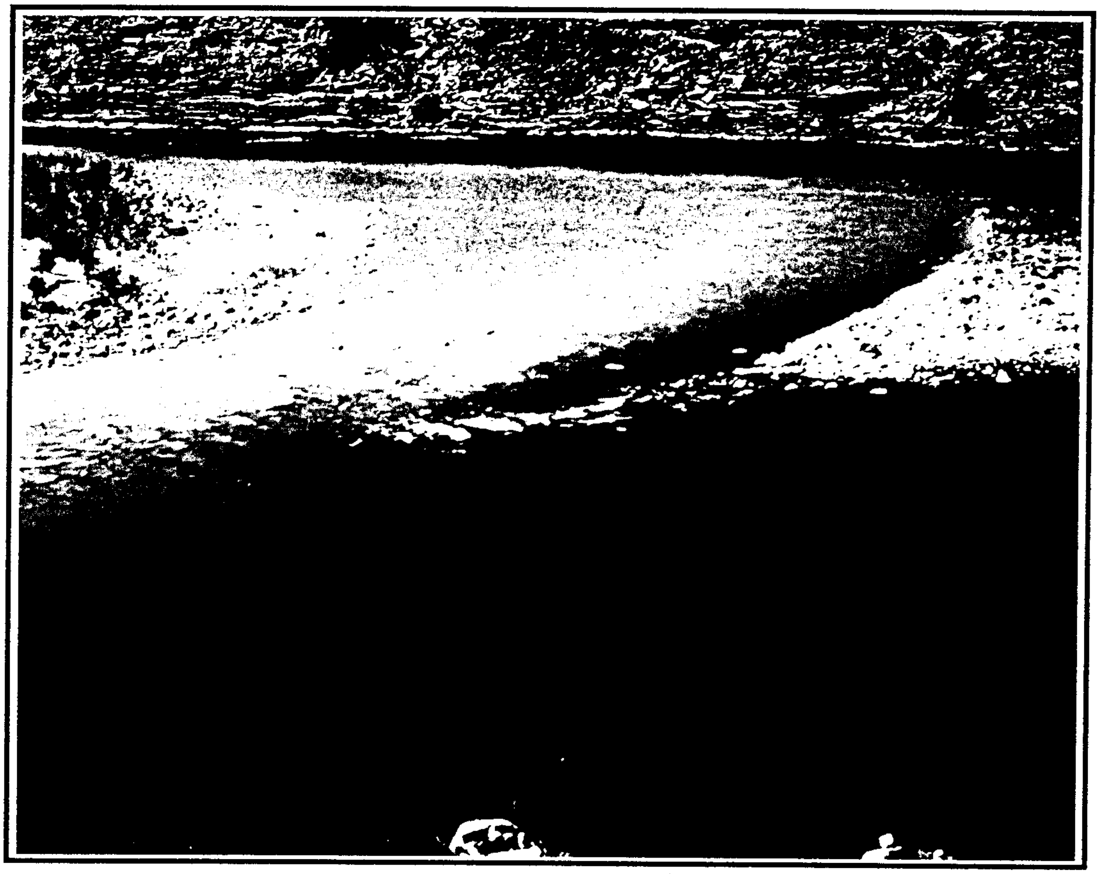
Fig. 2-9. Juvenile humpback chub with location of scale samples (A), and punches of dorsal fin (B), upper caudal fin lobe (C), and lower caudal fin lobe (D). Approximate fish length = 75 mm TL.

Table 2-3. Fin punch combinations used by B/W and AGF to mark juvenile humpback chub in the mainstem Colorado River, and fin clip combinations used by ASU to mark juveniles in the LCR.

Fin Punch Combinations (B/W, AGF)	Location (Colorado River)
dorsal fin	Malagosa Canyon to Lava Canyon (RM 57.6-65.4)
lower caudal fin lobe	Lava Canyon to Hance Rapid (RM 65.4-76.6)
upper caudal fin lobe	Hance Rapid to Havasu Creek (RM 76.6-156.7)
dorsal fin plus upper caudal lobe	Havasu Creek to Diamond Creek (RM 156.7-225.7)
Fin Clip Combinations (ASU)	**Location (LCR)**
upper caudal lobe plus right pelvic fin	Chute Falls to Salt Trail Camp (RK 14.9-10.8)
upper caudal lobe plus left pelvic fin	Salt Trail Camp to Sipapu (RK 10.8-7.5)
lower caudal lobe plus right pelvic fin	Sipapu to Powell Canyon Camp (RK 7.5-3.0)
lower caudal lobe plus left pelvic fin	Powell Canyon Camp to Confluence (RK 3.0-0.0)

Hydrology

Chapter 3



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CHAPTER 3 - HYDROLOGY

INTRODUCTION

The Colorado River drains an area of approximately 626,780 km² (242,000 mi²) and flows for about 2,330 km (1,450 mi) from the Rocky Mountains of Colorado to the Gulf of Lower California in Mexico. The river and its tributaries flow through seven arid western states (Colorado, Wyoming, Utah, Arizona, New Mexico, California, Nevada) draining approximately one-twelfth of the U.S. land area. Major tributaries include the Green, Yampa, White, Gunnison, Dolores, and San Juan rivers in the upper basin (above Lees Ferry) and the Little Colorado, Virgin, Bill Williams, and Gila rivers in the lower basin (below Lees Ferry).

Natural reconstituted inflows to Lake Powell, based on the periods 1895-1922 (LaRue 1925) and 1896-1956 (Leopold 1959), are estimated at about 13.85 million acre feet (maf) per year. Present annual upstream use of waters from the Colorado River are about 4 maf. For the period 1968-1974 upper basin depletions varied from 3.6 maf in 1969 to 4.96 maf in 1971, with an average of 4.28 maf. If 13.3 maf is available (estimated 0.55 maf is lost to evaporation, USGS 1990, 1992) and 4.3 maf is consumed in the upper basin, only 9.0 maf is available to meet the downstream requirement of 8.25 maf (7.5 maf to lower basin states plus half of the 1.5 maf to Mexico). Hence, under the present distribution of water from the Colorado River, only about 0.75 maf appears to be available for further basin use.

The Colorado River in Grand Canyon is the longest continuous portion of river remaining in the lower basin, flowing for 470 km (239 mi) from Glen Canyon Dam to Grand Wash Cliffs in upper Lake Mead. Major tributaries include the Paria River, Bright Angel Creek, Shinumo Creek, Tapeats Creek, and Kanab Creek flowing from the north rim, and the Little Colorado River (LCR), Havasu Creek, Diamond Creek, and Spencer Creek flowing from the south rim. The largest tributary in Grand Canyon is the LCR with a drainage basin of about 69,832 km² (26,964 mi²).

The Colorado River has flowed through Grand Canyon for the last 3-5 million years. During this time, natural streamflow has decreased because of an increasingly arid climate. The river also underwent many changes that greatly increased variability in streamflow regime, sediment loads, and water quality. Periodic geologic phenomena temporarily altered and reshaped the channel; e.g., late Cenozoic lava flows in western Grand Canyon formed at least 12 major lava dams in the last 1.2 million years. The largest of these dams was approximately 610 m (2,000 ft) high and backed the Colorado River for over 400 km (250 mi) for an estimated 3,000 years (Hamblin 1990).

The Colorado River is a high elevation desert stream, characterized by high spring snowmelt flows and low summer, fall, and winter flows. Periodic and erratic short-term flows occur during summer rainstorms. Natural streamflow is now substantially modified by anthropogenic effects, such as irrigation withdrawals, transbasin diversions, and dams. Thirteen mainstem dams regulate the flow of the Colorado River and hundreds of smaller dams control virtually every stream in the basin (Fradkin 1984). The first major mainstem dam was Hoover Dam, built in 1935.

Glen Canyon Dam, the largest dam on the Colorado River, was authorized under the Colorado River Storage Project Act of 1956. The dam began impounding the river on March 13, 1963 (Martin 1989). The dam is located 25 km (15.8 mi) upstream of Lees Ferry, the dividing point between upper and lower basins as designated by the Colorado River Compact of 1922 (Compact). Glen Canyon Dam is 223 m (730 ft) high and backs water in Lake Powell for approximately 322 km (200 mi) at a maximum lake elevation of 1,130 m (3,708 ft) above mean sea level. Lake Powell is used to provide storage replacement for upstream irrigation, to meet downstream requirements under the Compact, to store water for peaking power generation through Glen Canyon Dam, and for recreation.

Lake Powell has a total capacity of 27 maf and an active useable capacity of 25 maf. Water can be released through Glen Canyon Dam in the following three ways (U.S. Department of Interior 1995):

- Powerplant releases. The powerplant has eight generators with a maximum combined discharge capacity of about 33,200 cfs, although releases during fluctuations are limited to 31,500 cfs. Powerplant releases are preferred because of electrical production and associated revenues. Penstock intakes are located 70 m (229 ft) below the water surface at maximum lake elevation.

- River outlet works releases. Capacity of the river outlet works is 15,000 cfs, providing a total release capacity of 48,200 cfs, when used in conjunction with powerplant releases. The river outlet works (jet tubes) draw water from 6 m (20 ft) below the water surface at maximum lake elevation.

- Spillway releases. Spillway releases are made only when necessary to avoid overtopping the dam or to lower the level of Lake Powell. Combined capacity of right and left spillways is about 208,000 cfs. Spillway releases draw water from 6 m (20 ft) below the water surface at maximum lake elevation.

Although combined release capacity of the powerplant, river outlet works, and spillway is about 256,200 cfs, maximum combined releases from Glen Canyon Dam are not expected to exceed 180,000 cfs (U.S. Department of Interior 1995). Releases during the field trips of this investigation (October 1990 through November 1993) were entirely through the powerplant.

This chapter presents streamflow characteristics of the Colorado River and selected tributaries in Grand Canyon. An overview of the hydrology of Glen Canyon and Grand Canyon by Dawdy (1991) was used as a source of information for this chapter. Flow characteristics of the mainstem are presented for predam and postdam conditions to provide a perspective of hydrology during the term of this investigation. Although tributaries contribute a relatively minor component of flow to the mainstem, flow characteristics are presented because inflows were important areas for fish, providing food resources, warm flows, and possibly spawning and rearing areas for young. Access to tributaries for spawning and subsequent dispersal of young can be influenced by volume and timing of tributary flows.

METHODS

Flows of the Colorado River and its tributaries in Grand Canyon were characterized for this report from U.S. Geological Survey (USGS) stream gage records (Table 3-1, Fig. 3-1). The earliest USGS

Table 3-1. Stream gages used for hydrology analysis.

USGS Station Number	Station Name	Location[a]	Drainage Area (mi^2)	Period of Record (water years)
9380000	Colorado River at Lees Ferry, AZ	RM 0.2	111,800	1895-present
9383100	Colorado River above LCR, AZ	RM 61.2	N/A	Apr 1983-present
9402500	Colorado River near Grand Canyon, AZ	RM 87.4	~141,600	1925-present
9404120	Colorado River at National Canyon, AZ	RM 166.5	N/A	Apr 1983-present
9404200	Colorado River above Diamond Creek, AZ	RM 226.0	N/A	Apr 1983-present
9402000	Little Colorado River near Cameron, AZ	45 mi ups	26,459	1947-present
9402300	Little Colorado River near mouth, AZ	0.5 mi ups	26,964	1989-Jan 1993[bc]
9382000	Paria River at Lees Ferry, AZ	1.1 mi ups	1,410	1923-present
9403000	Bright Angel Creek near Grand Canyon, AZ	0.5 mi ups	101	1923-1974
9403780	Kanab Creek near Fredonia, AZ	31 mi ups	1,085	1963-1980

[a]RM = river miles downstream from Lees Ferry.
ups = miles upstream from Colorado River confluence.
[b]data inconsistent
[c]discharge based on stage elevations, periodically adjusted based on stream channel measures.

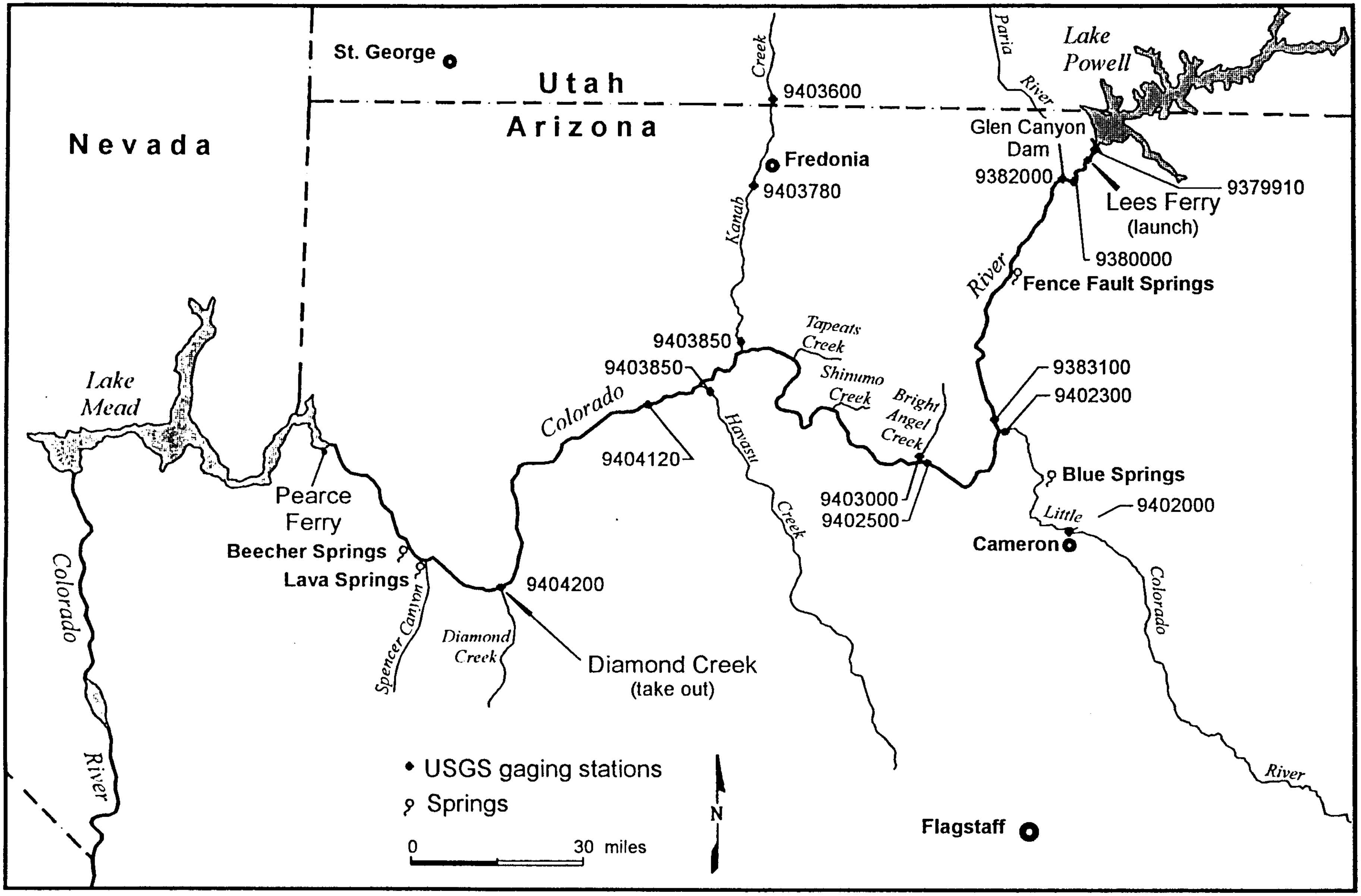


Fig. 3-1. Locations of stream gages (shown as 7-digit numbers) used for hydrology analysis.

records available were for the Colorado River at Lees Ferry starting in 1895. Early records were typically based on single daily measurements, while more recent records are for streamflow at 15-min intervals. Provisional, records were used for the analyses in this report because final published record were not available at the time of report preparation. Some provisional records were modified for this report using data from adjacent gaging stations when obvious data irregularities existed. Final published records of the USGS are not expected to vary significantly from those presented in this report.

A streamflow routing model (Supplement No. VI, Goodwin 1995) was developed for this study to provide site-specific flow information for correlation with radiotelemetry observations, habitat assessment, and collection of drift material. This model was based on the flood wave theory (Lazenby 1987) and used data from the nearest stream gages for calibration. Stage-discharge relationships were derived from USGS stream gages for determination of site specific flows.

Mainstem Colorado River

Flow data for the Colorado River in Grand Canyon were obtained from five USGS stream gages (Fig. 3-1), identified by the following gage numbers and descriptions:

- 9380000 - at Lees Ferry, AZ,
- 9383100 - above Little Colorado River, AZ,
- 9402500 - near Grand Canyon, AZ (i.e., Phantom Ranch),
- 9404120 - at National Canyon, AZ, and
- 9404200 - above Diamond Creek, AZ.

Historic records were available from the Lees Ferry gage (1895 to present) and from the Grand Canyon gage (1922 to present), but only intermittent records were available from above the LCR, at National Canyon, and above Diamond Creek (mid-1980s to present). Data from the gage above the LCR were used most frequently because of the proximity of the gage to many study sites that required time and site-specific streamflow information (e.g., fish movement from radiotelemetry observations, habitat assessments, drift samples). Missing or aberrant discharge measurements were estimated with a flow routing model using data from the Lees Ferry gage.

Little Colorado River

Flow data for the LCR were obtained from the following USGS stream gages (Fig. 3-1):

- 9402000 - near Cameron, AZ, and
- 9402300 - near LCR mouth, AZ.

The gage near Cameron provided an historic record of flow for the LCR since 1947. However, the gage was located 72 km (45 mi) upstream of the confluence with the Colorado River and did not record flow from Blue Springs (21 km upstream of the confluence), which is the major source of base flow for the LCR. The gage near the mouth was operated from 1989 to January 1993, when it was disabled by an unusually high flood. Collection of flow data in March 1993 was initiated by GCES with a nanometer pressure sensor, and correlations were developed between the two records to adjust the GCES data and provide a consistent record.

Other Tributaries

Flow data for other major tributaries in Grand Canyon were obtained from the following three USGS stream gages (Fig. 3-1):

- 9382000 - Paria River at Lees Ferry, AZ,
- 9403000 - Bright Angel Creek near Grand Canyon, AZ, and
- 9403780 - Kanab Creek near Fredonia, AZ.

The gages on the Paria River and Bright Angel Creek were each located within 2 km (1.2 mi) of the mouth, and were valuable for determining annual and seasonal inflow into the Colorado River. The Kanab Creek gage was located about 50 km (31 mi) upstream from the mouth and reflected general watershed hydrology. Gaged streamflow data were not available for Shinumo, Tapeats, or Havasu creeks.

FLOW CHARACTERISTICS

Mainstem Colorado River

Predam Flows

Prior to completion of Glen Canyon Dam in 1963, flow of the Colorado River through Grand Canyon was characterized by dramatic annual and seasonal variation. Year-to-year variation depended on snowpack that accumulated in the mountains. During high runoff years, annual flow volume exceeded 18 maf, while lowest recorded annual discharge at Lees Ferry was only 4.4 maf in 1934 (Fig. 3-2). Mean annual discharge for 51 water years (WY) prior to the dam (WY 1912-62) was 17,850 cfs, and mean volume was 12.93 maf. For 26 years after initial filling of Lake Powell (WY 1965-90), mean annual discharge was 14,350 cfs and mean volume was 10.40 maf.

Predam seasonal discharge patterns were characterized by exceptionally high spring and early summer flows and by low summer, fall, and winter flows (Fig. 3-2). Flows typically began rising in March with low elevation snowmelt and were generally highest in late May and early June at the peak of snowmelt. Although flows in June averaged nearly 60,000 cfs, peak daily flows were frequently over 100,000 cfs. Flows typically receded in late June and July, and average flow from August through March was 5,000-10,000 cfs. Lowest recorded flow at Lees Ferry since the USGS gage was installed in 1895, was 750 cfs on December 27, 1924, and highest flow was 220,000 cfs on June 18, 1921 (USGS 1990). Maximum discharge since at least 1868 was about 300,000 cfs on July 7, 1884. Climatological evidence from tree rings indicates that a flow of about 500,000 cfs occurred in the 1600s (Webb et al. 1991).

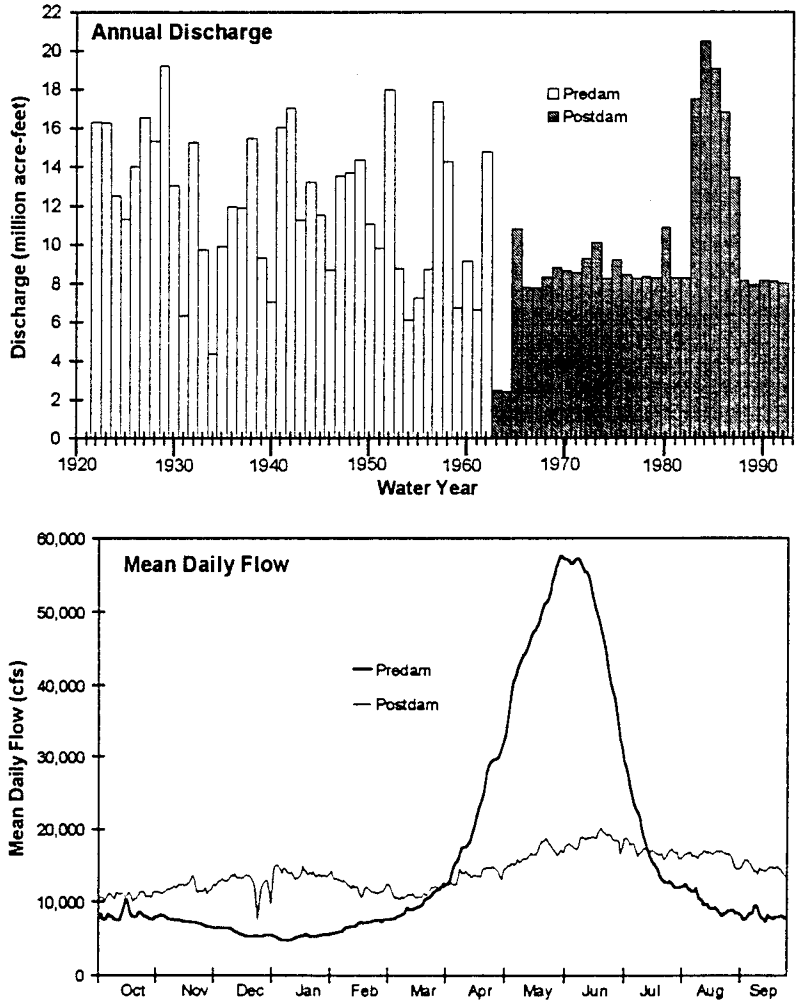


Fig. 3-2. Annual discharge (WY 1922-92) and mean daily predam (WY 1922-62) and postdam (WY 1965-92) flow of the Colorado River at Lees Ferry, AZ.

Postdam Flows

Annual and seasonal flow variation dramatically decreased, and daily fluctuations dramatically increased with operation of Glen Canyon Dam. Except in years of high-runoff (i.e., WY 1983-87), year-to-year variation in total annual discharge has been maintained between 8 and 9 maf (Fig. 3-2). Average daily postdam flows have exceeded 30,000 cfs only about 3% of the time and have been less than 5,000 cfs about 10% of the time. Seasonal streamflow regime has also been modified with mean daily springtime flows reduced from about 60,000 cfs to less than 20,000 cfs. Conversely, mean daily flow during late summer and winter has increased from a range of 5,000 to 10,000 cfs to a range of 10,000 to 15,000 cfs (Fig. 3-2).

Fluctuations within the day have varied dramatically for peaking power generation with a range in median (equaled or exceeded 50% of the time) daily fluctuations (difference between minimum and maximum daily releases) of about 12,000 cfs in October to about 16,000 cfs in January and August. Minimum flows during peaking power operations ranged from 1,000 to 4,000 cfs prior to August 1, 1991, when interim flows were implemented.

Hydroelectric power generation at Glen Canyon Dam is one of the more significant operational aspects affecting the character of the Colorado River in Grand Canyon. Since hydroelectric power is used primarily for "peaking power" (power needs above base loads brought about by daily changes in electrical demand), water is held in Lake Powell at night when demand for power is low and released at higher volumes during high daytime demand. Weekends and holidays are often extended periods of low flow. Daily release fluctuations generate long waves that travel downriver with a characteristic pattern (Fig. 3-3), but lack the long tails typical of natural streams (Graf 1995). Discharge and river flow velocities are substantially greater at wave peaks than at wave troughs. As the waves move downriver, wave peaks travel faster and tend to overtake wave troughs but because of flow hydraulics, wave peaks maintain similar magnitude while flows in wave troughs increase. Hence, the magnitude of oscillations associated with these kinematic waves are ameliorated with distance downstream. High tributary inflows may disrupt this pattern by increasing discharge for both wave peaks and wave troughs.

Six distinct operational scenarios were evident for postdam flows of the Colorado River in Grand Canyon for WY 1963-93 (Fig. 3-4):

- Initial reservoir filling from March 1963 through WY 1964,
- Long-term filling and operation from WY 1965 to WY 1982,
- High flood flows from WY 1983 through WY 1986,
- High fluctuating releases from WY 1987 to June 1, 1990,
- Research flows from June 1, 1990 through July 29, 1991, and
- Interim flows beginning August 1, 1991.

Initial Reservoir Filling. For the first 2 years following closure of Glen Canyon Dam in 1963, releases were low to allow for initial filling of the reservoir. Minimum daily flow on January 23 and 24, 1963 was 700 cfs, as a result of closing the coffer dam, and annual discharge in 1963 and 1964 was less than 2.5 maf.

Long-term Filling and Operation. Water released through the dam was of similar chemical and thermal nature to upstream river water through the late 1960s but the river below the dam became increasingly cold and clear as the reservoir filled and impounded sediments, eventually stratifying to trap cold water in the hypolimnion (See Chapter 4 - WATER QUALITY). Lake Powell reached maximum capacity of 26.373 maf on July 14, 1983

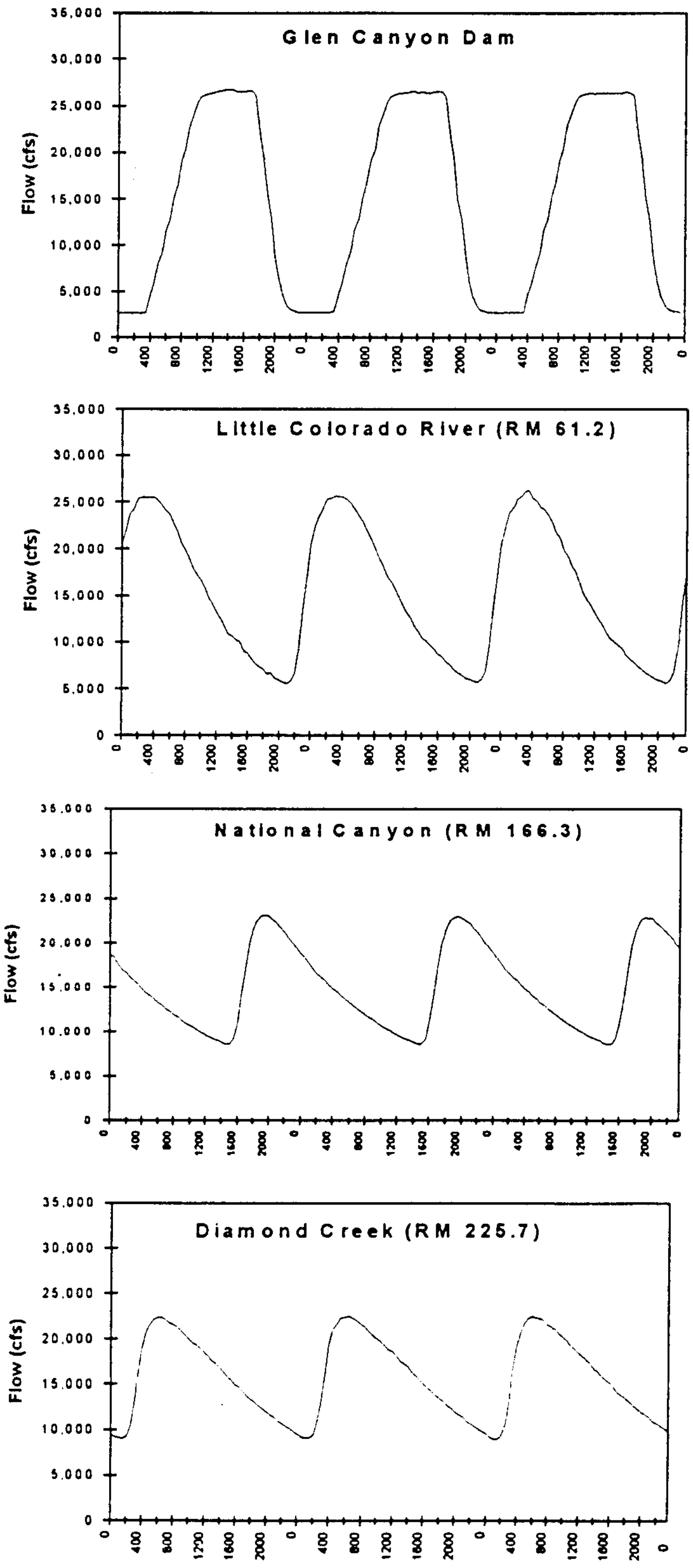


Fig. 3-3. Characteristic wave patterns of the Colorado River as generated by daily fluctuating releases over a 72-hr period. Flows were measured simultaneously during high fluctuating releases (~3,000 cfs to ~26,500 cfs) at Glen Canyon Dam, above the LCR, at National Canyon, and above Diamond Creek, May 10-12, 1991.

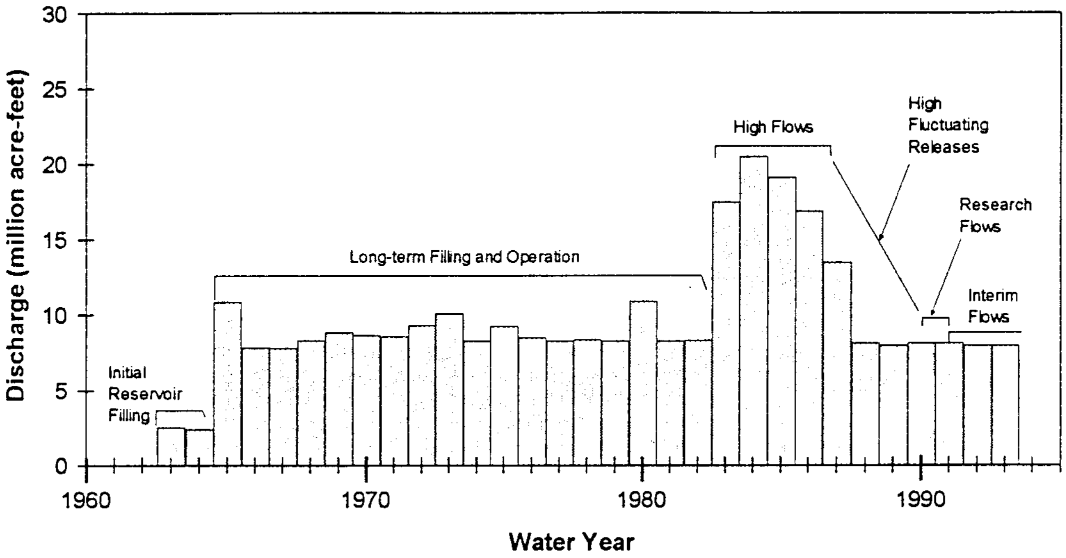


Fig. 3-4. Six operational scenarios during postdam discharges (WY 1963-93), as measured at Lees Ferry, AZ.

at 1,130 m (3,708 ft) elevation above mean sea level (USGS 1990).

High Flood Flows. The third operational scenario resulted from above average snowfall during the winters of 1982-83 and 1983-84, which produced an unusually high runoff and a maximum discharge of 97,300 cfs on June 29, 1983. Over 20 maf of water was released through the dam in WY 1984 (October 1, 1983 through September 30, 1984), more than any year since WY 1922. Annual releases from WY 1983 through WY 1986 averaged 12 maf as a result of this wet period.

High Fluctuating Releases. The period from WY 1987 to June 1, 1990 was characterized by low annual runoff, and high daily fluctuating releases as a result of increased regional peaking power demands. Typical daily release patterns (Fig. 3-5) for a low release year (WY 1989), moderate release year (WY 1987), and high release year (WY 1984) (U.S. Department of Interior 1995) illustrate the wide variation of operational scenarios caused by local weather patterns and peaking power demands. The magnitude of daily fluctuations was greater for low to moderate release years than for high release years, since constant high releases produced a consistently high level of hydropower.

Research Flows. Releases from June 1, 1990 through July 29, 1991 were identified as research flows. These releases were requested by GCES to evaluate the effects of controlled flows on canyon resources (Fig. 3-6). 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, and
- unrestricted ramping rate.

Constant releases during research flows were made according to the following criteria:

- 5,000 cfs for 3 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. In 1991, Secretary of Interior, Manuel Lujan, issued a decree to operate Glen Canyon Dam under "interim operating criteria" beginning August 1, 1991 and continuing until the Record of Decision for the Glen Canyon Dam Environmental Impact Statement was issued. Interim criteria were characterized by:

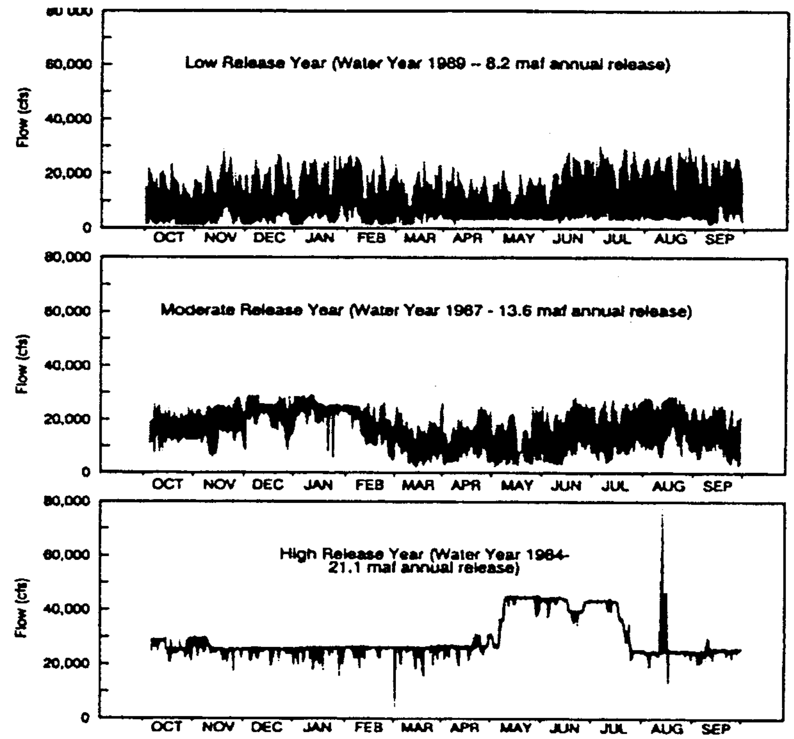


Fig. 3-5. Low, moderate, and high release water years for Glen Canyon Dam. The range is represented by lowest and highest hourly releases for each day. Used with permission of Bureau of Reclamation, Colorado River Studies Office, Salt Lake City, UT.

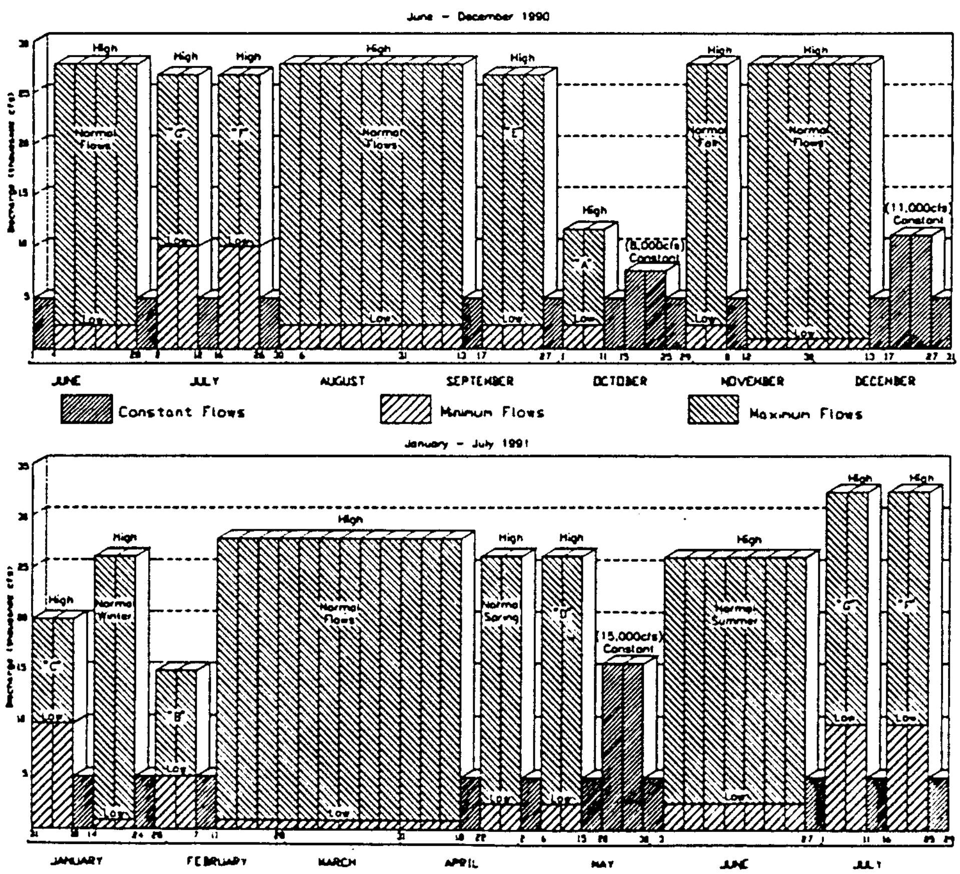


Fig. 3-6. Research flow schedule for releases from Glen Canyon Dam. The 3-day 5,000 cfs constant flows were scheduled to begin at 12:01 a.m. on Friday and conclude at 12:01 a.m. on Monday. The 8,000 cfs, 11,000 cfs, and 15,000 cfs constant flows each lasted 11 days.

- Flows limited to a maximum of 20,000 cfs,
- Daytime minimum of 8,000 cfs and nighttime minimum of 5,000 cfs,
- 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 rate of release change for rising flows (up ramp) no greater than 2,500 cfs/hr with a maximum of 8,000 cfs change during any 4-hr period, and
- Maximum allowable rate of release change for falling flows (down ramp) of 1,500 cfs/hr.

The B/W investigation spanned from October 1990 through November 1993 and included 3 complete water years (WY 1991, 1992, 1993), plus the first 2 months of WY 1994 (i.e., October and November 1993). Hydrographs showing daily high and low flows for this 3-year period for the Colorado River above the LCR are presented in Fig. 3-7. High fluctuating flows (i.e., research flows), with intermittent constant releases are evident from October through July of WY 1991, and more moderate fluctuations (i.e., interim flows) are seen from August of WY 1991 through WY 1993.

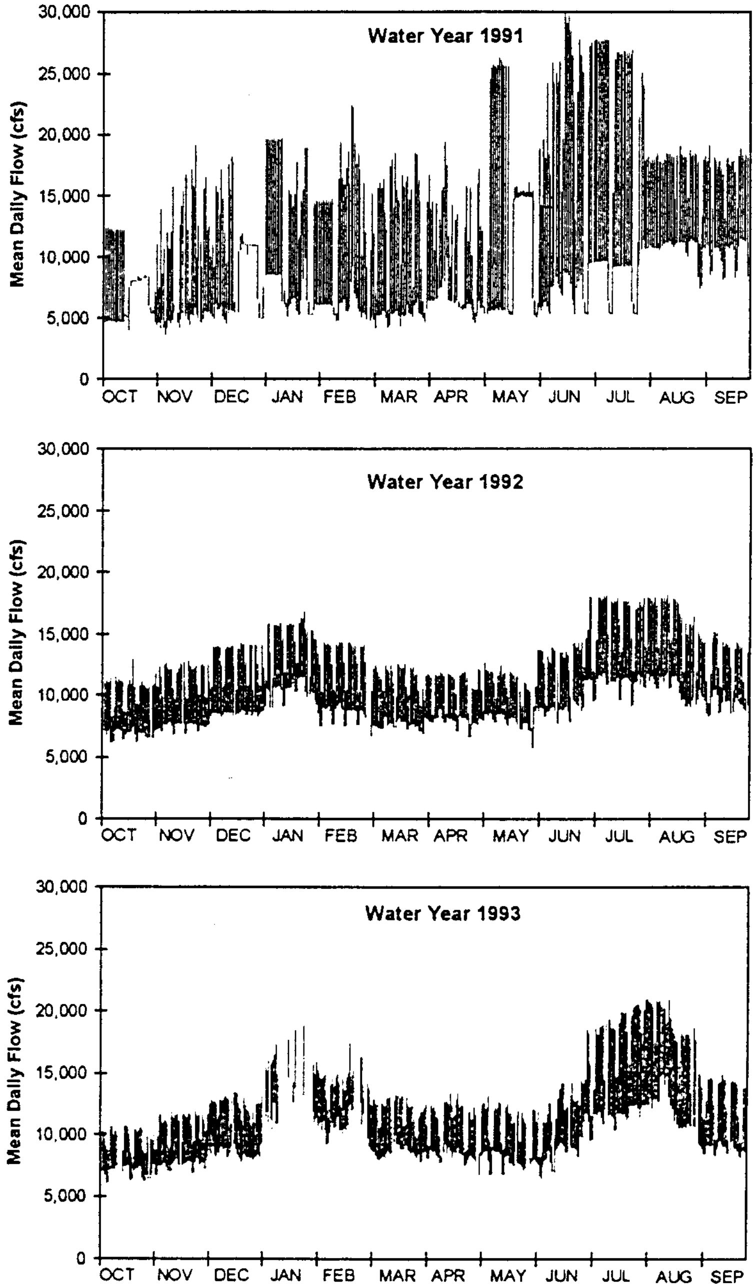


Fig. 3-7. Mean daily flow of the Colorado River for WY 1991, 1992, and 1993 as measured above the Little Colorado River, AZ.

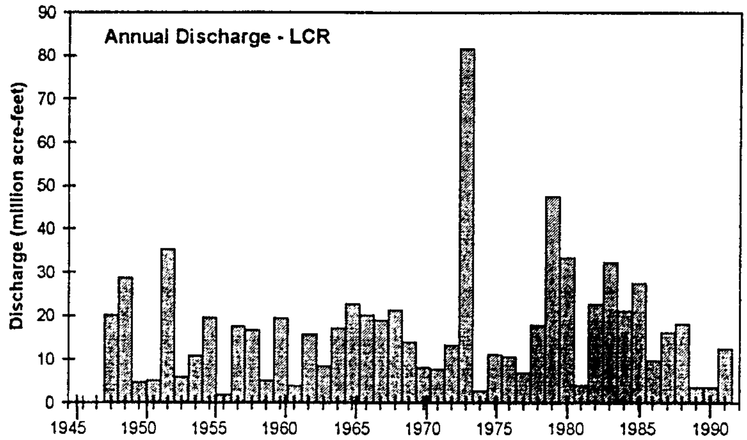
Little Colorado River

The LCR is the largest tributary to the Colorado River in Grand Canyon with a drainage area of about 69,832 km² (26,964 mi²) and an average annual discharge of 170,000 af (Johnson and Sanderson 1968). It is one of the most important tributaries in Grand Canyon providing the majority of known spawning and rearing habitat for humpback chub, a large influx of food supplies to fishes in the mainstem, and the major source of sediment to the mainstem. Although the LCR drainage comprises nearly 23% of the area of the Colorado River Basin, it contributes less than 2% of flow volume. The LCR originates on Mount Baldy in the White Mountains and flows north for about 412 km (256 mi) through northeastern Arizona, entering the Colorado River at RM 61.3 (i.e., 61.3 mi below Lees Ferry, 77.1 mi below Glen Canyon Dam). Stream gradient in the last 2 km is low at about 1.2 m/km. A characterization of the hydrology, climatology, sedimentation, and geochemistry of the LCR was reported by Morgan (1995).

The LCR, unlike the upper Colorado River, does not drain a large mountainous region and does not produce large snowmelt runoffs. The greatest annual flows generally originate from snowmelt in March and April, although high flows also occur from late summer to winter (Fig. 3-8) as a result of local high-intensity rainstorms.

The LCR is often dry near Cameron (72 km upstream from the mouth), but a series of springs located 5-21 km (3-13 mi) upstream from the mouth provide a relatively constant baseflow of 200-300 cfs. The largest spring, Blue Springs, is located 21 km (13 mi) from the mouth and imparts the characteristic aqua-blue color to the LCR.

Flows of the LCR during the study period (WY 1991-93) were variable (Fig. 3-9). The volume of water discharged by the LCR in WY 1991 was below normal as a result of low snowpack. Only three major flood events occurred with peaks of about 2,200 cfs in early January and March and about 2,700 cfs in mid-April. Above normal runoff occurred in WY 1992 and WY 1993. In WY 1992, an extended spring runoff occurred from February through April, and unlike WY 1991, several spike flows of about 2,200-2,500 cfs occurred throughout summer. The high rainfall-induced flow in June 1992 was unusual, since high intensity rainstorms on the Colorado Plateau usually occur in late summer (late July to mid-September). Water year 1993 was marked by an unusually high winter flood that peaked at about 17,000 cfs on January 13, 1993, and a second flood of about 14,000 cfs occurred in late January 1993. The first flood disabled the stream gage near the mouth (gage #9402300) and discontinued streamflow records for the lower LCR.



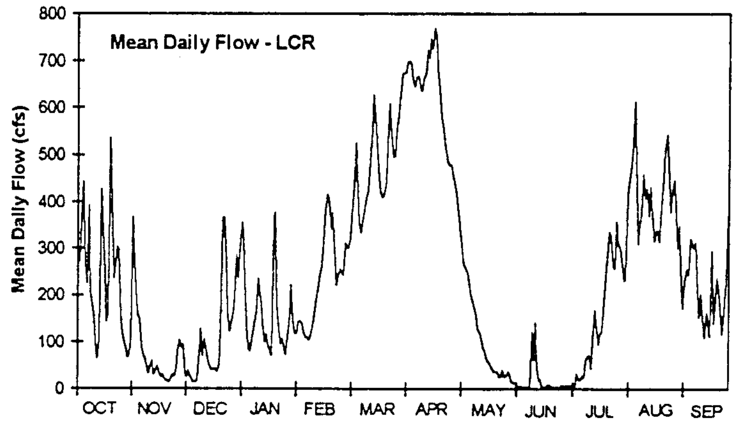


Fig. 3-8. Annual discharge and mean daily flow for WY 1948-91 of the Little Colorado River at Cameron, AZ.

Other Tributaries

Paria River

The Paria River enters the Colorado River about 1.6 km (1 mi) downstream from Lees Ferry (Fig. 3-1). It originates in the Escalante Mountains and the Paria Plateau of southern Utah and flows south for 88 km (55 mi), draining an area of approximately 3,650 km² (1,409 mi²). The lower 2 km of the channel has a low gradient of about 1.2 m/km. Unlike the Colorado River and LCR, the Paria River originates at a relatively low elevation of less than 2,000 m (6,560 ft), and springtime snowmelt runoff is not a large contributor to streamflow. The largest flows typically occur in late summer and fall following high-intensity rainstorms. This irregular and unpredictable streamflow pattern, caused by heavy rainfall on relatively barren and unvegetated ground, produces large sediment loads that enter the Colorado River about 27 km downstream of the dam (See Chapter 4 - WATER QUALITY).

Mean annual discharge of the Paria River is about 21,000 af with average streamflow of 29 cfs that varies widely (Fig. 3-10). Minimum annual flows typically occur from mid-May to mid-July when flow is often less than 10 cfs. Beginning about mid-July, summer storm activity often produces flash floods with discharges greater than 1,000 cfs. However, without such runoff, low flows are common. The probability of storm-generated runoff typically decreases in November.

Bright Angel Creek

Bright Angel Creek originates near Greenland Lake in the southern part of the Kaibab Plateau in northern Arizona. Bright Angel Creek flows south for about 20 km (12.5 mi) and enters the Colorado River at RM 87.6, near Phantom Ranch. The watershed of Bright Angel Creek is small with an area of about 260 km^2 (100 mi^2). The stream drains a karstic groundwater system with numerous springs providing a relatively constant baseflow of about 20 cfs. For the period of record, discharge typically increased with local snowmelt between April and early June, when flows often reached several hundred cubic feet per second (Fig. 3-10). However, in drought years flows never exceeded 50 cfs.

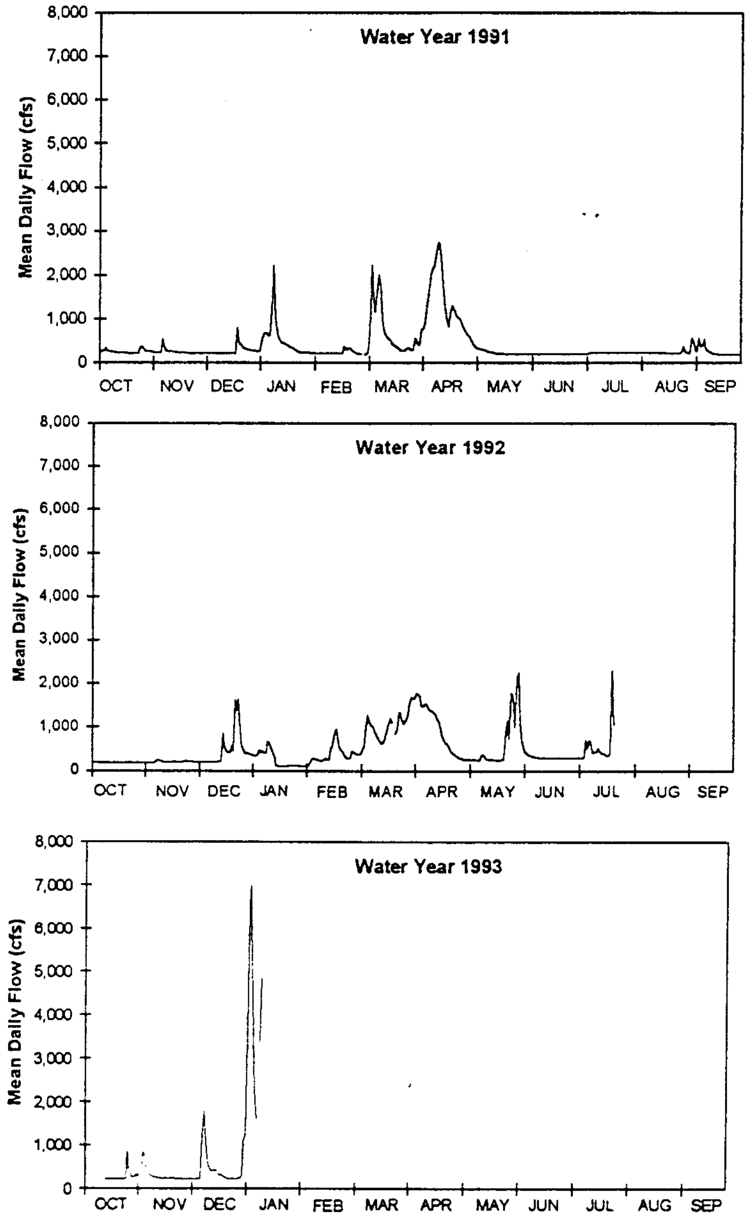


Fig. 3-9. Mean daily flow of the Little Colorado River for WY 1991, 1992, and 1993 near the mouth. Discontinuous line indicates missing data.

Shinumo Creek

Shinumo Creek originates at South Big Springs within the Shinumo Amphitheater and drains about 220 km^2 (85 mi^2) of the southern Kaibab Plateau in northern Arizona, similar to terrain drained by Bright Angel Creek. The stream flows south for about 20 km (12.5 mi) and enters the Colorado River at RM 108.5. Stream gradient is high, with an average elevational change of about 4.6 m/km in the last 2 km. Numerous springs support a year-round base flow, and the annual streamflow regime is probably similar to that of Bright Angel Creek. A USGS stream gage has never been installed in Shinumo Creek, and discharge information is based on measurements made by different investigators. Johnson and Sanderson (1968) found that flow at the mouth of Shinumo Creek ranged from 3.5 to 16 cfs. Maddux et al. (1987) reported a range of 10.5 to 108.0 cfs during a study from April 1, 1984 to May 30, 1986.

Tapeats Creek

Tapeats Creek originates in the Tapeats Amphitheater and drains about 100 km^2 (40 mi^2) of the southern Kaibab Plateau in northern Arizona. Tapeats Creek is formed by a number of springs, the largest of which is Tapeats Spring. It flows south for about 10 km (6 mi) to enter the Colorado River at RM 133.7. Springs originating from Monument and Crazy Jug points as well as Thunder Springs (feeds Thunder River and enters Tapeats Creek about 3 km (2 mi) above the Colorado River) also provide water to Tapeats Creek. Although a USGS stream gage has not been installed in Tapeats Creek, it is estimated that this stream has the highest discharge of any tributary originating from the north rim of Grand Canyon (Huntoon 1981). Maddux et al. (1987) reported a flow range of 78.4 to 281.9 cfs from April 1, 1984 to May 30, 1986. Stream gradient in the last 2 km is among the steepest of tributaries in Grand Canyon with an average change of about 4.9 m/km. Seasonal flow pattern of Tapeats Creek is probably similar to that of Bright Angel Creek (Fig. 3-10).

Kanab Creek

Kanab Creek originates in the Pausagunt Plateau of southern Utah and flows south for over 100 km (62 mi) to enter the Colorado River at RM 143.5. Stream gradient in the lower 2 km of Kanab Creek is low with an average change of about 1.2 m/km. The stream drains a watershed area of approximately 5,700 km² (2,200 mi²) and like the Paria River and LCR, has an irregular and unpredictable flow characterized by high short-term floods following severe rainstorms in late summer. Mean daily flow for WY 1963-1980, recorded at the USGS gage near Fredonia, Arizona (about 50 km, 31 mi, upstream from the mouth), varied dramatically from over 60 cfs in December to periods of no flow in June and July (Fig. 3-10). Maddux et al. (1987) reported a flow range of 2.8 to 38.0 cfs between April 1, 1984 and May 30, 1986. A description of historic changes in flow and the channel of Kanab Creek (Webb et al. 1991) shows that erosion in this tributary was attributed to arroyo initiation caused by large floods in the period 1882-1886, and poor land-use practices (e.g., overgrazing).

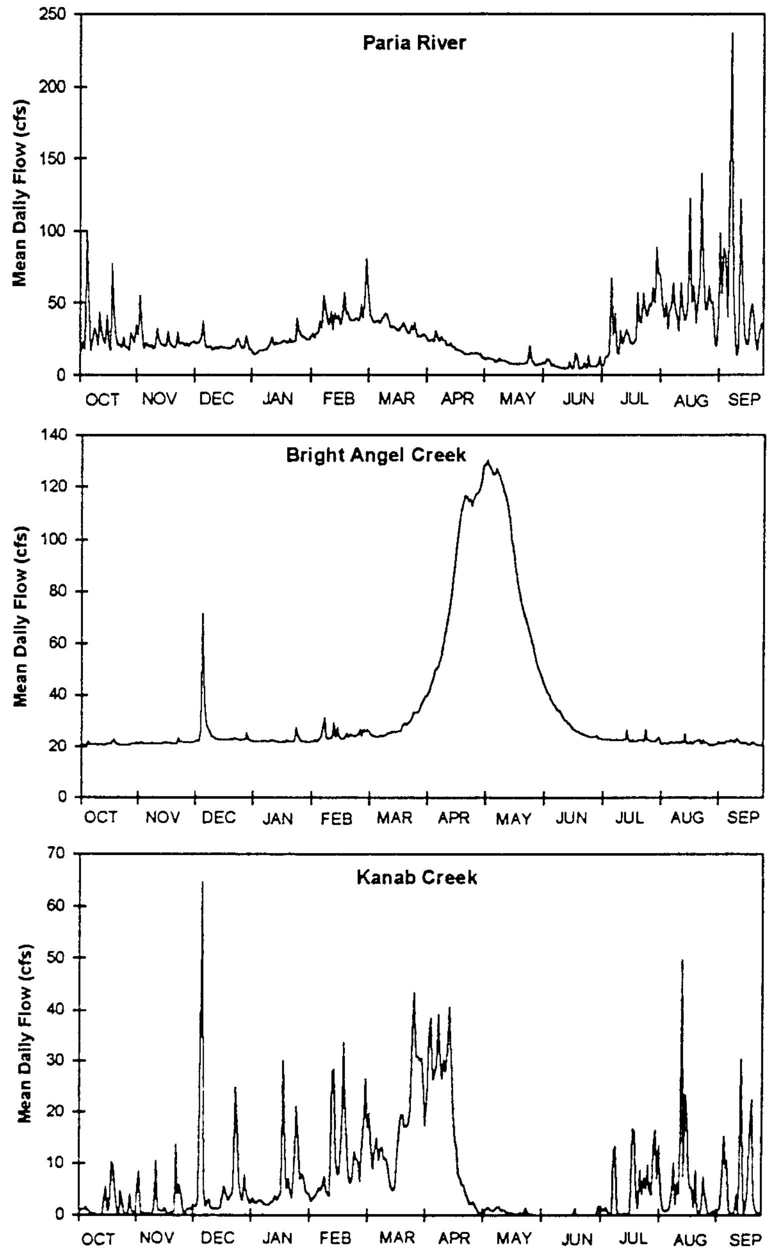


Fig. 3-10. Mean daily flow of the Paria River near Lees Ferry, AZ (WY 1923-93), Bright Angel Creek near Phantom Ranch, AZ (WY 1923-74), and Kanab Creek near Fredonia, AZ (WY 1963-80).

Havasu Creek

Havasu Creek is the major tributary draining Arizona's Coconino Plateau south of the Colorado River. A constant baseflow of about 70 cfs is provided by Havasu Springs, which is located about 16 km (10 mi) above the confluence with the Colorado River (Johnson and Sanderson 1968). Havasu Creek enters the Colorado River at RM 156.7 and is the only major perennial tributary for 111 km (69 mi) to Diamond Creek (RM 225.7). Maddux et al. (1987) reported a flow range of 60.6 to 207.4 cfs between April 1, 1984 and May 30, 1986. Large floods of about 20,000 cfs in January 1990 and 1991 scoured much of the riparian vegetation and travertine from the channel. Seasonal flow regime for Havasu Creek is similar to that of the other tributaries in Grand Canyon. High snowmelt flows occur in spring, and low summer, fall, and winter baseflows are marked by high short-term rainstorm floods. Gradient over the last 2 km of stream is moderate with an average elevational change of about 2.5 m/km.

DISCUSSION

Predam hydrology of the Colorado River in Grand Canyon shows the high annual and seasonal variability in flow characteristic of this southwestern river before impoundment. Highest annual flow volume (18 maf) from WY 1922 to WY 1962 was four times higher than lowest volume (4.4 maf), and highest mean daily flow in June (75,000 cfs) was more than one order of magnitude (10 times) greater than lowest mean daily flow in January (5,000 cfs). The most dramatic illustration of flow variability was the difference of nearly three orders of magnitude between record lowest flow (750 cfs) and estimated highest flow (500,000 cfs). Daily variation in summer, fall, and winter was low, except for periodic short-duration rainstorm floods in late summer that dramatically increased river volume.

Since completion of Glen Canyon Dam in 1963, annual and seasonal flow variation of the Colorado River in Grand Canyon has been greatly reduced, while daily variation has increased. Except for high flood flows during WY 1983-87, highest annual flow volume (11 maf) from WY 1965 through WY 1990 was only 38% higher than lowest volume (8 maf), and highest mean daily flow (20,000 cfs) was only four times greater than lowest mean daily flow (5,000 cfs). The difference between record lowest (1,000 cfs) and highest (31,500 cfs) flow was greatly reduced from predam conditions.

Release patterns during this investigation (October 1990 through November 1993) were unlike those of any comparable period of time and unlike those witnessed by previous investigators on the Colorado River in Grand Canyon (Fig. 3-11). Ichthyofaunal investigations in Grand Canyon since 1958 have experienced a variety of flows. Prior to construction of Glen Canyon Dam in 1963, monthly maximum flows exceeded 120,000 cfs with minimum flows of less than 5,000 cfs. After 1965, flows were irregular between 3,000 and 31,500 cfs, except for the period 1983-86 when monthly maxima peaked over 90,000 cfs (Fig. 3-11).

Flows during this investigation lacked the high spring floods of predam years (WY 1949-62), some exceeding 120,000 cfs, as well as the characteristic high daily fluctuating releases and periodic low flows of postdam years (WY 1964-93). The most dramatic contrast, for this investigation was with the period WY 1983-86, during the time of the last major mainstem investigation by AGF (Maddux et al. 1987). Researchers during that period witnessed three monthly maximums of over 40,000 cfs and many monthly minimums of over 20,000 cfs based on mean daily flows.

Flow of the Colorado River during the first 10 months of this study (i.e., research flows, October 1990-July 1991) was characterized by intervening periods of high fluctuating flows and constant releases. The last 28 months of the study (i.e., interim flows August 1991-November 1993) were marked by higher minimum flows, lower maximum flows, and less range in daily fluctuations. Maximum and minimum flow magnitude, flow volume, and ramping rate were important parameters used to evaluate the effects of Glen Canyon Dam operations on humpback chub.

Although high fluctuating releases (i.e., research flows) of 1,000 or 3,000 cfs to 31,500 cfs with unlimited ramping rates were similar to previous maximum peaking power operations (e.g., WY 1987-89), the intervening monthly constant flows of 5,000, 8,000, 11,000, and 15,000 cfs during research flows (June 1990-July 1991) were uncharacteristic of previous operations. Also, some elements of interim flows were atypical of previous operations (i.e., minimum of 5,000 or 8,000 cfs, maximum of 20,000 cfs and maximum daily variation of 5,000, 6,000, or 8,000 cfs) with limited ramping rates.

Stage-discharge relationships for the Colorado River above the LCR inflow illustrated the differences in flow magnitude and flow change rate observed in principal humpback chub habitat. Maximum change in river stage was 1.45 m during research flow releases of 3,000 to 31,500 cfs and 0.83 m during interim flow releases of 8,000 to 20,000 cfs. Average ramping rate at the gage above the LCR during research flows was 886 cfs/hr (SD=1,230) and 378 cfs/hr (SD=379) during interim flows, while magnitude of daily flow change decreased from an average of 5,643 cfs (SD=5,144) during research flows to an average of 4,014 cfs (SD=1,991) during interim flows.

Flow of seven principal tributaries in Grand Canyon (LCR, Paria, Bright Angel, Shinumo, Tapeats,

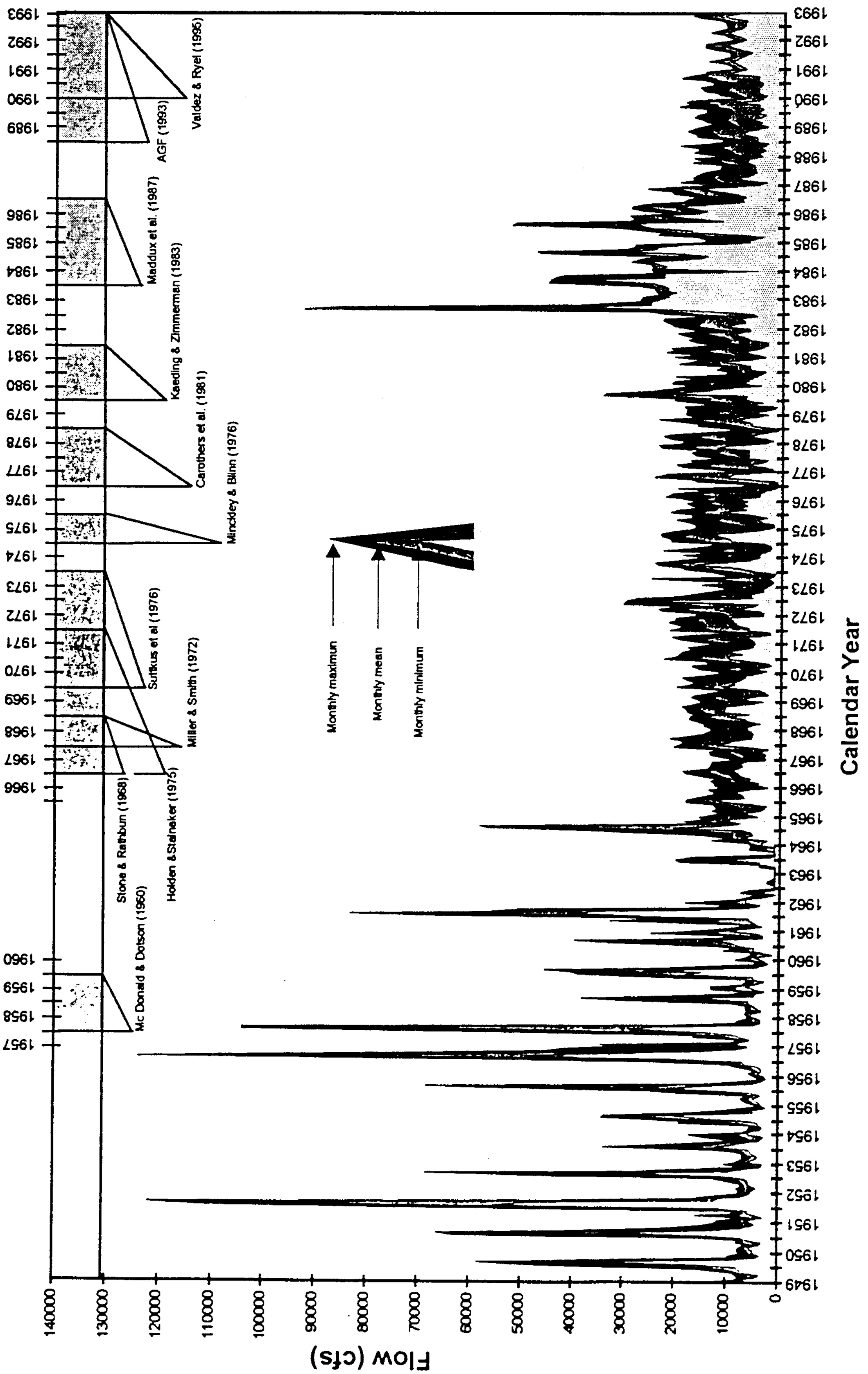
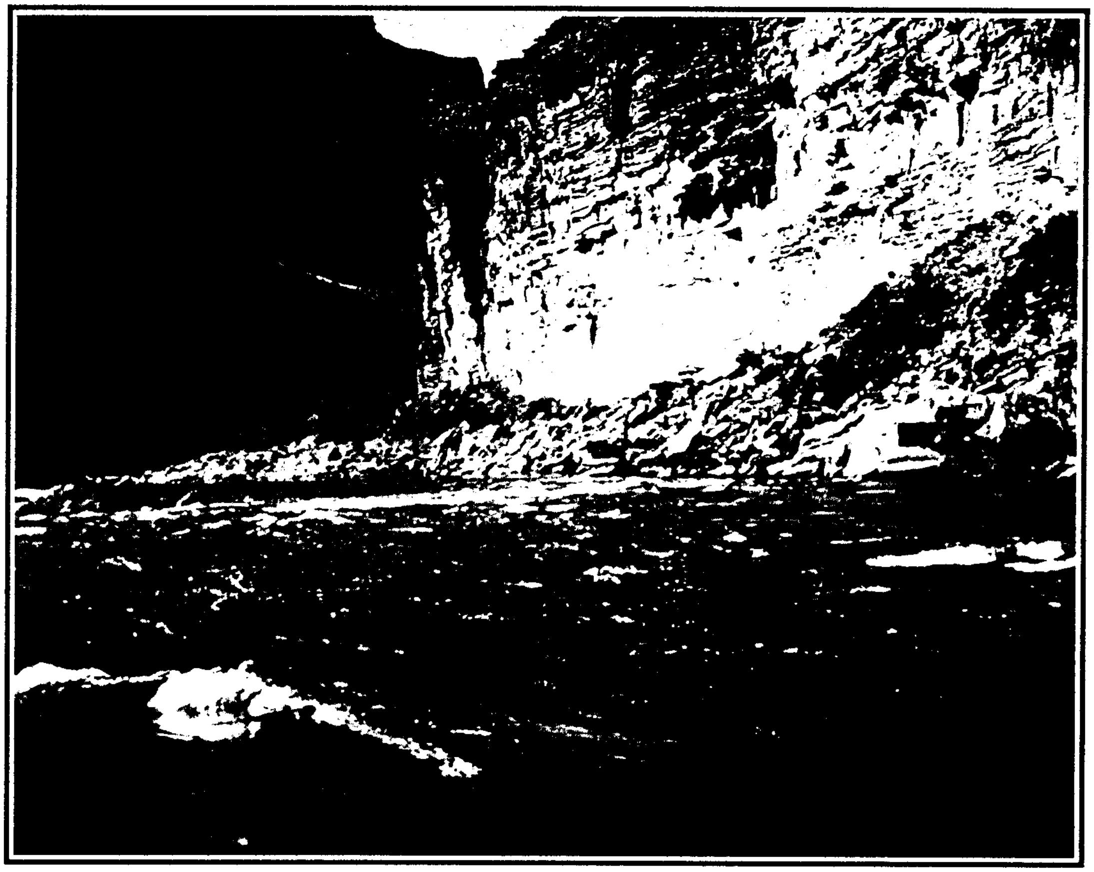


Fig. 3-11. Flow patterns during previous investigations.

Kanab, Havasu creeks) was characteristically variable with high spring runoff, low summer flows, and erratic late summer and winter floods. Large floods of about 20,000 cfs in Havasu Creek in January 1990 and 1991 and about 17,000 cfs in the LCR in January 1993 were dramatic and notable to this investigation. The Havasu Creek flood scoured much of the in-channel travertine and most of the streamside riparian vegetation, transporting large volumes of woody debris, sand, and silt to form an extensive alluvial fan into the Colorado River. This flood occurred early in this investigation and its effects on fish and fish habitat were largely undocumented. The LCR flood also scoured much of the in-channel travertine (Gorman et al. 1993) and transported large volumes of sand and silt into the Colorado River. This flood occurred immediately before a scheduled B/W trip and was the important aspect of several analyses in this report including dispersal of fish (See Chapter 5 - DISTRIBUTION AND ABUNDANCE) and reformation of channel morphology (See Chapter 7 - HABITAT). Sand beaches, formed primarily from reattachment bars in large recirculating eddies, received substantial deposits of sand downstream of the LCR.

Water Quality

Chapter 4



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CHAPTER 4 - WATER QUALITY

INTRODUCTION

Water quality of the Colorado River in Grand Canyon was substantially altered by the construction of Glen Canyon Dam. The major changes were to water temperature, sediment load, and distribution of particulate organic matter. Before Glen Canyon Dam, water temperature ranged widely from winter lows near freezing to highs of nearly 30°C in late summer (Table 4-1). After the dam, hypolimnetic releases from Lake Powell have ranged from about 7 to 11°C. Average predam sediment load through Grand Canyon was about 140 million tons per year (range 50 - 500 million tons). Average postdam sediment load has been about 15 million tons per year (Cole and Kubly 1976, National Research Council 1987). Sediments that were once carried by the Colorado River are now deposited in Lake Powell, and in 1986 these deposits ranged in thickness from 11 m (36 ft) near the base of the dam to 55.5 m (182 ft) near the mouth of Dark Canyon about 290 km (180 mi) upstream of the dam (Ferrari 1988). In addition to sediment deposition, the chemical dynamics of Lake Powell have also altered other water quality parameters including inorganic and organic elements (Stanford and Ward 1991)

Water quality parameters presented in this report include temperature, turbidity, specific conductance, dissolved oxygen (DO), and hydrogen ion concentration (pH). These parameters were used together with physical and biological components to characterize the riverine ecosystem in Grand Canyon, and to help evaluate responses by humpback chub to dam operations. Lowered water temperature and decreased turbidity have contributed substantially to a new set of environmental conditions. Relatively constant postdam temperatures have remained below optimum for warmwater fish species (Bulkley et al. 1981, Hamman 1982, Marsh 1985) and disrupted life cycles of many species of diatoms, algae, (Hardwick et al. 1992) and macroinvertebrates that were part of the predam ecosystem (Carothers and Brown 1991, Blinn et al. 1994). Reduced sediment has resulted in reduced organic levels, less suspended food, and increased water clarity which may reduce cover for escape from predators.

METHODS

Water quality data were collected with portable Hydrolab water quality instruments (Hydrolab Corp, Austin, TX), from USGS stream gaging stations, and with Ryan Tempmentors (Ryan Instruments, Redmond, WA). The following Hydrolab water quality instruments were used in this study:

Table 4-1. Summary of predam and postdam sediment transport and thermal characteristics of the Colorado River below Glen Canyon Dam.

Measurement	Lees Ferry		Grand Canyon	
	Predam	Postdam	Predam	Postdam
		Temperature(°C)[a]		
Range in mean daily	0 - 29.5	7.5 - 10	2 - 25	6 - 13
Mean annual	10	10	11	12
		Total Sediment (tons/year)[b]		
Mean annual load (years of record)	76.3×10^6 (1948-58)	8.6×10^6	138.7×10^6	14.6×10^6
		Suspended Sediment (mg/l)[c]		
Range in mean daily (years of record)	-	-	1,000-19,000 mg/l (1947-57)	500-7,000 mg/l (1967-71)

Sources: [a]Cole and Kubly 1976; USGS Water Supply Papers
[b]Schmidt and Graf 1990 - Lees Ferry
[b]Carothers and Brown 1991 - Grand Canyon
[c]USGS data from Earth Info on CD-Rom

- Surveyor 2: With Field Data Logger (Model 5100A),
- Surveyor 2: Display Unit (Model: SVR2-SU),
- Surveyor 3: 1100 Surveyor Data Logger (Model SVR3-DL), and
- DataSonde 2: (Model 2270 H).

Water quality parameters included temperature, specific conductance, DO, and pH. Water temperature was recorded in degrees Celsius (°C), and specific conductance was measured in micro siemens per centimeter (µS/cm), adjusted to 25°C. Dissolved oxygen was expressed as milligrams per liter (mg/L), and hydrogen ion concentration was recorded in pH units (0-14). Turbidity (as light transmisivity) was recorded in nephelometric turbidity units (NTUs) with a Hach Model 2100P turbidimeter, and depth of water transparency was measured with a standard 20-cm diameter Secchi disk.

Hydrolab instruments were calibrated before each field trip. Water quality data were downloaded from dataloggers using a laptop computer and Procomm Plus Version 1.1B communications program (Datastrom Technologies, Inc., Columbia, MO). Water quality parameters were recorded at camp locations, sample sites, tributary inflows, and special habitats (i.e., springs, shorelines, fish capture locations). Turbidity was measured daily at camp or under periods of observed change in water clarity. A summary of water quality instruments used by river mile and month for 1991, 1992, and 1993 is presented in Appendix Table D-1.

Data from USGS gages at six mainstem locations and six tributaries were used to provide historic and present overviews of water quality (Table 4-2, Fig. 3-1). Predam water quality and sediment data were obtained from two mainstem gages (Colorado River at Lees Ferry and Colorado River near Grand Canyon) and three tributary gages (Paria River at Lees Ferry, LCR near Cameron, and Bright Angel near Grand Canyon). Postdam data were collected from gages on the Colorado River below Glen Canyon Dam, above the LCR, at National Canyon, and at Diamond Creek; these gages were installed in 1983 as part of GCES Phase I to evaluate sediment transport and provide data for a flow routing model. Postdam data were also obtained from gages (minimonitors) installed in 1989 on the lower LCR, Bright Angel Creek, Kanab Creek, and Havasu Creek. Minimonitors recorded water temperature, DO, and conductivity and included pressure transducers for use with flow-rating curves to estimate stream discharge.

Table 4-2. Stream gages used for water quality analysis.

USGS Station Number	Station Name	Location[a]	Period of Record (water years)
9379910	Colorado River below Glen Canyon Dam, AZ	RM -15.5	Oct 1989-Sep 1990
9380000	Colorado River at Lees Ferry, AZ	RM 0.2	1895-present
9383100	Colorado River above LCR, AZ	RM 61.2	Apr 1983-present[b]
9402500	Colorado River near Grand Canyon, AZ (i.e., Phantom Ranch)	RM 87.4	1925-1988
9404120	Colorado River at National Canyon, AZ	RM 166.5	Apr 1983-present
9404200	Colorado River above Diamond Creek, AZ	RM 226.0	Apr 1983-present
9382000	Paria River at Lees Ferry, AZ	1.1 mi ups	1923-present
9402000	Little Colorado River near Cameron, AZ	45 mi ups	1947-present
9402300	Little Colorado River near mouth, AZ	0.5 mi ups	1989-Jan 1993[bc]
9403000	Bright Angel Creek near Grand Canyon, AZ	0.5 mi ups	1923-1974
9403850	Kanab Creek near mouth, AZ	1.0 mi ups	1989-present
9404115	Havasu Creek near mouth, AZ	0.3 mi ups	1990-present

[a]RM = river miles downstream from Lees Ferry.
ups = distance upstream from Colorado River confluence.
[b]data inconsistent.
[c]discharge based on stage elevations, periodically adjusted to stream channel measurements.

Ryan Tempmentors were installed by GCES in several tributaries and mainstem locations to supplement USGS gaging data and to provide data for a temperature model for the Colorado River in Grand Canyon. Tempmentors were located in lower Nankoweap Creek, LCR, Shinumo Creek, Kanab Creek, Tapeats Creek, and Havasu Creek, as well as select locations on the mainstem, such as RM 127.0 (Middle Granite Gorge).

Methods for gathering water quality parameters varied with location and condition. Water quality parameters in the mainstem were measured with a Hydrolab DataSonde deployed from the stern of an 11.3-m (37-ft) raft at each temporary campsite. Parameters were recorded electronically at 1-hr intervals, and manual readings were recorded three times daily from a Hydrolab Surveyor to supplement and validate the electronic data. Water temperature associated with fish and drift sampling was recorded with hand-held thermometers calibrated with a Surveyor 2 at the beginning of each trip. Water quality in the LCR was also recorded electronically at 15-min intervals with a Hydrolab DataSonde. Datasondes were deployed only when teams were in the vicinity for about 10 days/month and discontinued between field trips. Temperature data were supplemented with data collected with Ryan Tempmentors, CR10 dataloggers (Campbell Scientific, Inc., Logan, UT), and USGS ADAPs (Data Collection Platforms).

WATER QUALITY CHARACTERISTICS

Colorado River

Water Temperature

Predam. Mean monthly temperature of the Colorado River at Lees Ferry and near Grand Canyon (i.e., Phantom Ranch) before Glen Canyon Dam (1959 used as a representative year) ranged from about 2°C in winter to 26°C in late summer (Fig. 4-1). Mean daily temperature at Lees Ferry ranged from 0 to 29.5°C and from 2 to 25°C near Grand Canyon, suggesting some longitudinal cooling in summer as the river flowed through the deep shaded canyon (Table 4-1). Although the river usually began to warm in February, peak snowmelt from late May through early July maintained relatively cool water temperature through spring and early summer. As flow decreased in mid-summer, mean monthly water temperature reached 23-26°C in July and August and began cooling in September.

Postdam. Following construction of Glen Canyon Dam, the Colorado River in Grand Canyon was transformed into a cold clear river. The transformation was not abrupt and spanned from the start of impoundment on March 13, 1963 through about 1972. The difference between maximum (12.6°C) and minimum (7.9°C)mean monthly

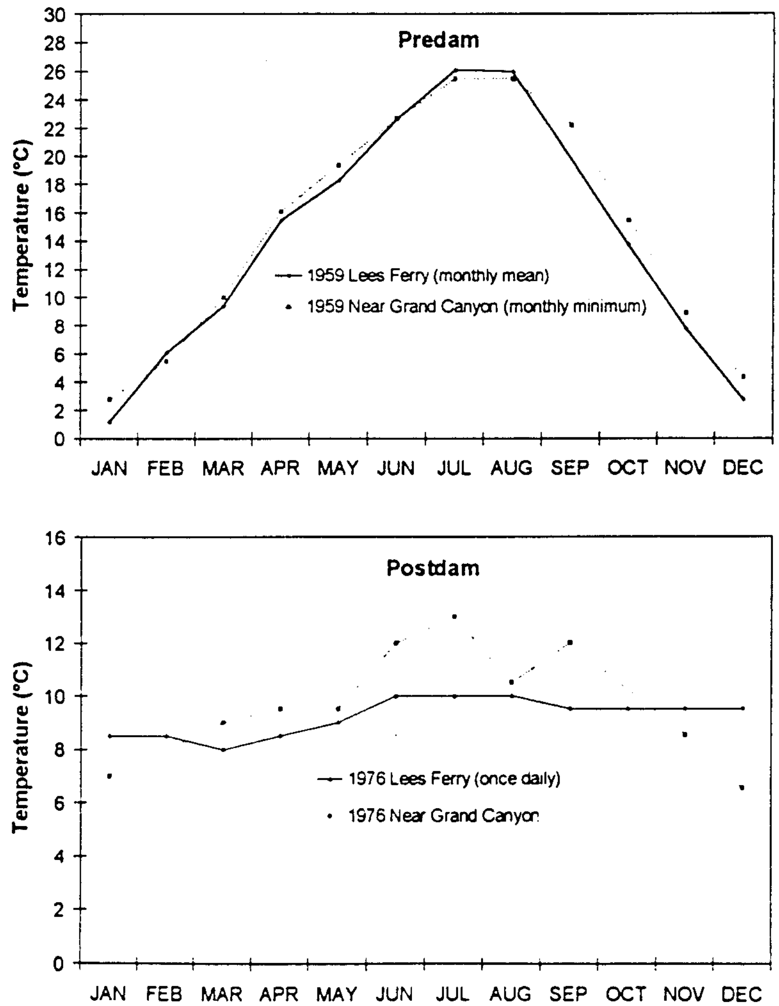


Fig. 4-1. Predam (1959) and postdam (1976) mean monthly temperatures of the Colorado River at Lees Ferry, AZ and near Grand Canyon, AZ (i.e., Phantom Ranch). USGS Water Resources Data.

water temperature at Lees Ferry was 4.7°C compared to a predam difference of about 25°C (Fig. 4-2, Appendix Table D-1). The last year in which mean monthly water temperature reached 16°C was 1970 (August-October). The same seasonal pattern of coldest water temperatures during December-January and warmest temperatures during June-August occurred after the dam was built, but the difference between winter lows and summer highs was only a few degrees Celsius. Mean monthly postdam water temperature at Lees Ferry (1976 used as a representative year) ranged from 8.0 to 10°C (Fig. 4-1), while temperature near Grand Canyon (i.e., Phantom Ranch) ranged from 6.5 to 13°C, suggesting longitudinal cooling in winter and warming in summer.

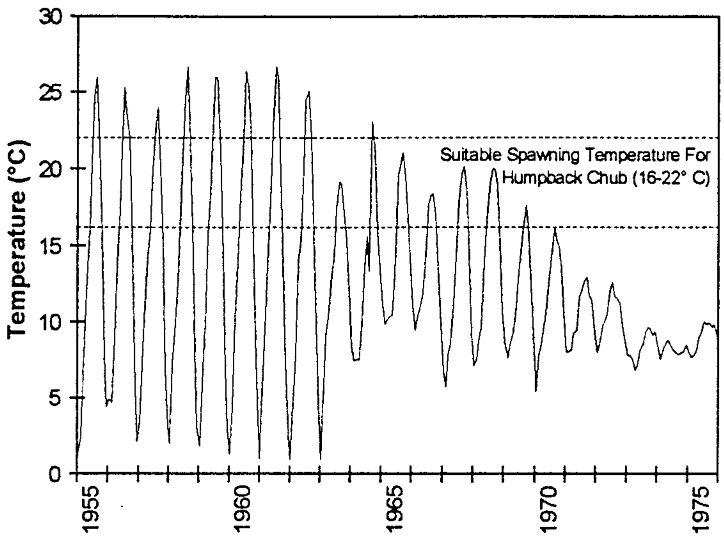


Fig. 4-2. Mean monthly water temperature at Lees Ferry following closure of Glen Canyon Dam and impoundment of Lake Powell on March 13, 1963. Monthly means are based on measurements at 15-min intervals. Suitable spawning temperature range for humpback chub is shown as 16-22°C.

Natural seasonal warming of the Colorado River downstream of Glen Canyon Dam is an important aspect of the aquatic ecosystem that can affect trophic levels spatially and temporally. Averages of mean daily temperatures for the middle months of each of the four seasons for WY 1992 (i.e., spring= April, summer = July, fall = October, winter = January) showed the greatest longitudinal increase during July (Fig. 4-3) of 8°C at the dam to 15.5°C at Diamond Creek or about 7.5°C for 386 km (240 mi), or a rate of 1°C/51 km (1°C/32 mi). Comparable warming during selected months was 1°C/60 km in spring, 1°C/97 km in fall, and no longitudinal warming or cooling was observed in winter. Similar longitudinal warming was seen when mean daily temperatures were averaged for the entire season for WY 1991, 1992, and 1993 revealing differences between water years, e.g., spring temperatures in WY 1992 were higher than in WY 1991 or WY 1993.

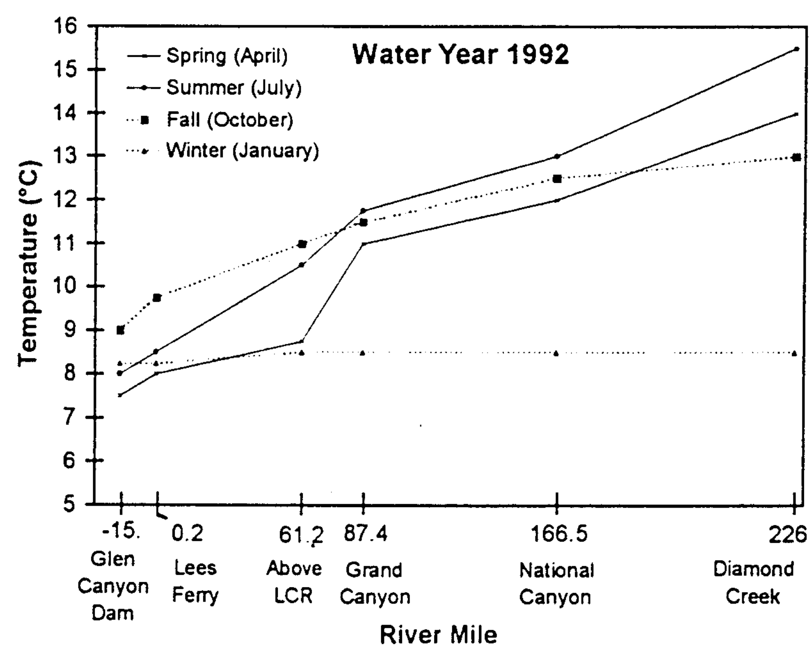


Fig. 4-3. Seasonal longitudinal warming of the Colorado River under interim flows from Glen Canyon Dam to Diamond Creek, as mean daily temperatures at six stations for WY 1992. The USGS gage below Glen Canyon Dam is 15.5 miles upstream of Lees Ferry.

Mean daily water temperatures for the mainstem Colorado River during research flows in 1991 were compared for constant flows of 5,000 cfs (May 16-20, May 31-June 3), 15,000 cfs (May 21-30), and normal summer fluctuating flows (June 4-27) to evaluate the effect

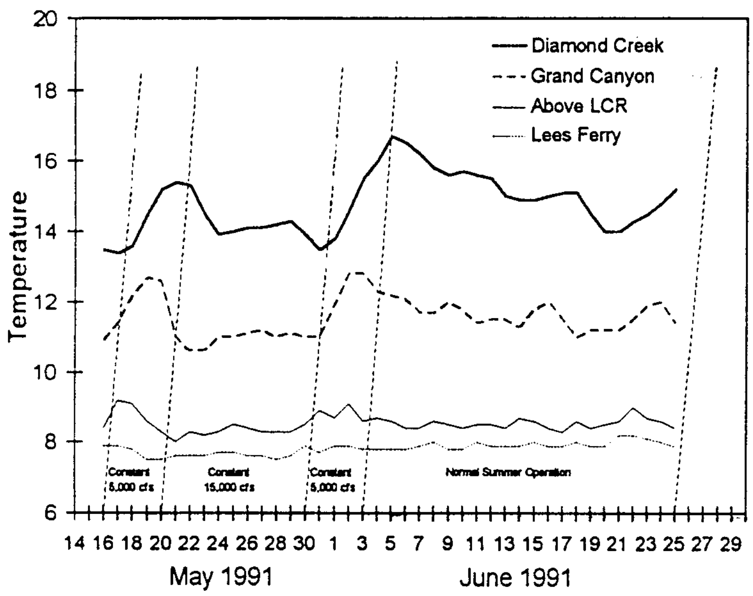


Fig. 4-4. Mean daily temperature of the Colorado river at four USGS stations (Lees Ferry, Above LCR, Grand Canyon, Diamond Creek) during 1991 research flows of constant 5,000 cfs (May 16-20, May 31-June 3), constant 15,000 cfs (May 21-30), and normal summer fluctuating flows (June 4-27). Diagonal dashed lines represent approximate travel time for flow to reach each of the four designated stations. USGS ADAPS data.

of flow volume on temperature (Fig. 4-4). Although time span for this analysis was short and precluded distinction of diurnal and seasonal influences, specific patterns are indicated. Assuming a travel time of about 15 hr for a mass of water from the dam to the LCR, about 19 hr to gage at Grand Canyon, AZ (Dawdy 1991), and about 60 hr to Diamond Creek, a relationship of water mass and temperature was evident longitudinally. While little temperature change was seen during the constant 5,000 cfs releases at Lees Ferry and above the LCR, an increase of about 1.5°C occurred near Grand Canyon, (i.e., Phantom Ranch) and about 3°C occurred at Diamond Creek (the combined influence of longitudinal warming and constant 5,000 cfs). Cooler and more isothermal conditions occurred during the constant 15,000 cfs releases. These gage data were confirmed through field measurements near Diamond Creek, which also showed an increase of up to 3°C during the 3-day constant 5,000 cfs release and a decrease of up to 3°C with return to normal operation or fluctuating releases. These observations suggest a need to better understand the relationship between water volume and temperature, particularly when considering high spring releases or constant low summer releases.

While mean monthly temperature patterns provided an understanding of ambient seasonal conditions, mean daily temperatures revealed variation within and between months at various distances downstream of Glen Canyon Dam. Annual water temperature pattern using mean daily values from six mainstem USGS gages (Glen Canyon Dam, Lees Ferry, above LCR, near Grand Canyon, National Canyon, and Diamond Creek) for WY 1991(Fig. 4-5), WY 1992 (Fig. 4-6), and WY 1993 (Fig. 4-7) revealed the phenomena of seasonal longitudinal warming and cooling with increasingly greater downstream daily and monthly variation. In WY 1991, dam releases ranged from about 7.5 to 9.5°C, while water temperature at Diamond Creek (445 km [240 mi] from the dam) ranged from about 5.5 to 18°C. In WY 1992, dam releases ranged from about 7 to 11°C, and water temperature at Diamond Creek ranged from about 8.5 to 17°C; warmer dam releases were probably the result of lower levels in Lake Powell, and withdrawal of warmer near-surface water. Dam releases in WY 1993 also ranged from about 7 to 11°C and recorded temperature at Diamond Creek was 7.5°C to nearly 14°C, although the gage record was incomplete for the warmest part of the year.

Sediment

Suspended sediment is composed of disintegrated or eroded rocks (< 2 mm diameter) and is the primary cause of turbidity in the Colorado River. Suspended sediment in the Colorado River originates from two sources; mountainous headwater areas contribute about 31% of sediment load, and tributaries draining the Colorado Plateau contribute the remainder (Andrews 1991). Within Grand Canyon, the main sources of sediment are the Paria River and LCR (Johnson and Sanderson 1968, Randle and Pemberton 1987, Graf et al. 1991). Sediments carried by the Colorado River during spring runoff consist primarily of coarse sand from headwaters, while local summer floods and intermittent winter rains transport primarily silts and clays (Carothers and Brown 1991). Suspended sediment, as milligrams/liter, was the standard measure of sediment load prior to Glen Canyon Dam.

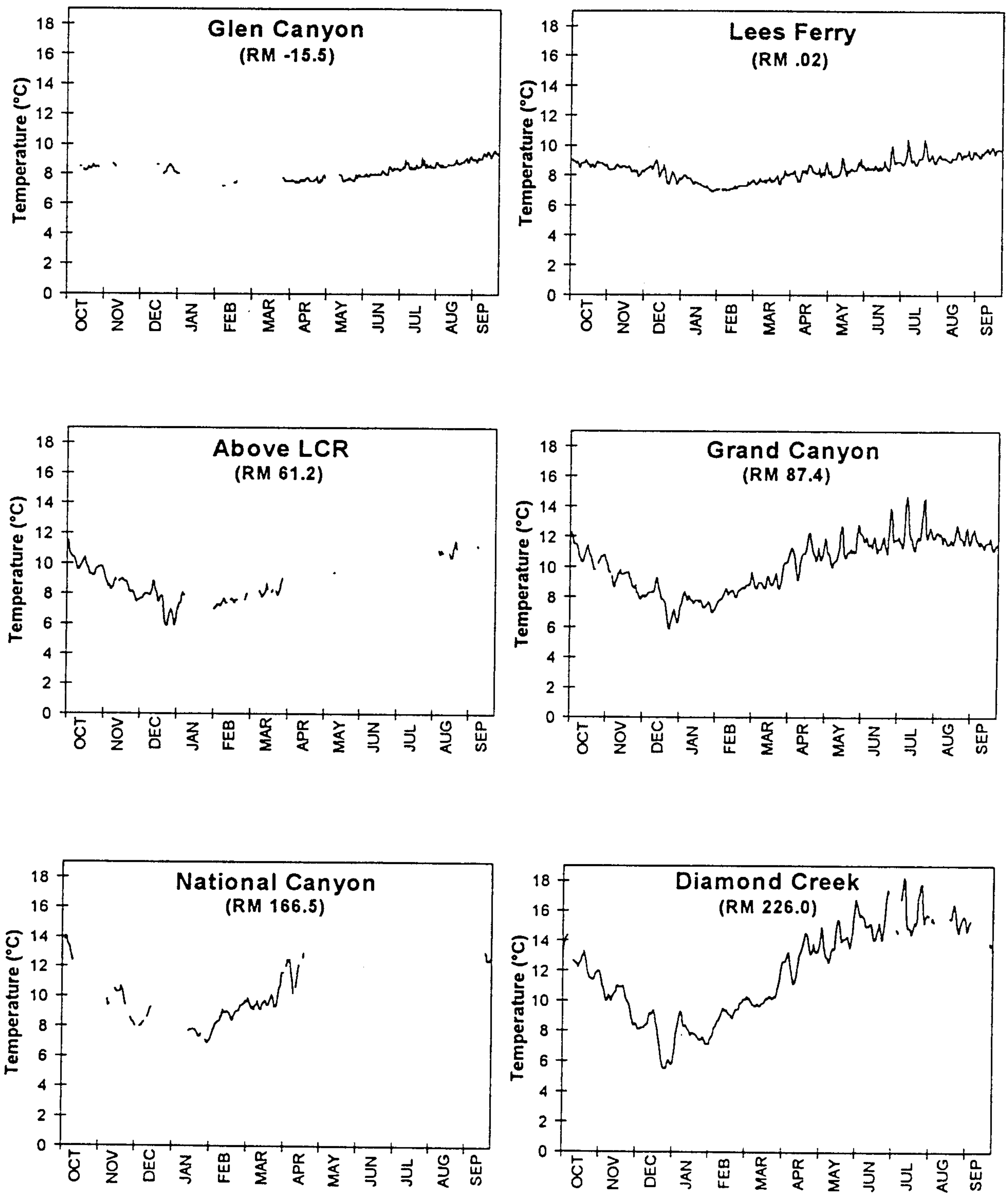


Fig. 4-5. Mean daily temperature of the Colorado River for WY 1991 at six stations (Glen Canyon Dam, Lees Ferry, Above LCR, Grand Canyon, National Canyon, Diamond Creek). Distance in kilometers downstream from Glen Canyon Dam is indicated in parentheses. Discontinuous line indicates missing data. USGS ADAPS data.

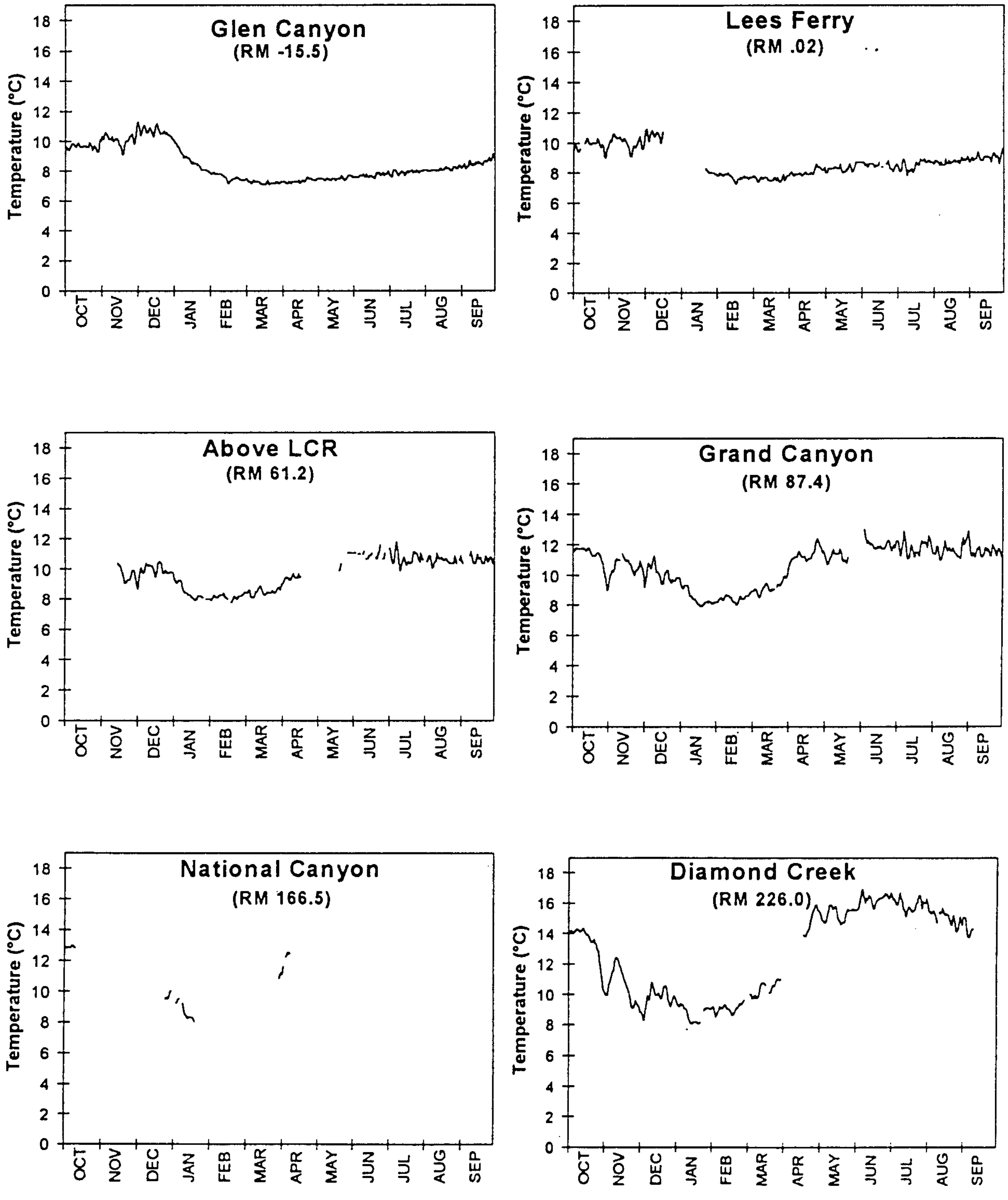


Fig. 4-6. Mean daily temperature of the Colorado River for WY 1992 at six stations (Glen Canyon Dam, Lees Ferry, Above LCR, Grand Canyon, National Canyon, Diamond Creek). Distance in kilometers downstream from Glen Canyon Dam is indicated in parentheses. Discontinuous line indicates missing data. USGS ADAPS data.

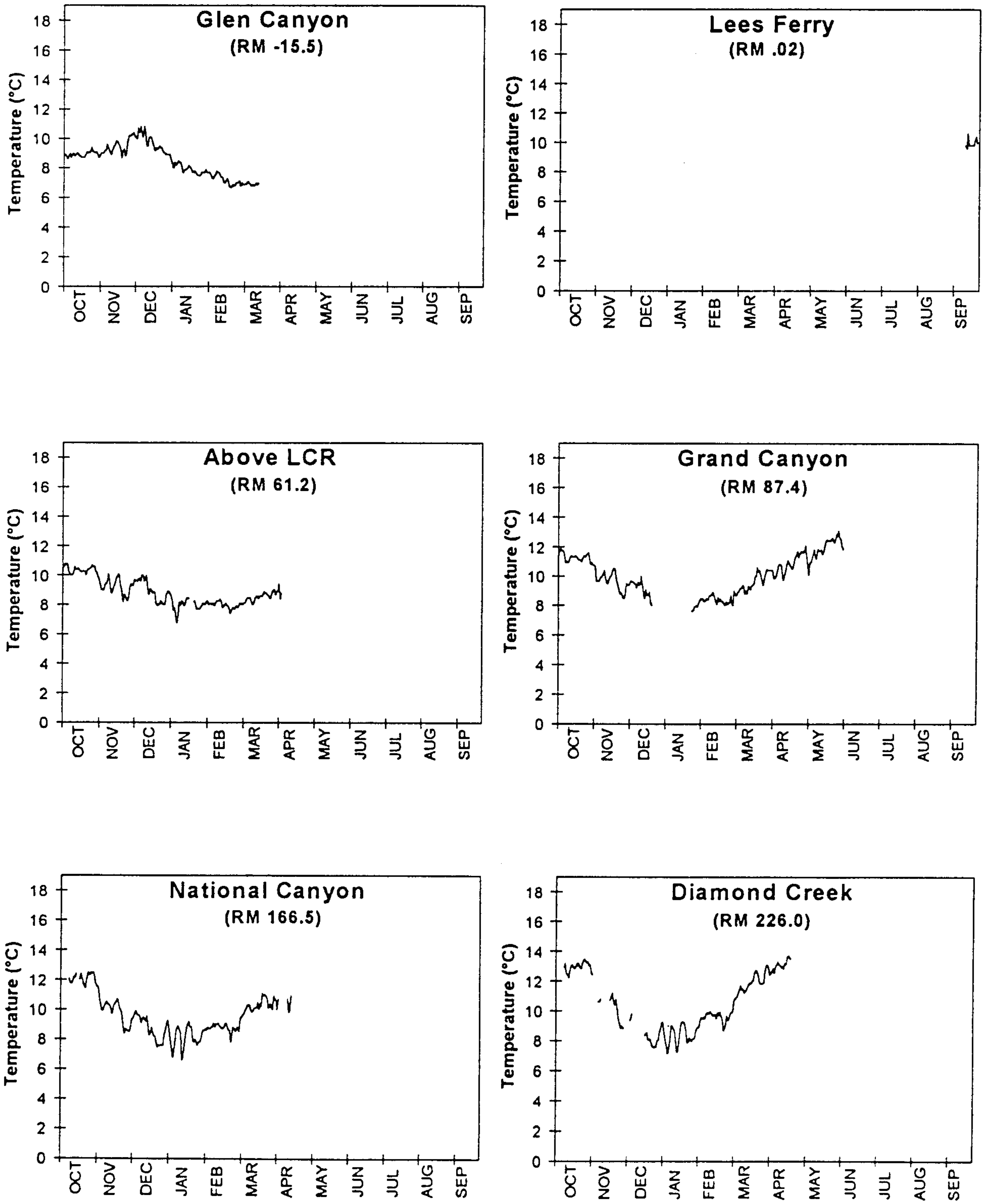


Fig. 4-7. Mean daily temperature of the Colorado River for WY 1993 at six stations (Glen Canyon Dam, Lees Ferry, Above LCR, Grand Canyon, National Canyon, Diamond Creek). Distance in kilometers downstream from Glen Canyon Dam is indicated in parentheses. Discontinuous line indicates missing data. USGS ADAPS data.

Turbidity, as a measure of transmiscivity, became a common system of measure after the dam was built.

Predam. The predam Colorado River was a sediment-rich system that experienced an annual cycle of erosion, transport, and deposition. Mean annual suspended sediment load at Lees Ferry was 76.3 million tons per year during a 10-year period (WY 1947-57) prior to dam construction (Laursen et al. 1976 in Schmidt and Graf 1990). The range in mean daily suspended sediment at the Grand Canyon gage (i.e., Phantom Ranch) varied from about 1,000 to 19,000 mg/L over the 10-year period (Fig. 4-8).

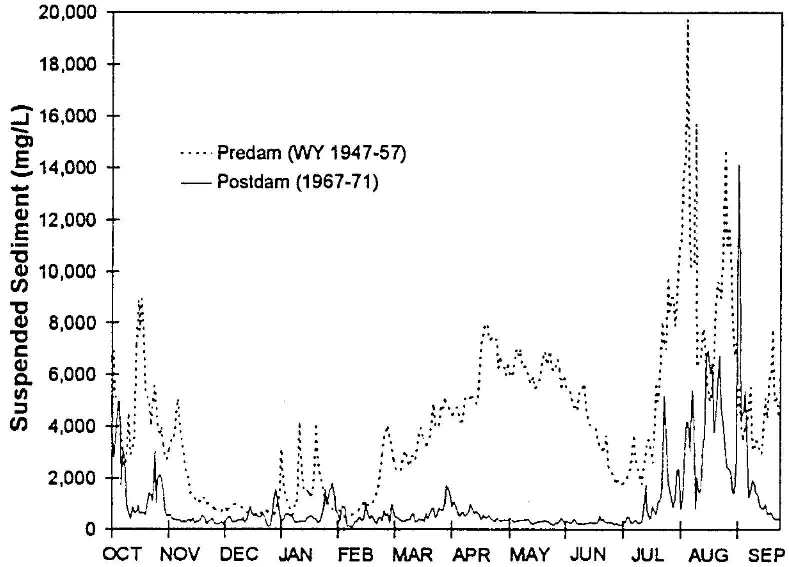


Fig. 4-8. Predam (WY 1947-1957) and postdam (WY 1967-1971) average daily sediment concentrations (mg/L) near Grand Canyon. USGS data from EarthInfo on CD ROM.

Historic climate changes on the Colorado Plateau have caused dramatic variations in warm-season rainfall, and hence sediment loads (Hereford and Webb 1992). Historically, suspended sediment was highest during three distinct seasonal periods. Spring runoff produced a consistent period of moderate sediment from late February through June, and summer rainstorms produced short-term floods with high sediment loads from July through mid-November. Also, winter flows were relatively stable and sediment loads were low, except during brief mid-winter rainstorms or intermittent snow melt events.

Postdam. Sediment originating from the headwaters of the Colorado River is presently deposited in a series of reservoirs, primarily Lake Powell. Sediment loads measured near Lees Ferry decreased by almost 90% (76.3 to 8.6 million tons/year) in WY 1963-65 just after dam construction (Laursen et al. 1976 in Schmidt and Graf 1990). The annual sustained sediment load during runoff (i.e., February-June) was eliminated by Glen Canyon Dam and Lake Powell, and the peaks in sediment load from summer rainstorms (i.e., July-November) and winter snowmelt events (i.e., January) in major tributaries are still apparent but reduced in magnitude (Fig. 4-8). Hence, the main volume of sediment into Grand Canyon now occurs in late summer from local rainstorms, instead of in spring and early summer from high elevation snowmelt.

Sediment input has persisted since dam closure, but the range in concentration has been reduced. Highest sediment loads are now a function of tributary floods, primarily from the Paria River and LCR. Mean annual sediment discharge of the Paria River for WY 1941-57 was 3.02 million tons, and sediment discharge for the same time period for the LCR near Cameron was 9.27 million tons (Andrews 1991). Other tributaries, such as Kanab Creek and ephemeral drainages, also contribute sediment intermittently.

Preliminary research by M. Yard (GCES, pers. comm.) indicates that suspended sediment loads in the Colorado River increase as a function of discharge, distance, and channel morphology (under tributary base flow conditions). These variables are independent of sediment loads from tributaries. However, under increased tributary and sediment discharge, distribution of suspended loads is dependent on location of the tributary inflow.

Turbidity

High spring snowmelt flows and erratic late summer rainstorms within a sparsely-vegetated and arid basin historically produced high sediment loads in the Colorado River. The sediment loads caused persistently low water clarity.

The relationship between light attenuation and turbidity depends on the variation in characteristic size, shape, and refractive index of suspended material (Roos and Pieterse 1994, Yard et al. 1993). The unique characteristics of sediment found in tributaries throughout Grand Canyon preclude direct correlation of turbidity with weight concentration of suspended matter (milligrams per liter) without concurrent sampling, i.e., turbidity may differ for the same sediment concentration, depending on the geologic source. Turbidity is a description of the optical property that causes light to be scattered and absorbed rather than transmitted through water. Turbidity in water may be caused by suspended matter, finely divided organic and inorganic elements, soluble colored organic compounds, plankton, or other microscopic organisms (Greenburg et al. 1992).

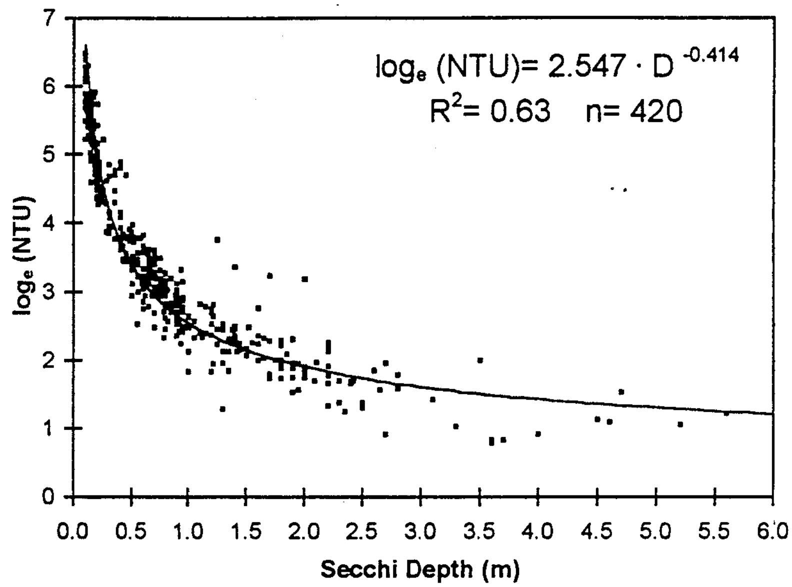


Fig. 4-9. Relationship between Secchi depth (D) and turbidity (NTU) for the Colorado River in Grand Canyon.

A power regression curve (Fig. 4-9) describing the relationship between concurrent field measurements of Secchi depth and turbidity (NTUs) was developed for a practical assessment of water clarity during this investigation. This relationship revealed that a Secchi depth of 0.5 m equates to about 30 NTUs. This enabled researchers to use either technique for assessing water clarity relative to fish catch information and movement (See Chapter 5 - DISTRIBUTION AND ABUNDANCE, Chapter 8 - MOVEMENT).

These patterns indicated higher water clarity at a constant flow of 5,000 cfs and lower water clarity at high fluctuating flows, but the data were inconclusive for a constant flow of 15,000 cfs. This relationship was observed during other transitions from fluctuating flows to low constant flows (e.g., 8,000 cfs), and needs to be further defined to better understand the effect of the steady summer flows identified in the Biological Opinion (See Chapter 1 - INTRODUCTION).

The relationship between turbidity and changes in flow of the Colorado River in Grand Canyon were illustrated during research flows in May 1991. In the absence of significant turbidity from tributaries, water transparency in the mainstem was 1-1.5 m Secchi depth at daily fluctuations ranging from 7,000 to 25,000 cfs. Secchi depth increased to a peak of 5.5 m during a 3-day steady flow of 5,000 cfs (Fig. 4-10). The 3-day steady release occurred at Glen Canyon Dam from May 16 (12:01 am) through May 19 (12:01 am) and was observed at the gage above the LCR about 15 hr later on May 17-20. Water transparency returned to a Secchi depth of about 2 m at the beginning of a constant flow period of 15,000 cfs.

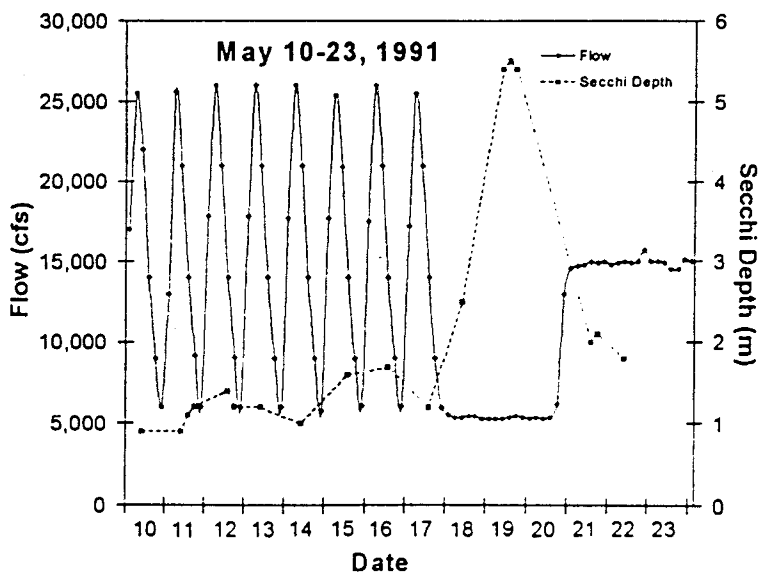


Fig. 4-10. Relationship of flow to Secchi depth during a transition of high fluctuating releases (7,000-25,000 cfs) to constant 5,000 cfs, May 10-23, 1991.

Conductivity

Conductivity is a measure of the ability of an aqueous solution to conduct an electric current and is dependent on concentrations of total dissolved solids (ions). Postdam conductivity of the Colorado River in Grand Canyon has varied slightly with the volume of water entering Lake Powell. Above-average flows dilute the lake water and reduce conductivity of releases, while below-average flows produce higher conductivities. Although individual tributaries within Grand Canyon have a minor influence on conductivity of the mainstem, collectively, these add to constituents from other streams to increase ionic concentrations in downstream reaches.

During this investigation, mainstem conductivity varied slightly with season and distance from Glen Canyon Dam. During WY 1992 (October 1, 1991 - September 30, 1992), mean daily conductivity of the Colorado River at Lees Ferry ranged from 874 to 981 µS/cm (USGS 1992), and mean daily conductivity above the LCR (RM 61.2) varied from 910 µS/cm in September to 1,010 µS/cm in April (Table 4-3).

Dissolved Oxygen

Mean daily DO concentrations in the mainstem ranged from 10.35 mg/L at 8.22°C (87% saturation) in February to 11.03 mg/L at 10.58°C (100% saturation) in July (Table 4-3). This relatively high DO was attributed to cool water temperatures and constant aeration by currents. A slight seasonal trend in DO resulted from seasonal changes in water temperature and associated saturation levels. All DO values recorded during the investigation approached saturation for the elevation of Grand Canyon.

pH

Mean daily pH of the Colorado River above the LCR (RM 61.2) varied slightly and ranged from 7.66 in October to 7.93 in May (Table 4-3). No longitudinal trends in pH were apparent, and only slightly higher pH values were recorded in summer months.

Little Colorado River

Water Temperature

Seasonal variation in water temperatures of the lower LCR during this investigation (WY 1991-93) was similar to the range of the predam Colorado River (Fig. 4-11). A low winter temperature of about 2°C was recorded in January with a maximum of 23-25°C in June and July. The effect of water temperature from the LCR on the mainstem was localized, with a characteristic downstream plume or mixing zone that varied with flow of both rivers and time of year (See Chapter 7 - HABITAT).

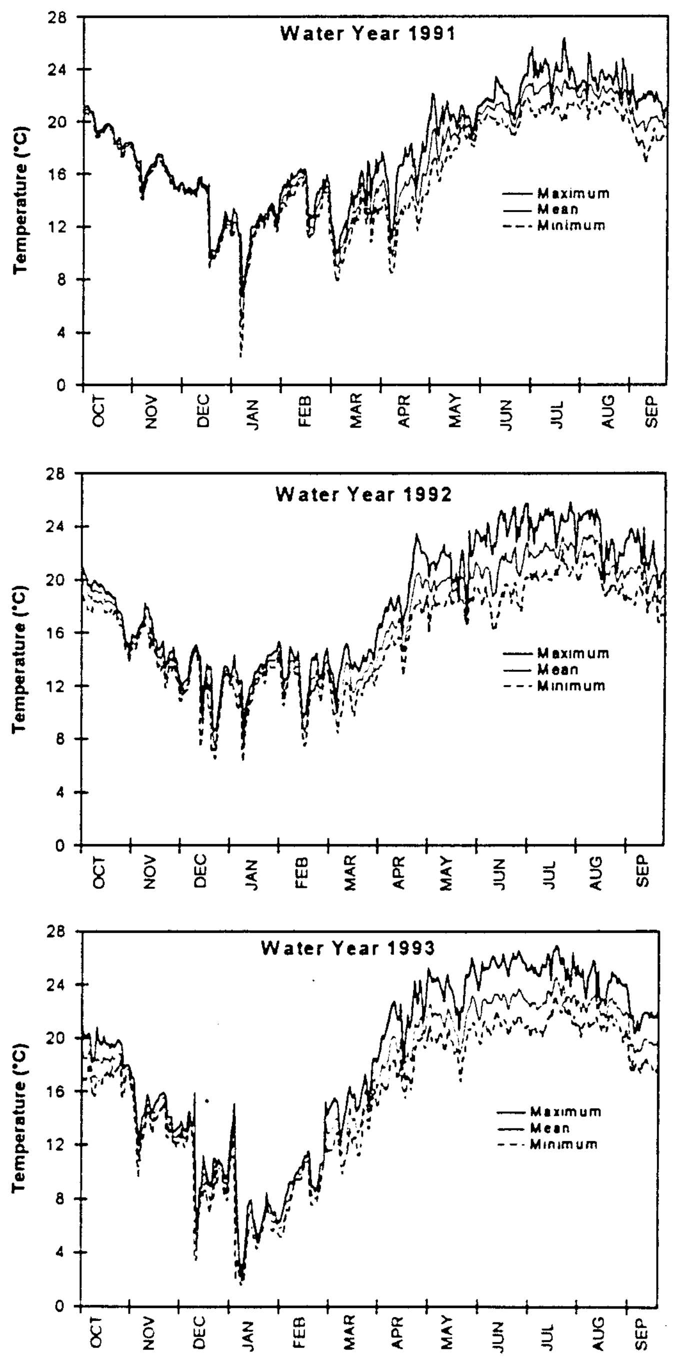


Fig. 4-11. Daily mean, minimum, and maximum temperature of the LCR for WY 1991, 1992, and 1993. GCES Ryan Tempmentor data.

Conductivity

Conductivity of the LCR varied with runoff. At base flow in June, conductivity was about 4,480 µS/cm. During runoff and floods in January, dilution decreased conductivity to less than 362 µS/cm (Table 4-3). Like temperature, conductivity of the LCR had only a local effect on mainstem conductivity.

Dissolved Oxygen

Dissolved oxygen (DO) in the LCR was generally lower than that of the mainstem and other tributaries, possibly because of warm tributary temperatures. Variation in DO levels in the LCR was caused by temperature fluxes and periodic flood events. In 1992, mean daily DO values in the LCR varied from 7.66 mg/L at 23.83°C (90% saturation) in August to 9.93 mg/L at 11.53°C (92% saturation) in February (Table 4-3).

pH

Mean daily pH in the LCR during 1992 ranged from 7.72 in January to 8.11 in April (Table 4-3). These values were similar to those in the mainstem Colorado River.

Bright Angel Creek

Water temperature of Bright Angel Creek ranged from a low of 1°C in December 1990 to a high of 24°C in August 1992 (Fig. 4-12A). Conductivity measured in November 1992 (Table 4-3) was 390 µS/cm, while DO ranged from 8.50 to 10.46 mg/L, and pH ranged from 8.26 to 8.30.

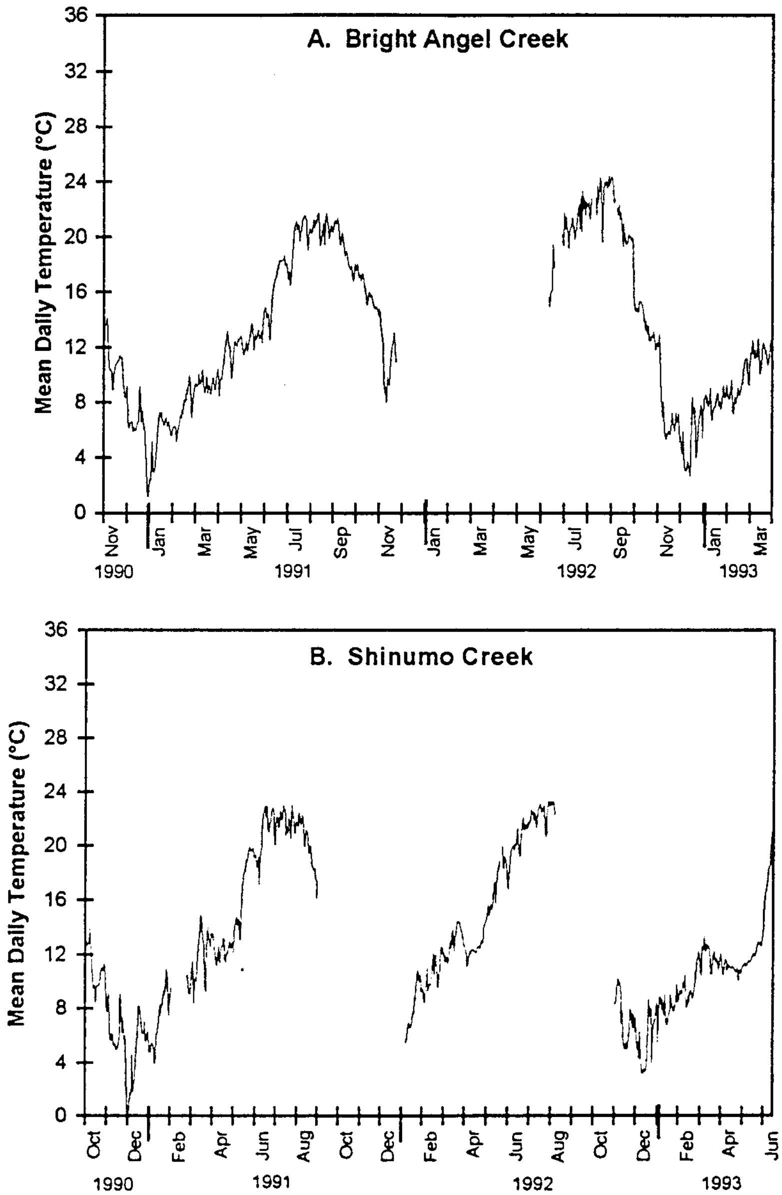


Fig. 4-12. Mean daily temperature of Bright Angel Creek (A) from November 1990 through March 1993 (USGS ADAPS data) and Shinumo Creek (B) from October 1990 through June 1993 (GCES Ryan Tempmentor data). Discontinuous line indicates missing data.

Shinumo Creek

The seasonal temperature pattern for Shinumo Creek was similar to that of Bright Angel Creek with a minimum of 1°C in December 1990 and a maximum of 23°C in July-August 1991 and 1992 (Fig. 4-12B). Mean conductivity in January, May, and November 1992 ranged from 370 to 1,900 µS/cm. Mean DO ranged from 10.34 to 13.31 mg/L, and pH ranged from 8.00 to 8.49 (Table 4-3).

Kanab Creek

Kanab Creek was the warmest tributary sampled during this investigation with a maximum temperature of 35°C in August 1991 (Fig. 4-13A). A minimum temperature of 0°C was recorded in December 1990 during lowest flow. Mean conductivity in May and November 1992 ranged from 1,220 to 1,260 µS/cm, mean DO ranged from 8.52 to 10.17 mg/L, and pH from 8.05 to 8.07 (Table 4-3).

Table 4-3. Minimum (min), maximum (max), and mean (ave) water quality parameters of the Colorado River and selected tributaries at 10 or 15-min intervals during monthly trips in 1992. BIO/WEST Hydrolab data.

Month	No. Days	Temperature (°C)			Conductivity (μS/cm)			Dissolved Oxygen (mg/l)			pH		
		min	max	ave	min	max	ave	min	max	ave	min	max	ave
Colorado River Above LCR (RM 61.2)													
Jan	-	-	-	-	-	-	-	-	-	-	-	-	-
Feb	7	7.76	8.57	8.22	910	950	930	9.76	10.63	10.35	7.79	7.88	7.84
Mar	6	7.78	9.14	8.36	970	1,000	990	10.14	10.67	10.51	7.71	7.81	7.77
Apr	7	9.21	10.38	9.75	990	1,030	1,010	9.51	10.92	10.78	7.71	7.84	7.77
May	6	9.85	11.39	10.49	930	1,010	980	-	-	-	7.83	8.00	7.93
Jun	-	-	-	-	-	-	-	-	-	-	-	-	-
Jul	5	9.64	11.22	10.58	920	950	930	10.73	11.34	11.03	7.84	7.92	7.88
Aug	3	10.16	11.11	10.74	910	950	930	-	-	-	6.92	7.76	7.72
Sep	6	10.40	11.45	10.84	890	920	910	-	-	-	7.85	7.98	7.92
Oct	7	10.15	19.99	10.63	880	910	890	8.88	10.76	10.46	7.44	7.72	7.66
Nov	-	-	-	-	-	-	-	-	-		-	-	-
Little Colorado River													
Jan	12	6.56	14.18	11.36	262	395	362	9.08	11.36	9.71	7.57	8.08	7.72
Feb	7	7.31	15.33	11.53	990	3,080	1,700	8.53	11.19	9.93	7.59	8.01	7.84
Mar	10	8.65	14.80	11.77	1,220	1,980	1,520	8.90	10.69	9.78	8.01	8.24	8.09
Apr	7	15.03	20.30	17.15	560	1,240	940	5.92	9.87	8.87	8.07	8.20	8.11
May	9	16.86	24.16	20.47	1,770	4,170	3,190	5.02	9.12	8.12	7.50	7.85	7.73
Jun	6	16.83	26.00	21.17	4,340	4,590	4,480	7.76	9.26	8.48	7.76	7.90	7.82
Jul	10	20.45	26.14	22.79	1,770	4,240	3,470	7.56	9.19	8.33	6.39	8.04	7.67
Aug	8	21.73	26.19	23.83	1,800	2,990	2,470	7.26	8.00	7.66	8.00	8.00	8.00
Sep	10	18.06	24.78	21.24	930	4,610	3,270	6.13	8.74	7.94	7.50	8.05	7.80
Oct	7	16.63	21.48	18.89	4,340	4,510	4,450	8.38	9.37	8.89	6.05	7.80	7.64
Nov	11	9.84	18.13	14.19	1,500	4,110	2,680	8.38	10.66	9.38	7.58	8.02	7.79
Bright Angel Creek													
Nov	2	10.07	12.65	11.43	390	390	390	8.50	10.46	10.08	8.26	8.30	8.27
Shinumo Creek													

Jan	2	2.69	5.77	4.60	340	380	370	12.74	13.88	13.31	7.61	8.57	8.49
May	3	11.37	17.00	13.20	1,800	1,900	1,900	9.52	10.76	10.34	7.96	8.08	8.00
Nov	3	8.31	13.70	10.57	380	390	390	9.30	11.42	10.68	8.25	8.37	8.29
Kanab Creek													
May	4	18.05	26.52	21.55	1,190	1,230	1,220	7.68	9.26	8.52	7.98	8.20	8.07
Nov	2	11.96	12.82	12.22	1,260	1,260	1,260	9.15	10.45	10.17	8.04	8.08	8.05
Havasu Creek													
May	3	18.69	20.81	19.19	710	740	720	7.87	9.41	8.93	7.93	8.23	8.06
Nov	3	11.83	14.53	12.65	700	740	720	9.91	10.68	10.46	7.87	8.14	7.98
Crystal Creek													
Jan	2	1.42	6.68	3.11	2,000	2,020	2,010	11.86	14.97	13.81	7.06	8.62	8.55
Tapeats Creek													
May	2	11.99	14.86	12.50	2,300	2,400	2,400	8.83	10.43	10.26	8.09	8.21	8.11
Nov	2	10.90	12.46	11.41	340	340	340	10.02	10.55	10.39	8.23	8.32	8.25
Deer Creek													
May	2	13.67	14.87	14.11	3,300	3,300	3,300	9.50	9.85	9.71	8.22	8.25	8.23

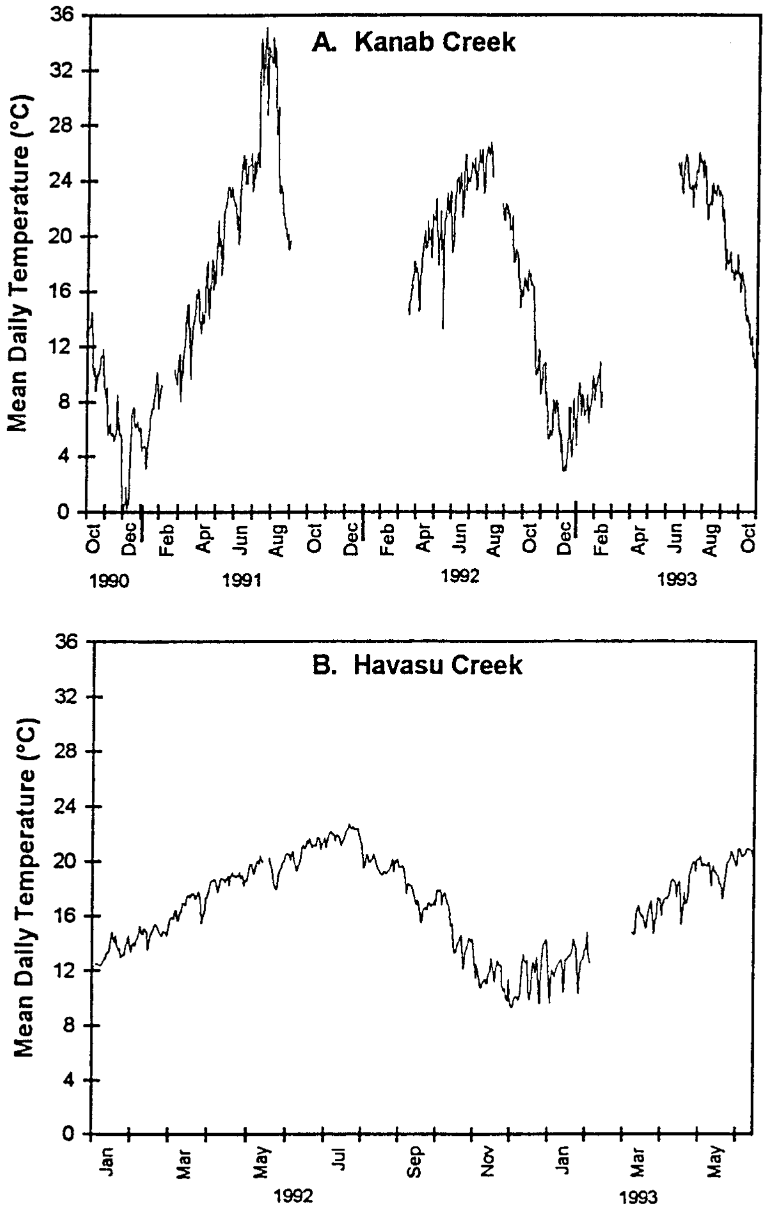


Fig. 4-13. Mean daily temperature of Kanab Creek (A) from October 1990 through October 1993 (GCES Ryan Tempmentor data) and Havasu Creek (B) from January 1992 through June 1993 (GCES Ryan Tempmentor and USGS ADAPS data). Discontinuous line indicates missing data.

Havasu Creek

Maximum water temperature of Havasu Creek was 22.5°C in July 1992, and minimum mean daily temperature was 9.5°C in December 1992 and January 1993 (Fig. 4-13B). The seasonal temperature pattern of Havasu Creek, unlike that of the other tributaries examined, was moderated by the warm temperature of Havasu Springs, resulting in relatively warm winter temperatures. Mean conductivity in March, May, and November 1992 was 720 µS/cm, while mean DO ranged from 8.93 to 10.46 mg/L, and mean pH ranged from 7.98 to 8.06 (Table 4-3).

Other Tributaries

Daily means for water quality parameters from Crystal, Tapeats, and Deer creeks were similar to those of other tributaries examined for comparable periods during this investigation (Table 4-3). Temperature of these tributaries could not be adequately characterized from periodic monthly samples. Limited measurements indicated high conductivity in Crystal Creek (2,000-2,020 µS/cm), Tapeats Creek (340-2,400 µS/cm) and Deer Creek (3,300 µS/cm). Dissolved oxygen was relatively high in all three tributaries; Crystal Creek (11.86-14.97 mg/L), Tapeats Creek (8.83-10.55 mg/L), and Deer Creek (9.50-9.85 mg/L).

Springs

Water quality parameters were also collected from four spring complexes. The spring areas were Fence Fault Springs (RM 30.1-31.8), Lava Springs (RM 179.5), Beecher Springs (RM 183.5), and Pumpkin Spring (RM 212.8).

Fence Fault Springs

Eight springs and numerous seeps were located in an 8-km subreach of river near South Canyon (RM 30.0-35.0) (Fig. 4-14). These springs were located on both sides of the river and were associated with the Fence Fault, as previously described by Huntoon (1968, 1981).

Locations, estimated discharges, temperatures, and geologic setting for the eight springs are compared in Table 4-4 for data collected by Huntoon (1981) on August 8, 1979 and data collected during this study on July 14, 1994 (Valdez and Masslich 1995). Discharges of springs during this study were visually estimated and were not considered reliable for comparison with the 1979 data, except for spring No. 5 where some velocity measurements were taken. Temperatures recorded at each spring

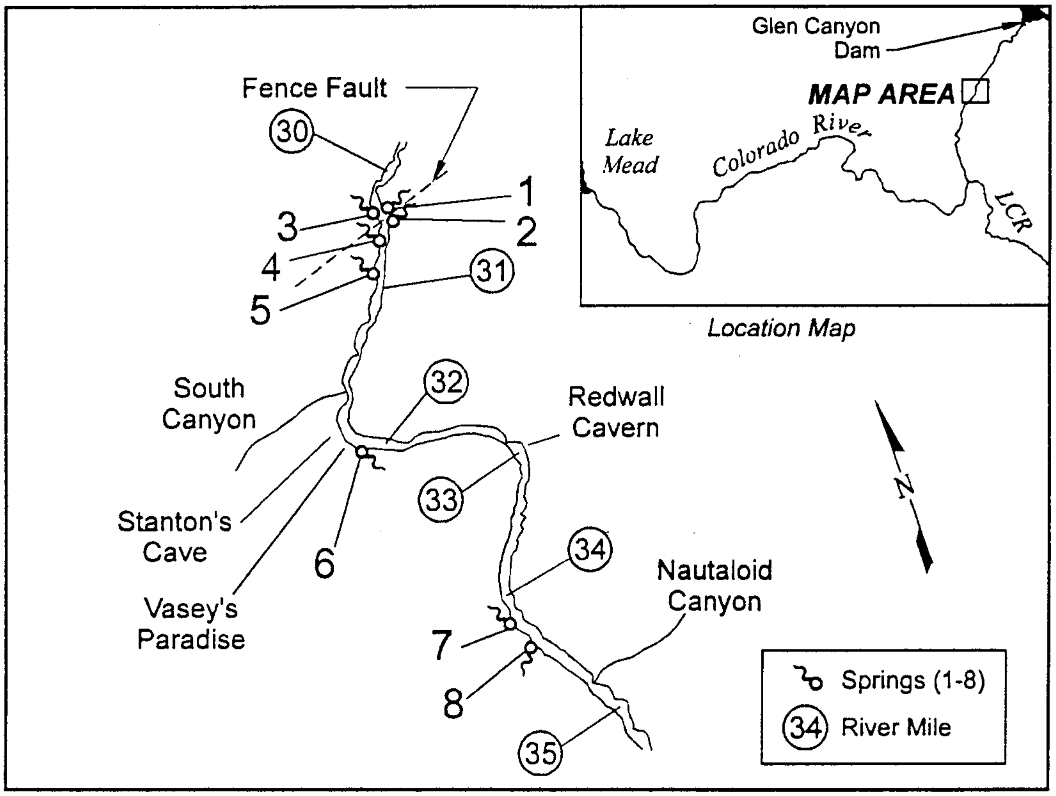


Fig. 4-14. Locations of eight springs in the Fence Fault area, as represented by Huntoon (1981).

Table 4-4. Location, estimated discharge, temperature, and geologic setting of springs in the vicinity of Fence Fault. Data from Huntoon (1981) and BIO/WEST (this study).

Spring No.	Name	Approximate River Mile[a]	Side of River	Discharge (gal/min) Huntoon (8/9/79)	Discharge (gal/min) BIO/WEST (7/14/94)	Temperature (°C) Huntoon[b] (8/8/79)	Temperature (°C) BIO/WEST (7/14/94)
1	East Fence No.1	30.1	East	500	–[c]	20.5	20.9
2	East Fence No.2	30.2	East	6,500	–	21.1	21.0
3	West Fence No.1	30.2	West	20	–	21.6	21.0
4	West Fence No.2	30.7	West	30	–	21.1	21.0
5	Diagonal	30.9	West	900	-900	21.6	21.5
6	Vasey's	31.9	West	2,500	–	16.7	17.0
7	Hanging No. 1	34.4	West	30	–	18.3	–
8	Hanging No. 2	34.5	West	10	–	17.8	–

[a] River Mile = miles downstream of Lees Ferry
[b] Converted from degrees Fahrenheit
[c] – = data not available

source in 1994 were similar to those recorded in 1979. The springs between RM 30.1 and RM 30.9 were similar with a range of 20.5 to 21.6°C,while temperatures of the three downstream springs ranged from 16.7 to 18.3°C.

The five springs between RM 30.1 and RM 31.9 were produced from the Mooney Falls member of the Redwall Limestone, and the three downstream springs were produced from the Whitmore Wash member of the Redwall Limestone. Huntoon (1981) found evidence from water quality analyses that some springs emitted water mixed from both sides of the river, suggesting that there is groundwater flow beneath the Colorado River in the Fence Fault zone and possibly very localized warm plumes along the river bed. Huntoon (1981) found no evidence of the river invading the springs and no evidence of proximate surface input, hence the springs are likely to maintain constant year-around temperature. All eight springs discharge at or near the river level, except for spring No. 6 (i.e., Vasey's Paradise).

Lava Springs

Lava Springs were located just downstream of Lava Falls (RM 179.5) on the left bank. These springs flowed into the river from low travertine rims at a temperature of 16°C (mainstem temperature was 14°C).

Beecher Springs

Beecher Springs were located near river level at RM 183.5 on the left bank. Temperature of the main spring at its source was 23.5°C, and temperature of the mixed plume was 17.5°C (mainstem temperature was 14°C).

Pumpkin Spring

Although Pumpkin Spring is a large feature located at RM 212.8, we found no evidence of a warm plum extending into the mainstem, despite a temperature of 21.5°C at the spring source.

DISCUSSION

Water quality of the Colorado River in Grand Canyon is largely influenced by Lake Powell (Stanford and Ward 1991). Many water quality parameters have changed since the reservoir was created by Glen Canyon Dam in 1963. Changes in some parameters have had a noticeable effect on fish populations, while others have indirectly affected fish or had little effect.

This chapter characterizes temperature, turbidity, DO, conductivity, and pH for the mainstem Colorado River and the major tributaries in Grand Canyon. Other water quality parameters were the subject of other GCES investigations (U.S. Department of Interior 1990). The most significant changes from predam conditions were for temperature and turbidity. Predam temperature extremes of 0-29.5°C were replaced by dam releases with annual variation of 7-11°C. Greatest longitudinal warming in summer (1°C/51 km) under interim flows produced mean daily temperatures of 10-11°C at the confluence of the LCR (RM 61.0), 13-14°C in Middle Granite Gorge (RM 127.0), and 15-16°C at Diamond Creek (RM 226.0). Maximum temperature range for the Colorado River in Grand Canyon observed under interim flows was about 6-8°C below the temperature preferenda of 21-24.4°C for juvenile humpback chub under laboratory conditions (Bulkley et al. 1981, Pimental and Bulkley 1983). This preferred range was based on juveniles that selected 21, 23.5, and 24.4°C at acclimation temperatures of 14, 26, and 20°C, respectively (mean temperatures selected were not significantly different at P=0.05).

Maximum temperature range observed under interim flows was marginally suitable for spawning, incubation, and larval survival of humpback chub, which have a reported suitable range of 16-22°C (Marsh 1985). Hamman (1982) found that hatching success of humpback chub in the laboratory was highest at 19-20°C, while larval survival was highest at 21-22°C. Incubation periods ranged from 102 to 146 hr at water temperatures of 21-22°C, 115 to 160 hr at 19-20°C, 167 to 266 hr at 16-17°C, and 340 to 475 hr at 12-13°C. Survival of eggs was 79% at 21-22°C, 84% at 19-20°C, 62% at 26-17°C, and 12% at 12-13°C. Survival of swim-up fry was 99% at 21-22°C, 95% at 19-20°C,. 91% at 16-17°C, and 15% at 12-13°C. Total length at hatching ranged from 6.7 to 7.4 mm, which doubled in 21 - 28 days. Length range 56 days after hatching was 36.9 to 47.5 mm. Marsh (1985) found similar results for humpback chub, with greatest hatching success at 20°C (60%), but significantly lower at 15°C (0.8%) and 25°C (2%); all embryos died at incubation temperatures of 5, 10, and 30°C.

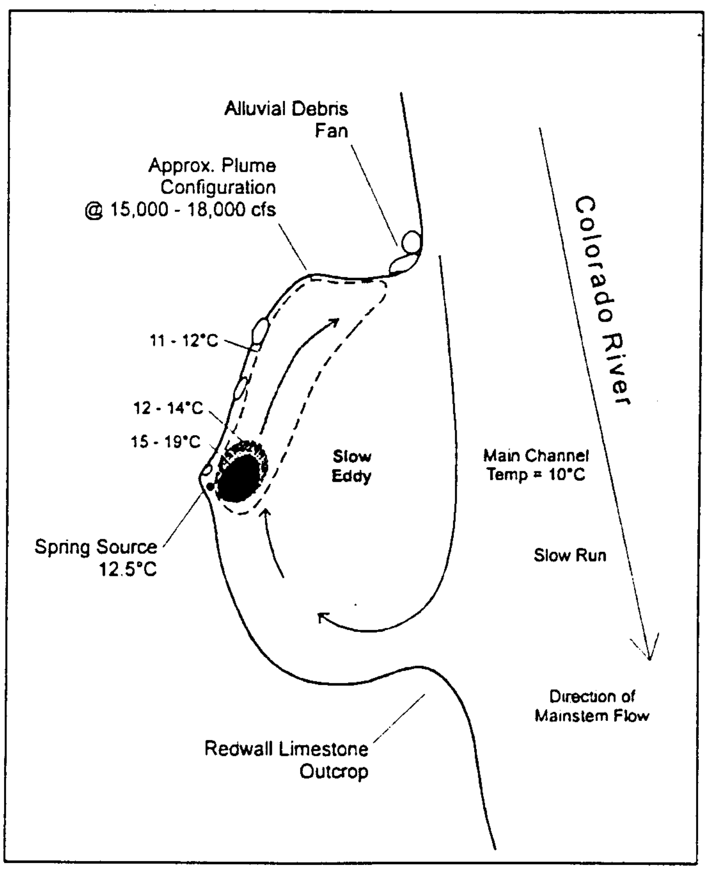
Lower maximum releases and less variation in flow under interim flows may make certain habitats, such as tributary inflows and warm springs, more stable than under high fluctuating flows. Perennial tributaries, such as the Paria River, LCR, Bright Angel Creek, Shinumo Creek, Kanab Creek, Havasu Creek, Crystal Creek, Tapeats Creek, and Deer Creek, warmed seasonally with temperatures higher than mainstem levels from about April through September and provided warm plumes extending into the mainstem. During base tributary flows, thermal influence on the mainstem was local, and typically extended as a warm plume less than 200 m from the outflow (See Chapter 7 - HABITAT).

Warm springs were also important fish habitat because of their thermal properties, but like tributary inflows, their influence on the mainstem was local, and their size and duration depended on mainstem flows. Of 12 springs located in four areas (Fence Fault, RM 30.2; Lava Falls, RM 179.5; Beecher Springs, RM 183.5; Pumpkin Spring, RM 212.8), source temperature was typically 21°C or higher, and plume diameter was highly variable with spring volume and mainstem flow. One spring with a source temperature of 21.5°C had a plume of 3 m x 10 m that was warmer than the mainstem (Box 4-1).

The river in and around Fence Fault may be one of the more important habitats for native fishes, particularly humpback chub, in the 115 km downstream of the dam. The presence of post-larval humpback chub in July 1994 indicated successful spawning in the area (See Chapter 5 - DISTRIBUTION AND ABUNDANCE). Also, the presence of eight major thermal springs along an 8-km subreach in this area, and the possibility of local warm plumes along the river bed may serve as an attraction to both coldwater and warmwater species in an otherwise relatively isothermal cold river (See Chapter 5 - DISTRIBUTION AND ABUNDANCE). In order for warmwater native fishes to spawn successfully

Box 4-1. Thermal Characteristics of a Mainstem Spring

Spring No.5 at RM 30.9 had certain thermal characteristics as a mainstem spring. In January 1992 the undiluted spring temperature was 21.5°C, with a plume (2 m x 2 m) extending into the mainstem at 17.5°C, while mainstem temperature was 10°C. When the spring was revisited on July 14, 1994, the temperature was still 21.5°C. Plume temperature was approximately 15°C at 2 m from the source, 12°C at 3 m from the source, and was not perceptibly different than the mainstem at 10 m from the source. Approximate area of the plume was 3 m wide and 10 m long. The mouth of the spring was located in a limestone shelf along the shoreline. Substrate in the plume was composed of bedrock limestone, boulders, and sand. Estimated discharge on July 14, 1994 was 900 gal/min.



Approximate plume shape and thermal characteristics of Spring No.5 at RM 30.9. Data collected July 14, 1994 with a Hydrolab Surveyor 3.

in these habitats, the thermal plume from the spring must remain relatively stable during egg incubation (5-20 days) and larval development (10-20 days). Hence, the relatively stable high releases from Glen Canyon Dam (i.e., 15,000-20,000 cfs) during June-August may have resulted in conditions which enhanced successful spawning and survival of YOY in 1994. Known springs and associated warm plumes should be monitored and characterized by river stage.

Other springs may be present along the Colorado River in Grand Canyon. Locating and mapping these springs may help locate additional aggregations of fish. Thermal infrared (FLIR) studies may be useful in locating these springs (Holroyd 1995).

The other water quality parameter that has been significantly altered in Grand Canyon is turbidity. Since turbidity is caused by suspended sediment, reduced sediment concentration from retention in Lake Powell has resulted in lower year-around turbidity and reduced frequency of turbid conditions. Average annual sediment load reduction of 140 million tons to 15 million tons is not a quantifiable relationship to turbidity (Yard et al. 1993) but provides a perspective of the relative magnitude and frequency of change in water clarity. The effects of reduced turbidity on humpback chub and sympatric fishes in Grand Canyon are further discussed in Chapter 8 (MOVEMENT) of this report. Turbidity in the river provides cover for native fishes from predators, and reduces feeding efforts by non-native sight feeders such as rainbow trout.

Dissolved oxygen, conductivity, and pH levels were not significantly different from predam conditions, and remained within tolerance ranges for the Colorado River native fishes. Bulkley et al. (1981) 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 600-1,100 mg/L, respectively. They also found that humpback chub had the highest tolerance level for conductivity at 8,500 μS/cm. Average mainstem TDS and conductivity and most monthly maxima were below the preferred range of humpback chub, and not considered detrimental to the species.

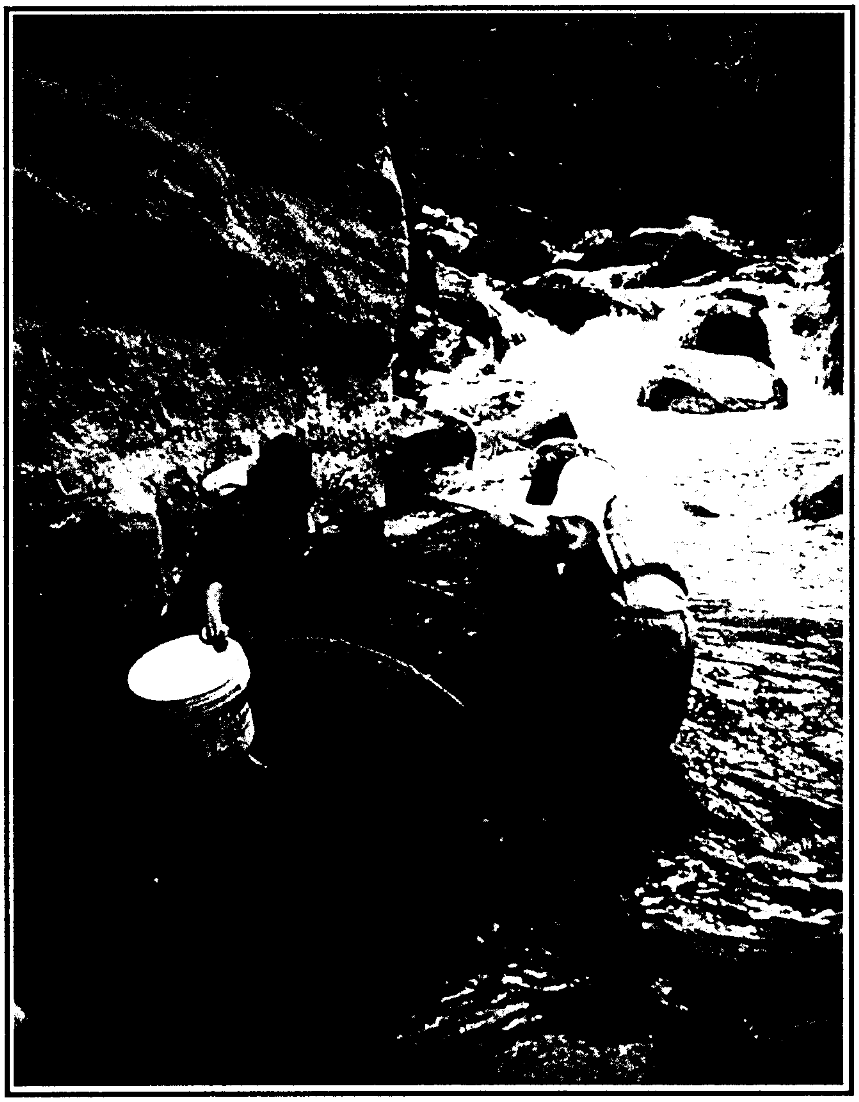
Minimum observed DO in the mainstem (not including backwater habitats) was 8.88 mg/L or higher, while average DO was above 10.35 mg/L. Although preferred and tolerance levels of DO for the Colorado River native fishes is unknown, other fish species require concentrations of 5 mg/L or higher for health, and 1 mg/L is usually lethal (Whitmore et al. 1960, Moss and Scott 1961, Bonn et al. 1976, Piper et al. 1982, Stickney 1986). Dissolved oxygen levels in the LCR in April and May were 5.92 and 5.02 mg/L, respectively, during spring runoff. No evidence of oxygen starvation in fish was observed in the mainstem.

Observed levels of pH were also within normal tolerance range for warmwater fishes (McKee and Wolf 1963). A range of 6.92 to 8.00 pH units was found in the mainstem and 6.05 to 8.24 pH units was found in the LCR.

Phototrophic productivity downstream of Glen Canyon Dam is significantly higher than before the dam, but productivity decreases substantially downstream of the Paria River and LCR. Blinn et al. (1994) identified that both primary and secondary productivity (i.e., standing crop biomass) decreased by an order of magnitude below each of the primary tributaries in a stairstep fashion. The causal factor was the increased frequency of sediment input which resulted in a reduction of light on available substrate, hence a decrease in photosynthetic productivity. Increased sediment also increased abrasion, thereby reducing standing crop biomass. There was also a distinct compositional shift in periphyton and invertebrates associated with distance downstream.

Distribution and Abundance

Chapter 5



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CHAPTER 5 - DISTRIBUTION AND ABUNDANCE

INTRODUCTION

The distribution and abundance of fishes in the Colorado River in Grand Canyon are not well understood despite numerous surveys and studies over the last 35 years (McDonald and Dotson 1960, Stone and Rathbun 1968, Miller and Smith 1972, Holden and Stalnaker 1975, Minckley and Blinn 1976, Suttkus et al. 1976, Carothers and Minckley 1981, Kaeding and Zimmerman 1983, Maddux et al. 1987, Arizona Game and Fish Department 1993). Hence, the status of fish populations prior to construction of Glen Canyon Dam in 1963 and effects of dam operations are difficult to assess because of a paucity of fisheries data. The present investigation adds new information to an existing pool of knowledge that will continue to expand with long-term monitoring, core research, and integration of historic and current data. Perhaps the distribution and abundance of each species in Grand Canyon can not be definitively described, but monitoring and research programs will provide the framework for systematic data collection that will enable scientists to relate dynamics of fish populations to management options.

Describing fish assemblages in Grand Canyon will continue to be challenged by logistical difficulties of accessing and sampling the deep, turbid river and by relatively inefficient gears that sample but a fraction of the river corridor. Implementation of new methodologies, such as radiotelemetry, timed sampling strategies, and use of small maneuverable research boats, will enhance opportunities for collecting information vital to understanding the fishes of this and other swift canyon regions (Valdez et al. 1993).

This chapter integrates predam and postdam information with data from this investigation to characterize fish assemblages in the Colorado River in Grand Canyon. Composition, distribution, and abundance are presented for all species, together with a discussion of causative effects of Glen Canyon Dam operations on these attributes for humpback chub.

METHODS

Species Composition, Distribution, Abundance

Historic species composition, distribution, and relative abundance were compiled from agency and university reports (i.e., gray literature) and published manuscripts. Present distribution and relative abundance were determined from spatial and temporal information gathered during this investigation using a variety of sampling methods and radiotelemetry (See Chapter 2 - STUDY DESIGN). Fish species composition reflected the types of fish species captured. Distribution was determined by noting the occurrence of individuals throughout the study area, and relative abundance was computed as catch-rate statistics. Mark-recapture population estimates for humpback chub are also presented in Chapter 6 - DEMOGRAPHICS.

Catch Rates

Catch per effort (CPE) statistics were used to make temporal and spatial comparisons of relative fish abundance by species. Problems inherent to catch rate statistics are magnified when dealing with endangered species, such as humpback chub. Because of the low numbers of individuals, the majority of samples yielded no humpback chub, thereby creating a skewed or non-normal catch distribution. Non-normal catch distributions limit parametric tests (Cryer and MacLean 1991) which are based on normality, and they distort nonparametric tests, which are based on measures of central tendency. Use of simple non-parametric tests, such as the Mann-Whitney 'U', provides lower statistical power than parametric tests (Zar 1984), and results can be distorted by the large number of zero values. Hence, catch rates are often computed as geometric mean to reduce dependence of the variance on the mean (Sokal and Rohlf 1987).

Catch rate statistics were expressed as arithmetic mean (AM_{CPE}) and geometric mean (GM_{CPE}) (Sokal and Rohlf 1987). Arithmetic mean was used to estimate relative fish abundance for comparison with previous investigations that also used arithmetic means. Geometric mean was used for comparative parametric tests. Use of catch rate statistics was limited to those datasets with robust sample sizes and to comparisons among identifiable and consistent variables.

Arithmetic mean catch per effort was calculated as the number of fish captured in each sample, divided by respective sampling effort and averaged for a given set of samples (Equation 5-1). This statistic (AM_{CPE}) was used to perform comparative tests for samples with normal catch distributions, or where sample efforts were similar. Where sample efforts were dissimilar and catch was zero, AM_{CPE} ignored variable effort from the catch rate calculation; e.g., two electrofishing efforts of 0.5 hr and 2.0 hr with no fish each yielded zero catch rates, but differences in effort were not reflected in the averaging statistic. Arithmetic mean was computed as:

(Equation 5-1)

$$AM_{CPE} = \sum (f/e)/n$$

where:

AM_{CPE} = arithmetic mean CPE,
f/e = number of fish captured divided by effort for each sample, and
n = number of samples.

Geometric mean catch per effort (Equation 5-2) was calculated with the catch rate for each sample (number of fish divided by effort) transformed to a natural logarithm. Sample catch rates were averaged and geometric mean was calculated as the antilog of the average. An adjustment for zero catches was made by adding '1' to each untransformed sample (Sokal and Rohlf 1987). Standard deviation was computed from log-transformed values, and the antilog was taken to provide bounds around the geometric mean. Geometric mean was computed as:

(Equation 5-2)

$$GM_{CPE} = \exp [(1/n) \sum \log_e (f/e + 1)] - 1$$

where:

GM_{CPE} = geometric mean CPE,
f/e = number of fish captured divided by effort for each sample, and
n = number of samples.

The main advantage of GM_{CPE} is reduced dependence of the variance on the mean (Sokal and Rohlf 1987) and reduced influence of single samples with exceptionally high CPE. As with AM_{CPE} disadvantages include the loss of individual efforts from samples with no fish. Geometric mean was used to compare datasets with variable efforts, numerous zero catches, and non-normal AM_{CPE} distributions. The GM_{CPE} statistic was used as an index of abundance and was not considered to yield realistic catch rates for comparison with AM_{CPE}. Geometric mean is used by the U.S. Fish and Wildlife Service (Service) (McAda et al. 1994) to monitor densities of age-0 Colorado squawfish in the Interagency Standardized Monitoring Program for the Upper Colorado River Basin.

Biomass

Indices of biomass (wet weight) of native and non-native fishes were estimated by geomorphic reach using electrofishing and seine catch date (Appendix E). Estimates were made by species for three age categories--young-of-year (YOY), juveniles, and adults. Numbers of individuals of juveniles and adults of large forms (e.g., flannelmouth sucker, bluehead sucker, rainbow trout, brown trout, carp, channel catfish) were estimated per kilometer by converting electrofishing time to average distance traveled (620m/hr), as computed for adult Colorado squawfish on the Green River (Tyus 1991). Electrofishing efficiency was estimated at 20% (Jacobs and Swink 1982). Numbers per kilometer of small forms (e.g., fathead minnow, plains killifish, green sunfish) were estimated from seine haul catch rates as numbers of fish per 100 m^2.

Numbers of fish per kilometer were converted to numbers per hectare for a 10-m strip along each shoreline--the approximate area sampled with electrofishing and seines. These estimates were used as indices of abundance. Average total length and weight were determined for each fish species by age category from field measurements and literature (Carlander 1969). The average weight was multiplied by total numbers of fish by species and age category to determine biomass per hectare.

Species Diversity

Species diversity indices were computed for fish assemblages in each of the 11 geomorphic reaches using a measure of information developed by Shannon and Weaver (1959) and applied to ecological situations by Margalef (1958, 1963, 1968). Species richness (i.e., number of fish species captured) and evenness (number of individuals captured per species) were also presented and discussed. Species diversity was computed as:

(Equation 5-3)

$$H = -\sum (p_i \log_e p_i)$$

where:

H = species diversity index, and
p_i = n/N, or number of individuals of a given species/sum of individuals of all species.

RESULTS

Composition, Distribution, And Abundance Of All Species

Predam (Before 1964)

The earliest evidence of fishes in Grand Canyon was found in 4,000-year old flood deposits in Stanton's Cave at RM 31.5 (Miller 1955, Euler 1978, Miller and Smith 1984). These deposits included skeletal remains of bonytail, humpback chub, Colorado squawfish, flannelmouth sucker, and bluehead sucker. Bones of Gila species were also discovered at an archeological site at RM 136.0 (Jones 1985) and in Catclaw Cave, an archeological site inundated by Lake Mead (Miller 1955). The original complement of fishes in Grand Canyon was also surmised from early explorers to the region including J.W. Powell (1875) in 1869, Dellenbaugh (1908) with J.W. Powell in 1871-72, R.B. Stanton (1965) in 1892, and Kolb and Kolb (1914) in 1908, and from initial fish surveys of the Colorado River Basin by Jordan (1891) and Everman and Rutter (1895). A preliminary checklist of fishes of Grand Canyon National Park was assimilated by Miller (1944).

The first comprehensive portrayal of historic fish assemblages of the Colorado River Basin was from paleontological records of Tertiary and Quaternary deposits (Miller 1959). The list consisted of 11 families, 22 genera, and 35 species with 27% and 74% levels of genus and species endemism, respectively. The primary (mainstem) ichthyofauna consisted of 2 families (Cyprinidae and Catostomidae), 12 genera, and 23 species with 50% and 87% levels of genus and species endemism, respectively. These records and archaeological findings indicate that the primary ichthyofauna in Grand Canyon prior to about 1850 consisted of 2 families, 5 genera, and 8 species--humpback chub, bonytail, roundtail chub, Colorado squawfish, speckled dace, bluehead sucker, flannelmouth sucker, and razorback sucker (Table 5-1 presents common and scientific names). Secondary or tributary-dwelling species were rare in the mainstem in Grand Canyon and included 2 Cyprinidae--Virgin spinedace and woundfin.

Establishment of Grand Canyon as a National Park on February 19, 1919 brought renewed attention to the area. Initial fish management efforts were directed at establishing a recreational fishery, with non-native trout introduced into clear coldwater tributaries (Williamson and Tyler 1932, Miller 1975). Also, numerous non-native species were brought into the region as sport fish, baitfish, and incidentals about the time that Lake Mead formed with construction of Hoover Dam in 1935 (Haden 1992, Table 5-2). Miller (1961) noted a marked decline in many native Colorado River fishes concurrent with land-use practices and invasion of alien fishes in the 1950s. Most notable introductions of non-native fishes were common carp into the U.S. in 1881 (Cooper 1987) and into the Colorado River in about 1890 (U.S. Fish and Wildlife Service 1980), channel catfish in about 1890 (Miller and Alcorn 1943, Hoffman 1981), rainbow trout in 1923 (Miller 1944, Stricklin 1950), and red shiners as baitfish in Lake Mead in the late 1940s (Hubbs 1954, Courtney and Robbins 1989).

The first ichthyofaunal survey of the Colorado River in Glen Canyon in 1958-59 (McDonald and Dotson 1960) reported 17 species of fish (6 native, 11 non-native) from the mainstem and various tributaries (Table 5-1). Of the native species, speckled dace were the most common shoreline inhabitant, flannelmouth suckers were common in the mainstem, and bluehead suckers were found primarily in tributaries. Only two immature razorback suckers and one Colorado squawfish were reported. Humpback chub were not reported, probably because the survey was concentrated in Glen Canyon, which is an intervening alluvial reach not usually considered preferred habitat for the species. Roundtail chub were rare and bonytail were not found.

Postdam (1964-90)

Following completion of Glen Canyon Dam in 1963, Stone and Rathbun (1968) reported 15 species of fish (5 native, 10 non-native) from the tailwater of Glen Canyon Dam in 1967-68 (Table 5-1). Non-native species such as red shiners, rainbow trout, and channel catfish were abundant, and carp were observed in large schools. Razorback suckers were not reported, but humpback chub and "bonytail" were common (probably roundtail chub since specific epithet Gila robusta was used). Colorado squawfish were "rare" in 1968; this was the last documented report of the species from Grand Canyon. Red shiners were common between Glen Canyon Dam and Lees Ferry in 1967, but rare in 1968. This survey also reported coldwater salmonids introduced by resource agencies, including rainbow trout, brown trout, and kokanee salmon.

In August 1968, Miller and Smith (1972) reported 10 species of fish (4 native, 6 non-native) between Lees Ferry and Diamond Creek, noting that introduced fishes greatly outnumbered native fishes. Channel catfish were particularly abundant as well as carp, fathead minnows, and red shiners. Holden and Stalnaker (1975) reported only 8 species (4 native, 4 non-native) from Glen, Marble, and Grand canyons in 1967-71, including humpback chub between Glen Canyon Dam and Lees Ferry, and Minckley and Blinn (1976) reported 10 species (4 native, 6 non-native).

In 1970-73, Suttkus et al. (1976) reported 18 species (5 native, 13 non-native) between Glen Canyon Dam and Pearce Ferry, including one Virgin spinedace from the mouth of the Paria River, humpback chub from various mainstem locations and the LCR, and flannelmouth suckers, bluehead suckers, and speckled dace from numerous tributary inflows. They also reported red shiners from five locations, including five fish from RM 194.5, one from RM 212.5, and unspecified numbers from three sites in Lake Mead (Spencer Creek, Scorpion Island, Pearce Ferry). This was the last record of red shiners between the dam and the Lake Mead inflow, except for one specimen caught by Arizona Game and Fish (AGF) in 1992 at RM 117.4 (T. Hoffnagle, AGF, pers.comm.). The disappearance of the red shiner from Grand Canyon appeared to coincide with consistently cold dam releases which occurred about 1973 (See Fig. 3-2 in Chapter 3 - HYDROLOGY).

Carothers and Minckley (1981), in a comprehensive treatise of fishes of Grand Canyon, identified 17 species (5 native, 12 non-native), with 6 species comprising nearly 100% of individuals (carp-42%, speckled dace-16%, flannelmouth sucker-14%, rainbow trout-13%, bluehead sucker-9%, humpback chub-6%). Razorback sucker were also reported.

Kaeding and Zimmerman (1982, 1983), as part of the U.S. Fish and Wildlife Service's Colorado River Fishery Project in 1980-81, reported 14 species of fish from 32 km of the Colorado River (16 km above and 16 km below the LCR inflow). Fathead minnows, speckled dace, and plains killifish were common to abundant along shorelines, flannelmouth suckers and bluehead suckers were present primarily downstream of the LCR inflow; and rainbow trout were abundant throughout. This study also reported 10 redside shiners from RM 61.4 to RM 71.7 as the only record of the species from the mainstem Colorado River in Grand Canyon.

As part of GCES Phase I, AGF conducted a complete fishery investigation of the Colorado River and tributaries between Glen Canyon Dam and Diamond Creek from April 1984 through June 1986 (Maddux et al. 1987). Twenty fish species (5 native, 15 non-native) were reported, and rainbow trout dominated total catch by number with 78%, 85%, 59%, 77%, and 42% of composition in five reaches sampled progressively downstream. The second most common species was carp with 5%, 13%, 18%, and 37% of numerical composition in the lower four reaches. Brown trout were the second most common fish between the LCR and Bright Angel Creek with 19% of composition. Native species were 17%, 8%, 8%, 2%, and 19% of fish composition in the five reaches. AGF also reported five golden shiners (range, 68-167 mm TL) from 1985 to 1988, from RM 66.0 to RM 165.0 and one specimen (124 mm TL) from the lower LCR. Red shiners were not reported from the mainstem, but two specimens (50, 70 mm TL) were collected in May 1989 from the lower LCR, about 100 m upstream from the confluence (Minckley 1989).

Present (1990-93)

Present composition, distribution, and abundance of fishes in the Colorado River in Grand Canyon are

Table 5-1. 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 (herrings)											
threadfin shad (Dorosoma petenense)	-	-	-	-	-	R	-	-	-	-	C[l]
Family: Cyprinidae (minnows)											
red shiner (Cyprinella lutrensis)	-	-	C/R	C	-	R	-	-	-	-	A[l]
common carp (Cyprinus carpio)	-	C	A	C	C	A	C	A	LC	A	A
Utah chub (Gila atraria)	-	R	-	-	-	-	-	-	-	R	-
humpback chub (Gila cypha)	P	-	C	R	R	R	R[m]	LC	LC	R	LC
bonytail (Gila elegans)	P	-	-	-	-	-	-	-	-	-	-
roundtail chub (Gila robusta)	P	R	C	-	-	-	-	-	-	-	-
Virgin spinedace (Lepidomeda mollispinnis)	P	-	-	-	-	R	-	-	-	-	-
golden shiner (Notemigonus crysoleucas)	-	-	-	-	-	R	-	R	-	R	R[l]
fathead minnow (Pimephales promelas)	-	A	-	A	R	C	A	C	A	A	LC
woundfin (Plagopterus argentissimus)	P	-	-	-	-	-	-	-	-	-	-
Colorado squawfish (Ptychocheilus lucius)	P	R	R	-	-	-	-	-	-	-	-
speckled dace (Rhinichthys osculus)	P	A	-	C	A	A	A	C	C	A	C
redside shiner (Richardsonius balteatus)	-	-	-	-	-	-	-	-	R	-	-
Family: Catostomidae (suckers)											
bluehead sucker (Catostomus discobolus)	P	C	C	C	C	C	A	C	C	C	C
flannelmouth sucker (Catostomus latipinnis)	P	C	A	C	C	C	A	C	C	C	C
razorback sucker (Xyrauchen texanus)	P	R	-	-	-	-	-	R	-	R	-
Family: Ictaluridae (catfishes, bullheads)											
black bullhead (Ameiurus melas)	-	C	R	R	-	-	R	-	R	R	R
yellow bullhead (Ameiurus natalis)	-	-	-	-	-	-	-	-	-	R	-
channel catfish (Ictalurus punctatus)	-	A	A	A	R	C	R	C	LC	R	LC
Family: Salmonidae (trout)											
cutthroat trout (Oncorhynchus clarki)	-	-	-	-	-	-	-	-	R	R	-
coho salmon (Oncorhynchus kisutch)	-	-	-	-	-	R	-	-	-	-	-
rainbow trout (Oncorhynchus mykiss)	-	-	A	C	C	C	C	A	A	A	A
kokanee (Oncorhynchus nerka kennerlii)	-	-	R	-	-	-	-	-	-	-	-
brown trout (Salmo trutta)	-	-	R	-	-	-	-	C	C	C	C

brook trout (Salvelinus fontinalis)	-	-	-	-	-	-	-	C	C	C	R
Family: Cyprinodontidae (killifishes)											
plains killifish (Fundulus zebrinus)	-	R	-	-	-	C	C	C	C	R	LC
Family: Poecilidae (livebearers)											
mosquitofish (Gambusia affinis)	-	R	-	-	-	R	-	-	-	-	LC[l]
Family: Percichthyidae (temperate basses)											
striped bass (Morone saxatilis)	-	-	-	-	-	-	-	R	-	R	R
Family: Centrarchidae (sunfish)											
green sunfish (Lepomis cyanellus)	-	C	C	-	-	R	-	R	-	R	R
bluegill (Lepomis macrochirus)	-	R	-	-	-	R	-	R	-	-	R[l]
largemouth bass (Micropterus salmonides)	-	R	C	-	-	R	-	R	-	R	R[l]
black crappie (Pomoxis nigromaculatus)	-	-	R	-	-	-	-	-	-	-	R[l]
Family: Percidae (perches)											
yellow perch (Perca flavescens)	-	R	-	-	-	-	-	-	-	-	-
walleye (Stizostedion vitreum)	-	-	R	-	-	-	-	-	-	-	R
Total Number of Species	10	17	15	10	8	18	10	21	14	20	22

[a]Miller (1959)
[b]McDonald and Dotson (1960)
[c]Stone and Rathbun (1968)
[d]Miller and Smith (1972)
[e]Holden and Stalnaker (1975)
[f]Suttkus et al. (1976)
[g]Minckley and Blinn (1976)
[h]Carothers et al. (1981)
[i]Kaeding and Zimmerman (1983)
[j]Maddux et al. (1987)
[k]Valdez and Ryel (1995)
[l]Valdez (1994), reported only below Diamond Creek
[m]reported as "Gila elegans"

Table 5-2. Dates and approximate locations of non-native fish introductions or the first reports in the area of Grand Canyon. See Table 5-1 for scientific names.

Species	Date	Location	Citation
Family: Cluperdae			
threadfin shad	1954[a]	Lake Mead	McCall (1979)
	1968[a]	Lake Powell	Miller et al. (1969)
Family: Cyprinidae			
red shiner	Late 1940s	riverside bait rearing ponds	Hubbs (1954)
common carp	~1890	lower Colorado River	U.S. Fish and Wildlife Service (1980)
Utah chub	1958	Glen Canyon	McDonald and Dotson (1960)
golden shiner	1976[a]	Kanab Creek	Suttkus (1976)
fathead minnow	1940s	Lake Mead baitshops	McCall (1979)
redside shiner	1982	Lees Ferry, bait fishermen	Kaeding and Zimmerman (1983)
Family: Ictaluridae			
black bullhead	1904	Lake Mead	U.S. Fish and Wildlife Service (1980)
yellow bullhead	1978	Lake Mead	McCall (1979)
channel catfish	1890s	lower Colorado River	Miller and Alcorn (1943)
Family: Salmonidae			
cutthroat trout	1978[a]	Lees Ferry	McCall (1979)
coho salmon	1970[a], 1971[a]	Lees Ferry, Lake Mead	Haden (1992)
rainbow trout	1923[a]	Tapeats Creek	Stricklin (1950)
kokanee	1967	Glen Canyon	Stone and Rathbun (1968)
brown trout	1926[a]	Shinumo Creek	Stricklin (1950)
brook trout	1920[a]	Bright Angel Creek	Stricklin (1950)
Family: Cyprinodontidae			
plains killifish	~1938	Little Colorado River	Miller and Lowe (1967)
Family: Poecilidae			
mosquitofish	1926	common before Lake Mead	Miller and Lowe (1967)
Family: Percichthyidae			
striped bass	1969[a]	Lake Mead	McCall (1979)
	1974[a]	Lake Powell	Gustavson et al. (1985, 1990)
Family: Centrarchidae			
green sunfish	1937[a]	Lake Mead	McCall (1979)
bluegill	1958	Glen Canyon	McDonald and Dotson (1960)
largemouth bass	1935[a]	Lake Mead	McCall (1979)
black crappie	1935[a]	Lake Mead	Wallis (1951)
Family: Percidae			
yellow perch	1960s	First released lower Colorado River	Minckley (1973)
walleye	1963	All ready present in Lake Powell Basin	Gustaveson et at. (1985, 1990)

[a] documented introductions by agencies

based primarily on the findings of this investigation. Some preliminary information from a concurrent mainstem investigation by AGF was available from progress reports and personal communications.

Fifteen species of fish (4 native, 11 non-native) and one hybrid form were captured in the Colorado River (not including tributaries) between Lees Ferry and Diamond Creek during this 1990-93 investigation (Table 5-3). An additional 7 non-native species (Table 5-1) were captured between Diamond Creek and Pearce Ferry in a separate study (1992-94) for the Hualapai Indian Tribe (Valdez 1993, 1994, 1995). Of the eight mainstem native species, only four were found--humpback chub, flannelmouth sucker, bluehead sucker, and speckled dace. Colorado squawfish, roundtail chub, bonytail, and razorback sucker were not captured, although five specimens were classified as flannelmouth sucker x razorback sucker hybrids, based on external morphological characters (McAda and Wydoski 1980). Morphologic variation (e.g., nuchal hump depth, caudal peduncle length and depth) and meristic variation (e.g., fin ray counts) of humpback chub handled in Grand Canyon indicated high morphologic plasticity and suggested historic introgressive hybridization between the three forms of Colorado River Gila (Gilbert 1961, Kaeding and Zimmerman 1983, Dowling and DeMarais 1993). This morphologic variation has led to considerable confusion in distinguishing the Colorado River Gila and to interchangeable use of common and scientific names by past investigations. There continues to be a lack of substantial evidence that confirms the occurrence of roundtail chub in the mainstem Colorado River in Grand Canyon.

Eleven non-native species found between Lees Ferry and Diamond Creek were also previously reported by other investigators (Table 5-1, Fig. 5-1); these include common carp, fathead minnow, black bullhead, channel catfish, rainbow trout, brown trout, brook trout, plains killifish, striped bass, green sunfish, and walleye. Carp and channel catfish were common throughout, rainbow trout and brown trout were abundant to common in upstream reaches, and fathead minnows and plains killifish were locally common along shorelines. A total of 39 striped bass and 1 walleye were caught in the lower canyon in July and August of 1991-93; these fish were probably summer spawning migrants from Lake Mead. Utah chub, yellow bullhead, and cutthroat trout, previously reported as rare, were not captured during this investigation. Red shiners were not found upstream of Bridge Canyon (RM 235.0), but were abruptly abundant in tributaries, tributary inflows, and shorelines downstream of Bridge Canyon. Lacustrine species (threadfin shad, bluegill, largemouth bass, black crappie, and walleye) were common transients from Lake Mead to below Bridge Canyon, and one golden shiner was captured near Lost Creek (RM 249.0)(Valdez 1994). The only red shiner reported between Glen Canyon Dam and Bridge Canyon since 1973 was a single specimen (38 mm TL) captured by AGF on June 26, 1992 at RM 117.4 (T. Hoffnagle, AGF, pers. comm).

Nine species of fish were regularly captured each year of this 1990-93 investigation, hence these species were considered common mainstem residents, and included rainbow trout, humpback chub, flannelmouth sucker, carp, brown trout, speckled dace, fathead minnow, bluehead sucker, and channel catfish. Six species were captured intermittently during the investigation; plains killifish, black bullhead, and green sunfish were locally uncommon to rare in sheltered shoreline habitats, brook trout were infrequently captured, and striped bass and walleye were midsummer spawning migrants from Lake Mead.

Annual changes in relative numbers of individuals of a given species and age category (Table 5-4) were difficult to assess because of changes in sampling effort, sampling variation caused by temporal and spatial distribution of fishes, and gear efficiency relative to river condition. Increased numbers of YOY humpback chub in 1993 were attributed to increased sampling of shorelines near the LCR and to high production in the LCR in 1993 (See Chapter 6 - DEMOGRAPHICS).

Total numbers of fishes were highest in Region I and lowest in Regions 0 and III. (Table 5-5, Fig. 5-2). The number of species also increased by geomorphic reach (See Table 2-1 in Chapter 2 - STUDY DESIGN,) in a downstream direction (Fig. 5-3), from a low of 3 in Reach 2 (RM 11.3-22.6) to a high of 14 in Reach 10 (RM 159.9-213.9). The four native species (i.e., humpback chub, flannelmouth sucker, bluehead sucker, and speckled dace) were present in all reaches, except for Reach 1 (RM 0.0-11.3) (bluehead sucker,

Table 5-3. Fish species captured during this investigation in the Colorado River from Lees Ferry to Diamond Creek, October 1990 - November 1993. See Table 5-1 for scientific names.

Common Name	Species Code	Status[a]	YOY	JUV	ADU	Total	Percent
Family: Cyprinidae (minnows)							
common carp	CP	EX	4	44	2,375	2,423	8.6
humpback chub	HB	EN	2,865[b]	1,638	1,791	6,294	22.3
fathead minnow	FH	NN	44	12	1,074	1,130	4.0
speckled dace	SD	NA	4	92	1,395	1,491	5.3
Family: Catostomidae (suckers)							
bluehead sucker	BH	NA	101	250	689	1,040	3.7
flannelmouth sucker	FM	EN	183	395	2,197	2,775	9.8
flannelmouth x razorback sucker	FR	-	0	0	5	5	<0.1
unidentified sucker	SU	-	32	0	0	32	0.1
Family: Ictaluridae (catfishes, bullheads)							
black bullhead	BB	NN	0	3	3	6	<0.1
channel catfish	CC	NN	4	5	104	113	0.4
Family: Salmonidae (trout)							
rainbow trout	RB	NN	169	1,152	9,800	11,121	39.4
brown trout	BR	EX	2	107	1,564	1,673	5.9
brook trout	BK	NN	0	0	6	6	<0.1
Family: Cyprinodontidae (killifishes)							
plains killifish	PK[c]	NN	1	0	75	76	0.3
Family: Percichthyidae (temperate basses)							
striped bass	SB	NN	0	0	39	39	0.1
Family: Centrarchidae (sunfish)							
green sunfish	GS	NN	1	1	1	3	<0.1
Family: Percidae (perches)							
walleye	WE	NN	0	0	1	1	<0.1
Totals			**3,410**	**3,699**	**21,119**	**28,228**	**100**

[a]NA = native to the drainage
EN = endemic to the drainage
EX = exotic, introduced from another continent
NN = non-native, introduced from another drainage in North America
[b]Does not include 14 specimens captured on July 14, 1994
[c]Common synonym Rio Grande killifish

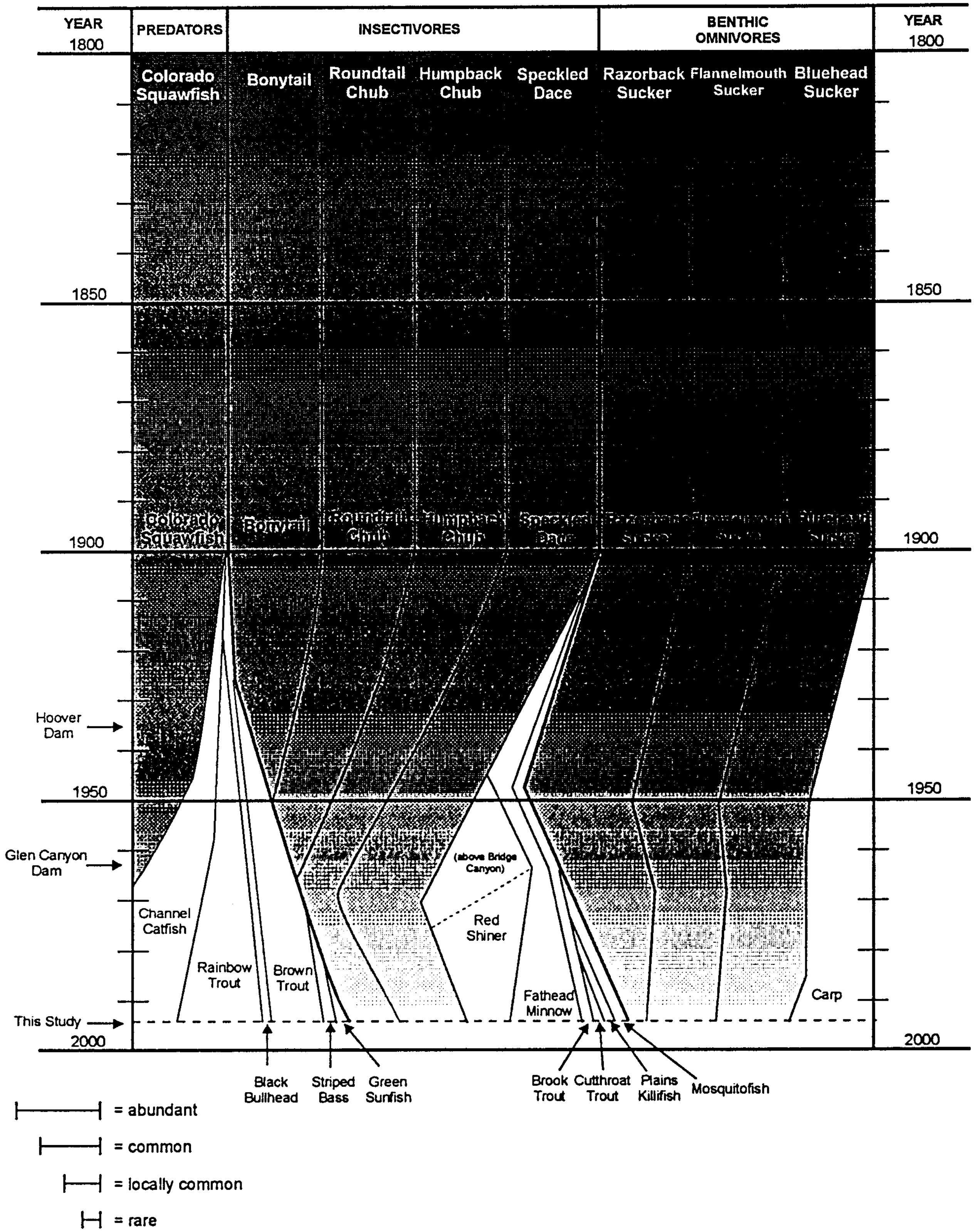

Fig. 5-1. Conceptual chronology of relative abundance of fish species in Grand Canyon from 1800-1993.

Table 5-4. Fish species captured by year and age category (in order of abundance) in the Colorado River in Grand Canyon, October 1990 - November 1993. See Table 5-3 for description of species codes. YOY = young-of-year, JUV = juvenile, ADU = adult.

Species Code	1990-91				1992				1993				TOTAL			
	YOY	JUV	ADU	TOTAL	YOY	JUV	ADU	TOTAL	YOY	JUV	ADU	TOTAL	YOY	JUV	ADU	TOTAL
RB	45	382	4,309	4,736	42	257	2,257	2,556	82	513	3,234	3,829	169	1,152	9,800	11,121
HB	117	241	608	966	119	527	422	1,068	2,629	870	761	4,260	2,865	1,638	1,791	6,294
FM	4	53	798	855	57	140	550	747	122	202	849	1,173	183	395	2,197	2,775
CP	2	15	1,168	1,185	2	9	787	798	0	20	420	440	4	44	2,375	2,423
BR	0	24	703	728	2	62	579	643	0	20	282	302	2	107	1,564	1,672
SD	1	0	163	164	1	0	385	386	2	92	847	941	4	92	1,395	1,491
FH	0	0	18	18	11	0	549	560	33	12	507	552	44	12	1,074	1,130
BH	1	14	198	213	8	48	179	235	92	188	312	592	101	250	689	1,040
CC	1	1	59	61	2	2	22	26	1	2	23	26	4	5	104	113
PK	0	0	5	5	1	0	65	66	0	0	5	5	1	0	75	76
SB	0	0	17	17	0	0	3	3	0	0	19	19	0	0	39	39
SU	0	0	0	0	28	0	0	28	4	0	0	4	32	0	0	32
FR	0	0	3	3	0	0	2	2	0	0	0	0	0	0	5	5
BB	0	0	1	1	0	2	0	2	0	1	2	3	0	3	3	6
BK	0	0	4	4	0	0	1	1	0	0	1	1	0	0	6	6
GS	0	0	0	0	0	1	0	1	1	0	1	2	1	1	1	3
WE	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Totals:	171	730	8,055	8,957	273	1,048	5,801	7,122	2,966	1,920	7,263	12,149	3,410	3,699	21,119	28,227

Table 5-5. Number and percentage of fish species by age category in the four study regions. See Table 5-3 for description of species codes. YOY = young-of-year, JUV = juvenile, ADU = adult.

	Region 0					Region I					Region II					Region III				
Species	YOY	JUV	ADU	Total	%	YOY	JUV	ADU	Total	%	YOY	JUV	ADU	Total	%	YOY	JUV	ADU	Total	%
RB	34	291	2,012	2,337	94.3	56	412	5,152	5,620	37.0	72	385	2,527	2,984	37.6	7	64	112	183	6.9
HB	0	0	26	26	1.0	2,885	1,537	1,569	5,991	39.4	37	45	181	263	3.3	0	2	12	14	0.5
FM	0	0	64	64	2.6	117	147	990	1,254	8.3	27	131	834	992	12.5	39	117	309	465	17.6
CP	0	0	37	37	1.5	2	25	203	230	1.5	0	7	1,292	1,299	16.4	2	12	843	857	32.4
BR	0	1	4	5	0.2	0	1	67	68	0.4	2	100	1,480	1,582	20.0	0	4	13	17	0.6
SD	0	0	4	4	0.2	2	0	712	714	4.7	2	0	279	281	3.5	0	92	400	492	18.6
FH	0	0	0	0	0.0	26	8	878	912	6.0	5	0	132	137	1.7	13	4	64	81	3.1
BH	0	0	2	2	0.1	79	108	157	344	2.3	9	49	242	300	3.8	13	93	288	394	14.9
CC	0	0	0	0	0.0	3	3	27	33	0.2	1	1	3	5	0.1	0	1	74	75	2.8
PK	0	0	0	0	0.0	0	0	10	10	0.1	0	0	56	56	0.7	1	0	9	10	0.4
SB	0	0	0	0	0.0	0	0	0	0	0.0	0	0	8	8	0.1	0	0	32	32	1.2
SU	0	0	0	0	0.0	1	0	0	1	<0.1	16	0	0	16	0.2	15	0	0	15	0.6
FR	0	0	0	0	0.0	0	0	4	4	<0.1	0	0	1	1	<0.1	0	0	0	0	0.0
BB	0	0	0	0	0.0	0	2	3	5	<0.1	0	1	0	1	<0.1	0	0	0	0	0.0
BK	0	0	2	2	0.1	0	0	1	1	<0.1	0	0	0	0	<0.1	0	0	3	3	0.1
GS	0	0	0	0	0.0	0	1	1	2	<0.1	0	0	0	0	0.0	1	0	0	1	<0.1
WE	0	0	0	0	0.0	0	0	0	0	0.0	0	0	0	0	0.0	0	0	1	1	<0.1
Total	**34**	**292**	**2,151**	**2,477**	**100**	**3,171**	**2,244**	**9,780**	**15,195**	**100**	**171**	**719**	**7,038**	**7,928**	**100**	**91**	**389**	**2,169**	**2,649**	**100**

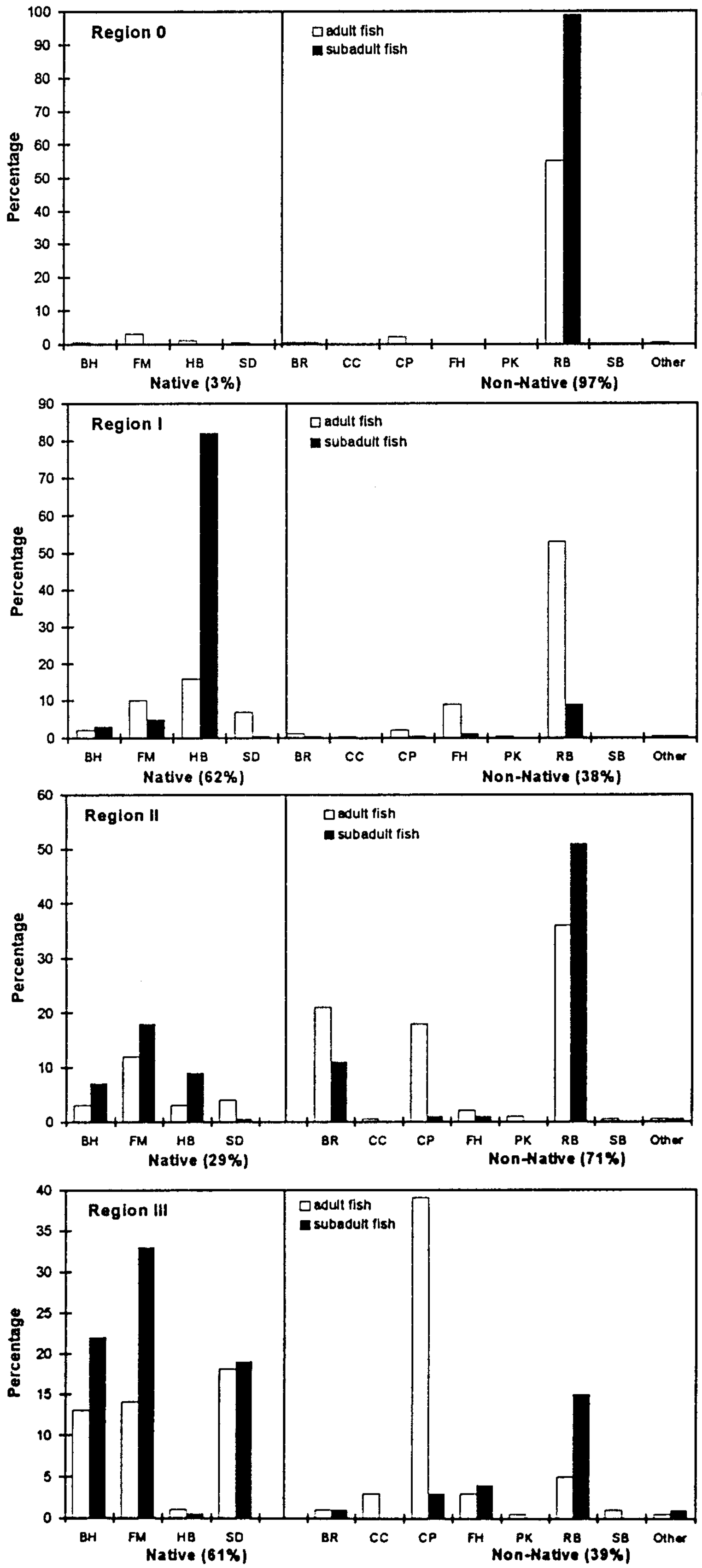

Fig. 5-2. Percentage of adults and subadults of common fish species by study region, 1990-1993. See Table 5-3 for description of species codes.

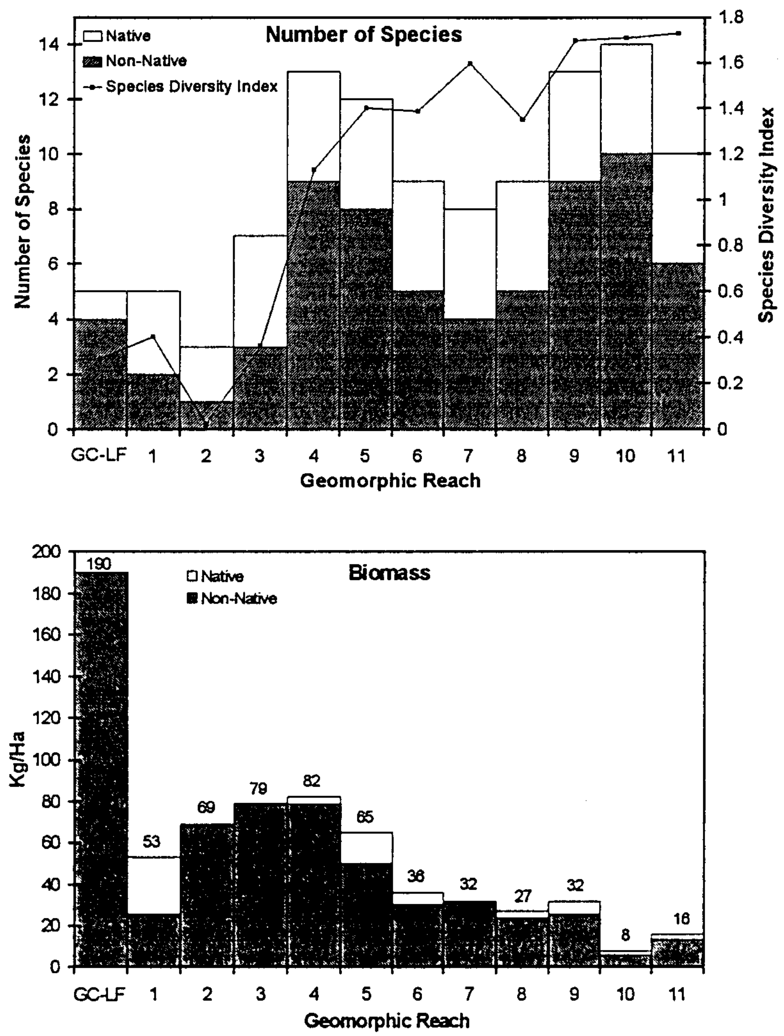

Fig. 5-3. Number of species, species diversity, and biomass of native and non-native fish species by geomorphic reach from Lees Ferry to Diamond Creek. Data for Glen Canyon Dam to Lees Ferry (GC-LF) from Arizona Game and Fish Department (1993).

flannelmouth sucker, and speckled dace were present) and Reach 2 (flannelmouth sucker were present). Numbers of non-native species increased downstream from a low of 1 in Reach 2 to a high of 10 in Reach 10. Non-native species in Reaches 1-3 (RM 0.0-35.9) were primarily coldwater salmonids, while non-native species in Reaches 4-11 (RM 35.9-226.0) were primarily warmwater cyprinids, ictalurids, and centrarchids. Numbers of non-native species increased dramatically from 3 in Reach 3 (RM 22.6-35.9) to 9 in Reach 4 (RM 35.9-61.5), a possible influence of the warm and productive LCR inflow at RM 61.3. Similarly, the increase in non-native species from 5 in Reach 8 (RM 125.5-139.9) to 9 in Reach 9 (RM 139.9-159.9) could also be attributed to warm inflows from Kanab Creek (RM 143.5) and Havasu Creek (RM 156.7).

Fish species diversity also increased dramatically downstream, with a low Shannon-Weaver index (H) of 0.022 in Reach 2 to a high of 1.728 in Reach 11 (RM 213.9-226.0) (Fig. 5-3). Maddux et al. (1987) reported the lowest diversity index of 0.20 in AGF Reach 20 (RM 0.0-61.5) and higher diversity indices of 0.77 and 0.63 in AGF Reaches 30 (RM 61.5-88.0) and 50 (RM 166.5-226.0) respectively. The AGF Reach 30 approximately corresponded to Reach 5 (RM 61.5-77.4) of this study (H=1.400), and AGF Reach 50 corresponded to Reach 10 (H=1.708) and Reach 11 (H=1.728) of this study (RM 159.9-213.9 and RM 213.9-226.0 respectively).

Estimated fish biomass followed a different longitudinal pattern than either species richness or species diversity (Fig. 5-3). Biomass varied from a high of 190 kg/ha between Glen Canyon Dam and Lees Ferry to a low of 8 kg/ha in Reach 10 (RM 159.9-213.9). The highest biomasses were recorded in Reaches 2 through 5, while lowest biomass occurred in Reaches 1 and in Reaches 6 through 11.

Abundances of the six most common fish species were quantified by AM_{CPE} for netting (Fig. 5-4) and electrofishing (Fig. 5-5) in each of the 11 geomorphic reaches. Catch rates of adults decreased downstream of Reach 2 for electrofishing and below Reach 3 for netting, while AM_{CPE} for subadults was variable. Netting and electrofishing catch rates of adult rainbow trout exceeded those of all other species in each of the first eight reaches, except for Reach 5 (Furnace Flats, RM 61.5-77.4) where AM_{CPE} for humpback chub was higher near the LCR inflow. Netting catch rates of adult flannelmouth suckers and bluehead suckers were generally lowest in lower reaches, except in Reach 9 (Muav Gorge, RM 139.9-159.9) in association with the Havasu Creek inflow.

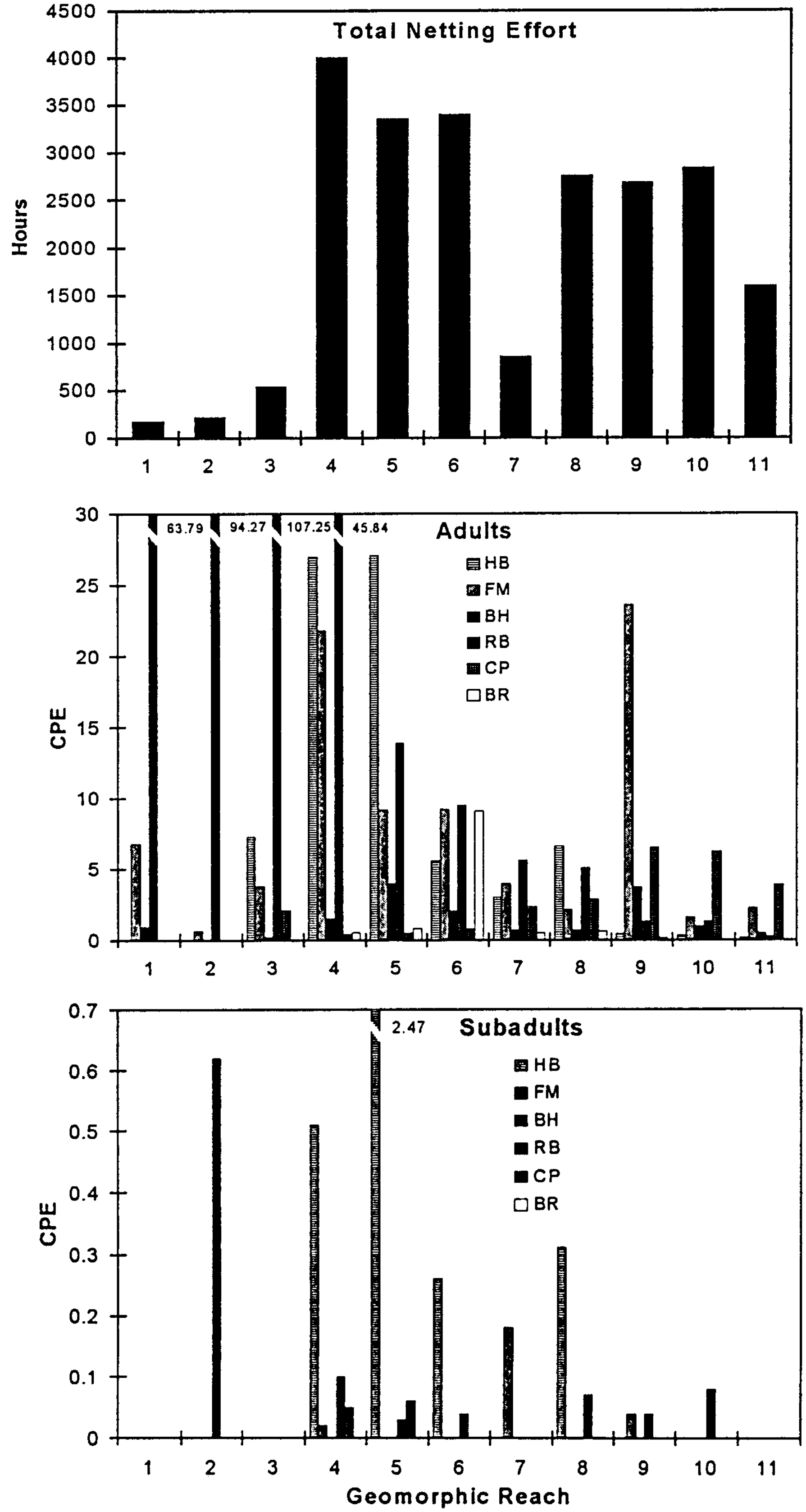

Fig. 5-4. Gill and trammel netting effort (hours) and CPE(AM$_{CPE}$ # fish/100 ft/100 hr) for adult and subadult humpback chub (HB), flannelmouth sucker (FM), bluehead sucker (BH), rainbow trout (RB), carp (CP), and brown trout (BR) in 11 geomorphic reaches. See Table 2-1 for description of geomorphic reaches.

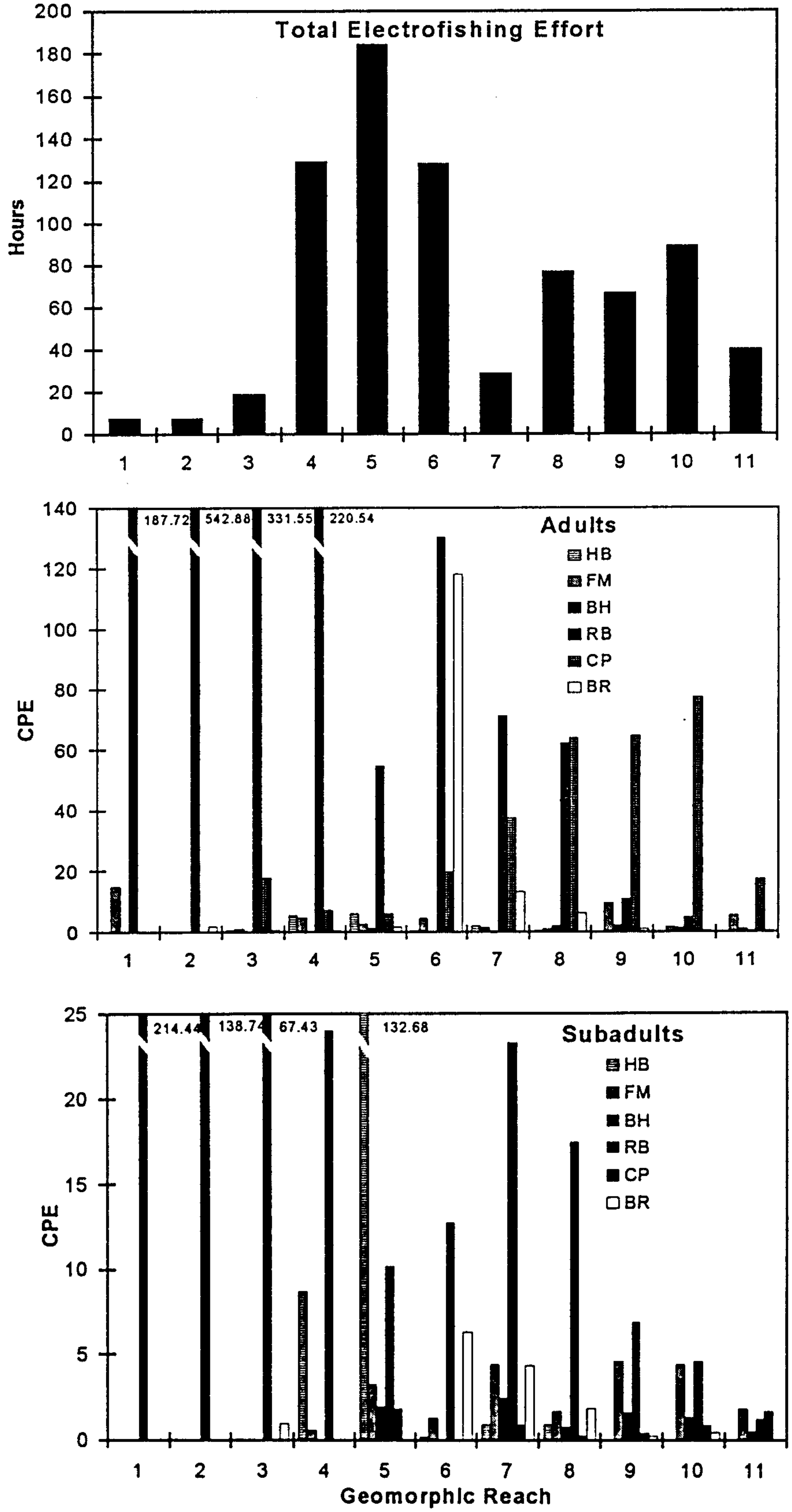

Fig. 5-5. Electrofishing effort (hours) and CPE (AM_{CPE} # fish/10 hr) for adult and subadult humpback chub (HB), flannelmouth sucker (FM), bluehead sucker (BH), rainbow trout (RB), carp (CP), and brown trout (BR) in 11 geomorphic reaches. See Table 2-1 for description of geomorphic reaches.

The association of high catch rates with tributary inflows was further examined by comparing species composition and AM_{CPE} for nets (Table 5-6) and electrofishing (Table 5-7) between 1-mi subreaches at six major tributary flows with randomly-selected 1-mi subreaches within the same geomorphic reach. Numbers of individuals and species captured by nets were higher near tributary inflows than in disjunct areas, except for Tapeats Creek. Numbers and catch rates of fish captured with nets at inflows of the LCR, Shinumo Creek, Kanab Creek, and Havasu Creek were dominated by native species, i.e., humpback chub at the LCR and Shinumo Creek, and flannelmouth suckers at the LCR, Kanab Creek and Havasu Creek. Brown trout and rainbow trout were most abundant at inflows of Bright Angel Creek and Tapeats Creek, respectively.

Non-native fish were dominant in electrofishing catches at inflows of all six major tributaries (Table 5-7). Carp were the most abundant species at Kanab Creek and Havasu Creek, rainbow trout at the LCR and Shinumo Creek, brown trout at Bright Angel Creek, and carp and rainbow trout at Tapeats Creek. Total numbers of fish captured by electrofishing were higher at tributary inflows than in disjunct areas, except for the LCR. Also, the number of species was higher at all inflows, except for Tapeats Creek. Discrepancies in species composition and numbers of fish captured with nets and electrofishing were attributed to inherent gear selectivity for species and habitat.

Distribution And Abundance Of Humpback Chub

Predam (Before 1964)

Predam records are too few to accurately characterize the historic distribution or abundance of humpback chub in Grand Canyon (Fig. 5-6). Emery and Ellsworth Kolb (Kolb and Kolb 1914), during May of 1911, provided the first known description and photographic documentation of the humpback chub. The fish were referred to as "bony tail", since a species description did not exist for the humpback chub. The report was from the Little Colorado River near Beamer's Cabin, about 200 m upstream from the outflow:

"On the opposite side of the pool the fins and tails of numerous fish could be seen above the water. The striking of their tails had caused the noise we had heard. The 'bony tail' were spawning. We had hooks and lines in our packs, and caught all we cared to use that evening."

The humpback chub was described in 1945 by Miller (1946) from a specimen collected in 1942 by N.N. Dodge near Phantom Ranch, a second specimen of unknown origin, and the head, nape, and pectoral fins of a third specimen of unknown origin. These specimens were probably from the Grand Canyon area.

The earliest catalogued collections of the Gila complex from the Grand Canyon were by R.R. Miller for specimens held at the University of Michigan (M. Douglas, ASU, pers. comm.). Sixteen bonytail (G. elegans) (11 from LCR, 3 from Lava Cliff Rapids, 1 from Lees Ferry, 1 from Marble Canyon), six roundtail chub (G. robusta), and five humpback chub (G. cypha) were reported in the 1940s. Morphometrics and meristics from these specimens were used to demonstrate morphologic differentiation using principal components analysis by Bookstein et al. (1985). The reader is referred to the Prologue for a description of those three species of the genus Gila.

Before Glen Canyon Dam was completed in 1963, humpback chub were captured at four locations, including the Phantom Ranch area (Miller 1946), Lees Ferry (Miller 1944), the LCR (Kolb and Kolb 1914), and Spencer Creek (O.L. Wallis reported eight juveniles from Spencer Creek in 1950 in Kubly 1990). Although these records fail to discern historic distribution for the species in Grand Canyon, knowledge of life history requirements and present distributions of other humpback chub populations suggest that the species was historically distributed through most of Grand Canyon with local concentrations. Similar historic flows in areas occupied by other populations (i.e., Westwater Canyon, Cataract Canyon, Desolation Canyon) suggest mainstem reproduction and population maintenance in Grand Canyon.

Postdam (1964-90)

Completion of Glen Canyon Dam in 1963 prompted a renewed interest in the ichthyofauna of the Colorado River in Glen Canyon and Grand Canyon.

Table 5-6. Arithmetic mean catch rate (AM_{CPE}) and percentage (in parentheses) captured by gill and trammel nets in 1-mi subreaches of tributary inflows (I) and adjacent main channel areas (A) in the same geomorphic reach of the Colorado River. See Table 5-3 for description of species codes.

	LCR		Bright Angel		Shinumo		Tapeats		Kanab		Havasu	
	I	A	I	A	I	A	I	A	I	A	I	A
Samples	767	483	381	55	762	30	186	532	473	29	414	29
Effort (hrs)	1,629.5	1,019.1	795.0	121.5	1,556.1	57.5	366.1	1,138.8	986.1	62.4	845.7	62.4
Number of Fish	1556	322	372	3	204	8	30	163	322	2	222	2
River mile	60.9-61.9	64-65	87.2-88.2	97-98	108-109	116-117	133.2-134.2	127-128	143-144	147-148	156.2-157.2	147-148
Species												
BH	6.4 (4.2)	1.8 (3.7)	2.7 (4.3)	0	2.5 (11.8)	0	0.2 (3.3)	0.4 (2.5)	3.5 (7.8)	0	5.6 (13.5)	0
BR	0.7 (0.5)	0.9 (2.8)	27.0 (40.6)	0	1.2 (5.4)	4.2 (12.5)	0	0.5 (1.8)	0.3 (0.6)	0	0	0
CC	1.1 (0.6)	0.2 (0.6)	0	0	0	0	0	0	0.4 (0.9)	0	0	0
CP	0.8 (0.6)	0.6 (1.2)	1.0 (1.1)	0	0.8 (3.4)	3.7 (12.5)	1.4 (13.3)	3.2 (13.5)	8.9 (19.9)	1.6 (50.0)	2.4 (5.4)	1.6 (50.0)
FM	48.7 (37.7)	2.0 (5.0)	26.7 (37.6)	0	3.9 (18.1)	0	0.3 (3.3)	2.8 (14.1)	29.4 (65.8)	0	30.8 (73.4)	0
FR	0.3 (0.2)	0	0	0	0	0	0	0	0	0	0	0
HB	54.0 (38.3)	21.5 (52.2)	0.7 (0.8)	0	11.4 (13.7)	0	0	13.6 (60.7)	0.1 (0.3)	0	1.0 (2.7)	0
RB	23.1 (17.7)	14.0 (34.5)	11.0 (15.6)	3.2 (100.0)	8.5 (47.5)	18.4 (75.0)	10.2 (80.0)	1.7 (7.4)	1.5 (3.1)	0	1.7 (5.0)	0
SB	0	0	0	0	0	0	0	0	0.7 (1.6)	0.2 (50.0)	0	0.2 (50.0)

Table 5-7. Arithmetic mean catch rate (AM_{CPE}) and percentage (in parenthesis) captured by electrofishing in 1-mi subreaches of tributary inflows (I) and adjacent main channel areas (A) in the same geomorphic reach of the Colorado River. See Table 5-3 for description of species codes.

	LCR		Bright Angel		Shinumo		Tapeats		Kanab		Havasu	
	I	A	I	A	I	A	I	A	I	A	I	A
Samples	163	154	72	15	144	4	27	47	45	3	32	3
Effort (hrs)	34.5	60.7	17.4	7.5	43.7	2.3	8.9	16.7	16.1	0.5	8.5	0.5
No. of Fish	732	822	822	153	912	26	154	98	191	3	100	3
River mile	60.9-61.9	64-65	87.2-88.2	97-98	108-109	116-117	133.2-134.2	127-128	143-144	147-148	156.2-157.2	147-148
Species												
BH	0.3 (0.3)	0.8 (0.5)	0.5 (0.1)	0	0.5 (0.2)	0	4.9 (1.3)	2.0 (3.1)	2.3 (2.1)	0	7.2 (60.0)	0
BR	0.3 (0.1)	0.6 (0.5)	499.6 (73.6)	50.4 (22.2)	42.2 (16.1)	22.1 (19.2)	10.5 (4.5)	5.9 (13.3)	0	0	2.5 (2.0)	0
CC	1.2 (0.5)	0.2 (0.1)	0	0	0	0	0	0	0	0	0	0
CP	8.3 (4.1)	13.2 (4.9)	6.0 (1.2)	34.8 (15.0)	36.9 (18.0)	39.3 (34.6)	140.2 (32.5)	15.9 (34.7)	59.0 (51.8)	35.2 (66.7)	47.4 (41.0)	35.2 (66.7)
FM	10.8 (4.6)	2.7 (1.1)	15.0 (1.9)	0	7.7 (2.0)	4.5 (3.8)	0	1.3 (3.1)	15.7 (11.0)	0	41.6 (27.0)	0
FH	11.3 (5.6)	18.7 (6.7)	0	0	0	0	0	0	10.1 (9.9)	0	1.4 (1.0)	0
HB	41.7 (21.6)	123.8 (48.5)	0	0	1.2 (0.2)	0	0	2.9 (4.1)	0	0	0	0
RB	106.2 (50.5)	68.7 (30.7)	191.4 (22.4)	156.4 (62.7)	167.3 (62.4)	48.0 (42.3)	141.0 (61.7)	20.6 (40.8)	15.2 (15.7)	11.9 (33.3)	18.5 (16.0)	11.9 (33.3)
SD	32.4 (12.2)	21.4 (6.8)	8.8 (0.7)	0	16.9 (1.1)	0	0	0.3 (1.0)	10.3 (9.4)	0	1.4 (2.0)	0
PK	0.3 (0.1)	0.2 (0.1)	0	0	0	0	0	0	0	0	2.8 (1.0)	0
BB	0.5 (0.3)	0.6 (0.1)	0	0	0	0	0	0	0	0	0	0
SB	0	0	0	0	0	0	0	0	0	0	8.3 (3.0)	0
BK	0	0	0	0	0	0	0	0	0	0	1.3 (1.0)	0

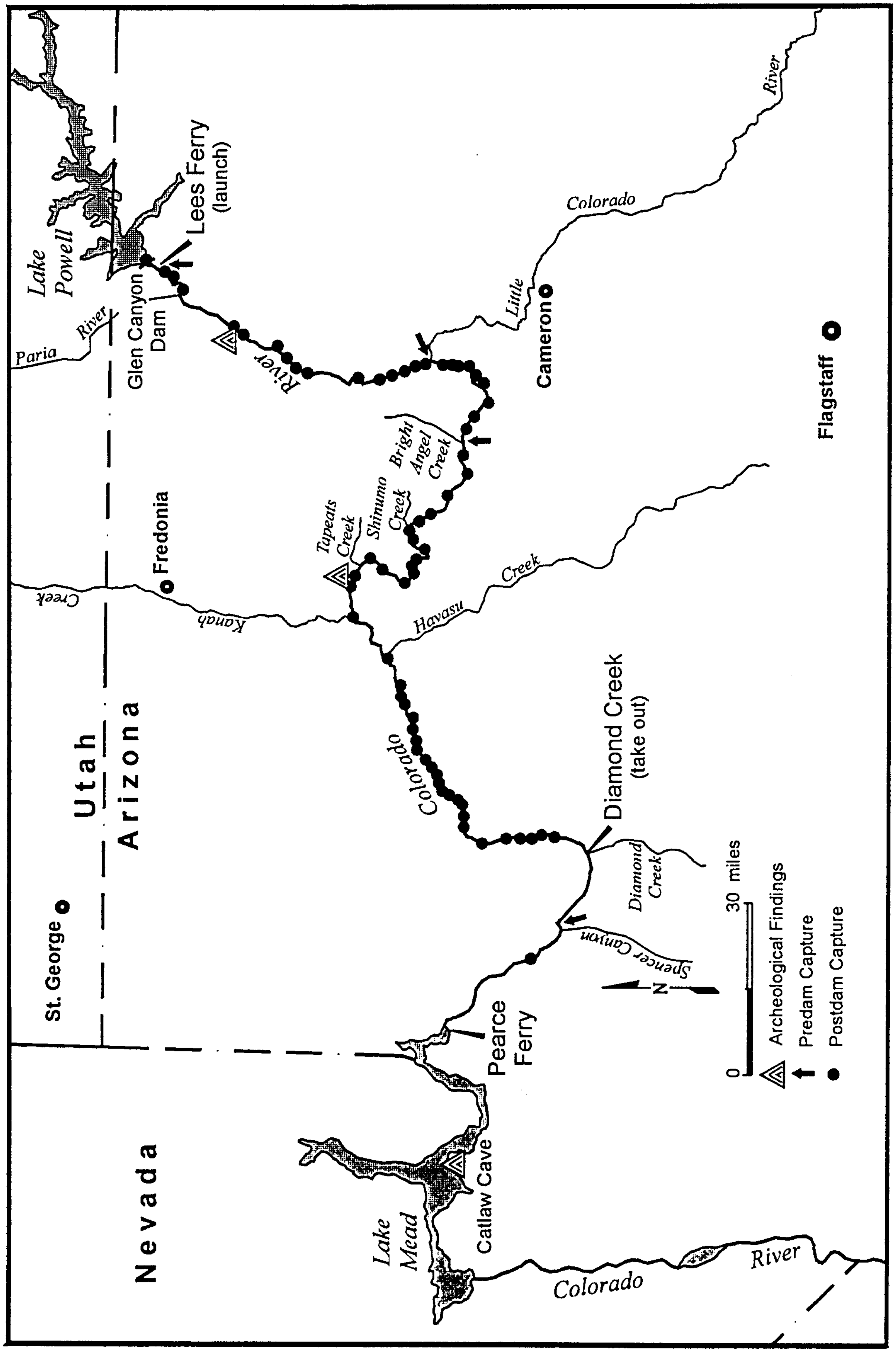

Fig. 5-6. Archeological finds and predam and postdam capture locations of humpback chub in the Colorado River, Grand Canyon.

Humpback chub were consistently reported in AGF creel census from Lees Ferry in 1963-68, although use of an ichthyocide in the lower 300 m of the Paria River in 1965 and 1967 yielded no humpback chub (Stone 1964, 1966; Stone and Queenan 1967; Stone and Rathbun 1968). Stone and Rathbun (1968) also sampled seven tributaries (excluding the LCR) between Lees Ferry and Lake Mead in 1968, and reported no humpback chub. P.B. Holden (BIO/WEST, pers. comm.) collected 15 humpback chub in July 1967 and 1 in August 1970, all within a few hundred meters downstream of Glen Canyon Dam. Humpback chub have not been captured above Lees Ferry since 1970, when dam releases became more consistently cold (See Fig. 3-2 in Chapter 3 - HYDROLOGY) and when a tailwater trout fishery flourished with large rainbow trout of up to 7 kg (Carothers and Brown 1991); the large trout could have preyed on the humpback chub or the humpback chub could have left the area because of consistent cold dam releases. Holden and Stalnaker (1970, 1975) reported humpback chub from Lake Powell in the early to mid 1960s, suggesting that the species was variously distributed throughout the region now inundated by the reservoir.

Humpback chub were captured during 15 scientific collecting trips through Grand Canyon from 1970 through 1976 (Suttkus et al. 1976, Suttkus and Clemmer 1977). Most were YOY or juveniles (<165 mm TL) captured between RM 44.0 (just below President Harding Rapid) and RM 108.7 (Shinumo Creek). Four adults were also caught at the mouth of the LCR in June 1976.

Researchers from the Museum of Northern Arizona captured humpback chub during six river trips in 1977-79 (Carothers and Minckley 1981), including adults between RM 19.5 (above North Canyon) and RM 194.0 (below Boulder Wash), and one juvenile (<100 mm TL) at RM 93.5 (just above Granite Rapid). Of 19 tributaries sampled from the Paria River to Travertine Creek (RM 229.1), humpback chub were captured only in the LCR.

In 1980-81, biologists from the U.S. Fish and Wildlife Service captured 504 adult humpback chub (>200 mm TL) between RM 52.2 (Nankoweep Canyon) and RM 72.3 (Unkar Rapid) (Kaeding and Zimmerman 1982, 1983). Their abundance was reported to assume a normal or "bell-shaped" distribution with greatest numbers at the LCR inflow. Humpback chub smaller than 145 mm TL were not caught from the Colorado River above the LCR confluence, although many small specimens were caught in spring and fall below the confluence.

Arizona Game and Fish Department sampled the Colorado River annually from 1984 through 1989 (Maddux et al. 1987, Kubly 1990) and reported humpback chub from RM 32.0 to RM 217.0, mostly in or around the LCR. Ninety-six percent of humpback chub were captured in AGF Reach 20 (RM 0.0-61.5) and AGF Reach 30 (RM 61.5-87.0). No humpback chub were electrofished from the tailwaters of the dam. Humpback chub were captured with trammel nets in AGF Reach 30 and Reach 40 (RM 87.0-166.0), with little difference in CPE between the two reaches. Humpback chub were also captured at the inflows of tributaries in AGF Reach 40, including Bright Angel, Shinumo, Kanab, and Havasu creeks.

Present (1990-93)

The present distribution of humpback chub in the mainstem is based on findings of this investigation. Preliminary findings from a concurrent mainstem study by AGF were integrated into this report where applicable. A total of 6,294 humpback chub, including 2,865 YOY, 1,638 juveniles, and 1,791 adults, were captured by B/W with 20 gear types (Table 5-8) during 36 trips from October 1990 through November 1993 (Table 5-9). Humpback chub were captured in 52 of 226 (23%) river miles between Lees Ferry and Diamond Creek (Table 5-10, Fig. 5-7); 72% of the fish were between RM 60.0 and RM 65.0. The subreach between RM 62.0 and RM 62.9 yielded the largest number of YOY (555), while RM 63.0-63.9 yielded the largest number of juveniles (410), and RM 61.0-61.9 yielded the largest number of adults (590). Maddux et al. (1987) reported a similar distribution pattern, except for a greater number of subadults in downstream reaches (Fig. 5-7).

Netting and electrofishing catch rates by linear mile (Appendix E Fig. E-1, E-2) further illustrate the clumped distribution for humpback chub in Grand Canyon. All humpback chub captured in Region 0 were between RM 29.0 and RM 31.9, while 99% of adults captured in Region I were between RM 57.0 and RM 65.9 (Malgosa Crest to Lava Canyon). Pooled netting catch rates (AM_{CPE}) for adults were

Table 5-8. Description of fish sample gear and numbers of humpback chub captured in the Colorado River in Grand Canyon, October 1990 - November 1993.

Sample Gear Code-Description	Number of Chub[a]				Gross CPE (no/hrs)[b]
	Y	J	A	T	
Gill Nets					(#/100 ft/100 hr)
GP - 100'x6'x1.5" gill net	0	1	143	144	5.2
GM - 100'x6'x2" gill net	0	0	65	65	3.3
GX - Experimental gill net (100'x6'x0.5, 1, 1.5, 2")	0	45	51	96	9.0
Trammel Nets					
TL - 75'x6'x1.5"x12" trammel net	0	2	586	588	11.6
TK - 75'x6'x1"x12" trammel net	0	33	553	586	11.6
TM - 50'x6'x1"x12" trammel net	0	12	107	119	15.4
TN - 50'x6'x1.5"x12" trammel net	0	0	119	119	14.9
TW - 75'x6'x0.5"x10" trammel net	0	0	0	0	0
TY - Floating TK	0	0	3	3	36.0
TZ - Floating TL	0	0	1	1	25.6
Hoop Nets					(#/100 hr)
HL - Large hoop net (4'x16'x1")	1	1	2	4	0.4
HM - Medium hoop net (3'x13'x1")	0	0	0	0	0
HS - Small hoop net (2'x10'x0.5")	0	0	2	2	0.1
Minnow Traps					
MT - Commercial minnow trap	629	298	0	927	1.1
Electrofishing					(#/10 hr)
EL - 220-V DC	1,272	767	138	2,177	27.8
Seines					(#/100m^2)[c]
SA - 10'x3'x0.125" seine	90	51	0	141	0.9
SB - 30'x4'x0.25" seine	135	42	2	179	1.7
SG - 30'x5'x0.25" seine	705	351	9	1,065	1.8
GF - Floated gill net	0	0	2	2	0.1
TF - Floated trammel net	0	0	0	0	0
Misc. qualitative seine hauls	33	35	5	73	-
Angling[d]					
AN - standard gear	0	0	2	2	-
AL - standard gear, lures	0	0	1	1	-
Total	**2,865**	**1,638**	**1,791**	**6,294**	

[a]Y = young-of-the-year, J = juvenile, A = adult, T = total.
[b]Gross catch-per-effort (CPE computed from total hour areas; all nets adjusted to 100 feet.)
[c]Seining CPE's exclude qualitative seine hauls.
[d]no effort recorded

Table 5-9. Total numbers of young-of-year (YOY), juvenile (JUV), and adult (ADU) humpback chub captured by trip, October 1990 - November 1993[a].

Trip No.	Month	YOY	JUV	ADU	Total
		1990			
1	October	0	1	45	46
2	November	0	2	48	50
3	December	-	-	-	-
		1991			
4	January	0	2	83	85
5	February	0	0	3	3
6	March	0	3	127	130
7	April	0	0	7	7
8	May	0	34	33	67
9	June	0	16	35	51
10	July	6	46	81	133
11	August	-	-	-	-
12	September	63	116	100	279
13	October	-	-	-	-
14	November	48	21	46	115
		1992			
15	January	23	11	27	61
16	February	0	0	6	6
17	March	22	10	44	76
18	April	3	3	38	44
19	May	0	151	54	205
20	June	0	2	38	40
21	July	3	137	102	242
22	August	2	60	6	68
23	September	4	68	48	120
24	October	3	0	0	3
25	November	59	85	59	203
		1993			
26	January	97	52	111	260
27	February	18	18	79	115
28	March	35	25	58	118
29	April	56	42	45	143
30	May	0	141	93	234
31	June	0	49	71	120
32	July	247	89	94	430
33	August	590	99	40	729
34	September	713	288	87	1,088
35	October	646	63	44	753
36	November	227	4	39	270
	Total	**2,865**	**1,638**	**1,791**	**6,294**

[a]Fish were not sampled on trips 3, 11, and 13 when only radio tracking was conducted.

Table 5-10. Ranking of river miles, according to total numbers of humpback chub captured by age category in the mainstem Colorado River, October 1990-November 1993. YOY-young-of-year, JUV=juvenile, ADU=adult.

Ranking	River Mile[a]	YOY	JUV	ADU	Total	Percent
1	61	235	188	590	1013	16.10
2	63	479	410	119	1008	16.02
3	62	555	215	132	902	14.33
4	64	413	320	137	870	13.82
5	60	25	31	346	402	6.39
6	65	141	134	88	363	5.77
7	76	257	76	4	337	5.36
8	68	242	36	3	281	4.47
9	75	104	64	3	171	2.72
10	67	119	24	0	143	2.27
11	58	0	2	123	125	1.99
12	127	0	7	97	104	1.65
13	72	72	20	0	92	1.46
14	71	64	19	1	84	1.33
15	70	65	17	0	82	1.30
16	108	4	13	27	44	0.70
17	74	20	14	0	34	0.54
18	73	17	10	0	27	0.43
19	66	12	10	3	25	0.40
20	30	0	0	24	24	0.38
21	126	1	5	18	24	0.38
22	119	0	7	13	20	0.32
23	78	13	2	0	15	0.24
24	59	0	1	13	14	0.22
25	69	9	1	0	10	0.16
26	128	0	3	7	10	0.16
27	87	5	1	2	8	0.13
28	57	0	0	7	7	0.11

29	156	0	0	6	6	0.10
30	83	1	0	4	5	0.08
31	213	0	0	5	5	0.08
32	86	4	0	0	4	0.06
33	122	1	3	0	4	0.06
34	82	3	0	0	3	0.05
35	85	3	0	0	3	0.05
36	92	1	0	2	3	0.05
37	91	0	1	1	2	0.03
38	114	0	0	2	2	0.03
39	120	0	1	1	2	0.03
40	129	0	0	2	2	0.03
41	187	0	2	0	2	0.03
42	0	0	0	1	1	0.02
43	29	0	0	1	1	0.02
44	31	0	0	1	1	0.02
45	118	0	0	1	1	0.02
46	125	0	1	0	1	0.02
47	142	0	0	1	1	0.02
48	143	0	0	1	1	0.02
49	155	0	0	1	1	0.02
50	195	0	0	1	1	0.02
51	212	0	0	1	1	0.02
52	219	0	0	1	1	0.02
53	221	0	0	1	1	0.02
Total		**2,865**	**1,638**	**1,791**	**6,294**	**100**

[a]Includes all fractions to next highest river mile, e.g. 29 = 29.00 to 29.99.
Excludes 10 fish from LCR, 13 with no age category, 9 with no designated mile of capture, for a total of 2,635 + 32 = 2,667.

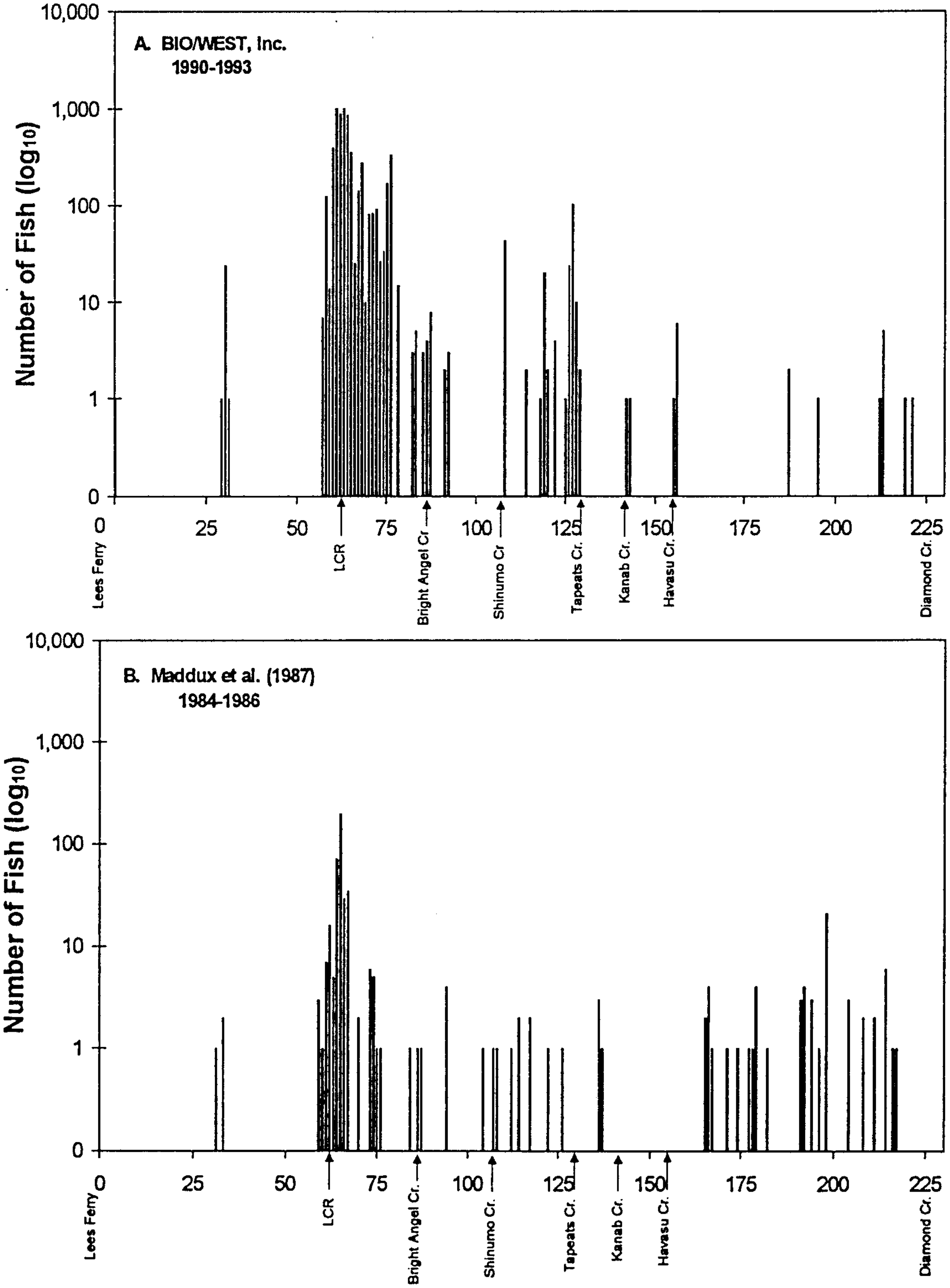

Fig. 5-7. Numbers of humpback chub captured by river mile from Lees Ferry to Diamond Creek by BIO/WEST, October 1990 - November 1993 (A), and by Maddux et al. (1987), April 1984-June 1986 (B).

highest at 56 fish/100 ft/100 hr (FPN) at the LCR inflow (RM 61.0-61.9). Pooled netting AM_{CPE} for humpback chub in Region II did not exceed 15 FPN for any 1-mi subreach--the highest was in RM 114.0-114.9 (Garnet Canyon), where effort was relatively low. Within Region II, adults were also captured with nets in RM 83.0-83.9 (above Clear Creek), RM 87.0-87.9 (Bright Angel Creek inflow), RM 92.0-92.9 (around Salt Creek), RM 108.0-108.9 (Shinumo Creek inflow), RM 119.0-119.9 (upper end of Middle Granite Gorge), RM 126.0-129.9 (below Fossil Canyon), RM 142.0-143.9 (Kanab Creek inflow), and RM 155.0-156.9 (Havasu Creek inflow). In Region III, adults were collected from RM 212.0-212.9 (Pumpkin Spring), RM 219.0-219.9 (Trail Canyon), and RM 221.0-221.9 (222 Mile Canyon). In a separate investigation (Valdez 1994), one adult female humpback chub (329 mm TL, 293 g), was caught on October 5, 1993 near Maxon Canyon (RM 253.2), about 44 km (27 mi) downstream of Diamond Creek.

Highest electrofishing AM_{CPE} for adult humpback chub in Region 0 was 2 fish/10 hr (FPH) in RM 30.0-30.9 (Fig. E-2). Within Region I, AM_{CPE} exceeded 16 FPH in RM 62.0-62.9 (Crash Canyon), but no adults were caught above RM 57.0 or below RM 69.0. In Region II, electrofishing AM_{CPE} was over 7 FPH in RM 118.0-118.9 (Stephen Aisle). Adults were also collected in RM 90.0-90.9 (near Horn Creek), RM 108.0-108.9 (Shinumo Creek inflow), RM 120.0-120.9 (near Blacktail Canyon), and RM 126.0-128.9 (upper end of Middle Granite Gorge). One adult was captured in Region III, at RM 195.6.

Of 4,503 subadult humpback chub captured (2,865 YOY, 1,638 juveniles) (Table 5-3), 99% and 1% of YOY were caught in Regions I and II, respectively, while none were captured in Regions 0 or III. In a subsequent field trip in July 1994, 14 YOY (range, 18-31 mm TL) were captured in Region 0 in a warm spring near RM 30.0 (See Chapter 6 - DEMOGRAPHICS). Of 1,638 juveniles, 97%, 3%, and less than 1% were caught in Regions I, II, and III, respectively, but none were caught in Region 0.

Distribution of subadult humpback chub was associated with distinct aggregations of adults (Table 5-10). Ninety-nine percent of subadults (2,859 YOY, 1,596 juveniles) were captured between RM 58.8 and RM 92.1 (above LCR to Salt Creek). Of these, only 2% were above the LCR confluence, 68% were between the LCR (RM 61.3) and Lava Canyon (RM 65.4), and 30% were between Lava Canyon and Salt Creek. Numbers of subadults captured were dramatically lower downstream of Salt Creek, with only 4 YOY and 13 juveniles near Shinumo Creek (RM 108.1-108.6), 2 YOY and 27 juveniles from Blacktail Canyon to Specter Rapid (RM 119.0-128.9), and 2 juveniles at Whitmore Wash (RM 187.6).

Pooled monthly AM_{CPE} for subadult humpback chub (<200 mm TL) captured with electrofishing, minnow traps, and seines along shorelines (excluding backwaters) between RM 61.3 (LCR inflow) and RM 65.4 (Lava Canyon) illustrates monthly and seasonal patterns of abundance (Fig. 5-8). This area of river provided the best index to year class strength of humpback chub from the LCR because it was the first area occupied by fish dispersing into the mainstem. Annual peaks in electrofishing AM_{CPE} occurred in September 1991 (159.7 FPH), May 1992 (154.7 FPH), and September 1993 (521.7 FPH). Typically, numbers of subadult humpback chub were highest in late summer and early fall, following dispersal of young from the LCR.

Distribution and relative abundance of subadult humpback chub in the mainstem indicate that more young were produced in 1993 than either 1991 or 1992. Over 22 times as many fish classified as YOY were captured in 1993 than in 1991 or 1992 (Fig. 5-8) (See Chapter 6 - DEMOGRAPHICS for discussion of densities and survival rates).

Mainstem Aggregations. Nine aggregations of humpback chub were identified in the mainstem as a result of the previous longitudinal analysis of distribution (Table 5-11, Fig. 5-9). An aggregation was a consistent and disjunct group of fish with no significant exchange of individuals with other aggregations, as indicated by recapture of PIT-tagged juveniles and adults and movement of radio-tagged adults (See Chapter 8 - MOVEMENT). These aggregations also had a high adult recapture rate, indicating long-term residence by individuals. The nine aggregations accounted for 94% of all humpback chub captured in the mainstem, or 92% of YOY (2,640 of 2,865), 94% of juveniles (1,545 of 1,638), and 98% of adults (1,755 of 1,791).

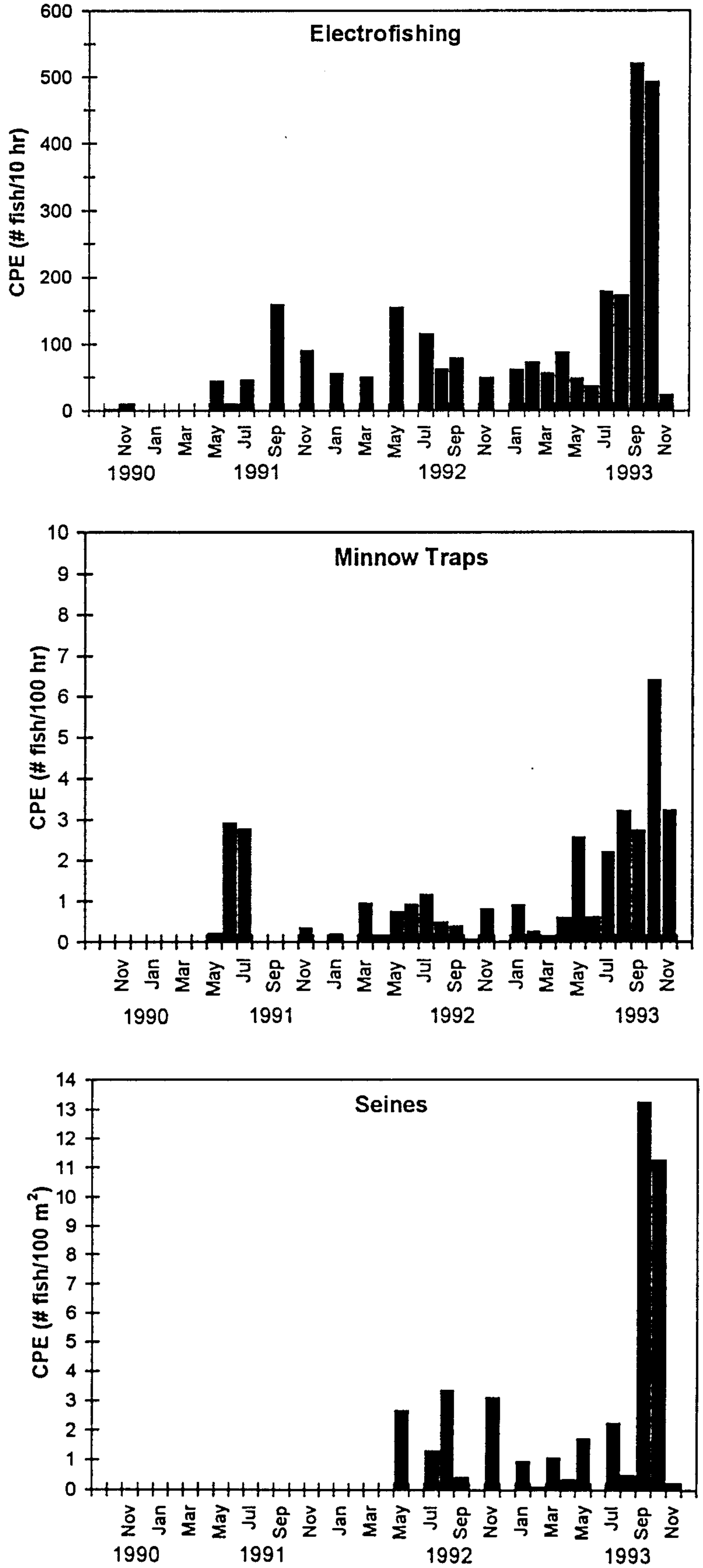

Fig. 5-8. Arithmetic mean catch per effort (AM_{CPE}) for subadult humpback chub (<200 mm TL) captured with electrofishing, minnow traps, and seines along shorelines between RM 61.3 and RM 65.4.

Table 5-11. Location and numbers of humpback chub in nine aggregations in the Colorado River in Grand Canyon, 1990-93.

Aggregations	Location (RM)	Number Captured[a]				% of Total Numbers	Number Recaptured[b]	Estimated Total[c]	Primary Association[d]
		YOY	Juv	Adu	Total				
1. 30-Mile	29.8 - 31.3	14[e]	0	26	26	0.4	6	52	WS
2. LCR Inflow	57.0 - 65.4	1,830	1,293	1,524	4,647	78.2	280	3,482	WT/ED
3. Lava to Hance	65.7 - 76.3	778	226	15	1019	17.2	3	ne	-
4. Bright Angel Creek Inflow	83.8 - 92.2	13	2	9	24	0.4	1	ne	WT
5. Shinumo Creek Inflow	108.1 - 108.6	4	13	27	44	0.7	6	57	WT
6. Stephen Aisle	114.9 - 120.1	0	7	17	24	0.4	2	ne	DF/ED
7. Middle Granite Gorge	126.1 - 129.0	1	4	124	129	2.3	48	98	DF/ED
8. Havasu Creek Inflow	155.8 - 156.7	0	0	7	7	0.2	1	13	WT
9. Pumpkin Spring	212.5 - 213.2	0	0	6	6	0.2	2	5	WS
Total		**2,640**	**1,545**	**1,755**	**5,940**	**100**	**349**		

[a] includes recaptures
[b] includes multiple recaptures, i.e., fish recaptured more than once.
[c] Mark-recapture estimate for adults using Chao M_h estimator (See Chapter 6), ne= no estimate.
[d] WS = warm spring, WT = warm tributary, ED = eddy complex, DF = debris fan.
[e] Captured from a school of about 100 YOY in a spring plume, July 14, 1994, not included in totals for October 1990-November 1993.

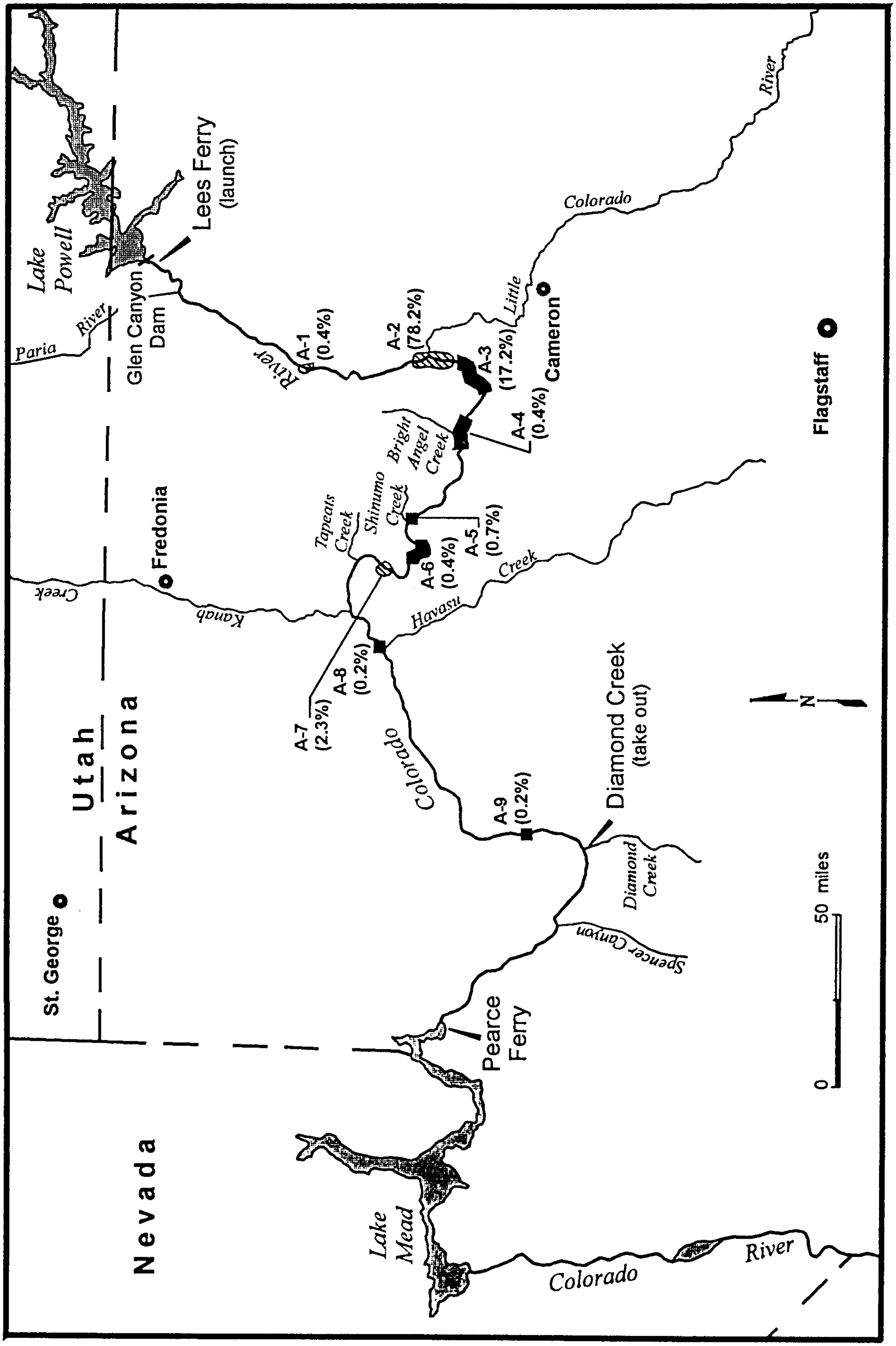

Fig. 5-9. Locations (percentage of total captures of fish within these aggregations) of nine aggregations of humpback chub in the Colorado River in Grand Canyon.

Estimated numbers of adults (mark recapture estimates) in six of nine aggregations ranged from 5 to 3,482 (See Chapter 6 - DEMOGRAPHICS). Estimates could not be made for Lava to Hance (A-3), Bright Angel (A-4), and Stephen Aisle (A-6) aggregations. The only major tributary inflow where aggregations were not found were the Paria River, Kanab Creek (2 found within 1.4 km above inflow), and Tapeats Creek. The following is a description of each aggregation and characteristic attributes of associated habitats.

1. 30-Mile Aggregation. The 30-Mile aggregation of humpback chub was distributed from RM 29.8 to RM 31.3. A total of 26 adults were captured and released in this area during eight sampling trips in 1993, the only year in which this region was sampled, although one sampling trip was conducted in July 1994, after the scheduled investigation (See Chapter 2 - STUDY DESIGN). Six of these fish were recaptured, all within the aggregation area. The 30-Mile aggregation was composed of an estimated 52 adults, based on mark-recapture estimates (See Chapter 6 - DEMOGRAPHICS).

Twenty of 26 humpback chub (77%) were captured with trammel nets in the warm plume of a shoreline spring above South Canyon, designated as Spring No. 5 (See Fig. 4-16 in Chapter 4 - WATER QUALITY). Six of these fish were recaptured in the warm plume of the spring in the same net location. Also, two of four adults observed in the plume during electrofishing in September 1993 were captured, two were captured with nets in the plume of Spring No. 4, and one was captured in a return channel adjacent to Fence Fault. All humpback chub were captured in the immediate vicinity of springs, indicating an attraction to the warmer water.

Spring No.5 was resampled July 12-14, 1994, and an estimated 100 YOY humpback chub were sighted among boulders in the warm plume. Fourteen specimens (range, 18-31 mm TL) were captured with a dip net and preserved to verify identification (note: these fish are not included in total fish reported in Table 5-3 since this trip occurred after the normal sampling period). Water temperature at the source of the spring was relatively constant at 21.5°C, compared to 10°C in the adjacent mainchannel. These young were presumed to belong to the 1994 year class and probably hatched from eggs deposited in the warm spring plume, since mainstem water temperature was too cold for survival of eggs or larvae (Hamman 1982, Marsh 1985). The fish were about 30 days old, based on age to length relationships developed by Muth (1990) for young humpback chub. It is unlikely that these young originated from other locations and moved through the cold mainstem with the large numbers of predators (i.e., rainbow trout) in the area. Spawning by humpback chub in this area is further discussed in Chapter 6 - DEMOGRAPHICS and Chapter 7 - HABITAT.

In 1993, AGF (Arizona Game and Fish Department 1994) captured 20 YOY humpback chub (range, 20-50 mm TL) (3 in July, 3 in September, and 14 in October) in a backwater at RM 44.3 (Eminence Fault just below President Harding Rapid). These fish could have emerged from eggs deposited in one of three areas--springs in the vicinity of Fence Fault (i.e., the 30-Mile aggregation), the Paria River, or an undiscovered warm spring below the river surface and near the subject backwater. It is unlikely that these young fish originated from the Paria River, since adult humpback chub have not been reported in that tributary, and a large number of young would be necessary to supply a distant backwater with 20 individuals, under normal dispersal patterns. Possibly, these fish originated from the 30-Mile aggregation, although cold mainstem temperature, transport distance (RM 30.0 to RM 44.0), and the presence of large numbers of predators probably substantially reduced survival. The potential for humpback chub spawning in the Eminence Fault area was difficult to assess because little was known about the area, and it was sampled only twice during this investigation. At least one juvenile humpback chub was captured near RM 44.0 between 1970 and 1976, but no lengths were reported (Suttkus et al. 1976, Carothers and Minckley 1981).

2. LCR Inflow Aggregation. The LCR Inflow (LCRI) aggregation was considered a component of the LCR population of humpback chub. The relationship between the mainstem and LCR components of this population are further discussed in Chapter 6 - DEMOGRAPHICS, Chapter 8 - MOVEMENT and Chapter 10 - INTEGRATION. Eighty-seven percent of 1,791 adults captured in this investigation were in the aggregation between RM 57.0 (Malgosa Crest) and RM 65.4 (Lava

Canyon). This area contained an estimated 3,482 adult humpback chub, based on a mark-recapture estimate (See Chapter 6 -DEMOGRAPHICS), but no mark-recapture estimate was developed for subadults. Lava Canyon was a relatively distinct lower boundary for this aggregation, i.e., from 1990 to 1993, 134 adult humpback chub were captured within 1.6 km (1 mi) upstream, but only 1 adult was captured within 1.6 km (1 mi) downstream. The upper boundary was also distinct, with 132 humpback chub captured within 3.2 km (2 mi) downstream of Malgosa Crest and none upstream for 42 km (26 mi) to RM 31.0. These distinct boundaries may be related to habitat distribution and quality (See Chapter 7 - HABITAT).

Many adults from this aggregation congregated annually prior to ascending the LCR for spawning. Numbers and catch rates of humpback chub in the LCR inflow varied dramatically by season in 1991, 1992, and 1993. This variation in numbers probably accounts for variable catch results reported by previous investigators (Table 5-1, Appendix E-3). Timing and magnitude of these seasonal congregations are illustrated by netting catch rates in a 1.6-km (1 mi) subreach at the LCR inflow, RM 60.9-61.9 (Fig. 5-10) and from radiotelemetry data (See Chapter 8 - MOVEMENT). Significantly higher mean monthly catch rates in March 1991 (ANOVA, F=6.64, P=0.001, df=8, 204; Fisher's LSD, P≤0.05) and February 1992 (ANOVA, F=3.86, P=0.001, df=8, 251; Fisher's LSD, P≤0.05) and higher catch rates in January and February of 1993, resulted from prespawn staging at the mouth of the LCR. Early floods from the LCR in January 1993 may have prompted early staging. Slightly higher catch rates in June and July of all 3 years were consistent with a post-spawning descent and little or no congregation by adults before redispersing into the mainstem.

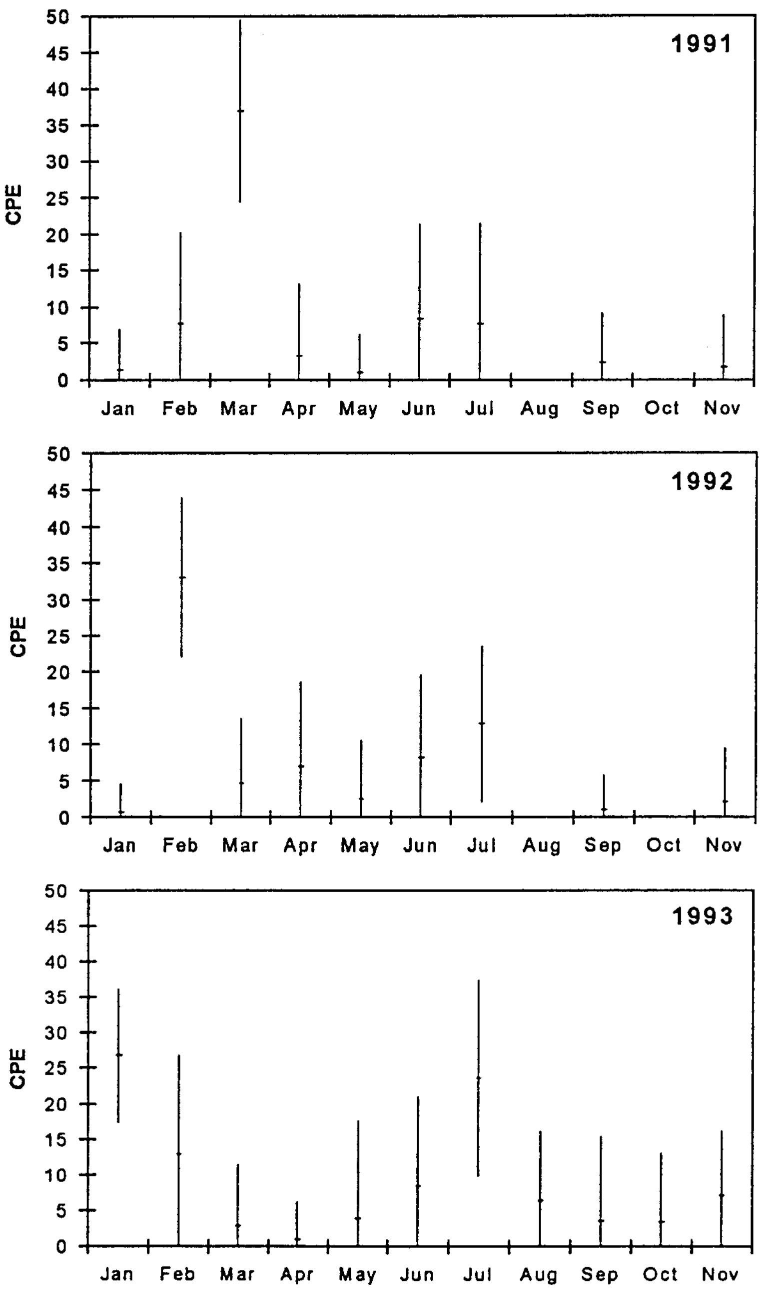

Fig. 5-10. Monthly geometric mean catch per effort (GM_{CPE}, # fish/100 ft/100 hr) for adult humpback chub captured in nets within RM 60.0-61.9 (LCR inflow), 1991-93. Standard error bars are shown.

The effect of turbidity on distribution and abundance of humpback chub and rainbow trout was evaluated by comparing catch rates above and below the LCR in 1991, 1992, and 1993 (Fig. 5-11). The LCR is a major source of sediment to the mainstem, causing turbidity with spring runoff or periodic rainstorms. While humpback chub evolved in a turbid system, rainbow trout are sight feeders with significantly decreased foraging success during

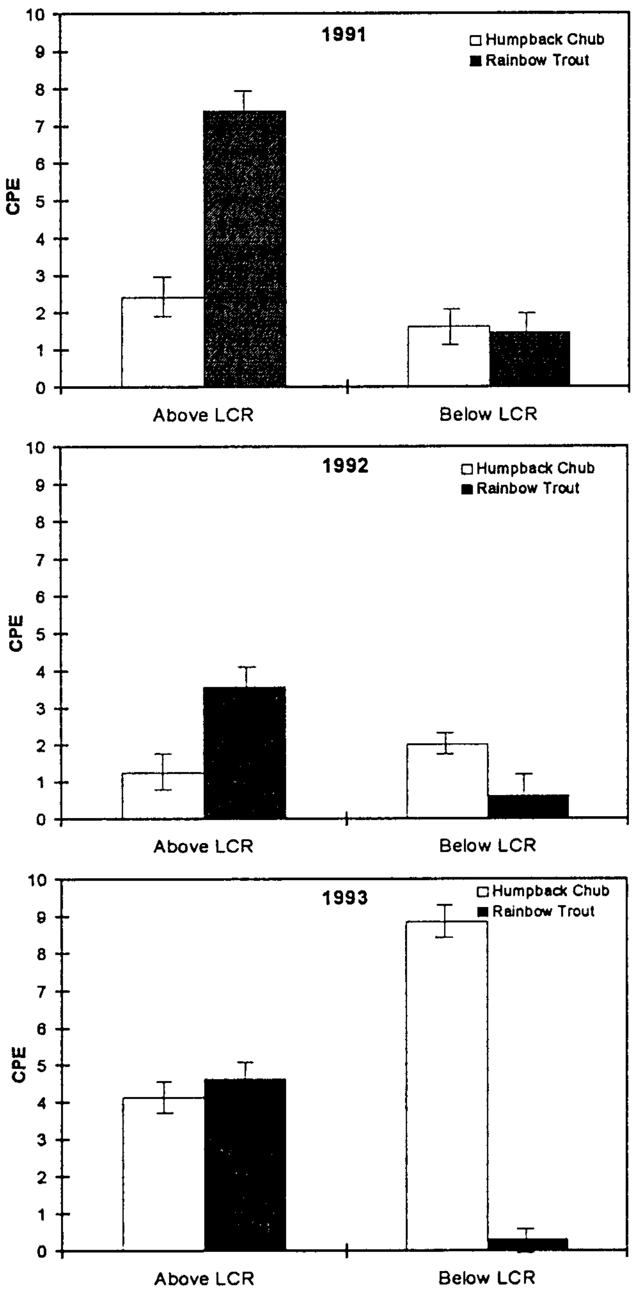

Fig. 5-11. Monthly geometric mean catch per effort (GM_{CPE}, # fish/100 ft/100 hr) for adult humpback chub and rainbow trout captured in nets above the LCR (RM 52.85-60.85) and below the LCR (RM 61.85-65.55) for 1991-93. Standard error bars are shown.

turbidity of greater than 30 NTU (Barrett et al. 1992).

Catch rates (GM_{CPE}) of adult humpback chub were significantly different (t-test, P<0.05) for the subreaches above and below the LCR inflow for 1993, but not for 1991 and 1992, indicating that the LCR inflow and associated turbidity may not affect the local distribution and abundance of this species. Conversely, catch rates of adult rainbow trout were significantly higher (t-test, P<0.05) above than below the inflow for the 3 years, indicating that turbidity from the LCR affected this species. Catch rates of rainbow trout were also higher in 1991 than in 1992 or 1993; a change that is attributed to a higher frequency of turbidity during 1992-93 and to a series of large floods from the LCR in January and February 1993 (See Chapter 3 - HYDROLOGY).

3. Lava to Hance Aggregation. This aggregation contained primarily subadults. Increased densities indicate that subadults from the LCR dispersed downstream into both aggregations, providing a unidirectional link. Although this aggregation was immediately downstream of the LCR inflow aggregation, no exchange of marked adults was recorded from October 1990 through November 1993. Upstream movement of fish may be impeded by Lava Canyon Rapid at certain flows. Fifteen adults captured between RM 65.7 (below Lava Canyon Rapid) and RM 76.3 (below Papago Creek) were found with no apparent pattern of distribution. Four adults were captured within 0.5 km (0.3 mi) of seasonal tributaries (i.e., 3 below Papago Creek, 1 below Cardenas Creek), and the remaining 11 were captured within 0.5 km (0.3 mi) above major rapids (i.e., 3 above Tanner Rapid, 3 above Nevills Rapid, 5 above Hance Rapid).

4. Bright Angel Creek Inflow. This aggregation was distributed from RM 83.8 to RM 92.2, or about 6.4 km (4 mi) upstream and 6.4 km (4 mi) downstream of the Bright Angel Creek inflow. Of 9 adult humpback chub captured in this aggregation, 2 were within 0.3 km (0.2 mi) above the Bright Angel Creek inflow, and 4 were within 0.5 km (0.3 mi) of the Clear Creek inflow. The 15 subadults captured at this inflow probably originated from the LCR (42 km upstream), although reproduction by humpback chub in Bright Angel Creek cannot be discounted. The presence of this aggregation was attributed to Bright Angel Creek and Clear Creek which are warm tributaries. Most humpback chub associated with this and other tributary inflows were found upstream of the inflow in waters ponded by the alluvial inflow fan, rather than in the swift areas below the inflows.

5. Shinumo Creek Inflow. This aggregation extended only 0.8 km (0.5 mi) above the Shinumo Creek inflow, from RM 108.1 to RM 108.6. Sampling yielded 4 YOY, 13 juveniles, and 27 adults. This aggregation contained the highest density (fish/mile) of humpback chub downstream of the LCR aggregation and an estimated 57 adults (mark-recapture estimate). The occurrence of this aggregation was attributed to the warm inflow of Shinumo Creek.

6. Stephen Aisle. The aggregation in Stephen Aisle was distributed from RM 114.9 to RM 120.1. Although 7 juveniles and 17 adults were captured in this area, there were no perennial tributaries present. This aggregation was associated with Muav Limestone, Bright Angel Shale, and Tapeats Sandstone, a shoreline association similar to that found at the LCRI aggregation (See Chapter 7 - HABITAT).

7. Middle Granite Gorge Aggregation. The Middle Granite Gorge (MGG) aggregation of humpback chub was distributed between RM 126.1 (below Fossil Rapid) and RM 129.0 (Specter Rapid). Of 181 adults captured in Region II, 124 (69%) were in this aggregation. The recapture for this aggregation was 48 of 76 unique adults (63%). The MGG aggregation was composed of an estimated 98 adults, based on mark-recapture estimators.

The MGG aggregation occupied an area with high diversity of fish habitat, including deep eddy complexes and various shoreline types such as talus, debris fans, and cobble bars. Of 124 adult humpback chub captured from the MGG aggregation, 106 (86%) were found below the first exposure of Vishnu schist (RM 127.0), where convoluted walls and rooms enhanced shoreline complexity. Warm springs were not detected in this area and the only perennial stream was 128-Mile Creek, which had low discharge and a confluence morphology that seemed unsuitable for humpback chub. (See Chapter 7 - HABITAT for further discussion of habitat associations for this aggregation.)

8. Havasu Creek Inflow Aggregation. This aggregation occupied the area between RM 155.8 and RM 156.7. The seven adults captured in this area were within 1.4 km (0.9 mi) upstream of the Havasu Creek inflow. It is believed that these fish were associated with this warm tributary, but occurred in more suitable habitat upstream of the inflow. Access to Havasu Creek was blocked by a series of natural falls and only the lower 400 m was accessible to mainstem fish.

9. Pumpkin Spring Aggregation. This aggregation extended from RM 212.5 to RM 213.2. Although six adult humpback chub were captured within 1.1 km (0.7 mi) of Pumpkin Spring (1 above, 5 below), which is a warm shoreline spring, field measurements revealed no detectable plume or localized increase in mainstem temperature near the spring. Two of the 6 fish were recaptured once and the estimated number of adults was 5, based on mark-recapture estimators.

Species Accounts - Native Species

Humpback Chub

A summary of PIT-tagged humpback chub is provided in Table 5-12. Of 6,294 humpback chub captured, only those fish 175 mm TL or larger were candidates for PIT tags. Hence, 1,220 unique chubs were PIT-tagged by B/W. B/W handled 1,572 unique PIT-tagged fish, including 352 fish tagged by other researchers and 1,220 tagged by B/W. A total of 805 PIT-tagged humpback chub were handled by B/W and at least one other investigative group.

Flannelmouth Sucker

Flannelmouth suckers were caught throughout the study area, from Lees Ferry to Diamond Creek. A summary of flannelmouth sucker catch rates by gear type and reach is presented in Appendix E. Greatest numbers were found in Region I, with declining abundance downstream to Region III, although catch rates were sporadically high at or near major tributary inflows (i.e., LCR, Bright Angel, Kanab, and Havasu creeks). Of 2,775 specimens captured, only 578 were subadults (183 YOY, 395 juveniles), indicating low reproductive success or survival, or both. Pooled netting catch rate (AM_{CPE}) for adults was highest at 60 FPN between RM 61.0 and RM

Table 5-12. A summary of catch statistics for PIT-tagged humpback chub handled by BIO/WEST during October 1990 through Novermber 1993.

Description of Captors	Numbers of Fish
Unique PIT-tagged fish handled by B/W	1,572
Total recaptures of PIT-tagged fish previously handled by B/W	356
Total captures of PIT-tagged fish handled by B/W	1,928 (1,572 + 356)
Unique PIT-tagged fish handled by B/W + others	805
Unique PIT-tagged fish handled only by B/W	767 (805 + 767 = 1,573)
Unique PIT-tagged fish tagged by ASU, handled by B/W	340
Unique PIT-tagged fish tagged by AGF, handled by B/W	12
Unique PIT-tagged fish tagged by FWS, handled by B/W	0
Unique PIT-tagged fish tagged by B/W, handled by B/W	1,220 (340 + 12 + 1,220 = 1,572)
Total captures of PIT-tagged fish captured by B/W, tagged by B/W	1,516
Total captures of PIT-tagged fish captured by B/W, tagged by others	412 (1,516 + 412 = 1,928)
Total captures of PIT-tagged by B/W	296 (1,516 - 1,220 = 296)

61.9 (LCR inflow area) (Fig. E-4), which was the same 1.6 km (1-mi) subreach with highest netting catch rate for adult humpback chub (Fig. E-1). Catch rates for adults in Region 0 were highest within the first 6 river miles, because of the proximity to a spawning tributary, the Paria River (Weiss 1993) i.e., seasonal congregations of adult flannelmouth suckers in the vicinity of this tributary inflated catch rates.

Highest electrofishing AM_{CPE} for adult flannelmouth suckers was over 1,700 FPH between RM 0.0 and RM 0.9 (Fig. E-5). This catch rate was based on four electrofishing efforts in the inflow of the Paria River in April 1993, when adults were staging to spawn. Catch rates and electrofishing in Regions I through III were approximately uniform, but highest near major tributaries, as with net catches.

The majority of PIT-tagged adult flannelmouth suckers (1,071 tagged, 202 recaptured) that were recaptured (190 of 202 = 94%) were found less than 16 km (10 mi) from their original capture locations in the Colorado River over periods of up to 790 days (Fig. 5-12). Some adults moved long distances, but no distinct pattern was evident for seasonal movement or direction, although inflated catches of adults at tributary inflows in spring (April-May) confirmed seasonal spawning congregations. Greatest displacement (distance from capture to recapture) was 247 km (153.5 mi) upstream from RM 214.0 to RM 60.5 over 79 days (July 26 to October 13, 1993). Other long-distance displacements were often associated with one or more tributary inflows, e.g., two adults were captured near the LCR inflow (RM 61.3) and recaptured near the Havasu Creek inflow (RM 156.6), and one adult was captured near Havasu Creek and recaptured near the LCR. Weiss (1993) also reported long-distance displacement by adults captured in spawning areas in the Paria River; of 77 fish recaptured spawning in the Paria River in 1992-93, 15 were originally tagged in the LCR (up to 6 km [3.7 mi] above the mouth), and one originated in Kanab Creek, 228.0 km (141.7 mi) downstream.

Five specimens captured in this 1990-93 investigation were classified as flannelmouth sucker x razorback sucker hybrids (Table 5-3). These fish averaged 497 mm TL (range, 332-631 mm TL), and they were typically larger than adult flannelmouth suckers (mean = 430 mm TL). These presumed hybrids were distinguished by the presence of a small but distinct dorsal keel, dark olive back fading to yellow belly, and 13 or fewer anal fin rays (McAda and Wydoski 1980). Four of these presumed hybrids were captured in Region I, near

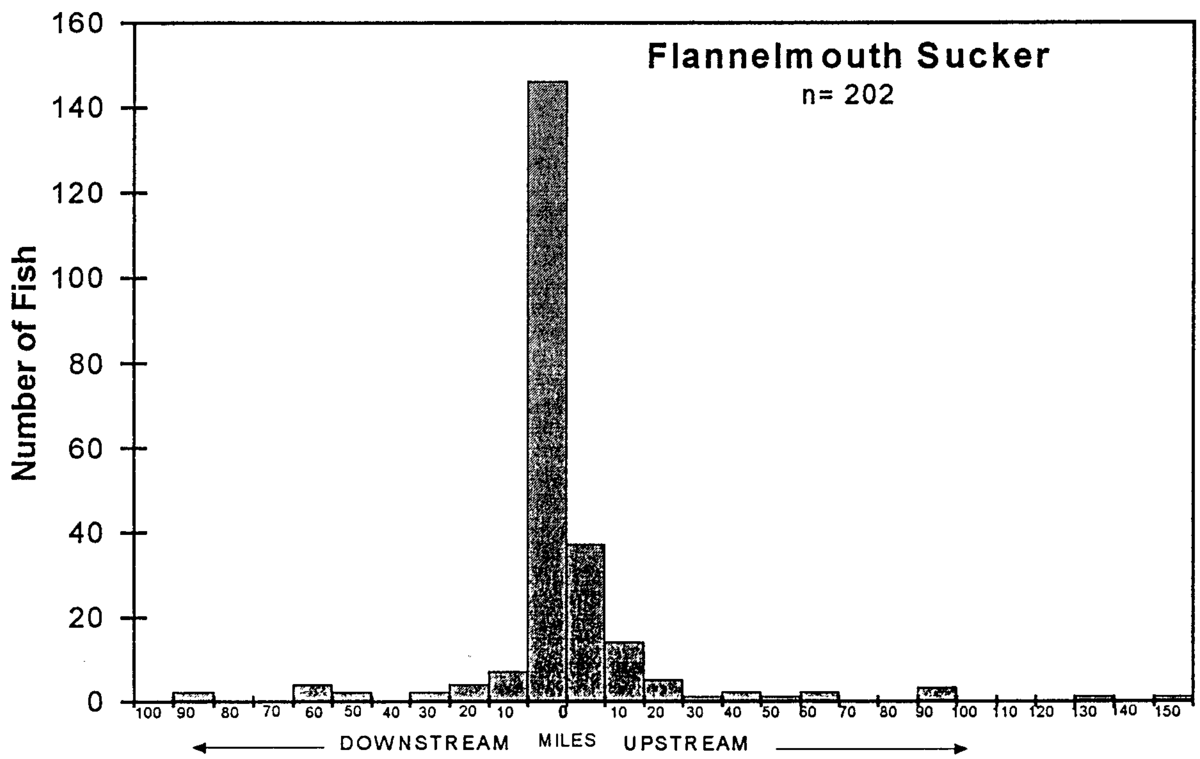

Fig. 5-12. Displacement of 202 PIT-tagged flannelmouth suckers (>200 mm TL) from capture locations in the Colorado River, Grand Canyon.

the LCR, and one was found in Region II (Table 5-5).

Subadult flannelmouth suckers (range, 21-198 mm TL) were captured in return channels and other quiet shoreline habitats. Subadults were distributed from RM 55.7 to RM 222.0, with concentrations in the inflows of the LCR, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek. Large numbers of flannelmouth suckers were observed spawning in Kanab Creek in April 1992 (R. VanHaverbeke, ASU, pers. comm.).

Bluehead Sucker

Bluehead suckers were caught throughout the study area, but were found in smaller numbers and more infrequently than flannelmouth suckers. A summary of bluehead sucker catch rates by gear type and geomorphic reach is presented in Appendix E. Greatest numbers were found in Region II, with declining abundance downstream to Region III. Like flannelmouth suckers, catch rates of bluehead suckers were sporadically high at or near major tributary inflows (i.e., LCR, Bright Angel, Kanab, and Havasu creeks). Of 1,040 specimens captured, only 351 were subadults (101 YOY, 250 juveniles), indicating low reproductive success or low survival, or both. Pooled netting catch rates (AM_{CPE}) for adult bluehead suckers were highest at about 60 FPN between RM 88.0 and RM 88.9 (i.e., below Bright Angel Creek) (Fig. E-6). Relatively low catch rates (<5 FPN) occurred downstream of Havasu Creek.

Pooled electrofishing AM_{CPE} for adult bluehead suckers peaked at over 50 FPE between RM 146.0 and RM 146.9 (i.e., below Olo Canyon) (Fig. E-7). No bluehead suckers were captured by electrofishing in Region 0, and catch rates throughout Regions I-III were low, except for tributary inflows.

Movement patterns of adult bluehead suckers were inconclusive because of the small number of recaptured PIT-tagged fish. Of 12 recaptured adults (394 PIT-tagged) at large up to 431 days, 9 were captured and recaptured near Havasu Creek, 2 were near the LCR, and only 2 moved more than 0.2 km (0.1 mi) from the original capture location (Table E-

4). The greatest displacement was 47.8 km (29.7 mi) from Havasu Creek to a site near Whitmore Wash.

Subadult bluehead suckers (range, 28-150 mm TL) were captured in return channels and other quiet shoreline habitats. Their distribution was similar to that of subadult flannelmouth suckers, extending from RM 61.4 to RM 184.1, with concentrations below the LCR and in the inflows of Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek. Maddux and Kepner (1988) observed bluehead suckers spawning in Kanab Creek.

Razorback Sucker

Razorback suckers were not captured during this investigation. As previously discussed, five presumed flannelmouth sucker x razorback sucker hybrids were captured.

Speckled Dace

A total of 1,491speckled dace (range, 17-86 mm TL) were captured in 1990-93. Of these, 4 (<1%) were captured in Region 0, 714 (48%) in Region I, 281 (19%) in Region II, and 492 (33%) in Region III. Speckled dace in Regions 0 and II were concentrated around thermal inputs, including the Fence Fault spring complex, and inflows of Clear Creek, Bright Angel Creek, Shinumo Creek, and Kanab Creek. Most speckled dace in Region III were captured near the Havasu Creek inflow, but low numbers were consistently found in the mainstem to Diamond Creek.

Species Accounts-Non-Native Species

Black Bullhead

Six black bullheads (range, 70-232 mm TL) were captured in 1990-93 including 5 adults between RM 61.3 and RM 70.9 and 1 juvenile at RM 143.5 (mouth of Kanab Creek). Bullheads have been considered rare in Grand Canyon since completion of Glen Canyon Dam in 1963 (Maddux et al. 1987), probably because cold mainstem temperatures have limited their distribution and abundance.

Black bullheads are omnivorous voracious feeders that can be a threat to young fish in enclosed habitats such as backwaters (Valdez 1990, Sigler and Sigler 1987). Although currently not a significant threat to native fishes in the mainstem Colorado River, black bullheads have successfully spawned in the LCR (Haden 1992), and proliferation of this species could have a serious impact on native fishes in that tributary. Black bullheads are present in the warm waters of the upper basin, but are reported in large numbers only in riverside ponds and gravel pits (Valdez and Wick 1982, Valdez et al. 1982, Valdez 1990). Black bullheads are primarily nocturnal feeders and could be significant predators on larval fishes, which are negatively phototaxic and most active at night.

Brook Trout

Six brook trout (range, 318-436 mm TL, range, 342-657 g) were collected in the mainstem including 3 in 1990, and 1 each in 1991, 1992, and 1993. These fish were captured at RM 30.3, RM 32.5, RM 60.1, RM 156.7 (two fish), and RM 165.1. Brook trout have not been stocked into the mainstem or its tributaries since 1979, and their present status below Lees Ferry is considered rare (Haden 1992). Unless stocking is resumed, brook trout are not numerous enough to represent a significant predator threat to humpback chub or other native species in Grand Canyon.

Brown Trout

A total of 1,673 brown trout (range, 69-730 mm TL, range, 3-4,423 g) were captured during 1990-93. The longitudinal distribution of brown trout was 5 (<1%), 68 (4%), 1,582 (95%), and 17 (1%) in Regions 0, I, II, and III, respectively. over half of the brown trout in Region II were captured near the tributaries Bright Angel Creek, and Shinumo Creek. In Region 0, 3 of 5 brown trout were captured in the vicinity of the Fence Fault Spring complex, and one was captured 0.5 km (0.3 mi) upstream of Nankoweap Creek.

Although brown trout have not been stocked in the mainstem or its tributaries since 1934, they remain locally common in Grand Canyon and reproduce in Bright Angel Creek and other tributaries (Haden 1992). Numerous ripe fish were captured near the inflows of Bright Angel Creek, Shinumo Creek, and Kanab Creek during this investigation. R. Lechleitner (GCES, pers. comm.) reported that brown trout had replaced rainbow trout as the most abundant fish in Bright Angel Creek.

Brown trout are aggressive predators, consuming fish at an earlier age than most other salmonids (Sigler and Sigler 1987). Brown trout are considered a serious threat to native fish populations in Grand Canyon, including humpback chub. Otis (1994) observed congregations of rainbow trout and brown trout behind groups of spawning suckers in Bright Angel Creek, and found over 100 flannelmouth sucker eggs in one sacrificed brown trout. Predation by brown trout on humpback chub is further discussed in Chapter 6 - DEMOGRAPHICS.

Channel Catfish

A total of 113 channel catfish (range, 39-712 mm TL, range, 2-5,500 g) were captured in 1990-93, including 33 (29%) in Region I, 5 (4%) in Region II, and 75 (67%) in Region III. Seventy-nine percent of all channel catfish captured in Region III were in the lower 21 km (13 mi). Channel catfish were not captured in Region 0.

Channel catfish have been reported spawning in the LCR and Kanab Creek (Carothers and Minckley 1981). Numerous large (< 5 kg) channel catfish were seen in the LCR inflow during unusually clear water in July 1993. BIO/WEST biologists observed and photographed a congregation of 30-40 large adults under a boulder along the mixing zone at the mouth of the LCR. Subadult humpback chub and unidentified suckers were occupying the same deep boulder and ledge habitat and often swam in close proximity to the large channel catfish.

Kaeding and Zimmerman (1983) and AGF (Kubly 1990) observed humpback chub with apparent catfish bite marks, and suggested that channel catfish may be predators on humpback chub in the LCR. Stomach analyses were performed on channel catfish from the mainstem to determine extent of predation by this species (See Chapter 6 - DEMOGRAPHICS).

Common Carp

A total of 2,423 common carp (range, 23-827 mm TL, range, 2-9,440 g) were captured in the mainstem Colorado River during 1990-93. Carp were abundant in Regions I-III and consistently captured from RM 56.8 (below Kwagunt Canyon) to RM 226.0 (Diamond Creek). Within Region 0, carp were captured only between RM 26.9 and RM 32.9, where they were congregated with humpback chub in warm spring plumes of the Fence Fault spring complex. Carp are omnivorous and opportunistic feeders (Sigler and Sigler 1987, Cooper 1987), and are suspected of preying on eggs and larvae of native fishes in the LCR (Minckley 1990). Carp could be a serious threat to the viability of the 30-Mile aggregation of humpback chub where they may compete for limited space and food, and prey on young confined by the warm spring plumes. Carp may reproduce in several warm Grand Canyon tributaries or in warm shoreline springs that satisfy the preferred spawning and egg incubation temperature range of 14 to 19°C (Sigler and Sigler 1987).

Four of 2,423 carp captured in 1990-93 were previously marked with Floy tags or Carlin tags by other researchers (Table 5-13). Of these, two were traced to their original capture locations (B. Persons, AGF, pers. comm.). Both fish were originally tagged by AGF in 1985; one at RM 182.0 and the other at RM 204.0. The fish were recaptured by B/W at RM 208.0 in 1991 and at RM 208.6 in 1992, respectively. One fish had moved 42 km (26 mi) downstream in 6 years and 2 months, and the other had moved 7.4 km (4.6 mi)downstream in 5 years and 10 months, respectively. The length and weight of each carp remained relatively unchanged between captures.

Fathead Minnow

A total of 1,130 fathead minnows (range, 13-84 mm TL) were captured in 1990-93, including 912 (81%) in Region I, 137 (12%) in Region II, and 81 (7%) in Region III. Fathead minnows were notably absent in the mainstem Colorado River above the LCR. This distribution is explained as dispersal of individuals from a large population in the LCR (Clarkson 1993), and by an absence of spawning in at least the uppermost colder mainstem reaches.

Numbers of fathead minnows captured in the mainstem increased dramatically after 1991. Only 18 were captured in 1990-91, 560 in 1992, and 552 in 1993. Greater numbers in 1992 and 1993 may be attributed to 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 May-June 1992 and January-February 1993. Electrofishing effort of 196.5, 172.7, and 183.2 hr during 1990-91, 1992, and 1993, respectively, yielded higher GM_{CPE} for 1992 and 1993, compared to 1990-91.

Fathead minnows are known to act aggressively toward young fishes in backwaters (Pflieger 1975), although it is not known if present densities in Grand Canyon are high enough to represent a threat (Haden 1992). Fathead minnows spawn at or above a temperature of 15.6°C, which probably restricts

Table 5-13. Fish species captured, tagged and recaptured during this investigation in the Colorado River from Lees Ferry to Diamond Creek, October 1990 - November 1993.

		B/W PIT Tags		Recapture - All Tags			
Common Name	**Total Captured [a]**	**Unique Tagged**	**Recaptured**	**PIT**	**Carlin**	**Floy**	**Coded Wire**
Family: Cyprinidae (minnows)							
common carp	2,423	0	-	0	1	3	-
humpback chub	6,294	1,516	296	412	50	27	-
fathead minnow	1,130	0	-	-	-	-	-
speckled dace	1,491	0	-	-	-	-	-
Family: Catostomidae (suckers)							
bluehead sucker	1,040	394	13	13	-	-	-
flannelmouth sucker	2,775	1,071	176	219	1	18	-
flannelmouth x razorback sucker	5						
unidentified sucker	32	0	-	-	-	-	-
Family: Ictaluridae (catfishes, bullheads)							
black bullhead	6	0	-	-	-	-	-
channel catfish	113	0	-	0	-	-	-
Family: Salmonidae (trout)							
rainbow trout	11,121	0	-	0	-	6	3[b]
brown trout	1,673	0	-	0	-	-	-
brook trout	6	0	-	0	-	-	-
Family: Cyprinodontidae (killifishes)							
plains killifish	76	0	-	-	-	-	-
Family: Percichthyidae (temperate basses)							
striped bass	39	0	-	-	-	-	-
Family: Centrarchidae (sunfish)							
green sunfish	3	0	-	-	-	-	-
Family: Percidae (perches)							
walleye	1	0	-	-	-	-	-
Totals	**28,228**	**3,292**	**485**	**644**	**52**	**54**	**3**

[a] Total captured includes numbers recaptured.
[b] Fish marked and released between Lees Ferry (RM 0) and Glen Canyon Dam and recaptured at RM 2.9, 3.2, and 3.2.

spawning to warm tributaries or local warm shoreline habitats or springs. Specimens from the mainstem included tubercled males and egg-laden females, suggesting that mainstem temperatures were sufficiently warm for maturation of gametes, but may be too cold for significant survival of eggs and larvae.

Green Sunfish

Three green sunfish were captured during 1990-93, including 1 adult (120 mm TL) at RM 60.1 in January 1993, 1 juvenile (60 mm TL) at RM 62.5 in September 1992, and 1 juvenile (28 mm TL) at RM 173.9 in September 1993. Small numbers of green sunfish were reported in springs below Glen Canyon Dam in the mid-1980s, and collections near the LCR inflow have always been incidental (Maddux et al. 1987). Green sunfish are opportunistic predators and can be a threat to young fish in enclosed habitats such as backwaters (Valdez 1990, Sigler and Sigler 1987, B. Muth, CSU Larval Fish Laboratory, pers.comm.). Currently, because of low numbers, green sunfish do not represent a significant threat to humpback chub or to other native species in Grand Canyon.

Plains Killifish

Seventy-six plains killifish (range, 39-70 mm TL) were captured in the mainstem during 1990-93, including 10 in Region I, 56 in Region II, and 10 in Region III. All killifish captured in Region II were in tributary inflows of Deer Creek, and Kanab Creek. Distributions of individuals in Regions I and III appeared relatively random. Although killifish may compete with juvenile native species in backwaters, their limited abundance and distribution precludes a serious threat. A common synonym for this species is Rio Grande killifish (American Fisheries Society 1991) and the specific epithet, Fundulus zebrinus, is preferred to the junior synonym of F. kansae (Poss and Miller 1983).

Rainbow Trout

A total of 11,121 rainbow trout (range, 24-708 mm TL, range, 1-6,641 g) were captured in the mainstem Colorado River in 1990-93. Netting catch rates peaked at over 185 FPN between RM 12.0 and RM 12.9, while electrofishing catch rates in the same mile were highest at over 1,300 FPE (Fig. E-8, E-9). Both netting and electrofishing catch rates generally decreased with downstream direction, although adult, juvenile, and YOY rainbow trout were captured in all four study regions. A summary of rainbow trout catch rates by gear type and region is presented in Appendix E.

Nine of 11,121 rainbow trout captured had been previously marked with Floy tags (6) or coded wire tags (3) by other researchers (Table 5-13). According to AGF (B. Persons, AGF, pers. comm.), four were Floy-tagged in the Nankoweap Creek inflow (RM 52.1) in January and February 1991 by bald eagle researchers and were recaptured from June through September 1991 between RM 56.7 and RM 61.8. Furthest individual movement was 15.6 km (9.7 mi) downstream in 107 days. Two fish were Floy-tagged by AGF at RM 105 in 1984 and at RM 5.7 in 1992. The first was recaptured at RM 56.7 in 1990, after having moved 77.7 km (48.3 mi) upstream in just over 5 years and 11 months. The other was recaptured at RM 60.2 in 1992 and moved 87.7 km (54.5 mi) downstream in 75 days. The three rainbow trout (112, 131, 265 mm TL) with coded wire tags were recaptured in July 1993 at RM 3.2, RM 3.2, and RM 2.9, respectively, and were among hatchery-reared fish tagged and released by AGF between Glen Canyon Dam and Lees Ferry. Arizona Game and Fish Department released 78,000 rainbow trout with coded wire tags in 1992 and 73,000 in 1993 (S. Reger, AGF, pers.comm.). Rainbow trout released in the dam tailrace (as indicated by coded wire tag) were not reported in areas occupied by humpback chub.

Red Shiner

Red shiners were not captured during this investigation between Lees Ferry and Diamond Creek. However, the species was abruptly abundant downstream of Bridge Canyon (RM 235.0), approximately 15 km downstream of Diamond Creek (Valdez et al. 1995).

Striped Bass

A total of 39 striped bass (range, 315-857 mm TL, range, 229-5,829 g) were captured in the mainstem Colorado River, including 17 in 1991, 3 in 1992, and 19 in 1993. All striped bass were captured between May and July at river temperatures of 12.7-17.0°C, presumably during upstream spawning-related migrations from Lake Mead. The apparent reduction in numbers of striped bass caught in 1992 was unexplained, but fewer numbers of fish may have ascended following the dramatic reduction in water level of Lake Mead in spring of 1992.

Most striped bass were captured in the lower end of Region III; 16 were between RM 212.0 and RM 220.0, 4 were near Havasu Creek, and 6 were near Kanab Creek. Also, 4 striped bass were captured in 1 day just below Lava Falls Rapid, indicating that this rapid may be a temporary impediment to upstream migration. The furthest upstream capture of a striped bass during this study was RM 142.3, although other investigators reported striped bass in the LCR at RM 61.3 in 1989 (C.O. Minckley, AGF, pers. comm.). Weiss (1993) reported a single moribund striped bass (stomach empty) at the mouth of the Paria River in September 1992. This fish could have ascended over 400 km upstream from Lake Mead, or it could have passed from Lake Powell through Glen Canyon Dam.

Walleye

One adult walleye (426 mm TL) was captured in July 1991 at RM 179.7 (base of Lava Falls Rapid). Few walleyes have been collected in Grand Canyon, and their present status is considered rare (Haden 1992). Despite their psicivorous nature, walleye are too low in numbers to represent a significant threat to humpback chub or other native species in Grand Canyon.

DISCUSSION

Historic status and trends in fish species composition, distribution, and abundance in the Colorado River in Grand Canyon were difficult to characterize because of a lack of past quantitative information. Early explorers through the canyon did not have the technology to document native ichthyofaunal assemblages, and earliest fish management efforts targeted development of sports fisheries with introduced salmonids. Intensive ichthyofaunal surveys of Grand Canyon were not possible until the relatively recent advent of inflatable motorized rafts.

While fish assemblages from tributaries and tributary inflows were known as early as the 1940s, information on mainstem distributions and abundances was fragmented until the late 1970s, largely because of logistical difficulties of accessing and sampling the deep, swift mainstem. By the time the first fish survey was conducted in Glen Canyon (1958-59), many non-native fishes had already invaded the area, and most native species were declining with causal factors largely unidentified and undescribed. When Glen Canyon Dam was completed in 1963, many changes had already taken place in the riverine ichthyofauna that remained unquantified and inseparable from effects of dam construction and some aspects of operation. Predam and postdam fishery surveys focused on developing a recreational sport fishery in Lake Powell and a cold tailwater fishery below the dam. These surveys were primarily descriptive with little attention to effects of dam construction or operation.

Mainstem and tributary investigations in the 1970s refined information on species composition, distribution, and abundance, but infrequent sampling and dynamic fish populations precluded accurate assessments. The first fishery investigations with repeated trips and intensive mainstem sampling were conducted in the late 1970s and early 1980s. These studies provided the first accounts of mainstem ichthyofauna and established a foundation for hypothesis development to test causal factors for changes in species composition, distribution, and abundance.

Comparisons of present fish assemblages with predam assemblages must be inferred, based on existing life history information for native species and known distributions from similar areas. Effects of dam construction on the Colorado River in Glen Canyon and Grand Canyon cannot be fully known for lack of comparative data, and because of pre-existing anthropogenic effects (e.g., non-native fishes, watershed practices, etc., Miller 1961) that confound comparisons. Similarly, evaluation of dam operations is confounded by a lack of quantitative data for comparative flow regimes, and a plethora of pre-existing conditions.

Of 34 fish species reported in Grand Canyon since 1958, only 10 were native to the Colorado River Basin. Seventeen of the 24 non-native species were already present in the region by the time Glen Canyon Dam was built in 1963. Their invasion is attributed to bait fish releases, coincidental releases, dispersal from other introduction sites, and establishment of sport fisheries. Carp, fathead minnow, and channel catfish have remained common to abundant in Grand Canyon for 35 years, while plains killifish, black bullhead, yellow bullhead, mosquitofish, and green sunfish have remained low in numbers or only locally common. Other warmwater species are lacustrine in Lake Powell and Lake Mead, and occur incidentally in the canyon. These lake species include threadfin shad, striped bass, bluegill, largemouth bass, black crappie, yellow perch, and walleye. Although red shiners were common before Glen Canyon Dam was built, they were rare by the early 1970s, and except for one specimen captured in 1992 from RM 117.4, the species was not reported upstream of Diamond Creek after 1973. Other cyprinids were reported only incidentally, including redside shiner, Utah chub, and golden shiner.

Of six coldwater species introduced since 1920, only rainbow trout have remained common to abundant in the upper reaches of the canyon. Brown trout have increased in relative abundance in the middle reach (near Bright Angel Creek) since about 1976. Brook trout are rare and cutthroat trout are rare or absent, but kokanee salmon and coho salmon have not been reported since the 1960s and 1970s, respectively.

Native humpback chub continue to be reported as rare or locally common, speckled dace as abundant, and bluehead sucker and flannelmouth sucker as common. Bonytail, roundtail chub, and Colorado squawfish have been extirpated, and razorback sucker are extremely rare, or perhaps extirpated.

Non-native warmwater and coldwater species dominated fish composition and biomass (Fig. 5-13) in Grand Canyon during this investigation. Approximately 81% of fish biomass was attributed to rainbow trout (53%) and carp (28%). Cold hypolimnetic releases from Glen Canyon Dam were a dominating influence on distribution of fish assemblages, coldwater species were dominant for 225 km (140 mi) below the dam, and warmwater species were dominant in the lower 177 km (110 mi) to the Lake Mead inflow. Rainbow trout comprised about 90% of biomass between Glen Canyon Dam and Lees Ferry (Arizona Game and Fish Department 1993) and over 63% (47-98% by reach) of biomass from Lees Ferry to Middle Granite Gorge (225 km [140 mi] below the dam), where a shift in dominant biomass occurred from coldwater to warmwater species. While carp comprised only 18% of biomass from Lees Ferry to Middle Granite Gorge, this warmwater species was dominant with over 70% of biomass from Middle Granite Gorge to Diamond Creek. Rainbow trout biomass decreased dramatically over the same area from over 63% to only 7%. An overall longitudinal decrease in fish biomass is similar to that reported by Blinn et al. (1994) for benthic macroinvertebrates.

The majority of fish biomass between Glen Canyon Dam and the Diamond Creek inflow was stored as rainbow trout and carp. Native fish biomass was associated primarily with warm tributary inflows, but was 25% or less of total biomass in each of the 11 geomorphic reaches. Greatest biomass of native forms was 23% (bluehead sucker, humpback chub, and flannelmouth sucker) in Reach 5 (area immediately downstream of LCR inflow), 20% (flannelmouth sucker, bluehead sucker) in Reach 9 (Kanab Creek to Havasu Creek), and 25% (flannelmouth sucker, bluehead sucker) in Reach 10 (below Havasu Creek).

Cold releases from Glen Canyon Dam have left few habitats suitable for reproduction, survival, and growth of warmwater fishes. Tributary inflows consistently had highest catch rates, and aggregations of fish were frequently found in and near tepid springs. Mainstem temperatures appear sufficient for maturation of gametes of warmwater species but are too cold for survival of eggs and larvae. Eggs deposited in inflows or in tepid springs are not likely to survive when fluctuating flows bathe gametes and larvae with cold lethal temperatures. While an abundance of spawning activity was not seen in these habitats, their use may be increased under more stable thermal regimes in lower fluctuations associated with interim flows. This was demonstrated by the discovery of about 100 YOY humpback chub from a warm spring near Fence Fault in July 1994. These fish probably hatched and survived in a warm plume that apparently persisted for at least 30 days under interim flows.

While the predam status of humpback chub in Grand Canyon remains unknown, it is reasonable to surmise the historic distribution and possibly abundance from known life history requirements and current distribution. Based on a present affinity for whitewater canyon regions, humpback chub were probably distributed throughout the 67 km (41 mi)of Cataract Canyon, described by Dellenbaugh (1908) as ending at the Dirty Devil River. A small population of humpback chub in the remaining 18 km (11 mi) above Lake Powell (Valdez 1990, Valdez and Williams 1993) and specimens collected from the lake during filling in 1962-67 (Holden and

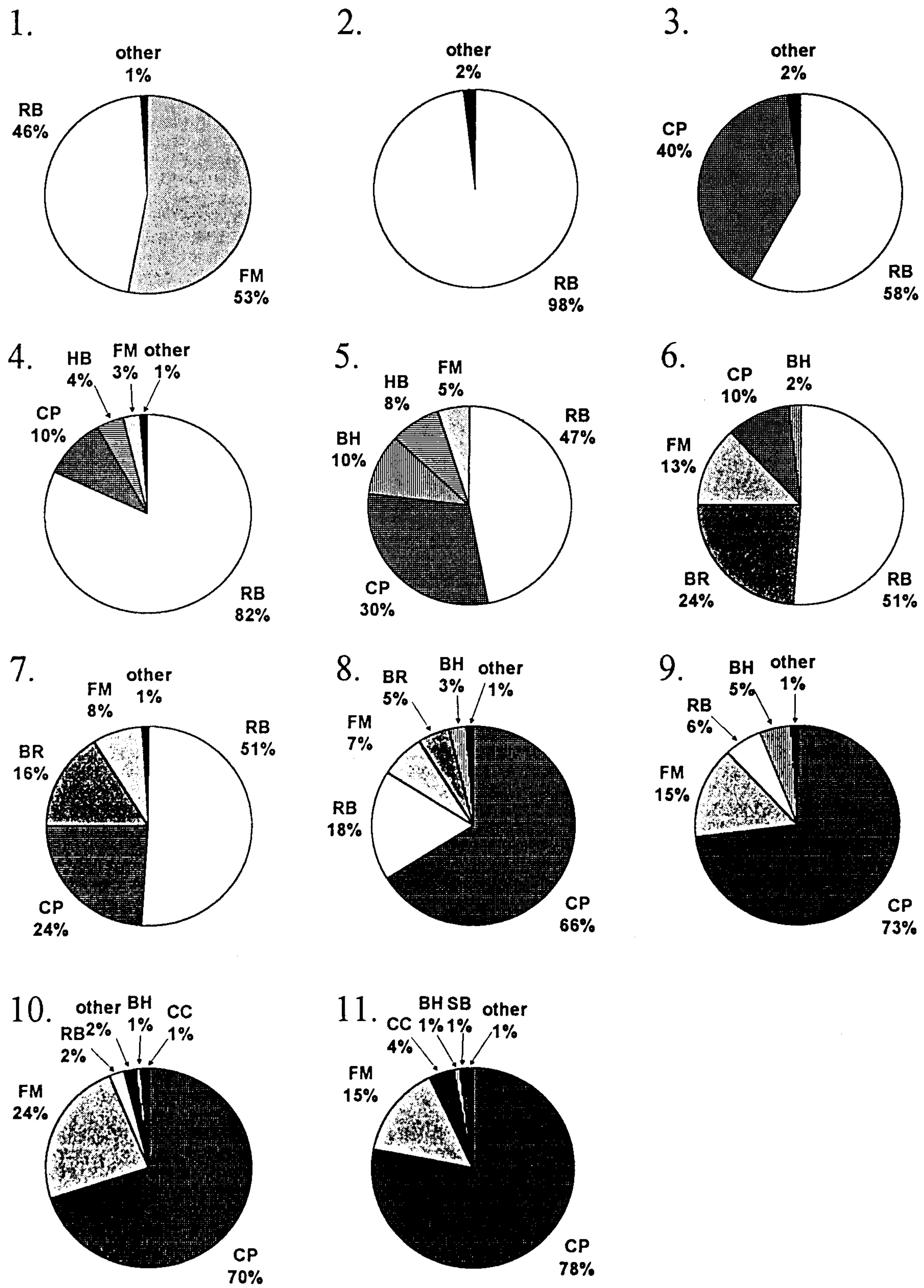

Fig. 5-13. Percentage biomass for fish species in 11 geomorphic reaches of the Colorado River from Lees Ferry to Diamond Creek. See Table 5-3 for species codes and Table 2-1 for geomorphic reach descriptions.

Stalnaker 1975) support this contention. However, humpback chub were probably not common in Glen Canyon (Dirty Devil River to the Paria River), described as a gentle meandering river cut through sandstone (Dellenbaugh 1908); photographs by Stephens and Shoemaker (1987) show an alluvial region not commonly used by the species. Based on present distributional patterns in the upper Colorado River basin, humpback chub were probably distributed through most of Marble and Grand canyons as far downstream as Grand Wash Cliffs, a distance of about 443 km (275 mi). While the species may have been common near tributary inflows and possibly ascended these to spawn, it is noted that upper basin populations are not associated with tributaries and spawn in the mainstem (Valdez and Clemmer 1982, Valdez 1990).

Postdam distribution suggests the demise of humpback chub from 66 km (41 mi) of Cataract Canyon, now inundated by Lake Powell. In Marble and Grand canyons, distribution has been reduced by 98 km (61 mi), or 24% of the original estimated distribution since Glen Canyon Dam was completed in 1963. Postdam capture locations spanned 412 km (256 mi), from the base of Glen Canyon Dam to Separation Canyon (RM 241.0), while the most recent distribution is 307 km (191 mi), from above South Canyon (RM 30.0) to Granite Spring Canyon (RM 221.0). Except for a specimen near Maxson Canyon (RM 253.7), humpback chub have not been captured recently downstream of Diamond Creek, and researchers have consistently found the majority of the postdam population within a small area around the confluence of the LCR (RM 61.3).

Reduction in abundance of humpback chub in Marble and Grand canyons has probably been at least as great as reduction in distribution. Of nine distinct aggregations of humpback chub identified in this study, 74% of total numbers captured were in the LCRI aggregation (RM 57.0-65.4), an area of about 13.5 km (8.4 mi). The LCRI aggregation appears to be a component of the LCR population, the only known self-sustaining humpback chub population in Grand Canyon. Size structure of eight other disjunct aggregations indicates a lack of reproductive success, and suggest that the source of fish to downstream aggregations is primarily from the LCR population. Lack of mainstem recruitment and absence of humpback chub from large intervening reaches between aggregations indicates reduced abundance of the species since 1963. While recruitment in seven aggregations downstream of the LCR is probably supplemented by the LCR population and possibly some local reproduction in warm springs or tributary inflows, an aggregation of adults near RM 30.0 (50 km [31 mi] above the LCR) may be relicts of fish produced shortly after the dam was completed in 1963 or progeny of the fish from as late as the early 1970's when mainstem temperatures became too cold for successful spawning (See Fig. 4-2). Post-larval humpback chub in a warm spring near RM 30.0 indicate successful reproduction, but the lack of subadults in the aggregation indicates little or no survival and recruitment.

Although mainstem temperature has had a dominating influence on fish species composition, distribution, and abundance in Grand Canyon, water clarity or turbidity have also affected species distribution and composition for given river reaches. Turbidity was a main deterrent to rainbow trout below the LCR, and probably limited downstream distribution and abundance by reducing sight feeding opportunities. Conversely, humpback chub were more abundant downstream of the LCR, and possibly used turbidity as a cover element for feeding and to escape predators.

Demographics

Chapter 6

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CHAPTER 6 - DEMOGRAPHICS

INTRODUCTION

This chapter provides a basic understanding of population demographics for the humpback chub in Grand Canyon. Demographics are population attributes important to understanding the life history and ecology of a species. Population size, survival rates, length-weight and age-growth relationships, condition factor, sex ratio, predation, parasites and diseases, and reproductive potential and success are described for humpback chub from the Colorado River in Grand Canyon. Understanding these attributes is fundamental to identifying life history requirements and hence, the factors that limit the species as a result of Glen Canyon Dam operations. This chapter also presents some population attributes of sympatric native and non-native species, in order to compare biological responses by different species to similar and simultaneous environmental conditions.

Surveys and various investigations have been conducted on the six known populations of humpback chub, including Black Rocks (Valdez et al. 1982, Valdez and Clemmer 1982, Kaeding et al. 1990), Westwater Canyon (Valdez et al. 1982, Chart 1995), Cataract Canyon (Valdez et al. 1982, Valdez 1990, Valdez and Williams 1993), Desolation Canyon (Tyus et al. 1982, Moretti et al. 1989), Yampa Canyon (Tyus et al. 1982, Karp and Tyus 1990), and Grand Canyon (Kaeding and Zimmerman 1983, Miller and Smith 1972, Suttkus et al. 1976, Carothers and Minckley 1981, Maddux et al. 1987, Kubly 1990). These studies describe distribution, relative abundance (i.e., catch rates), habitat use, and fish assemblages, but there is little information on population demographics. Many population attributes described in this chapter have not been previously reported for the species. Understanding the characteristics of one population will help scientists understand other populations and the requirements of this endangered species throughout the Colorado River Basin.

METHODS

Length-Frequency

Length-frequency analysis was used to characterize the size of fish in different aggregations. Length-frequency analyses were performed separately for recognized mainstem aggregations (See Chapter 5 - DISTRIBUTION AND ABUNDANCE) to avoid pooled analyses of groups of fish with possibly different spawning times, growth characteristics, and age compositions. Monthly length-frequency histograms were developed for the Little Colorado River Inflow (LCRI) aggregation. Pooled length-frequency histograms were developed to characterize size and possibly age composition of the 30-Mile (RM 29.8-31.3), LCRI (RM 57.0-65.4), and Middle Granite Gorge aggregations (RM 126.1-129.0). Length-frequency analyses were also used to better understand the size relationships of humpback chub in the mainstem and those in the LCR.

Relationships were developed for all humpback chub captured by B/W to provide conversions between standard length and total length for use with missing data, or when the caudal fin of fish was damaged. These relationships were expressed as:

(Equation 6-1)

$$TL = 1.217 \cdot SL$$

(Equation 6-2)

$$SL = 0.822 \cdot TL$$

where:

TL = total length, and
SL = standard length.

Length-Weight Relationship

Length-weight relationships were determined separately for humpback chub captured in 1990-91, 1992, and 1993 using a power function (Anderson and Gutreuter 1983):

(Equation 6-3)

$$W = aTL^b$$

where:

W = weight in grams,
TL = total length in millimeters,
a = a constant, and
b = an exponent.

The coefficients 'a' and 'b' were estimated by least squares linear regression using:

(Equation 6-4)

$$\log_{10}W = \log_{10} a + b \log_{10}TL$$

Generally, a slope (b) of less than 3.0 describes fish that become less rotund as length increases, and a slope greater than 3.0 describes fish that become more rotund as length increases. A slope of 3.0 describes fish that do not change shape as length increases (isometric growth), such that the weight of a fish in pounds is the cube (10^3) of the length in feet (i.e., "cube law", Lagler 1956).

Condition Factor

An index of well-being, or condition factor, was calculated to describe the relationship of length to weight by aggregation, gender, and season, and to evaluate environmental factors (e.g., flow, food supplies, etc.) affecting condition and therefore, health of fish (Murphy and Willis 1992). Relative condition factor (Kn) was used to compensate for allometric growth (LeCren 1951), since humpback chub change shape appreciably with maturity (i.e., development and enlargement of a nuchal hump).

Relative condition factor was calculated as:

(Equation 6-5)

$$Kn = \frac{W}{aL^b}$$

where:

W = weight in grams,
L = total length in millimeters, and
a and b = constant and exponent from the length-weight relationship estimated using the least squares regression technique presented in Equation 6-4.

Relative condition factor was used to compare the condition of individual fish or groups of fish with average condition of all fish within the sample group. Fish with a Kn greater than 1.0 were considered more robust than the average condition fish of the same length, while fish with a Kn less than 1.0 were considered less robust.

Relative condition factors were computed for humpback chub 200 mm TL or greater by using constants derived from least squares regression from the pool of humpback chub handled in 1990-1991 (n=550). Recaptured fish bearing Carlin fingerling tags or Floy tags, which were previously tagged by other investigators, were not included in the analysis because of possible effects of these tags on growth and condition (Scheirer and Coble 1991).

Sample values were tested for normality to confirm the appropriateness of parametric statistics. One-way analysis of variance (ANOVA) was used to test for differences in average condition factor between sample periods. Fisher's least-significant-difference (LSD) test (Sokal and Rohlf 1987) was used for multiple comparisons when ANOVA tests were significant.

Age and Growth

Age and growth of humpback chub were determined with the scale method. Growth rates were also derived from lengths of recaptured individuals (Busacker et al. 1990) from the mainstem and the LCR. Length-frequency analyses were attempted to confirm age group designations, but lengths of different ages of humpback chub overlapped substantially and limited interpretation.

The Scale Method

Scales were collected from subadult humpback chub (<200 mm TL) during 1992-1993 to assess age and growth of young fish, and to determine size and age at dispersal from the LCR to the mainstem (Prats and Valdez In Review). Scales of adults (≥200 mm TL) were examined but were not used because annular rings were indistinct indicating that scale margins were reabsorbed, perhaps because of energy demands during spawning (Lagler 1956). Kaeding and Zimmerman (1983) used scales of humpback chub from the LCR as indicators of age, and found that annuli were directly correlated with modes of length-frequency distributions for fish up to about 3 years of age and 250-300 mm TL. Otolith bones (i.e., the lapilli) have been used to age humpback chub from the LCR (Hendrickson 1993), but this technique has not been validated and requires sacrificing the fish.

Scales were taken from 154 humpback chub captured in the mainstem by B/W and from 44 captured in the upper LCR by AGF. Of these, reliable measurements and interpretation were made on 84 fish from the mainstem and 44 fish from the LCR. These scales were examined for the presence of a "transition check", or a disruption in scale growth rings or circuli. This disruption was caused by a change in water temperature as fish hatched in the LCR, at about 20°C, dispersed to the mainstem, at about 10°C. Assuming young fish captured in the upper LCR had not been in the mainstem, disruption of early circular rings was not expected. Conversely, fish captured in the mainstem had presumably hatched and descended from the LCR, and circular disruptions were expected to correspond to the time of transition. This check was visible on scales of most young fish and was used to back-calculate length at the time that fish descended from the LCR to the mainstem.

Scales were taken from an area on the fish above the lateral line and below the insertion (posterior end) of the dorsal fin, approximately where scale development begins (Muth 1990). Scales from this region were expected to have a full complement of circular rings, and were less variable thereby reducing the incidence of false annuli (Hirschhorn and Small 1987). Approximately 2-6 scales were plucked with forceps or scraped with a scalpel, placed on waxed paper, and stored in labeled envelopes. In the laboratory, scales of each sample were removed from the wax paper, moistened, placed on a microscope slide beneath a coverslip, and dried into place with low heat from a cigarette lighter. Each microscope slide was labeled with sample and fish number for future reference.

Scales were measured with an ocular micrometer on an Olympus microscope under 20X magnification. Two scales were selected from each fish and examined with reflected light. Scales were examined by first locating the focus, or growth center of the scale, and overlaying it with the micrometer origin so the micrometer lines were 45° from the median posterior margin of the scale. Scale radius and distance to each annulus were measured from the focus along either posterior-lateral margins (A-B or A-B', See Box 6-1.) as described by Hawkins (1991) for scales of Colorado squawfish. Only the lateral margin with greatest clarity and annulus definition was used.

Annular rings were identified by crowding, cross-over, or discontinuity of circuli indicating disrupted or slowed growth. The distance from the focus of the scale to the outermost disrupted circulus of the annulus was measured for use in back-calculation of fish length as described by Hawkins (1991) for Colorado squawfish.

The Lee method was used to describe the relationship of fish length to scale radius (Lagler 1956, Chugunova 1963) as:

(Equation 6-6)

$$TL = a + b \cdot SR$$

where:

TL = total length (mm),
SR = scale radius (micrometers),
a = y-intercept, and
b = slope.

This mathematical relationship assumes that the coefficient 'a' (i.e., the y-intercept) represents the size of fish at initial scale development. The relationship in Equation 6-6 yielded a coefficient of determination (R^2) of 0.77 for fish lengths of up to 200 mm TL and corresponding scale radius of up to 14 microns. This linear relationship was used to back-calculate lengths of fish at annulus formation, since attempts to fit the data to Carlander's third degree polynomial (Lagler 1956, Bagenal and Tesch 1978) yielded considerably lower R^2 values. Although the relationship of fish length to scale radius for all sizes of humpback chub is probably a third degree polynomial, the relationship for fish less than 200 mm TL was best described by the linear model.

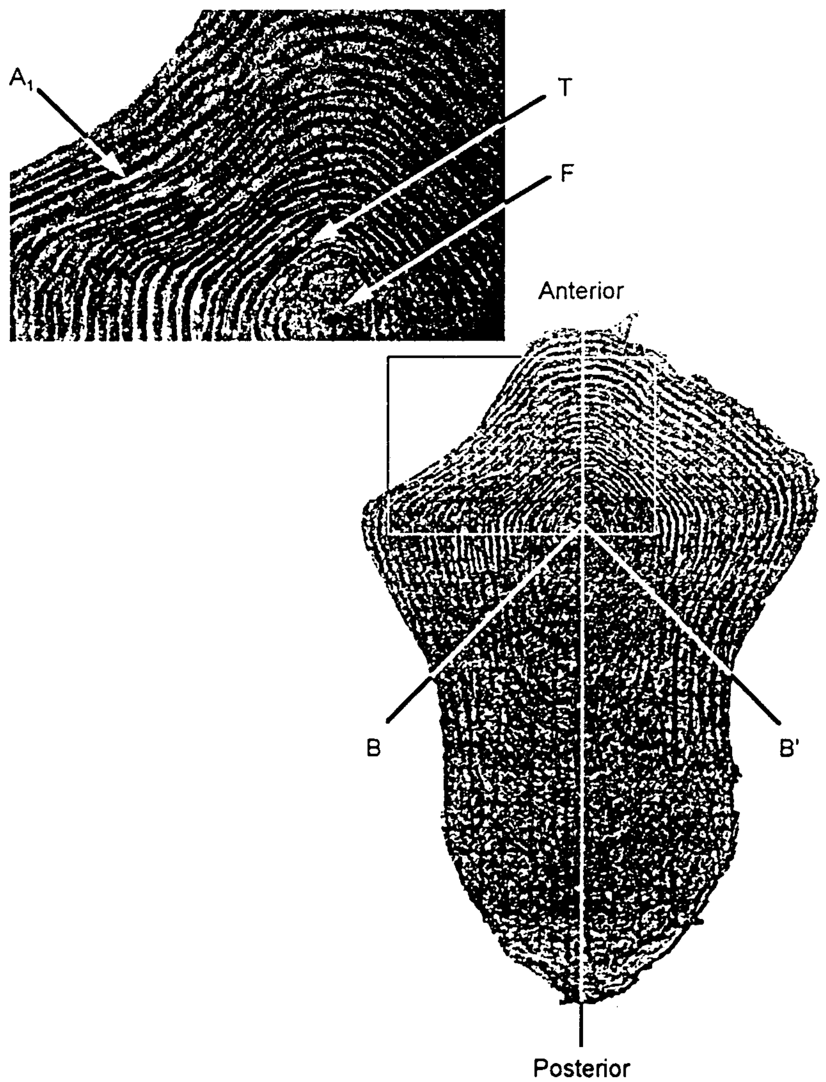
The previous relationship of fish length to scale radius was developed for two partitions of data, including the mainstem fish and fish from the upper LCR. The sample of fish from the LCR contained few fish with one or more annular rings, and the fish length to scale radius relationship was not used. The relationship for fish from the mainstem was used to develop a table of back-calculated lengths to determine age, size at annulus formation, growth, and length of fish at time of descent from the LCR to the mainstem. Back-calculated lengths at the time of transition were compared with lengths of humpback chub captured in the mainstem, using length-frequency analyses.

Lengths of Recaptured Fish

Lengths of humpback chub measured at consecutive capture events were used to compute growth rates of fish by size group. These data were compared with growth rate information reported from the LCR

Box 6-1. Age Determination from Scales.

Humpback chub have small, delicate, cycloid scales that may be useable for age determination of younger fish. The scales have an elongated posterior field (exposed toward tail of fish), and shortened anterior field (embedded in skin) with a central focus (F), circular growth rings, and annular rings (A). Humpback chub are born without scales. Scales first form on the base of the caudal peduncle, below the insertion of the dorsal fin, when the fish are less than 32 mm TL (~44 days old), and are throughout the body by about 64 mm TL (~69 days old; Muth 1990, Suttkus and Clemmer 1977). Scales are developed as a series of daily growth rings appearing under low magnification as circular rings, indicating events of growth or environmental factors. Disruption of circuli may indicate transition of fish from the warm (>20°C) LCR to the colder mainstem Colorado River (<10°C), caused by interrupted metabolism and growth. Closely-spaced and irregularly-formed presumptive daily growth rings observed by Hendrickson (1993) from otoliths (lapilli) of LCR humpback chub captured in the mainstem support the existence of a "transition check" and closely-spaced growth circuli. Proportional back-calculation using the transition check (T) indicates the size of a fish at transition from the LCR to the mainstem. The scale shown below is of an age 1+ humpback chub (TL=146 mm) from Grand Canyon, captured in August 1994. Measurements were made from the focus (F) along the posterior-lateral lines B or B'. Inset shows transition check (T) and first annulus (A).



(Minckley 1992). Growth rates computed from these length differences were expressed on a 30-day basis and an annual basis.

Population Estimates

Numbers of adult humpback chub (≥200 mm TL) in six distinct aggregations in the mainstem Colorado River were estimated. Eleven estimators in two classes (open and closed population models) were used for estimating numbers of adults in the LCRI aggregation. Fewer population estimators were used for the other aggregations as numbers of recaptures were much lower.

Adult humpback chub were captured with nets or electrofishing, marked with PIT tags, and released in 32 monthly sampling trips from October 1990 through November 1993. Sampling for marked fish was not conducted in December 1990, August, October and December 1991, and October and December 1992. Only humpback chub captured by B/W personnel were considered in these population estimates. It is important to note that capturing adult humpback chub for population estimation was not a high priority of this study (distributional and radio-tagging studies were highest priority), and capture-recapture data did not reflect an optimal sampling design for population estimators.

Closed Population Models

Closed population models are used to estimate the size of populations with no mortality, recruitment, immigration or emigration, and where population size remains constant during the sampling period. No animal population is permanently closed as mortality, recruitment, emigration and/or immigration will eventually occur, but the sampling period can be often be chosen to minimize the influence of these factors (White et al. 1982). Assumptions associated with models for estimating the size of closed populations are outlined by Seber (1982) and Otis et al. (1978).

Familiar estimators for closed populations are the Lincoln-Peterson index (Le Cren 1965) and its extension, the Schnabel estimator (Schnabel 1938). More recently, Otis et al. (1978) developed a framework of models for estimating the size of closed populations under variations in capture probabilities. These models, while assuming demographic closure, permit variation in capture probabilities due to time, behavioral response to sampling, and individual heterogeneity.

Estimators presented by Otis et al. (1978) for each model emphasize the use of maximum likelihood estimators (MLE) as the most desirable formulation. The following is a brief overview of these models and the estimators used in this study. The reader is referred to the cited references for specific equations for each estimator of population size and associated variance. The comprehensive computer program CAPTURE (Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991) calculates estimates for all of the following estimators except Schnabel $M_t t$, many of which require iterative methods to solve for N (i.e., population estimate).

Model M_o. This model assumes constant capture probabilities at each sampling period and for all individuals. The MLE's of population size (N) and capture probability (P) for this model were derived in Otis et al. (1978).

Model M_t. This model assumes that all individuals of the population have the same probability of capture, but that the capture probability may change from one sampling period to the next. Such changes in capture probability may result from different sampling efforts, sampling methods, seasonal or weather effects, or combinations of all factors. The MLE's of N and P_i (i=1, number of sample periods) for this model were derived in Otis et al. (1978), and variance of N was derived by Darroch (1958), and presented in Otis et al. (1978). This formulation is referred to in this study as the Darroch M_t estimator.

The Schnabel estimator is the original formulation for model M_t, but it is only an approximation of the MLE for N (Otis et al. 1978). This formulation is most appropriate when P_i is less than 0.1 at each sampling period, a condition met with this study (Seber 1982). Results of the Schnabel estimator are presented in this study for comparative purposes since this is a commonly used estimator. Equations for this estimator of N and associated variance developed by Chapman (1952) are presented in Seber (1982).

A third estimator for model M_t was developed by Chao (1989). This formulation was developed to reduce bias in the Darroch M_t estimator of N that can occur when P_i is small. Equations for the bias-corrected Chao M_t estimator of N and associated variance are presented in Chao (1989).

Model M_h. This model allows capture probabilities to vary by individual within the population. Such variation may result from different accessibility of individuals to traps or nets, or age and sex differences in behavior and activity (Otis et al. 1978). Use of estimators which do not assume such heterogeneity in capture probabilities, when such heterogeneity is prevalent, result in underestimation (negative bias) of the population size (Edwards and Eberhardt 1967, Carothers 1973). Maximum likelihood estimators for model M_h can be developed only when the distribution of capture probabilities is known (this is unlikely). An alternative approach to estimating N, using the generalized 'jackknife' statistic (Gray and Schuncany 1972), was developed by Burnham and Overton (1979). Equations for jackknife estimates of N and associated variance are presented in Otis et al. (1978).

Chao (1987) developed another estimator for N under the assumptions of model M_h. This development was in response to the underestimation of N by the jackknife estimator when most individuals were captured only once or twice, the case with captured adult humpback chub in this study. Equations for estimated N and variance are shown in Chao (1989).

Model M_b. This model allows capture probabilities to change after the initial capture, although the probability of capture of all individuals are the same prior to initial capture. Otis et al. (1978) derives the MLE estimator of N which is nearly equivalent to the Zippin removal estimator (Zippin 1956, 1958). This estimator relies only on first capture records, and is most appropriate in removal sampling (physically removed or 'removed' through marking) where the number of newly captured individuals must decline over the study period. Equations for this estimator are contained in Otis et al. (1978).

Models M_{tb}, M_{th}, M_{bh}, M_{tbh}. Combinations of models M_t, M_b, and M_h have also been proposed. Estimators for all but M_{tbh} have been developed. Program CAPTURE contains an unpublished estimator for M_{tb} (referred to as Burnham M_{tb}) where the probability of recapture (r) is related to the probability of initial capture (c) as follows: $c=p^{1/e}$ (Rexstad and Burnham 1991). An iterative procedure is used to find the MLE's of N, c and s (survival).

Chao (1992) proposed an estimator of N for M_{th} based on a nonparametric approach. The bias-corrected estimator N_3 in Chao (1992) was used in this study.

Estimators for model M_{bh} are presented in Otis et al. (1978) and Pollock and Otto (1983). As with the Zippin estimator for model M_b, these estimators are best suited to removal experiments, requiring a decline in numbers of newly captured individuals over the course of the study.

Estimations. In this study, closed population estimates were made for adult humpback chub captured within each of 3 calender-years (1991, 1992 and 1993), where additions and losses to the population were assumed to have minimal effect on the population estimate. Each monthly sampling trip was considered to be a sampling period. The number of sample periods were 9 in 1991, 10 in 1992 and 11 in 1993. Program CAPTURE was used to calculate most of the parameter estimates except for the Schnabel M_t estimator. A FORTRAN program was created to make calculations to estimate parameters with the Schnabel M_t estimator using equations from Seber (1982). The assumption of population closure for the LCRI aggregation for each year was supported by statistical tests for closure performed by CAPTURE. Closure could not be rejected for any of the 3 years of capture data. Meaningful closure tests could not be performed on the data from the other aggregations because of small numbers of recaptures.

Model Selection. Program CAPTURE contains an extensive routine to aid in the selection of the best closed population model for the data collected. Statistical comparisons between models and goodness-of-fit tests of individual models were made using the supplied capture data. When capture probabilities were low, however, the effectiveness of this selection routine was limited (Menkens and Anderson 1988, Pollock et al. 1990). When applied to much of the capture-recapture data from this study, CAPTURE was often unable to perform one or more of the tests due to insufficient data. This problem combined with the ineffectiveness of the selection routine with low capture probabilities resulted in limited use of these test results in this study. Instead, estimates produced by estimators robust to low capture probabilities, Chao M_h and M_t (Chao 1989), were considered to be the most reliable. Estimates and confidence intervals of N produced with these models were compared with those of the other estimators to provide a more complete evaluation of the estimated N.

Confidence Intervals. Confidence intervals around individual estimates of N were calculated as suggested by Burnham et al. (1987). This method is based on the assumption that the number of individuals in the population not captured is log-normally distributed. Chao (1989) and Rexstad and Burnham (1991) provide the necessary equations for the 95% confidence intervals about N. Confidence intervals of the mean of two or more estimates of N were calculated assuming the variance of the means is a linear combination of the variances of each mean (Blum and Rosenblatt 1972).

Open Population Models

Demographically open population models provide estimates of population size without the constraints of assuming no additions or losses to the population. Pollock et al. (1990) provided a series of estimators for open populations, within the framework of the general Jolly-Seber model (Jolly 1965, Seber 1965). Estimates are made of the population size (N_i), survival rate (s_i) number of additions to the population (B_i), and capture probability (P_i) at each sampling period "I". While these open models are not subject to the closure restriction of closed population models, estimation of additional parameters (i.e., s, B and N at each time period) often result in less precise estimates.

Models A, A', B, C, D. Maximum likelihood estimators for five related models are presented by Pollock et al. (1990). Model A assumes time specific survival (s_i) and probability of capture (P_i). Model A' is the same as model A but assumes no immigration (B = 0). Model B assumes constant survival (s), and time specific probability of capture (P_i). Model C assumes constant probability of capture (P) but time specific survival (s_i). Model D assumes constant survival (s) and constant probability of capture (P). All five models assume no differences in capture probability by individual or changes in capture probability after initial capture. Equations for MLE of models A and A' are contained in Pollock et al. (1990). Jolly (1982) provides equations for MLE of models B, C and D.

Estimations. The comprehensive computer program JOLLY was used to estimate parameters for models A, B and D for the LCRI aggregation. Because insufficient data existed from each monthly sampling trip, sampling periods were combined into seasonal sampling periods to provide sufficient numbers of humpback chub captured to estimate N and s. This resulted in 13 sampling periods from October 1990 through November 1993. December through February was defined as the winter sampling period, March through May as the spring period, June through August as the summer period, and September through November as the fall period.

Model Selection. The program JOLLY (Pollock et al. 1990) provides parameter estimates and associated confidence intervals for models A, B, and D, as well as two other related models. Goodness-of-fit tests and tests between models are conducted by JOLLY to aid in model selection. Estimators for the simplest model that fits the data are usually selected for parameter estimation.

Confidence Intervals. Confidence intervals for N_i and s_i (SE ± 1.96) were calculated by program JOLLY. Confidence intervals of the mean of two or more estimates of N were calculated assuming the variance of the means was a linear combination of the variances of each mean (Blum and Rosenblatt 1972).

Survival Estimates

Adults. Survival estimates of adult humpback chub (≥200 mm TL) were calculated in conjunction with N_i using estimators for the open population models A, B and D presented in the previous section. Brownie et al. (1985) provide estimators of survival from band recovery data which could also be applied to estimating survival of adults. They show, however, that estimators of survival derived from their methods are equivalent to those of Jolly-Seber model estimators discussed in the preceding section (Brownie et al. 1985).

Subadults. Survival of subadult humpback chub was determined from densities of subadults (<200 mm TL), from the LCR inflow (RM 61.3) to Lava Canyon (RM 65.4). These densities were determined monthly from catch rates of shoreline electrofishing, seining, and minnow traps. Decreased densities in this area were attributed to mortality (i.e., predation, starvation, thermal shock, parasites and diseases) and emigration, and offset by immigration from the LCR. These decreases in catch rates were used as indices of survival for periods of time when emigration and immigration were low, based on presence or absence of high LCR flows. Peak mainstem densities in September 1991, May 1992, and September 1993 reflected downstream dispersal of subadults from the LCR, concurrent with high LCR flows. Decreases in monthly densities were evaluated for 6-month periods starting with peak mainstem densities. These decreases were best described as a negative exponential (Z_t), that served as an index to monthly decline of subadults during that sample period (Ricker 1958, 1975, Everhart and Youngs 1981), and expressed as:

(Equation 6-7)

$$N_{(t)}=N_{(o)}e^{-zt}$$

where:

$N_{(t)}$ = **number of fish at time(t),**
$N_{(o)}$ = **number of fish at start of sample period, and**
z = **instantaneous mortality rate.**

Sex Ratios

Humpback chub, flannelmouth suckers, and bluehead suckers over 175 mm TL were externally examined to determine gender. Slight pressure was applied to the abdomen of each fish for expression of milt from males or eggs from females. If gametes could not be expressed, male humpback chub were distinguished from females on the basis of size and shape of the urogenital papillae (Suttkus and Clemmer 1976). Males exhibited a more pronounced, erect, and anteriorly-oriented papillae when palpated with slight pressure to the anterior region of the vent. Papillae of females was less pronounced, oriented posterior, and broader than that of males. This technique of external examination is used by personnel at the Willow Beach National Fish Hatchery to sort male from female Colorado squawfish, bonytail, and humpback chub when eggs and milt are not being expressed by the fish (B. Jensen, USFWS, pers. comm.). Douglas (1993) failed to find reliable external morphological characters by which to distinguish male from female humpback chub, but did not consider the urogenital papillae.

Gender of flannelmouth suckers and bluehead suckers was determined from expression of gametes or examination of the urogenital papillae, as described above for humpback chub, and from the size and shape of the anal fin. Male suckers had a narrower and longer anal fin than the shorter, broader, and rounded fin of females.

Reproductive Potential and Success

Reproductive potential of humpback chub in the mainstem was derived from information found in literature, primarily from laboratory and hatchery studies. Fish were not sacrificed during this investigation to supplement these data because of the endangered status of the species. A relationship between fish length and fecundity (number of eggs per female) was developed for the size range reported in literature.

Reproductive success of humpback chub in the mainstem was assessed from reproductive condition of adults (i.e., expression of milt or eggs, tuberculation, coloration), presence of larvae, and aggregations of adults that indicated possible spawning activity in the area. Widespread sampling and radiotelemetry were used to locate staging fish and to identify congregations suggesting reproductive readiness or spawning activity.

Predation

Diet analyses were conducted on the four most common large predatory fish species in Grand Canyon: brown trout, rainbow trout, channel catfish, and striped bass (See Chapter 9 - FOOD HABITS). Total numbers of humpback chub potentially consumed by these predators were estimated with the aid of predator to prey size relationships and predation rates determined from these diet analyses.

Prey potential on humpback chub was evaluated by relating predator mouth gape (maximum diameter) to maximum body depth of humpback chub. The relationship of total length to maximum body depth was developed for humpback chub from morphometric measurements taken in the field during this investigation (See Chapter 2 - STUDY DESIGN). The relationship between predator length and maximum mouth gape was developed using measurements reported for brown trout (Bannon and Ringler 1986), channel catfish (T. Crowl and L. Alder, USU, pers.comm.), and striped bass (Chervinski et al. 1989). The length to mouth gape relationship for rainbow trout was taken from a relationship developed for the closely related cutthroat trout (Reimchen 1991).

These relationships were used to determine maximum size of humpback chub susceptible to predation by each predator species. It was assumed that mouth gape for each predator was equivalent to maximum body depth of humpback chub that could potentially be consumed. This relationship was confirmed by examining size of fish actually consumed by specific predators. It was also assumed, and confirmed in the literature cited above, that digestive rates of all four predators at 10-12°C were about 24 hr. Potential numbers of humpback chub consumed daily were based on average numbers per stomach by predator species examined in the field.

Parasites and Diseases

Incidence of apparent diseases and kinds and numbers of macroparasites were recorded for each native fish captured incidental to field measurements and observations. No attempt was made to conduct a complete or thorough survey of diseases and parasites during this investigation. Locations and effects (e.g., lesions, open sores, etc.) of external parasites were noted, and internal parasites were recorded when possible. Internal parasites were revealed during handling and with the aid of a pump used to evacuate gut contents for diet analysis (See Chapter 9 - FOOD HABITS).

RESULTS

Length-Frequency

Pooled length-frequency histograms from all gear types (Fig. 6-1) were generated to characterize size distributions of humpback chub in the 30-Mile aggregation (RM 29.8-31.3), MGG aggregation (RM 126.1-129.0), and the LCRI aggregation subdivided into a group above the LCR (RM 57.0-61.3) and a group below the LCR (RM 61.3-65.4) (See Table 5-11 in Chapter 5 - DISTRIBUTION AND ABUNDANCE). Size of fish in the 30-Mile aggregation (range, 330-460 mm TL) indicated that all specimens handled were adults with average length significantly greater than that of the other groups (ANOVA, $F=108.21$, $P<0.001$, df=3, 1,127; Fishers LSD, $P \leq 0.05$) (Fig. 6-2). Absence of

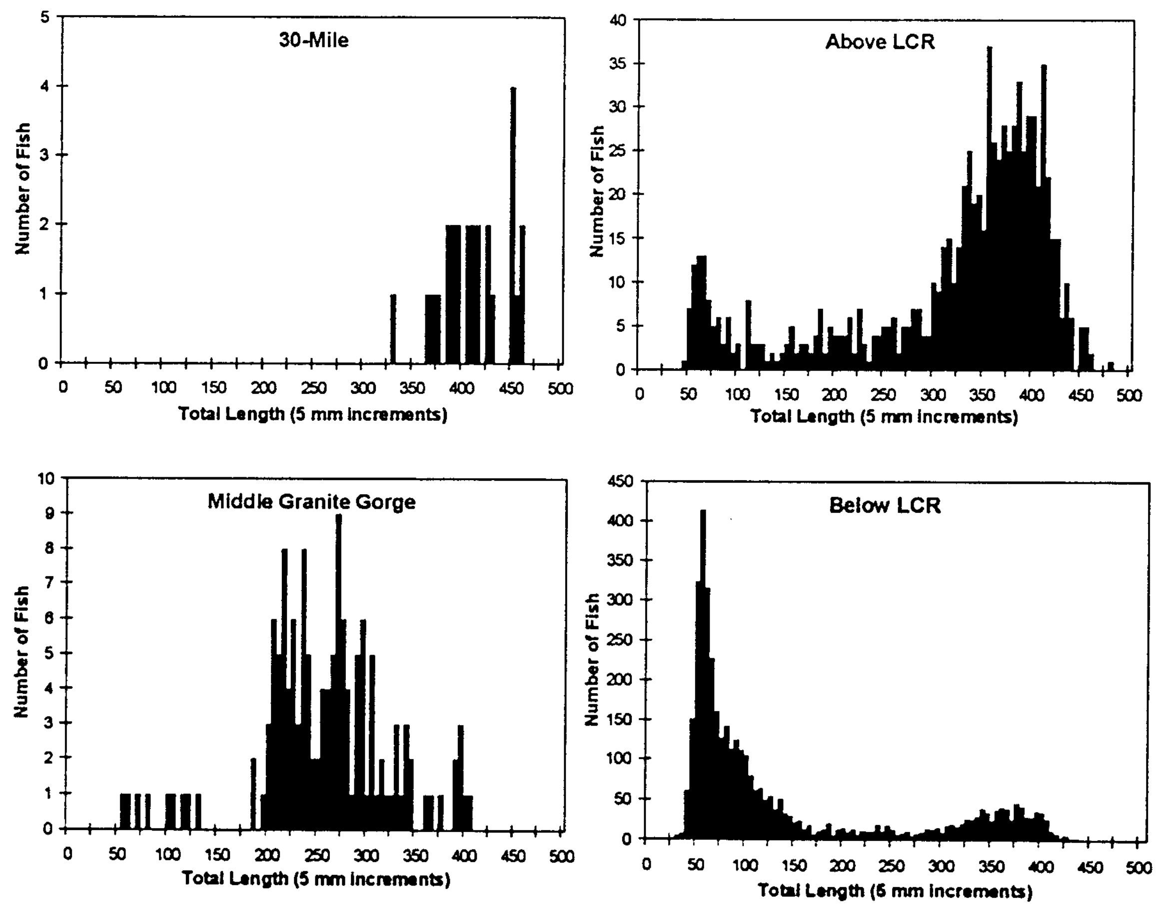


Fig. 6-1. Length-frequency histograms for four major aggregations of humpback chub in the Colorado River, October 1990-November 1993. Note differences in vertical scales.

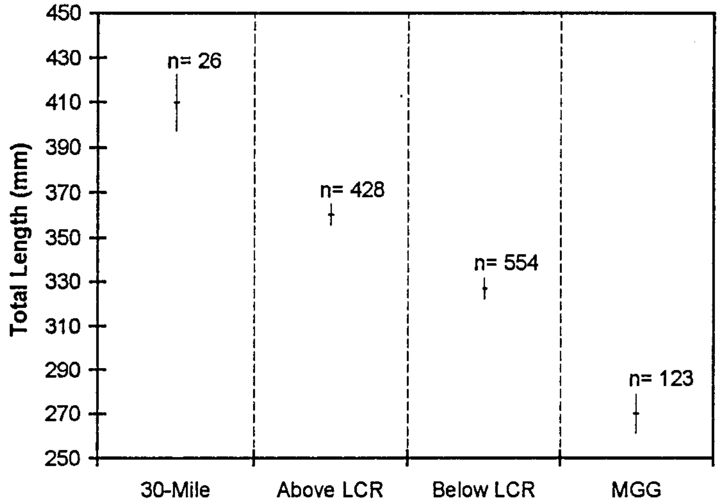


Fig. 6-2. Mean total length for adult humpback chub (≥200 mm TL) in four mainstem aggregations in Grand Canyon, 1990-93. Means, 95% confidence intervals and sample sizes are shown.

subadults and adults smaller than 330 mm TL indicated little, if any, successful recent reproduction and recruitment.

Length-frequency histograms for humpback chub near the LCR revealed a greater proportion of small fish downstream of the LCR inflow than above. Most individuals less than 150 mm TL above the LCR inflow were within 0.8 km (0.5 mi) of the confluence, indicating these fish originated in the LCR and swam short distances upstream. Four fish (range, 74-88 mm TL) captured in January through November 1992 were within 0.4 km (0.25 mi) upstream of the LCR inflow. Kaeding and Zimmerman (1983) failed to collect humpback chub smaller than 145 mm TL in the mainstem upstream of the LCR in October and November 1980-81, and in April and May 1981.

Mean length of adults in the MGG aggregation (range, 53-405 mm TL) was significantly less (ANOVA, F=108.21, P<0.001, df=3, 1,127; Fishers LSD, P≤0.05) than mean length of the other three groups (Fig. 6-2). Overall, the MGG aggregation was composed of few small fish and numerous large subadults and adults. Successful reproduction was not confirmed in this area, and there appears to be substantial immigration of subadults from the LCRI aggregation. This aggregation appeared to be maintained by immigration of young fish from the LCR and longevity of adults.

Monthly length-frequency histograms were generated for the LCRI aggregation for 1991 (Appendix F, Fig. F-1), 1992 (Fig. F-2), and 1993 (Fig. F-3). Faster growth occurred in the LCR (Kaeding and Zimmerman 1983, Hendrickson 1993) than in the mainstem with differential dispersal of young from the LCR (i.e., young moved from the LCR to the mainstem at different ages) precluding distinct segregation of age 0, I, and II cohorts (<200 mm TL). Adults (≥200 mm TL) could not be segregated into cohorts by length-frequency analysis, apparently because of disrupted growth from spawning, slowed growth at maturity, and longevity of adults.

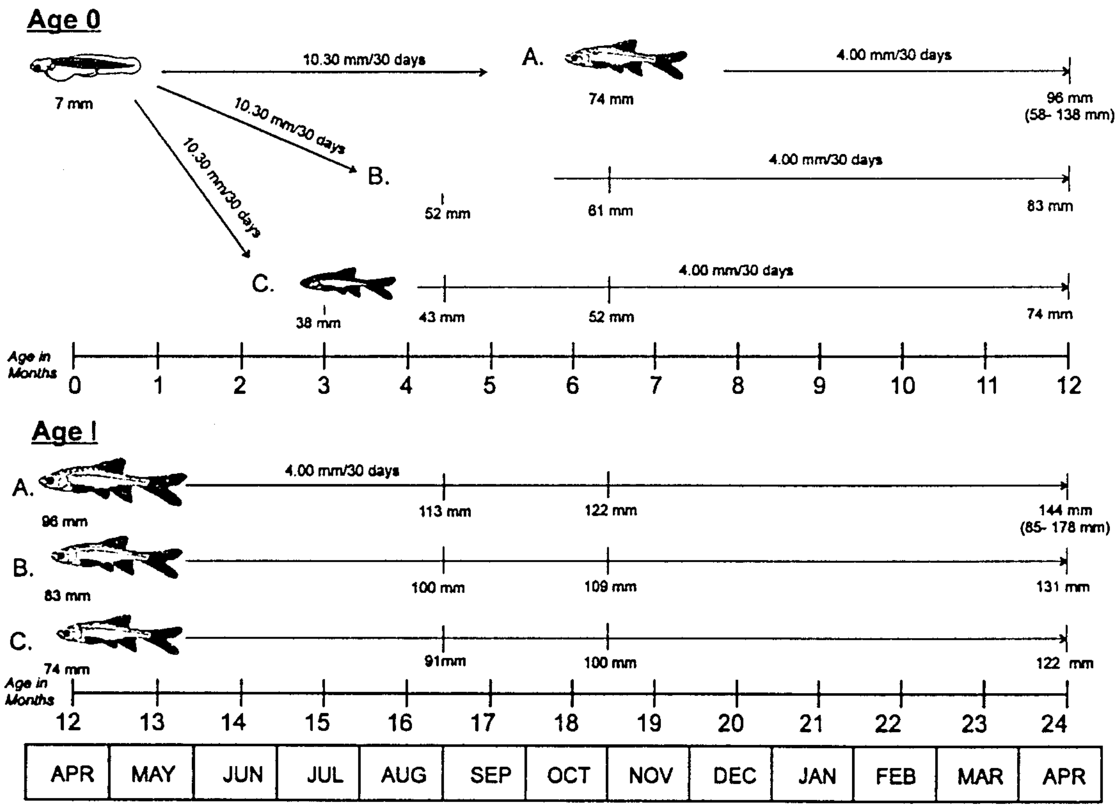
The appearance of large numbers of humpback chub less than 75 mm TL at the LCR inflow in September 1991, May 1992, and September 1993 was the result of dispersal of young from the LCR concurrent with summer, rain-induced floods. This frequency mode persisted and was dominant for about 6 months, during which time either mortality or emigration dramatically reduced monthly mainstem densities (See Survival section of this chapter). Scale back-calculations indicate that the majority of these young fish were age 0, but also included age I fish. The age 0 fish were variable sizes, apparently because of extended spawning and hatching times in the LCR (i.e., late March to early June), and the variable time of transition from the warm faster-growing environment of the LCR to the cold slower-growing environment of the mainstem. Age 0 fish remaining in the LCR most of the first summer of life were nearly as long as age I fish hatched late in the previous spawning period and moving to the mainstem at a small size (See Box 6-2.).

Length distribution of captured humpback chub over 150 mm was very different between the LCR (Fig. 6-3A, ASU data) and the mainstem LCRI aggregation (Fig. 6-3B). The length distribution of the LCRI was highly skewed toward chubs 300 mm TL or greater (72% were >300 mm TL and 28% <300 mm TL). Humpback chub under 175 mm TL may be under-represented in the LCRI as PIT-tagging of individuals 150-175 mm TL was not instituted in the mainstem sampling until February 1991. The length distribution of chubs captured in both the LCRI aggregation and in the LCR (Fig 6-3C) was nearly identical to that of chubs captured in the LCRI aggregation, particularly for fish 200 mm

Box 6-2. Similar Lengths of Subadult Humpback Chub of Different Age.

Subadult humpback chub (age groups 0, I, II) from Grand Canyon are difficult to differentiate by cohort from length-frequency analyses because of apparent overlap from similar lengths of fish of different age. Differential growth rates of fish residing in the warm Little Colorado River (LCR, >20°C) and in the colder mainstem Colorado River (<10°C), with mixing of individuals in both systems, leads to fish of similar age having different lengths, or fish of different age with similar lengths. Three growth scenarios are illustrated in the associated figure and theoretical total lengths of fish determined for 2 years: (A) mean total length of 74 mm for fish descending from the LCR to the mainstem, based on scale back-calculations, (B) minimum total length of 52 mm for fish descending from the LCR to the mainstem, based on scale back-calculations, and (C) calculated total length of 38 mm for fish descending from the LCR to the mainstem during early transition. Growth rates of 10.30 mm/30 days and 4.00 mm/30 days were used for the LCR and mainstem, respectively, from scale back-calculations.

Assuming total length of 7 mm at hatching (Muth 1990), fish are theoretically 96 mm, 83 mm, and 74 mm TL for scenarios A, B, and C, respectively, and by September of the second year, the fish are theoretically 113, 100, and 91 mm TL, respectively. At the end of the second year, the fish are 144, 131, and 122 mm TL. Although means in length estimates appear to be distinct for age groups 0 and I, ranges in mean back-calculated lengths for age 0 (58-138 mm) and age I (85-178 mm) indicate that the overlap in length between age groups occurs over respective ranges.



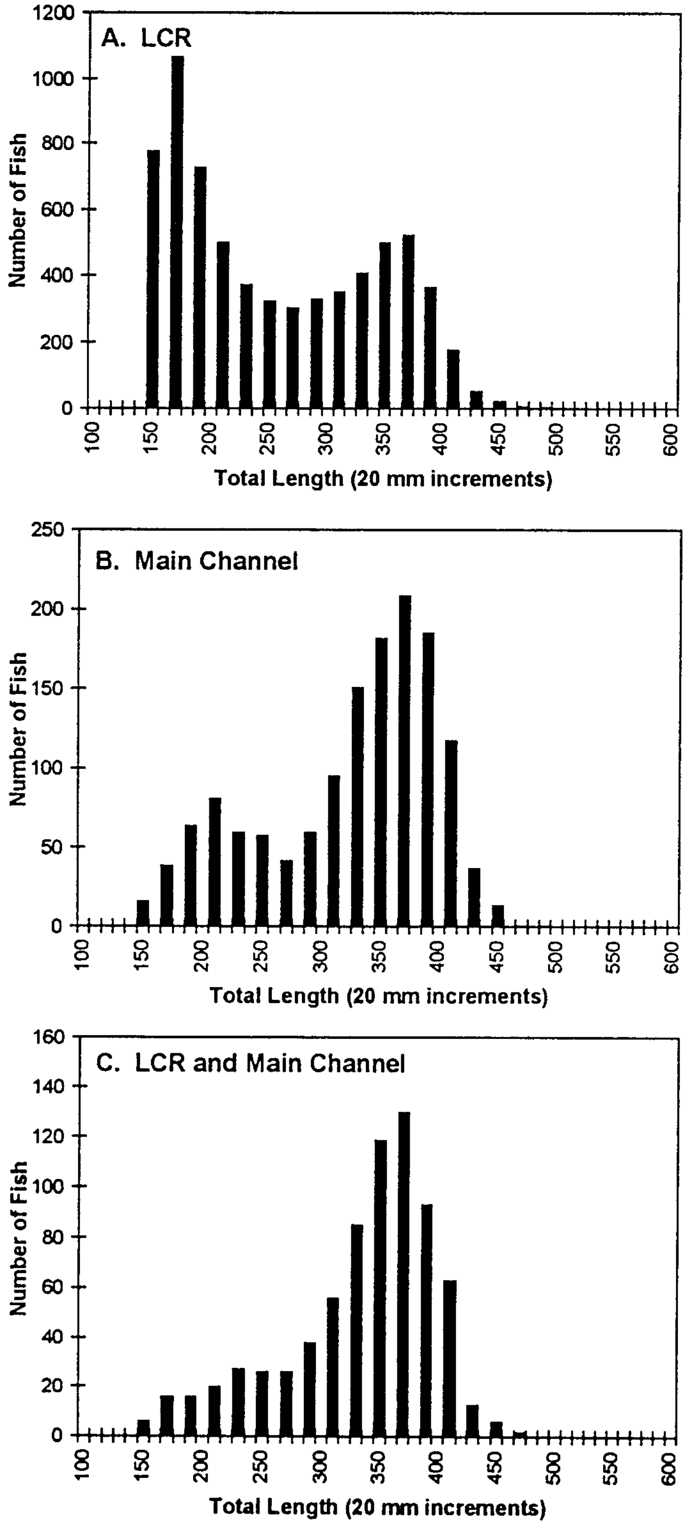


Fig. 6-3. Length-frequency of individual PIT-tagged humpback chub capture in the LCR (A) (ASU data), in mainstem LCRI aggregation (B), and in both LCR and mainstem LCRI aggregation (C).

TL or greater. This suggests a portion of chubs 200 mm TL or greater use both systems, and that larger individuals (≥300 mm TL) were more likely to be found in both systems.

Length-Weight Relationship and Condition Factor

Humpback Chub

Length-weight relationships for humpback chub (Fig. 6-4, Table 6-1) were described for 1990-91, 1992, and 1993. Exponents of 3.117, 3.056, and 2.986 indicate that growth pattern was approximately isometric as an exponent of 3.0 indicates 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), the length to weight relationship was constant, as reported for other species (Anderson and Gutreuter 1983).

Monthly trends in relative condition factor (Kn) of adult humpback chub (≥200 mm TL) from October 1990 through November 1993 (Fig. 6-5, Table 6-1) reflected robustness prior to spawning by the LCRI aggregation, loss of weight during spawning, and regained weight following spawning. Except for October 1990, monthly mean Kn was highest in January, February, March or April of 1991, 1992, and 1993, which was prior to spawning by the LCRI aggregation. Condition was lowest in June of 1991 and 1992, and August 1993 when post-spawned adults were dispersing from the LCR to the mainstem. Relative condition increased most dramatically from June to September, when fish were recovering from spawning, and from November to March, in advance of spawning. Increased Kn from June to September may also be associated with increased robustness by adults in other mainstem aggregations involved in later spawning (See Reproductive Potential and Success section of this chapter).

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≤0.05). Higher Kn for October 1990 were possibly related to greater availability of food under research flows, which

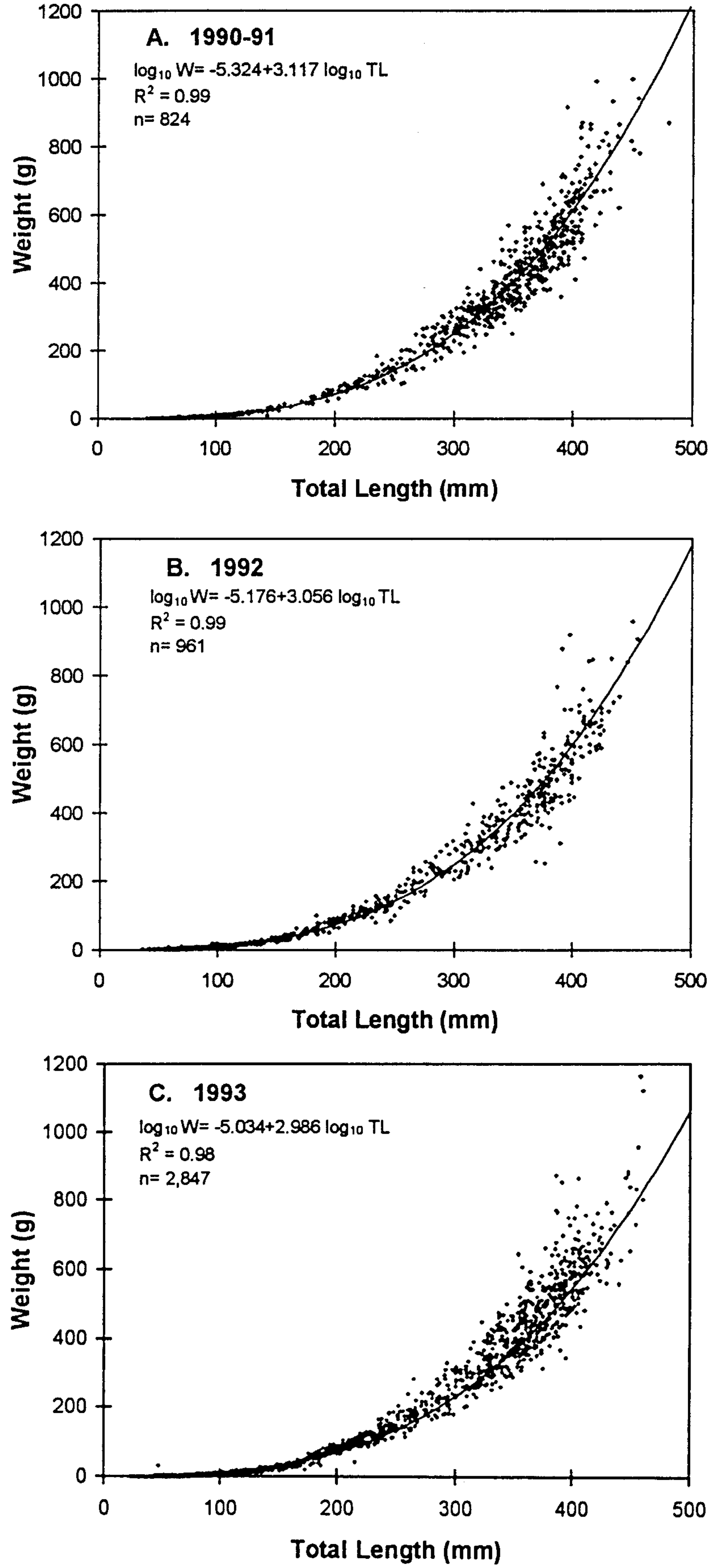


Fig. 6-4. Length-weight relationship for humpback chub from the Colorado River in Grand Canyon for 1990-91 (A), 1992 (B), and 1993 (C).

Table 6-1. Mean monthly relative condition (Kn) for 1,693 humpback chub (≥200 mm TL) from the Colorado River in Grand Canyon, October 1990 - November 1993.

Month	No. Fish	Mean Relative Condition	Standard Error
		1990	
October	38	1.061	0.023
November	43	1.020	0.022
		1991	
January	76	1.052	0.013
March	109	1.054	0.014
April	7	0.993	0.048
May	33	0.997	0.025
June	30	0.930	0.020
July	72	0.986	0.020
September	96	0.997	0.015
November	40	0.989	0.021
		1992	
January	25	1.020	0.024
March	42	1.057	0.021
April	37	1.058	0.016
May	52	0.949	0.022
June	34	0.824	0.018
July	98	1.009	0.014
August	6	1.047	0.039
September	46	1.047	0.022
November	56	0.997	0.018
		1993	
January	108	1.044	0.013
February	78	1.058	0.014
March	58	1.102	0.023
April	45	1.076	0.021
May	92	0.949	0.018
June	71	0.925	0.016
July	93	0.977	0.013
August	39	0.935	0.022
September	86	0.977	0.015
October	44	0.996	0.021
November	39	0.983	0.019

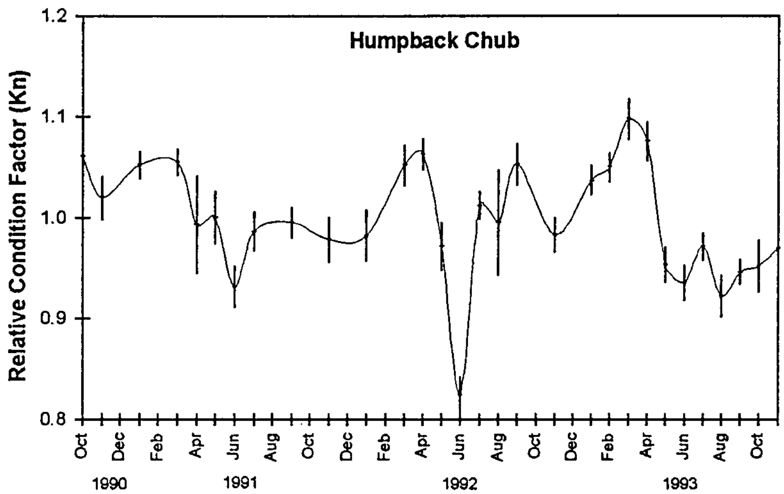


Fig. 6-5. Mean monthly relative condition (Kn) of adult humpback chub (≥200mm TL) from the Colorado River in Grand Canyon, October 1990 - November 1993. Values represent means ± one standard error. Means are connected with a smooth line to enhance visual representation of trends.

were replaced by interim flows on August 1, 1991 (See Chapter 3 - HYDROLOGY). The extremely robust appearance of some adults in October 1990 suggests an exceptionally high condition at that time. Lower Kn in October 1991, 1992, and 1993 suggests reduced availability of food from lower fluctuations associated with interim flows (See Chapter 9 - FOOD HABITS), although the lower Kn did not reflect fish that appeared starved or physiologically stressed. The only fish that appeared emaciated were individuals captured at the LCR inflow following high floods in January 1993. These fish were believed to be LCR residents temporarily transported by high flows into the mainstem.

Pooled relative condition of adult female humpback chub (Kn=1.022) was significantly greater (t-test, t=2.643, P=0.009, df=358) than that of males (Kn=0.980), indicating gender differences in robustness (Fig. 6-6). Monthly Kn was significantly higher for females in June, July, and November of 1992 (Table 6-2), suggesting that differences in condition were not related to egg masses in females, i.e., most females spawned in March through May.

Relative condition of adults above and below the LCR inflow was compared to assess the importance of the input of LCR water to fish condition. Fish caught in the LCR inflow staging area (RM 60.9-61.9) were excluded from the analysis to reduce bias from exceptionally robust fish during prespawning aggregations. The analysis showed that Kn of fish caught below the confluence (RM 61.9-65.4) did not differ significantly (t-test, P=0.003, df=1, 462) from Kn of fish caught above the inflow (RM 60.9-57.0).

Flannelmouth Sucker

A length-weight relationship was developed for 1,903 flannelmouth suckers captured in the mainstem from October 1990 through November 1993 (Fig. 6-7A). The exponent of 3.076 indicates that growth of flannelmouth suckers was approximately isometric. Average monthly relative condition of adults did not followed a particular seasonal pattern (Fig. 6-8A).

Bluehead Sucker

A length-weight relationship was also developed for 693 bluehead suckers captured in the mainstem from October 1990 through November 1993 (Fig. 6-7B). An exponent of 3.090 indicates that growth of bluehead suckers was approximately isometric. Annual patterns in average monthly relative condition were irregular, perhaps because of small sample size (Fig. 6-8B).

Rainbow Trout

A length-weight relationship was developed for 3,568 rainbow trout captured in the mainstem in 1990-91 and represented by:

(Equation 6-8)

$$\log_{10}W = -4.013 + 2.582 \log_{10}TL \quad (R^2=0.99)$$

An exponent of 2.582 indicates that rainbow trout did not exhibit isometric growth, but became less robust with length. Average monthly Kn of adult rainbow trout failed to follow the same seasonal pattern over the 3 years observed, 1991, 1992, and 1993 (Fig. 6-8C, Table 6-3). Assuming that robustness is affected primarily by spawning activity and food availability (Anderson and Gutreuter 1983), rainbow trout in Grand Canyon were expected to exhibit high Kn in late fall and early winter in preparation for spawning in January

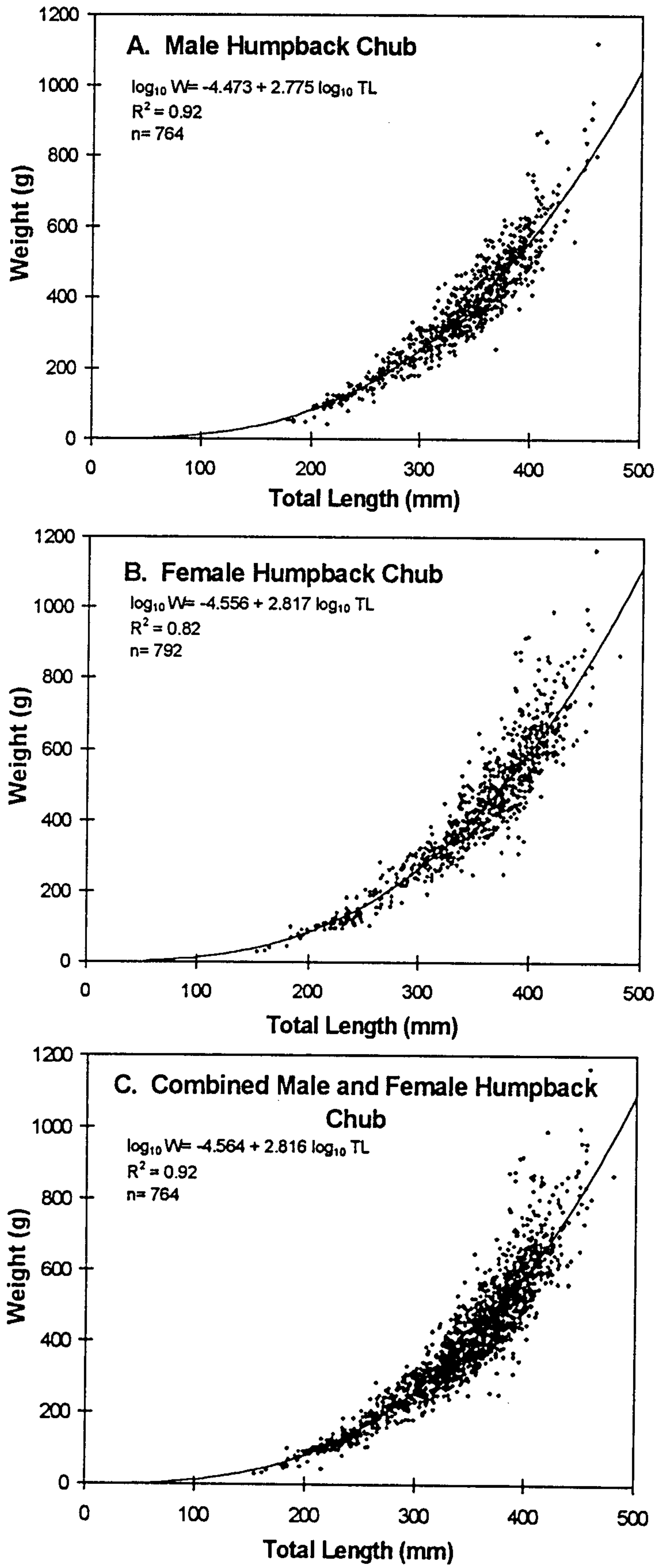


Fig. 6-6. Length-weight relationship for males (A), females (B), and combined (C) from the Colorado River in Grand Canyon, October 1990-November 1993.

Table 6-2. A comparison of mean monthly relative condition (Kn) for male and female humpback chub (≥200 mm TL) from the Colorado River in Grand Canyon, 1992.

	Males		Females		
Month	No	Kn	No.	Kn	P values [a]
January	9	0.996	14	1.050	0.280
March	17	1.080	19	1.069	0.813
April	17	1.070	14	1.063	0.853
May	14	1.023	32	0.939	0.108
June	18	0.783	15	0.883	0.003*
July	38	0.969	55	1.031	0.024*
September	22	1.017	22	1.092	0.096
November	25	0.960	25	1.050	0.014*

[a]'t' test significant at P≤ 0.05, indicated by '*'

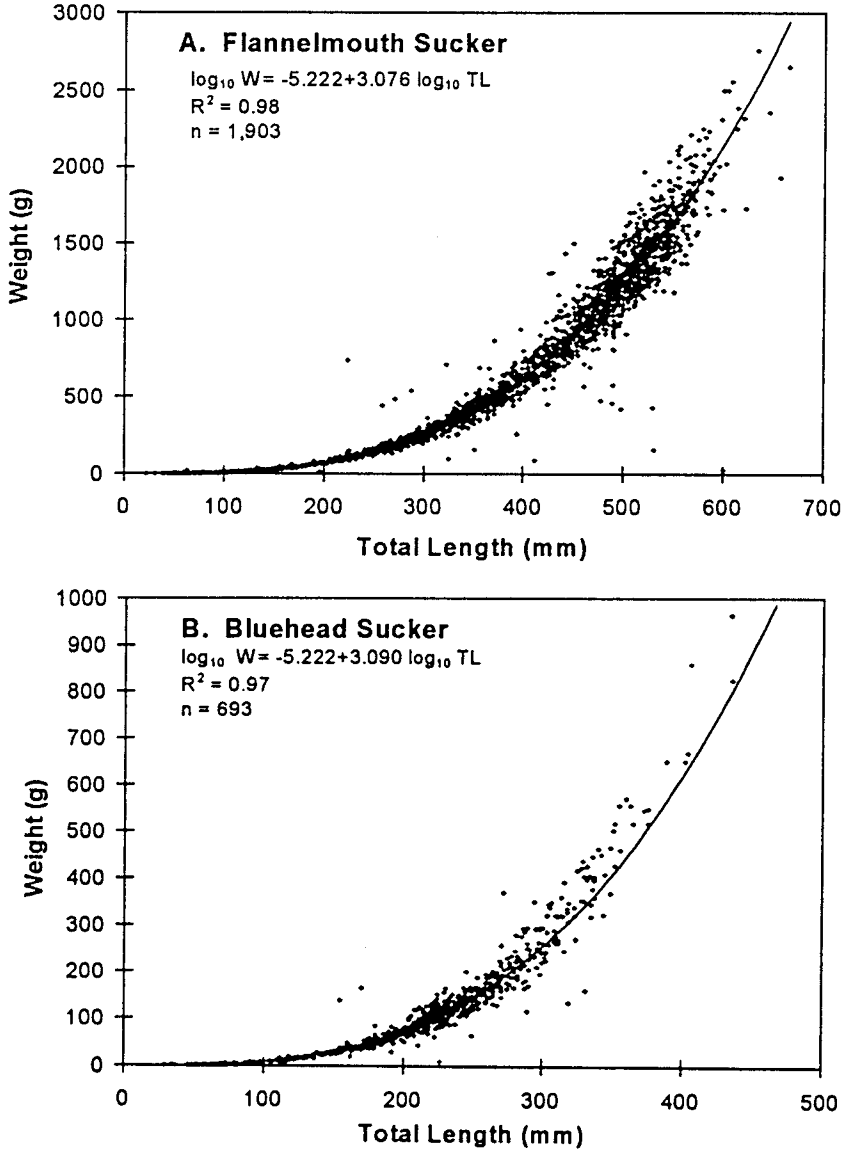


Fig. 6-7. Length-weight relationships for flannelmouth sucker (A) and bluehead sucker (B) from the Colorado River in Grand Canyon, October 1990 - November 1993.

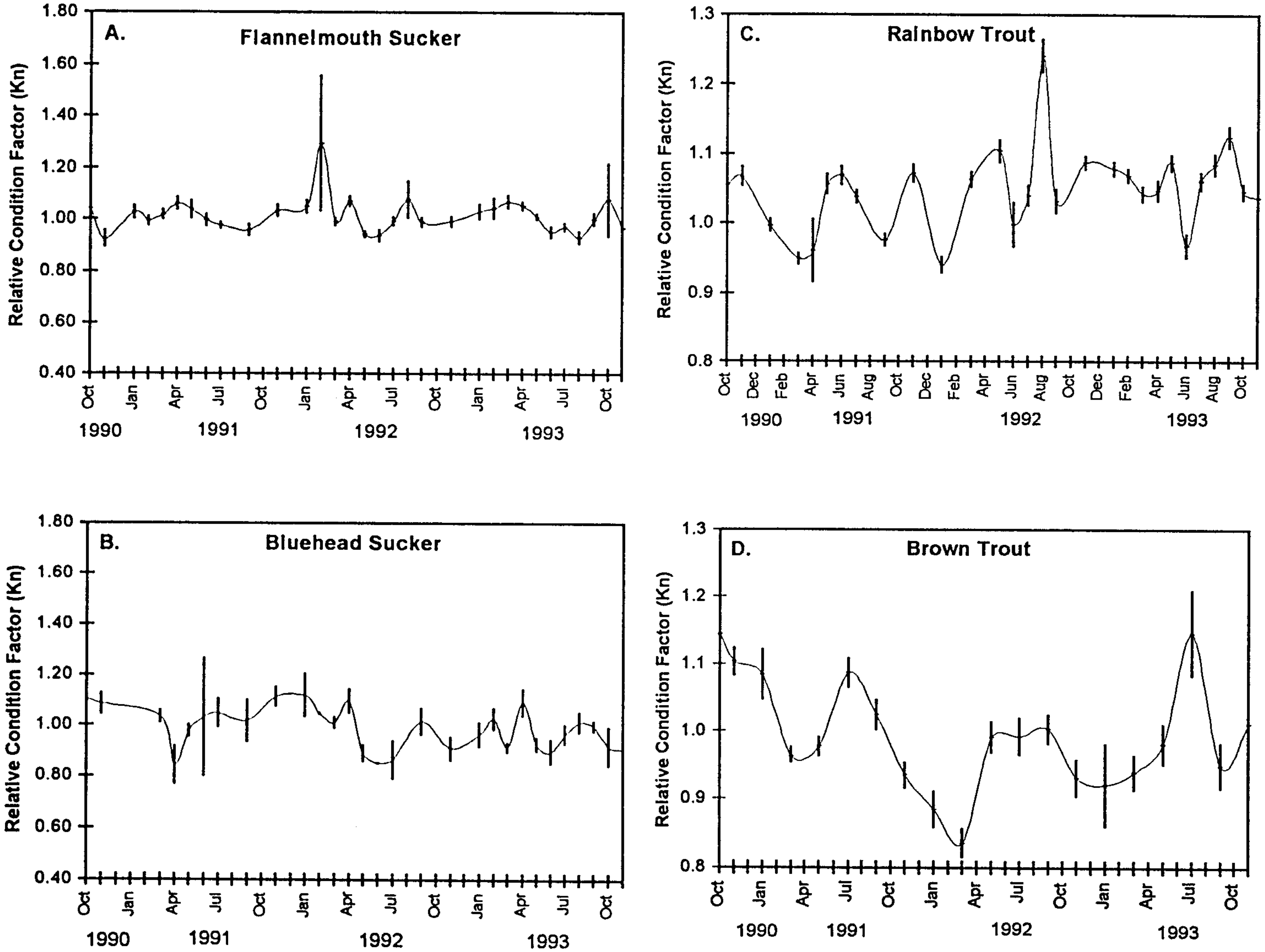


Fig. 6-8. Mean monthly relative condition (Kn) for flannelmouth sucker (A) and bluehead sucker (B) (≥150 mm TL), and for rainbow trout (C) and brown trout (D) (≥200 mm TL) from the Colorado River in Grand Canyon, October 1990-November 1993. Values represent means ± one standard error. Means are connected with a smooth line to enhance visual representation of trends.

Table 6-3. Mean monthly relative condition (Kn) of 9,126 rainbow trout (≥200 mm TL) from the Colorado River in Grand Canyon, October 1990 - November 1993.

Month	No. Fish	Kn	Standard Error
		1990	
October	84	1.054	0.028
November	336	1.067	0.014
		1991	
January	522	0.997	0.009
March	518	0.949	0.008
April	10	0.962	0.044
May	643	1.056	0.011
June	161	1.069	0.013
July	667	1.038	0.009
September	672	0.976	0.008
November	433	1.072	0.012
		1992	
January	478	0.941	0.011
March	406	1.066	0.011
May	256	1.104	0.016
June	14	0.998	0.031
July	280	1.044	0.015
August	120	1.241	0.023
September	190	1.032	0.017
November	401	1.091	0.010
		1993	
January	411	1.076	0.010
February	301	1.068	0.009
March	500	1.042	0.010
April	182	1.047	0.014
May	340	1.087	0.011
June	112	0.968	0.016
July	290	1.061	0.012
August	190	1.085	0.015
September	181	1.124	0.014
October	348	1.046	0.011
November	80	1.037	0.021

through March (Maddux et al. 1987), followed by low Kn through spring and early summer, and increasing in late summer and fall.

The pattern in condition of rainbow trout from fall to spring of each year was as expected with respect to spawning activity, but variable high and low Kn through 1991, 1992, and 1993 suggests that the fish were also responding to environmental factors, such as flow, turbidity, or food availability. Relative condition of rainbow trout tended to be low in late winter (January-March) and late summer (August-October), when tributary floods were most frequent, and mainstem turbidity was generally high. Hence, increased turbidity could be reducing feeding activity of rainbow trout, as reported in laboratory studies (Barrett et al. 1992).

Brown Trout

A length-weight relationship was also developed for 603 brown trout captured during 1990-91, and described as:

(Equation 6-9)

$$\log_{10}W = -4.967 + 2.958 \log_{10}TL \quad (R^2=0.98)$$

An exponent of 2.958 indicates that the growth pattern for brown trout was approximately isometric. Annual patterns in average monthly Kn were irregular and variable, like those of rainbow trout (Fig. 6-8D, Table 6-4). Average Kn for brown trout in Grand Canyon was expected to be high in late summer and early fall in preparation for spawning in October through November, followed by low Kn through winter and early spring, and

Table 6-4. Mean monthly relative condition (Kn) of 1,421 brown trout (≥200 mm TL) from the Colorado River in Grand Canyon, October 1990 - November 1993.

Month	No. Fish	Kn	Standard Error
		1990	
October	5	1.144	0.053
November	29	1.103	0.020
		1991	
January	24	1.084	0.037
March	131	0.963	0.013
May	137	0.977	0.013
July	66	1.087	0.021
September	114	1.024	0.022
November	109	0.935	0.018
		1992	
January	71	0.885	0.025
March	70	0.836	0.020
May	154	0.991	0.022
July	73	0.992	0.027
September	98	1.003	0.021
November	73	0.931	0.026
		1993	
January	24	0.920	0.059
March	61	0.939	0.025
May	84	0.981	0.029
July	31	1.146	0.062
September	48	0.949	0.032
November	19	1.011	0.051

increasing in summer and fall. The decrease in Kn from fall to winter occurred in all years sampled, but other seasonal patterns were irregular and probably caused by variable flow patterns or food availability. Feeding activity of brown trout does not appear to be as affected by turbidity as feeding by rainbow trout.

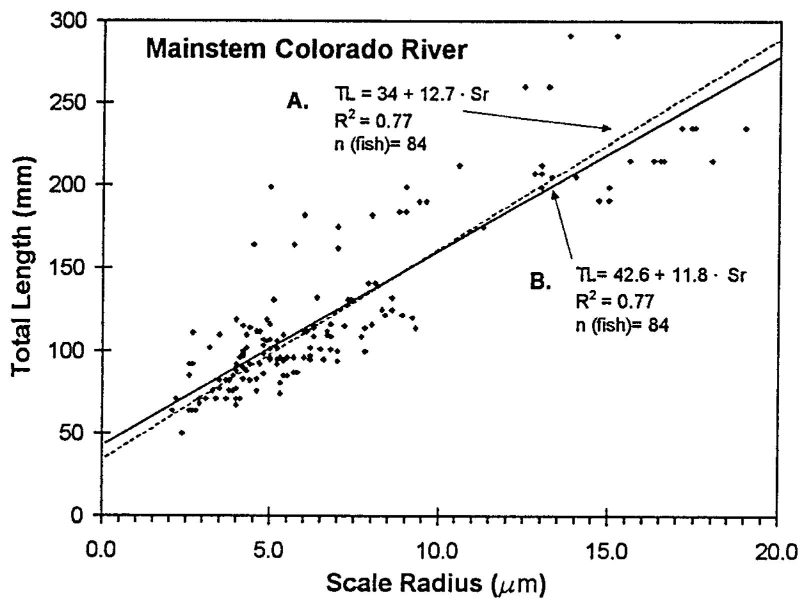


Fig. 6-9. Total length to scale radius relationship for humpback chub from the Colorado River in Grand Canyon, with (A) and without (B) a specified y-intercept.

Age and Growth

Length at Annulus Formation

Total length to scale radius relationships were developed for humpback chub less than 200 mm TL from the mainstem Colorado River (Fig. 6-9). The y-intercept coefficient, or fish length at scale formation, was 42.6 mm TL, about 9 mm larger than known length at scale formation (<34 mm TL,<26 mm SL) for laboratory-reared humpback chub (Muth 1990). This discrepancy demonstrates Lee's phenomenon where, at a given annulus, back-calculated lengths are relatively larger in younger fish (Miranda et al. 1987). The typical body length to scale radius relationship is a third degree polynomial with a specified y-intercept (Lagler 1956), but this model was not used because the data for these subadult fish more closely fit a linear model; hence, a linear model with a specified y-intercept of 34 mm TL was used to calculate body length at annulus formulation.

(Equation 6-10)

$$TL = 34 + 12.7\ SR$$

where:

SR = scale radius in millimeters.

Annular rings were distinguished by crowding, cross-over, and disruption of several adjacent circuli. The first annulus usually began to form with disruption of the 10th to 13th circulus from the focus. Scales of fish captured in November showed crowded or discontinuous circuli, indicating the start of the winter annular ring. Scales collected between January and March usually displayed crowding and discontinuity of several circuli at or near the outer margin of the scale, indicating the presence of an annular ring. Those scales collected in April and May showed complete circuli at the margin, indicating that annulus formation occurred during the winter period of about November through March. Kaeding and Zimmerman (1983) observed crowded circuli at scale margins during October-November, few scales with new annuli (resumed growth) in February, and new annuli on many scales during April-May.

Average back-calculated lengths of mainstem subadults at 1, 2, and 3 annuli were 96, 144, and 186 mm TL, respectively (Table 6-5). Only 5 of the 44 subadults from the LCR had one or more annular rings, and back-calculations for the LCR fish are not presented in this report because of small sample size. Kaeding and Zimmerman (1982, 1983) reported 1st annulus formation for LCR fish at 100 mm TL, and they also reported that humpback chub 250-300 mm TL were approximately 3 years of age. This appears to be an underestimate of age since we found from scale back-calculations that humpback chub with 3 annular rings averaged 186 mm TL. With annulus formation complete by the end of March, and most spawning and hatching in April, scale interpretation for this population closely approximated calendar years of age, i.e., back-calculated length at 1st annulus formation approximated length at 1 calendar year of age.

Growth

A logarithmic relationship similar to that proposed by Von Bertalanfly (1938, see also Ricker 1975, Everhart and Youngs 1981) is presented to

Table 6-5. Summary of back-calculated total length (mm) at each annulus (A_i) and transition check (T_x), based on the linear regression formula: TL = 34 + 12.7 (Sr), for 84 humpback chub collected from the mainstem Colorado River in Grand Canyon, 1992-93. n = number of fish.

Age	No. Fish		T_x	A_1	A_2	A_3	A_4
0	32	Mean	71				
		Range	52-98				
		n	32				
I	40	Mean	76	95			
		Range	58-132	67-127			
		n	40	40			
II	5	Mean	78	107	155		
		Range	57-103	85-138	117-178		
		n	5	5	5		
III	5	Mean	62	995	152	206	
		Range	62	75-118	130-168	149-231	
		n	1	5	5	5	
IV	2	Mean	-	70	95	136	157
		Range	-	58-82	85-105	128-144	151-163
		n	-	2	2	2	2
Summary	84	Mean	74	96	144	186	157
		Range	52-132	58-138	85-178	129-231	151-163
		n	78	52	12	7	2

represent growth of humpback chub in the mainstem (Fig. 6-10). The relationship was based on scale back-calculations for ages 0-3 and measurements of recaptured PIT-tagged fish for ages 4+. Assuming a length of 7 mm at hatching (Muth 1990), annual growth increments from back-calculations were 89 (7 to 96 mm TL), 48 (96 to 144 mm TL), and 42 mm (144 to 186 mm TL) for years 1, 2, and 3, respectively. Back-calculated length on transition checks indicated that the young fish left the LCR at an average size of 74 mm TL, hence, average 30-day growth rate in the LCR was 10.30 mm (7 to 74 mm TL). Average 30-day growth rates for 2 and 3 year old mainstem fish were 4.00 mm (96-144 mm TL), and 3.50 mm (144-186 mm TL). Lupher and Clarkson (1994) reported average 30-day growth

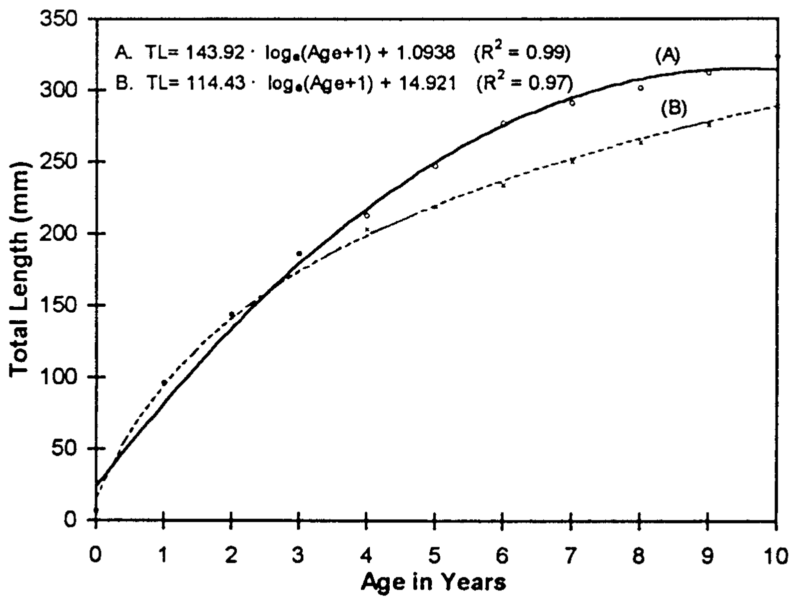


Fig. 6-10. Logarithmic growth curve for humpback chub in the mainstem Colorado River in Grand Canyon (A). Hatching length of 7 mm from Muth (1990); length at 1-3 years from scale back-calculations; lengths at 50 mm increments for 4+ years from PIT-tag recaptures. Growth curve for humpback chub in the LCR (B) from Minckley (1992).

of laboratory humpback chub of about 10.63 mm at 20°C and about 2.30 mm at 10°C. The 30-day growth rate of 10.63 mm is comparable to 10.30 mm determined for the pre-transition (i.e., LCR) fish from this study, but the higher rate of 4.00 mm for mainstem fish (compared to 2.30 mm for laboratory fish) may be attributed to wild fish spending time in shallow shorelines or backwaters that were warmer than 10°C.

Growth rates of age 4+ fish were determined from consecutive measurements of recaptured PIT-tagged individuals for 50-mm length intervals (Table 6-6). Growth rates were computed on an annual basis for respective length groups and age in years assigned to consecutive lengths as shown in Fig. 6-10.

The average 30-day growth rate of PIT-tagged fish was 2.25 mm for the 150-200 mm TL increment, which was less than 3.5 mm than the average length from scale back-calculations. Average 30-day growth rate ranged from 2.79 mm (33.95 mm/year) for fish 200-250 mm TL to 0.79 mm (9.61 mm/year) for fish 350-400 mm TL. Mean growth rate dropped dramatically from 2.50 mm to 1.16 mm/30 days for fish over 300 mm TL.

As a comparison with mainstem growth, Minckley (1992) reported average 30-day growth rates of humpback chub from the LCR by size group, i.e., 1.4 mm (23 mm for 497 days) for fish less than 200 mm TL, 1.3 mm (22 mm for 497 days) for 200-250 mm TL, 1.1 mm (18 mm for 497 days) for 250-300 mm TL, 0.4 mm (7 mm for 497 days) for 300-350 mm, 0.5 mm (8 mm for 497 days) for 350-400 mm, and 0.1 mm (2 mm for 497 days) for over 400 mm TL. Average growth for all sizes and ages of fish handled by Minckley in the LCR was 0.037 mm per day, 1.1 mm per month, and 13.5 mm per year. These growth rates are considerably lower than those presented above for adults from the mainstem. It appears, from these data, that growth of young fish (<200 mm TL) is higher in the LCR, but growth of older fish (>200 mm TL) is higher in the mainstem (Fig. 6-10).

Length At Transition

Scales of humpback chub from the two systems were examined to determine fish length at transition from the LCR into the Colorado River. Transition checks were usually identified as cross-overs or discontinuities in one to three of the innermost circuli from the scale focus. This disruption in growth was attributed to the transition in water temperature from the LCR (~20°C) to the mainstem (~10°C). Transition checks usually preceded annular rings, indicating that most mainstem humpback chub less than 3 years of age descended from the LCR at less than 1 year of age. Back-calculated lengths of humpback chub at these transition checks averaged 74 mm TL (range, 52-132 mm TL) (Table 6-5). Hence, the majority of growth in the first year occurred in the LCR. Minimum size of fish at transition was 52 mm TL, indicating little or no survival of smaller fish descending from the LCR. The most likely cause of mortality was thermal shock or predation elicited by aberrant thermal-shock behavior, i.e., erratic swimming, flashing.

Table 6-6. Growth rates of humpback chub (≥150 mm TL) in the mainstem Colorado River by 50-mm length intervals, based on recapture of PIT-tagged fish, October 1990 - November 1993. Data are compared to growth rates reported by Minckley (1992). SD=standard deviation.

TL Increment (mm)	No. Fish	Mean Growth Rate (mm/30 days)	SD	Annual growth (mm/year)	Minckley (1992) (mm/year)
150-200	19	2.25	2.05	27.38	17
200-250	106	2.79	2.44	33.95	16
250-300	157	2.5	2.62	30.42	13
300-350	324	1.16	1.17	14.11	5
350-400	383	0.79	1.17	9.61	6
400-450	131	0.91	1.47	11.07	1
450-500	5	0.96	1.03	11.68	1
Total:	1125	Means: 1.36	1.8	16.55	

Histograms of back-calculated lengths at transition checks and actual captures of humpback chub less than 200 mm TL (Fig. 6-11) revealed that a substantial number of fish captured in the mainstem were shorter than the minimum back-calculated size. The discrepancy is explained by errors in the back-calculation relationship, Lee's phenomenon, or the lack of long-term survival by humpback chub descending from the LCR less than about 52 mm TL. Survival of juvenile humpback chub exposed to thermal gradients is not well known. Hamman (1982) reported only 15% survival for "swim-up fry" (6.9 mm long) at 12-13°C, and Bulkley et al. (1981) reported a temperature preference by juveniles of 24°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°C to 10°C. These findings suggest low survival related to thermal shock or perhaps to predation for humpback chub less than about 52 mm TL following descent from the LCR to the mainstem.

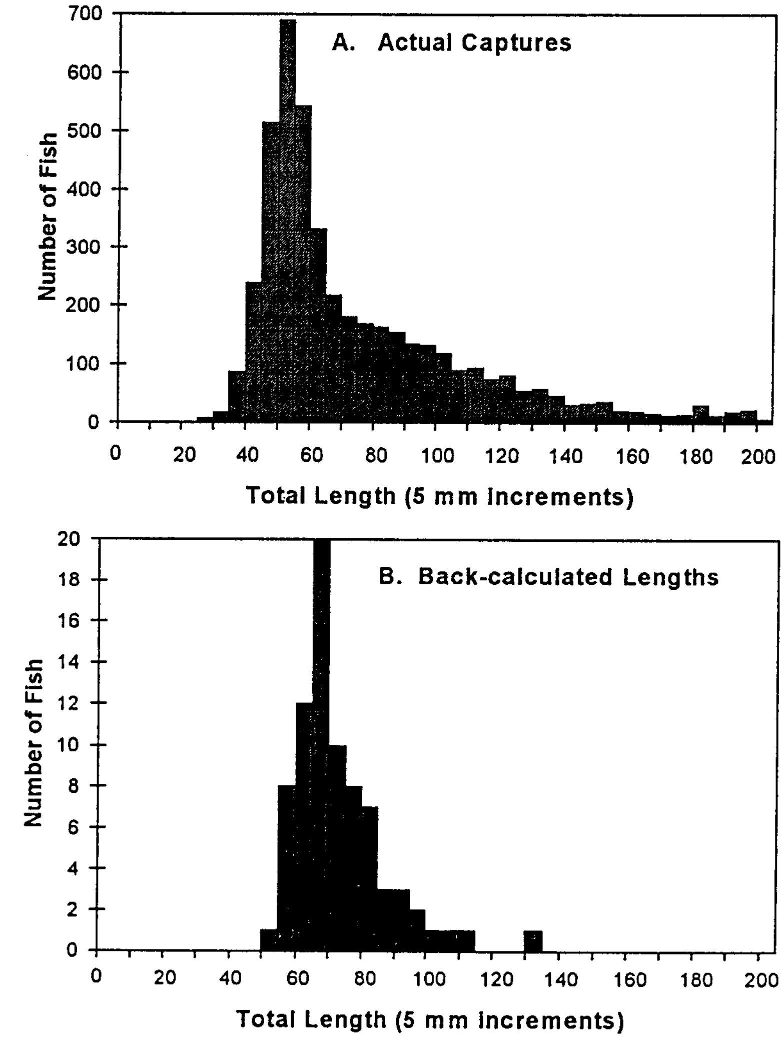


Fig. 6-11. Length-frequency histograms for humpback chub (<200 mm TL) captured in the Colorado River, 1990-93 (A), and for back-calculated lengths from scales of subadult humpback chub taken in the Colorado River (B).

Scales from 7 of 88 (8%) fish examined from the mainstem did not exhibit transition checks, indicating that either these fish failed to show scale disruption at transition, or they were spawned and hatched in the mainstem. Conversely, scales of 7 of 44 (16%) humpback chub sampled from the LCR exhibited a disruption in circuli, indicating that other environmental conditions altered early scale growth, including floods, food shortages, or fluxes in calcium carbonates and salinity (Morales-Nin 1987). None of the 36 LCR fish classified as age 0 (lacking annuli) exhibited disruptions of circuli.

Subtle disruptions in scale growth patterns have been used to differentiate hatchery stocked salmon from naturally-spawned fish (Schwartzberg and Fryer 1993). Circular disruptions on scales of humpback chub have not been used previously to determine lengths of fish in transition between thermal regimes, although Hendrickson (1993) recognized the possible use of otolith daily growth increments as indices of warm backwater or cold mainstem occupation. Although Kaeding and Zimmerman (1983) failed to discern "false checks" in scales of LCR fish less than 3 years of age, Hendrickson (1993) observed abrupt transitions in early growth rates from otoliths (i.e., lapilli) of humpback chub from the LCR. These transitions, indicated by spacing of circuli, were similar to those seen in hatcheries following temperature manipulation.

Population Estimates

The estimated number of adult humpback chub (≥200 mm TL) in the mainstem LCRI aggregation was 3,482 (95% C.I. = 2,682-4,281, Table 6-7, 6-8, 6-9). The next largest mainstem aggregation, located in Middle Granite Gorge, had an estimated 98 adults (95% C.I. = 74-153), followed by aggregations at the Shinumo inflow (N=57, 95%

Table 6-7. Estimated numbers (N) and 95% confidence intervals (C.I.) of adult humpback chub (≥200 mm TL) in nine mainstem aggregation. Estimates and confidence intervals are from the Chao M_h closed population estimator.

Aggregation	No. Adults Captured	No. Adults Recaptured	N	SE(N)	Range of 95% C.I.
1. 30-Mile	26	6	52	23	28-136
2. LCR Inflow	1,524	280	3,482	408	2,682-4,281
3. Lava to Hance	15	3	--[a]	--	--
4. Bright Angel Inflow	9	1	--[a]	--	--
5. Shinumo Inflow	27	6	57	26	31-149
6. Stephen Aisle	17	2	--[a]	--	--
7. Middle Granite Gorge	124	48	98	19	74-153
8. Havasu Inflow	7	1	13	12	5-70
9. Pumpkin Spring	6	2	5	2	4-16

[a] no population estimates computed.

C.I. = 31-149), 30-Mile (N =5 2, 95% C.I. = 28-136), Havasu inflow (N = 13, 95% C.I. = 5-70), and Pumpkin Spring (N = 5, 95% C.I. = 4-16). Population estimates for other aggregations could not be made because of a lack of recaptures between sampling periods (all had multiple capture of the same fish within a single sampling period). The numbers of unique fish captured in the three other aggregations were Stephen Aisle (15), Bright Angel (8), and Lava to Hance (12). The sum of these estimates indicates that about 3,750 adult humpback chub were in the mainstem during this investigation.

These estimates were based on recapture rates within aggregations that ranged from 16% to 39%, and an overall recapture rate of about 23%, i.e., 356 of 1,572 adults were marked and recaptured by B/W. Rates of recapture, however, were much lower between individual sample periods, generally less than 10%, and resulted in estimates with relatively high confidence intervals. Fish tagged by other researchers were not considered in estimates, except when fish were captured, released, and recaptured by B/W.

LCRI Aggregation

Closed Population Estimators. Estimates of total population (N) for adult humpback chub (≥200 mm TL) in the LCRI aggregation for 1991, 1992 and 1993, using 11 estimators for 7 closed population models are presented in Table 6-8. Population estimates for estimators M_0, Darroch M_t, Schnabel M_t, Chao M_t, Chao M_h, and Chao M_{th} are very similar for each year, and were not significantly different (z-test, P>0.05). The other five estimators produced estimates of N which were generally much lower and often significantly different than the first six (z-test, P<0.05). The Zippin M_b estimator failed to meet the necessary requirements for declining numbers of newly caught individuals in 1991 and 1992. The jackknife M_h estimator produced intermediate estimates of N in 1991 and 1992. Chao (1987, 1989) and Pollock and Otto (1983) indicate that the jackknife M_h estimator can severely underestimate N when the probability of capture of many individuals is low, and when many individuals are captured only once or twice. This was the situation with captures of adult humpback chub in the LCRI aggregation (all other aggregations as well).

As discussed in METHODS, the program CAPTURE was not able to effectively select an appropriate model for estimation of N. However, the estimates of N under models M_b(N=856), M_{bh} (N=902), and M_{tb} (N=896) are likely underestimates since during the course of the study 1,267 distinct fish were captured. In addition, the sampling of adults did not effectively meet the requirements for a removal study (note failure of Zippin M_b estimator in 1991 and 1992), casting doubt on estimates produced under models M_b and M_{bh}. Finally, significant behavioral changes due to capture are not likely, unless humpback chub can effectively sense nets and relate nets to the capture experience.

Table 6-8. Estimated population (N) of adult humpback chub (≥200mm TL) in the LCRI aggregation using 11 estimators for closed population models. Estimates are shown for individual years 1991, 1992, and 1993 and for all samples collected 1990-1993. Mean estimates for the years 1991-1993 are also shown.

	1991			1992			1993			Mean 1991-1993			1990-1993		
Estimator	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.
M_0	3191	570	2280-4550	2276	452	1571-3380	3331	444	2587-4347	2933	284	2375-3490	4176	241	3740-4687
Darroch M_t	2817	463	2066-3910	2151	364	1564-3013	3358	458	2593-4408	2775	249	2287-3263	4616	283	4105-5218
Schnabel M_t	2941	567	2051-4317	2819	706	1772-4624	3223	465	2454-4299	2994	339	2329-3660	4111	269	3630-4689
Chao M_t	2749	492	1967-3927	2986	732	1893-4843	3186	453	2438-4233	2974	331	2325-3622	4208	297	3681-4852
Chao M_h	3315	619	2334-4803	3572	917	2213-5913	3558	521	2699-4764	3482	408	2682-4281	4564	327	3982-5269
Jackknife M_h	1826	96	1650-2028	1582	93	1411-1779	2659	145	2393-2964	2022	66	1893-2152	4870	252	4408-5399
Chao M_{th}	3126	554	2239-4447	3362	868	2078-5586	3320	489	2515-4456	3269	380	2524-4014	4681	300	4142-5321
Zippin M_b		--failed to run--			--failed to run--		856	69	748-1025		--not calculated--			--not run--	
Otis M_{bh}	566	69	483-777	1234	1457	426-8629	905	393	621-2632	902	504	538-1889		--not run--	
Pollock M_{bh}	718	51	634-836	751	65	641-898	846	55	756-977	772	33	706-837		--not run--	
Burnham M_{tb}	922	403	551-2435	708	361	407-2158	1058	433	677-2737	896	231	538-1349		--not run--	

Table 6-9. Estimated total population (N) and survival (S) for adult humpback chub (≥ 200 mm TL) for the LCRI aggregation for 13 seasonal periods, 1991-1993, using estimators for open population models A, B, and D. The estimated number of chubs recruited into the adult population (B) and estimated total number of marked chubs at the beginning of each sample period (M) are also shown. Survival rates are expressed on a seasonal basis.

Period	N	SE(N)	N: 95% C.I.	S	SE(S)	S: 95% C.I.	B	SE(B)	M	SE(M)
Model A										
Jan-Feb, 1991	1820	1116	-367-4007	1.124	0.306	0.531-1.1718	2312	2122	93	25
Mar-May, 1991	4152	2003	225-8079	1.011	0.269	0.484-1.539	-11	2557	173	38
Jun-Aug, 1991	4456	1946	642-8270	1.076	0.298	0.492-1.659	-913	1316	340	85
Sep-Nov, 1991	2377	733	939-3814	0.738	0.216	0.315-1.162	-382	510	334	73
Jan-Feb, 1992	1108	518	92-2125	0.627	0.238	0.161-1.093	3473	1756	286	97
Mar-May, 1992	4944	1890	1240-8647	1.327	0.524	0.301-2.354	-620	837	449	108
Jun-Aug, 1992	1750	503	764-2735	0.479	0.128	0.228-0.731	-21	812	278	50
Sep-Nov, 1992	2623	910	839-4406	1.511	0.468	0.594-2.428	985	660	566	158
Jan-Feb, 1993	2924	790	1375-4472	0.739	0.244	0.262-1.216	744	858	498	107
Mar-May, 1993	3670	1222	1275-6065	1.001	0.327	0.360-1.642	-92	935	663	187
Jun-Aug, 1993	4062	1794	545-7579	1.132	0.547	0.060-2.204	--	--	934	392
Mean	3080	405	2286-3875	0.979	0.060	0.861-1.097	547	197	--	--
Geometric Mean				0.931						
Model B										
Jan-Feb, 1991	2014	1088	-119-4148				2197	2035	96	13
Mar-May, 1991	4077	1728	690-7464				96	2150	161	16
Jun-Aug, 1991	3887	1358	1224-6550				-1123	1416	270	19
Sep-Nov, 1991	2477	526	1444-3509				-551	776	320	23
Jan-Feb, 1992	1743	520	724-2762				3220	1574	387	29
Mar-May, 1992	4849	1448	2011-7687				-1357	1548	387	35
Jun-Aug, 1992	3140	717	1734-4546				-395	859	440	43
Sep-Nov, 1992	2579	530	1540-3619				983	749	543	53
Jan-Feb, 1993	3380	622	2161-4599				615	849	564	62
Mar-May, 1993	3784	729	2355-5212				-298	770	680	74
Jun-Aug, 1993	3231	530	2192-4271				-764	510	748	84
Sep-Nov, 1993	2224	339	1560-2889				--	--	799	94
Mean	3116	352	2425-3806				238	100	--	--

S = 0.932

SE(S) = 0.021

SE(S) = 0.021

95% C.I. = 0.890-0.973

Model D							
Jan-Feb, 1991	2081	314	1466-2697	1891	414	86	14
Mar-May, 1991	3866	509	2864-4865	-797	426	146	17
Jun-Aug, 1991	2862	389	2099-3625	567	374	247	22
Sep-Nov, 1991	3271	432	2424-4119	-2100	408	306	26
Jan-Feb, 1992	973	154	671-1276	2397	390	353	31
Mar-May, 1992	3354	441	2490-4218	-293	376	389	38
Jun-Aug, 1992	2906	385	2151-3662	-365	337	480	48
Sep-Nov, 1992	2490	328	1846-3134	2230	434	630	62
Jan-Feb, 1993	4646	573	3522-5770	-429	438	710	78
Mar-May, 1993	4032	501	3049-5014	695	413	850	100
Jun-Aug, 1993	4667	567	3555-5779	-1291	427	1055	135
Sep-Nov, 1993	3154	420	2331-3977	--	--	1132	192
Mean	3192	330	2544-3840	228	50	--	--

S =

SE(S) = 0.020

95% C.I. = 0.914-0.991

Estimates using models M_t and M_h and M_{th} are probably most appropriate (except jackknife M_h with its negative bias with sparse data) as sample intensity varied between trips based on research objectives and study design (model M_t), and different capture probabilities between individual fish were possible (model M_h). If both sources of heterogeneity in capture were significant, model M_{th} would be the most appropriate. However, similarities in estimates for models M_t, M_h and M_{th} do not suggest one model over another to best fit the data. The Chao M_h estimator suggested by Chao (1989) as robust to low capture probabilities (independent of underlying model M_t, M_h or M_{th}) consistently produced the highest estimation of N, although estimated N was less than 10% higher than the next highest estimate. Estimated N using Darroch M_t and the estimator under model M_0 were noticeably lower in 1992 suggesting that capture data from this year may have been more affected by heterogeneity in catchability than in the other 2 years. With the exception of these two estimators in 1992, the population estimates under models M_t, M_h and M_{th} were relatively constant (and not significantly different: z-test, P>0.05) for 1991-1993.

Since estimates of N for the LCR aggregation were relatively constant for 1991-1993, the estimates were averaged for the 3 years (Table 6-8). Results of estimation under closed population models suggest a population of adult humpback chub in the LCR aggregation of 3,000-3,500 (95% C.I. ±20% of estimated N).

Population size was also estimated using estimators for closed population models M_0, M_t, M_h, and M_{th} for all data from October 1990 through November 1993 (Table 6-8). These estimates of N were about 1,000 chubs higher (significantly higher, z-test, z=2.58, P=0.0049) than the corresponding average of estimates for separate years. This higher total resulted from the violation of closure as the number of marked chubs was reduced by mortality, and sizable recruitment likely occurred. Disproportionately low numbers of recaptures related to inflated numbers of marked chubs would cause inflated estimates of N. This phenomenon was clearly seen with the Schnabel M_t estimator when the number of marked individuals was corrected by estimated mortality (see section on adult survival). Estimated N for this period, correcting the number of marked fish for mortality, was 3,035 adults (SE(N)=171, 95% C.I.=2,681-3,465), nearly the same as the average of Schnabel M_t estimate of 2,994 based on averages of individual years. When mortality was considered in Schnabel M_t estimates of N for individual years of 1991 through 1993, estimates ranged from 2,570 to 2,886 (mean = 2,711). This mean was only 9.4% below the mean Schnabel M_t estimate of N assuming closure (mean = 2,994), and well within the 95% confidence intervals of 2,329-3,660 adults. This analysis clearly shows the importance of approximating closure when applying these estimators. It is important to note that the estimated SE(N) using Schnabel M_t with mortality assumes the number of marked fish (M_i) was exact. This was not the case, however, as M_i has its own probability structure related to the probability of survival. Including such variability would increase the true SE(N) (See Seber, 1982, for Schnabel M_t estimator for N).

Open Model Estimators. Seasonal population estimates from estimators for open population models A, B and D are shown in Table 6-9. Estimated N from all models were highly variable. This variability reflects the low numbers of fish sampled and recovered in each of the 13 sampling periods. Also, N was estimated for each sampling period instead of a single estimate over an extended period as with estimators for closed population models. The mean N's calculated for each model, however, were not significantly different (z-tests, p>0.05) and ranged from 3,080 adults for model A to 3,192 adults for model D. These means were nearly identical to mean estimates of N from close population estimators (z-tests, P>0.05), although the 95% confidence intervals were greater (±25%). The similarity of this estimate and estimates for closed population models M_0, M_t, M_h (Chao estimator) and M_{th} strongly supports the validity of these estimates over estimates under assumptions of models M_b, M_{bh} and M_{tb}.

Model goodness-of-fit tests performed by the program JOLLY indicated that all models fit the data at the P=0.05 level (χ^2 test), but model D (constant capture probabilities and survival) failed to fit the data at P=0.10. Tests between models B and D, and between A and D showed significant differences (χ^2 test, $P \leq 0.05$), indicating variability in capture probabilities between sampling periods, consistent with the variable sampling program. No significant differences were found between model A and B (χ^2 test, P=0.20), indicating that model B was the simplest to fit the data, suggesting that survival was relatively constant over the course of the study (see section on adult survival).

MGG Aggregation

Estimates of total population (N) for adult humpback chub (≥200 mm TL) in the MGG aggregation for 1993 using seven estimators for closed population models M_0, M_t, M_b and M_{th}, are presented in Table 6-10. Estimates were conducted on 1993 capture data since this was the only relatively complete annual dataset. All estimators provided similar and not significantly different (z-test, P>0.05) estimates (range, 89-103). The ranges of 95% confidence intervals place this estimate between 68 and 155 adults, or 3-5% of the estimated population size of the LCRI aggregation (Tables 6-8, 6-9). Data were insufficient to use open population estimators.

Estimates were also calculated using all capture data for the MGG aggregation (Table 6-10). Estimates were 16-77% higher than for 1993. This higher estimate was likely the result of mortality and recruitment (lack of population closure) as was the case with similar estimates for the LCRI aggregation.

Other Aggregations

Population size was estimated for four other aggregations of humpback chub (Table 6-11) from limited capture-recapture data. Three other aggregations did not have recaptures between sampling periods (all had 2 captures of a single chub within one sampling period, however), and estimations of N could not be made. Only five estimators for three models were used as sufficient data did not exist to calculate estimates with other estimators. Estimates ranged from 4-5 adult humpback chub in the Pumpkin Springs area to

Table 6-10. Estimated population (N) of adult humpback chub (≥ 200mm TL) in the MGG aggregation using seven estimators for closed population models. Estimates are shown for 1993 and for all data collected (1990-1993).

	1993			1990 - 1993		
Estimator	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.
M_0	99	15	77-140	115	12	97-145
Darroch M_t	96	14	76-135	112	11	96-141
Schnabel M_t	91	20	68-155	106	16	86-158
Chao M_t	89	15	70-132	152	31	112-238
Chao M_h	98	19	74-153	168	37	119-273
Jackknife M_h	103	15	82-141	182	29	138-256
Chao M_{th}	96	15	75-139	167	33	122-256

Table 6-11. Estimated population (N) of adult humpback chub (≥ 200mm TL) in four aggregations in the mainstem Colorado River in Grand Canyon.

	30-mile			Shinumo Inflow			Havasu Inflow			Pumpkin Spring		
Estimator	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.
M_0	57	25	31-141	60	25	33-145	10	7	5-40	4	1	4-6
Darroch M_t	47	18	28-107	58	23	33-135	8	4	5-26	4	0	4-4
Schnabel M_t	41	23	23-143	48	28	26-163	6	7	5-52	4	3	4-16
Chao M_t	37	12	24-81	45	16	27-102	7	2	5-19	4	1	4-9
Chao M_h	52	23	28-136	57	26	31-149	13	12	5-70	5	2	4-16

about 50-60 in the 30-Mile and Shinumo inflow aggregations. All aggregations had population estimates less than 2% of the LCR aggregation. Sufficient data did not exist to apply open population estimators to these aggregations.

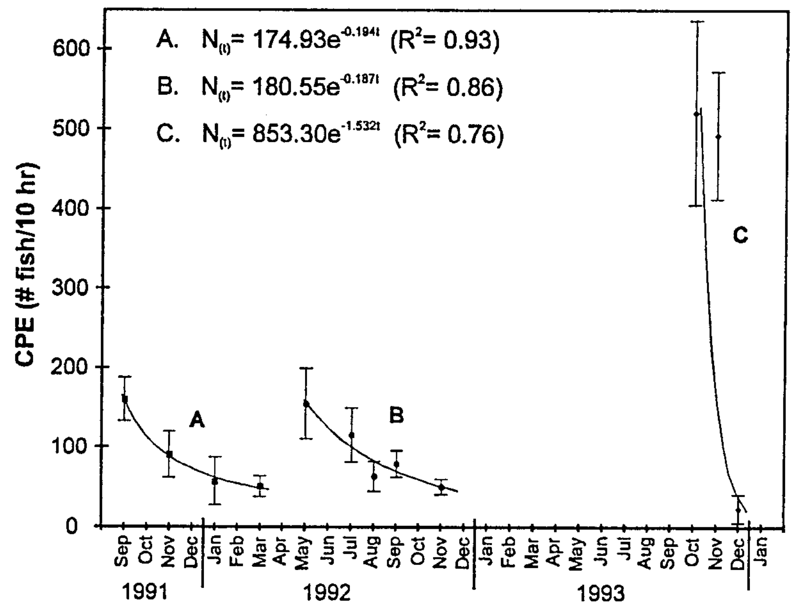


Fig. 6-12. Exponential decreases in densities of subadult humpback chub in the mainstem Colorado River from the LCR (RM 61.3) to Lava Canyon (RM 65.4) for September 1991 through March 1992 (A), May through November 1992 (B), and September through November 1993 (C).

Survival Estimates

Adults

Estimates of adult survival were made for the LCRI aggregation using estimators for open population models A, B, and D (Table 6-9). These estimates were made simultaneous to estimates of N. Model B, the simplest model that fit the data produced a survival estimate of 0.932 (95% C.I.=0.890-0.973) between seasons which translates to annual survival of 0.755 (95% C.I.=0.627-0.896). As with seasonal estimates of population from model A, seasonal estimates of survival were also highly variable and often greater that 1.0. The estimated mean seasonal survival rate with model A was 0.979 (95% C.I.=0.861-1.097) translating to an annual survival rate of 0.919 (95% C.I.=0.5496-1.4482). The rate estimated for model A was higher than estimated for model B, but the estimated variance was higher and the 95% confidence intervals for model A included the entire 95% confidence intervals for model B. In addition, the geometric mean (perhaps more appropriate) of seasonal survival rates for model A was 0.931, nearly identical to that of model B.

The mean estimated number of recruits for model B of 238 humpback chub per season was very similar to the number of fish lost based on a seasonal survival rate of 0.932. With this survival rate, 204-238 chubs would be lost each season out of a population size of 3,000-3,500. On an annual basis, roughly 735-857 adult chubs (≥200 mm TL) could be lost from the population each year, and would have to be replaced by a similar number of recruits.

Subadults

Decreases in mainstem catch rates for subadult humpback chub for 6-month periods following maximum densities in the subreach from the LCR inflow to Lava Canyon, were similar for 1991-92 and 1992-93 (Fig. 6-12). Negative exponentials showed decrease rates of 0.824, 0.312, and 0.097 for 1, 6, and 12-month periods using electrofishing catch rate data from September 1991 through March 1992 (Table 6-12). Similar rates of 0.829, 0.326, and 0.106 respectively, were found with electrofishing catch rate data for May through November 1992. Decrease rates for 1993 using electrofishing catch rate data for September through November 1993 were 0.216, $1x10^{-4}$, and $1x10^{-8}$ for 1, 6, and 12-month periods respectively. The decrease in numbers of subadults in fall 1993 was dramatic with a 95% decrease in catch rate from September to November (521.72 to 24.37). This was comparable to a 98% decrease in total numbers of subadults (2,082 to 58) caught in backwaters by AGF during the same time period (Doster et al. 1993a, 1993b). Similar rates of 0.137, less than 0.001, and less than 0.001, respectively, were found using seine catch rate data for September through November 1993. Assuming an annual survival rate of about 0.100, survival rate of young to adulthood at 3 years of age is estimated at 0.001 (0.100 • 0.100 • 0.100 = 0.001).

These rates may approximate survival of subadults in the mainstem following descent from the LCR, and when the youngest fish were about 2 months of age. 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

Table 6-12. Exponential decreases in density of subadult humpback chub (<200 mm TL) for electrofishing, seines, and minnow traps in the mainstem Colorado River from the LCR (RM 61.3) to Lava Canyon (RM 65.4).

Gear	Period	Exponential Function	Survival Rate 1 mo	6 mo	12 mo	Coefficient of Determination r^2
Electrofishing	9/91-3/92	$N_{(t)}=174.93e^{-0.194t}$	0.824	0.312	0.097	0.93
	5/92-11/92	$N_{(t)}=180.55e^{-0.187t}$	0.829	0.326	0.106	0.86
	5/92-4/93	$N_{(t)}=112.53e^{-0.053t}$	0.948	0.728	0.529	0.33
	9/93-11/93	$N_{(t)}=853.3e^{-1.532t}$	0.216	$1x10^{-4}$	$1x10^{-8}$	0.79
Seines	5/92-4/93	$N_{(t)}=3.14e^{-0.170t}$	0.844	0.361	0.130	0.33
	5/92-9/92	$N_{(t)}=4.35e^{-0.323t}$	0.724	0.144	0.021	0.36
	9/93-11/93	$N_{(t)}=177.03.43e^{-1.985t}$	0.137	<0.00	<0.001	0.78
Minnow Traps	5/92-10/92	$N_{(t)}=2.05e^{-0.403t}$	0.668	0.089	0.008	0.66
	5/92-4/93	$N_{(t)}=0.80e^{-0.079t}$	0.924	0.623	0.388	0.13
	9/93-7/94	$N_{(t)}=5.32e^{-0.168t}$	0.845	0.365	0.133	0.78

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.

Analysis of Adult Length-Frequency

Inherent to good population estimation is the availability and susceptibility of most individuals to capture. If sampling gear or methods do not effectively capture a significant portion of the population, population estimates may be low. The length-frequency distribution for adult humpback chub in the LCRI aggregation suggests that individuals 200-300 mm TL may be under-sampled in the mainstem (Fig. 6-3). When length distributions were created for an assumed stable population using the estimated annual survival of 0.755 and the growth and age-length relationships in Fig. 6-10 and Table 6-6, the number of chubs captured between 200 and 300 mm TL appeared greatly under-represented (Fig. 6-13). Even using a survival rate equal to the upper 95% confidence interval (0.896), the numbers of medium-size chubs (200-300 mm TL) seem under-sampled, relative to the number greater than 300 mm TL.

Two possible explanations for the low number of humpback chub captured in the size range of 200 to 300 mm TL in the LCRI aggregation were addressed: 1) sampling gear was unable to capture many of these chubs, either through inadequate net mesh size, or differential habitat distribution of chubs 200-300 mm TL, and 2) lower survival rates for chubs 200-300 mm TL than for those greater than 300 mm TL. These hypotheses were assessed by calculating population and survival estimates for the individual groups (i.e., 200-300 mm TL and >300 mm TL). Annual population estimates for 1991-1993 using estimators for closed population models for each group are contained in Table 6-13 and Table 6-14. Mean population size for adults greater than 300

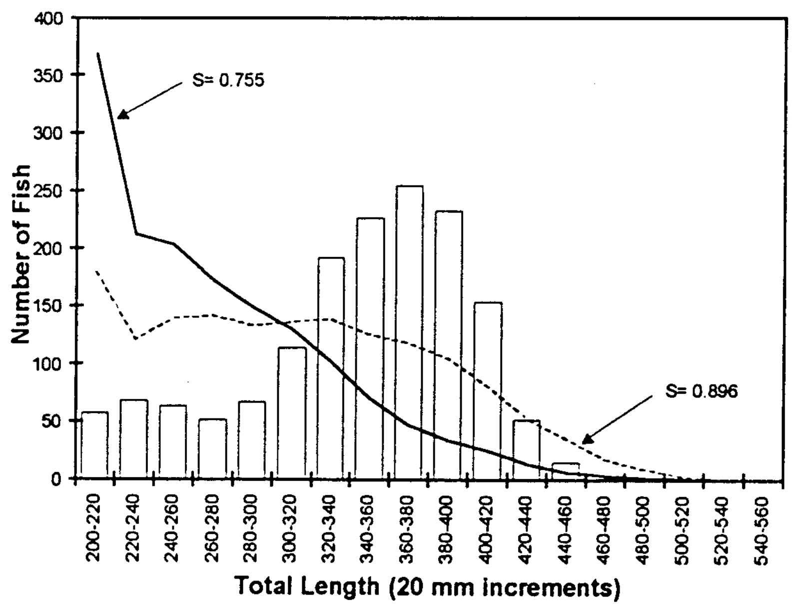


Fig. 6-13. Survival rates (s) and length distribution of adult humpback chub in the mainstem Colorado River.

Table 6-13. Estimated total population size (N) of adult humpback chub (>300mm TL) in the LCRI aggregation. Annual estimates of N are shown for 1991, 1992 and 1993. Mean estimates are also shown for 1991-1993.

	1991			1992			1993			Mean 1991 - 1993		
Estimator	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.
M_0	1999	338	1458-2803	1607	342	1085-2456	2910	419	2218-3878	2172	213	1755-2589
Darroch M_t	2434	470	1696-3575	2013	489	1283-3257	2962	442	2235-3989	2470	270	1940-2999
Schnabel M_t	2332	487	1583-3537	1903	510	1166-3237	2356	382	1740-3261	2197	267	1673-2721
Chao M_t	2181	419	1526-3202	2045	533	1266-3425	2815	435	2107-3833	2347	269	1820-2874
Chao M_h	2637	531	1810-3935	2488	685	1496-4274	3167	505	2346-4351	2764	334	2108-3419
Chao M_{th}	2491	476	1742-3644	2372	657	1423-4091	2967	477	2198-4093	2610	314	1995-3225

Table 6-14. Estimated population size (N) of adult humpback chub (200-300mm TL) in the LCRI aggregation. Annual estimates of N are shown for 1991, 1992 and 1993. Mean estimates are also shown for 1991-1993, and for 1991 and 1993 (excluding 1992) combined.

	1991			1992			1993			Mean 1991 - 1993			Mean 1991 and 1993		
Estimator	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.
M_0	664	315	295-1649	1637	1303	450-6567	984	309	559-1831	1095	459	196-1994	824	221	391-1257
Darroch M_t	583	268	268-1415	738	309	352-1653	961	300	548-1782	761	169	429-1092	772	201	377-1167
Schnabel M_t	491	282	200-1464	1122	1485	207-8271	874	310	470-1762	829	514	134-1837	683	210	271-1094
Chao M_t	472	203	229-1095	1131	789	360-3968	820	251	476-1508	808	284	250-1365	646	161	329-963
Chao M_h	705	350	303-1814	2738	2737	578-14136	1002	330	556-1916	1482	926	134-3298	854	241	382-1325
Chao M_{th}	697	350	298-1812	2761	2793	576-14454	967	302	552-1793	1475	944	134-3325	832	231	378-1285

mm TL ranged from 2,172 to 2,764, depending on the estimator (Table 6-13). Mean estimates for adults 200-300 mm were more variable (Table 6-14), and were influenced by highly variable estimates in 1992 when only one chub within this length class was recaptured. However, variability of estimates was much less between estimators for 1991 and 1993, when more chubs were recaptured (Table 6-14), and may more accurately reflect the size of this length class.

Whether estimates from 1992 were included or not, the estimated mean population of humpback chub 200-300 mm TL (Table 6-14) was much lower than expected by the stable size distribution shown in Fig. 6-3A. The combined total population estimates that resulted from summing the two separate estimates (Table 6-15) were very similar (z-test, P>0.05) to estimates for this aggregation made using capture data for all chubs greater than or equal to 200 mm TL. Exceptions (although not significant, z-test, P>0.05) were estimates using the Chao M_h and M_{th} estimators when the mean estimate 1991-1993 for chubs 200-300 mm TL was used. However, the estimates from these estimators was much closer to the other estimates when the 1992 estimates for chubs 200-300 mm TL were excluded (Table 6-15).

These results indicate that the numbers of humpback chub 200-300 mm TL were lower in the mainstem than those greater than 300 mm TL, and much lower than would be expected for a stable size distribution. In addition, estimates of adults in the LCRI aggregation using capture data for all chubs greater than 200 mm TL appear adequate. Estimated mean capture probabilities from the program CAPTURE, however, indicate that chubs 200-300 mm TL had lower capture probabilities (mean P=0.0094 per sampling period, Chao M_h) than chubs greater than 300 mm TL (mean P=0.0143 per sampling period, Chao M_h), but these differences did not significantly affect the population estimate or suggest a vast under-sampling of chubs 200-300 mm TL. This length analysis and population estimators indicate that movement of small adults from the LCR may contribute more to mainstem recruitment than survival of resident young (i.e., young hatched in the LCR and disbursed to the mainstem).

Survival estimates were also calculated for humpback chub greater than 300 mm TL to assess survival rates by length category. Unfortunately, similar estimates could not be calculated for chubs 200-300 mm TL because of insufficient data. Seasonal survival estimates for chubs greater than 300 mm TL using estimators for open models were 0.974 for model A and 0.927 for model B, nearly identical (z-test, P>0.05) to those calculated for all chubs 200 mm TL or greater in the LCR aggregation (Table 6-9). Thus it does not appear that substantially lower survival rates for chubs 200-300 mm TL biased the survival estimates for fish greater than 300 mm TL. However, rates for these smaller chubs could be less, but not likely enough to cause the disparity in the length-frequency distribution seen in Fig. 6-13.

Sex Ratios

Sex ratios and average total length and weight were summarized for adult humpback chub capture during 1990-93 in three mainstem aggregations, including 30-Mile (RM 29.8-31.3), LCRI (RM 57.0-65.5), and MGG (RM 126.1-129.0). Male to female sex ratios for the three aggregations were

Table 6-15. Estimated total population size (N) of adult humpback chub in the LCRI aggregation by combining estimates for chubs 200-300 mm (Table 6-14) and greater than 300 mm TL (Table 6-13). Combined estimates are sum of means of each group. Estimates are shown for all years, 1991-1993 and without 1992.

	Combined Estimate			Combined without 1992		
Estimator	N	SE(N)	95% C.I.	N	SE(N)	95% C.I.
M_0	3267	505	2276-4258	2996	306	2395-3597
Darroch M_t	3230	318	2606-3855	3242	337	2581-3902
Schnabel M_t	3026	580	1889-4162	2880	340	2213-3546
Chao M_t	3155	391	2388-3921	2993	313	2378-3607
Chao M_h	4246	985	2315-6176	3618	412	2810-4425
Chao M_{th}	4085	994	2135-6035	3442	390	2678-4206

50:50, 48:52, and 52:48, with an overall ratio of 49:51 (Table 6-16). Overall average total length of females was 355 mm TL (range, 200-480 mm TL), or 17 mm greater than average length of males at 338 mm TL (range, 202-460 mm TL). Average weight of females was 454 g or 79 g more than males at 375 g (Table 6-17). Minimum size of fish that were distinguished by gender (i.e., 200 mm TL for females, 202 mm TL for males) indicate that male and female humpback chub in Grand Canyon mature at about 200 mm TL, or in their fourth year of life (i.e., age 3).

Reproductive Potential and Success

Fecundity

This investigation did not attempt to determine fecundity of fishes handled, but instead relied on existing literature. Fewer attempts have been made to propagate and culture humpback chub than any of the Colorado River endangered species. Hamman (1982) reported stripping an average of 2,523 eggs per female from eight females (range, 355-406 mm TL, range, 350-690 g) 20 hr after injection with carp pituitary (Table 6-18, Fig.6-14). These fish yielded an average of 5,262 eggs/kg of body weight.

Table 6-16. Sex ratios for adult humpback chub (≥200 mm TL) from three major aggregations in the Colorado River in Grand Canyon, October 1990 - November 1993.

Aggregation	Location (RM)	Year	No. Fish	Ratio (Male:Female)
30-Mile	29.8 - 31.3	1990	-	-
		1991	-	-
		1992	-	-
		1993	20	50:50
		Summary	20	50:50
LCR Inflow	56.0 - 65.5	1990	73	41:59
		1991	372	47:53
		1992	264	45:55
		1993	399	53:47
		Summary	1108	48:52
Lava to Hance	126.1 - 129.0	1990	-	-
		1991	8	25:75
		1992	21	38:62
		1993	34	68:62
		Summary	63	52:48
	Overall Summary	1990-1993	1246	49:51

Table 6-17. Average total length (TL in mm) and weight (WT in g) for adult male (M) and female (F) humpback chub (≥ 200 mm TL) from the Colorado River in Grand Canyon, October 1990 - November 1993.

Year	No. Fish	Sex	TL (range)	WT (range)
1990	31	M	351 (225-451)	432 (125-790)
	45	F	373 (294-439)	529 (250-865)
1991	185	M	345 (220-423)	385 (106-870)
	207	F	359 (221-480)	470 (104-999)
1992	131	M	331 (202-455)	358 (64-908)
	162	F	339 (200-451)	396 (85-959)
1993	252	M	336 (204-460)	371 (43-1122)
	209	F	360 (210-458)	467 (98-1165)
Summary	599	M	338 (202-460)	375 (43-1122)
	623	F	355 (200-480)	454 (85-1165)

Table 6-18. Number of eggs per female and corresponding lengths and weights of humpback chub reported by different investigators. TL = total length, WT = weight.

Investigators	No. Fish	Origin	Mean TL (mm)	Mean WT (g)	Eggs Per Female		Eggs/g Fish WT		Mean Egg diameter (mm)
					Mean	Range	Mean	Range	
Hamman 1982	8	Black Rocks	382	507	2,523	330-5,445	4.9	0.65-10.7	2.7
Hamman 1982	9	LCR, AZ	395	588	3,333[a]	–	5.7	–	2.8
Clarkson 1993	11	LCR, AZ	362	401	4,831	320-11,717	12	0.8-29.2	–

[a]Based on estimate number of eggs voluntarily deposited by 9 females = 30,000.

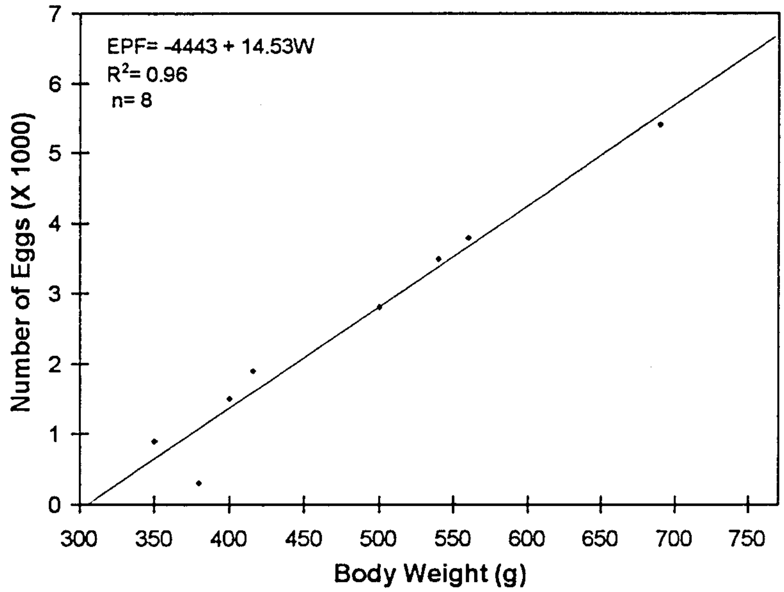


Fig. 6-14. Fecundity of humpback chub, as a relationship between body weight of fish and number of eggs. Data from Hamman (1982).

Egg diameter ranged from 2.6 to 2.8 mm (mean=2.7 mm). Number of eggs per female was determined volumetrically by measuring displacement in water, and using a conversion of 55 eggs/ml (range, 51-58 eggs/ml). The relationship of body weight (W) to number of eggs per female (EPF) for this sample of fish is expressed as:

(Equation 6-11)

$$EPF = -4443 + 14.53W (R^2=0.96)$$

Hamman (1982) also estimated 30,000 eggs were deposited by nine females injected with carp pituitary at 24-hr intervals and allowed to spawn unassisted over cobble substrates in raceways. Egg diameters varied from 2.6 to 2.9 mm (mean=2.8 mm), and the eggs were adhesive. Assuming the estimated number of eggs was accurate, these fish yielded approximately 3,333 eggs per female.

Clarkson (1993) reported higher fecundity using egg weight as a conversion for field-stripped humpback chub from the LCR in 1992. An average fecundity of 4,831 eggs per female (range, 320-11,717 eggs) was reported for 11 females that were manually stripped. Some fish were injected with carp pituitary up to three times and others were spawned without injection.

Mainstem Observations Related to Spawning

A total of 178 adult humpback chub captured in the mainstem LCRI aggregation during 1990-93 exhibited spawning characteristics (i.e., expression of milt or eggs, tuberculation, coloration) with the highest frequency in March, associated with spawning in the LCR (Table 6-19, Fig. 6-15). A total of 49 adults from seven aggregations, other than the LCRI, also displayed spawning characteristics, but the highest mode of occurrence was in May. The greatest numbers of adults that displayed spawning characteristics were caught in the MGG aggregation (n=23) and the 30-Mile aggregation (n=7). Fifteen of these 49 fish (31%) were captured near tributaries, including 4 within 0.5 km (0.3 mi) of Clear Creek, 1 within 0.5 km (0.3 mi) of Bright Angel Creek, 5 within 1.0 km (0.6 mi) of Shinumo Creek, and 5 within 1.4 km (0.9 mi) of Havasu Creek.

Ripe fish found in the mainstem, away from the LCRI aggregation, were captured from March through July at water temperatures of 10-14°C, a range that is marginal for survival of eggs and larvae of humpback chub. Hence, it appears that

Table 6-19. Spawning condition of adult humpback chub in nine aggregations in the Colorado River.

Aggregation	Males				Females				
	Milt	Tubercled	Spent	Colored	Eggs	Tubercled	Spent	Colored	Total
1. 30-Mile	2	2	0	0	0	2	1	0	7
2. LCR Inflow	10	91	3	13	3	25	11	22	178
3. Lava to Hance	0	0	0	1	0	0	0	0	1
4. Bright Angel Inflow	1	4	0	0	0	0	0	0	5
5. Shinumo Inflow	1	2	0	0	0	1	0	1	5
6. Stephen Aisle	1	0	0	1	0	0	0	0	2
7. Middle Granite Gorge	6	8	0	0	0	7	0	2	23
8. Havasu Inflow	0	3	0	0	0	2	0	0	5
9. Pumpkin Spring	0	1	0	0	0	0	0	0	1
Totals	**21**	**111**	**3**	**15**	**3**	**37**	**12**	**25**	**227**

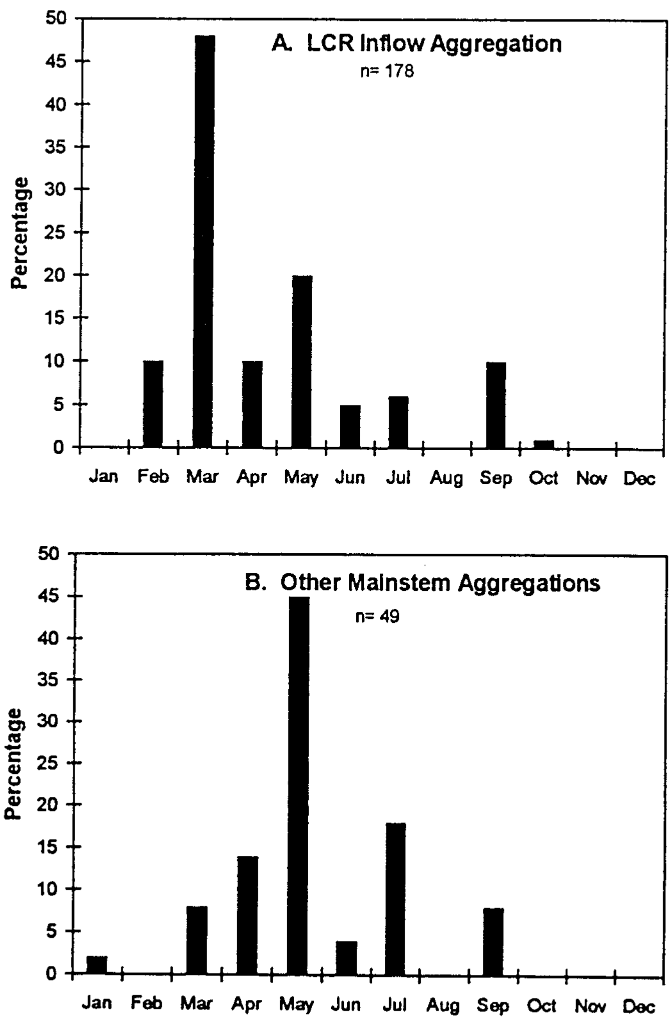


Fig. 6-15. Percentage of adult humpback chub in spawning condition from monthly samples in the LCR inflow aggregation (A) and eight disjunct mainstem aggregations (B). See Table 5-10 for location of aggregation sites.

gonodal maturation occurs at the cold mainstem temperatures, but spawning activity and success appear to be limited.

Ripe humpback chub were recorded in water temperatures of 16°C in Cataract Canyon, Utah, in June 1988 (Valdez and Williams 1993), and in 11.5°C water in Black Rocks, Colorado, in June 1980 (Valdez and Clemmer 1982), where Kaeding et al. (1990) also reported spawning at 13-17°C in June 1983 and at 15-23°C in July 1984. Reports of spawning by humpback chub in the LCR were in water temperatures of 16-20°C (Suttkus and Clemmer 1977, Carothers and Minckley 1981, 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%, respectively (Hamman 1982). Thus, although hatching success was highest in 19-20°C, larval survival was highest at warmer temperatures of 21-22°C.

The best evidence of mainstem reproduction during this investigation was the presence of ripe fish and post-larvae in and near a warm spring near RM 30. Spring No. 5 is a small warm spring inhabited by individuals of the 30-Mile aggregation near Fence Fault (See Chapter 4 - WATER QUALITY). Seven adults (range, 330-451 mm TL) were found in spawning condition in this area, including 1 in May 1993 (milting male), 3 in September 1993 (2 tubercled males, 1 tubercled female), and 3 in July 1994 (1 tubercled male, 1 milting male, 1 spent female). Also, during July 12-14, 1994 about 100 YOY humpback chub were sighted among boulders in the warm plume, and 14 specimens (range, 18-31 mm TL) were captured and preserved to verify identification. Water temperature at the spring source was constant at 21.5°C, compared to 10°C in the adjacent mainchannel. These young fish were from the 1994 year class, and probably hatched from eggs deposited in the warm spring plume, since mainstem water temperature was too cold for survival of eggs or larvae (Hamman 1982, Marsh 1985). Based on average length of 24 mm TL (20 mm SL), these young were approximately 36 days old (hatched about June 8, 1994) based on the following relationship (Muth 1990):

(Equation 6-12)

$$D = \frac{\log_e SL - \log_e 7.2843}{0.0280}$$

where:

D = days from hatching, and
SL= standard length of fish.

It is unlikely that these young originated from upstream locations, because of the thermal restriction and large numbers of predators (i.e., rainbow trout) in the area. Spawning by humpback chub in this area is further discussed in Chapter 5 - DISTRIBUTION AND ABUNDANCE.

Young humpback chub have also been found downstream of this Fence Fault area by other investigators. Historically, at least one juvenile humpback chub was captured at RM 44 between 1970 and 1976, but no length information is available (Carothers and Minckley 1981, Suttkus et al. 1976). In 1993, AGF (Arizona Game and Fish Department 1994) captured 20 YOY (range, 20-50 mm TL) humpback chub (3 in July, 3 in September, and 14 in October) in a backwater at RM 44.3 (just below President Harding Rapid). The origin of these fish is unclear. They could have hatched from eggs deposited in one of three areas--springs in the vicinity of Fence Fault (30-Mile area), the Paria River, or an undiscovered spring below the river surface and near RM 44 . Although it is unlikely that larval humpback chub could survive the thermal shock of a transition from a spring plume of 20°C to a mainstem temperature of 10°C, sufficient size and temperature of some plumes may persist under interim flows to allow fish to age and acclimate to greater thermal tolerance. If young fish reached sufficient size to survive the thermal transition, chances of survival would be further reduced by transport through 23 km (14 mi) (RM 30 to RM 44) of clear water and high densities of predators (e.g., rainbow trout). It is unlikely that these young fish originated from the Paria River, since adult humpback chub have not been historically reported in that tributary, and a large number of young would be necessary to supply a distant backwater with 20 individuals under normal dispersal patterns. The potential for humpback chub spawning in the Eminence Fault area was difficult to assess because little is known of the area, and because it was sampled only twice during this investigation. A geologic fault (Eminence Break Fault) indicates the potential of warm springs, but none were visible along the shoreline or reported by Huntoon (1981).

Small subadults captured downstream of the LCR inflow could have originated from tributaries, mainstem spawning, or dispersal from the LCR. Of 3,503 subadults captured in shoreline habitats outside of backwaters (AGF sampled backwaters) in 1990-93, the smallest was 23 mm TL, and nine (0.3%) were less than 30 mm TL. Most of these young fish were captured near the LCR inflow, but subadult humpback chub were captured as far downstream as the Blacktail Canyon area (RM 119-129) and below Whitmore Wash (RM 187.6).

Aside from the 15 ripe fish captured near four tributaries, no substantial evidence of mainstem reproduction was found in any other inflow sampled. Five eggs (range, 1.9-2.5 mm diameter) recovered from substrate in the LCR inflow in May 1991 were believed to be eggs of humpback chub that were dislodged from upstream spawning areas rather than eggs deposited in the inflow. We found no definitive evidence of reproduction by humpback chub in the LCR inflow, but the occurrence of large numbers of adults in this area during spawning in the LCR suggests the likelihood of at least some spawning activity. Reproductive success in the LCR inflow was probably low because of the daily inundation of the area by cold mainstem fluctuating flows.

Predation

The total number of humpback chub subject to predation by the four major mainstem predators (i.e., brown trout, rainbow trout, channel catfish, and striped bass) was estimated by calculating the average numbers of humpback chub in the diet of each predator and extrapolating the estimate for the numbers of predators in the population. Humpback chub were recovered from stomachs of brown trout and channel catfish during this investigation. Estimates of predation by rainbow trout were assumed based on observations and informal data from other Grand Canyon investigations (P. Marsh, ASU, pers. comm.). Susceptible prey size was determined by comparing predator size and mouth gape (Fig. 6-16) with prey size and body depth; the following equation was used to describe the relationship of total length to body depth of humpback chub:

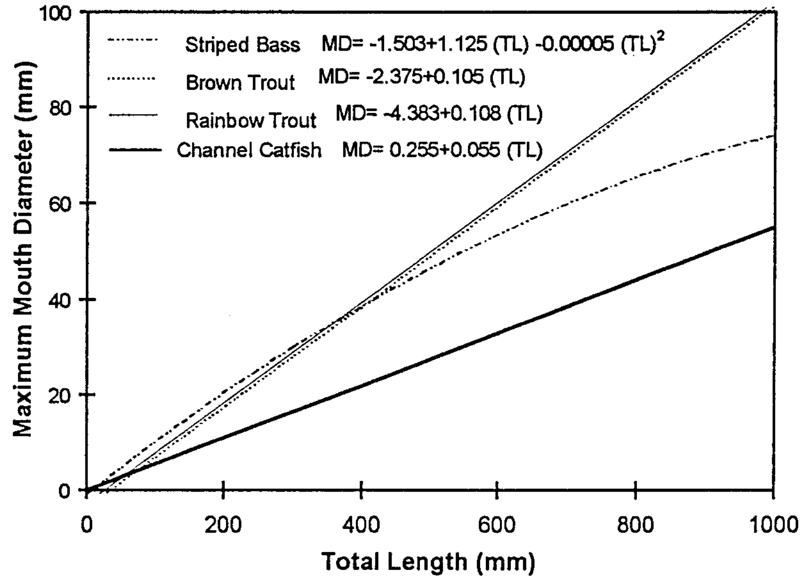


Fig. 6-16. Total length to maximum mouth diameter relationships for three predaceous fish species in Grand Canyon. Brown trout relationship from data presented in Bannon and Ringler (1986); rainbow trout relationship from cutthroat trout equation by Reimchen (1991); channel catfish relationship from data obtained from T. Crowl and L. Alder (pers. comm.); striped bass relationship from Chervinski et al. (1989).

(Equation 6-13)

$$BD = 4.6364 + 02.20514\ TL\ (R^2 = 0.70)$$

where:

D = maximum body depth in millimeters, and
TL = total length in millimeters

Brown Trout

Ten humpback chub were found in 5 of 48 (10.4%) brown trout stomachs examined for an average of 2.0 chubs per stomach. One brown trout stomach contained four humpback chub. The five trout were 393-500 mm TL, and the ingested chubs were 78-130 mm SL (mean= 95 mm SL). Tail fins of ingested fish were too frayed for total length measurements, so the conversion of TL=1.217 • SL (Equation 6-1) was used to yield total lengths of 95-158 mm TL (mean=116 mm TL). All brown trout with ingested humpback chub were caught in Region 1, between RM 57.0 and RM 65.4, above and below the LCR inflow (RM 61.3).

The lengths of predaceous brown trout (i.e., 393-500 mm TL) were related to maximum mouth diameters of 38.9-50.1 mm (Fig. 6-17). Using a relationship of total length to maximum body depth for humpback chub (Fig. 6-17), maximum size range of chubs potentially consumed by predaceous brown trout was 167-222 mm TL (body depth of 38.9-50.1 mm, or equivalent to mouth diameter of brown trout). Size range of ingested humpback chub was 78-130 mm SL (range, 95-158 mm TL), which was within the maximum range of expected prey size.

Size range of 1,466 adult brown trout captured and measured was 200-730 mm TL (mean = 332 mm TL). Adult brown trout of average size were able to ingest humpback chub with a maximum body depth of 32.5 mm or a length of 136 mm TL. The largest brown trout captured during this investigation (730 mm TL) was capable of ingesting fish with a body depth of 74.3 mm, or a humpback chub 340 mm TL.

Brown trout are reported to be primarily piscivorous as adults, or a size of over 200 mm TL (Carlander 1969). Elliott (1991) determined that large adult brown trout evacuated 93% of stomach contents after 24 hr at 10°C, the approximate temperature of the Colorado River in middle Grand Canyon. Assuming only brown trout greater than 200 mm TL were preying on humpback chub, and that 10.4% of these each consumed 2.0 humpback chub per day, estimated annual consumption of chubs depends on

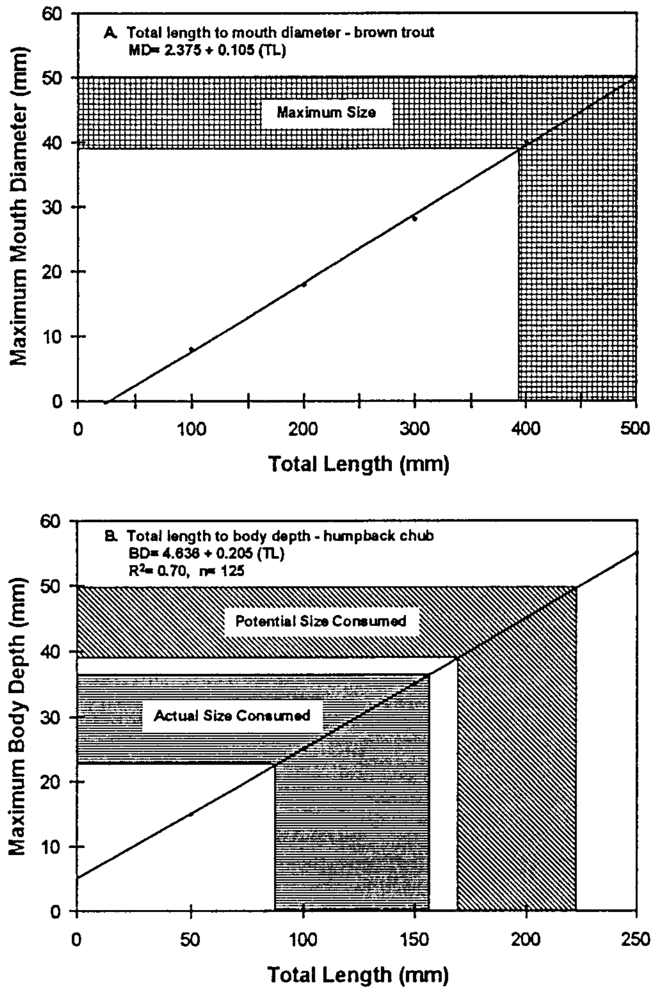


Fig. 6-17. Potential and actual size of humpback chub consumed by brown trout, based on total length to mouth diameter of predaceous brown trout (A) and total length to body depth of humpback chub (B).

total numbers of brown trout in the river sympatric with humpback chub. Highest consistent densities of subadult humpback chub sympatric with brown trout, were reported from the LCR inflow (RM 61.3) to Red Canyon (RM 76.6) (See Chapter 5 - DISTRIBUTION AND ABUNDANCE). A relationship was developed for different numbers of trout, using the previous assumptions (Fig. 6-18). This relationship indicates that 500 adult brown trout could consume 104 humpback chub daily, or 37,960 chub annually. A population of 10,000 adult brown trout could consume 2,080 chubs daily or 759,200 chubs annually. Electrofishing catch rates of brown trout converted to numbers per reach (See Chapter 5 - DISTRIBUTION AND ABUNDANCE) indicate that the area from the LCR inflow to Red Canyon had an estimated 3,000 adult brown trout. If 10.4% of 3,000 adult brown trout consumed 2.0 humpback chub daily, total annual consumption would be 227,760 chubs (Table 6-20). The size of adult brown trout handled were all capable of consuming subadult humpback chub (<200 mm TL) and some were capable of consuming adults, although Bannon and Ringler (1986) found that optimal prey size for brown trout is from sizes smaller than maximum buccal diameter. A length-frequency distribution of brown trout from the LCR inflow to Red Canyon indicates that about 31% of brown trout in this area were large enough to ingest adult humpback chub (≥200 mm TL), and 69% could ingest only subadults.

Rainbow Trout

Although humpback chub were not confirmed in stomachs of rainbow trout during this investigation, we assumed predation levels of 1%, 5%, and 10%,based on previous informal communications with other investigators. For the purposes of this treatise, and to provide a perspective of possible predation by rainbow trout on humpback chub, an analysis was performed similar to that previously presented for brown trout.

A relationship of standard length to mouth diameter for cutthroat trout (Reimchen 1991) was used in the absence of literature for rainbow trout. The relationship was generated for total length, using a conversion factor of TL = 1.15 • SL for cutthroat trout (Carlander 1969) to facilitate comparison with other predator species and with data collected during this investigation.

Size of 9,358 adult rainbow trout measured (range, 200-579 mm TL) was related to maximum mouth diameter of 17.2-58.1 mm. Humpback chub of corresponding body depth were 61-261 mm TL, or the size range susceptible to predation by rainbow trout. Hence, rainbow trout with an average of 339 mm TL were capable of consuming fish with a body depth of 32.2 mm or a humpback chub 135 mm TL. Windell et al. (1976) determined that rainbow trout evacuated 80% of stomach contents after 24 hr at 10°C. Assuming a 24-hr digestive rate, and a consumption rate of 1.0 humpback chub per day,

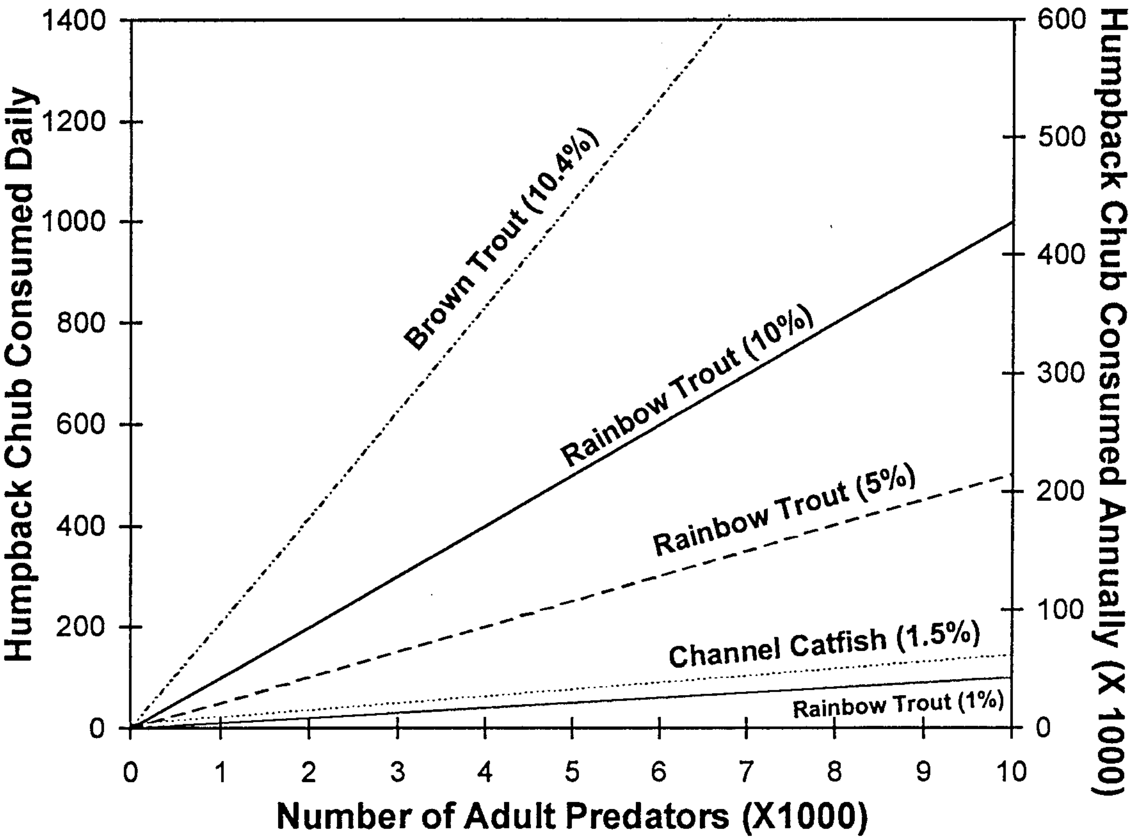


Fig. 6-18. Potential daily and annual consumption of humpback chub by adults of three predator fish species in the Colorado River in Grand Canyon. Relationships assume 2.0 chubs consumed daily by 10.4% of adult brown trout; 1.0 chub consumed daily by 1, 5, or 10% of adult rainbow trout; 1.0 chub consumed daily by 1.5% of adult channel catfish.

Table 6-20. Sizes of four predaceous fish species and susceptible sizes of humpback chub (HB).

Species	n	Size of Adult Predators (TL - mm)		Susceptible size of HB (TL - mm)		Estimated Annual Consumption[a]
		Range	Mean	Range	Mean	
brown trout	1,466	200-730	332	68 - 340	136	227,760
rainbow trout	9,358	200-579	339	61 - 261	135	32,850
channel catfish	103	200-712	368	47 - 165	86	1,095
striped bass	39	315-857	453	138-313	196	no estimate
					TOTAL	261,705

[a]See assumptions in text.

daily and annual consumption rates were estimated from relationships for 1%, 5%, and 10% predation levels, i.e., percentage of adults consuming humpback chub.

Assuming only rainbow trout greater than 200 mm TL were predaceous (Carlander 1969), estimated annual consumption of humpback chub depends on total numbers of rainbow trout sympatric with humpback chub. A relationship was developed for different numbers of trout, using the previous assumptions (Fig. 6-17). This relationship indicates that 1% of 500 adult rainbow trout or five trout could each consume one humpback chub daily for a total of five (500 x 0.01 = 5) or 1,825 humpback chub annually. A population of 10,000 adult rainbow trout could consume 100 humpback chub daily or 36,500 annually. Electrofishing catch rates of rainbow trout converted to numbers per reach indicate that the area of highest juvenile humpback chub concentrations, LCR inflow (RM 61.3) to Red Canyon (RM 76.6), had an estimated 9,000 adult rainbow trout. One percent of 9,000 adult rainbow trout each consuming 1.0 humpback chub daily, could consume 32,850 chub annually, while 5% of 9,000 adult rainbow trout each consuming 1.0 subadult humpback chub daily, could consume 164,250 chub annually, and 10% of adult rainbow trout could consume 328,500 humpback chub annually.

A length-frequency distribution of rainbow trout from the LCR inflow to Red Canyon indicates that the majority of rainbow trout in this area were capable of consuming primarily subadult humpback chub (<200 mm TL). The relationship presented by Reimchen (1991) (Fig. 6-16) indicates that only rainbow trout greater than or equal to 464 mm TL were capable of consuming adult humpback chub (≥200 mm TL).

Channel Catfish

The predation analysis for channel catfish was based on an observed predation rate of 1.5%, i.e., one humpback chub (~95 mm SL) was found in 1 of 68 (1.5%) channel catfish stomachs examined from the mainstem. The catfish was 475 mm TL, and was captured at RM 61.7, immediately below the LCR inflow. Predation of humpback chub by channel catfish was also reported in the LCR by AGF (C.O. Minckley, AGF, pers. comm.) and ASU (M. Douglas, ASU, pers. comm.).

Total length to maximum mouth gape relationship for channel catfish (Fig. 6-16) (T. Crowl and L. Alder, USU, pers. comm.) indicates that a fish 475 mm TL was capable of ingesting a fish with a body depth of 26.4 mm and a length of 111 mm TL. Assuming a digestive rate of 24 hr, it was determined that 1.5% of predaceous channel catfish consumed an average of 1.0 humpback chub per day. Shrable et al. (1969) determined that adult channel catfish evacuated 80% of stomach contents after 24 hr at 10°C, the approximate temperature of the Colorado River in middle Grand Canyon.

Size range of 103 adult channel catfish measured was 200-712 mm TL (mean = 368 mm TL). Relationship of total length to mouth diameter indicates that catfish in this size range were capable of ingesting humpback chub with body depths of 11.3-39.4 mm, or 47-165 mm TL. Average adult channel catfish were able to ingest humpback chub with a maximum body depth of 20.5 mm and a length of 86 mm TL.

Channel catfish are reported to have a primarily piscivorous diet as adults, starting at about 200 mm TL (Carlander 1969). Assuming only channel catfish greater than or equal to 200 mm TL were preying on humpback chub, and that 1.5% of these each consumed 1.0 humpback chub per day, the estimated annual consumption of chubs depends on total numbers of channel catfish in the river sympatric with humpback chub (Fig. 6-18). This relationship indicates that 100 adult channel catfish could consume 548 humpback chub annually, and a population of 200 adult channel catfish could consume 1,095 humpback chub annually. Electrofishing catch rates of channel catfish converted to numbers per reach indicate that the area of highest juvenile humpback chub concentrations, LCR inflow (RM 61.3) to Red Canyon (RM 76.6), had an estimated 200 adult channel catfish. Like brown trout and rainbow trout, the majority of humpback chub consumed by channel catfish were probably subadults, because of the predominate size of catfish and selection for minimal size prey. Because of the relatively low efficiency in catching channel catfish with electrofishing, numbers of channel catfish and hence their predation effect on humpback chub, are probably herein underestimated.

Striped Bass

A relationship of total length to mouth gape is presented for striped bass (Fig. 6-16) to identify size range of humpback chub susceptible to predation by this migratory predator in Grand Canyon. Humpback chub were not found in 39 adult striped bass examined. The striped bass were 315-857 mm TL (mean = 453 mm TL), and corresponding mouth gape were 32.9-68.9 mm (mean=44.9 mm). Using this relationship, striped bass captured in the mainstem could potentially consume humpback chub ranging from 138 to 313 mm TL.

Although adult striped bass typically fast during spawning migrations (Thomas 1967, Stevens et al. 1987), individuals will strike aggressively at lures or occasionally ingest other fishes. Four of 39 adults captured in the mainstem contained fish remains, including 3 trout and 4 unidentified fish (See Chapter 9 - FOOD HABITS). The likelihood of predation on humpback chub in Grand Canyon is unknown, and needs to be further investigated in light of its highly piscivorous diet (Engeling 1990).

Other Predators

On September 6, 1991, an adult osprey was observed flying over the mainstem Colorado River with a fish in its talons. The bird passed overhead along the shoreline at low level and the fish was positively identified by two B/W biologists as an adult humpback chub (Wasowicz and Yard 1993). The fish was identified by its distinct deep body shape, its elongated, slender caudle peduncle with a deeply forked tail, and its light gray color. This observation occurred at river mile 57.1 about 6.9 km upstream of the confluence with the LCR. It is not known whether the osprey captured the chub in the mainstem Colorado River or in the LCR.

Further evidence of possible avian predation was discovered several months prior to this observation. On May 14, 1991, a radiotransmitter, which was previously implanted by B/W biologists into an adult humpback chub, was discovered on the bank of the LCR, approximately 30 m upstream of the confluence. The transmitter was found among boulders, 3-4 vertical meters above the water surface. No remains of the fish were located in the area, but one white feather was found stuck to the transmitter. An osprey was observed frequenting the LCR confluence area on May 12th and 13th. We believe this fish was taken by an osprey, rather than found dead and removed from the water by a scavenger (e.g., coyote, raven, ringtail cat). Before the radiotransmitter was found, the fish was successfully monitored for 3 months following implanting and had moved nearly 2 km to the confluence and then up the LCR, indicative of a healthy fish.

Parasites and Diseases

Lernaea cyprinacea

The only external parasite noted on humpback chub from the mainstem was Lernaea cyprinacea. This parasitic copepod was found on 8 of 6,294 humpback chub examined for an infection rate of 0.13% and an average of 1.25 copepods (range, 1-2 copepods) per fish. None of the infected fish showed signs of stress or illness, although some had open lesions where the parasites had attached. Valdez et al. (1982) reported this parasitic copepod in 26% of 234 humpback chub examined from the Upper Colorado River. Higher infection rate in the upper basin is attributed to warmer mainstem temperature than in Grand Canyon. In the upper basin, the parasite was not found in YOY, but 17% of juveniles, and 31% of adults were infected with 1-13 copepods. Lernaea cyprinacea was reported on most species of fish examined from the upper basin, including largemouth bass, green sunfish, channel catfish, black bullhead, roundtail chub, red shiner, flannelmouth sucker and bluehead sucker (Flagg 1982). This parasite was first reported in native fishes of Grand Canyon by Carothers et al. (1981).

Approximately 40 species of the genus Lernaea (Copepoda, Cyclopoida) have been reported (Hoffman 1967). Most are found in marine species (Amlacher 1970), and many are specific to families or genera of fishes, e.g., L. esocina is found primarily on pikes and L. phoxinacea is found primarily on daces. Species reported in the Colorado River Basin include L. cyprinacea and L. elegans (from Harvey Gap Reservoir) (Williams 1993). Only the former is reported from the Colorado River proper. This group of parasites has no intermediate host.

Lernaea cyprinacea is cosmopolitan and is the best known of the copepod parasites. Adult females are 9-22 mm in length, and live in the muscles of fish. The majority of the body is outside the host, and is attached by a cephalic region, characterized by four cephalic horns, of which the anterior two are digitiform and the posterior two are "T" shape. These cephaic horns are situated around the mouth and enable the parasite to fix itself into the host musculature. Only females penetrate the host to form the typical "anchor worms", while the smaller males enter into permanent copulation with females. Host fish show irritation and local hemorrhaging from initial penetration by the females. These anchor points may be secondarily infected with bacteria.

Females develop large egg sacs that retain up to 700 eggs until hatching. The life cycle is temperature dependent, and maturation can take as little as 15 days at 30°C (Stoskopf 1993). Females release eggs into the water, which hatch into microscopic, elliptically-shaped, free-swimming nauplii about 140 μm long and 80 μm wide. Within 80 hr, the nauplii molt into metanauplii, which molt again in 20-40 hrs into the first of six copepodid stages (Hoffman 1976). The first copepodid stage, at about 230 μm long and 110 μm wide, must find a host within 3 days or it will die (Khalifa 1973). All copepodid stages feed on fish mucous, but only the female is parasitic and attaches. Lernaea cyprinacea is unable to complete its life cycle at pH levels below 7.0, temperature below 15°C, and salinity level at or above 1.8% (Hoffman 1976).

The favorable temperature range of L. cyprinacea is 14-32°C, and a constant relationship between temperature and development from hatching to transformation of female larvae is reported (Nakai and Kokai 1931, Shields and Tidd 1968). From transformation of female larvae to the end of the life cycle, temperature effects were slight. Copepods have been observed parasitizing fish only during summer, when water temperatures exceeded 25°C (Marcogliese 1991).

Asian Tapeworm

The only internal parasite observed on humpback chub during this investigation was the Asian tapeworm (Bothriocephalus acheilognathi). This parasite was found in the gut of 6 of 168 (3.6%) adults flushed with a stomach pump (See Chapter 9 - FOOD HABITS). An average of 6.7 tapeworms (range, 1-28) were found for the six infected fish. Subadults humpback chub were not examined internally or subjected to stomach flushing, and these young fish were not evaluated for internal parasite load.

The Asian tapeworm was first reported from North America in 1975 in golden shiners and fathead minnows, and in the United States in grass carp (Ctenopharyngodon idella) (Hoffman 1976). It is believed to develop in any member of the minnow family, but has been found in non-cyprinids in Asia and Europe (Babaev 1965, Bauer et al. 1969), where it is considered a dangerous parasite to fish (Bauer and Polyanski 1981). It is well established in the southeastern U.S., where it often has an adverse impact on the baitfish industry (Granath and Esch 1983, Riggs and Esch 1987).

Asian tapeworm were first reported in humpback chub from Grand Canyon in 1990 (D. Hendrickson, AGF, pers. comm.). Angradi et al. (1992) reported tapeworms in 80% of juvenile humpback chub (range, 13-35 mm TL) from the LCR in 1990, and none from humpback chub examined in 1989. Asian tapeworms were also reported from the Virgin River in woundfin (Plagopterus argentissimus), speckled dace (Rhinichthys osculus), Virgin River chub (G. robusta seminuda), Virgin spinedace (Lepidomeda mollispinis), and red shiner (Cyprinella lutrensis) (Heckman et al. 1986). Asian tapeworms were not reported in a survey of Colorado squawfish, humpback chub, bonytail, and razorback suckers from the upper Colorado River basin (Flagg 1982).

The Asian tapeworm has a complex life cycle with operculate eggs shed into the water via feces from an infected fish. After a period of development (e.g., 96 hr at 20°C), a motile coracidium emerges (Granath and Esch 1983) and is ingested by a primary host; one of several species of cyclopoid copepods, some of which occur in the Colorado River and its tributaries in Grand Canyon (Haury 1988). A procercoid stage develops in the copepod and matures to an adult tapeworm when ingested by the final fish host. Development of the adult occurs in the intestine of the fish and adult tapeworms can be rather large, up to 100 mm long and 2 mm wide (Hoffman 1980). The scolex or head is large and triangular and diagnostic for the species.

Temperature has a significant effect on maturation and growth of B. acheilognathi (Granath and Esch 1983). Maximum egg hatching and development of all life stages occurred at 30°C, although highest densities of tapeworms were found at 20°C (temperatures below 20°C were not tested). Stimulation for growth, development, and maturation of eggs in adults occurred above 25°C. Coracidia failed to develop into procercoids, and procercoids failed to develop into adults at 20°C.

Saprolegnia

Other external maladies noted on 17 of 6,294 (0.27%) humpback chub included "fungus" or "bacterial infections", and "growths" or "tumors". The "fungus" was characteristic of the fungus Saprolegnia spp., which is a facultative pathogen that attacks necrotic tissue, but can also breach the integrity of the host skin, or invade external abrasions or cuts (Davis 1967). Flagg (1982) identified Saprolegnia spp. from Gila sp. in the upper basin, and cautioned that "*Abrasions from net capture and tagging were also prime targets for Saprolegnia but no mortalities could be attributed to this alone.*" Saprolegnia was not observed on net scars during this investigation, but was reported from the tail region of adult humpback chub, and likely caused by abrasions inflicted during spawning. No evidence of whirling disease (Myxobolus cerebralis) was seen from any fish handled. Whirling disease is a protozoan parasite that is known to cause cartilage damage only in salmonids, resulting in frenzied, tail-chasing behavior by the fish (Stoskopf 1993).

DISCUSSION

Population estimates for adult humpback chub (≥200 mm TL) were made for six of nine aggregations, from RM 30 (Fence Fault) to RM 213 (Pumpkin Spring), in the mainstem Colorado River (see Chapter 5 - DISTRIBUTION AND ABUNDANCE). Estimates within the LCRI aggregation were 3,000-3,500 adults depending upon the estimator chosen, while estimates for the other five aggregations were less than 5% of this total. Since 98% of adults were captured in the nine aggregations, an approximate estimate of adults in the mainstem using the Chao M_n estimator for six aggregations, and assuming 90 fish total in the other three aggregations, was 3,800 (95% C.I. = ± 25% of total). These represent some of the first population estimates for native fishes in the Colorado River Basin. Lanigan and Tyus (1989) estimated numbers of adult razorback suckers in the upper Green River and Tyus (1991) estimated an upper bound for adult Colorado squawfish in the Green River.

Estimation of populations for the other three aggregations was not possible because of the lack of fish captured in two or more sample periods. Numbers of adult humpback chub in these aggregations were likely higher than the numbers of individuals actually captured. However, capture rates for these aggregations were low (see Chapter 5 - DISTRIBUTION AND ABUNDANCE) indicating that these populations were small, probably within the range of aggregations other than the LCRI aggregation.

Estimated numbers of adult humpback chub in the LCRI aggregation (Table 6-13, Table 6-14) strongly suggest that the numbers of fish 200-300 mm TL were well below those expected for a population with a stable size and age distribution. Stable age and size distributions place the expected number of chubs 200-300 mm TL higher than the number for fish greater than 300 mm TL. While this skewed length distribution could reflect a population with recent recruitment substantially below replacement level, recruitment of adults greater than 300 mm TL may be largely from the LCR. If the population of adults was relatively stable, most recruitment to the mainstem would have to be coming from smaller adults (perhaps 250-350 mm TL) leaving the LCR. This also indicates that recruitment to the mainstem adult component from juveniles and subadults living in the mainstem may be lower than recruitment by small adults from the LCR. Low growth rates for humpback chub greater than 300 mm TL in the LCR compared to higher growth rates in the mainstem suggest that large chubs may reach resource limitations in the LCR and migrate to the adjacent portion of the mainstem. Length-frequency data and population estimates of humpback chub in different size categories from the LCR need to be evaluated to better understand this relationship.

Monthly length-frequency analyses of the LCRI aggregation indicated substantial overlap in lengths of fish less than 200 mm TL from different cohorts. A large and distinct mode of fish less than 100 mm TL reached peak densities in September 1991, May 1992, and September 1993, and was attributed to dispersal of young (ages 0, 1, and possibly 2), concurrent with summer freshets from the LCR. Considerable overlap in lengths of fish of different ages was suspected and attributed to timing of descent from the warmer LCR to the colder mainstem, i.e., slow-growing fish from the cold mainstem were older, but of similar size to faster-growing, younger fish from the LCR. Separation of cohorts was also difficult because of expanded spawning time, perhaps as much as 3 months (March-May).

The only aggregation upstream of the LCR inflow, the 30-Mile aggregation (RM 29.8-31.3), was composed entirely of adults, significantly larger (≥330 mm TL) than adults of other aggregations. Although a concentration of about 100 post-larval humpback chub (range, 18-31 mm TL, n=14) was observed in a warm shoreline spring near RM 30 (constant temperature of 21.5°C), the absence of juveniles and subadults from this aggregation indicates little or no past survival of young or recruitment to adults. The group of humpback chub at 30-Mile will likely go extinct when the large adults die. Recruitment from the LCR aggregation may explain the existence of this aggregation, however, movements to areas this far upstream would have to be by larger subadults or adults. Such movements appear to be rare, and humpback chub were not captured in a 40-mile subreach, between RM 32 and RM 57, during this investigation.

While age determination of adults in the 30-Mile aggregation was not possible, large sizes and distinct morphological characters (i.e., enlarged nuchal humps) implied a relict group of fish that could have hatched in the early 1970s, before hypolimnetic releases occurred following construction of Glen Canyon Dam in 1963. Assuming little or no recruitment to this aggregation, some of these fish may be 25 years old or more and may represent a unique genetic stock of mainstem fish isolated from the LCR population.

Length-frequencies in other aggregations indicate that humpback chub in these areas have had recent recruitment. Small humpback chub found in these aggregations could be from local reproduction, but the majority were probably dispersed from the LCR population, as cold mainstem temperatures likely limit or prohibited successful mainstem spawning in these areas. Spawning in tributaries adjacent to some aggregations is possible, but survival of young in the mainstem is likely limited by cold temperature, minimal habitat, and high predation potential. Individuals of all sizes may have migrated to these regions, however, adult fish may be less likely than young fish (which may be passively transported) to make such movements. The size distribution of larger subadults and adults in MGG was much closer to a stable size distribution than was observed for the LCRI aggregation. This suggests a relatively steady flow of small-sized recruits to this aggregation over time from the LCRI aggregation.

None of the aggregations outside the LCR region may have large enough numbers of adults to form viable populations without input from the LCR population. Population sizes less than 50 individuals may place the rate of inbreeding at intolerable levels (i.e., <2%,Frankel and Soulé 1981), while 500 individuals may be necessary to maintain sufficient genetic variability for adaptation to environmental changes (Franklin 1981). Several larger populations may be necessary to maintain long-term evolutionary potential at the species level (Soulé 1980). The probable influx of chubs from the LCRI aggregation to aggregations below the LCR would likely aid in supplementing genetic diversity if suitable spawning conditions were present. Sex ratios of nearly 50:50 measured in the 30-Mile and MGG aggregation indicate that sufficient numbers of both sexes are available for reproduction.

The similarity in population estimates of adult humpback chub in the LCRI aggregation between several estimators for closed population models M_0, M_t, M_h, and M_{th} and for open population models was encouraging. Relatively similar estimates from closed population models were also found for estimates from other aggregations. This consistency occurred in spite of a variable sampling program that was necessitated by sampling for multiple objectives (and time and personnel limitations) through the course of the study. Monitoring population size will require sampling that is more intensive and uniform in effort to reduce the variability in estimates. The large 95% confidence intervals (±20-25% for LCRI aggregation, larger for other aggregations) from this study would preclude effective monitoring of population size, except when major changes in numbers occur (on the order of 30-40%).

Length-weight relationships and Kn for adult humpback chub were typically highest prior to spawning, in March and April, and lowest in June, after spawning for the LCRI aggregation. Greatest increases in Kn were from June to September, when fish were recovering from spawning, and from November to March, in advance of spawning. Significantly higher Kn for October 1990 was possibly related to high releases and greater drift food availability during research flows. Lower Kn in October 1991, 1992, and 1993 suggested differential effects of interim flows, i.e., possibly less food from lower magnitude fluctuations. Relative condition of humpback chub may be a useful indicator to local environmental conditions, because the absence of a pyloric caecum (i.e., fat absorption and storage organ at the posterior end of the stomach of most fishes, Lagler et al. 1962) restricts fat storage to mesenteries and muscle. Fat from these sites is more quickly metabolized, reflecting rapid weight changes of individual fish. Condition of males and females was not significantly different prior to spawning, indicating that both sexes directed substantial energy into gonadal and ovarian development. The adult component of the population may have different winter physiological characteristics than subadults, as indicated by high Kn and spawning activity. Relative condition of adults of other species, including flannelmouth sucker, bluehead sucker, rainbow trout, and brown trout, showed no distinct pattern, but there was some indication that Kn reflected physiological events.

Estimated hatching time of early June for post-larval humpback chub captured within the 30-Mile aggregation, and peak in spawning condition of adults in May indicate that mainstem chubs in areas other than the LCRI aggregation reached spawning readiness 2 months later than the LCR fish (which showed peak spawning condition in March), or approximately the same time as humpback chub in the five Upper Colorado River Basin populations. While maturation and spawning cues were not apparent, temperature-degree days, light intensity, and water temperature (average mainstem temperature was about 3-5°C higher in summer than winter) were probably major factors in timing of mainstem spawning.

Scales of subadult humpback chub were cycloid, with a center focus, concentric growth circuli, and annular rings composed of closely spaced circuli that formed from November through March. Winter annular ring establishment was consistent with most temperate species (Lagler et al. 1962), although maximum mainstem temperature variation near the LCR inflow was from a monthly mean of 6°C in January to 11°C in July. Circuli in scales of adults were too distorted and disrupted to distinguish annular rings. Average back-calculated lengths of mainstem subadults at 1, 2, and 3 years were 96, 144 and 186 mm TL, respectively, with 74 mm TL as the average length at time of transition from the LCR to the mainstem. Apparently the majority of growth in these juveniles occurred in the first year while in the LCR. Minimum size of fish at transition was 52 mm TL, indicating little or no survival of smaller fish descending from the LCR; thermal shock or predation elicited by aberrant thermal-shock behavior (i.e., erratic swimming, flashing) may be the most likely causes of mortality.

Estimated annual survival rates of 0.755 for adult humpback chub (≥200 mm TL) was surprisingly low considering the longevity of some individuals of this species (Hendrickson 1993). Survival estimates calculated for adults greater than 300 mm TL were similar indicating that potentially higher mortality for chubs 200-300 mm TL did not bias this estimate. Relatively large 95% confidence intervals were associated with these estimates due to limited data, however, and the upper confidence interval placed survival at 0.896. The difference in annual losses from these estimates would be one in four chubs versus one in ten.

Estimated 'survival' rate included both true survival and emigration from the LCRI aggregation. Such emigration may have been to the LCR or downstream. Movement data, however, indicate minimal downstream emigration of adults from the LCRI aggregation. Emigration into the LCR would have to be substantiated by mark-recapture data in the LCR. If emigration was minimal for these adult chubs, survival rate would largely reflect mortality.

Densities of subadult humpback chub from the LCR inflow (RM 61.3) to Lava Canyon (RM 65.4), followed a typical negative exponential relationship that was attributed to mortality (i.e., predation, thermal shock, diseases and parasites, starvation) and emigration (i.e., downstream dispersal), offset by immigration (i.e., dispersal from the LCR). Decreases in peak densities for 1991 and 1992 were similar, and believed to be indicative of survival since fish densities below this subreach decreased dramatically. Annual survival rates of subadult chubs estimated from electrofishing catch rates were below 0.10. Hence, survival from hatching to adults, at 3 years of age, is about 0.001. Such high mortality rates support the hypothesis that recruitment to the adult portion of the population may be primarily small adults (i.e., 200-300 mm TL) from the LCR. While reproductive success in spring of 1993 and densities of subadults were three times as high as in 1991 and 1992, a density of dramatic decrease in number of subadults occurred between September and November 1993. The density of subadults in November was similar to that of previous years, indicating density dependence possibly caused by limited food resources or a combination of limited food and predation.

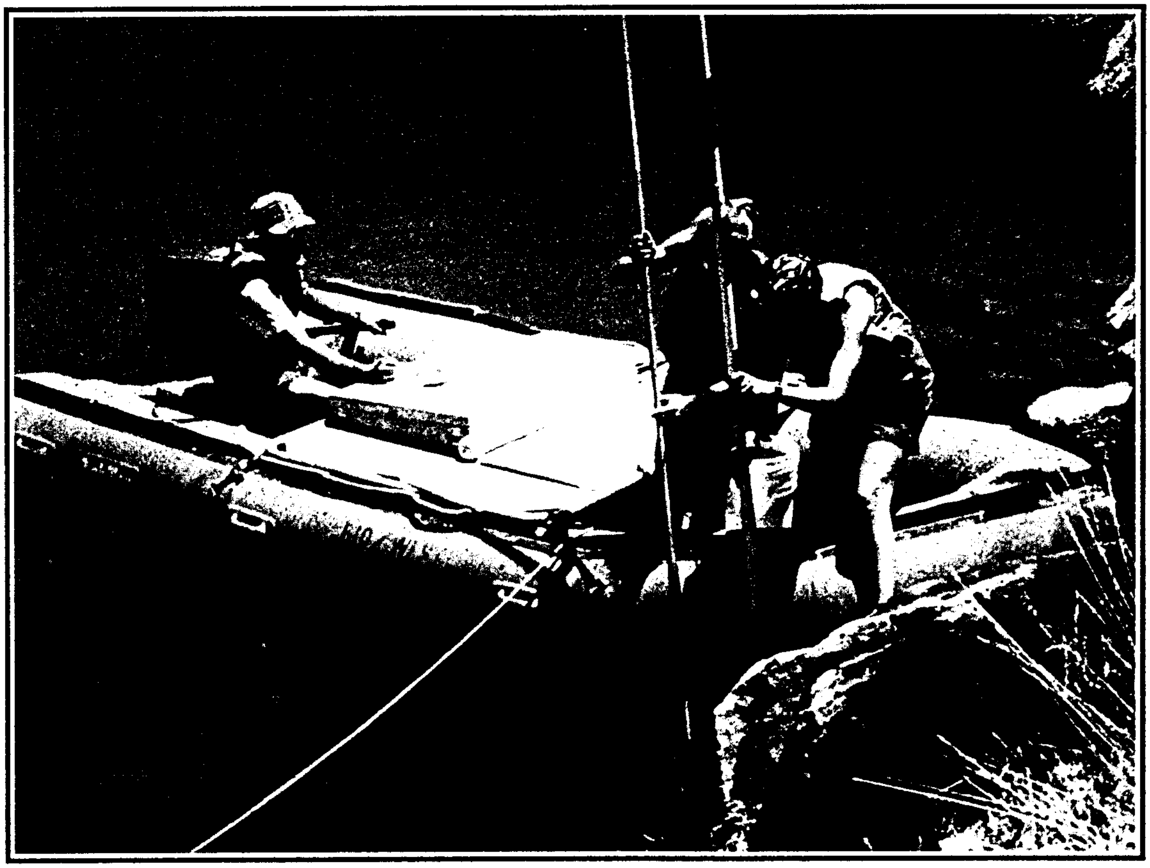
Predation by non-native fishes may be a significant mortality factor for humpback chub of all ages and it may be partially responsible for relatively low survival rates. Of fish examined, 10.4% of adult brown trout, and 1.5% of adult channel catfish had subadult humpback chub (range, 95-158 mm TL) in their stomachs. Adult brown trout (range, 200-730 mm TL) could consume humpback chub of up to 340 mm TL, although 90% of all fish predators were of a size that could consume only subadults (<200 mm TL), and neither brown trout nor channel catfish feed on prey as large as their mouth gapes will allow.

Assuming 10.4% of 3,000 adult brown trout consumed 2.0 humpback chub daily in the area of highest subadult densities, annual consumption was an estimated 227,760 chubs. Predation by 1.0% of an estimated 9,000 adult rainbow trout, and 200 adult channel catfish (1.0 chubs/day) in the area of highest subadult densities could result in estimated annual consumption rates of 33,850 and 1,095 humpback chub, respectively. Given these assumptions, brown trout, rainbow trout, and channel catfish could consume over 260,000 subadult humpback chub annually. Barrett et al. (1992) determined turbidity (>30 NTU) significantly reduced reactive distance by rainbow trout to prey items, suggesting that predation by rainbow trout on humpback chub is reduced during high turbidity. Predation of native fishes in Grand Canyon by brown trout is of particular concern, since it appears turbidity had less effect on this species. Also, brown trout are increasing in abundance in the Bright Angel area; the proportion of brown trout to rainbow trout at Bright Angel Creek in 1980 was one in ten (Usher et al. 1984), but results of this investigation suggest that this proportion has been reversed.

Other causes of mortality for mainstem humpback chub were identified in addition to predation, and included thermal shock, parasites and diseases, starvation, and avian predators, although no attempt was made to quantify these causes. Incidence of two parasite species was recorded for humpback chub. The parasitic copepod, L. cyprinacea, was found on 0.13% (8 of 6,294) of fish examined, and the Asian tapeworm, (Bothriocephalus acheilognathi) was found in the intestine of 3.6% (6 of 168) of adults flushed for gut content with a stomach pump. Some subadult humpback chub with tapeworms appeared emaciated, but the incidence of tapeworms in subadults could not be accurately assessed.

Habitat

Chapter 7



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CHAPTER 7 - HABITAT

INTRODUCTION

Fish habitat is the sum of physical, chemical, and biological elements that surround a fish throughout its life (Hynes 1970, Lotspeich and Platts 1982, Orth 1983, and references cited therein). Habitat is determined by water quality (e.g., temperature, dissolved oxygen, conductivity, pH, etc.), water quantity (i.e., flow magnitudes, ramping rate, fluctuations), channel geomorphology (i.e., size, shape, substrate type), and associated life forms (i.e., plants, macroinvertebrates, other fish). Fish of a given species and age frequently select similar sites that best meet immediate needs for resting, feeding, spawning, and escape from predators. This chapter focuses on physical habitat features that affect humpback chub in the mainstem Colorado River in Grand Canyon.

Flow regulation of the Colorado River has had dramatic effects on native fish and their habitats, but the mechanisms are poorly understood (U.S. Department of Interior 1988, National Research Council 1987). Mainstem dams, such as Glen Canyon Dam, have lowered spring flood peaks, elevated base flows, and caused daily fluctuations from hydropower production (See Chapter 3 - HYDROLOGY). These changes have had long and short-term effects on fish habitat and, together with invasion by non-native fishes, have limited native fish populations, such as the humpback chub.

Habitat of humpback chub has been variously described for each of the six known populations, including those in Black Rocks and Westwater Canyon (Valdez et al. 1982, Valdez and Clemmer 1982), Cataract Canyon (Valdez et al. 1982, Valdez 1990, Valdez and Williams 1993), Yampa Canyon (Tyus et al. 1982, Karp and Tyus 1990), Desolation/Gray canyons (Holden 1978, Tyus et al. 1982, Karp and Tyus 1990), and Grand Canyon (Kaeding and Zimmerman 1983, Gorman et al.1994). Kaeding et al. (1990) suggested that the habitat characteristics common to all populations were the presence of main channel and shoreline structure, such as boulders, and constrictions that cause obstructions of flow and variable current velocity and direction.

Habitat data from the five upper basin populations were recently assimilated by consensus of species experts into habitat suitability index (HSI) curves for four age categories, including larvae, young-of-year (YOY), juveniles, and adults (Valdez et al. 1990). Development of these HSI curves revealed a lack of quantitative information, that hindered defining flow requirements for the species. Lack of data on water depth, velocity, substrate, and cover 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).

Flow requirements for humpback chub also remain undescribed because of a poor understanding of the relationships between flow, channel geomorphology, and fish habitat. Flow patterns shape channel features, such as sand bars, side channels, and bottom contours, and the combination of flow and channel morphometry determines current patterns and hence habitat quality.

Channel geomorphology in Grand Canyon is dictated by the local geology at river level, processes of shoreline formation or deposition, and flow. Local geology at river level changes as the river cuts through layers of rock. Because some layers are more resistant than others, channel morphology changes as well. Based on these lithologic changes, reaches can be designated that are relatively homogeneous in channel width, depth, and shoreline features. In turn, hydraulic and shoreline features vary between reaches. Furthermore, microhabitat parameters, such as velocity, depth, substrate, and cover depend on reach characteristics as well as hydraulic and shoreline features. Debris fans reflect interactions of frequency and magnitude of tributary debris flows as well as frequency and magnitude of mainstem floods; these reflect basin characteristics such as lithology and slope.

This investigation evaluated the present use of physical habitat by humpback chub in the mainstem Colorado River in Grand Canyon and inferred effects of Glen Canyon Dam operations on habitat availability and use. Habitat features deemed important to different life stages were identified, and factors influencing the availability of these features were addressed. This study of habitat use and availability was conducted to better understand life history aspects of humpback chub and effects of Glen Canyon Dam operations.

A standard system of habitat nomenclature is not available for large western streams, such as the mainstem Colorado River, although several habitat classification systems have been developed for salmonids in small streams (Bisson et al. 1982, Sullivan 1986, Hawkins et al. 1993). 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 1991, 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.

The classification system used for fish habitat in the Colorado River in Grand Canyon is based on geomorphic processes and was designed to be integrated with existing descriptors of channel geomorphology in order to better describe the greater Grand Canyon ecosystem. This habitat classification system is based on the hypothesis that predominant shoreline geology and channel geomorphology change longitudinally and affect hydraulic characteristics, thus forming code pendant relationships between cover, substrate, depth, and velocity of fish habitat.

METHODS

Riverine habitat in the Colorado River of Grand Canyon was described by physical attributes of the river channel and shorelines and resultant surface hydraulic characteristics within defined geomorphic reaches. Habitat analysis was discreet for subadults (YOY and juveniles) and adults, because of an ontogenetic habitat shift at maturity (~200 mm TL) from littoral zones to open water. Humpback chub habitat use was determined by fish capture locations and radiotelemetry observations. Habitat selection was inferred through comparisons of habitat availability and use. Shoreline types, such as debris fans, and sand beaches are directly linked to tributary processes such as debris flows and seasonal floods.

Habitat Descriptions and Availability

Habitat availability was described at four levels of resolution (Fig. 7-1), including

- Level 1: geomorphic reach,
- Level 2: shoreline type,
- Level 3: hydraulic unit (i.e., macrohabitat), and
- Level 4: habitat parameter (i.e., microhabitat).

Adult habitat availability was described at levels 1, 3, and 4, while subadult habitat was described at levels 1, 2, and 4. These levels contained descriptions and definitions consistent with those used by other investigators in the Colorado River Basin (Valdez and Wick 1983, Tyus 1984, Osmundson et al. 1995, Harvey et al. 1983, Stanford 1994) and consistent with an integrated description of resources in Grand Canyon (Werth et al. 1993). A similar classification system was used by Anderson et al. (1986) to analyze aquatic habitat for low and high flows of the Colorado River in Grand Canyon from video imagery that provided a comparative data set.

Availability of habitat in selected subreaches of the mainstem was determined from

- maps with visual interpretations of surface hydraulics, (i.e., macrohabitat and shoreline types),
- channel bathymetry,
- velocity isopleths,
- temperature isopleths, and
- maps with visual interpretation of substrate types.

Map products 1 through 5 were incorporated into the GCES Geographic Information System (GIS) developed for resource monitoring of the Colorado River in Grand Canyon (Werth et al. 1993). Shoreline microhabitat measurements were integrated into a fisheries database and stored in dBASE IV files. Each map product was referenced to an established control network for use as

Fig. 7-1. Four levels of fish habitat classification in the Colorado River, Grand Canyon.

informational layers on the GIS. A multi-temporal, multi-accuracy GIS database was developed to accommodate the different data types and accuracies associated with these maps (Hougaard and Valdez 1994).

Level 1: Geomorphic Reach

The 11 geomorphic reaches described by Schmidt and Graf (1990) were the basis for major longitudinal comparisons of fish habitat (See Tables 1-3 and 2-1). Major geologic units at river level, width to depth ratio, channel width, channel slope, and bed composition were described for each reach to provide a longitudinal characterization of channel geomorphology. A more detailed analysis was conducted for two subreaches that contain the largest aggregations of humpback chub, the LCR Inflow (LCRI) and Middle Granite Gorge (MGG) aggregations, and compared with a third subreach containing few fish in order to identify important geomorphic variables in determining reach selection. That analysis compared numbers of debris fans, slope, and average width to depth ratio. Water temperature was also considered because of the dominating influence of cold hypolimnetic releases from Glen Canyon Dam.

Level 2: Shoreline Type

Shoreline types were classified according to the predominant formative shoreline geology. Shoreline types included bedrock, cobble bars, debris fans, sand bars, and talus (Table 7-1, Fig. 7-2); vegetated banks were usually associated with sandy or earthen banks and were identified as a sixth type because of their influence on fish distribution and abundance. Shoreline and macrohabitat types (See Level 3: Hydraulic Unit) were visually delineated at seven map sites and various flows, between RM 59.75 and RM 63.24, to determine changes in availability with fluctuating flows. This classification was similar to that used by Werth et al. (1993), except that "rock ledge" and "rock face" categories were combined into the bedrock type, and alluvial fan was termed debris fan. This shoreline classification was

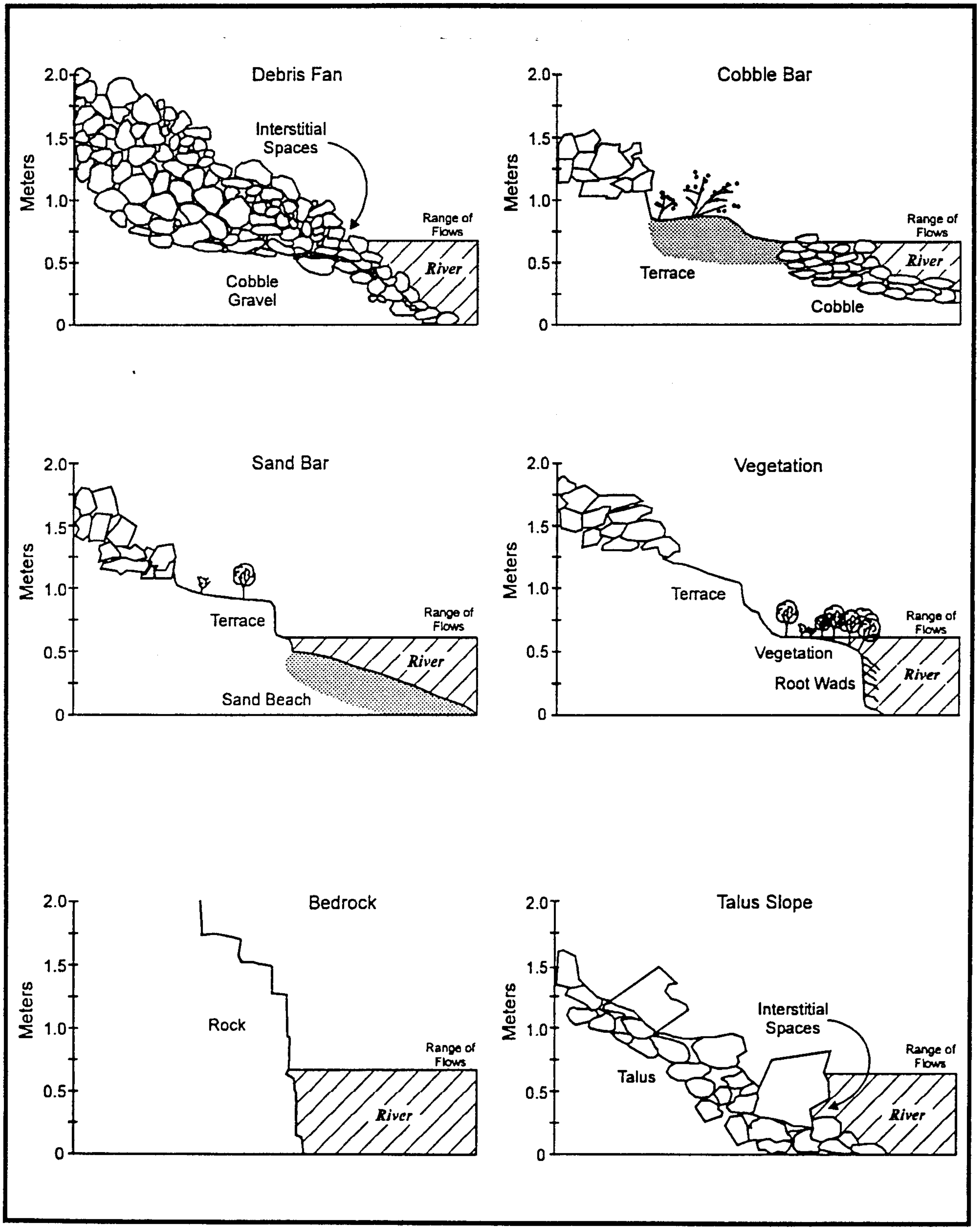


Fig. 7-2. Cross sections of hypothetical shoreline types.

Table 7-1. Shoreline types and definitions associated with fish habitat of the Colorado River in Grand Canyon.

Shoreline Type	Definition
Bedrock	Exposed underlying parental rock material.
Cobble Bar	Cobble transported and rounded by main channel activity, characteristically well worked and imbricated. May show embededness.
Debris Fan	Material transported from a tributary during flood events, primarily boulders and cobble rounded by transport processes. Material is often embedded, and the angle of repose is generally less than talus.
Sand Bar	Predominantly exposed sand.
Talus	Unconsolidated colluvium, predominantly angular boulders, deposited by rockfalls or rockslides from canyon walls. Talus is characteristically not embedded, and has a steeper angle of repose than debris fans.
Vegetation	Inundated plant material, consisting of stems, leaves, and/or root wads.

designed to reflect geomorphic processes and transposition of material with the greatest influence on fish habitat. For example, cobble bars were composed of material rounded and embedded by river processes with limited spaces for fish cover, while talus consisted of irregular, angular boulders formed from shoreline rockfalls and slides with many interstitial spaces.

Linear distance of shoreline types and surface area of macrohabitat types were delineated, irrespective of flow, from the LCR inflow (RM 61.3) to Hance Rapid (RM 76.4). The longitudinal shoreline geomorphology of this reach was compared to the occurrence and densities of juvenile humpback chub and with shoreline microhabitat measurements. These relationships were the subject of a Master's Thesis (Converse 1995) and are described in the section under Subadult Habitat Use entitled Habitat Selection.

Level 3: Hydraulic Unit

Fish macrohabitat described the general area occupied by a fish. Six habitat classifications were defined on the basis of hydraulic units, including eddies, pools, rapids, return channels, riffles, and runs (Table 7-2, Fig. 7-3). Terms and definitions for macrohabitats were consistent with those adopted by the American Fisheries Society (Helm 1985), with elements of the GCES/GIS classification scheme for aquatic biology (Werth et al. 1993), and with common usage of terms throughout the Colorado River Basin (Tyus et al. 1982, Valdez et al. 1982, Maddux et al. 1987, Stanford 1994). These hydraulic units reflected areas of differential fish use distinguishable at the water's surface, so that changes in flow were reflected in changes in surface area. These changes implied effects of dam operations on fish macrohabitat.

Twenty-five habitat maps were developed for seven sites in the vicinity of the LCR (Table 7-3, Fig. 7-4) for determination of flow to habitat relationships.

Aerial photographs at a 1:1200 scale (1 cm = 12 m) were used as base maps to simultaneously delineate macrohabitats and shoreline types for a subreach of river about 400 m long at each site. Two to four maps were developed at each site for different flows during interim flow criteria in 1991 and 1992 (See Chapter 3 - HYDROLOGY).

Maps were developed by the same observer using visual interpretations of macrohabitat margins and shoreline delineations from two or three established shoreline vantage points. Binoculars were used to better define water levels, habitat interfaces, and shoreline types. All observations were made early and late in the day to minimize solar reflection and water surface disturbances from wind.

Habitat maps were rectified to orthophoto base maps for GCES/GIS monitoring site #5 (Werth et al. 1993), from the LCR to Cardenas (RM 61.3-72). Surface area of each macrohabitat type in square meters, and linear distance of each shoreline type in meters were calculated by the GIS software and

Table 7-2. Fish macrohabitat types and definitions for the Colorado River in Grand Canyon.

Macrohabitat Type	Definition
Eddy	A circular current of water, sometimes quite strong, diverging from and initially flowing contrary to the main current. It is usually formed at a point at which the flow passes some obstruction or on the inside of river bends (Helm 1985). In the Colorado River, an eddy forms in a channel expansion where flow separates from the bank, creating a zone of relatively weak recirculating current (Rubin et al. 1990). Bars accumulate at the weak points of flow where the current separates from the bank (separation point) and where flow reattaches to the bank (reattachment point). Increasingly restricted countercurrent behind the reattachment bar creates a recirculating eddy return channel.
Pool	A portion of the stream with reduced current velocity, often with water deeper than the surrounding areas, and which is frequently usable by fish for resting and cover (Helm 1985). In the Colorado River, a pool usually occurs in a deepened scour basin, and there may be small surface boils and upwellings.
Rapid	A relatively deep stream section with considerable surface agitation and swift current. Some waves may be present. Rocks and boulders may be exposed at all but high flows. Drops up to one meter (Helm 1985). In the Colorado River, rapids are whitewater, high velocity area caused by a constriction and drop in elevation. A rapid is deeper than a riffle, and has large, broken standing waves.
Return Channel	A topographic feature of a recirculating eddy that serves as the main pathway for upstream circulation, and forms a narrow channel (Rubin et al. 1990). When flows are below the crest of the reattachment bar, a sheltered body of water forms, bound on three sides by land with one opening to the river. A return channel is one type of backwater.
Riffle	A shallow rapids where the water flows swiftly over completely or partially submerged obstructions to produce surface agitations, but standing waves are absent (Helm 1985).
Run	An area of swiftly flowing water, without surface agitation or waves, which approximates uniform flow and in which the slope of the water surface is roughly parallel to the overall gradient of the stream reach (Helm 1985).

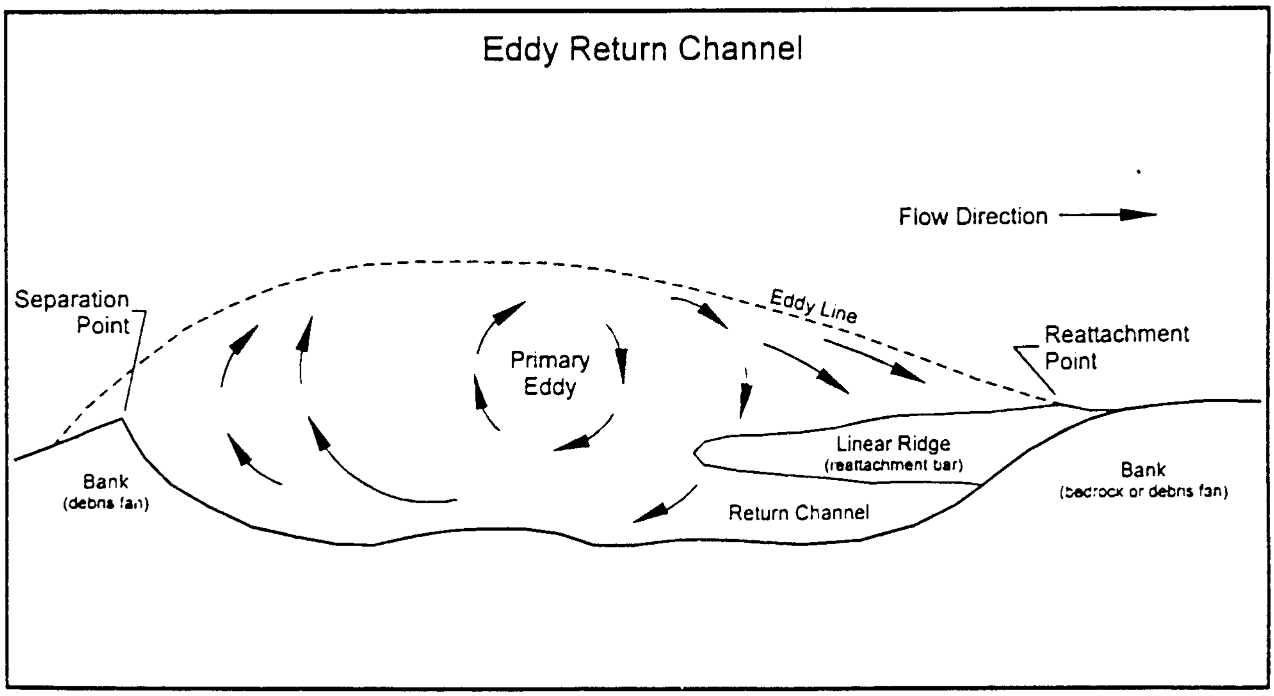


Fig. 7-3. Surface flow pattern of an eddy (adopted from Rubin et al. 1990).

Table 7-3. Habitat map sites for the Colorado River in Grand Canyon with flows and dates in which maps were rendered.

Map Site	Flow Range	Midpoint (cfs)	Date (time) Map was Rendered
ESPN (RM 59.75-61.00)	5,318-5,467	5,385	May 19, 1991 (1300-1400)
	11,089-11,089	11,089	August 19, 1991 (1830-1856)
	14,792-15,502	14,920	May 22, 1991 (1130-1230)
	17,249-16,749	17,148	August 18, 1991 (0850-0920)
	12,378-12,016	12,085	June 17, 1992 (1130-1245)
CAMP (RM 61.00-61.25)	5,318-5,268	5,234	May 20, 1991 (0830-0930)
	11,297-11,237	11,250	August 19, 1991 (1730-1750)
	15,017-14,888	14,888	May 21, 1991 (1515-1630)
	17,651-17,249	17,500	August 18, 1991 (0800-0834)
	12,916-12,443	12,696	June 17, 1992 (1015-1100)
LCRI (RM 61.25-61.50)	5,335-5,451	5,400	May 19, 1991 (1000-1130)
	11,446-11,326	11,400	August 18, 1991 (1800-1830)
	14,856-14,984	14,920	May 21, 1991 (1330-1430)
	16,451-16,155	16,300	August 18, 1991 (1000-1032)
	8,000	8,000	May 30, 1993 (0630-0700)
HOPI (RM 62.20-62.40)	10,052-10,043	10,050	September 16, 1991 (1530-1618)
	16,122-15,762	16,000	August 20, 1991 (1030-1050)
	11,979-11,643	11,708	June 18, 1992 (1215-1250)
SALT (RM 62.40-62.60)	9,257-10,266	10,266	May 20, 1991 (1720-1815)
	10,043-10,057	10,054	September 16, 1991 (1415-1508)
	14,824-14,888	14,952	May 22, 1991 (0830-0930)
	14,920-14,600	14,500	August 20, 1991 (1200-1230)
WHAL (RM 62.60-62.90)	14,920-14,920	14,920	May 22, 1991 (1810-1900)
WEEP (RM 62.90-63.25)	10,033-10,023	10,030	September 16, 1991 (1630-1718)
	17,517-17,115	17,300	August 20, 1991 (0830-0850)
	8,500	5,500	May 29, 1993 (1500-1530)

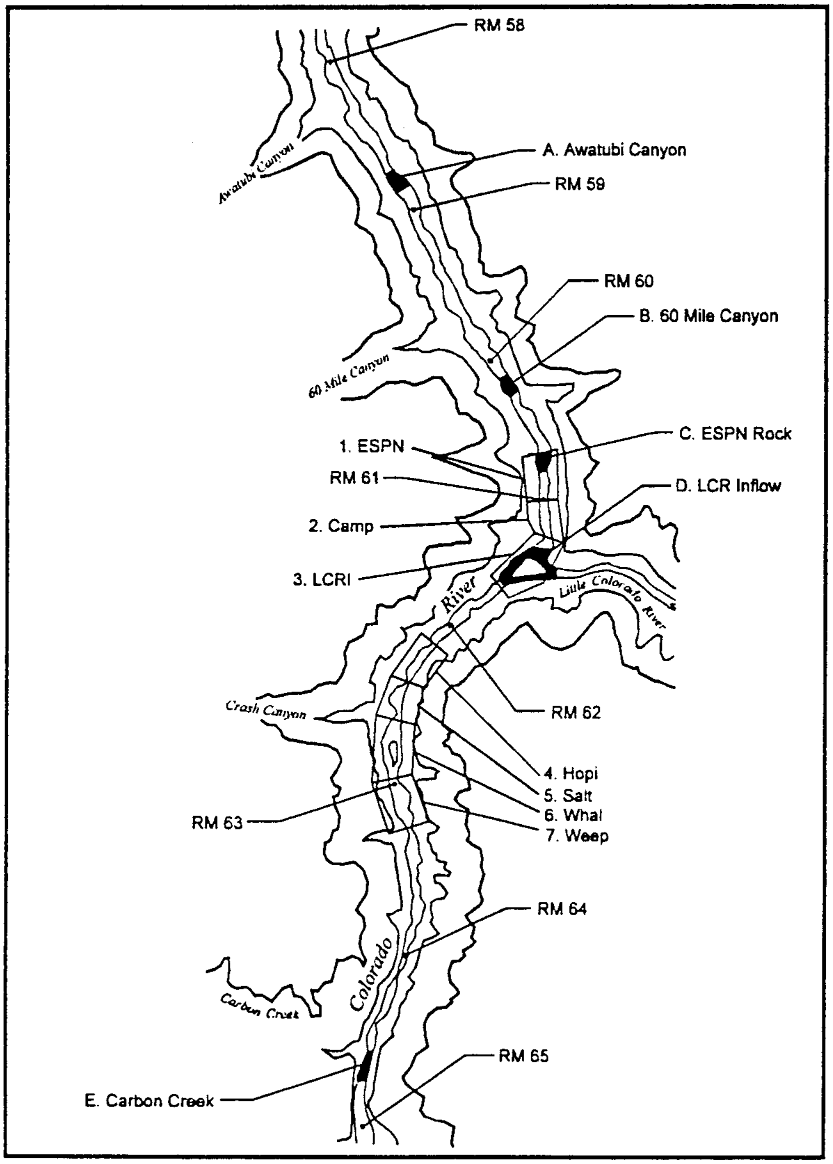


Fig. 7-4. Locations of five bathymetry map sites (A-E) and seven macrohabitat map sites (1-7) on the Colorado River in Grand Canyon. RM = river mile.

related to river flow at the midpoint of map development (habitat maps were developed in 35-60 min). A flow routing model (Supplement No. VI, Goodwin 1995) was used to estimate flow at the site during each period of map development.

Level 4: Habitat Parameter

Depth, velocity, substrate, and cover of shorelines and the main channel were characterized with a variety of techniques. Channel bathymetry, velocity isopleths, substrate maps, and temperature isopleths were developed for the main channel with the aid of a Super-Hydro bathymetry system, and shoreline parameters were measured for near shore transects.

Channel Bathymetry. Channel morphology was further described with bathymetry maps of five sites (Fig. 7-4), including:

A. Awatubi Canyon, RM 58.5,
B. 60-Mile Canyon, RM 60.1,
C. ESPN Rock, RM 60.8,
D. LCR Inflow, RM 61.3, and
E. Carbon Creek, RM 64.7.

The first four sites contained large recirculating eddy complexes regularly used by humpback chub, and the LCR Inflow site was used as a staging area by prespawning adults.

A Super-Hydro bathymetric system was used to map underwater topography of the mainstem (F. Protiva, M. Gonzales, GCES, pers. comm.), and presented as two-dimensional isopleths or three-dimensional bathymetry enhanced with computer imagery. The system consisted of a shore station, located by coordinates with the aid of an Ashtech Global Positioning System (GPS), to track and send position information to a main computer located on a boat. The boat computer included a graphics screen to guide the helms person along a pre-determined sampling pattern of transects set 10 m apart. Survey readings, including distance and angle, were made with the aid of a prism on the traversing boat, and simultaneous to measurements of depth (using a Lowrance depth finder) and velocity (using a Marsh-McBirney current meter). Data point collection interval for depth was adjustable, from once every 2 sec to 4 points/sec; i.e., over 10,000 points were collected to develop a bathymetric map for the LCR site (1.6 km distance of river). Elevational starting points for each map were based on a local coordinate system above the high water line in order to reliably reestablish control points and allow for future resurveys.

Field information was stored on a personal computer, and transferred to GCES for processing and plotting. Data processing included editing erroneous points, generating a database from surveyed points, visual reality check of data points, depth reductions to relative elevation, generation of a surface model, and orientation to established network coordinate points (Werth et al. 1993). Bathymetric plots were generated with contour intervals of 0.5 m (consistent with GCES/GIS).

Velocity Isopleths. Velocity isopleths were also developed with the aid of the Super-Hydro system for the ESPN Rock (RM 60.8) and Carbon Creek (RM 64.7) sites (Fig. 7-4). Velocity was measured 1 m below the water surface with a Marsh-McBirney current meter, and recorded simultaneous to depth readings. Velocity was plotted with contour intervals of 0.1 m/sec. Although flow volume changed during these measurements, and multi-directional velocity shears were common in a single vertical transect, these isopleths provided a characterization of velocity magnitude and distribution, as well as location of high and low velocity zones relative to channel morphology.

Temperature Isopleths. Thermal isopleths of the LCR inflow were developed from water temperature data collected with hand-held thermometers over a series of points located on a latice grid system. Data were collected May 16, 20, and 21, and July 21, 22, 23, 24, and 25 of 1992. Data were grouped by four mainstem flow ranges including: (1) 9,200-9,600 cfs, (2) 12,130-12,809 cfs, (3) 13,947-14,504 cfs, and (4) 17,470-17,798 cfs. A relationship of LCR temperature (at base flow of 230 cfs) to mainstem flow was established and thermal gradients were plotted at 2°C intervals, from 10°C to 24°C.

Substrate Maps. Substrate of the LCR inflow was also delineated with the aid of the Super-Hydro system, simultaneous to development of bathymetry maps. Observers used the tracking boat or waded in shallow areas to classify substrate according to a modification of the Wentworth system (Table 7-4). Substrate was segregated as a separate layer of the GIS. Surface area of each substrate type was recorded in square meters.

Shoreline Microhabitat. Depth, velocity, substrate, and cover of shorelines commonly used by juvenile humpback chub were evaluated to describe habitat attributes and determine relationships of flow to microhabitat. Parameters were measured and classified at three 1-m intervals from shore, along each of ten parallel transects separated by 10 m. Depth was measured with a graduated staff, velocity with a Marsh-McBirney current meter, substrate was classified according to Table 7-4, and cover was classified as instream, lateral, or overhead (Helm 1985). Measurements were made at 84 sites at different flows to evaluate changes in available habitat components within sites and among shoreline types. These sites were also sampled with electrofishing to relate fish density to shoreline type and to evaluate effects of dam operations (i.e., fluctuating flows) on juvenile habitat.

Table 7-4. Modified Wentworth classification for substrate particle sizes (Cummins 1962).

Classification		Code	Particle size range (mm)
Boulder		BO	>256
Cobble (Rubble)		CO	64 - 256
Pebble	- large	PE	32 - 64
	-small		16 - 32
Gravel	-coarse	GR	8 - 16
	-medium		4 - 8
	-fine		2 - 4
Very coarse sand		SA	1 - 2
Coarse sand			0.5 - 1
Medium sand			0.25 - 0.5
Fine sand			0.125 - 0.25
Very fine sand			0.0625 - 0.125
Silt		SI	0.0039 - 0.0625
Clay		CL	<0.0039

Habitat Use

Radiotelemetry was recommended by species experts as the most effective method for determining habitat used by the Colorado River endangered fishes (Valdez et al. 1990), and has been applied to humpback chub (Valdez and Nilson 1982, Valdez and Clemmer 1982, Kaeding et al. 1990), Colorado squawfish and razorback sucker (Tyus et al. 1982, Valdez and Masslich 1989), and bonytail (Chart and Cranney 1991). Habitat used by humpback chub and sympatric species in the mainstem was determined from radiotelemetry and capture information, and habitat selection was determined by comparing availability with use. Radio-tagged adults (n=75) were located and observed as described in Chapter 8- MOVEMENT, and habitat use was determined as percentage of radio contacts in respective macrohabitats. Contact locations were mapped during each of two to four daily boat surveillances through areas occupied by radio-tagged fish. Efforts to measure microhabitat (depth, velocity, substrate, cover) of adults were abandoned because water depth, channel width, and high, multi-directional velocity shears precluded accurate measurements. Capture locations of adults were used to supplement and confirm radiotelemetry data. Macrohabitat of juvenile and YOY humpback chub, and sympatric species, was determined from catch locations associated with electrofishing, nets, seines, minnow traps, and hoop nets.

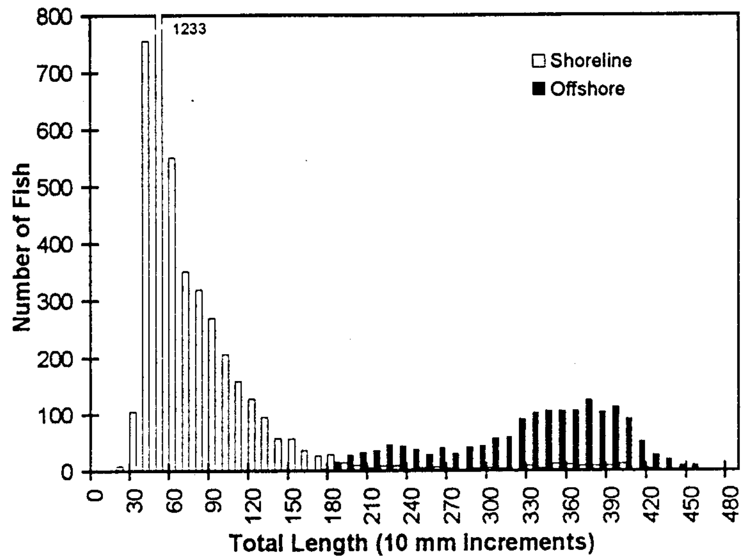


Fig. 7-5. Length-frequency distribution of humpback chub captured in shoreline habitats (with electrofishing, seines, minnow traps) and in offshore habitats (with gill nets, trammel nets) for 1991-93.

Radio contact locations and sample sites (i.e., net sets, electrofishing runs, seine hauls, and minnow traps) were transferred onto a GIS with linkage information to an associated digitized database. The contact and capture locations became a set of geographic information for comparison with physical river attributes (e.g., bathymetry, velocity, etc.).

Microhabitat of subadult humpback chub (<200 mm TL) was determined within shoreline types sampled with electrofishing (Table 7-1). Depth, velocity, substrate, and cover were determined from measurements taken along each of 10 parallel transects, as previously described in Shoreline Microhabitat. Although subadult habitat was characterized from shorelines sampled with electrofishing, individual capture locations were not used to quantify habitat since electrofishing commonly displaces fish from microhabitat sites (Bovee 1986, Valdez et al. 1990).

RESULTS

A transition in habitat use occurred with size and age of humpback chub, such that subadults used primarily shorelines and adults used primarily offshore habitats (Fig. 7-5). Numbers and sizes of fish captured indicates a transition from shorelines to offshore habitats beginning at about 1 year of age (i.e., age I+) and ending at about 3 years of age (i.e., age III+) , approximately the same age of field-observed maturity for males (min = 202 mm TL) and females (min = 200 mm TL) (See Chapter 6 - DEMOGRAPHICS). The length mode for fish caught nearshore with all gears was 40-60 mm TL (range, 20-460 mm TL); smaller fish were present in return channels that were sampled by AGF (See Chapter 2 - STUDY DESIGN). Fish in offshore habitats were 100-460 mm TL; smaller fish were not captured in offshore habitats despite sampling with small mesh experimental gill nets.

Adult Habitat Use

Reach Selection

Humpback chub in the Colorado River between Glen Canyon Dam and Lake Mead were found in aggregates associated with one or more of four canyon features: (1) warm tributaries, (2) warm springs, (3) a unique geologic association, and (4) debris fans (Table 7-5). These features were believed to be the most important influences to selection for these areas or subreaches. Although cold releases from Glen Canyon Dam have limited physiological functions of warmwater fish, such as reproduction and growth, three of the seven aggregates were associated exclusively with the

Table 7-5. Geomorphic attributes of the river channel and numbers (percentage of total) of adults captured in areas occupied by nine aggregations of humpback chub.

Aggregation	Location River Mile	No. Adults Captured (%)	Key Element[a]	Channel Slope (ft/1,000 ft)	Average Width to Depth Ratio
1. 30-Mile	29.8-31.3	26(1%)	WS, DF	1.5	9.5
2. LCR Inflow	57.0-65.4	1,524(87%)	WT, GA, DF	1.7	19.6
3. Lava to Hance	65.7-76.3	15(1%)	GA	2.1	28.2
4. Bright Angel Inflow	83.8-92.2	9(1%)	WT	2.3	10.2
5. Shinumo Inflow	108.1-108.6	27(2%)	WT	2.3	10
6. Stephen Aisle	114.9-120.1	17(1%)	GA, DF	1.7	10.5
7. Middle Granite Gorge	126.1-129.0	124 (7%)	GA, DF	2.1	8.2
8. Havasu Inflow	155.8-156.7	7(<1%)	WT	1.2	9.1
9. Pumpkin Spring	212.5-213.2	6(<1%)	WS, DF	1.3	21.1

[a]Key elements are features that are believed to influence selection by fish for a particular area or subreach, i.e., WT = warm tributary, WS = warm spring, GA = geologic association of Muav limestone, Bright Angel shale, Tapeats sandstone, Unkar group, DF = debris fans.

unique geologic association of Muav limestone, Bright Angel shale, Tapeats sandstone, and the Unkar group at or immediately above river level (see Fig. 1-5). Four of the seven aggregates were associated with warm tributaries or warm springs.

As presented in Chapter 5 - DISTRIBUTION AND ABUNDANCE, the distribution of adult humpback chub varied greatly by geomorphic reach. The largest mainstem aggregation (LCRI aggregation, 1,524 adult captures or 87% of total) was in a 13.5-km subreach near the LCR inflow, and the second largest (MGG aggregation, 124 adult captures or 7% of total) was in a 4.7-km subreach in Middle Granite Gorge. Other aggregations were found scattered from RM 29.8 to RM 213.2.

The majority of adults of the LCRI aggregation were found in the relatively narrow position of the geomorphic reach (i.e., Lower Marble Canyon) with width to depth ratio (w:d) of 19.1, and average channel width of 115 m (350 ft) (Table 1-3, Fig. 7-6). Although this aggregation depended on the LCR for spawning, occurrence of relatively large numbers of adults in the mainstem was attributed to the frequency of large closely spaced, and alternating recirculating eddies, which adults selected disproportionately by availability (see next section--Habitat Selection). The major geologic units at river level for these reaches were Muav limestone, Bright Angel shale, Tapeats sandstone, and members of the Unkar group, successive layers of varying resistance that together formed irregular talus shorelines and a high frequency of debris fans with associated downstream channel expansion zones and large recirculating eddies (Melis and Webb 1993). The next largest aggregations of adults and large subadults were

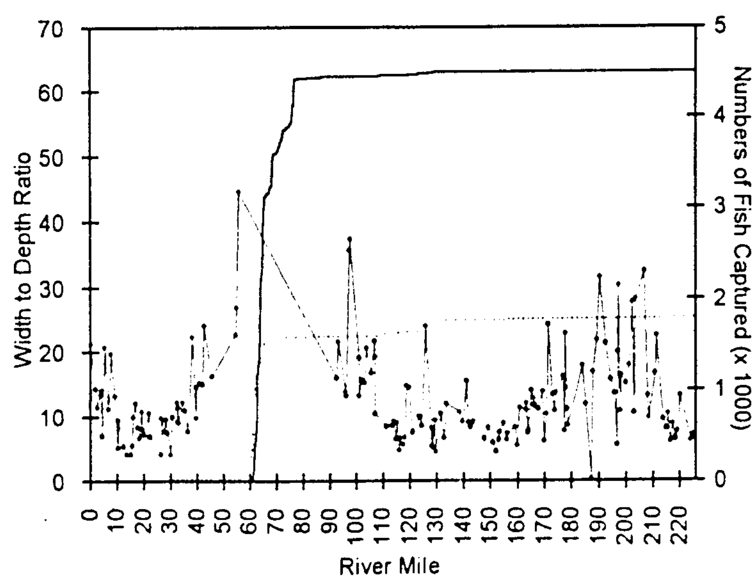


Fig. 7-6. Channel width to depth ratio compared to cumulative numbers of juvenile and adult humpback chub captured in the mainstem Colorado River from Lees Ferry (RM 0.0) to Diamond Creek (RM 226.0), October 1990-November 1993. Subreaches occupied by the nine humpback chub aggregations are indicated.

found in the Aisles and Middle Granite Gorge reaches. These reaches had similar shoreline geologic units (i.e., Muav limestone, Bright Angel shale, Tapeats sandstone, members of the Unkar group) as well as Vishnu Schist, but relatively narrow channel width of 75 m and 69 m (230 and 210 ft), respectively.

Other geomorphic reaches, where few or no humpback chub were captured, were dominated by more resistant geologic units that precluded large, closely-spaced debris fans and expansion zones. Supai Gorge and Redwall Gorge were dominated by relatively resistant limestones, sandstone, and silt stones; Upper Granite Gorge by precambrian Zoraster granite and Vishnu Schist; Muav Gorge by Muav limestone; and Lower Granite Gorge by Vishnu Schist. These reaches contained the narrowest channel widths where debris fans tended to form rapids instead of expansion zones and large recirculating eddies. Channel slope tended to be greatest in the wider, more erodible lithology, but this attribute failed to clearly indicate reach differences.

The numbers of debris fans and the average width-to-depth ratio in areas where adult chubs were captured were characterized for three subreaches: (1) RM 57-65.4, occupied by the LCRI aggregation, (2) RM 122-130.4, occupied by the MGG aggregation, and (3) RM 140-148.4, where only two humpback chub were captured (Fig. 7-7). Subreach lengths were standardized to 15.5 km (8.4 mi) to facilitate comparisons. The greatest number of debris fans (27) and the highest channel width-to-depth ratio (19.6) were correlated with subreach 1 (LCRI aggregation), where the largest number of adults were found. Fewer debris fans (16) and lower width-to-depth ratio (8.2) for subreach 2 (MGG aggregation), and low number of debris fans (3) and width to depth ratio (7.9) for subreach 3 suggest that these geomorphic attributes may contribute to reach selection by adult humpback chub. Selection for subreaches with a moderately-wide channel and high frequency of debris fans was consistent with high use of eddy complexes by adults. Large recirculating eddies and expansion zones were more common in subreach 1 than in subreach 2, where fewer debris fans and a narrower channel resulted in fewer and smaller eddies. Debris fans in subreach 3 were few and associated with hard resistant Muav limestone. The two adult humpback chub captured in this subreach were near the Kanab Creek inflow and not associated with debris fans.

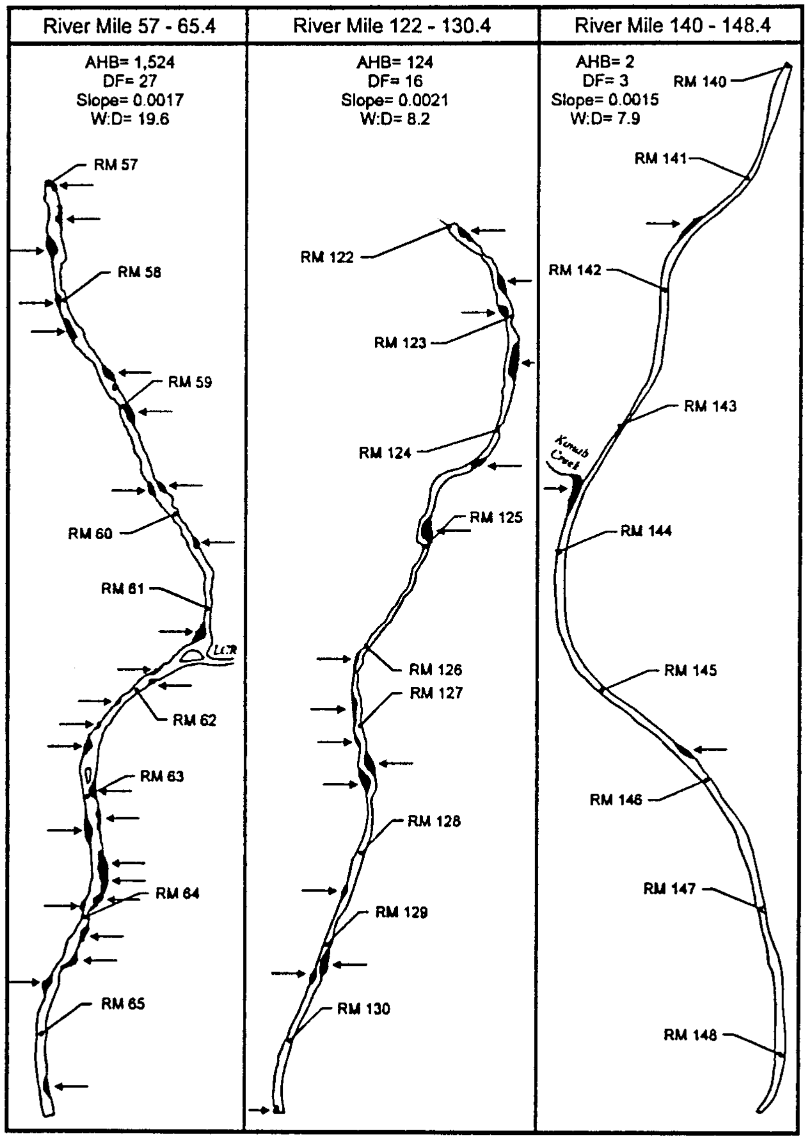


Fig. 7-7. Number of adult humpback chub captured (AHB), debris fans (DF), slope and width to depth ratio (W:D) for three 8.4-mi subreaches of the Colorado River: RM 57-65.4, LCR Inflow Aggregation (A), RM 122-130.4, Middle Granite Gorge Aggregation (B), RM 140-148.4, no aggregations (C).

An association of adults with recirculating eddy complexes was also indicated for the subreach from the LCR inflow (RM 61.3) to Hance Rapid (RM 76.4). Cumulative surface area of eddies at 0.16-km (0.10 mi) intervals showed a sizable reduction in area of eddies per mile of river downstream of Lava Canyon (Fig. 7-8). A dramatic reduction in numbers of adult humpback chub corresponded to fewer eddy complexes below Lava Canyon.

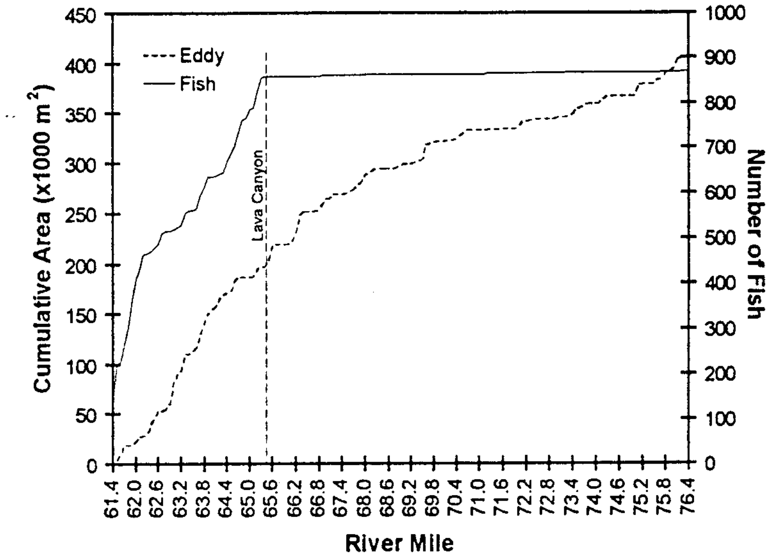


Fig. 7-8. Cumulative surface area of eddies and numbers of adult humpback chub captured from RM 61.4 (LCR Inflow) to RM 76.4 (Hance Rapid).

Habitat Selection

Mainstem Colorado River. Adult humpback chub in the mainstem Colorado River were found disproportionately in selected eddies, (i.e., 88% of adults captured and 74% of radio contacts were in eddy complexes Table 7-6), that constituted an average of only 21% of surface area in the subreach occupied by the LCRI aggregation. Smaller percentages of adults were captured or radio contacted in runs (7% and 16%, respectively) that constituted an average of 56% of surface habitat. Conversely, return channels, which were less than

Table 7-6. Number and percentage (%) of humpback chub captured and radio contacted in offshore and nearshore macrohabitats compared to surface area of macrohabitats, RM 57-65.4, 1990-93. YOY=young-of-year, JUV=juvenile, ADU=adult. Radio contacts represent 73 radio-tagged adults.

Macrohabitat Type	Percentage Surface Area Mean[a] (range)	Fish Captured YOY (%)	Fish Captured JUV (%)	Fish Captured ADU (%)	Radio Contacts ADU (%)
		Offshore Habitats			
Eddy	21 (2-44)	0 (-)	49 (52)	1391 (88)	617 (74)
Run	56 (35-73)	0 (-)	5 (5)	109 (7)	133 (16)
Pool	16 (0-43)	0 (-)	2 (2)	10 (1)	26 (3)
Riffle	4 (0-30)	0 (-)	0 (-)	0 (-)	3 (<1)
Rapid	4 (0-20)	0 (-)	0 (-)	0 (-)	0 (-)
Return Channel	0.1 (0-1)	0 (-)	38 (41)	69 (4)	56 (7)
Subtotals:		0	94 (100)	1579 (100)	835 (100)
		Nearshore Habitats			
Eddy	-	1261(43)	782 (53)	90 (60)	-
Run	-	792 (27)	244 (17)	19 (12)	-
Pool	-	25 (1)	22 (1)	1 (1)	-
Riffle	-	0 (-)	0 (-)	0 (-)	-
Rapid	-	0 (-)	0 (-)	0 (-)	-
Return Channel	-	551 (19)	282 (20)	30 (20)	-
Embayment	-	156 (5)	7 (<1)	0 (-)	-
Shoreline	-	141 (5)	137 (9)	11 (7)	-
Subtotals		2926 (100)	1474 (100)	151 (100)	

[a] average of surface area for seven habitat map areas, each about 400 m long

1% of surface area, accounted for 4% of captured adults and 7% of radio contacts. Small numbers of adults were also captured or contacted in pools and riffles, and although fish were neither caught nor radio contacted in rapids, movement patterns indicate that the fish ascended and descended rapids with 1-1.3 m drops, rated 2-4; i.e., 60-Mile Rapid (rated 4, with a drop of 1 m), (Belknap and Evans 1989). Opportunities were not available to radio-track fish through rapids to determine if they moved along the shoreline or through the central channel.

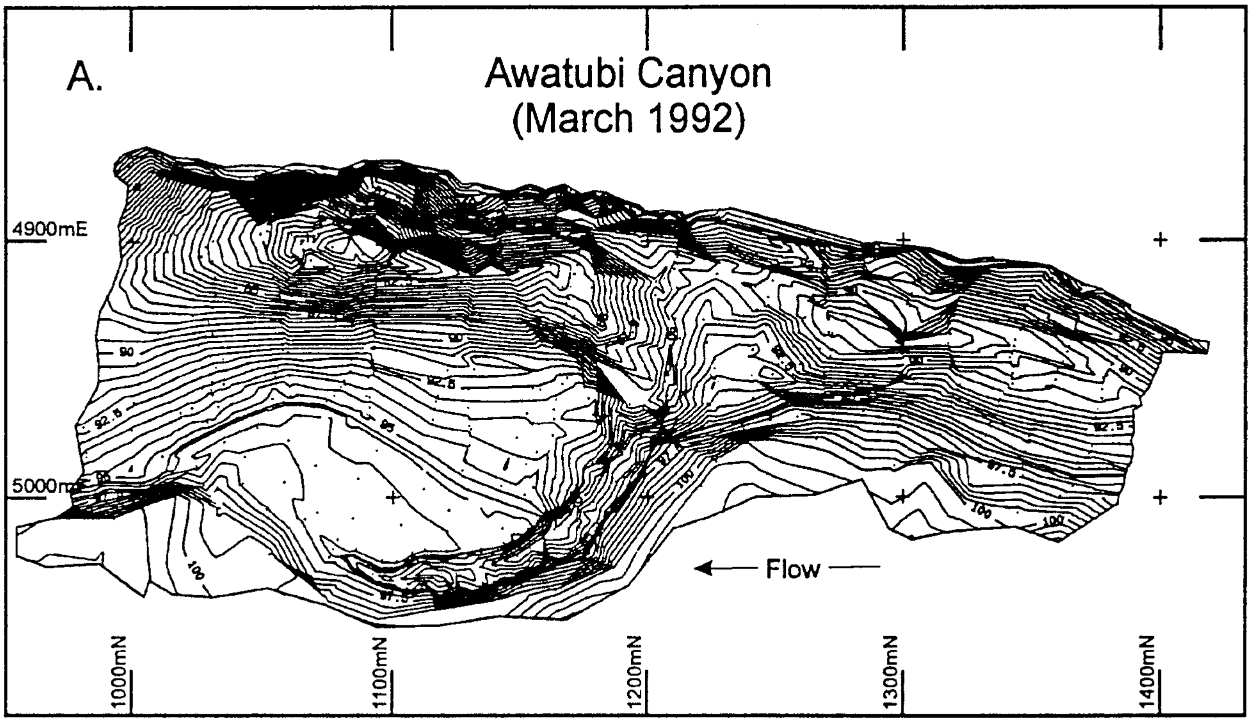
For the seven habitat sites (Fig. 7-4) within the area occupied by the LCRI aggregation,relationships of flow to surface area of eddies, runs, and rapids were positive and linear but weak (R^2<0.50) for the range of flows observed (i.e., 5,318 - 17,249 cfs) and negative for pools and riffles. No relationship was evident for return channels, although a 50% decrease in numbers and a 33% decrease in area of this habitat were observed when flow volume increased from about 5,000 cfs to 17,000 cfs. Weiss (1992) showed a 75% decrease in total numbers of backwaters (36 to 9) and an 82% decrease in total area (32,301 to 5,708 m^2) with increase in flow from 5,000 cfs to 15,000 cfs in 1991 (RM 50-72). Anderson et al. (1986) reported a 95% decrease in numbers of backwaters (from 62 to 3) when flow increased from 4,800 cfs to 28,000 cfs in 1985 (RM 61.5-77.0). McGuinn-Robins (1995) found significantly more backwaters at a flow of 5,000 cfs (42) than at 8,000 cfs (21) in 1990, 1992, 1993, and 1994 in Glen, Marble, and Grand canyons.

Bathymetric maps of four expansion zones/eddy complexes within the range of the LCRI aggregation (Fig. 7-9), showed characteristic topographic features described by Rubin et al. (1990): (1) a main platform, (2) a linear ridge or reattachment bar, (3) an eddy-return channel, and (4) accretionary banks. These features were formed by hydraulic patterns of the associated eddy complex. At median flow of about 12,000 cfs, the main platform of these complexes was a gentle sloping depositional zone of 0.5-5 m water depth, that changed abruptly to a steep slip face and sand dune at the accretionary bank. Maximum water depth of the scour channel in these expansion areas ranged from about 12 m at Carbon Creek (RM 64.7) to about 17.5 m at Awatubi Canyon (RM 58.5) (Table 7-7). The recirculation zone and associated features occupied a range of about 30% (60-Mile Canyon) to 50% (Carbon Creek) of the channel expansion area.

Velocity isopleths for ESPN Rock and Carbon Creek (Fig. 7-10) reflected a high-velocity scour channel with lower velocity shorelines and recirculation zones. Velocity in the recirculation zones was less than 1 m/sec, and typically less than 0.5 m/sec, and velocity in the midchannel scour zone was 1-3 m/sec. Characteristics of velocity in these eddy complexes were low velocity vortices over corresponding depositional areas, such as the main platform, on the river side of the reattachment bar, and near the separation point. Abrupt changes in velocity occurred at the accretionary banks from low velocity over the main platform to high velocity at the slip faces of the sand dunes.

Radio-tagged adult humpback chub in the area occupied by the LCRI aggregation (RM 58.0-65.4) selected macrohabitats associated with eddy complexes (Fig. 7-11). Twenty radio-tagged adults tracked and monitored for periods of 24-72 hr in four eddy complexes selected areas with similar depth, velocity, and substrate. Fish observed near Awatubi Canyon (n=3), 60-Mile Canyon (n=6), ESPN Rock (n=7), and Carbon Creek (n=5) were contacted most often on the main sand platforms or in the return channels. Fish used shallower areas of the main platforms and return channels (<2 m deep) primarily at dawn, dusk, and night, and remained in deeper areas of the platforms (2-5 m deep) during the day. Vortices of low-velocity (<0.3 mps) were selected and continuous local activity by some fish suggested a soaring behavior on vacillating currents, enabling the fish to remain within low velocity vortices at low energy expenditure. Association of fish with sand substrate was not considered selection, but coincidental to locations of low-velocity depositional areas created by eddy complexes. We believe that the fish selected these areas of low-velocity adjacent to high velocity shears and recirculation zones to feed on entrained drifting food organisms and particles, at low energy expenditure (See Chapter 9 -FOOD HABITS).

Radio contact locations outside of eddy complexes were associated with long-range movement between eddy complexes or as part of a pre- or post-spawning migration (See Chapter 8 - MOVEMENT), although the fish tended to follow shorelines and selected sheltered areas of low



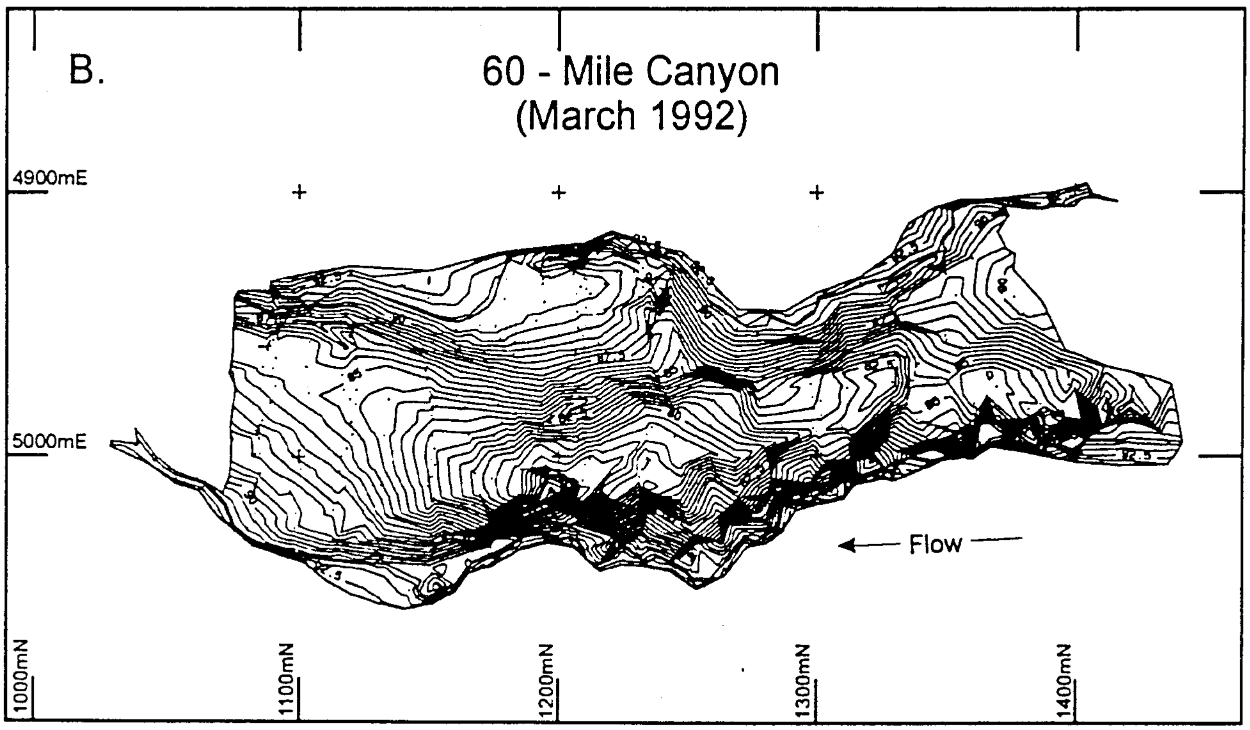
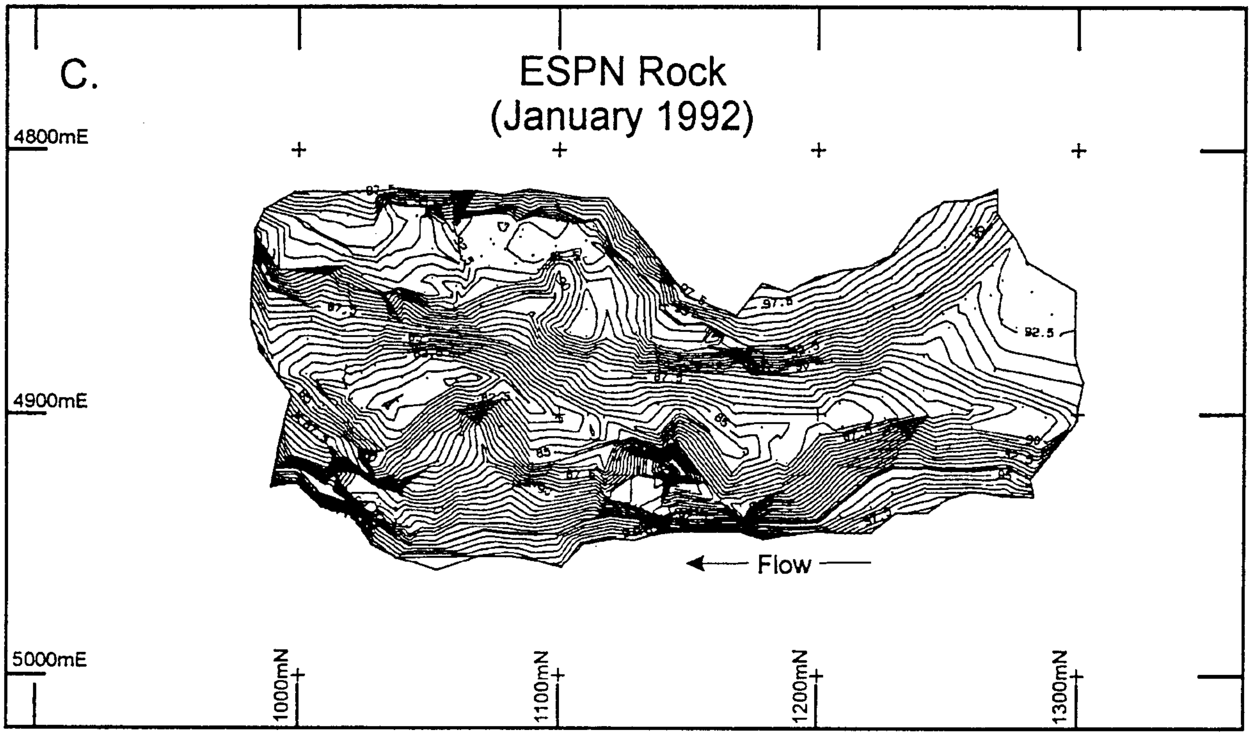


Fig. 7-9. Bathymetric maps of the Colorado River channel at Awatubi Canyon (RM 58.5) (A), 60-Mile Canyon (RM 60.1) (B), ESPN Rock (RM 60.8) (C), and Carbon Creek (RM 64.7) (D). Contour interval is 0.5 m. Data collected by GCES Survey Department.


C.
ESPN Rock
(January 1992)
4800mE
4900mE
5000mE
1000mN
1100mN
1200mN
1300mN
Flow

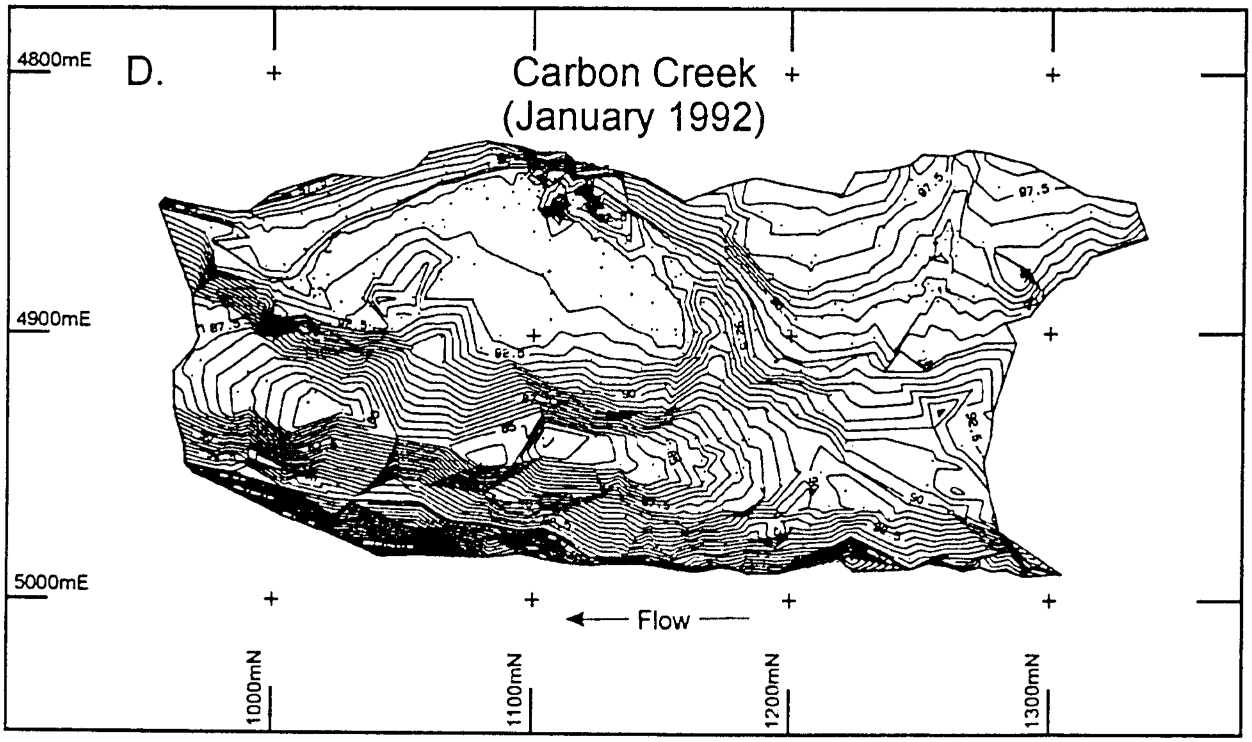

D.
Carbon Creek
(January 1992)
4800mE
4900mE
5000mE
1000mN
1100mN
1200mN
1300mN
Flow

Fig. 7-9. Cont.

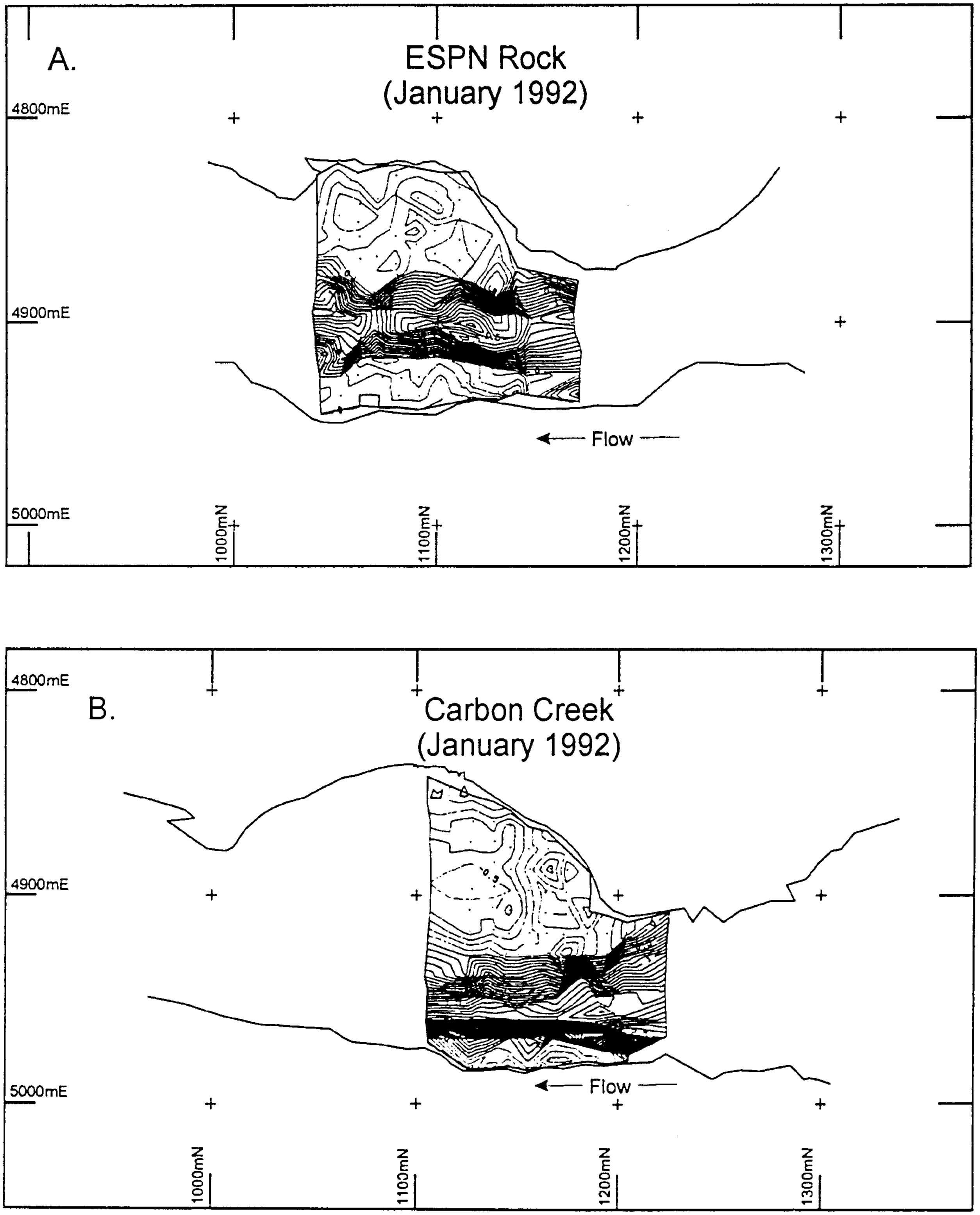


Fig. 7-10. Velocity isopleths for the Colorado River at ESPN Rock (RM 60.8) (A) and Carbon Creek (RM 64.7) (B). Contour interval is 0.5 mps. Data collected by GCES Survey Department.

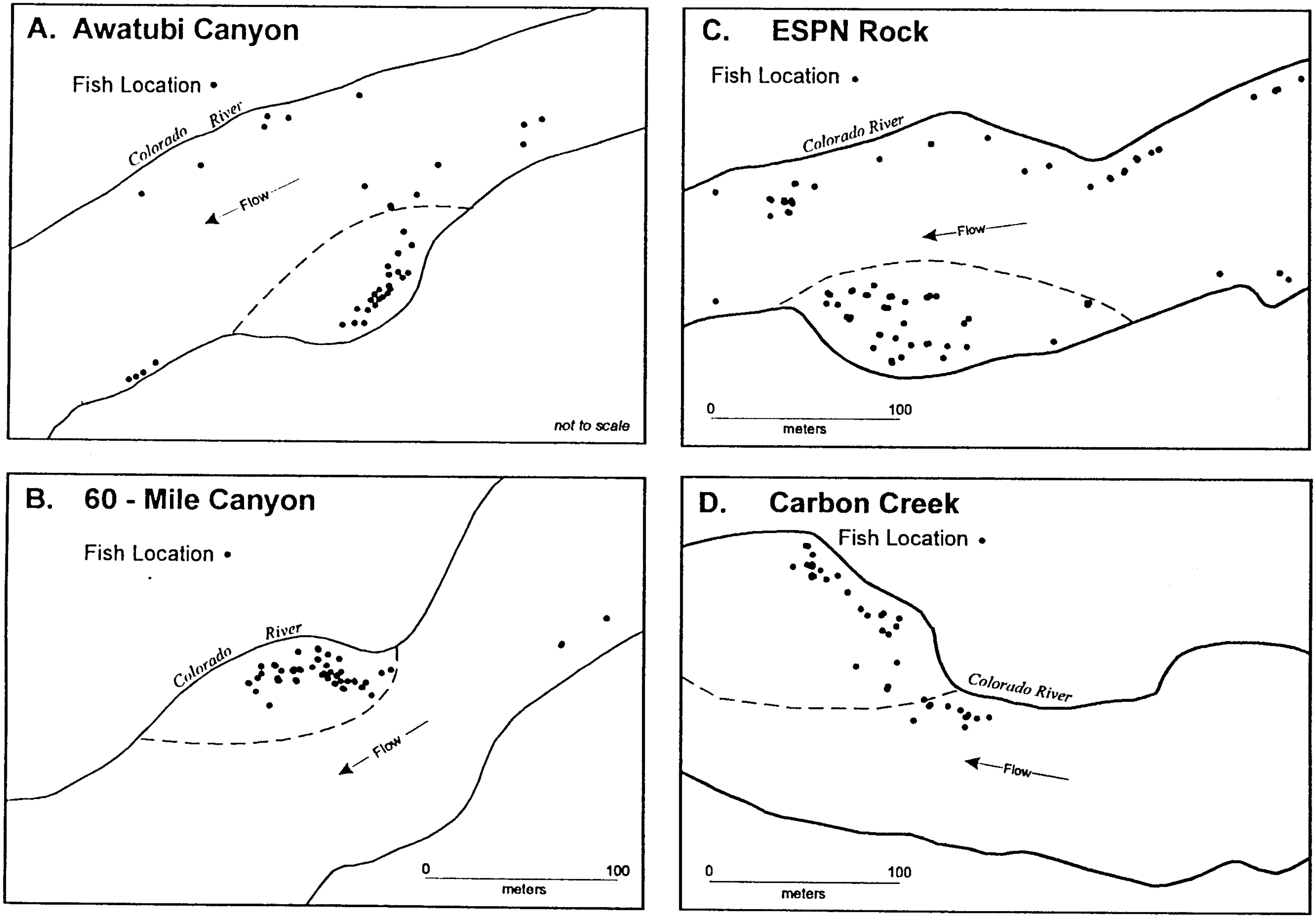


Fig. 7-11. Location of radio-tagged adult humpback chub near Awatubi Canyon (RM 58.5) (A), 60-Mile Canyon (RM 60.1) (B), ESPN Rock (RM 60.8) (C), and near Carbon Creek (RM 64.7) (D), 1991-92. Points represent radio contact locations occupied 15 min or more at a full range of flows. Shoreline shown is at approximately 12,000 cfs. Approximate area of eddy complexes shown by dashed lines.

Table 7-7. Characteristics and attributes of bathymetry for four eddy complexes in the Colorado River, Grand Canyon.

Bathymetric Map Site	River Mile	Size of Eddy Complex		Platform Depth (m)[a]			Maximum Scour Pool Depth (m)
		Area (m^2)	% of Expansion Zone	Max.	Min.	Ave.	
Awatubi Canyon	58.5	4,000	40	8.0	1.0	1.5	17.5
60-Mile Canyon	60.1	2,500	30	4.0	0.5	2.5	13.5
ESPN Rock	60.8	3,000	34	4.0	2.0	3.0	14.0
Carbon Creek	64.7	4,500	50	4.0	0.5	1.0	12.0

[a] Depth of main platform at 12,000 cfs

velocity for resting. Radio-tagged fish were not contacted in the central part of the channel, more than about 40 m from shore, except in low velocity zones of large eddy complexes, near midchannel islands, or behind instream structure (e.g., large midstream boulders at ESPN Rock). Radio signal patterns indicated that radio-tagged adults crossed the river channel by apparently remaining near the bed surface (See Box 8-1).

LCR Inflow. The inflow of the LCR into the mainstem Colorado River may be an important area for humpback chub in Grand Canyon. The inflow is used as a staging area for prespawning adults, and may provide a thermal acclimation zone for young dispersing from the LCR to the mainstem, as well as food washed from the LCR, and spawning habitat. Depth bathymetry illustrates the geomorphic complexity of the inflow, created primarily by a large cobble/sand island of alluvial material deposited by the LCR. The LCR enters the mainstem through a primary channel, but is often pushed to a secondary, downstream channel by high mainstem flows.

During this investigation, the LCR at base flow of 230 cfs flowed through the primary channel at mainstem flow of less than about 15,000 cfs. At mainstem flows greater than 15,000 cfs, the LCR was pushed into the secondary channel. The relationship between flows of the LCR and the mainstem greatly influence water depth, velocity, and temperature, and thus the degree of fish use of the inflow.

The primary channel at low mainstem flow (5,000 cfs) and base LCR flow (230 cfs) had a maximum depth of about 1.5 m, and an average depth of about 1.0 m. At high mainstem flow (30,000 cfs), maximum depth was about 4 m, and average depth was about 3 m. No restriction to passage by adult humpback chub was seen in water depth at base flows, assuming minimum depth of 1.5 times the body depth of a large adult (i.e., 100 mm x 1.5 = 150 mm water depth required).

The secondary channel at low mainstem flow (5,000 cfs) and base LCR flow (230 cfs) had little flow, with two or three small shoreline pools of about 1 m depth. At high mainstem flow (30,000 cfs), the secondary channel had both mainstem and LCR water with maximum depth of about 1.5 m and average depth of about 0.5 m.

Thermal gradient in the LCR inflow was dynamic for mainstem flows of 9,000-17,000 cfs, as indicated by the expanse of the 18°C+ plume from the edge of the inflow area at the mainstem high water line (at 31,500 cfs). The point of reference was "Mort Rock", a large boulder located along the LCR bank at the approximate main channel high water line. The main factors influencing thermal gradients were flow magnitude and temperature of the mainstem and LCR. Periodic photography of the LCR inflow indicated that at the LCR base flow of 230 cfs and a mainstem flow of 14,500 cfs, the inflow was through the primary channel. The inflow was forced into the secondary channel when mainstem flows were 14,500-15,000 cfs. At mainstem flows of 12,130-14,504 cfs and LCR base flow (230 cfs), temperature in the primary channel in July 1992 was 18-22°C for about 260 m below "Mort Rock" (Table 7-8). Temperature in the secondary channel was 18-24°C for about 460 m

Table 7-8. Sample dates, times, flow, and temperature of the mainstem and LCR for development of temperature isopleths in the LCR inflow.

Sample Dates - Times (1992)	Mainstem		LCR		Expanse of 18°C+Plume (meters)[a]
	Flow (cfs)	Temp. (°C)	Flow (cfs)	Temp. (°C)	
May 16 - 0015 May 21 - 0015 May 21 - 0045	9200-9600	11.0	230	21.0	150
July 23 - 1755 July 24 - 1730 July 25 - 2012 July 25 - 1900 May 20 - 0615	12,130-12,809	12.0	230	21.5-25.3	260
July 21 - 2200 July 22 - 1430 July 24 - 1430	13,947-14,504	11.5	230	21.9-24.8	260
July 22 - 1015 July 25 - 1000 July 25 - 1016	17,470-17,798	11.0	230	22.3-22.7	60

[a]Measured from high water mark, or "Mort Rock", along primary channel

downstream of "Mort Rock" and cooled abruptly at a mixing zone with the mainstem at its lower terminus. In May 1992, at a low mainstem flow of 9,200-9,600 cfs, a temperature of 18°C extended only about 150 m below "Mort Rock". Temperature in the secondary channel was also cooler during May, and the 18°C plume extended only about 240 m below the high water line. The warm plume of the LCR in the primary channel was forced to the downstream bank by the colder and higher mainstem flow. At observed mainstem flows of 17,470-17,798 cfs, the LCR was forced into the secondary channel, and temperature in the primary channel was 12-14°C. The 18°C plume ended dramatically about 60 m downstream of the high water line.

Substrate of the primary LCR channel below "Mort Rock" consisted primarily of boulders and cobble, with varying amounts of intermixed silt just below "Mort Rock" (Fig. 7-12). A small amount of gravel occurred at the lower end of the primary channel, and small gravel deposits were common behind the larger boulders. The secondary channel consisted primarily of silt and sand, that were deposited during high flows from the LCR. Some cobble and boulders were present at the upper end of the secondary channel.

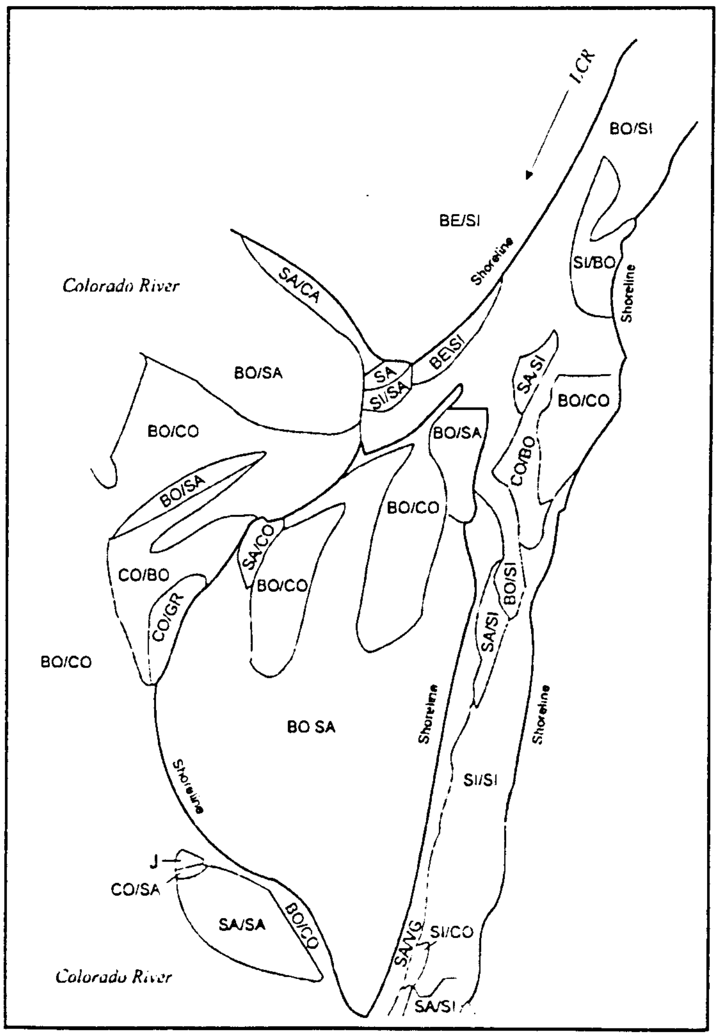


Fig. 7-12. Distribution of substrate types in the LCR inflow, May 15-17, 1993. See Table 7-4 for substrate codes.

Radio-tagged adults gathered at the LCR inflow in February-May, together with large numbers of staging adults (Fig. 7-13). During staging, adults moved between the primary channel and a deep (8-10 m) adjacent shoreline immediately upstream (See Chapter 8 - MOVEMENT). Velocity in the LCR inflow was higher than observed in eddy complexes, and radio-tagged fish frequently remained behind instream boulders or at the low velocity interface between the inflow and mainstem. Fish ascending the LCR frequently moved between the downstream cover of large boulders, entering swift current (>1 mps) for only short periods.

Radiotelemetry data collected during both 1991 and 1992 showed that large aggregations of radio-tagged fish spent time in various mainstem habitats near the inflow before moving into the LCR for spawning. Of interest was the different locations of staging radio-tagged fish around the inflow between pre-interim flows in 1991 and interim flows in 1992. During February through May of 1991, radio-tagged fish were primarily located in deep eddies and runs above the inflow except during April when the majority of fish were located in the mixing zone of the LCR. For the same time period in 1992, staging radio-tagged fish utilized different habitats. Although use of eddies and runs above the inflow was still evident, radio-tagged humpback chub utilized the LCR plume more frequently in 1992.

We attributed the shift in use of the inflow between 1991 and 1992 to differences in stability of the LCR plume associated with Glen Canyon Dam operations. During field trips in February through May of 1991, daily flows in the mainstem varied widely under pre-interim flows. Average daily change in flows during field trips ranged from 6,690 cfs in February to more than 12,800 cfs in May. During 1992, the magnitude of mainstem fluctuations under interim flows was 27-74 % less for corresponding months. Decreased fluctuations during 1992 resulted in a more stable plume configuration.

Location and extent of the LCR plume was related to flows of the mainstem and LCR. At base LCR flow, mainstem flow fluctuations dictated the location of the plume. During low mainstem flow (i.e., below 10,000 cfs), discharge from the LCR enters the mainstem on the upstream side of a large island at the confluence. Under this scenario, LCR water enters the mainstem along a series of runs and riffles and does not mix with mainstem water for 200-300 m below the inflow point.

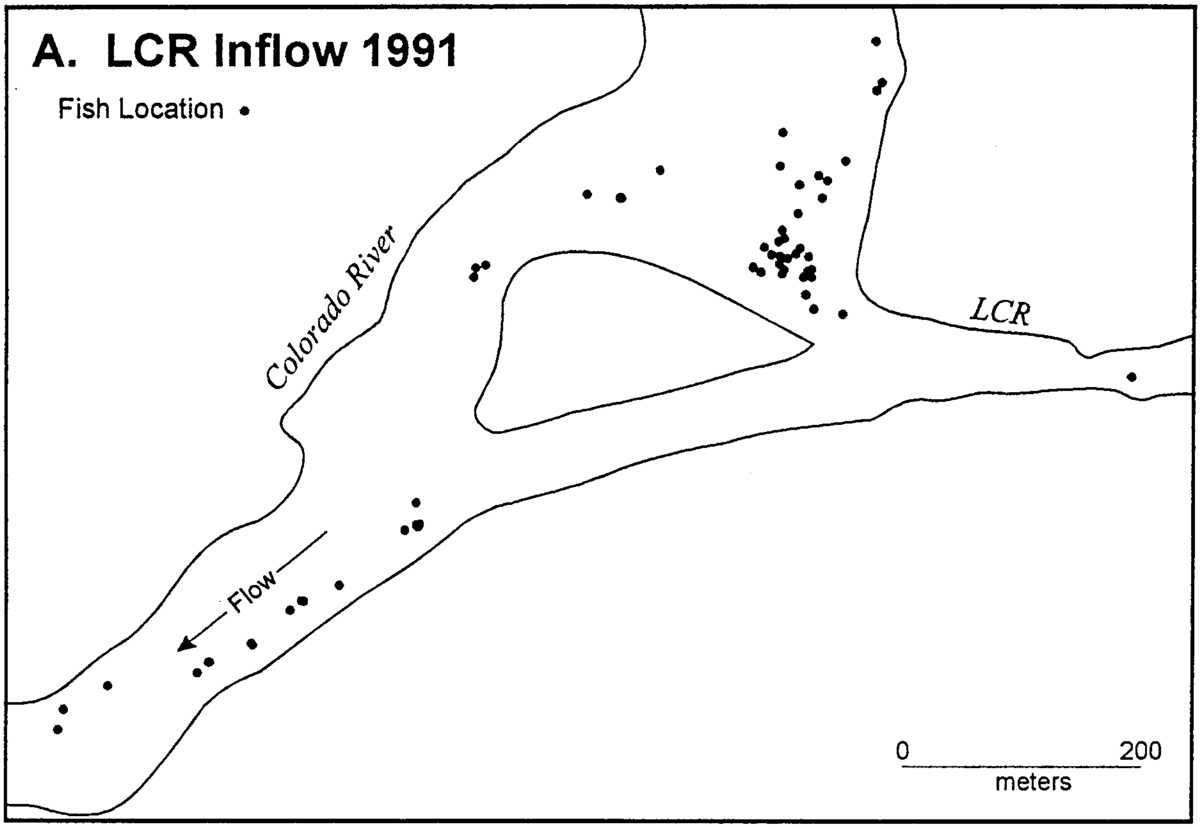
High flows from the LCR ameliorated effects of mainstem fluctuations on plume location. Despite mainstem flow fluctuations, the greater the flow from the LCR, the more stable the plume. For flows observed during this investigation, the LCR had a greater effect on plume location during interim flows in 1992 than during pre-interim flows in 1991. In April 1991, a flood in the LCR flow dominated the hydrology at the confluence, creating a stable plume configuration, and use of the plume by radio-tagged fish was highest in 1991. During 1992, reduced fluctuations in the mainstem resulted in a more stable plume configuration even during modest flow from the LCR, and use of the plume by radio-tagged fish was consistently high during all four spring months (i.e., February, March, April, May).

Use of the plume by radio-tagged fish appeared to be associated primarily with temperature, and perhaps turbidity and food availability. Temperatures in the plume were generally 1-5°C warmer than the mainstem depending on location. Higher temperatures along the plume may have attracted staging fish and possibly resulted in spawning attempts over suitable substrates. Cover provided by turbidity in the plume may also have served as an attractant to staging fish particularly when mainstem turbidities were low. Fish in the plume may have been utilizing the increased food availability from allocthonous materials from the LCR.

Subadult Habitat Use

Reach Selection

Principal factors that corresponded to the distribution of young were direction and distance from the main spawning source (LCR), shoreline type, presence of other humpback chub, and possibly presence of predators. Seventy percent of subadults (3,146 of 4,503) were captured within 9.5 km (5.9 mi) of the LCR (RM 60.0-65.9), the main spawning source, 28% (1,272) were captured in the next 17.5 km (10.9 mi) (RM 66.0-76.9), but only 1% (32) were captured in the 15.9 km (9.9 mi) section below Hance Rapid (RM 77.0-86.9) (Fig. 7-6). Ninety-three percent (4,185 of 4,503) of



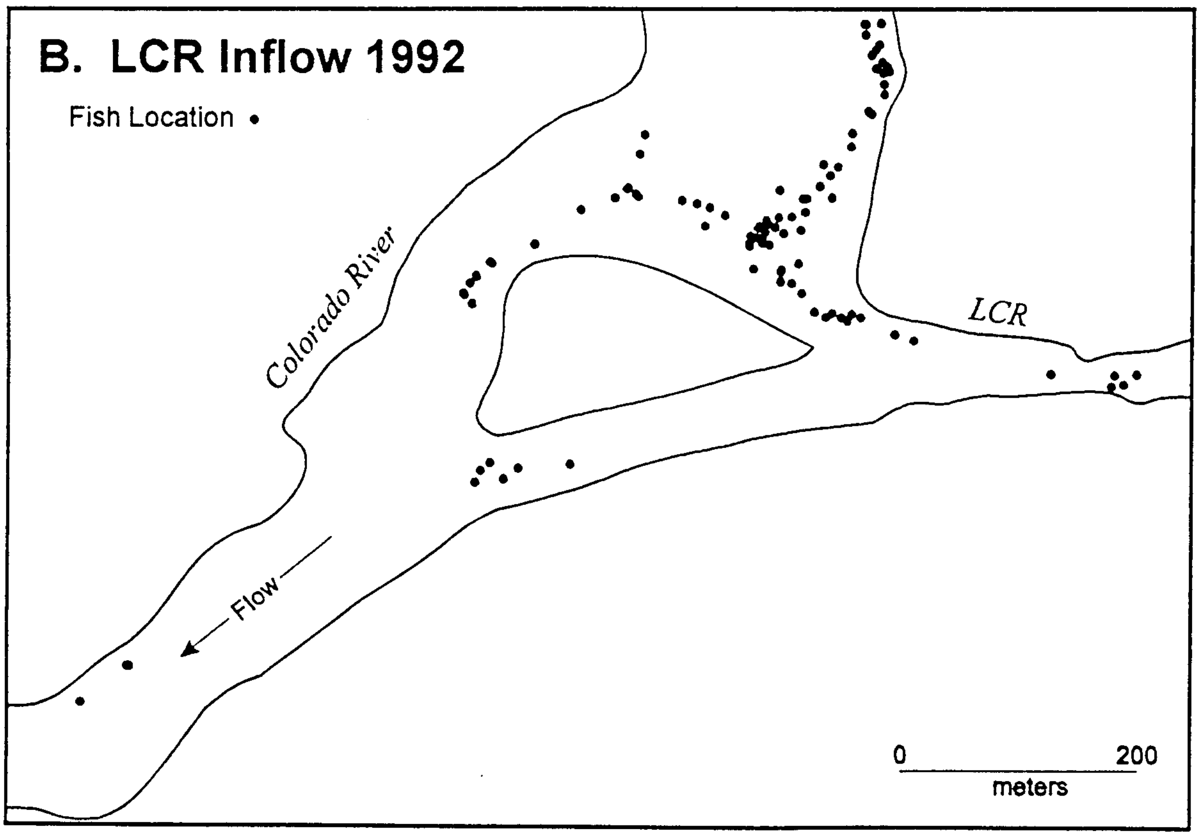


Fig. 7-13. Locations of radio-tagged adult humpback chub near the LCR inflow (RM 61.3) in February-May, 1991 (A) and 1992 (B). Points represent radio contact locations occupied for 15 min or more at various flows. Shoreline is at approximately 12,000 cfs.

subadults were found within the nine aggregations of humpback chub identified in the mainstem. The occurrence of subadults in aggregations was attributed to habitat availability and to social attraction for others of the same species, observed both in the wild (Valdez and Clemmer 1982) and in hatcheries (R. Hamman, USFWS, pers. comm.). While subadults lacked the affinity for recirculating eddies displayed by adults, subadults occurred in the greatest densities along complex shorelines, including vegetated banks, talus slopes, or debris fans.

Habitat Selection

The majority of subadults were caught along shorelines in a pattern of clumped distribution, indicating selection for particular shoreline types and attributes. This association was the basis for a special study to determine effects of fluctuating flows on subadult shoreline habitat and forced dispersal. The study was the subject of a Master's Thesis (Converse 1995) summarized in the following subsection. The study evaluated shoreline habitat use with fluctuating flows from Glen Canyon Dam, and related longitudinal distribution of subadults with channel geomorphology and shoreline types in the area of highest subadult densities, from the LCR inflow (RM 61.4) to Hance Rapid (RM 76.4).

Assuming the primary source of young humpback chub to this area was the LCR, a hypothetical distribution of young from the spawning outlet would show progressively fewer fish downstream. Instead, catch rates in 1.6-km (1 mi) strata in the 24-km (15 mi) area showed three distinct modes, consistent for all sample periods (Fig. 7-14). These modes corresponded to three geomorphic subreaches (1 = RM 61.4-65.4, 2 = RM 65.4-73.4, and 3 = RM 73.4-76.4), each with rock layers of different erosional resistance and distinct reach characteristic (Converse 1995).

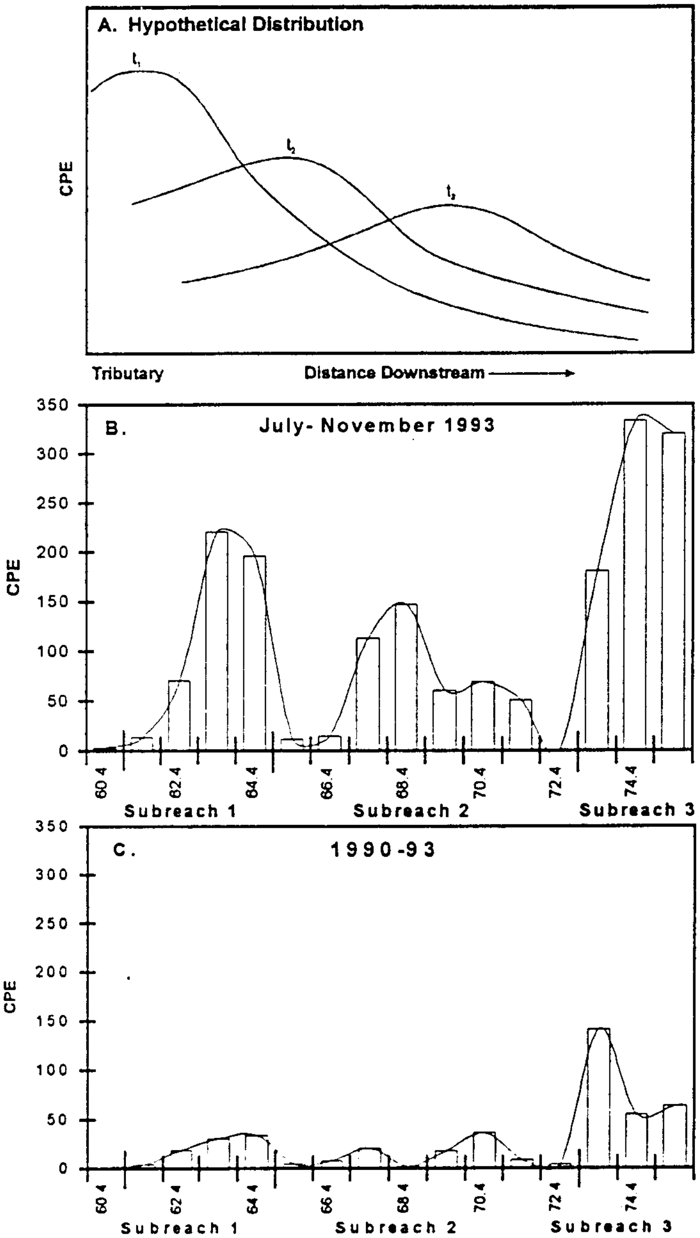


Fig. 7-14. Longitudinal distribution of subadult humpback chub, as hypothetical distribution from a spawning outlet (A), as geometric mean CPE (no. fish/10 hr) by 1-mile strata from the LCR (RM 61.3) to Hance Rapid (RM 76.5) for July-November 1993 (B),and November 1990-November 1993 (C). Hypothetical distribution in A relates hypothesized passive movement at those time periods (t_1, t_2, t_3) following a single movement from the LCR just prior to t_1.

This distribution of subadults was hypothesized to be the result of significant differences in availability of shore line types used differentially by the fish. The first part of this hypothesis was tested by comparing subadult catch rates for six shoreline types, independent of subreaches (Fig. 7-15). Subadult catch rates were significantly higher (ANOVA, P=0.05) in debris fans, talus, and vegetation than in the other three shoreline types. Catch rates along vegetated shorelines were significantly higher than in all other shoreline types, indicating selection for vegetated habitats.

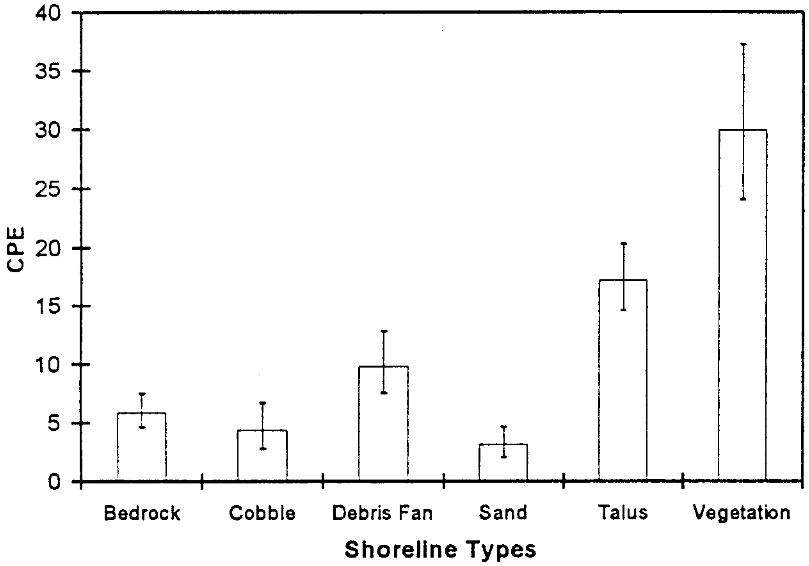


Fig. 7-15. Densities of subadult humpback chub from electroshocking catch rates for six shoreline types, November 1990-November 1993. Geometric mean catch per effort (CPE as no. fish/10 hr) are shown with standard errors.

Having identified a significant relationship between subadult densities and shoreline types, the second part of the hypothesis examined the distribution of the three selected shoreline types (i.e., vegetation, talus, debris fan) relative to fish densities. Channel width to depth ratios, shoreline types, and microhabitat parameters were compared with subadult catch rates for the three subreaches. Mean channel width to depth ratios of subreaches 1 (20) and 3 (17) were similar, while the mean ratio of subreach 2 (34) was substantially greater, corresponding to a wider channel in subreach 2 (mean = 400 m) than 1 (mean = 360 m) or 3 (mean = 340 m). Differences in channel width were attributed to local geology. The lithology of subreach 1 was dominated by relatively resistant Tapeats sandstone and the upper member of the Dox sandstone, while the subreach 2 shoreline consisted of more erodible members of Dox sandstone. Subreach 3 shoreline was dominated by a more resistant member of Dox sandstone, and Shinumo Quartzite and Hakatai shale between RM 75 and RM 76.4.

Local geology also influenced shoreline type. The more erosional shoreline of subreach 2 had a lower proportion of exposed bedrock and fewer sand beaches, but a substantially greater proportion of cobble bars. Subreaches 1 and 3 contained approximately the same percentage of bedrock shoreline, while shorelines in subreach 3 typically contained a high percentage of vegetation, i.e., root wads, inundated shoreline willows, tamarisk, or rushes. While some subreach differences were evident, patterns in distribution of shoreline types were not evident or consistent, because of the apparent variation within subreach. Possibly inreach variation was related to the width and styles of debris fans, i.e., size and height of fans determine shoreline irregularity.

This within subreach variation was evident from longitudinal distribution of shoreline types, which was not uniform between 1-mi strata (Fig. 7-16). Bedrock (primarily tapeats sandstone) was dominant in the upper two strata, while talus dominated the shoreline between RM 63.4 and RM 68.4. Alluvial fans and cobble bars were intermittent in dominance, while sand bars composed less than 30% of shoreline throughout the reaches, and vegetation increased for most downstream strata. Percentage of shoreline composed of debris fans, bedrock, and talus remained relatively constant between subreaches, while cobble bars and sand bars varied, and vegetation increased downstream. These analyses showed that shoreline types were regularly interspersed, and overall availability of the six shoreline types was approximately equal between subreaches.

Catch rates for all sample trips combined, as well as for three independent sample periods, were consistently highest in subreach 3 and lowest in subreach 2 (Fig. 7-17), suggesting that geomorphic reach had an effect on fish distribution, despite approximately even proportions of shoreline types. Two-way ANOVA revealed no significant differences in subadult CPE between subreaches (F=1.7, P=0.181), but did indicate significant differences among shoreline types (F=4.2, P=0.001) and interaction of reach and shoreline types (F=2.1, P=0.021). This analysis indicated that shoreline type was a more significant indicator of subadult density than reach, but that other factors within reaches also contributed to variability.

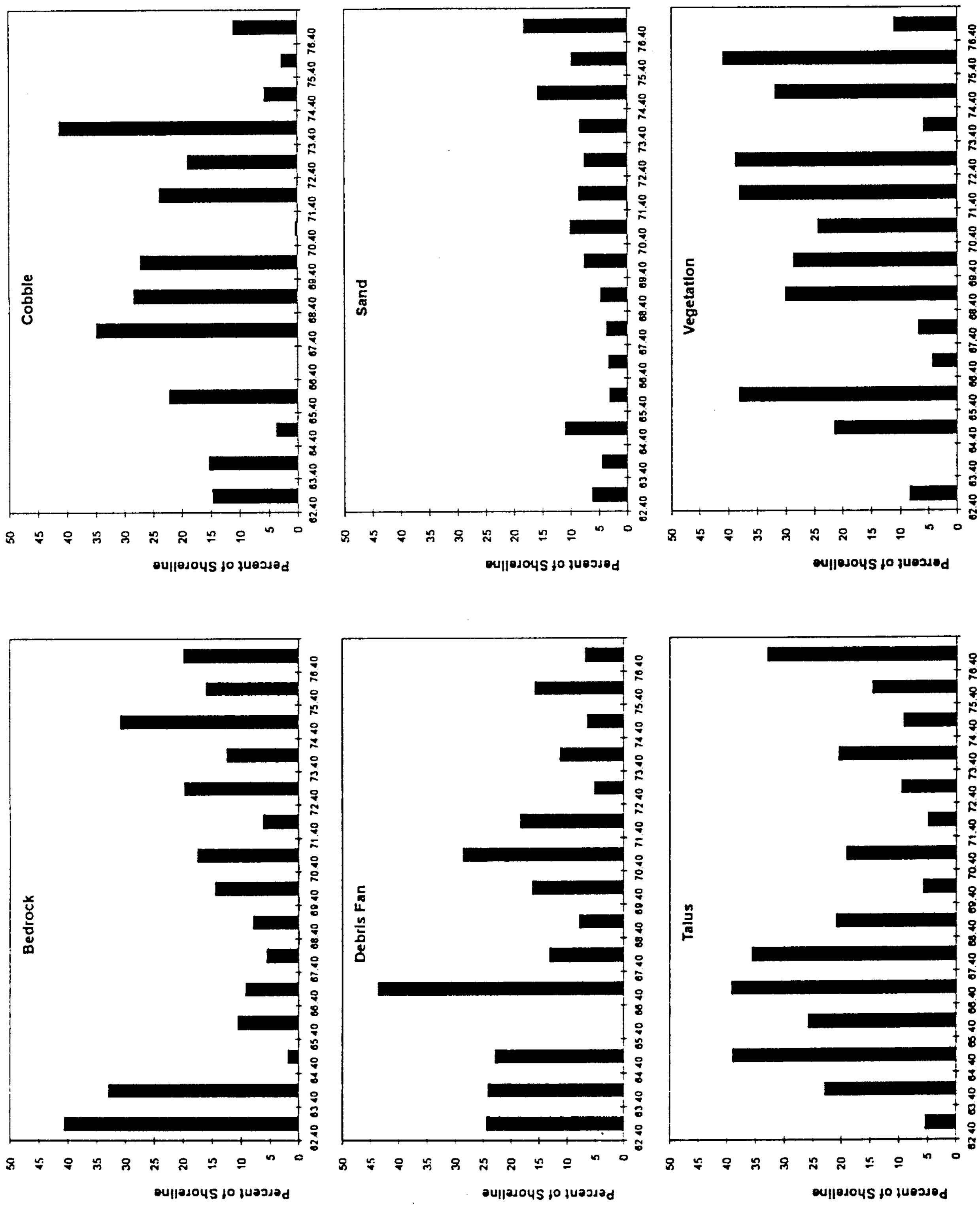


Fig. 7-16. Percentage of shoreline types by river mile from the LCR Inflow (RM 61.4) to Hance Rapid (RM 76.4)

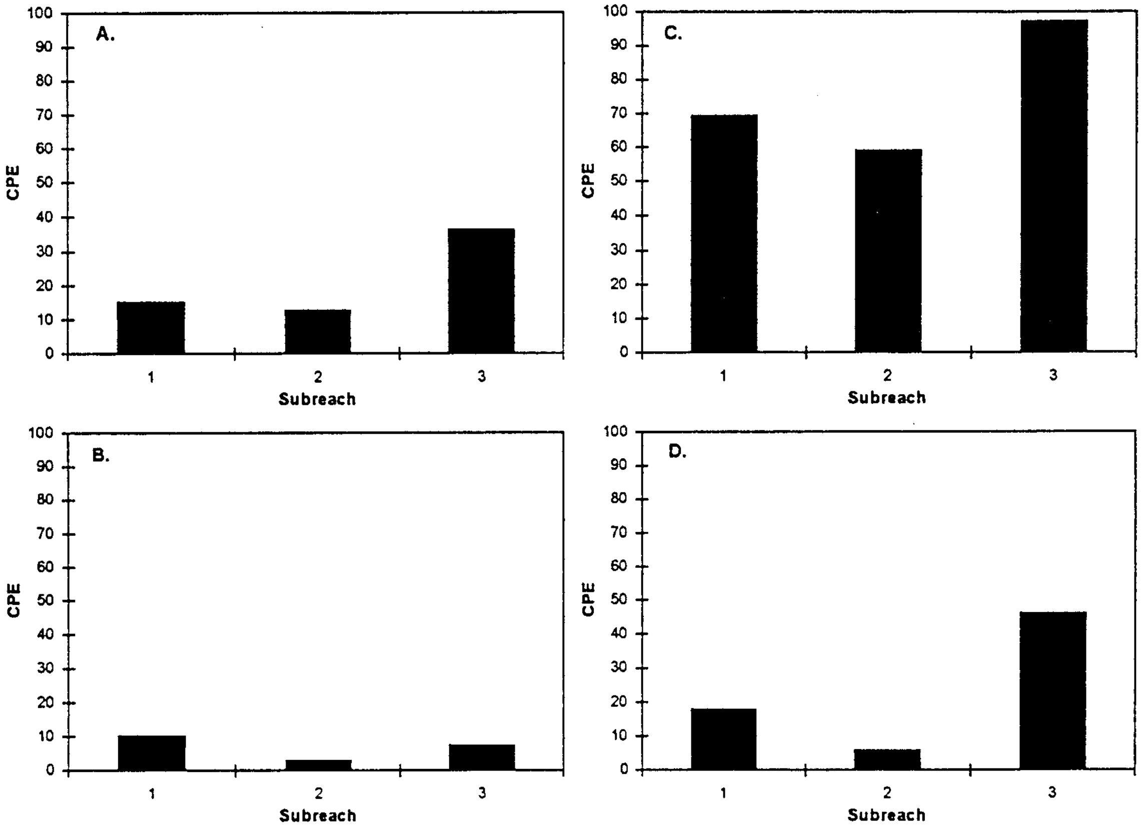


Fig. 7-17. Densities of subadult humpback chub from electroshocking catch rates (geometric mean, no. fish/10 hr), in subreaches 1, 2, 3, for all sample trips (A), November 1990-June 1993 (B), July-November 1993 (C), and July 1994 (D).

Attributes of shoreline habitats within each subreach were not satisfactorily quantified to account for the longitudinal distribution pattern of subadult humpback chub below the LCR inflow. The wider more open channel of subreach 2 contributed to shallower shorelines than those of subreach 1. It was hypothesized that although these attributes appeared favorable for young humpback chub, daily fluctuations from dam operations created greater instability in these more exposed shorelines than in shorelines of subreach 1. Thus, young fish forced from these shorelines by flow changes expended greater energy and were more exposed to predation when relocating suitable habitat.

This hypothesis was tested by comparing water depth and velocity of the different shoreline types with swimming ability of the fish. Mean depth was greater and velocity was higher at 2.5 m from shore in all shoreline types measured. Talus shorelines had the lowest average velocities (0.04-0.11 m/sec) of the six shorelines measured, and debris fans, sand beaches, and vegetated banks had similar velocity characteristics of about 0.07 to 0.20 m/sec (Fig. 7-18). Cobble bars and bedrock had the highest velocities, with ranges of 0.22-0.62 and 0.20-0.31 m/sec, respectively.

Minimum, average, and maximum velocity selected by YOY (range, 21-74 mm TL) humpback chub of 0.0, 0.06, and 0.30 m/sec, respectively (Valdez et al. 1990), suggested that all shoreline types were within maximum selected velocity. Similarly, selection by juveniles (range, 75-259 mm TL) of 0.0, 0.18, and 0.79 m/sec, respectively, also suggested suitable velocity conditions for this age category. However, Bulkley et al. (1982) reported that swimming ability of juvenile (range, 73-134 mm TL) humpback chub was positively and significantly related to temperature; others have reported the same phenomenon with other species, particularly juveniles (Brett 1967, Jones et al. 1974). While juvenile humpback chub (n=10) forced to swim at a velocity of 0.51 m/sec fatigued after an average of 85 min at 20°C, a similar group fatigued after an average of only 2 min at 14°C; a decrease of 6°C reduced time to fatigue by 98% (Bulkley et al. 1982).

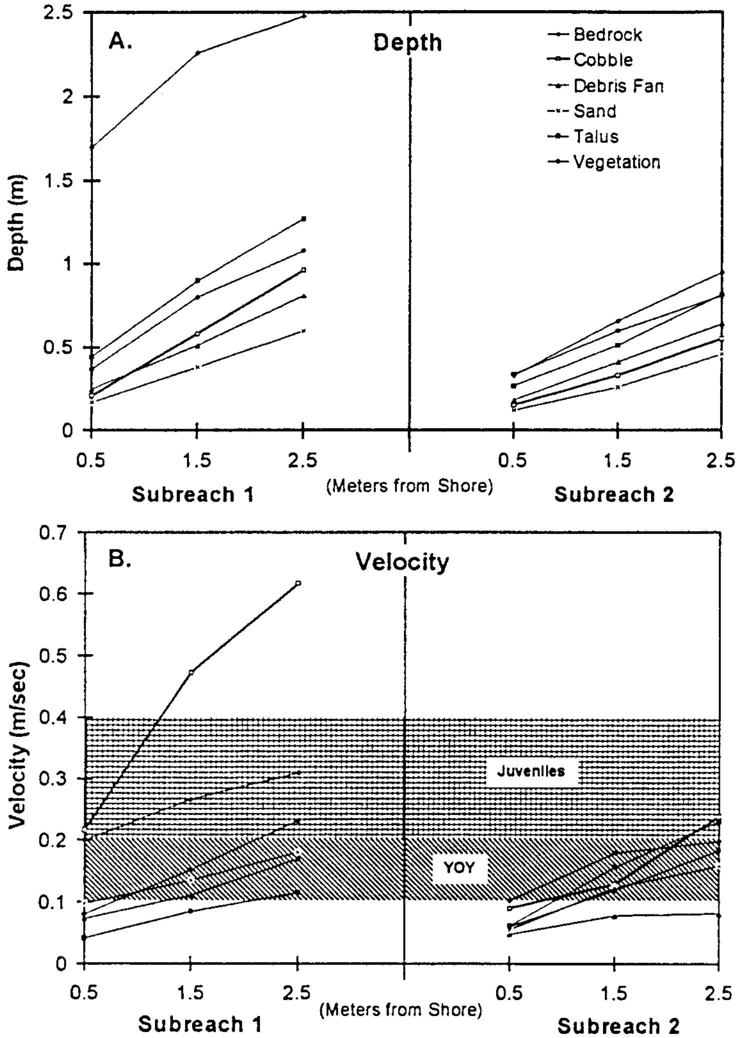


Fig. 7-18. Average depth (A) and velocity (B) at three distances from shore (0.5, 1.5, and 2.5 m) for six shoreline types in Subreach 1 (RM 61.4-65.4) and Subreach 2 (RM 65.4-73.4). The ranges in capable cruising speed for YOY and juveniles adjusted to 14°C are shaded (from Bulkley et al. 1982).

Temperature was also found to affect swimming performance of juveniles under different velocities, as indicated by burst speed (darting for a few seconds at 8-12 body lengths/sec), sustained speed (swimming for several minutes at 4-7 body lengths/sec), and cruising speed (swimming for hours at 2-4 body lengths/sec). From relationships of fish length to swimming speed and stamina (Bainbridge 1958), and information on temperature effects provided by Bulkley et al. (1982, and references therein), YOY humpback chub in the mainstem (range, 30-100 mm TL) at 14°C are capable of burst speed of 0.40-0.80 m/sec, sustained speed of 0.20-0.40 m/sec, and cruising speed of 0.10-0.20 m/sec (test fish were not temperature acclimated). By the same criteria, juveniles (range, 100-200 mm TL) are capable of burst speed of 0.80-1.60 m/sec, sustained speed of 0.40-0.80 m/sec, and cruising speed of 0.20-0.40 m/sec. 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 marginally suitable for juveniles. Talus, vegetated banks, debris fans, and sand bars provided suitable velocities for maintenance of position by these young fish, although sand bars lacked cover.

DISCUSSION

Reach Selection

The geomorphic framework of the river channel and shoreline, together with flow levels, were major determinants of fish habitat characteristics of the Colorado River in Grand Canyon. These characteristics are prominent in longitudinal transition through the canyon, as the river encounters successive rock layers of varying hardness. Softer, more erodible rocks allow the river to widen, while harder, more resistant strata form a narrower river channel. These erosional attributes, together with debris fan frequency, spacing, and size create distinct channel conditions and shoreline habitats related to hydraulic features of fish habitat that greatly influenced longitudinal distributional patterns and densities of adult and subadult chubs.

The patchy distribution of humpback chub in the Colorado River in Grand Canyon suggests that, under present conditions, suitable habitat is not distributed evenly throughout the canyon, nor is distribution a function of temperature where greater numbers of fish would be expected with higher downstream temperatures. Longitudinal distribution of nine aggregations suggests that reach selection is influenced by physical habitat, cold mainstem temperature, warm springs, tributary inflows, food production, and possibly predators. While the combination of these six factors greatly influences numbers and occurrence of fish, physical habitat, as affected by geomorphology, may be the most important factor affecting distribution.

Cold hypolimnetic releases from Glen Canyon Dam of 8-10°C have limited life history functions of the species in the mainstem, including reproduction and growth. Although juveniles and adults survive and grow, and their gonadal products mature in these cold temperatures (Kaeding and Zimmerman 1983), survival of eggs and larvae is low below 12°C (Hamman 1982, Marsh 1985). The presence of warmer water sources are important contributors to reach selection. Six of the nine aggregations reported during this study were associated with warm tributary inflows or springs. The largest aggregation at the LCR inflow was associated with a warm tributary suitable for spawning and adjoining mainstem habitat. The other five aggregations associated with springs and tributaries had small numbers of fish, indicating close association with small thermal sources, but a lack of associated spawning, nursery, and adult habitat. Small numbers of young fish near these springs or inflows indicate low reproductive success in the area or dispersal of young from the LCR population. The only conclusive evidence of mainstem reproduction was the discovery of about 100 post-larval humpback chub in a spring near RM 30.0 (Valdez and Masslich 1995, In Review) in July 1994. Survival of young produced in the Fence Fault springs may be low because of the lack of suitable shoreline habitat for nearly 20 km downstream.

The three aggregations not associated with thermal influence were in areas of characteristic channel geomorphology and habitat, particularly in more downstream subreaches (209-241 km [130-150 mi] below the dam), where summer temperatures were higher (maximum longitudinal warming was 1°C/51 km). These aggregations were in reaches characterized by large numbers of debris fans, expansion zones, and recirculating eddies. Minimal spawning opportunities likely limit the size of these small populations which may be comprised of individuals moving downstream from the LCRI aggregation. Low numbers of fish in seemingly suitable habitat further downstream (322-370 km [200-230 mi] below the dam) suggest a food shortage from low nutrient levels and low phototrophic production as a result of persistent sediment loads.

Habitat Use

Humpback chub in the mainstem used habitat with low-velocity, primarily shorelines as subadults and large eddy complexes as adults. Subadults made a transition in habitat use from nearshore to offshore habitats starting at about 1 year of age (approx. 100 mm TL) and ending at about 3 years of age (≥200 mm TL), or approximately at maturity. Disproportionate use of available habitat by mobile adults strongly suggests selection for specific low velocity habitat, particularly those associated with eddy complexes.

Catch rates of subadults indicated selection for shorelines of vegetation, talus, and debris fans. Talus shorelines had the lowest average velocities (range, 0.04-0.11 m/sec) of the six shorelines measured, and debris fans, sand beaches, and vegetated banks had similar velocity characteristics of about 0.07 to 0.20 m/sec. Cobble bars and bedrock had the highest velocities with ranges of 0.22-0.62 and 0.20-0.31 m/sec, respectively. Highest catch rates in habitats with lowest average velocities were consistent for vegetated banks, talus, and debris fans, but not sand bars, where low catch rates were attributed to lack of cover.

The vegetated shorelines used by subadults appear to serve as replacement cover, formerly provided by high turbidity and irregular shorelines with high food production. Vegetated shorelines were absent at pre-dam base flows. Today, these vegetated shorelines occur more often on sand beaches and irregular shoreline areas with abundant geomorphic control such as debris fans or shoreline irregularities that promote deposition and storage of sand.

Lack of widespread dispersal of humpback chub in all populations and consistently high fidelity for given reaches of river suggest that one key survival strategy for this species is the ability to remain in a relatively small area of river. Adults have adapted to these needs in swift riverine conditions by occupying low velocity regions that are supplied by drifting food. Subadults appear to have adapted the strategy of using low velocity shorelines and lack the propensity for long-distance drifting (commonly seen in larvae of Colorado squawfish, razorback sucker, and roundtail chub).

Although the mainstem habitat in Grand Canyon appears to fulfill these needs, in some reaches cold temperatures substantially reduce the swimming ability of young humpback chub and limit habitat suitability to those areas of lowest velocity. While shoreline velocities appear suitable for subadults at 20°C, colder temperatures may reduce swimming ability, and thus suitability of shoreline areas; i.e., laboratory tests showed a 98% decrease in time to fatigue of juveniles from 20°C to 14°C at sustained speed. These interactions may explain highest juvenile densities in shorelines with vegetation, talus, and debris fans, where velocity is buffered by an abundance of interstitial spaces with a minimum of change at different river stage. Literature suggests that colder water temperature does not affect swimming ability of adults as dramatically as that of subadults (Bainbridge 1958).

Although mean catch rates of subadults were significantly higher for shorelines with vegetation, talus, and debris fans, catches by subreach with approximately equal proportions of these shoreline types were significantly different. These differences indicate a subreach effect that could be related to shoreline instability resulting from fluctuating flows, greater exposure of young fish to predation, or to an interaction of the two effects. Lower subadult densities in the more alluvial subreaches were attributed to greater shoreline instability resulting from daily dam flow fluctuations that displaced the fish, increasing their energy expenditure and exposure to predation.

Adult humpback chub were found (88% captures, 77% radio contacts) in large, closely-spaced recirculating eddy complexes, frequently occupying internal vortices of low velocity (<0.5 m/sec) over sand platforms or in and near eddy return channels. We believe that recirculating zones entrained drifting food organisms and particles, and the low-velocity vortices provided energy-efficient feeding and resting sites. Local activity of radio-tagged adults suggests a "soaring" behavior to maintain position in vascilating currents. Fish were observed in clear water using their large falcate fins to glide through water currents in a manner analogous to raptors soaring on wind currents. Combined with the stabilizing effect of a nuchal hump and hydrodynamic body, this feeding mode was unique to adults as an energy-efficient strategy, adaptable to a range of flows.

Water depth (<5 m) and substrate (sand) within recirculating eddies and did not appear to be as critical in determining site selection as did velocity and food availability. Loss of radio contact for fish below 4 m depth precluded accurate determination of deep water habitats. Movement patterns and known selection for low-velocity zones suggest that daytime resting sites were near the bed shear zone or behind large instream structure such as boulders, often in deep water. Radiotelemetry data suggests that adults used shorelines primarily at night or in the daytime under high turbidity (>30 NTU), although individuals were sighted during daytime swimming casually near shore, often in the company of rainbow trout of similar size. Stomach analyses, radiotelemetry data, and direct observations indicate that fish may also feed on organisms trapped in sand riffles on reattachment bars and on bottom substrate and woody debris.

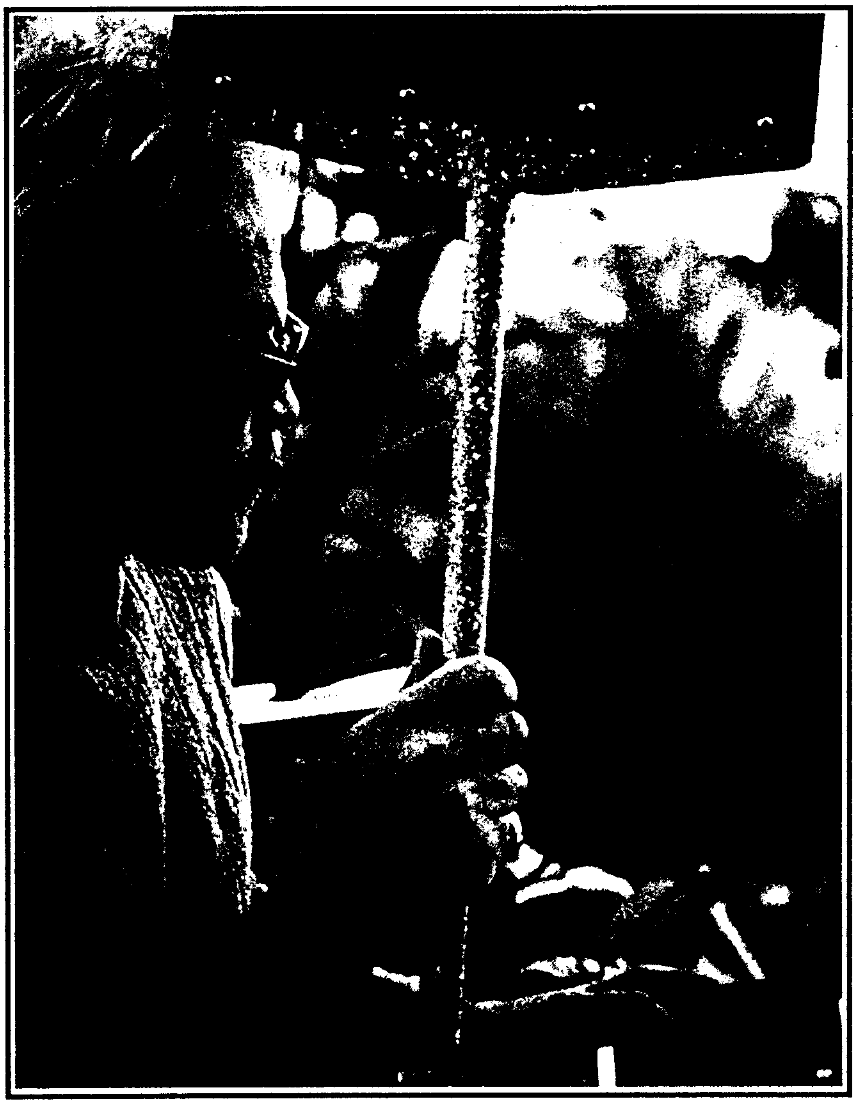
Adult humpback chub selected eddy complexes in all months, except for staging and spawning during February through April. Pre-spawning aggregations were identified in some eddies prior to migration and staging near the LCR inflow. Radio-tagged adults at the inflow typically remained behind boulders and in low-velocity interfaces during high turbidity and at night. Movement patterns inferred from radiotelemetry indicate that adults descended to adjacent deep (6-8 m) areas with irregular bed structure, similar to inferred daytime resting habitats used at other times of the year.

While detailed habitat measurements and ongoing monitoring of radio-tagged fish were largely restricted to the area of the LCR inflow, information obtained from habitat selection and distribution helps explain the present distribution of the species in other areas of Grand Canyon and perhaps other regions of the basin. Since large recirculating eddies are formed by debris fans with a frequency dependent on shoreline type and local geology, a relationship emerges between fish habitat and longitudinal lithology as a primary factor determining longitudinal fish distribution. While shoreline types selected by subadult humpback chub may be common throughout the canyon, recruitment of these fish to adults is dependent on the presence of large recirculating eddies for food, shelter, and associated proximate spawning sites. Suboptimal water temperatures have precluded use of most available mainstem spawning areas and confined the fish to spawn in warm tributaries or warm springs. The highest frequency of debris fans between Lees Ferry and Diamond Creek occurs from approximately Buck Farm Canyon (RM 41.0) to Hance Rapid (RM 76.5), which includes the identified range of the LCR inflow aggregation of humpback chub (RM 56.0-65.4). The fish were most abundant in the subreach from Malagosa Canyon (RM 57.6) to Lava Canyon (RM 65.4), where debris fans had a higher angle of repose (geologically determined) and were less subject to inundation by high flows (T. Melis, USGS, pers. comm.). Similar geomorphic reaches in Grand Canyon that are more limited in area and occur further downstream, include the area from Stephen Aisle (RM 117) to Specter Rapid (RM 129) which corresponded to the Stephen Aisle and Middle Granite Gorge aggregations of humpback chub; these are the only aggregations not associated with tributary inflows or warm springs.

The relationship of flow to habitat is determined by channel size and shape and appears to be unique for a given reach of river (Bisson et al. 1988). In the upper Colorado River, surface area of fish habitat in an alluvial region remained relatively constant at base and midrange flows, but dramatically changed in a threshold response to small increases at higher flows (Carter et al. 1985). Similarly, optimal flow range for maintenance of nursery backwaters for young Colorado squawfish in the Green River occurred at 1,100-1,800 cfs (Pucherelli and Clark 1989). Small changes in river volume may have a greater affect on fish habitat than large changes. These relationships appear unique for rivers and river regions and are important to understand in order to help ascertain responses by aquatic communities to mainstem facilities such as Glen Canyon Dam and to recommend flow management.

Movement

Chapter 8



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CHAPTER 8 - MOVEMENT

INTRODUCTION

Humpback chub move in response to spatial and temporal changes in life-history requirements and habitat attributes, and to daily requirements for food and cover. In this chapter, movements of humpback chub in the mainstem Colorado River were characterized as part of a description of life-history attributes for the species. This information was used to infer effects of Glen Canyon Dam operations on humpback chub in Grand Canyon by observing and comparing movement with time of day, season, flow magnitude, ramping rate, and turbidity.

Prior research on humpback chub in Grand Canyon has not dealt with movements in the mainstem. Movement of adults from the mainstem into the LCR for spawning was hypothesized (Kaeding and Zimmerman 1983, Angradi et al. 1992), and young fish had been captured in drift nets and pools at the mouth of the LCR (Valdez 1989, Angradi et al. 1992) indicating dispersal to the mainstem. Beyond this minimal information, exchange of individuals between the mainstem and LCR, and spatial and temporal movements in the mainstem had not been previously described.

Adult humpback chub in Black Rocks and Westwater Canyon in the Upper Colorado River Basin were reported to remain in specific sites year-around (Valdez and Clemmer 1982, Kaeding et al. 1990). Significant movements for spawning or between these two populations were not indicated by radiotelemetry or recapture of tagged individuals. This contrasts with sizable movements recorded for four other endemic species, Colorado squawfish, razorback sucker, (Archer and Tyus 1984, Valdez and Masslich 1989, Archer et al. 1985, McAda and Kaeding 1991), roundtail chub (Kaeding et al. 1990), and flannelmouth suckers (Chart and Bergerson 1992, Weiss 1993).

Flow variation from operation of Glen Canyon Dam and tributary floods is responsible for changes in water quality (See Chapter 4 - WATER QUALITY), arrangement of macrohabitats, and characteristics and distribution of microhabitats (See Chapter 7 - HABITAT). Fish movement in response to changes in these variables may cost energy and influence feeding efficiency and predator avoidance. Local movements were hypothesized to be affected by time-of-day, season, turbidity, flow regime, flow level, ramping rates, and magnitude of flow change. Movements related to these changes in the physical environment were assessed to infer effects of dam operations.

METHODS

Movement of adult humpback chub between the mainstem and LCR, and between aggregations were used to identify possible linkages between components or aggregations within the population in Grand Canyon. Also, patterns of long-range movement were used to identify spatial and seasonal movements. Understanding the dispersal of young chubs from the LCR is important in evaluating recruitment potential for a second population, and the existence of mainstem spawning sites.

Movement and activity of humpback chub in Grand Canyon were evaluated with radiotelemetry and recapture of uniquely-marked individuals. Radiotelemetry data were used to identify patterns of long-range and local movements, and to assess responses of chubs to changing flows from Glen Canyon Dam operations. Recapture locations of tagged fish were used to assess long-range movement of humpback chub within the mainstem, and between the mainstem and LCR.

Radiotelemetry

Adult humpback chub were monitored with radiotelemetry in two areas of the Colorado River in Grand Canyon. Seventy-five adults were equipped with radio transmitters and tracked in a 13.5-km (8.4 mi) subreach (RM 57.0-65.4) occupied by the LCR Inflow (LCRI) aggregation, from October 1990 through January 1993. Also, three adults were equipped and tracked in a 4.7-km (2.9-mi) subreach (RM 126.1-129.0) in the Middle Granite Gorge (MGG) aggregation, from February through August 1993 (Table 8-1, see Chapter 5 - DISTRIBUTION AND ABUNDANCE for description of aggregations). Of 75 radio-tagged humpback chub released into the LCRI aggregation, 69 were used to

Table 8-1. Effort expended for telemetry surveillance and observation of radio-tagged adult humpback chub of the LCRI and Middle Granite Gorge (MGG) aggregations.

Aggregation	Telemetry Effort	Day	Night	Total
	Surveillance			
LCRI	Boat Surveillance (mainstem)	285	175	460
	Foot Surveillance (LCR)	73	6	79
	Aerial Surveillance (helicopter)	6	0	6
MGG	Boat Surveillance (mainstem)	21	10	31
	Observations			
LCRI	Implant	-	-	75
	Locate	-	-	58
	2 hour observation	-	-	33
	24 hour observation	-	-	73
	Test flow observation	-	-	21
MGG	Implant	-	-	3
	2-hr Observation	-	-	5
	24-hr Observation	-	-	5

evaluate movement (Appendix H-1), and six were excluded from analysis because of loss of contact.

Receivers, Antennas, and Transmitters

Advanced Telemetry Systems (ATS) Model R2000 and Smith-Root (SR) Model SR-40 receivers were used to monitor humpback chub in Grand Canyon. The ATS Model R2000 was a programmable, sequential-scanning receiver used to monitor radio frequencies of 40 - 41 MHZ in omni-directional searching, directional triangulation, and remote stations. The Smith-Root Model SR-40 was a programmable, simultaneous-scanning receiver used exclusively for omni-directional searching. The two receivers were frequently used simultaneously to insure thorough searches for radio-tagged fish. Larsen-Kulrod omnidirectional whip antennas, Smith-Root loop antennas, and directional Proline low band yagi antennas (30-75 MHZ) were used for omni-directional searching, directional searching, and remote stations, respectively.

Five remote radiotelemetry stations were established at high points on the banks of the Colorado River in Grand Canyon to constantly monitor presence or movement of radio-tagged fish within predetermined receiving zones. Remote stations were equipped with an ATS Model R2000 receiver and a DCC-II Model R5041 datalogger. Two stations with directional yagi antennas were operated from February through August 1991 and 1992 near the LCR inflow to monitor movement of fish to and from the LCR (Fig. 8-1). One station was located about 50 m upstream of the LCR inflow (KLCR, RM 61.3) and one was located about 1,200 m downstream of the LCR inflow (KRSH, RM 62.1). A third station (KILR, RM 60.5), about 1,500 m above the inflow, was equipped with an omni-directional antenna to monitor occurrence of radio-tagged fish above the vertical signal extinction depth (4.5 m) between RM 60 and RM 61.3. This station was operated from August through December 1991, in January 1992, and August through November 1992. Two omni-directional stations, established in MGG, were operated from February through September 1993 (KBNE, RM 126.1), and from March through September 1993 (KMGG, RM 127.4).

Data from remote telemetry stations were downloaded at the beginning and end of each field trip on a portable computer, using Procomm Plus Version 1.1B (1987, 1988) communications software. Data were used to evaluate long-range and local movement and near-surface activity. Information collected from station KILR was also

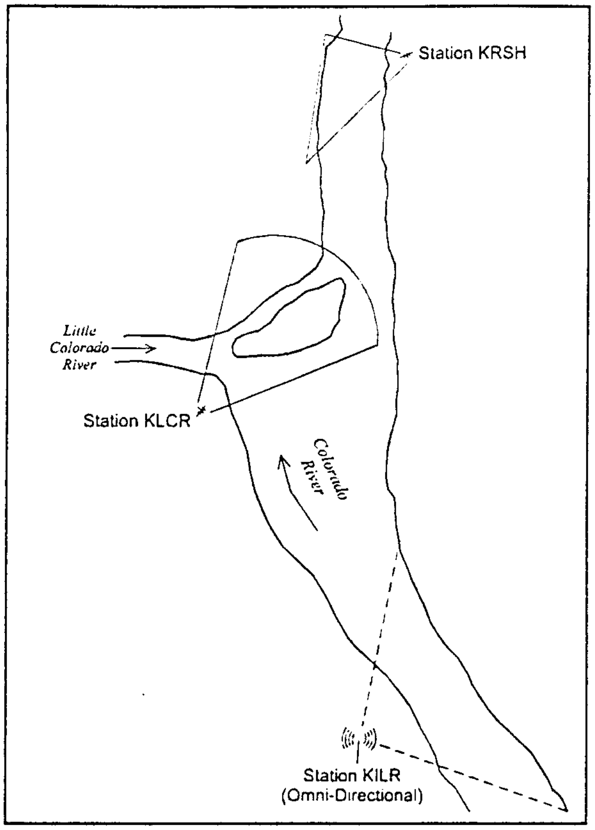


Fig. 8-1. Approximate receiving zones for three remote telemetry stations near the confluence of the Little Colorado River.

used to identify fish signatures (frequency/pulse combinations) in the area to expedite locating radio-tagged fish during field trips.

Two models of ATS radio transmitters were used, including the Model 1 BEI 10-18 (3.8 cm long, 1.3 cm diameter, 9-g, with a battery life expectancy of 50 days), and the Model 2 BEI 10-35 (6.0 cm long, 1.3 cm diameter, 11-g, with a battery life expectancy of 75-120 days). Both models were oblong, capsule-shaped transmitters, with an external cable antenna, 25 cm long and 1.2 mm diameter. Transmitters emitted signals in the frequency range of 40.600-40.740 MHZ, and were separated by 10 Hz intervals (i.e., 40.600, 40.610, 40.620, etc.) to distinguish individual transmitters. This 10-Hz separation yielded 15 different frequencies, which in combination with three pulse rates (40, 60, and 80 pulses/min), allowed for a total of 45 unique signatures to identify individual fish. A particular combination of frequency and pulse was reused following expiration of a transmitter.

Yard et al. (1990) reported from field tests in Grand Canyon that radio signals from 9-g external-antenna transmitters were received from a maximum water depth of 4.63 m, at a horizontal distance of 48 m in the Colorado River (10°C, 860 μS/cm), but only 0.91 m depth in the more saline LCR (23°C, 4,630 μS/cm). Radio signals from 11-g external-antenna transmitters, field tested for this investigation, were received at a maximum water depth of 4.5 m at 50 m distance (11°C, 950 μS/cm), and maximum horizontal reception for a transmitter 1 m deep was 1,200 m (11°C, 950 μS/cm).

Surgical Procedures

A surgical protocol was established from procedures developed for humpback chub (Valdez and Nilson 1982, Kaeding et al., 1990), Colorado squawfish, and razorback sucker (Tyus 1982, Valdez and Masslich 1989). Fish were selected for radio implant on the basis of weight, condition, and location of capture. Transmitter weight did not exceed 2% of fish weight (Bidgood 1980, Marty and Summerfelt 1990), such that 9-g transmitters were implanted in fish weighing 450-550 g, and 11-g transmitters were implanted in fish weighing more than 550 g. Care was taken to select fish that were healthy and showed no signs of stress. Females were not implanted from March through May to prevent stress to gravid fish, avoid resorption of eggs from handling, and eliminate the risk of transmitter expulsion from enlargening egg masses (Bidgood 1980, Marty and Summerfelt 1990).

Surgical implants were performed in an enclosed tent at a central processing station in a riverside camp. Two trained members of the B/W staff were designated with the primary responsibility of insuring that all aspects of surgical protocol were followed and monitored. Three people were involved with surgery--a surgeon, an assistant, and an anesthetist to administer anesthesia and monitor respiration of the fish. Fish were anesthetized with Finquel®, a brand of tricaine methanesulfonate (MS-222), at a concentration of 100 mg/L for 2-4 min, or until fish lost equilibrium but continued moderate opercular movement. During surgery, gills were bathed with anesthetic at 50 mg/L, as needed, and then with fresh water about half way through the surgery to expedite post-surgical recovery.

A primary incision, 2-3 cm long, was made either along the abdominal midline (linea alba) or lateral to the midline, between the pectoral and pelvic girdles (Fig. 8-2). A radio transmitter was inserted through the primary incision and positioned on the pelvic girdle with the antenna protruding through the abdominal wall, posterior to the pelvic girdle and anterior to the vent. The antenna was exerted through a small incision in the body wall with the aid of mosquito forceps or punched through the wall with a specially-designed sheathed needle. Primary incisions were closed with four absorbable Maxon® sutures (Gore Laboratories, Flagstaff, AZ) and antenna incisions were closed with two sutures. The trailing antenna extended to the end of the hypural plate of the fish and no fraying of the tail fin was noted. The incision area was washed with sterile saline before and after implant. Following surgery, fish were held in a live well until completely recovered--usually 10-30 min--then returned to the capture location for release.

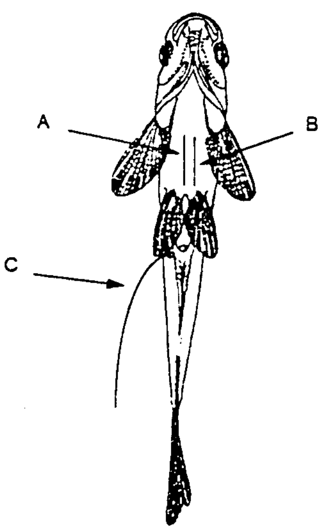


Fig. 8-2. Primary abdominal incision along the midline (A) or lateral to the midline (B), and external antennae (C) of implanted radio transmitter in adult humpback chub.

Recaptured radio-tagged fish were weighed, measured, and examined to document recovery or complications associated with radio implant procedures. Photographs were taken of the fish to document general condition, and of the primary incision and antenna exit to document rate and degree of healing or signs of necrosis. Protruding antennae from expired transmitters were cut approximately 1-2 cm from the body wall to remove frictional drag and reduce stress to the fish. Expired radio transmitters were not removed from the fish.

Surveillance

Surveillances were conducted to locate radio-tagged fish, and to characterize daily patterns of near surface activity and long-range movement. Each surveillance was conducted by 2-3 monitors from a slow moving research boat (See Box 2-1). Helicopter surveillances were conducted three times, but discontinued because fidelity by radio-tagged fish to specific sites precluded the need for widespread searches.

Signal locations were marked on 1:2400-scale aerial photographs, and a confidence level of high (<10 m), medium (10-100 m), or low (100-400 m) was assigned to each location as an index of observer confidence for location accuracy, i.e., triangulation was usually less accurate with low visibility at night, from signal distortion caused by proximity to canyon walls, during inclement weather, and with faint or inconsistent signals. Habitat type was recorded at each radio contact location, and water clarity was measured at least once daily with a Secchi disk. Beginning in March 1992, turbidity was measured daily as NTUs (See Chapter 4 - WATER QUALITY). Turbidity was classified as high (>30 NTU, ≤0.5 m Secchi disk) or low (≤30 NTU, >0.5 m Secchi disk).

Because surveillances were not continuous in time, displacement of individual radio-tagged fish between surveillances was used as an index to movement. "Net displacement" (expressed as distance upstream or downstream) was defined as longitudinal distance from release site to last contact site, while "gross displacement" was defined as cumulative distance between successive contact sites (Fig. 8-3). "Mean displacement" was computed as average distance between contact points. Only surveillance locations with confidence levels of high or medium were used in these analyses.

An index of near-surface activity was also determined from telemetry surveillance of radio-tagged adult humpback chub. Radio contacts above the signal extinction depth of approximately 4.5 m (Yard et al. 1990), were used to indicate near-

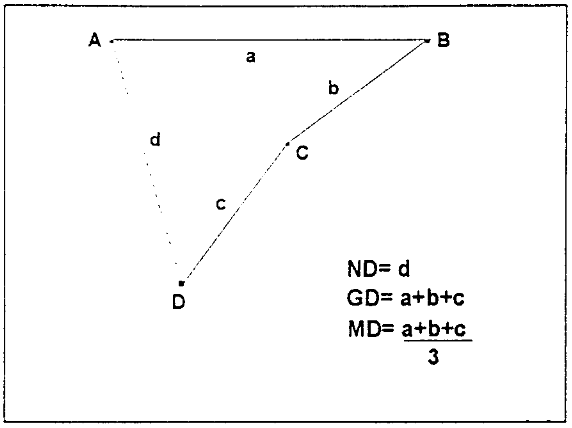


Fig. 8-3. Schematic to define movement of radio-tagged fish as net (ND), gross (GD), and mean (MD) displacement between contact sites. Contact sites are A, B, C, D and distance between consecutive contact sites are a, b, c. Distance d is linear distance from first to last contact.

surface activity. During surveillances, it was assumed that fish below this depth could not be contacted, but were within the area of radio coverage based on recent contacts. Average proportion of fish contacted (APFC) was used as an index of near-surface activity:

(Equation 8-1)

$$APFC = \sum(FC/FE)/n$$

where:

FC = number of radio-tagged fish contacted in the surveillance area (above 4.5 m),
FE = number of fish expected in the area based on release records, previous surveillances, and remote telemetry data, and
n = number of observation periods.

This index was used to compare fish activity by season, time-of-day, and turbidity level. Seasons were designated by 3-month periods (winter: December-February, spring: March-May, summer: June-August, fall: September-November), and spawning period (February-May) was distinguished from non-spawning period (June-January). The period of spawning was inferred from observed movement of radio-tagged fish into the LCR and was similar to that reported by Kaeding and Zimmerman (1983). Time-of-day was divided into day (sunrise to sunset) and night (sunset to sunrise), with sunrise and sunset calculated for a date in the middle of each monthly trip (Sun and Moon Events Worksheet, Heizer Software, Inc., Palo Alto, CA).

Remote Telemetry

Two directional remote telemetry stations (KRSH and KLCR) were deployed to evaluate use of the LCR confluence by identifying specific times in which radio-tagged fish were present (Fig. 8-1). Maximum antenna range was approximately 500 m, as determined from test tags at a 1-m depth and increasing distances upstream and downstream from each station. Upstream or downstream movement to and from these areas monitored was inferred from surveillance locations identified before and after contact by a station. Season and duration of use of the LCR inflow and specific timing of movements by adults between the mainstem and LCR were determined with this monitoring system.

Three omni-directional remote telemetry stations were deployed to assess near-surface activity of radio-tagged fish in the LCRI aggregation (KILR) and MGG aggregation (KBON and KMGG). Although antenna ranges were not established for KBON or KMGG, effective ranges were assumed to be similar to KILR, or about 1,500 m. To permit comparisons with telemetry surveillance data, only remote telemetry data collected during field trips (when turbidity data were collected) were analyzed.

Average proportion of radio contacts with remote telemetry (APFC) was also used as an index of near surface activity. The acronym 'APFC' was also used for this index of remote telemetry data because it was virtually the same as the previously described index of surveillance data. The difference was in the data types and specific analyses. Hence, the average proportion of radio contacts with remote telemetry was:

(Equation 8-2)

$$APFC = \sum(CO/CE)/n$$

where:

CO = number of radio contacts of single fish within a specified time period,
CE = number of possible contacts of same fish within the same time period, and
n = number of radio-tagged fish contacted.

Average APFC was related to turbidity and time-of-day, but seasonal effects could not be evaluated because KILR was operated only during non-spawning periods, and an appropriate spawning season could not be identified for the MGG aggregation. Diel periods and high-low turbidity levels were the same as defined for telemetry surveillance. For statistical analysis, values of APFC were arcsin transformed (Sokal and Rohlf 1987).

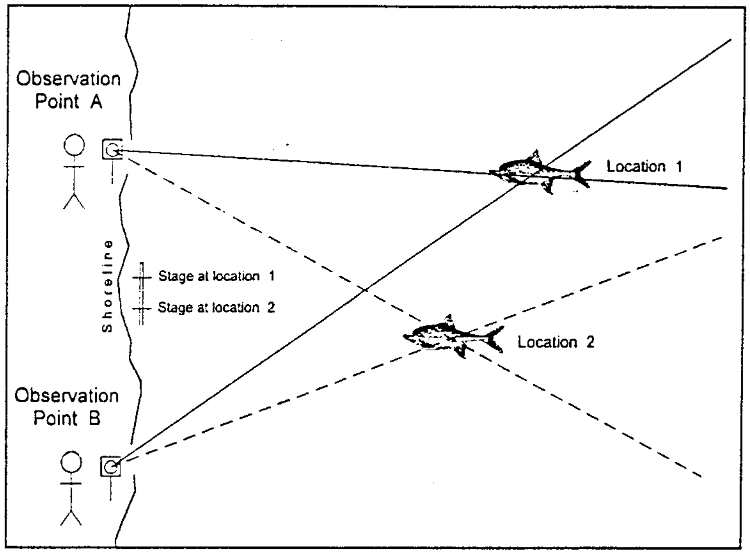


Fig. 8-4. Location of radio-tagged adult humpback chub by triangulation and relationship to river stage.

Observation

Individual radio-tagged adult humpback chub were observed for periods of 2 - 72 hr (mean=14.5 hr) to assess local movement by season, time-of-day, turbidity, flow, ramping rate, and magnitude of flow change. Local movement or activity was defined as movement within macrohabitats or habitat complexes and was represented two-dimensionally as horizontal movement. Sequential observations of radio-tagged fish were conducted with relocation attempts approximately every 0.25-2.0 hr.

Locations of radio-tagged fish under observation were determined by triangulation from the nearest riverbank (Fig. 8-4), and marked on mylar overlays on 1:2400-scale aerial photographs of the contact site. Start and end contact times, river stage, and macrohabitat (e.g., eddy, run, pool, riffle) were simultaneously recorded on data sheets. Locations and movements between subsequent locations were transferred to GIS as a record of movement for comparison with channel bathymetry, macrohabitat, substrate type, temperature, and flow (See Chapter 7 - HABITAT).

Observation periods were divided into blocks for analysis with each observation spanning time between consecutive radio-contact locations. A given observation period was usually composed of many blocks, each representing movement by fish under specific conditions. To standardize blocks for analysis, only those with elapsed time of 0.25-1.0 hr were used, and included 1,831 blocks (90% of total) with a total elapsed time of 962.8 hr. Detectable fish movement during a block was defined as movement of 5 m or more, the usual approximate observer triangulation error.

Proportion of movement (Pm) was used as an index of fish movement or activity:

(Equation 8-3)

$$P_m = BM/BT$$

where:

BM = number of blocks with movement, and
BT = total number of blocks.

Categories of season, time-of-day and turbidity were the same as described for surveillance. Mainstem flow was determined at 0.5-hr intervals from the Colorado River USGS gaging station (#9383100) just above the LCR confluence. Flow was classified as high (≥ 10,000 cfs) or low (<10,000 cfs), with the dividing point close to the mean flow during observations (mean=10,874 cfs; range, 4,778 - 29,916 cfs). On-site ramping rates were calculated from flow measurements using a flow routing model for start and end times of an observation period, and were classified as high (≥300 cfs/hr) or low (<300 cfs/hr). Ramping rates ranged from 0 to 8,833 cfs/hr and averaged 454 cfs/hr during observations. Periods of continuous 24-hr observations were used to evaluate fish movement under research and interim flow regimes, since flow changes typically cycled through 24 hr. Proportion of movement from 24-hr observations was also related to magnitude of flow change, i.e., the difference between high and low flows within a flow cycle.

Radiotelemetry in MGG was used primarily for tracking movement and dispersal of adults from a small disjunct aggregation of humpback chub prior to the expected spawning period of April and May. The area was surveyed and radio-tagged fish were monitored in the same manner as described for the LCR inflow area.

Recaptures of Marked Fish

Displacement of PIT-tagged humpback chub recaptured by electrofishing, netting, and seining were also used to evaluate long-distance movement. Sampling efforts used to capture these fish are described in Chapter 5 - DISTRIBUTION AND ABUNDANCE. Net movement was defined as displacement between successive captures. Humpback chub recaptured with Carlin dangler tags or Floy tags, marked during previous studies, were also used to assess long-distance movement, although original capture information was not available for all fish.

A joint marking program was conducted by ASU in the LCR, and B/W and AGF in the mainstem to determine dispersal of subadult (<150 mm TL) humpback chub. In 1992-93, B/W marked 1,042 subadults in the mainstem and AGF marked 186 according to the four fin-punch combinations (codes) described in Chapter 2-STUDY DESIGN. Also, fish marked with fin clips or punches by ASU, beginning in January 1992, were used to evaluate movement of juveniles from the LCR into the mainstem. Fin-clip combinations were associated with reaches in the LCR where fish were originally marked.

RESULTS

Categories of long-range and local movement were identified and described for humpback chub in this study. Long-range movement was usually between large habitat hydraulic units and associated with spawning migrations or dispersal of subadults. Local movement was related to daily activities of feeding, resting, or seeking cover in response to changes in the riverine environment.

Long-range Movement

Long-range movement of humpback chub was evaluated for the mainstem Colorado River, between the mainstem and LCR, and between aggregations. Extent of movement was described, and the timing of movement was related to flow regime, season, and age category of fish.

Mainstem Movement

Mean net displacement of 69 radio-tagged adult humpback chub in the LCRI aggregation (Fig. 8-5,

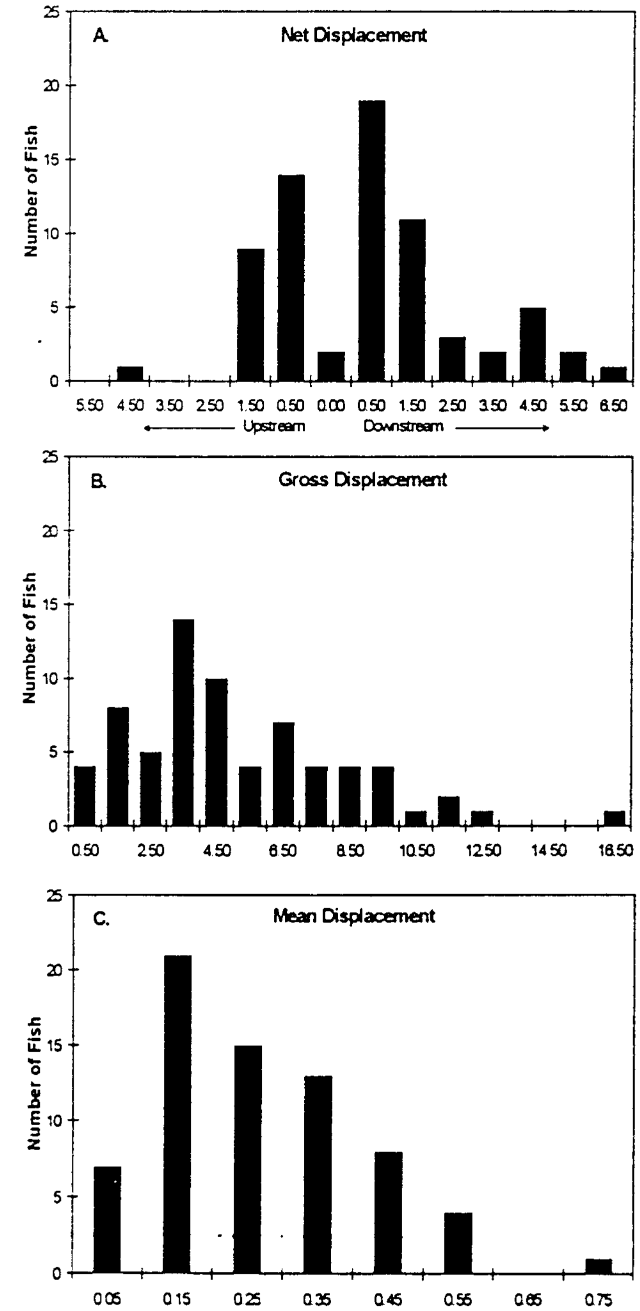


Fig. 8-5. Net (A), gross (B), and mean (C) displacement of 69 radio-tagged adult humpback chub, November 1990-November 1992.

Appendix H-1) was 1.49 km (range, 0.00-6.11 km). Mean gross displacement was 5.13 km (range, 0.32-16.93 km), and mean displacement between contacts was 0.26 km. Time between release date and last contact ranged from 30 to 170 days (mean = 93 days). All observed movements were within a 13.5-km subreach of the mainstem (RM 57.0-65.4) and the lower 5 km of the LCR, although radiotelemetry in the LCR was limited by high conductivity water that interfered with signal transmission. Net (t-test, t=0.341, P=0.734, df=63) and gross (t-test, t=0.073, P=0.942, df=63) movements were not significantly different between males and females.

Movement of three radio-tagged adult humpback chub in MGG was similar to that of fish in the LCRI aggregation, with mean net and gross displacements of 1.88 and 3.38 km, respectively (Appendix H-1). Net displacement of MGG fish was not significantly different from LCRI fish (t-test, t=0.38, P=0.704, df=70), and mean displacement of MGG fish of 0.20 km was not significantly different from that of mean displacement of LCRI fish (t-test, t=0.76, P=0.450, df=70). Movement by MGG fish was confined to a 4-km reach (RM 126.1-128.5), the approximate boundaries defined for this aggregation (See Chapter 5 - DISTRIBUTION AND ABUNDANCE).

Strong spatial fidelity was exhibited by radio-tagged adult humpback chub in the mainstem. Of 69 fish radio tracked in the LCRI aggregation, net displacement of 35 (51%) was less than 1 km, and net displacement of 58 (84%) was less than 3 km. Despite strong fidelity, adults moved considerably between eddy complexes before and after spawning, as illustrated by movements of two radio-tagged adults during portions of 3 months (Fig. 8-6). Fish spent one to several days within an area before moving and tended to reoccupy specific sites.

Similar movement was reported for PIT-tagged humpback chub (≥150 mm TL) in the mainstem.

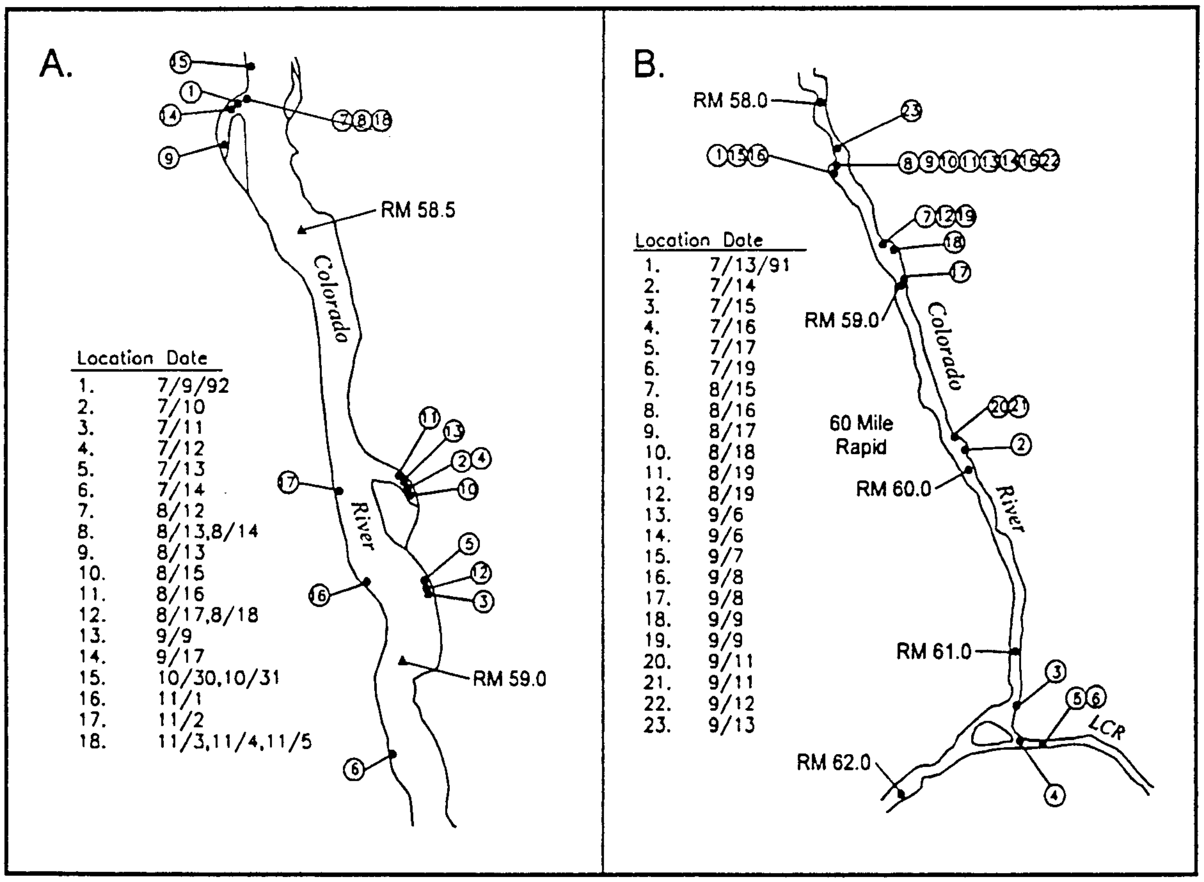


Fig. 8-6. Locations of two radio-tagged adult humpback chub determined from telemetry surveillance in Region I, July 9-November 5, 1992 (A) and July 13-September 13, 1991 (B). RM = river mile.

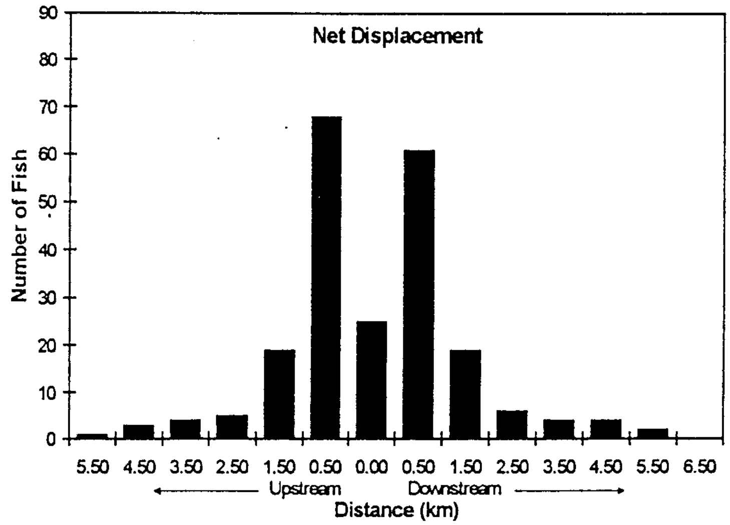


Fig. 8-7. Net upstream and downstream displacement of 188 PIT-tagged humpback chub (225 movements) between consecutive captures separated by ≥20 days within the LCR Inflow aggregation, October 1990-November 1993.

Net displacement between consecutive captures of 238 marked fish (285 movements) averaged 1.64 km (range, 0.0-99.8 km). To eliminate the potential for bias from fish caught a few hours to a few days apart, net displacement was calculated for consecutive captures separated by at least 20 days (188 fish, 225 movements), and resulted in a slightly higher net displacement of 1.94 km (range, 0.0-99.8 km). Net displacement for 185 PIT-tagged fish (222 movements) was 0.99 km (range, 0.0-8.9 km) when three displacements over 9 km (movements between aggregations) were omitted. Displacements were equally divided between upstream and downstream movements, with 85% of net displacements less than 2 km (Fig. 8-7). Mean net displacements were not significantly different for captures separated by 20-120, 121-365, and 366-1,065 days (ANOVA, F=0.80, P=0.45, df=2, 291); means were 0.85 km (range, 0.0-8.9 km), 1.10 km (range, 0.0-4.8 km) and 1.02 km (range, 0.0-5.6 km) for the three respective periods. Net displacement in the mainstem was not significantly different (t-test, t=1.66, P=0.098, df=192) between males (mean=0.89 km, range, 0.0-4.9 km) and females (mean=1.22 km, range, 0.0-8.9 km), and between 238 PIT-tagged fish (285 movements) and 69 radio-tagged fish (t-test, t=0.17, P=0.867, df=352).

Estimated net displacement was greater for PIT-tagged humpback chub in the LCRI aggregation than in the MGG aggregation. Net displacement of 1.11 km (range, 0.0-8.9 km) in the LCRI aggregation for 166 movements was significantly greater (t-test, t=3.11, P=0.0022, df=209) than 0.64 km (range, 0.0-2.8 km) for 45 movements in MGG. Differences in displacement between aggregations was possibly related to subreach size of respective areas occupied by the two aggregations (13.5 km and 4.7 km), and to spawning-related movement by the LCRI aggregation.

Movement between nine aggregations of humpback chub (See Chapter 5 - DISTRIBUTION AND ABUNDANCE) was rare; only 7 of 356 (2.0%) PIT-tagged fish recaptured in the mainstem (total fish PIT-tagged=1,572) moved between aggregations (Fig. 8-8). Four of these fish (1 adult, 3 subadult) moved downstream from the LCRI aggregation to aggregation 3 (RM 65.7 to RM 76.3), suggesting some downstream dispersal from the LCR population center. Two other fish (1 adult, 1 subadult) made extensive downstream movements from the LCRI aggregation, including one with gross displacement of 99.8 km to the MGG aggregation (RM 127.0). This radio-tagged adult exhibited normal behavior during 57 days of tracking near the LCR inflow, but possibly moved as a result of delayed effects of radio-implant. Another fish (subadult) was recaptured 87.6 km

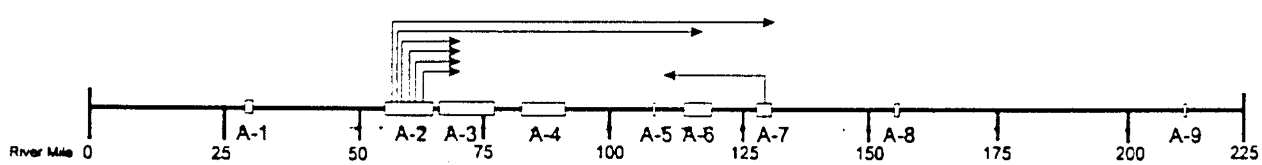


Fig. 8-8. Movement of seven PIT-tagged humpback chub between mainstem Colorado River humpback chub aggregations (A-1 through A-9).

downstream in a movement from the LCRI aggregation to aggregation 6 (RM 119.1). Upstream movement between aggregations was observed for only one fish (subadult) that moved 30.7 km, from RM 127.6 (MGG aggregation) to RM 108.5 (aggregation 5).

A total of 92 humpback chub, originally marked with Carlin dangler tags or Floy tags in the LCR by other investigators, were recaptured in the mainstem. Original tagging records for 50 of these fish showed that all were tagged in the LCR by AGF, between the confluence (RK 0.0) and RK 9.0 during 1980-90. Of these, 49 (98%) were recaptured in the mainstem, between RM 57.0 (6 km above LCR) and RM 65.0 (5 km below LCR), in the period October 1990 to November 1993 (Fig. 8-9); one fish was recaptured 11 km below the LCR confluence (RM 68.1). Average distance between original capture and recapture was 4.29 km, (range, 0.1-14.4 km). Average elapsed time between captures was 8.2 years (i.e., 2,990 days, range, 304-4,496 days). Humpback chub recaptured with Floy and Carlin tags were dispersed approximately evenly above and below the LCR (23 fish upstream, 22 downstream, and 5 at the confluence).

Movement between Mainstem and LCR

Extent of Movement. The greatest long-range movement by radio-tagged adult humpback chub was related to spawning activity in the LCR. Of 69 fish monitored in the mainstem (RM 57-65.4), 35 (51%) were contacted in the LCR or LCR inflow (RM 61.3-61.4) at least once. Nearly all of the fish monitored in the mainstem during spawning season were contacted in the LCR inflow. Timing of these movements corresponded with spawning activity in the LCR, but high conductivity in the LCR precluded adequate relocation and tracking of radio-tagged fish in that tributary (See next section--

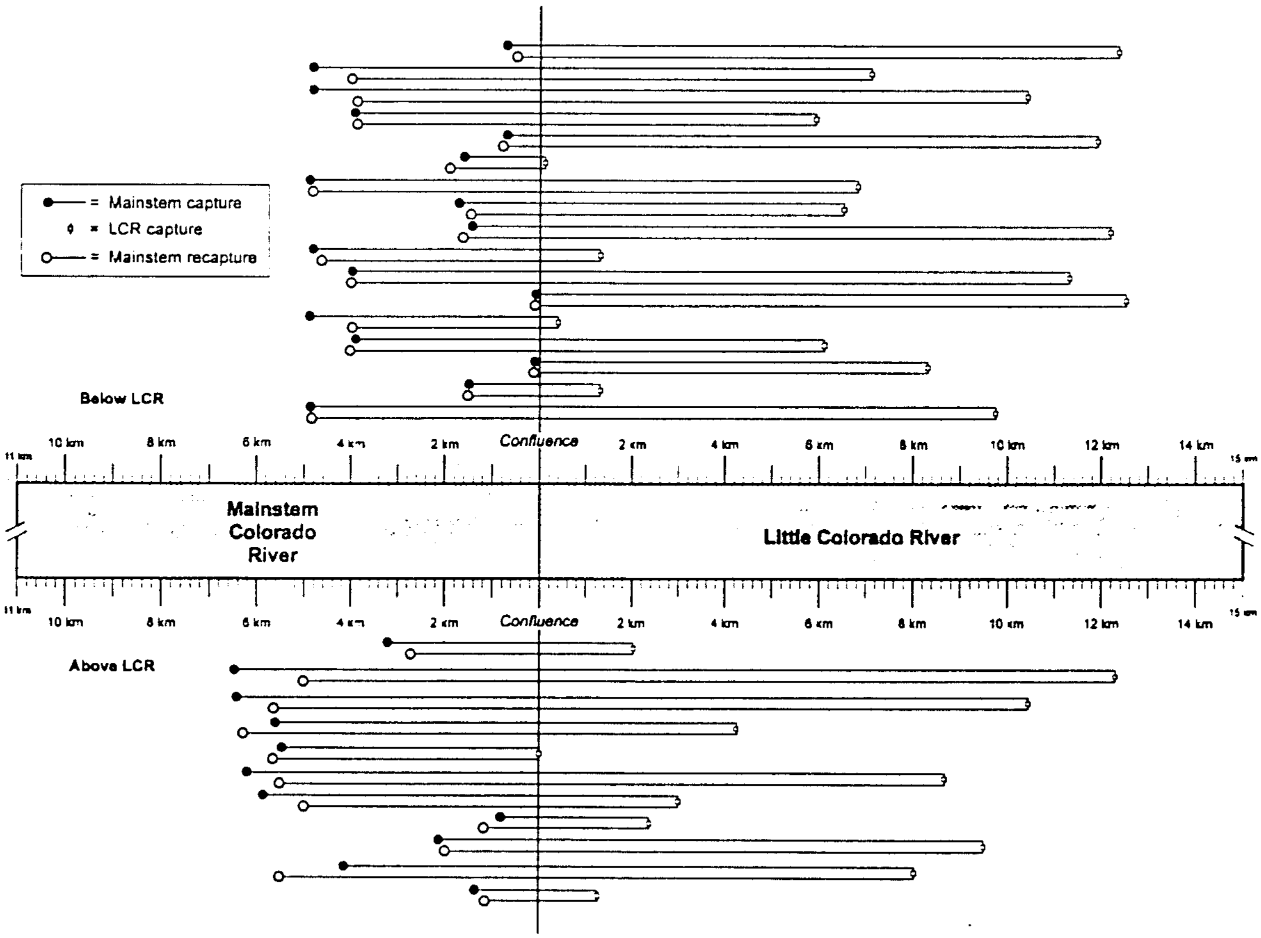


Fig. 8-9. Net displacement of 50 Floy- and Carlin-tagged humpback chub originally tagged by AGF in the LCR 1980-90 and recaptured by B/W in the mainstem, October 1990-November 1993.

Timing of Movement). Despite movements to the LCR, these fish demonstrated strong spatial fidelity for specific river locations; 70% of spawning migrants returned to within 2 km of pre-migration sites.

Net displacement of PIT-tagged fish, sampled year-around from October 1990 through November 1993, between the mainstem and LCR also demonstrated substantial movement between the two systems. PIT-tagged humpback chub captured and released in the mainstem were recaptured by ASU, AGF, and the Service up to 14.9 km into the LCR, with 44% more than 3 km, and 36% more than 5 km from the mouth (Fig. 8-10). Mean net displacement of 419 PIT-tagged chub (431 movements) from the mainstem to LCR was 6.4 km (range, 0.10-20.0 km), while mean displacement in the mainstem was 2.0 km (range, 0.0-6.5 km) and 4.4 km (range, 0.0-14.6 km) in the LCR. Mean net displacement from the mainstem to LCR of fish for which gender was determined (n=372) was not significantly different between males (6.5 km) and females (5.8 km) (t-test, t=1.41, P=0.075, df=370). Gender differences in timing of staging and movement into the LCR were not identified; i.e., males and females seemed to stage and ascend the LCR simultaneously.

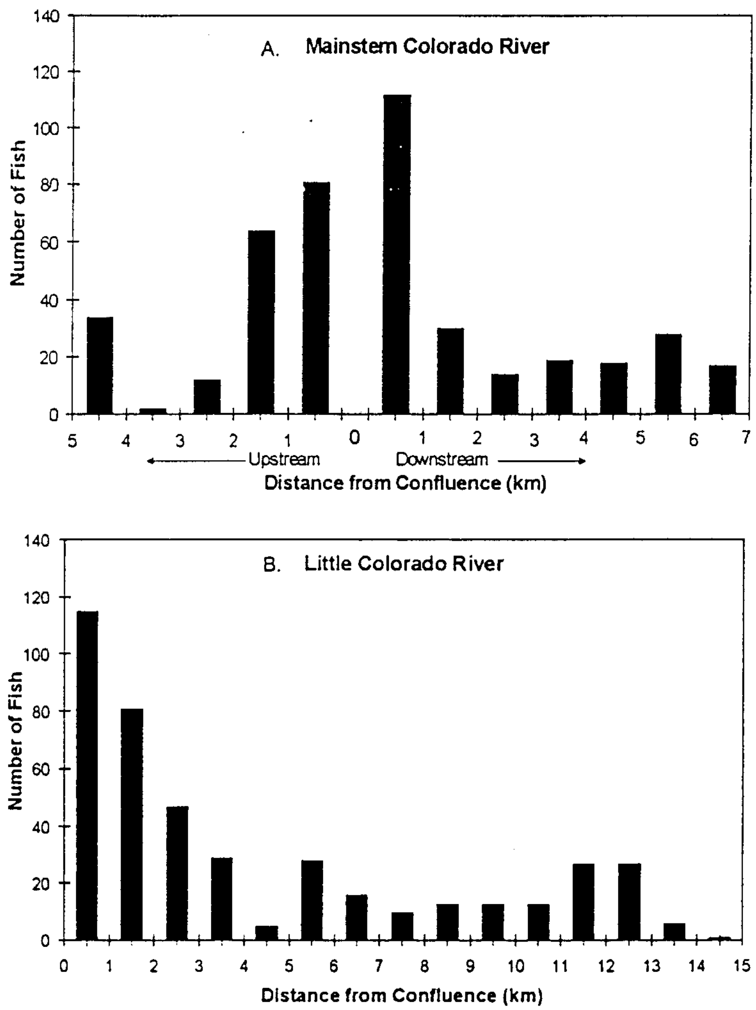


Fig. 8-10. Capture locations of 419 PIT-tagged humpback chub (431 movements) in mainstem Colorado River (A) and recapture locations in the LCR (B), October 1990-November 1993.

Net displacements of PIT-tagged fish captured in the LCR and recaptured in the mainstem were similar to the previous analysis (Fig. 8-11). Fish captured between RK 0.0 and RK 14.9 in the LCR were recaptured in the mainstem up to 4.9 km upstream (RM 58.2) and 24.2 km downstream of the confluence (RM 76.4); 24% were recaptured more than 3 km from the confluence, but only 8% were more than 5 km (RM 58.2-64.4). Mean net displacement of 401 fish (415 movements) from the LCR to the mainstem was 7.2 km (range, 0.08-34.1 km), with mean net displacement of 5.3 km (range, 0.0-14.9 km) in the LCR and 1.9 km (range, 0.0-24.2 km) in the mainstem. Mean net displacement from the LCR to the mainstem was not significantly different between males (7.4 km) and females (7.2 km) (t-test, t=0.30, P=0.76, df=357). Mean net displacements were significantly greater (t-test, t=9.96, P<0.00005, df=1,129) for all movements of PIT-tagged fish (820 fish) between the mainstem and LCR (6.72 km) than for all movements within the mainstem (mean = 1.64 km).

Over 99% of PIT-tagged fish captured in both systems remained within a 13.5-km subreach of the mainstem, i.e., 6.9 km upstream to 6.6 km downstream of the LCR confluence (Fig. 8-10 A, Fig. 8-11 B). Based on these recaptured fish, the home range of the mainstem component of the LCR population of humpback chub was defined as approximately 28.4 km, 13.5 km in the mainstem and 14.9 km in the LCR. Although the majority of

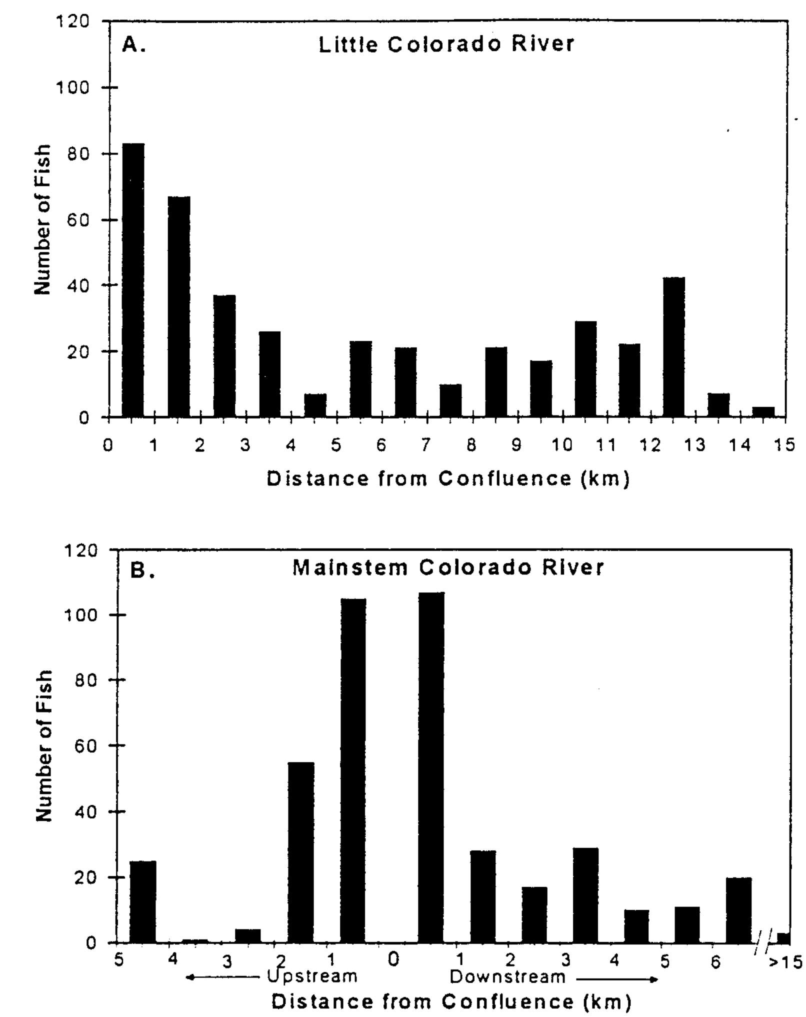


Fig. 8-11. Capture locations of 401 PIT-tagged humpback chub (415 movements) in the LCR (A) and recapture locations in mainstem Colorado River (B), October 1990-November 1993.

fish remained within this range, three (2 subadults, 1 adult) moved further downstream including one that moved 34.1 km in 359 days between recaptures (from RK 9.8 in the LCR to RM 76.4 in the mainstem). The greatest cumulative displacement for an individual fish was entirely within the home range, i.e., 54.9 km for an adult recaptured six times in 626 days, twice moving between RK 10.0 in the LCR and RM 58.3 in the mainstem. Both movements were during spawning periods, and in both cases the fish returned to the original mainstem location.

Fidelity of PIT-tagged humpback chub to specific locales or reaches in the mainstem was similar to that observed for radio-tagged fish. Of 60 PIT-tagged fish consecutively captured in the mainstem, LCR, and again in the mainstem, 54 (90%) returned to within 2 km of specific mainstem locales; i.e., 31 (52%) were recaptured within 0.5 km and 10 (17%) within 0.1 km (Fig. 8-12).

PIT-tagged humpback chub (≥ 150 mm TL) moving between the mainstem and LCR for presumed spawning tended to be large individuals. Most individuals (81%) caught in both systems were 300 mm TL or greater (Fig. 8-13).

Timing of Movement. Timing of movements to and from the LCR was evaluated using remote and surveillance telemetry equipment, and from data of recaptured PIT-tagged fish. Average number of radio contacts per day by the remote telemetry station near the LCR inflow (KLCR) were highest from February through April (Fig. 8-14), indicating movements between the mainstem and LCR were not direct, but preceded by a period of staging near the inflow. In 1991 and 1992, 39 fish were continuously contacted an average of 17.1 days (range, 1-64 days) by KLCR (Appendix H-2), a rough estimate of time spent by radio-tagged fish in the confluence staging area. Lowest contact rates from May to August may correspond to rapid post-spawning dispersal of adults to the mainstem.

Movements of 35 radio-tagged humpback chub from the mainstem to the LCR inflow and into the lower LCR were documented by using telemetry surveillance in 1991 and 1992. Spawning-related movements appeared to occur in four phases. The first was marked by local aggregations in mainstem eddy complexes in February, and the second by long-distance movements to a staging area near the LCR inflow from March through May. Largest aggregations of radio-tagged fish in the LCR inflow staging area were observed in March and April of 1991, and March of 1992 (Fig. 8-15). Peak numbers occurred on March 8 and 11 of 1991, and March 11 of 1992, when 60% of radio-tagged fish were located in a deep mainstem eddy just above the LCR inflow. Adults upstream and downstream of the LCR inflow moved simultaneously to the

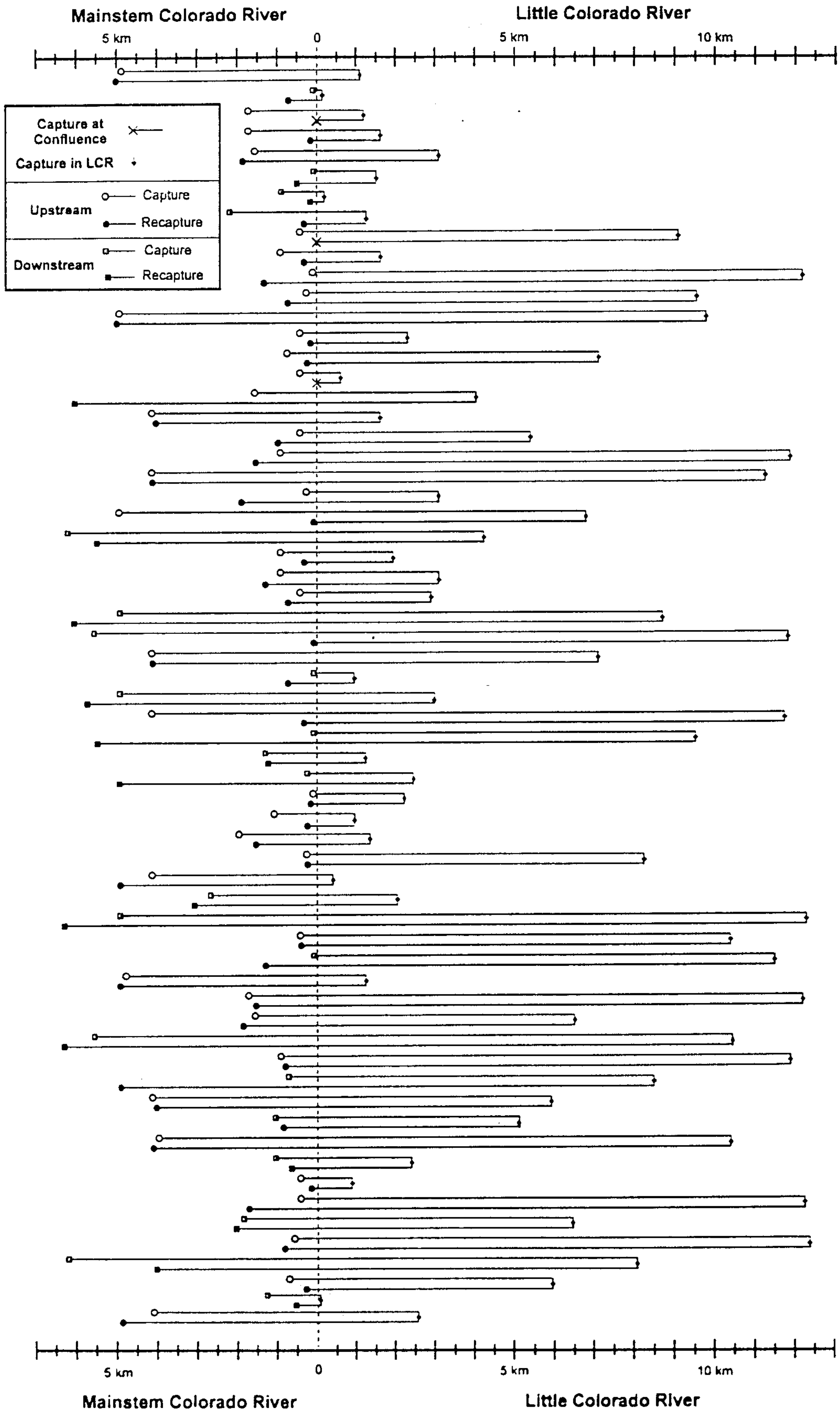


Fig. 8-12. Fidelity of 60 PIT-tagged humpback chub in the mainstem Colorado River following presumed spawning in the LCR, October 1990-November 1993.

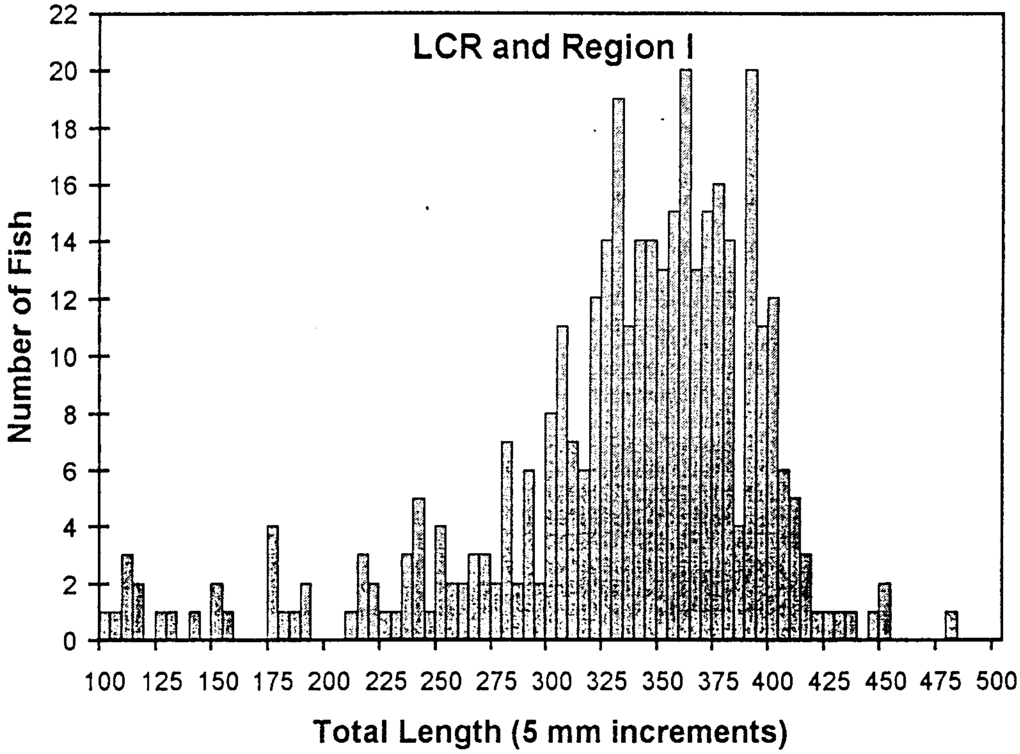


Fig. 8-13. Length-frequency of humpback chub captured in both LCR and Region I of mainstem, October 1990-November 1993.

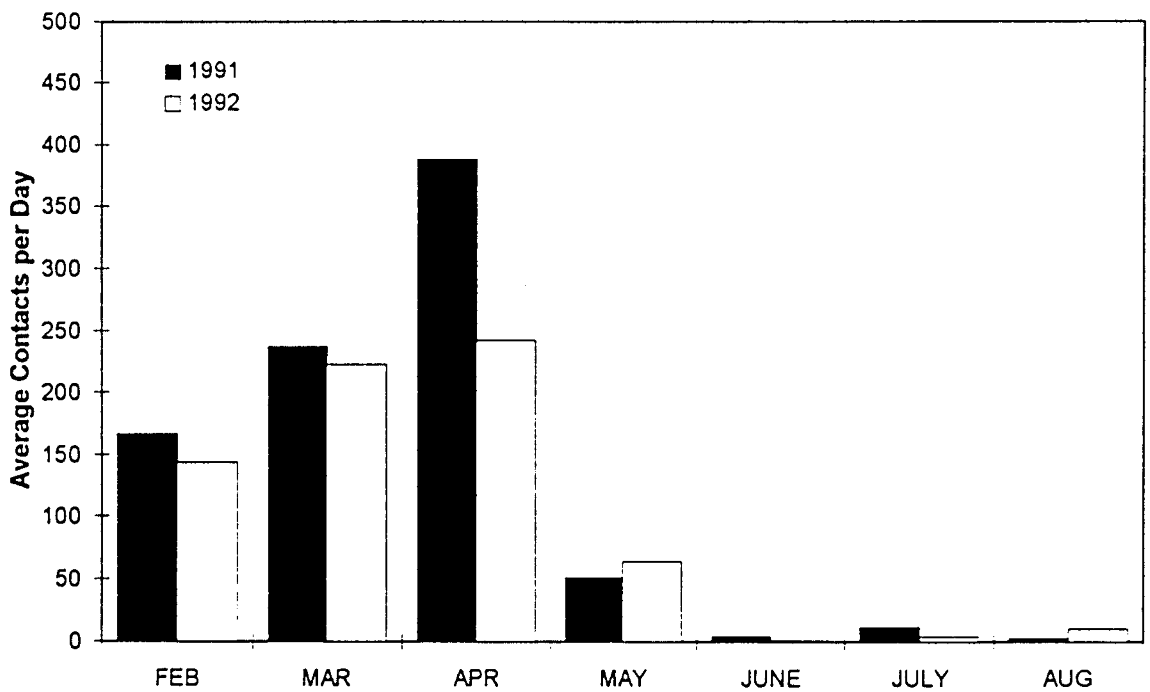


Fig. 8-14. Average number of radio contacts per day by remote telemetry station KLCR, February-August of 1991 and 1992.

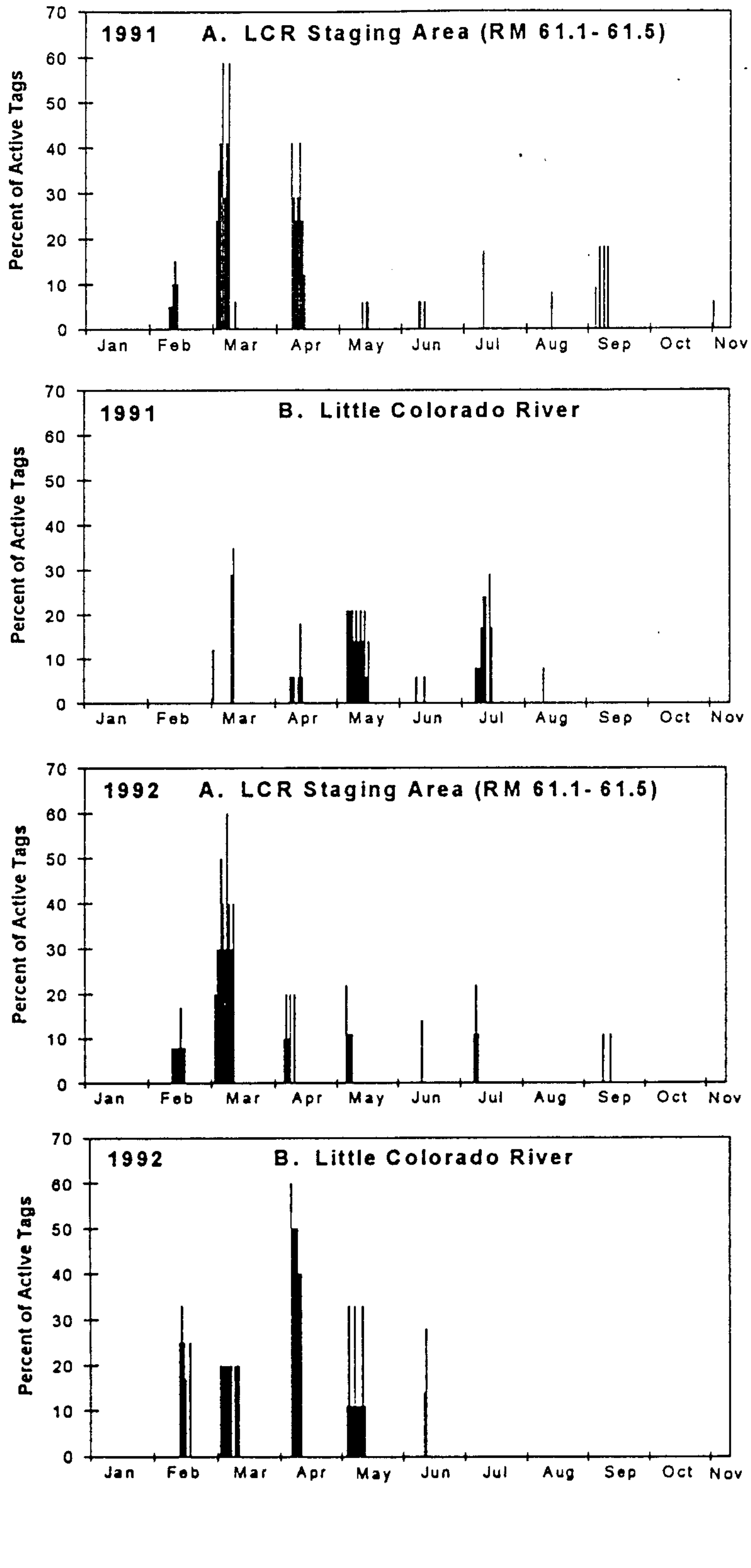


Fig. 8-15. Percent of radio-tagged adult humpback chub with active radio transmitters (tags) located during telemetry surveillance in the LCR staging area (RM 61.1-61.5 (A), and the Little Colorado River (B), during 1991 and 1992.

staging area, indicating initial spawning cues were unrelated to LCR flows.

The third phase of spawning-related movement was ascent into the LCR, primarily from February through May in 1991, and mid-March through mid-April in 1992 (Fig. 8-15). In both years, movements of radio-tagged fish were irregular, with several fish moving between the mainstem and LCR two or more times when spring runoff and rainstorms periodically increased flow and turbidity in that tributary; fish moved into the LCR during descending flow and decreased turbidity, but temporarily returned to the mainstem when LCR flow and turbidity increased substantially.

The fourth stage of migration involved return of fish to the mainstem after presumed spawning. Timing of these movements was not clear, since battery life of radio transmitters did not span the full period of activity in the LCR. Movement appeared to occur over an extended time period from June through September with little time spent by individuals at the LCR inflow before redispersing to the mainstem.

Movement of 20 radio-tagged fish into the LCR appeared related to decreasing or steady low flows and rising temperatures. Eleven (55%) fish moved into the LCR during decreasing flows in a range of 213-1,760 cfs, seven (30%) moved during steady low flows in a range of 198-276 cfs, one moved during rising flows at 1,220 cfs, and one moved during a small flow peak of 1,140 cfs (Fig. 8-16). Seventeen (74%) fish moved during rising temperature of 9.6-22.7°C and four moved during steady temperature of 20.5°C.

Timing of movement between the mainstem and LCR was determined

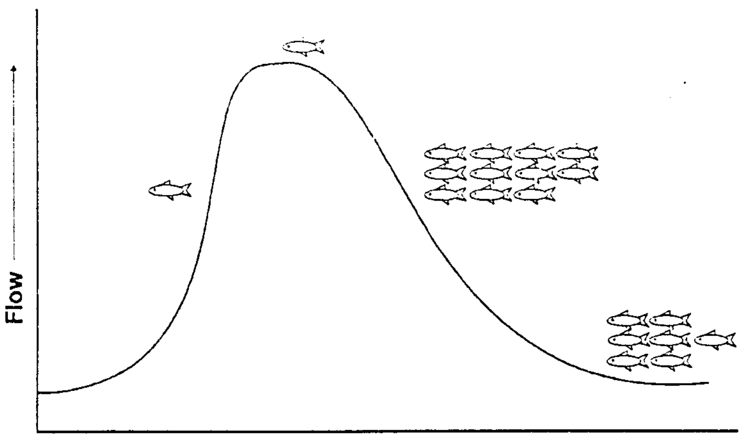


Fig. 8-16. Conceptual flow spike in the LCR illustrating timing of movements by 20 radio-tagged adult humpback chub into the LCR from the mainstem Colorado River.

Movement Related to Flow Regime

Movement of radio-tagged adult humpback chub, as indicated by displacement between contact sites from random surveillances, was compared between two time periods of different flow regimes under Glen Canyon Dam operations, i.e., research flows (June 1, 1990 to July 29, 1991) and interim flows (after August 1, 1991) (See Chapter 3 - HYDROLOGY). No significant differences in mean net displacement (t-test, t=0.777, P=0.440, df=52) or mean gross displacement (t-test, t=0.253, P=0.802, df=52) were observed.

for 23 PIT-tagged humpback chub captured in the mainstem and recaptured in the LCR, and 17 captured in the LCR and recaptured in the mainstem (Fig. 8-17). Only fish at large less than 30 days between successive captures were considered for this analysis. Movement occurred primarily during the LCR spawning period (February through June), and only 3 of 23 fish (13%) moved into the LCR during the remainder of the year. Movement of 17 fish from the LCR was later than movement into the LCR; 15 fish (88%) moved out from May through November.

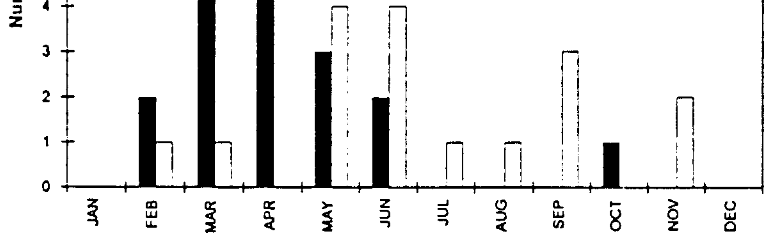


Fig. 8-17. Timing of movement for 23 PIT-tagged humpback chub between the mainstem Colorado River and LCR, October 1990-November 1993.

Seasonal Movement

Net displacement of radio-tagged humpback chub from surveillance data were not significantly different among winter, spring, and summer, but significantly lower (ANOVA, F=3.15, P=0.027, df=3, 122) in fall (Fig. 8-18). Absolute differences by season were not great with mean net displacements in fall only 0.4-0.8 km less than other seasons. Net upstream and downstream movement of these fish was not significantly different from zero for each season (t-test, P>0.05), indicating no seasonal net upstream or downstream displacement. Similar results were found from consecutive captures of PIT-tagged chubs in the mainstem. Although no significant differences were found among seasons (log-transformed data: ANOVA, F=2.46, P=0.091, df=3, 21), net displacement in fall was lowest.

Movement of Subadults

Movement of YOY and juvenile humpback chub too small to PIT tag was assessed from fin punches. Only 10 of 1,228 (0.8%) fish fin-punched in the mainstem by B/W and AGF were recaptured, all within the subreach of initial capture. Time between mark and recapture, and length of time in the subreach, could not be determined. Ten recaptured

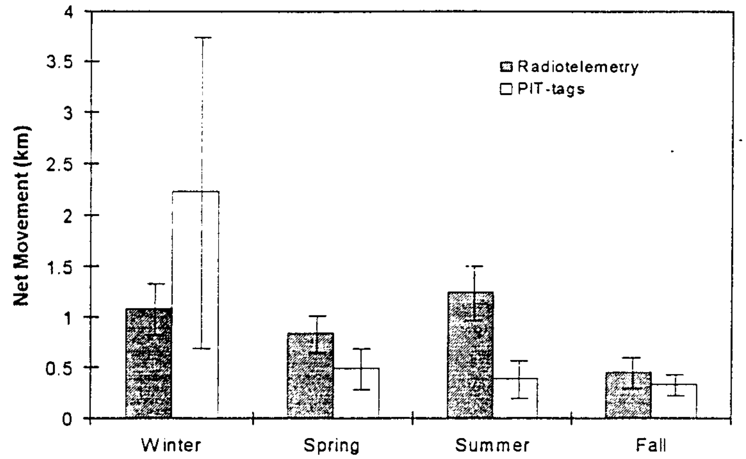


Fig. 8-18. Net displacement by season of radio-tagged and PIT-tagged adult humpback chub in Region I October 1990-November 1993. Bars represent standard error.

fish were considered an insufficient sample to assess movement of young chubs in the mainstem. Additional information on dispersal of young humpback chub, based on catch rates, is discussed in Chapter 5 - DISTRIBUTION AND ABUNDANCE and Chapter 7 - HABITAT.

In addition to the young fish fin-punched by B/W and AGF, 11 fish marked by ASU in the LCR were recaptured in the mainstem in 1993. These fish dispersed from three of four LCR study reaches (RK 0-3.1, RK 7.5-10.8, RK 10.8-14.8) originating from as high as 14.6 km in the LCR. Five were recaptured below the confluence of the LCR (RM 61.9 - RM 64.9), and one was recaptured 1.8 km (1.1 mi) above the confluence at RM 60.2 (Table 8-2). Appearance of these fin-clipped fish in the mainstem coincided with dispersal of young chubs from the LCR during large floods in the LCR in January and February 1993 (See Chapter 5 - DISTRIBUTION AND ABUNDANCE).

Local Movement

Local movement of adult humpback chub in the mainstem was related to spawning/non-spawning seasons, time of day, turbidity, flow level, flow regime, ramping rates, and magnitude of flow change. Vertical and horizontal movements were used to assess these relationships. Evaluation of vertical movement was based on occurrence of radio-tagged fish within 4.5 m of the water surface (radio signal extinction depth) and termed near-surface activity. Near-surface activity was often a manifestation of fish utilizing shallow nearshore habitats. Horizontal movement was based on consecutive contact sites during ongoing telemetry observations.

Effect of Season, Time-of-day, and Turbidity

Near-surface activity was expressed as average proportion of radio-tagged fish located (APFC) during telemetry surveillance for each trip, and related to season, time-of-day, and turbidity. Data were pooled over years, since no significant differences were found for APFC (ANOVA, F=0.80, P=0.371, df=1, 441) between years. Turbidity had a significant influence on near-surface activity (ANOVA, F=99.41, P<0.00001, df=1, 441), with mean APFC greater during high turbidity (Table 8-3, Fig. 8-19). Near-surface activity was also significantly higher during spawning than non-spawning season (ANOVA, F=19.97, P<0.00001, df=1, 441). Smaller but no significant differences (ANOVA, F=2.16, P=0.141, df=1, 441) were found for APFC between day and night (Table 8-3).

Table 8-2. Monthly numbers of YOY and juvenile humpback chub fin-clipped in the LCR and recaptured in the mainstem Colorado River. LCLP = lower caudal, left pelvic; UCLP = upper caudal, left pelvic, UCRP = upper caudal, right pelvic.

Month	LCLP	UCLP	UCRP	Total
January	2	1	2	5
March	0	1	0	1
April	1	0	1	2
May	1	0	0	1
July	1	0	0	1
October	0	1	0	1
Total	5	3	3	11

Table 8-3. Near-surface activity of radio-tagged adult humpback chub as average proportion of fish contacted (APFC) during spawning and nonspawning periods, between day and night, and under low and high turbidity. Fish were located during telemetry surveillance in the mainstem, November 1990 - November 1992. n=number of observations, SD = standard deviation.

Factor	n	APFC	SD
Spawning[a]	148	0.40	0.31
Non-Spawning[a]	295	0.25	0.27
Day	280	0.28	0.29
Night	163	0.33	0.30
Low Turbidity[b]	288	0.20	0.25
High Turbidity[b]	153	0.48	0.29

[a,b]Factors with the same letter are significantly different at P = 0.05.

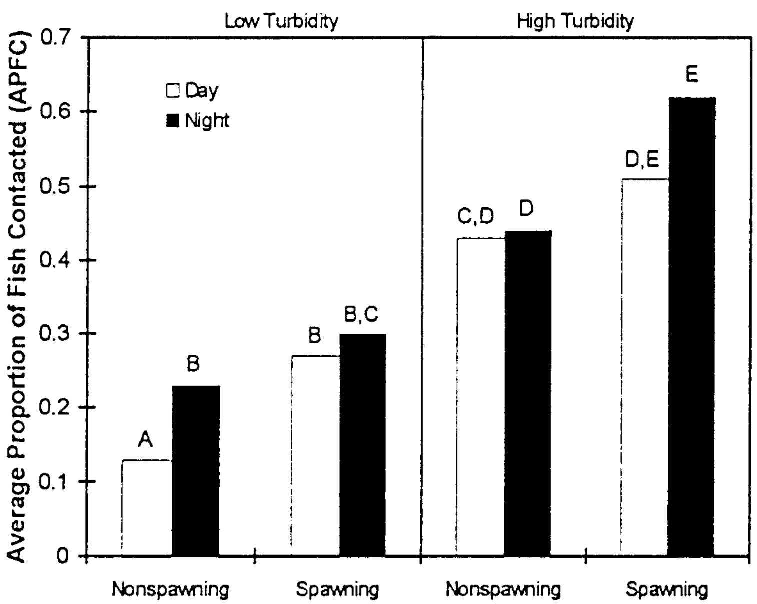


Fig. 8-19. Average proportion of fish contacted (APFC) for radio-tagged adult humpback chub located with telemetry surveillance in Region I under different turbidity levels, season and time-of-day, November 1990-November 1992. (Bars with same letter were not significantly different at P=0.05 with Fisher's LSD test after significant ANOVA).

Although nighttime near-surface activity was consistently higher under all conditions, APFC was significantly lower in the day under low turbidity and during non-spawning periods. While a diel pattern may have existed, it was less pronounced during periods of spawning or high turbidity.

Average proportion of fish contacts (APFC), using remote telemetry in the LCRI aggregation, was also related to time of day and turbidity. No significant differences were found between trips for APFC in 1991 and 1992 (ANOVA, F=2.35, P=0.128, df=1, 138) and data were pooled during additional analysis. The APFC index was significantly greater (ANOVA, F=28.46, P<0.001, df=1, 138) during high turbidity (Table 8-4), but there was no significant difference (ANOVA, F=2.37, P=0.126, df=1, 138) between day and

Table 8-4. Near-surface activity of radio-tagged adult humpback chub as average proportion of fish contacted (APFC) during low and high turbidity and between day and night. Data were collected by remote telemetry station (KILR) within LCRI aggregation, August 1991 - December 1991 and August 1992 - December 1992.

Factor		APFC	SD
	Turbidity		
Low Turbidity[a]		0.06	0.13
High Turbidity[a]		0.18	0.23
	Time of Day		
Day		0.09	0.17
Night		0.14	0.20

[a]Factors with same letter are significantly different at P = 0.05.

night. Also, APFC was significantly higher under high turbidity during both day and night, and lowest during daytime under low turbidity (Fig. 8-20). These patterns of increased near-surface activity during high turbidity and at night were consistent with observations made with telemetry surveillance.

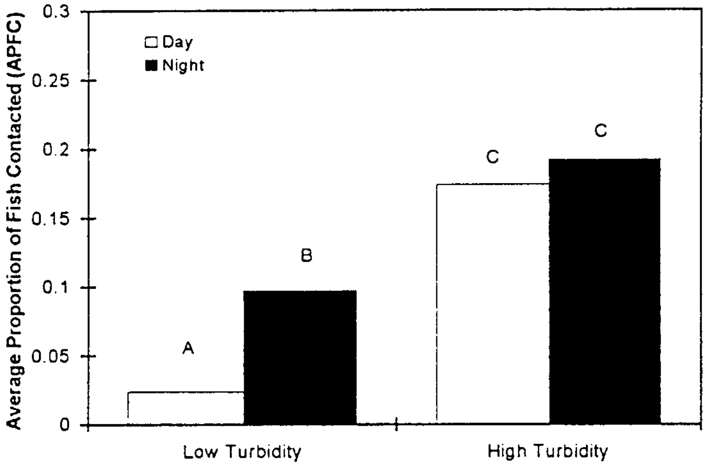


Fig. 8-20. Average proportion of fish contacts (APFC) at low and high turbidity, during day and night, for adult humpback chub contacted by remote telemetry station KILR. (Bars with same letter were not significantly different at P=0.05 with Fisher's LSD test after significant ANOVA).

Remote telemetry was also used to calculate APFC for three radio-tagged fish in MGG. As with fish of the LCRI aggregation, APFC for fish in MGG was higher during periods of high turbidity, but diel patterns of near-surface use were opposite those observed in the LCRI group (Fig. 8-21). Although not significant, APFC for MGG fish was greater during the day under both high and low turbidity. Dam releases produced daily flow patterns in MGG opposite those near the LCR (i.e., mainstem flows at MGG were typically high at night and low during the day, whereas flows near the LCR were usually high in the day and low at night), which may have influenced near-surface activity more than ambient light condition.

Telemetry observations of radio-tagged humpback chub were also used to relate horizontal movement to season, time-of-day and turbidity (Table 8-5). Horizontal movement was indicated as the proportion of times fish moved (P_m) during observation blocks. Significantly higher movement was recorded during spawning season than non-spawning season in the LCRI aggregation (χ^2=22.25, P<0.00001, df=1). Proportion of movement was significantly higher during high turbidity (χ^2=10.89, P=0.001, df=1), but no difference was detected between day and night (χ^2=0.02, P=0.887, df=1). Proportion of movement in the MGG group was similar during day (16%) and night (13%) (χ^2=0.30, P=0.58, df=1), and overall P_m of the MGG group (17%) and LCR group (16%) were similar (χ^2=0.61, P=0.436, df=1). Influence of turbidity on fish movements in MGG could not be examined because all observations in this reach were conducted during high turbidity. Patterns of horizontal movement of radio-tagged fish in both aggregations were similar with greater movement observed under high turbidity and during spawning season.

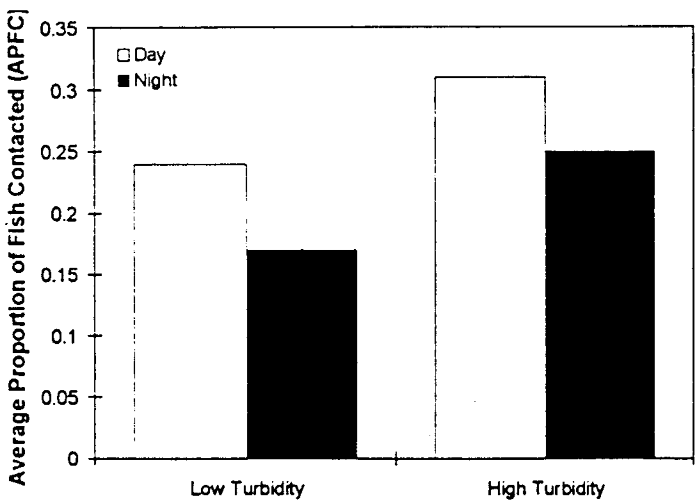


Fig. 8-21. Average proportion of fish contacted (APFC) for radio-tagged adult humpback chub at low and high turbidity, during day and night, for fish contacted by remote telemetry stations in MGG, February 1993-September 1993. (ANOVA was not significant at P=0.05).

Movement of adult radio-tagged fish with time of day was probably not random, but rather directed at optimizing position in habitat, feeding, or relocation to other resting sites. These movements occurred within large hydraulic units or macrohabitats and some were associated with fish moving across the channel (See Box 8-1).

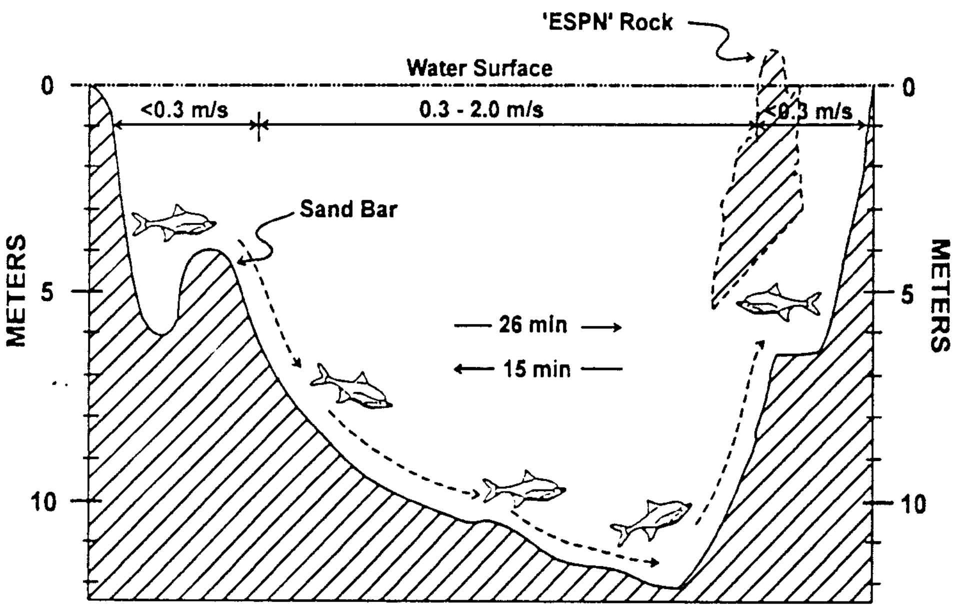
Table 8-5. Horizontal activity of radio-tagged adult humpback chub as proportion of movement (> 5 m) during spawning and nonspawning periods, between day and night and under low and high turbidity. Fish were monitored November 1990 - November 1992. n=number of observations.

Factor	n	No. Movements > 5 m	Proportion of Movement > 5 m
Spawning[a]	705	151	0.21
Non-Spawning[a]	1,126	147	0.13
Day	947	153	0.16
Night	884	145	0.16
Low Turbidity[b]	651	81	0.12
High Turbidity[b]	1180	217	0.18

[a,b] Factors with the same number are significantly different at P = 0.05.

Box 8-1. Moving Across a Swift River.

Humpback chub select feeding and resting sites with low water velocity (<0.5 m/sec) associated with large recirculating eddies, instream structure, and shorelines. They apparently move across a swift river channel by staying near the shear zone of the bed surface, avoiding high mid-column velocities. The strategy was surmised from radio-tagged adult No. 7F7F3F3626 (TL=432), during a 41.5-hr continuous observation period in which the fish moved from low-velocity vortices (<0.1 m/sec) in a large recirculating eddy at RM 60.8 across the river to a similar, low velocity site (<0.2 m/sec) behind a large emergent rock (ESPN Rock). The fish returned to the original site 31.3 hr after the first crossing; cross-channel movements took place in 26 and 15 min. Maximum channel depth at the crossing location was 14 m, and maximum water velocity 1 m below the surface was 2.5 m/sec. Although water depth and conductivity extinguished radio signals 4.5 m below the water surface, use of the bed surface shear zone was surmised from velocity measurements of the water column and knowledge of the swimming ability of the species. Juvenile humpback chub in a laboratory stamina tunnel (Bulkley et al. 1982) had a maximum swimming speed of 0.51 m/sec for 2.22 min, and sustained swimming speed of 0.45 m/sec for 28.05 min at 14°C. Maximum swimming speed at 20°C was 0.72 m/sec for 4.0 min, and sustained swimming speed was 0.63 m/sec for 23.77 min. Maximum swimming speed observed was 0.78 m/sec for 2.08 min at 26°C (time in minutes is average of 10 fish tested). Swimming ability of adults was estimated to be about twice that of juveniles, i.e., sustained swimming speed of adult humpback chub at 20°C might be about 1.2 m/sec for about 20 min, compared to 1.06 m/sec for 4 min for adult Colorado squawfish, and 3.29 m/sec for adult coho salmon (Bell 1973). Selection for low-velocity sites is consistently demonstrated by humpback chub, even when crossing a swift river such as the Colorado River.



Effect of Flow, Ramping Rate, and Magnitude of Flow Change

Observations of radio-tagged adult humpback chub were used to relate horizontal movement (P_m) under different flow regimes, flow levels, ramping rates, and magnitude of flow change. Magnitude of flow change was defined as the difference between highest and lowest flows in a daily cycle, while ramping rate was the hourly rate of flow change in cubic feet per second. Implementation of interim flows in August 1991 resulted in a substantial decrease in ramping rate and magnitude of flow change. Average ramping rate during telemetry observations was 886 cfs/hr (SD=1,230) prior to interim flows (November 1990 - July 1991), and 378 cfs/hr (SD=379) during interim flows (August 1991 - November 1992). Magnitude of daily flow change during telemetry observations decreased from an average of 5,643 cfs (SD=5,144) during research flows to an average of 4,014 cfs (SD=1,991) during interim flows. Hydrological differences between research and interim flows are described in detail in Chapter 3 - HYDROLOGY.

The proportion of movement of radio-tagged adult humpback chub varied with different flow regimes and flow characteristics. When observations were pooled by flow regime, P_m was significantly higher during research flows than during interim flows (χ^2=5.18, P=0.023, df=1) (Table 8-6). Horizontal movement also differed with flow level (Table 8-7, Fig. 8-22), with P_m approximately three times higher (0.19 vs. 0.06) at flows above 10,000 cfs (χ^2=39.31, P<0.00001, df=1). Proportion of times fish moved (P_m) was also higher when ramping rates were greater than 300 cfs/hr during both high and low flows, but this relationship was significant only for flows greater than 10,000 cfs (ANOVA, F=15.37, P<0.00005, df=3, 1,260). Only telemetry observations during non-spawning season were used in this analysis, since it was assumed that higher movement rates during spawning season would bias fish response to flow.

Horizontal movement of adult humpback chub varied with the daily hydrograph (Fig. 8-23); P_m was highest (0.21) during rising and falling flows, but remained high (0.16) during the high portion of the flow cycle and low during low flow periods.

Less movement observed during interim flows (Table 8-6) may have been related to reduced magnitude of daily flow changes and lower ramping rates. Although daily regularity of high and low flows were similar under research and interim flow regimes, magnitudes of flow change were

Table 8-6. Comparison of horizontal activity of radio-tagged adult humpback chub as proportion of movements (> 5 m) during research and interim flows in Region I of the mainstem, October 1990 - November 1992. n=number of observations.

Flow Type	n	No. Movements >5 m	Proportion of Movement > 5 m
Research Flows	310	66	0.21
Interim flows	1715	275	0.16

Table 8-7. Horizontal movement of radio-tagged adult humpback chub as proportion of movement (> 5 m) at high and low flows, and high and low absolute ramping rates as monitored during telemetry observation, November 1990 - November 1992. n=number of observations.

Flow (cfs)[a]	Absolute Ramping Rate (cfs/hr)[a]	n	No. Movements > 5 m	Proportion of Movement > 5 m
<10,000	<300	318	16	0.05
	>300	130	10	0.08
>10,000	<300	353	55	0.16
	>300	463	97	0.21

[a]Flows and ramping rates were determined from local gages or from a flow routing model (Goodwin 1995).

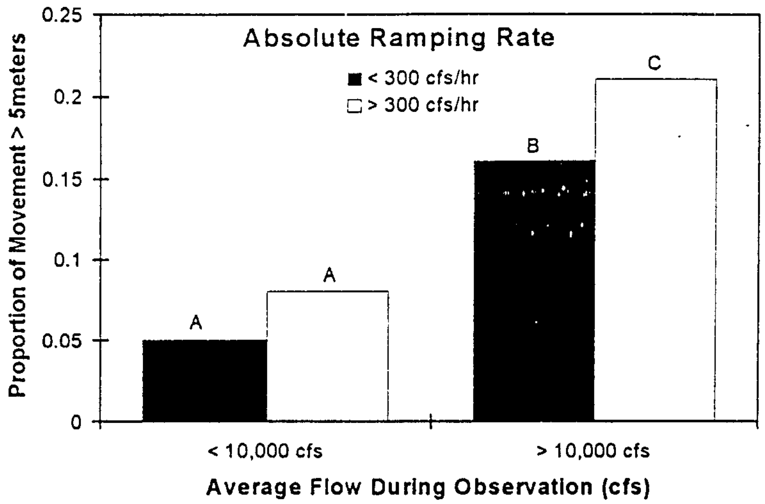


Fig. 8-22. Fraction of telemetry observation time blocks with horizontal movement of radio-tagged adult humpback chub in Region I as related to ramping rate and flow, November 1990-November 1992. (Bars with same letter were not significantly different at p=0.05 with Fisher's LSD test after significant ANOVA).

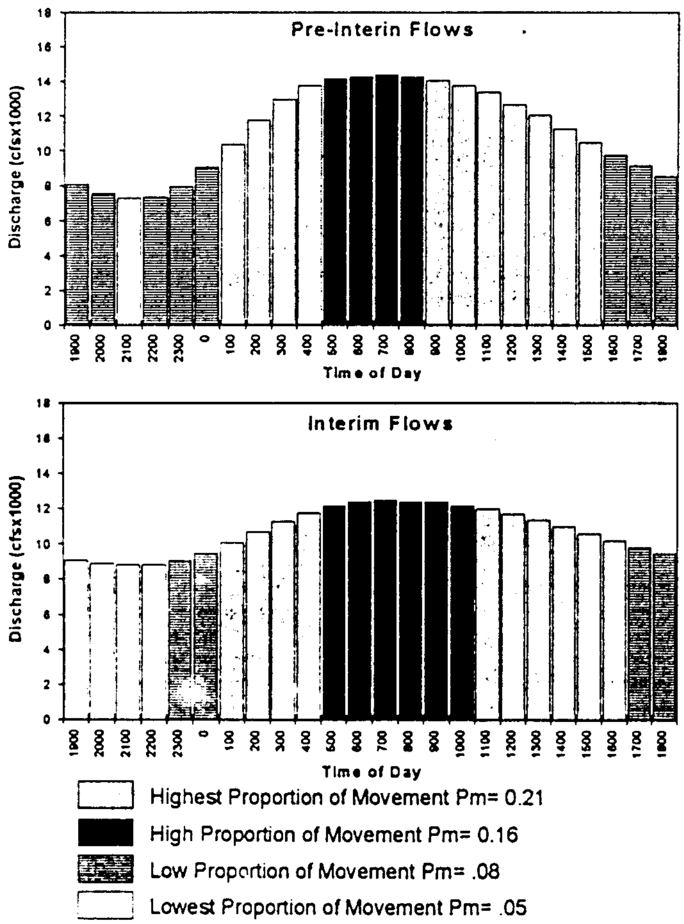


Fig. 8-23. Fraction of telemetry observation time blocks with horizontal movement of radio-tagged adult humpback chub in Region I during average research and interim flow cycles.

substantially different. Mean daily flow change observed at the LCR Inflow during research flows (October 1990 - July 1991) was approximately 6,500 cfs, but only 3,000 cfs during interim flows (August 1991 - November 1992) (Fig. 8-23). Reduced fluctuations in daily flow under interim flows corresponded to shorter intervals of high flows (>10,000 cfs) and high ramping rates (>300 cfs/hr), periods when P_m was greatest.

Total distance traveled by adult humpback chub during telemetry observations was greater with higher magnitude of flow change. When total fish movement was related to magnitude of flow change during observations, a general trend of increased total movement with was found (n=91, $P<0.005$, $R^2=0.18$), particularly when the daily difference between high and low flows exceeded 4,000 cfs.

DISCUSSION

Long-range Movement

Long-range movement of adult and subadult humpback chub in the vicinity of the LCR, determined from radiotelemetry and PIT-tag recaptures, indicated a home range for this aggregation of approximately 28.4 km (13.5 km in mainstem, 14.9 in LCR). Movement within a second aggregation in MGG was similar but restricted to 4.7 km of mainstem habitat. Strong spatial fidelity for discrete locations was observed for radio-tagged fish following upstream or downstream movements. Such fidelity may have been associated with an affinity for specific habitats or habitat complexes, as areas utilized by radio-tagged fish often included large recirculating eddies and associated eddy return channels (See Chapter 7 - HABITATS).

Movement of adult and subadult humpback chub within the mainstem Colorado River in Grand Canyon was similar in extent to that reported for the species in Black Rocks, a turbulent deepwater reach of the Colorado River in the upper basin. Net displacement in Grand Canyon averaged 1.49 km for radio-tagged adults from first to last contact and 0.99 km for PIT-tagged fish between captures. Mean maximum displacement of humpback chub in Black Rocks was 0.8 km for radio-tagged and 1.67 km for Carlin-tagged adults (Valdez and Clemmer 1982), which was similar to mean net (0.8 km) and maximum displacement (1.4 km) of radio-tagged adults reported by Kaeding et al. (1990). Similarity in net movements by males and females of the Grand Canyon population was also observed for fish in Black Rocks (Kaeding et al. 1990). Strong spatial fidelity also reported by Valdez and Clemmer (1982) and Kaeding et al. (1990) in Black Rocks, and return to discrete locations following presumed spawning migration, is indicative of strong homing ability by humpback chub.

Humpback chub in Grand Canyon moved substantially less than reported for other Colorado River cyprinids. Mean maximum displacement of 43 radio-tagged adult Colorado squawfish in fall and spring in the Colorado River was 31.8 km (calculated from data in Archer et al. 1985), while mean maximum displacement of 33.9 km was reported for roundtail chub in spring and summer by Kaeding et al. (1990). Relatively small movements by humpback chub during all seasons may be attributed to proximity of feeding, resting, and cover habitats within small reaches of river, although the age at which this "spatial imprinting" occurs was not determined. Selection of eddy complexes in Grand Canyon may be related to low velocity habitat and greater food availability from entrainment of drifting material.

Although most movements by adults and large subadults (≥ 150 mm TL) in the mainstem were over short distances, three were substantially greater with the longest movement by an adult of 99.8 km. Large but infrequent movements have also been documented for humpback chub in the Upper Colorado River Basin (Valdez and Clemmer 1982, Kaeding et al. 1990), i.e., three adults moved 22 km between populations in Black Rocks and Westwater Canyon. These relatively large movements, observed in a few adults and large subadults--and suspected for greater number of small subadults (>150 mm TL)--may be a dispersal mechanism for these relatively sedentary fishes and may be more prevalent with high population densities. Long-distance dispersal from the LCRI aggregation may represent the primary source of humpback chub to other aggregations in Grand Canyon, particularly downstream.

While adult humpback chub exhibited limited movements and strong spatial fidelity in the mainstem, sizable movements were observed from the mainstem into the LCR for presumed spawning. Mean net displacements of PIT-tagged fish between the mainstem and LCR were significantly greater than mean net displacement within the mainstem. Movements of radio-tagged adults from mainstem locations to the LCR occurred predominately from February through April and were likely associated with spawning activities within the LCR, reported primarily as March through July (Suttkus and Clemmer 1977, Minckley 1990, Kaeding and Zimmerman 1983). Staging behavior by adults was also observed near the LCR inflow with movement into the LCR primarily under descending flows and decreased turbidity, and rising water temperatures, conditions presumably favorable for spawning. Although not well documented, movements from the LCR after spawning appeared to occur over an extended period, with individuals spending little time in the inflow. Movements from the LCR coincided with reduced captures of adults in hoop nets in the LCR in fall (Angradi et al. 1992) and increased catch rates in the mainstem (See Chapter 5 - DISTRIBUTION AND ABUNDANCE). Significant spatial fidelity was observed for individuals migrating to the LCR and returning to similar mainstem locations.

Movements from the mainstem to the LCR for spawning were different from those observed for humpback chub in Black Rocks. Valdez and Clemmer (1982) and Kaeding et al. (1990) suggested that suitable habitat for spawning was found within the confined reaches of Black Rocks, while Kaeding and Zimmerman (1983) hypothesized that suitable temperature was not available in the mainstem Colorado River for survival of eggs and larval humpback chub. Thus, suitable spawning habitat for humpback chub of the LCRI aggregation was likely limited to the LCR, necessitating annual migrations. Also, adults living year-round and spawning in the LCR may eventually exploit the mainstem when populations in the LCR become large enough to limit resources, but return to the LCR to spawn. These movements suggest homing behavior by spawning humpback chub, as hypothesized for Colorado squawfish (Tyus 1985), or these movements may be a search for suitable spawning habitat, limited in the mainstem by suboptimal water temperature.

Long-range movements of radio-tagged adult humpback chub in the LCRI aggregation were not different between research flows and interim flows. Also, there was no apparent large-scale movement of adults when flow regimes were changed, a phenomenon that may have occurred if major habitat changes had occurred. Instead, relatively stable geomorphic features, and similarities in gross habitat complexes were observed between flow regimes. Kaeding and Zimmerman (1983) speculated that common to all humpback chub habitat was the occurrence of large, angular boulders and shoreline rock outcrops that buffer velocity during flow. Flow regimes observed in this study did not change basic adult habitat characteristics, and suitable habitat was apparently available for the numbers of adults observed.

Daily Movement

Near-surface activity was highest under conditions of high turbidity and lowest during daylight hours when turbidity was low. Adults apparently used shallow habitats or the upper portion of the water column more often when cover was provided by turbidity, darkness, or both. Although larger subadults and adults were minimally susceptible to predation by large brown trout, channel catfish, and striped bass (See Chapter 6 - DEMOGRAPHICS), they were also vulnerable to avian predators, primarily osprey (Pandion haliaetus) (Wasowicz and Yard 1993) and bald eagles (Haliaeetus leucocephalus).

The pattern of near-surface activity for adult humpback chub in Grand Canyon differed from that reported for adults in the upper basin. When turbidity was consistently high, and flows relatively constant, patterns of near-surface activity of adults in Black Rocks varied with time-of-day. Valdez and Nilson (1982) found adults in shallow shorelines (<5 m) during crepuscular periods, in slightly deeper waters in midmorning and late afternoon (5-7 m), and in deepest waters (>7 m) at night and midday. In Grand Canyon, near-surface activity appeared to be related to flow and possibly availability of food (i.e., drifting macroinvertebrates), and was significantly reduced at low turbidity, suggesting use of turbidity as cover, or less availability of drifting food with lower concentrations of suspended material.

Highest rates of daily horizontal movement by radio-tagged adults were observed under conditions associated with high-fluctuating flows, i.e., high flow, high ramping rates, high magnitude of flow change. Higher movement rates may have resulted from chubs moving to more favorable microhabitats after flow changes altered conditions at the original position. Microhabitat changes could involve changes in cover (through fluctuations in water depth) and local hydraulics. Higher local movement rates did not translate to greater long-range movements as net long-range displacement of adults did not differ between research flows and interim flows.

Movement of Juveniles

Movement of juvenile humpback chub (< 150 mm TL) from the LCR to the mainstem, as presumed by Kaeding and Zimmerman (1983) and Angradi et al. (1992), was documented with marked individuals. Based on catch rates and recapture records, movement of large numbers of YOY and juveniles from the LCR to the mainstem were associated with flood events in the LCR. This study did not determine whether this movement was passive or active. Passive movement may occur when flows are sufficient to involuntarily move fish from suitable habitat, while active movement may involve opportunistic use of high flows to disperse to more favorable habitat. John (1964) and Harvey (1987) found that larvae and small post-larvae were most susceptible to passive downstream transport, and that for young cyprinids, vulnerability was greatly reduced for individuals 10-25 mm in length (Harvey 1987). If susceptibility to passive transport was similar for humpback chub, the bulk of young fish observed in the mainstem after floods from the LCR (>40 mm TL) moved concurrently with floods, rather than under passive transport. Flows in the LCR for 3-4 months after presumed spawning, during March - May, usually remain low and stable, hence the young fish are well past the larval stage when flooding occurs from late summer convection storms. Absence of humpback chub from drift nets downstream of population centers in the upper basin (Valdez et al. 1985, Valdez and Williams 1993), suggest that humpback chub are not prominent in drifting ichthyofaunal assemblages.

Dispersal of juvenile humpback chub from the LCR to the mainstem may be the major contributor of fish to downstream aggregations, since cold water temperatures in summer (i.e., 10-15 °C) likely preclude successful spawning in the mainstem (Hamman 1982, Marsh 1985). Although young humpback chub marked in the LCR or the LCRI aggregation were not subsequently captured in these lower reaches, annual increases in numbers suggest downstream dispersal. Small numbers of marked fish, short duration of fin-clips and punches, and probable high mortality of young fish in the mainstem contributed to low recapture probability.

Management Considerations

Although long-range movement of adults was not different under the two flow regimes, daily activity differed significantly at different flow magnitudes, ramping rates, and levels of turbidity. The proportion of times fish moved was significantly higher during local ramping rates greater than 300 cfs/hr when flows were 10,000 cfs or greater. The effect of greater daily movement by subadult and adult humpback chub under high-fluctuating flows could be increased energy expenditure and greater risk of predation. Energy costs would be associated with movements between areas of suitable habitat and could result from reduced feeding efficiency. High condition factors for adults throughout the study (See Chapter 6 - DEMOGRAPHICS), however, indicate no negative energetic effects from increased energy demands. Increased predation of subadults and adults could be associated with higher movement rates when fish leave protective cover. Sizable populations of large brown trout, rainbow trout, and channel catfish are predators on humpback chub in Grand Canyon and are capable of preying on individuals up to 340 mm TL. Flow conditions which reduce turbidity may also increase the potential for predation, while negative phototaxis may reduce available foraging time for humpback chub.

The effects of flow regime on dispersal and movement of young humpback chub were not clearly determined. Relatively low densities of juveniles were observed in the mainstem during high-fluctuating flows (1991), and low densities (1992) and high densities (1993) were observed during interim flows (See Chapter 5 - DISTRIBUTION AND ABUNDANCE). These variable densities precluded evaluation under the two flow regimes. If young humpback chub were passively transported in large numbers or moved concurrently under high flows from the LCR, it is likely that high flows in the mainstem would have a similar effect. Two unanswered questions, however, are: 1) what flow levels, ramping rates, and magnitude of flow changes will passively transport large numbers of young humpback chub in the mainstem, and 2) at which point in the mainstem are transported young chubs unable or unlikely to return to the LCRI aggregation and effectively lost from the reproducing LCR population? Within Black Rocks and Westwater Canyon of the upper basin, numerous young individuals were found in areas within or adjacent to reaches inhabited by adults, and few juveniles were found in reaches outside of population centers (Valdez and Clemmer 1982). Recruitment of young may be dependent on their ability to remain and mature in habitats required by adults.

Low mainstem temperatures may also affect the ability of juvenile humpback chub to maintain position under large flow fluctuations that significantly alter microhabitat characteristics, particularly velocity. Bulkley et al. (1982) found that low temperatures significantly reduced maximum and sustained swimming speed in juvenile humpback chub during experiments in a laboratory stamina tunnel. At 20°C, swimming speed of 0.51 m/sec was sustained for an average of 85 min, maximum swimming speed was 0.72 m/sec for 4 min, and sustained swimming speed was 0.63 m/sec for 24 min. At 14°C maximum swimming speed was 0.51 m/sec for 2 min, and sustained swimming speed was 0.45 m/sec for 28 min. Hence, subadult humpback chub may experience greatly reduced swimming ability in the mainstem, particularly when they are hatched and acclimated in the warmer LCR.

Food Habits

Chapter 9

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CHAPTER 9 - FOOD HABITS

INTRODUCTION

Food habits studies of humpback chub were conducted as part of this investigation to increase the understanding of their diet in Grand Canyon, and to determine how food items and their availability are affected by Glen Canyon Dam operations. Integration of this information with past and ongoing studies will provide insights into life history strategies of the species and identify management options that will enhance these strategies.

Because of the endangered status of the humpback chub and the intrusive nature of food habits studies, little information has been collected in the past on the diet of the species. Methods used to assess the diet of fish include emetics, stomach pumping, or dissection and removal of the gut. Emetics are useful on robust, piscivorous species, but are generally considered less effective and potentially harmful to some species, including many cyprinids (Bowen 1983). Dissection and removal of the gut was not considered a viable option for humpback chub because sacrifice of adequate numbers of fish for a food habits study could seriously deplete the population. Previous humpback chub investigations have relied on incidental mortalities or small numbers of sacrificed fish to evaluate food habits (Carothers and Minckley 1981, Kaeding and Zimmerman 1983, Maddux et al. 1987, Kubly 1990).

Stomach pumping was considered the most applicable method for recovering gut contents of humpback chub for this investigation. The technique has been widely applied and is shown to be effective on a variety of fish groups, including the salmonids, centrarchids, ictalurids, percids, and esocids (Meehan and Miller 1978, Swenson and Smith 1973, Seaburg and Moyle 1964). Since the use of a stomach pump on humpback chub had not previously been reported, a pilot study was conducted on the closely-related roundtail chub during January 1991 and August 1992 to evaluate the technique. Results of these studies indicated that stomach pumping was a safe and efficient means for recovering gut contents of roundtail chub, and hence the technique was considered safe for humpback chub (Wasowicz and Valdez 1994).

Items in the diet of humpback chub were related to items in river drift in order to compare use with availability. Drift samples were collected at the same time and place that fish were captured for stomach pumping. Benthic samples were not taken since that mode of sampling was beyond the scope of this investigation. Information on benthic standing crop of the Colorado River in Grand Canyon was assimilated by Blinn et al. (1992, 1994) and was integrated into this discussion of food availability and use.

This chapter presents a summary of food items found in the gut of humpback chub, as well as a comparison of diets between the fish from the Little Colorado River Inflow (LCRI) aggregation and the Middle Granite Gorge (MGG) aggregation (See Chapter 5 - DISTRIBUTION AND ABUNDANCE). A summary of food items collected in the drift is also presented together with longitudinal and seasonal analyses. The relationship between items consumed and items in the drift is presented as electivity indices. Information on food habits of other species collected during this investigation, including predation of humpback chub by piscivorous species, is also presented in this chapter.

METHODS

Food Habits

Food habits of adult humpback chub (>250 mm TL) from the LCRI aggregation and MGG aggregation were examined during 1992-93. Within the LCRI aggregation, gut contents of humpback chub from above and below the LCR were sampled and partitioned for analysis to determine possible effects of input from the LCR on diet. Consequently three groups of humpback chub were identified for food habits analysis including:

Subregion Ia -	**RM 60.0 to 61.3 (LCRI aggregation, above LCR)**
Subregion Ib -	**RM 61.3 to 65.4 (LCRI aggregation, below LCR)**
Region II -	**RM 126.0 to 129.0 (MGG aggregation)**

Gut contents of humpback chub were sampled using a non-lethal stomach pumping technique described by Wasowicz and Valdez (1994) (Fig. 9-1) which evacuated items in the gut (mouth to anal vent) of the fish. Humpback chub have a simple 'S' shaped intestine (i.e., gut) with no distinction between the stomach and lower intestine as in some other fishes. Hence, all food in the intestine was flushed and referred to as 'gut contents'. Gut contents were individually placed in plastic bags, preserved in 70% ethanol, and sorted in the laboratory. Identifiable material and macroinvertebrates were counted by taxonomic group (i.e., order, family, genus, or species), and displacement volume of each taxon was determined. Analysis of Variance (ANOVA) and Fisher's Least Significant Difference (LSD) were used to compare differences among seasons (spring, summer, and fall) and groups (above LCR, below LCR, and MGG).

Food habits of adult non-native predaceous species (i.e., channel catfish, brown trout, rainbow trout, striped bass, walleye) were sampled to assess predation (See Chapter 6 - DEMOGRAPHICS) and compare sympatric competition with humpback chub for food. Stomach contents of non-native fish were generally sampled using stomach pumping techniques similar to those described above for humpback chub. Occasionally, where the likelihood of predation on humpback chub was high, (e.g., tributary inflows in spring and summer), large non-native predators were sacrificed for removal of stomach contents.

Drift

Material drifting in the river was sampled during 1991-93 at various camp locations, but primarily in association with the areas identified for fish groups 1-3. Drift nets used were made of a rectangular tubular frame (30.48 cm x 45.72 cm) with a 3-m long net of 560 μm mesh and a detachable catchment cup (Fig. 9-2). Nets were placed in pairs, one collecting surface drift and one collecting subsurface drift. A Swoffer current meter was used to determine current velocity at the net-mouth at the beginning and end of each set, usually 15-20 min. Volume of water filtered through each net was calculated as:

(Equation 9-1)

$$VOL = WHV$$

where:

VOL = Volume of water filtered in cubic meters per hour,
W = width of net opening (0.4572 m),
H = height of net opening (0.3048 m), and
V = average water velocity as meters per second at the net mouth, (start + end velocity)/2.

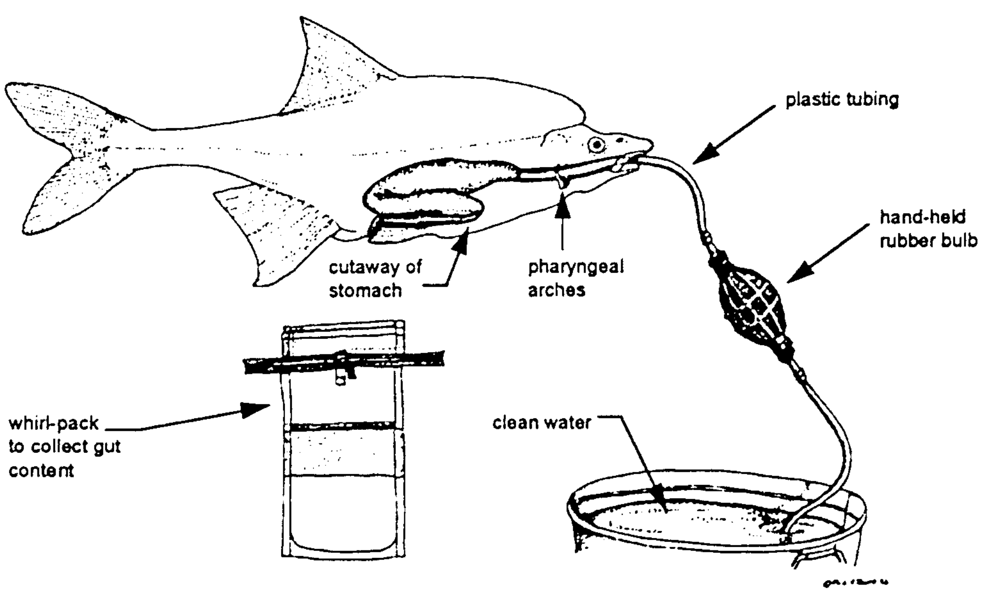


Fig. 9-1. Stomach pump used to recover gut contents of adult humpback chub.

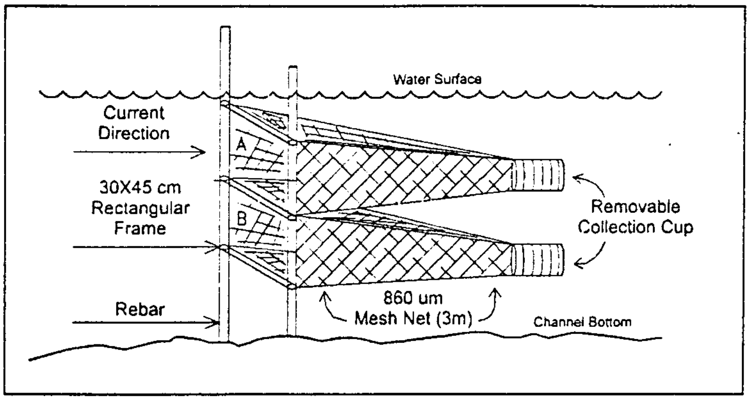


Fig. 9-2. Drift nets set in tandem to sample near-surface (A) and midwater (B).

In 1991 and 1992, a permanent sampling site was established just upstream of the LCR (RM 61.2) to determine the effects of discharge and time of day on drifting macroinvertebrates. Drift was sampled monthly to evaluate seasonal variation, and to provide an ongoing dataset for the term of the investigation. Drift was also sampled at various sites between the LCR (RM 61.2) and Diamond Creek (RM 226).

The contents of each drift net was placed in appropriately-labeled whirl-pacs or Ziplock bags, preserved with 70% ethanol, and returned to a laboratory. Macroinvertebrates were sorted from detritus and identified and counted by taxonomic group (i.e., order, family, genus, or species). Dry weight of remaining detritus (algae, woody debris, etc.) was measured. Sample drift density, as reported by Allen and Russek (1985), was calculated as:

(Equation 9-2)

$$DD = \frac{N}{VOL} \times 100$$

where:

DD = Sample drift density, as number of macroinvertebrates/100 m^3 of water filtered,
N = number of organisms per net hour, and
VOL = volume of water filtered in cubic meters per hour.

Data collected from drift samples are presented as volume in milliliters (ml) and number of organisms in 100 cubic meters of water filtered (orgs/100 m^3 wf). For algae, all results are presented as milliliters displacement volume in 100 cubic meters of water filtered. Analysis of drifting food items was based on the volume of material (i.e., algae, macroinvertebrates) drifting in the river by season, flow ramp direction (i.e., rising, falling, and steady flow), and region of the river in order to relate drift material to dam operations and to food habits of fish. Analysis of Variance (ANOVA) and Fisher's LSD were used to compare differences among seasons (spring, summer, and fall) and Regions I, II, and III.

Electivity Indices

A statistical procedure proposed by Johnson (1980) was used to relate food items consumed by humpback chub to food items in the drift. This procedure provides consistency in evaluating preferences in food. Calculated preferences using most standard methods (e.g., forage ratio, index of electivity, difference in proportions, contingency tables) depend on the array of items present or available. Changing the availability of items can change food preference. In Johnson's method, the availability and use of food are each ranked from highest to lowest (1 being highest), and statistics are performed on the differences in ranks. The method is minimally affected by the range of items available.

Average volume of items in the drift by study region (Region I above the LCR, Region I below LCR, Region II, and Region III) and by season (spring, summer, and fall) was used as estimates of availability of drift food items and ranked from most to least abundant. Food items were placed into six categories: Cladophora, simuliids, chironomids, Gammarus, other aquatic invertebrates, and terrestrial invertebrates. Food use was estimated by ranking the categories by volume in the gut of each fish from highest to lowest. Differences in rank of categories in gut samples and in drift were then calculated for each fish resulting in an electivity index for each food item. A positive difference indicated relatively higher use than availability. Differences between electivity indices for each food item were evaluated using ANOVA and Fisher's LSD.

RESULTS

Food Habits

Gut contents of 168 humpback chub were collected during 1991-93. Of these, 10 fish (5.9%) had empty guts and were not included in analyses. The remaining 158 fish were used to describe the composition of diet and to evaluate effects of location, season, and daily fluctuations (i.e., rising, falling, steady flows) caused by the operation of Glen Canyon Dam.

A total of 14 aquatic invertebrate taxonomic groups and 9 terrestrial groups were found in gut contents (Table 9-1). Also, 16 aquatic and 14 terrestrial groups were found in drift samples. Orthoptera (grasshoppers), Tipulidae (crane flies), and Gastropoda (snails) were found in guts but were absent in drift. Cladophora glomerata, a common green algae in Grand Canyon, was also found in gut contents, as well as human food remains and plant seeds and pods.

Gut contents of humpback chub captured during this investigation indicated that the most frequent items in the diet were simuliids, Gammarus lacustris, chironomids, Cladophora glomerata, cladocerans, and terrestrial Hymenoptera (primarily ants) and Coleoptera (beetles) (Table 9-2).

Simuliids were found in 77.8% of humpback chub examined and represented the most commonly occurring food item in fish of both the LCRI and MGG aggregations. Chironomids (57.6%) were the next most common item, followed by Gammarus (50.6%), Cladophora (23.4%), Hymenoptera (20.9), and cladocerans (19.6%). The high incidence of simuliids and chironomids in gut contents was consistent for the LCRI and MGG aggregations. Notable differences between the two aggregations included a higher incidence of chironomids, cladocerans, ants, and Cladophora in fish captured from the LCRI aggregation, and a higher incidence of other aquatic and terrestrial invertebrates in fish from the MGG aggregation. Seeds and human food remains were found in 8 (5.1%) and 7 (4.4%) fish, respectively.

Longitudinal Analysis

Comparisons of total gut volume and volumetric composition by taxonomic group indicated little difference in gut contents of fish captured above and below the confluence of the LCR, while substantial differences existed between fish from the LCRI and MGG aggregations (Table 9-3). The lack of differenees above and below the confluence of the LCR indicated that the LCR had little effect on the diet of humpback chub. It should be noted however, that highest densities of drifting food items probably occurred during flood events from the LCR. These events and the associated increase in food availability were generally ephemeral in nature and varied in magnitude depending on the timing and size of the flood. Most fish were captured for diet analyses at times other than these short term floods. These floods introduced large amounts of debris into the mainstem that reduced the efficiency of netting which was the primary means of capturing adult humpback chub. It is unknown if these periodic pulses of food from tributaries are retained in mainstem reaches used by humpback chub, or whether the materials are quickly transported downstream and become unavailable to the fish. Presumably, recirculating eddies entrain large volumes of drifting material, and hence, regions with a high incidence of eddy complexes, such as near the LCR inflow, have a longer retention time for allochthonous material. Higher percentages of terrestrial invertebrates in gut contents of fish captured below the LCR were not significant, but suggest some effect of this tributary.

Significant differences in composition of gut contents (invertebrates only) between fish from the LCRI and MGG aggregations were found for all taxonomic categories except simuliids and chironomids (Table 9-3, Fig. 9-3). Hence, although these two groups occurred more frequently in guts of LCRI fish, average of total volume and percent of volume did not differ from fish of the MGG aggregation. Mean total volume of gut contents was significantly higher for the LCRI aggregation than the MGG aggregation. Differences in volumetric proportion of the diet composed of invertebrates (all categories except Cladophora) and algae (Cladophora only) were also significant between the two aggregations. This difference was primarily associated with the absence of algae in stomach contents of 24 fish captured from the MGG aggregation, compared to algae comprising 23.6% of the diet of fish from the LCRI aggregation. A significant decrease in the percentage of diet composed of Gammarus, and an increase in other aquatic invertebrates and terrestrial invertebrates

Table 9-1. Aquatic and terrestrial invertebrates found in gut contents of 158 humpback chub and in 603 drift samples from the mainstem Colorado River, Grand Canyon, 1992-93.

Taxa	Gut Contents n=158		Drift Contents n=603	
	Aquatic	Terrestrial	Aquatic	Terrestrial
Thysanura (bristletails)				x
Collembola (springtails)				x
Ephemeroptera (mayflies)	x		x	
Odonata (dragonflies)			x	
Orthoptera (grasshoppers)		x		
Isoptera (termites)				x
Plecoptera (stoneflies)	x		x	
Hemiptera (true bugs)	x	x	x	x
Homoptera (cicadas)		x		x
Neuroptera (dobsonflies)	x		x	
Coleoptera (beetles)	x	x	x	x
Mecoptera (scorpionflies)				x
Trichoptera (caddisflies)	x		x	
Lepidoptera (butterflies)				x
Diptera (flies)	x	x	x	x
Chironomidae (midges)	x		x	
Simuliidae (blackflies)	x		x	
Culicidae (mosquitos)	x		x	
Tipulidae (craneflies)	x			
Hymenoptera (ants, wasps)		x		x
Formicidae (ants)		x		x
Amphipoda (amphipods)				
<u>Gammarus</u> <u>lacustris</u>	x		x	
Annelida (earthworms)		x		x
Cladocera (water fleas)	x		x	
Copepoda (copepoda)			x	
Acarina (mites, ticks)				
Hydrocarina (water mites)			x	
Araneida (spiders)		x		x
Tubellaria (worms)			x	
Isopoda (isopods)				x
Gastropoda (snails)	x			

Table 9-2. Frequency of occurrence of principal food categories (number and percentage of total) in gut contents of humpback chub in Grand Canyon during 1992-93. n=number of fish sampled.

Food Category	All Fish n = 158	LCRI Aggregations Region I n= 135	MGG Aggregations Region II n = 23
	Aquatic Organisms		
Simuliidae	123 (77.8)	104 (77.6)	19 (82.6)
Chironomidae	91 (57.6)	86 (64.2)	5 (21.7)
Gammarus lacustris	80 (50.6)	68 (50.7)	12 (52.2)
Cladocera	31 (19.6)	31 (23.0)	0 (0)
Trichoptera	8 (5.1)	5 (3.7)	3 (13.0)
Neuroptera	9 (5.7)	4 (3.0)	5 (21.7)
Other	21 (13.3)	12 (8.9)	9 (39.1)
	Terrestrial Organisms		
Hymenoptera	33 (20.9)	30 (22.2)	3 (13.0)
Coleoptera	24 (15.2)	19 (14.1)	5 (21.7)
Diptera	18 (11.4)	15 (11.1)	3 (13.0)
Hemiptera	5 (3.2)	4 (3.0)	1 (4.3)
Orthoptera	3 (1.9)	2 (1.5)	1 (4.3)
Homoptera	3 (1.9)	2 (1.5)	1 (4.3)
Other	28 (17.7)	18 (13.3)	10 (43.5)
	Miscellaneous		
Cladophora glomerata	37 (23.4)	37 (22.2)	0 (0)
Seeds or Pods	8 (5.1)	8 (5.9)	0 (0)
Human Food Remains	7 (4.4)	7 (5.2)	0 (0)

Table 9-3. Average total volume and percent of total volume of principal food categories in gut contents of humpback chub collected from three fish groups of the Colorado River in Grand Canyon, 1992-93. n = numbers of fish sampled; SE = standard error.

	(1) Above LCR Subregion Ia n=73		(2) Below LCR Subregion Ib n=55		(1 and 2) LCRI Region I n=128		(3) MGG Region II n=23		ANOVA[a] (df=2,149)
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
					Average Total Volume (ml)				
	1.0	0.1	1.4	.04	1.2	0.2	0.1 (1)	0.1	F=4.03, P=0.02
					Percent of Total Volume				
Cladophora	21.8	4.4	26.0(3)[b]	5.6	-	-	0 (1,2)	0	F=4.52, P=0.01
Invertebrates[c]	78.2	4.4	74.0(3)	5.6	76.1	3.4	100.0	0	F=4.52, P=0.01
Simuliids	42.6	4.6	39.7	4.7	40.2	0.4	49.1	7.7	F=0.83, P=0.44
Chironomid	5.7	2.3	4.3	1.9	5.3	0.2	4.6	1.7	F=0.04, P=0 97
Gammarus	44.2	4.9	43.8 (3)	5.4	44.8	0.5	10.4 (1,2)	5.3	F=8.19, P<0 01
Other	0.1 (3)	0.1	0.6 (3)	0.2	0.3	0.1	6.3 (1,2)	1.5	F=46.39, P<0 01
Terrestrial	7.4 (3)	2.2	11.6 (3)	3.3	9.4	0.2	29.6 (1,2)	7.5	F=7.4, P<0 01

[a]ANOVA includes data from Subregions Ia, Ib, and Region II.
[b]Number in parenthesis indicates a significant difference with the mean in the corresponding column in the same row (Fisher's LSD, P<0.05), e.g., mean total volume above LCR (Column 1) is significantly different than the mean for MGG (Column 3).
[c]includes invertebrates only, excludes Cladophora;

was also observed in guts of fish from the MGG aggregation, compared to those from the LCRI aggregation.

Seasonal Analysis

Seasonal comparisons of gut contents (all reaches pooled) showed differences between spring and summer/fall in diet of adult humpback chub (Fig. 9-4). Significant differences in volumetric composition of the diet were found only for simuliids and terrestrial invertebrates (Table 9-4). The percentage of gut contents composed of simuliids was significantly higher in summer and fall than in the spring. Percentage of terrestrial invertebrates was significantly lower in fall than in spring and summer. No differences were detected in

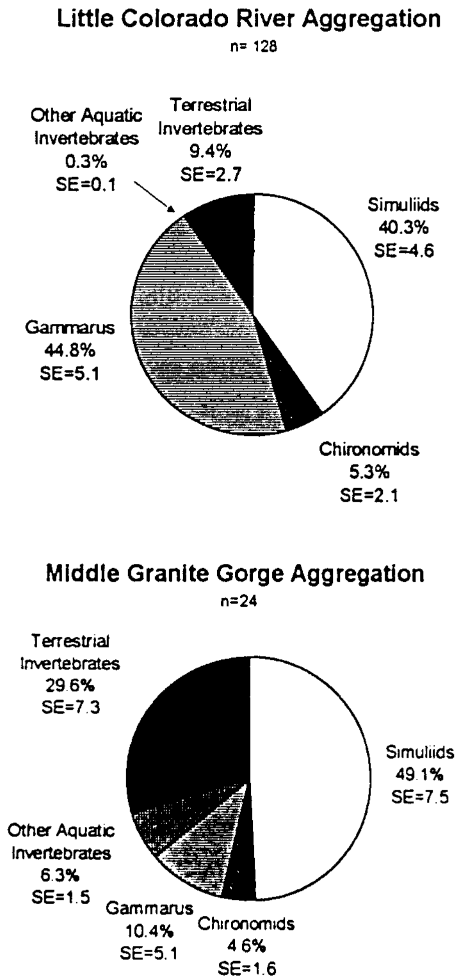


Fig. 9-3. Volumetric composition of invertebrates (excluding Cladophora) found in stomach contents of humpback chub from the Little Colorado River aggregation and the Middle Granite Gorge aggregation during 1992-93.

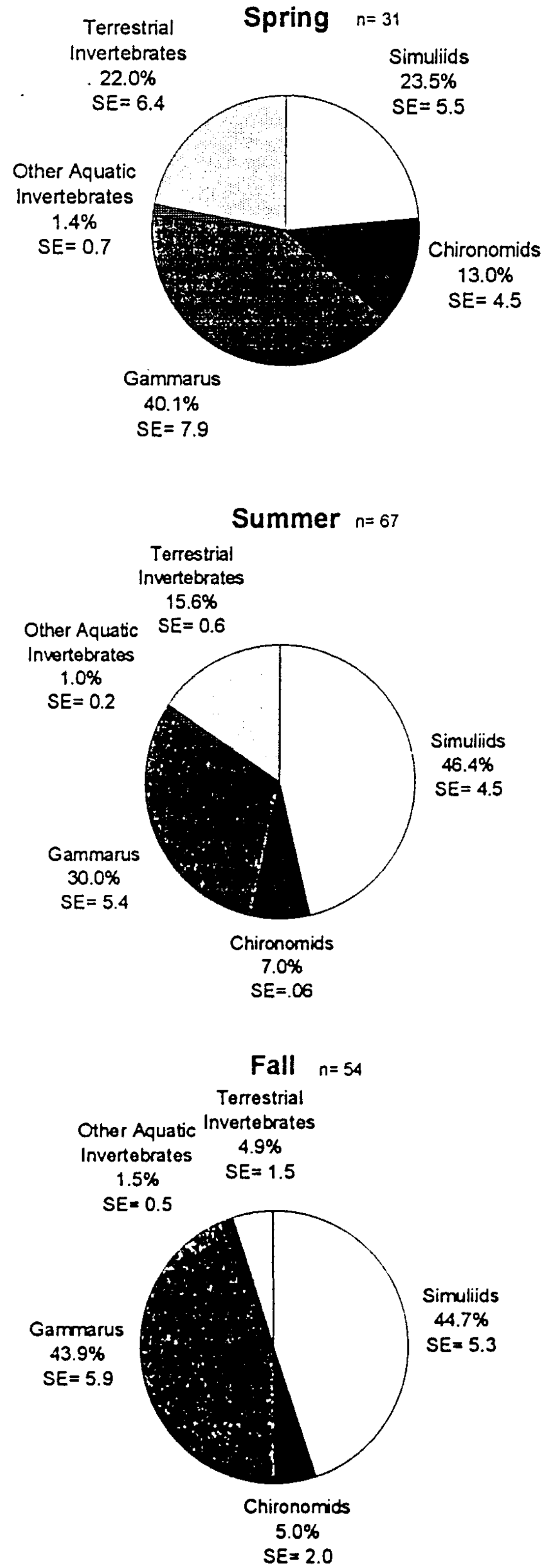


Fig. 9-4. Seasonal volumetric composition of invertebrates (excluding Cladophora) found in stomach contents of humpback chub captured between RM 57 and RM 130, Colorado River, Grand Canyon, 1992-93.

Table 9-4. Average total volume and percent volume of principal food categories in gut contents of humpback chub by season, collected between RM 57 and RM 130, Colorado River in Grand Canyon, 1992-93. n = number of drift samples; SE = standard error.

	(1) Spring n=31		(2) Summer n=67		(3) Fall n=54		ANOVA (df=2,149)
	Mean	SE	Mean	SE	Mean	SE	
Average Total Volume (ml)							
	1.1	0.3	1.0	0.2	1.0	0.3	F=0.02, P=0.98
Percent of Total Volume							
Cladophora	18.5	6.9	20.4	4.1	20.0	5.2	F=0.03, P=0.97
Invertebrates[b]	81.5	6.9	79.6	4.1	80.0	5.2	F=0.03, P=0.97
Simuliids	23.5	5.5	46.4	4.5	44.7 (1)[a]	5.3	F=4.30, P=0.02
Chironomids	13.0	4.5	7.0	0.6	5.0	2.0	F=1.70, P=0.19
Gammarus	40.1	7.9	30.0	5.4	43.9	5.9	F=2.34, P=0.10
Other	1.4	0.7	1.0	0.2	1.5	0.5	F=0.80, P=0.45
Terrestrial	22.0 (3)	6.4	15.6	0.6	4.9 (1,2)	1.5	F=4.94, P=0.01

[a]Number in parenthesis indicates a significant difference with the mean in the corresponding column in the same row (Fisher's LSD, P<0.05), e.g., % Simuliids in spring (Column 1) is significantly different than the mean for summer (Column 2) and fall (Column 3).
[B]includes invertebrates only, excludes Cladophora;

total volume, percent of diet composed of invertebrates and algae, or percent of diet composed of organisms within other categories (i.e., chironomids, Gammarus and other aquatic invertebrates).

Drift

Invertebrates from a total of 30 taxonomic categories, including 16 aquatic groups and 14 terrestrial groups, were collected in 603 drift samples during this investigation (Table 9-1). Algae (Cladophora glomerata) and organic debris were present in all samples collected in the mainstem Colorado River.

Longitudinal Analysis

Volumetric and numerical composition of drift samples collected from four sampling reaches indicated significant longitudinal variation in several taxonomic groups (Tables 9-5, 9-6). Greatest differences in the composition of drift were observed between Region I (RM 56.0-77.4, Subregion Ia, above the LCR inflow and Subregion Ib, below the LCR inflow) and Regions II (RM 77.4-159.9) and III (RM 159.9 and 226.0). Total volume of Cladophora in drift increased steadily downstream with significantly different means between regions I and regions II and III. In contrast, the volume of invertebrates decreased with distance downstream, with significant differences between Region I and Regions II and III. Relative volumetric compositions of invertebrates and Cladophora in drift samples were reflective of patterns in absolute volumes for each category. Drift samples collected in Region I and in combined Regions II and III contained significant amounts of algae (Fig. 9-5), which increased significantly in volume between Region I and Region III (Table 9-5, Fig. 9-6).

In contrast to algae, total invertebrate volume decreased significantly in a downstream direction between Region I and Regions II and III (Table 9-5). The relative composition of other aquatic invertebrates and terrestrial invertebrates increased between Region I and Regions II and III. No significant changes were observed in percentage of simuliids, chironomids or Gammarus. The only significant difference between relative composition of any category in drift samples collected above and below the LCR was for terrestrial invertebrates. An increase in terrestrial invertebrates downstream of the confluence of the LCR was probably associated with periodic flooding from the LCR which transported these organisms into the mainstem. No significant differences in volumetric composition of drift were detected between Regions II and III. Patterns in absolute numbers of different taxa in the drift differed slightly from volumetric composition.

Table 9-5. Average total volume and percent of total volume of principal food categories in drift samples by region in the mainstem Colorado River, Grand Canyon, 1991-93. n = number of drift samples; SE= standard error.

	(1) Subregion Ia n=331			(2) Subregion Ib n=80			(3) Region II n=131			(4) Region III n=30			ANOVA
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	
Average Total Volume (ml)													
Cladophora	26.76 (3,4)[a]	2.96	144	21.33 (3,4)	5.17	47	50.95 (1,2,4)	3.56	99	72.94	8.60	17	F=17.94, P<0.01,
Invertebrates[b]	0.87 (3,4)	0.11	331	0.77 (3,4)	0.15	80	0.31 (1,2)	0.03	131	0.21 (1,2)	0.05	30	F=8.75, P<0.01,
Percent of Total Volume													
Cladophora	86.9 (3,4)	1.9	144	90.4	3.3	47	94.6 (1)	2.3	99	99.5 (1)	5.5	17	F=4.92, P<0.01,
Invertebrates[b]	13.1 (3,4)	1.9	144	9.6	3.3	47	5.4 (1)	2.3	99	0.5 (1)	5.5	17	F=4.92, P<0.01,
Simuliids	38.9	1.6	331	35.2	3.5	80	33.7	2.2	131	47.6	5.0	30	F=1.86, P=0.14,
Chironomids	17.2	1.2	331	16.1	2.5	80	13.9	1.5	131	15.8	3.7	30	F=0.27, P=0.85,
Gammarus	36.4	2.0	331	36.0	4.2	80	32.8	2.9	131	18.1	5.0	30	F=2.54, P=0.06,
Other	2.7 (3,4)	0.5	331	4.3 (3)	1.2	80	9.0 (1,2)	1.4	131	6.8 (1)	3.3	30	F=14.66, P<0.01,
Terrestrial	4.8 (2,3,4)	0.7	331	8.4 (1,3)	1.8	80	10.6 (1,2)	1.4	131	11.7 (1)	4.1	30	F=11.57, P<0.01,

[a]Number in parenthesis indicates a significant difference with the corresponding column in the same row (Fisher's LSD, P<0.05), e.g., the mean Cladophora volume for Subregion Ia (Column 1) is significantly different than the mean for Region II (Column 3) and Region III (Column 4).
[B]includes invertebrates only, excludes Cladophora;

Table 9-6. Numbers of invertebrates in 100 m^3 of water filtered in drift samples by region, in the mainstem Colorado River, Grand Canyon 1991-93. n = number of drift samples; SE = standard error.

	(1) Subregion Ia n=331		(2) Subregion Ib n=80		(3) Region II n=131		(4) Region III n=30		ANOVA (df=3,568)
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Simuliids	65.0 (3,4)[a]	4.5	56.5 (3)	8.0	27.4 (1,2)	2.4	30.3 (1)	7.0	F=10.12, P<0.01
Chironomids	166.8 (3,4)	16.2	132.5	22.5	71.3 (1)	8.6	52.3 (1)	11.1	F=6.11, P<0.01
Gammarus	17.7 (3,4)	2.0	18.2 (3,4)	5.3	4.7 (1,2)	0.7	2.7 (1,2)	1.1	F=6.44, P<0.01
Other Aquatic	6.5	1.7	13.2	4.9	11.7	1.8	3.1	0.9	F=1.89, P=0.13
Terrestrial	10.8	1.3	14.4	3.6	17.3	3.3	7.5	2.5	F=2.01, P=0.11
Total Number	266.8 (3,4)	21.0	234.8 (3,4)	32.0	132.4 (1,2)	12.9	96.0 (1,2)	17.0	F=7.22, P<0.01

[a]Number in parenthesis indicates a significant difference with the corresponding column in the same row (Fisher's LSD, P<0.05). The mean number of Simuliids in Subregion Ia (Column 1) is significantly different than the mean for Region II (Column 3) and Region III (Column 4).

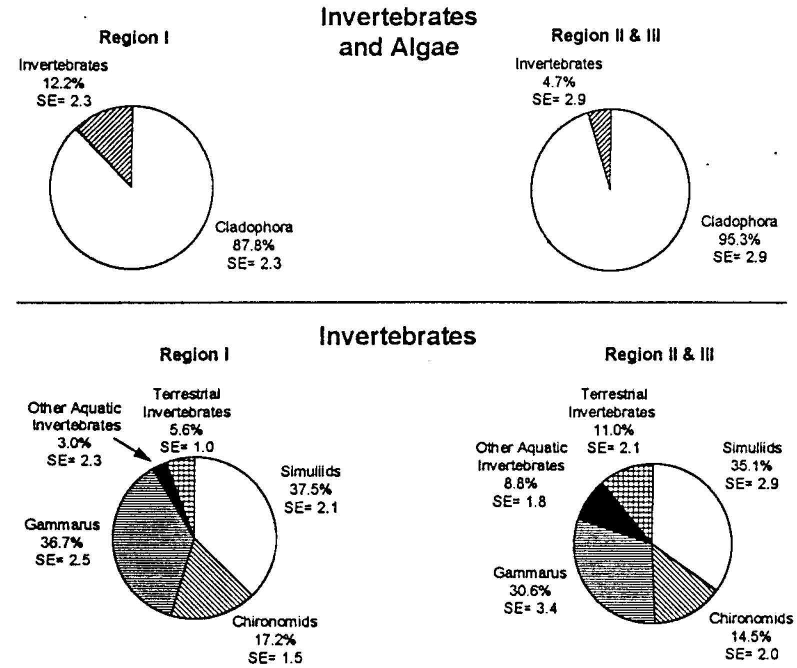


Fig. 9-5. Volumetric composition of drift collected from Region I and Regions II and III of the Colorado River, Grand Canyon, 1991-93.

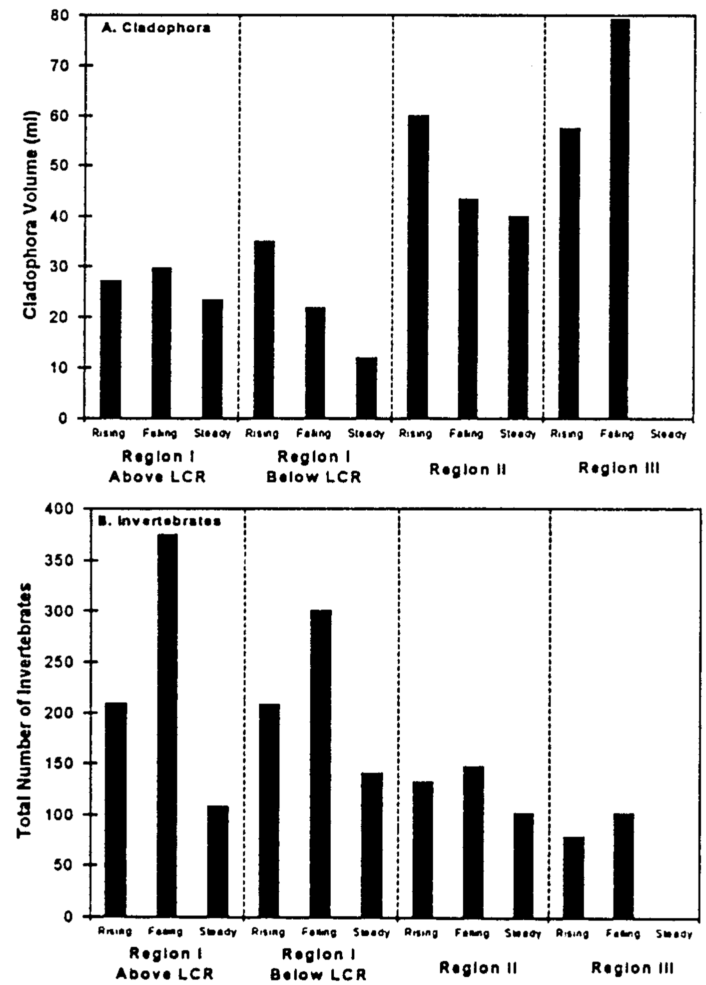


Fig. 9-6. Volume of Cladophora (A) and total number of invertebrates (B) collected in drift samples during rising, falling and steady limbs of the hydrograph, by region in the Colorado River, Grand Canyon, 1991-93.

Numbers of simuliids/100 m^3 wf and total invertebrates/100 m^3 wf were higher in Region I than in Regions II and III (Table 9-6).

Seasonal Analysis

Data for seasonal analysis were partitioned into Region I, representing samples collected above and below the LCR (RM 57 to 76.5), and the pool of data from samples collected in Regions II and III (RM 76.5 to 226).

Significant seasonal patterns were detected in relative composition of the drift in four taxonomic categories in Region I and two in Regions II and III (Table 9-7). Volumes of simuliids were not significantly different between seasons in either region, while volumes of chironomids exhibited the most seasonal variability in both regions. In Region I, chironomid volume peaked in the spring and continued to decrease in summer and fall. In contrast, peak chironomid volumes occurred in summer in Regions II and III, followed by spring and fall. In Region I, relative volume of Gammarus was highest in summer, followed by fall and spring; in Regions II and III, volume was highest in spring, followed by fall and summer. The relative composition of other aquatic invertebrates showed significant seasonal variation in both reaches, with highest relative volumes in the fall. Terrestrial invertebrates also varied seasonally in Region I, with highest relative volumes observed in summer. In Regions II and III, highest relative volumes of terrestrial invertebrates were observed in spring.

Effect of Flow Change on Drift

Numbers of drifting organisms and total volume of Cladophora were significantly different among rising (up-ramping), falling (down-

Table 9-7. Percentage composition by volume of invertebrates in drift samples by season for Region I and Regions II and III, collected in the mainstem Colorado River, Grand Canyon, 1991-93. n = number of drift samples; SE = standard error.

	(1) Spring			(2) Summer			(3) Fall			ANOVA
	Mean	SE	n	Mean	SE	n	Mean	SE	n	
Region I										
Simuliids	38.4	2.6	130	33.2	2.3	141	34.6	2.8	140	F=1.16, P=0.31, df=2,408
Chironomids	24.6 (2,3)[a]	2.3	130	15.6 (1,3)	1.5	141	11.4 (1,2)	1.4	140	F=14.68, P<0.01, df=2,408
Gammarus	30.6 (2)	3.3	130	34.8 (1)	2.9	141	35.0	3.2	140	F=4.31, P<0.01, df=2,408
Other Aquatic	2.3 (3)	0.7	130	9.8 (3)	0.3	141	13.4 (1,2)	1.1	140	F=9.68, P<0.01, df=2,408
Terrestrial	4.1	0.6	130	6.6 (3)	1.0	141	5.6 (2)	1.6	140	F=3.39, P<0.01, df=2,408
Regions II and III										
Simuliids	27.6	3.3	48	37.3	4.3	26	37.3	3.1	87	F=0.94, P=0.39, df=2,158
Chironomids	14.2 (2)	1.8	48	24.3 (1,3)	4.4	26	14.7 (2)	1.8	87	F=7.51, P<0.01, df=2,158
Gammarus	35.9	4.4	48	24.3	5.0	26	28.5	3.9	87	F=1.26, P=0.29, df=2,158
Other Aquatic	8.7 (2)	2.1	48	2.4 (1,3)	1.8	26	10.4 (2)	1.9	87	F=3.92, P=0.02, df=2,158
Terrestrial	13.6	2.2	48	11.7	3.7	26	9.1	1.0	87	F=3.02, P=0.05, df=2,158

[a]Number in parenthesis indicates a significant difference with the mean in the corresponding column in the same row (Fisher's LSD, P<0.05), e.g., the mean percent chironomids in spring (Column 1) is significantly different than the mean for summer (Column 2) and fall (Column 3).

ramping), and steady flows associated with daily release cycles from Glen Canyon Dam. Average total volume of Cladophora was significantly higher in samples collected during up-ramp and during down-ramp than those collected during steady flows (Table 9-8). Differences in average Cladophora volume in drift collected during up-ramp and down-ramp were not significant. Total numbers of invertebrates were also higher during down-ramp than during either up-ramp or steady flows. Numbers were higher during up-ramp than during steady flows, but these differences were not significant.

When partitioned by season and reach, the pattern of highest invertebrate numbers during down-ramp was remarkably consistent (Fig. 9-6, Fig. 9-7). The consistency of this pattern strongly suggests that diel flow fluctuations affected invertebrate drift throughout the year and throughout the canyon, although the effects appeared to diminish in the lower end of the canyon. Patterns of algal drift did not exhibit the same consistency between seasons or reaches as with invertebrate numbers. Differences in patterns of algal and invertebrate drift suggest that unique mechanisms may be affecting the drift of these groups.

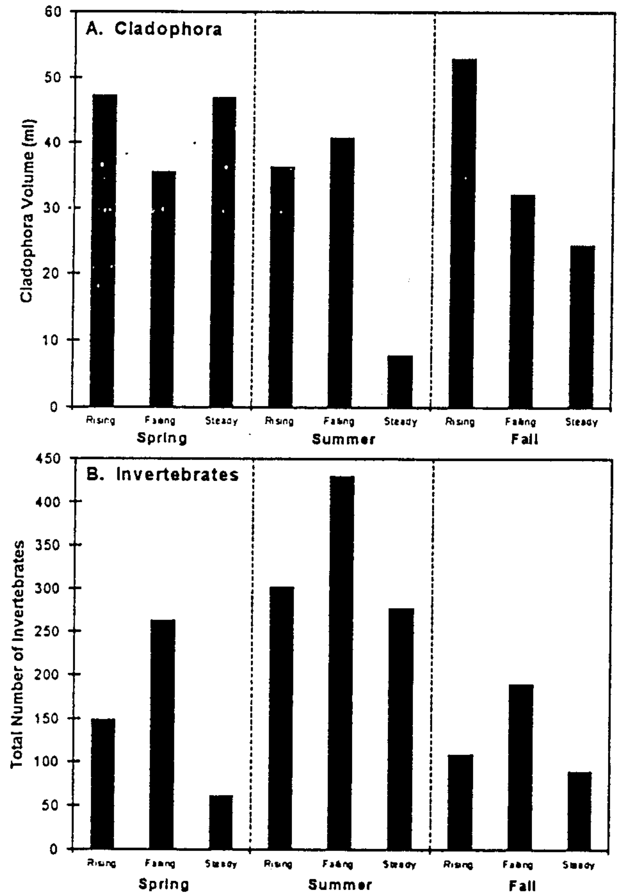


Fig. 9-7. Volume of Cladophora (A) and total number of invertebrates (B) collected in drift samples during rising, falling and steady limbs of the hydrograph, by season, in the Colorado River, Grand Canyon, 1991-93.

Table 9-8. Numbers of invertebrates and volume of Cladophora in drift during rising (up-ramp), falling (down-ramp) and steady flows in the mainstem Colorado River, Grand Canyon, 1991-93. n = number of drift samples; SE = standard error.

	(1) Rising n=195		(2) Falling n=261		(3) Steady n=116		ANOVA (df=2,569)
	Mean	SE	Mean	SE	Mean	SE	
Volume of Cladophora (ml) [a]	44.5 (3)[b]	3.7	37.1 (3)	3.4	24.8 (1,2)	4.1	F=6.38, P<0.01
Invertebrates[c]	178.4 (2)	22.6	304.1 (1,3)	19.5	113.5 (2)	29.3	F=17.58, P<0.01
Simuliids	45.6 (2)	5.1	65.2 (1,3)	4.4	39.8 (2)	6.6	F=6.98, P<0.01
Chironomids	99.6 (2)	17.0	198.8 (1,3)	14.7	46.7 (2)	22.1	F=19.61, P<0.01
Gammarus	15.8	2.4	13.6	2.1	11.6	3.1	F=0.57, P=0.56
Other Aquatic	5.3	2.2	11.3	1.9	7.4	2.8	F=2.28, P=0.10
Terrestrial	12.1	2.1	15.1	1.8	7.8	2.7	F=2.60, P=0.08

[a] Sample size for analysis of Cladophora volume is as follows: Rising - n=104; Falling - n=120; Steady - n=83; ANOVA - df=2,304.

[b] Number in parenthesis indicates a significant difference with the mean in the corresponding column in the same row (Fisher's LSD, P<0.05), e.g., the mean for volume of Cladophora during rising flows (Column 1) is significantly different than the mean for steady flows (Column 3).

[c] includes invertebrates only, excludes Cladophora;

Further evaluation of the six invertebrate taxa indicated that flow changes had the greatest effect on simuliids and chironomids, with significantly higher numbers during down-ramp than during up-ramp and steady flows (Table 9-8). Although numbers of other aquatic and terrestrial invertebrates also exhibited the same pattern, differences between rising, falling, and steady flows were not significant. Total numbers of Gammarus in the drift were not significantly affected by flow changes, but did exhibit a different pattern than the other invertebrates with highest numbers during up-ramp.

Electivity Indices

Johnson's Electivity Indices (JEIs) indicated that the relative abundance of food items in guts of humpback chub were different than relative availability of food items in drift (Table 9-9). Cladophora was the most abundant food item in drift (rank = 1) during all seasons and in all regions, but on average ranked approximately fourth (rank = 4) in abundance in gut contents during all seasons of the year. JEI for Cladophora was significantly lower than for any other food item during all seasons examined. Highest JEIs were consistently observed for other aquatic invertebrates and terrestrial invertebrates (primarily ants and beetles) during all seasons, suggesting that these food items were consumed at a disproportionately higher level than their availability in the drift. Johnson's Electivity Indices for simuliids, chironomids and Gammarus indicated that these organisms were consumed in approximate proportion to their availability in the drift. Of the three categories, simuliids were preferred over the other two taxa, particularly during summer, when the JEI for simuliids was significantly higher than for all food items except other aquatic invertebrates and terrestrial invertebrates.

Food Habits of Non-Native Fishes

The food habits of five non-native fish species (i.e., channel catfish, striped bass, walleye, brown trout and rainbow trout, n = 328) were determined during the course of this study. Analyses were based on combined samples for 1991, 1992, and 1993.

Of the five species, rainbow trout contained the greatest mean numbers of invertebrates per stomach (mean = 58.8) (Table 9-10). Channel catfish contained an average of 25 invertebrates per stomach, while striped bass, brown trout, and walleye contained few invertebrates but higher numbers of fish. Brown trout averaged 0.31 fish per stomach. Percent relative abundance of simuliids was greatest for channel catfish, striped bass, and rainbow trout. Gammarus were in greatest proportions in channel catfish, rainbow trout, and brown trout. Chironomids and terrestrial invertebrates were relatively rare except in channel catfish.

The filamentous green alga, Cladophora glomerata, was present in four of the five non-native species, but overall accounted for about 1% of combined stomach volume. Channel catfish and rainbow trout contained the greatest volumes of Cladophora. The presence of Cladophora in rainbow trout is similar to the findings of Leibfried (1988), Maddux et al. (1987) and Bancroft and Sylvester (1978) that reported this alga as a major component in the diets of rainbow trout in the Colorado River in Grand Canyon. Leibfried (1988) also provided data suggesting that diatoms attached to Cladophora enhance the trout diet by providing high energy lipids.

Predation By Non-Native Fishes

Of 328 stomach samples taken from non-native fishes, only 6.1% contained fish remains. Species with fish remains included channel catfish, striped bass, walleye, brown trout, and rainbow trout. Brown trout contained the highest incidence of fish with 9 of 48 (18.8%) stomachs examined containing remains of 15 fish. Five brown trout consumed 10 humpback chub, therefore 10.4% of the brown trout sampled preyed on chub. One brown trout contained four humpback chub (range, 78-130 mm SL) in its stomach. All brown trout with fish remains were captured between the LCR inflow (RM 61.3) and RM 68.

Five of 68 (7.4%) channel catfish stomachs examined contained fish remains. A total of 8 fish were found in these 5 stomachs, including 1 humpback chub, 1 bluehead sucker, 1 flannelmouth sucker, 1 unidentified sucker, and 4 unidentified fish. The humpback chub was approximately 95 mm SL and the identified suckers were 150 and 170 mm SL, respectively.

A total of 48 striped bass were taken for stomach contents, including 39 from this study and 9 from a

Table 9-9. Summary of mean Johnson's electivity indices by season for food items including Cladophora and five taxonomic categories of invertebrates collected from 152 humpback chub in the Colorado River, Grand Canyon 1991-93. High numbers indicate relatively higher use than availability.

	(1) Cladophora	(2) Simuliids	(3) Chironomids	(4) Gammarus	(5) Other Aquatics	(6) Terrestrial	ANOVA
Spring	-3.08 (2,3,4,5,6)[a]	0.05 (1,5,6)	-0.50 (1,5,6)	0.15 (1,5,6)	1.66 (1,2,3,4)	1.73 (1,2,3,4)	F=42.2, P<0.01, df=5,180
Summer	-2.89 (2,3,4,5,6)	0.79 (1,3,4,5,6)	-0.10 (1,2,4,5,6)	-0.72 (1,2,3,5,6)	1.41 (1,2,3,4)	1.51 (1,2,3,4)	F=95.77, P<0.01, df=5,396
Fall	-2.91 (2,3,4,5,6)	-0.11 (1,4,5,6)	0.59 (1,5,6)	0.16 (1,2,6)	0.91 (1,2,3)	1.36 (1,2,3,4)	F=64.95, P<0.01, df=5,318
Combined	-2.94 (2,3,4,5,6)	0.31 (1,4,5,6)	0.07 (1,5,6)	-0.23 (1,2,5,6)	1.28 (1,2,3,4)	1.5 (1,2,3,4)	F=185.56, P<0.01, df=5,906

[a]Mean electivity index is significantly different than mean index in corresponding column in same row (Fisher's LSD; P<0.05), e.g., electivity index for Cladophora (Column 1) is significantly different than mean indices for all other categories (Columns 2-6).

Table 9-10. Mean numbers per stomach and percent relative abundance of stomach contents for non-native fishes collected from the Colorado River in Grand Canyon, 1991-1993.

Fish Type	n	Gammarus		Chironomid		Simuliid		Other Aquatics		Terrestrials		Cladophora	Fish
		Mean No.	% Rel. Abun.	Mean No.	% Rel. Abun.	Mean No.	% Rel. Abun.	Mean No.	% Rel. Abun.	Mean No.	% Rel. Abun.	Displacement Volume	Displacement Volume
CC	68	6.25	24.53	3.15	12.36	9.82	38.54	1.54	6.04	4.72	18.53	1.49	0.12
SB	48	0.06	2.50	0.15	6.25	1.75	72.92	0.23	9.58	0.21	8.75	0.38	0.15
WE	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
BR	48	4.02	85.71	0.02	0.43	0.17	3.62	0.13	2.77	0.35	7.46	0.06	0.31
RB	163	14.9	25.34	2.47	4.20	36.69	62.41	3.38	5.75	1.35	2.30	0.62	0.006

CC = channel catfish
SB = striped bass
WE = walleye
BR = brown trout
RB = rainbow trout

study for the Hualapai Tribe (Valdez 1993, 1994, 1995). Four of the 48 (8.3%) stomachs contained 7 fish, including 3 trout and 4 unidentified specimens. All striped bass were captured in Regions II and III. No identifiable native fish were observed in striped bass.

Only one unidentified fish was found in the stomachs of 163 rainbow trout examined (0.6%). This trout was captured at RM 63.9 and the remains were digested beyond identification. No other fish remains were found in rainbow trout stomachs. The dominance of invertebrates and algae in rainbow trout stomachs (Table 9-10) and the lack of fish reflect the feeding habits of rainbow trout in Grand Canyon as described by Maddux et al. (1987), and Leibfried (1988).

DISCUSSION

A food habits study conducted during this investigation indicated that humpback chub in Grand Canyon utilized a variety of food items in their diet including numerous species of invertebrates of aquatic and terrestrial origin. Simuliids were the most common food item by number, while Gammarus, simuliids, chironomids, and terrestrial invertebrates (primarily ants and beetles) composed the bulk of the diet by volume. The green algae, Cladophora glomerata, made up about 20% of the gut volume of fish from the LCRI aggregation, but it was not determined if this item was a food staple or ingested incidental to other items. Comparisons between items in drift with those found in gut contents indicated that humpback chub were general in their feeding habits, utilizing most available taxa. The presence of seeds or pods and human food remains also demonstrates that these fish were opportunistic in their feeding habits.

Kaeding and Zimmerman (1983) reported that larvae of simuliids and chironomids were numerically dominant in stomach contents of 18 humpback chub collected from the mainstem during 1980. These taxa were also the numerically dominant food items found during this investigation, although volumetrically, simuliids and Gammarus were equally important. Chironomids averaged only about 5% of the volume of gut contents. Kaeding and Zimmerman (1983) noted that Gammarus were not utilized to a large extent despite their apparent abundance in littoral areas of the mainstem Colorado River. They found that, numerically, Gammarus composed approximately 1% of stomach contents and were found in only 11% of the fish examined. In contrast, this investigation determined that Gammarus were an important component of the diet in all seasons, composing approximately 44% of food volume in Region I and occurring in 64% of all guts examined.

Examination of 17 humpback chub from the mainstem Colorado River in 1985-86 by Kubly (1990) indicated that the filamentous green alga, Cladophora glomerata, composed 77% of the volume of stomach contents, and chironomids and adult terrestrial insects represented 10% of volume. The present investigation showed that Cladophora was not used as extensively by humpback chub, composing approximately 20% of gut volume of 128 fish captured in Region I, but this algae was absent from gut contents of 23 humpback chub captured in Middle Granite Gorge (Region II). Ingestion of Cladophora by humpback chub may be related to foraging on diatoms or other invertebrates associated with the algae. Minckley et al. (1981) and Leibfried (1988) found that epiphytic diatoms on Cladophora consumed by rainbow trout provided 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 the algae in rapids. The decreased use of Cladophora by humpback chub in Middle Granite Gorge may reflect this loss of epiphytic diatoms and associated organisms, hence, reducing the value of the algae as a food item. Or, perhaps the algae is too pulverized in downstream regions for the fish to ingest as pockets.

Food habits information for humpback chub from populations outside of the Grand Canyon is limited. Analysis of 25 YOY and juvenile Gila sp. from the Green and Upper Colorado Rivers indicates that ephemeroptera and diptera were important food items (Jacobi and Jacobi 1982). The diet of "Colorado chub" (roundtail chub and bonytail) was chironomid larvae and ephemeroptera nymphs for small fish (<200 mm TL), and aquatic and terrestrial insects (adult beetles, grasshoppers and ants) for larger fish (>200 mm TL) (Vanicek 1967). Tyus and Minckley (1988) reported that humpback chubs utilized migrating Mormon crickets (Anabrus simplex), a large terrestrial, flightless locust in the

Green and Yampa rivers within Dinosaur National Monument. These studies suggest that humpback chub are opportunistic in their feeding habits, utilizing food sources as they become available. Periodic increases in availability of terrestrial and aquatic invertebrates from irregular flood events or insect hatches may have been an important factor in the evolution of the feeding strategies of this species. Selection of terrestrial invertebrates as well as some relatively uncommon taxa of aquatic origin may reflect these strategies.

Patterns in selectivity of drifting food items by humpback chub, based on JEIs, indicates that humpback chub selected terrestrial invertebrates relative to their occurrence in the drift. Blinn et al. (1994) reported that terrestrial insects were not an important component of stream drift in the Colorado River through Grand Canyon and suggested that availability may be greatly increased during and after rainstorm events. The relatively high use of this food source by humpback chub indicates that these fish were either very adept at foraging on these organisms in the drift, or they were able to locate areas where these items were entrained and concentrated. Blinn et al. (1994) indicated that entrapment of drifting material in the Colorado River in Grand Canyon occurs in recirculation zones (i.e., eddies) and pools. Observations of radio-tagged adult humpback chub during this investigation indicated that eddies were used extensively and fish moved frequently between different eddies (See Chapter 7-HABITAT). These movement patterns suggest a feeding strategy focused on areas where food items are entrained such as drifting invertebrates.

Simuliids, Gammarus, and chironomids represented dominant food items in the diet of humpback chub in Grand Canyon, particularly in the LCRI aggregation. Electivity indices, based on availability of these food items in the drift, suggest that humpback chub utilized these taxa in approximately the same proportion as their availability in the drift. Simuliids were selected over the other two taxa during the summer, and other aquatic invertebrates and terrestrial invertebrates (primarily ants and beetles) were selected in all seasons.

Since calculation of electivity indices for this study only considered availability of food items in the drift, these results should be interpreted with caution. Availability of benthic food items were not evaluated during this investigation, but may contribute substantially to the food base of humpback chub. Blinn et al. (1992) found that standing crop biomass of most macroinvertebrates, particularly Gammarus and chironomids, significantly declined with increasing distance downstream of Glen Canyon Dam. Declines of these invertebrates were directly related to decreased standing crop of Cladophora downstream of the dam. In contrast, Blinn et al. (1992) also found that standing crop biomass of simuliids increased in downstream reaches. Consequently, selection for simuliids, based on comparison with food availability in the drift, may be misleading if humpback chub were utilizing benthic standing crops of simuliids instead of drift. Conversely, low standing crop biomass of Gammarus and chironomids in downstream reaches used by humpback chub, suggests that drift of these organisms from upstream reaches may be the key mechanism related to their availability as food items.

Numbers of drifting invertebrates and volume of Cladophora during rising, falling, and steady flows indicates that diurnal fluctuations associated with operations of Glen Canyon Dam differentially affected food availability. High numbers of invertebrates, particularly simuliids and chironomids during down-ramp, suggests a behavioral response, while high Cladophora volumes during up-ramp suggests a dislodging effect of epiphytic algae. Cessation of daily flow cycles from Glen Canyon Dam would likely alter diel patterns of invertebrate drift observed during this study, possibly reducing numbers of drifting simuliids and chironomids, two primary food items of humpback chub. Direct effects on food availability for humpback chub would depend on how extensively drift is utilized as a food resource compared to benthos.

Competition between humpback chub and non-native fish species for food resources appears to exist in the reach occupied by the LCRI aggregation. Rainbow trout have a similar diet to that of humpback chub and represent a potential competitor when food resources are limited. However, differences in habitat use and feeding behavior between the two species act to create a degree of spacial segregation and reduce competition.

Relatively high condition factors for adult humpback chub throughout this investigation indicate that food was not limiting for adults in the mainstem. However, condition of rainbow trout in the mainstem near the LCR was more variable and often low, indicating that adult humpback chub were more efficient at foraging than rainbow trout, particularly during periods of high turbidity associated with either flow fluctuations or tributary input.

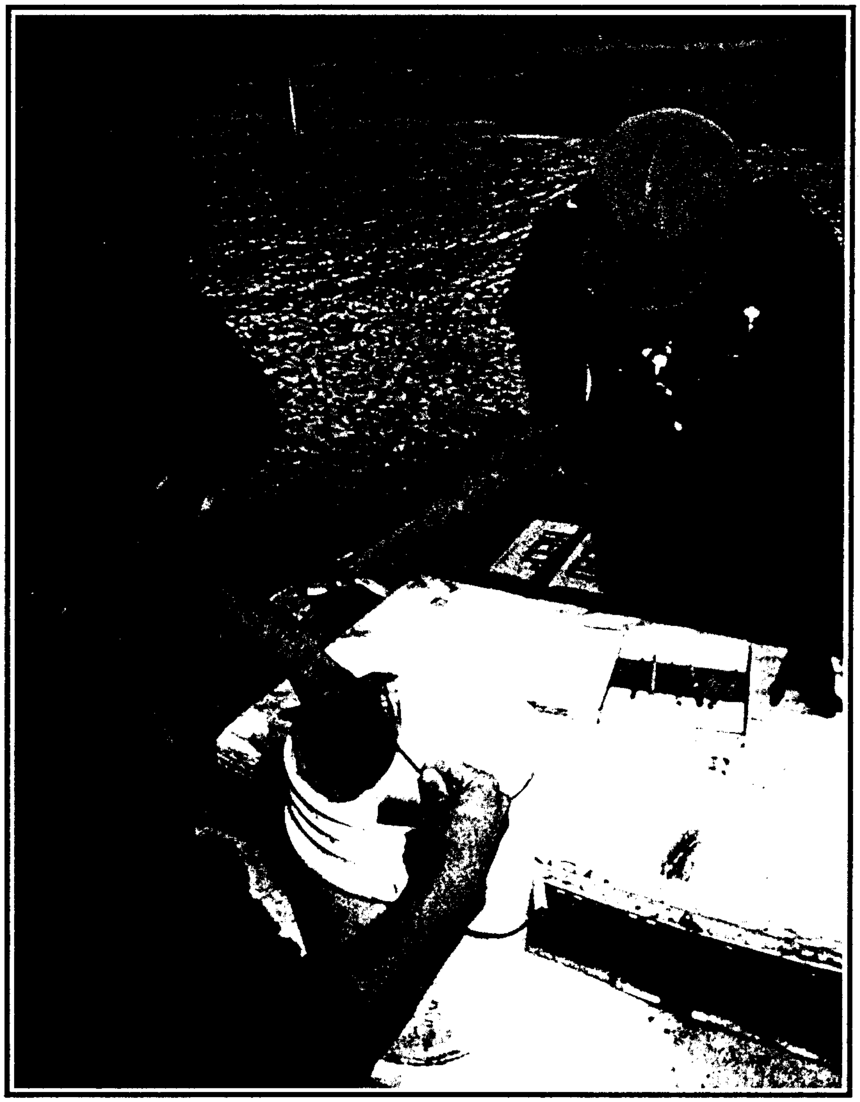
We hypothesize that research flows from June 1, 1990, through July 29, 1991, maintained high fluctuating releases that enhanced drift and sediment loads which kept water clarity low and reduced foraging opportunities for sight-feeding trout. Hence, the condition of rainbow trout late in 1990 and early in 1991 was substantially reduced while the condition of humpback chub remained high (See Chapter 6 - DEMOGRAPHICS).

Although food for adults may be adequate, it may be limiting for subadults since the smaller fish select shoreline habitats that may have low in-situ production, particularly in the more downstream reaches of reduced phototrophy. If adults feed primarily in large recirculating eddies and subadults use shallow shorelines, feeding strategies may differ and hence, the present aquatic ecosystem in Grand Canyon may not supply food to all ages.

Examination of stomach contents of piscivorous non-native fishes during this investigation suggests that brown trout were the most significant predator on humpback chub in the mainstem. This piscivorous feeding behavior is typical for the species (Carlander 1969). The increase in abundance of brown trout since about 1980 in the Inner Gorge of Grand Canyon (Carothers and Minckley 1981) has increased concern over their impact on native fishes. The proportion of brown trout to rainbow trout at Bright Angel Creek in 1980 was one in ten (Usher et al. 1984), but results of this investigation suggest that this proportion has been reversed. The piscivorous habits of brown trout and their apparent expansion in abundance is worthy of further investigation. Further studies addressing causes for the increase in non-native fishes and documenting predation of native fishes should be included in future monitoring of the Colorado River in Grand Canyon.

Integration and Recommendations

Chapter 10



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CHAPTER 10 - INTEGRATION

INTRODUCTION

This chapter integrates information assimilated on the life history and ecology of the humpback chub in Grand Canyon and identifies limiting factors related to the operation of Glen Canyon Dam. The effects of dam operations on life history aspects are described, and some management options are evaluated and discussed that could help conserve the humpback chub and other native fishes in Grand Canyon. We view this report as an assimilation of information to provide insight into management options. These options are discussed with respect to our findings and those of other investigations. We also offer recommendations for future core research and long-term monitoring.

This chapter is presented in four sections: (1) life history and ecology of the humpback chub, (2) effects of Glen Canyon Dam operations, (3) management options, and (4) recommendations. The first section describes the evolutionary history of the humpback chub and provides a characterization of the life history and ecology of the species in the Colorado River Basin with emphasis on the Grand Canyon. The second section identifies and describes the effects of Glen Canyon Dam operations on each life history aspect and distinguishes predam conditions from effects of dam construction and operation. The third section presents management options for conserving the native ichthyofauna and associated ecological benefits and risks. The fourth section presents recommendations for future core research and long-term monitoring.

LIFE HISTORY AND ECOLOGY OF THE HUMPBACK CHUB

This section describes the evolutionary history of the humpback chub and its life history and ecology. Knowing the evolutionary history of the species is important in understanding its life history requirements and survival strategies, and in determining how these strategies have been affected by anthropogenic activities, including the construction and operation of Glen Canyon Dam. Information from past investigations in Grand Canyon and from other populations is integrated to provide a perspective of life history for the known range of the species.

Evolutionary History

The humpback chub is one of 35 fish species native to the Colorado River Basin. The species is part of an ichythofaunal assemblage with the highest level of species endemism (74% or 26 species) of any major basin in North America (Miller 1959). A long period of geographic isolation for the Colorado River, together with high gradient, high sediment, and variable flow volumes and temperatures have combined to shape this unique assemblage. It is surmised that the humpback chub speciated from a G. elegans-like (i.e., bonytail-like) form in canyons of Northern Arizona (i.e., Grand Canyon) about 3 million years ago (Miller 1946, Minckley et al. 1986). It was during these mid-Pliocene and early Pleistocene epochs that the Colorado River was cutting through the Kaibab upwarp of the Colorado Plateau to join the ancient upper basin with the lower Hualapai Drainage System (McKee et al. 1967).

The species is part of the Gila complex and one of six forms inhabiting the basin, including the humpback chub (G. cypha), bonytail (G. elegans), roundtail chub (G. robusta), Virgin River chub (G. robusta seminuda), Pahranagat roundtail chub (G. r. jordani), and Gila chub (G. intermedia). The humpback chub, bonytail, and roundtail chub are mainstem sympatric species with substantial evidence of introgressive hybridization (Dowling and DeMaris 1993), while the Virgin River chub, Pahranagat roundtail chub, and Gila chub are isolates and primarily tributary inhabitants, although historic hybridization with other forms of Gila is also evident.

Roundtail chub are sympatric in all upper basin populations of humpback chub and morphologic integrades are common. Nevertheless, the mainstem species are considered morphologically and ecologically distinct (Holden and Stalnaker 1970, Valdez and Clemmer 1982, Douglas et al. 1989). Roundtail chub typically inhabit mid to upper elevation rocky reaches, humpback chub are primarily canyon-bound inhabitants, and bonytail were probably inhabitants of middle and lower basin regions. Bonytail are nearly extinct in the upper basin (Valdez et al. 1995), and are confined as wild adults to Lake Mohave in the lower basin (Minckley et al. 1989). Roundtail chub are common in rocky reaches of the upper basin (Tyus et al. 1982, Valdez and Clemmer 1982), but remain only locally common in tributaries of the lower basin.

The population of humpback chub in Grand Canyon is presently allopatric with respect to congeneric species, but bonytail and roundtail chub were reported from the Colorado River in Grand Canyon and from the LCR as recently as the 1940s (morphometric and meristic data collected by R.R. Miller and received from M. Douglas), indicating long-term sympatry. Roundtail chub were recently reported from Chevelon Creek of the upper LCR (R. Clarkson, AGF, pers. comm.), but none have been found recently with humpback chub in the LCR or other waters in Grand Canyon.

Life History And Ecology

The life history and ecology of the humpback chub in Grand Canyon are similar in many respects to those of the species in the five other recognized populations. All populations are restricted to canyon-bound regions in which individual adults exhibit high fidelity for particular sites (Valdez and Clemmer 1982, Kaeding et al. 1990, Karp and Tyus 1990), and long-range dispersal of young is not evident (Muth 1990). Spawning by all populations is suspected to occur in local or centralized mainstem sites, except in Grand Canyon where the main population spawns primarily in the LCR from March through May. Spawning related movements from the mainstem to the LCR ranged up to 40 km, round-trip. Eight other mainstem aggregations of humpback chub, largely isolated from the aggregation that spawns in the LCR, reach spawning readiness from May through July or approximately the same time as upper basin populations and probably about the same time that spawning occurred predam in Grand Canyon.

The majority of humpback chub in the mainstem Colorado River in Grand Canyon appear to have originated from the LCR. Reproduction in this tributary appears to be the primary source of fish for the mainstem downstream of about RM 56 (Kwagunt Rapid). The only possible exceptions are predam relicts of what is hypothesized to have been a larger mainstem population. These relicts are suspected to persist as a small aggregation of fish (40-60 adults) near RM 30 and as small numbers of adults mixed with LCR progeny in the mainstem scattered in aggregations from the LCR downstream. Reproduction by the 30-Mile aggregation appears to occur in small shoreline tepid springs, but survival of young and recruitment to adults appears very limited or nonexistent. Reproduction by other mainstem fish may also occur, but apparently with minimal, if any success.

We hypothesize that before the dam, humpback chub were distributed throughout much of the mainstem Colorado River in Grand Canyon. This mainstem population was the main reproducing group, and the fish that ascended the LCR were a small component or stock of that group. Construction and operation of Glen Canyon Dam essentially reversed the relative importance of the mainstem and the LCR. We believe that the fish that spawn in the LCR are largely the progeny of an historic LCR stock. We further believe that the mainstem stock is largely lost, except for about 40-60 adults in warm springs near RM 30, and possibly some adults mixed with LCR progeny in downstream reaches.

Today, the major population of humpback chub in Grand Canyon is associated with the lower 14.9 km of the LCR, and with the adjacent 13.5 km of the mainstem (6.9 km upstream and 6.6 km downstream of the LCR inflow). This population is composed of a full complement of age groups, with young produced annually in the LCR. The population appears to be centered in the LCR with many fish using the mainstem (i.e., LCRI aggregation). The fish in the LCR appear to be composed of all age groups, while the fish in the mainstem are composed of 3,000-3,500 adults, with varying numbers of young subadults depending on reproductive success in the LCR and time of descent to the mainstem.

Genetic exchange between the two groups of fish is likely since spawning in the LCR appears to overlap spatially and temporally. Of mainstem adults recaptured during spawning ascent of the LCR, 36% were found upstream of the lower 5 km of the LCR. Smaller numbers were found up to 14.9 km from the mouth, suggesting the likelihood of mixed spawning. Humpback chub are social broadcast spawners and there is probably at least some if not nearly complete mixing of stocks.

Although many young emerged from the LCR, it was not possible to link their parental origin to the mainstem fish or to the LCR fish. The social nature of the species suggests mixed schooling of young from LCR and mainstem "stocks", and young descending to the mainstem are probably progeny of both components; segregational descent by progeny of mainstem fish is unlikely. Conversely, the numbers of young chubs remaining in the LCR may be determined by available habitat and food, suggesting density dependence, which we hypothesized forced young to leave the LCR during low clear flows in 1993 (i.e., earlier in the summer than observed in 1991 and 1992).

It appears from the length distribution of the LCR component that many young remain in the LCR for more than one year and recruit to adulthood within that system. It also appears from length-frequency analysis and size-specific population estimates that many fish descend from the LCR to the mainstem as adults (>200 mm TL), particularly when over 300 mm TL. These fish could comprise a significant source for mainstem recruitment, and may provide greater numbers of adults than survival of young fish maturing in the mainstem. It appears that substantial numbers of adults descend from the LCR to take residence in the mainstem, but it is also possible that some mainstem adults may remain in the LCR for extended periods following spawning ascent. Greater average length of mainstem adults and higher growth rates indicate that mainstem conditions are more suitable for adults, while age-growth analyses show that the young fish have higher growth rates in the LCR.

This mainstem investigation did not enable us to definitively determine the interrelationships between the fish of the mainstem and the fish of the LCR. An integration of information gathered in the LCR by other investigators (i.e., Arizona State University, Arizona Game and Fish Department, and U.S. Fish and Wildlife Service), and a synthesis with mainstem data, are needed to better understand this population. Preliminary analyses with recapture data of mainstem chubs in the LCR indicate that most chubs 200 mm TL or greater found in the mainstem LCRI aggregation used the LCR as well. A population model is being developed to better understand and integrate data from all aspects of this population in Grand Canyon (Ryel and Valdez 1995).

The life history of the LCRI aggregation (i.e., mainstem group of fish) is depicted in Fig. 10-1, based on observations during 1990-93. Adults were typically found in or near large eddy complexes between RM 57 and RM 65.4 from about July through January. In February and March, adults congregated locally in a few large eddy complexes before moving to stage at the LCR inflow. Adults staged primarily in March, April, and May, with individuals remaining in the inflow an average of 17 days and ascending primarily when flows in the LCR were decreasing, clearing, and warming. There was no evidence of differential movement by gender. Most mainstem adults were in the LCR during March through June and many returned to mainstem eddy complexes within 2 km from their original location before the spawning movement. This spatial fidelity is notable for the species and commonly reported in other populations. Length-frequency analyses and catch rate data suggest that most mainstem adults from the LCRI aggregation ascend the LCR at some time during the year.

Large numbers of young were seen in the mainstem, primarily downstream of the LCR inflow, during and immediately after floods from the LCR drainage. The largest numbers of young fish

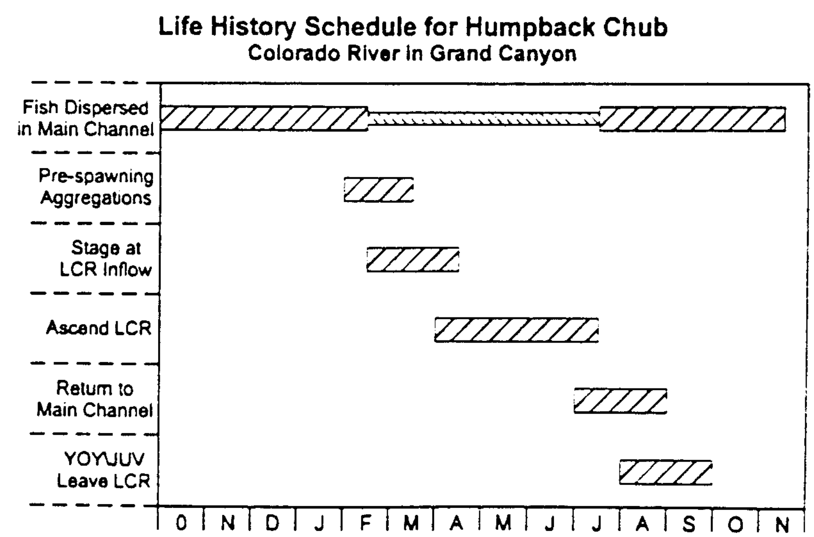

Fig. 10-1. Life history schedule for the LCR inflow aggregation of humpback chub in the mainstem Colorado River in Grand Canyon.

appeared following floods from late summer rainstorms. The timing of these "monsoon rains" determined the appearance of these young chubs in the mainstem, indicating that dispersal from the LCR was concurrent with floods; floods occurred in September 1991, May 1992, and July 1993. Large numbers of subadults descended from the LCR into the mainstem in September 1991 and May 1992, concurrent with floods. However, in 1993 large numbers of young began to descend to the mainstem in July, during low and clear flow in the LCR; the 1993 cohort was large and movement to the mainstem during low flows in July suggests that dispersal was density-dependent and the result of food shortage or habitat limitation in the LCR.

EFFECTS OF GLEN CANYON DAM OPERATIONS

Construction and operation of Glen Canyon Dam has variously affected the life history and ecology of the humpback chub in Grand Canyon. This section distinguishes and discusses those effects. Information from past investigations in Grand Canyon, and from the five other populations in the basin is integrated into this discussion to provide a perspective of the requirements of the species and to establish a foundation for the sections on management options and recommendations.

The native fishes of Grand Canyon have been exposed to a variety of effects from anthropogenic activities over the last 130 years leading to a decline in their distributions and abundances. Land use practices, water diversions, and introduction of non-native fishes initiated this decline well before construction and operation of Glen Canyon Dam (Miller 1961). The construction and presence of the dam also brought changes to the aquatic ecosystem, independent of operations. These changes and effects are identified and distinguished from dam operations in order to determine reasonable management options available through reoperation.

Distribution

Historic

The distribution and abundance of humpback chub in Grand Canyon have historic and recent perspectives that predate Glen Canyon Dam and anthropogenic activities of the last century. At least 12 major late Cenozoic lava dams in the last million years impounded the Colorado River in Grand Canyon (Hamblin 1990), dramatically altering riverine habitat. The largest of these dams was at present-day Lava Falls Rapid (RM 179.3). At an estimated 610 m high, this lava dam created an impoundment larger than modern-day Lake Powell that persisted an estimated 3,000 years (Hamblin 1990). This lava plug probably created conditions that at times were similar to those associated with present-day Glen Canyon Dam; i.e., sediments were impounded while cold hypolimnetic flows eroded through the bottom of the plug, and seasonally-warmed water flowed over the top of the lava dam. Paleontological evidence indicates that the ichthyofauna in these reservoirs was similar to the recent (pre 1900) native assemblage of 10 to 15 species, mostly cyprinids (minnows) and catostomids (suckers).

Remains of humpback chub from Tertiary and Quaternary deposits indicate that the species was subjected to the effects of the lava dams, and a large proportion of habitat in eastern Grand Canyon and Marble Canyon was inundated. Survival strategies during this period are unclear. While the species does not currently seem to persist or thrive in reservoirs, their absence in modern-day impoundments may be attributed to large predator loads rather than to an incompatibility for lentic environments. The Colorado squawfish was the only large predator inhabiting the mainstem during these lava dams, and humpback chub may have persisted in the reservoirs and riverine inflows, despite native predation and physical habitat changes.

Recent

Perhaps the most dramatic and threatening changes to the native fishes of the Colorado River Basin have occurred in the last 130 years, as a result of man's influence. Although the Colorado Plateau was inhabited by paleo-Indians for about 1,500 years, they were few in numbers and lacked the technology to make major land and water modifications. Archaeological remains indicate that native Colorado squawfish, chubs, and suckers were used as food by native Americans (Miller 1959). The Hopi Indians recognize a fish katchina, "Pakiowik" (Bromberg 1986), symbolic of the life form but having no resemblance to a particular species. Although the Sipapu (a large travertine dome about 7.5 km up the LCR) is a significant religious site for the Hopi and Navajo Indians, no known association was made to fishes, inspite of possible opportunities to observe or capture humpback chub in the clear LCR. We also note that fishes are the only large life form absent from petroglyphs on sandstone walls along the banks of the river.

Settlement of the region by European immigrants and their need for redistribution of water starting in the late 1800s imposed severe and long-lasting impacts on aquatic ecosystems and their fish communities throughout the West (Minckley and Deacon 1991, Reisner 1986). Fish assemblages in Grand Canyon responded to these activities long before Glen Canyon Dam was completed in 1963. Reduced flows and altered water quality beginning in the late 1800s, combined with introduction and expansion of non-native fishes in the early 1900s, dramatically degraded the native ecosystem. All eight native mainstem species had begun to decrease in distribution and abundance by the late 1950s as a result of reduced water quality, altered flows from tributary dams, mainstem diversions, and construction of Hoover Dam in 1935 (Miller 1961 and references therein). By the time Glen Canyon Dam was completed, Colorado squawfish were nearly extirpated from the lower basin and bonytail and roundtail chub were no longer reported in Grand Canyon. At least 15 non-native species had invaded the mainstem by the time the dam was built; red shiners, common carp, and channel catfish were common to abundant in the mainstem, and rainbow trout were abundant in some tributaries.

Present

Cold releases from Glen Canyon Dam dramatically influenced the distribution of fishes through Grand Canyon starting in about 1970. Of 24 species recently found between the dam and Lake Mead, only 5 were native and 19 were non-native. While only four of these species (rainbow trout, brown trout, brook trout, cutthroat trout) are considered coldwater forms, rainbow trout and brown trout dominate fish biomass in the upper half of the canyon and the warmwater species tend to be concentrated near warm tributary inflows (Fig. 10-2).

Today, humpback chub are found primarily in canyon-bound regions of the Colorado River Basin. They remain in 6 of 11 areas historically reported (U.S. Fish and Wildlife Service 1990), including:

1. Black Rocks, Colorado (Kidd 1977, Valdez and Clemmer 1982),
2. Westwater Canyon, Utah (Valdez et al. 1982, Valdez and Clemmer 1982),
3. Cataract Canyon, Utah (Valdez and Clemmer 1982, Valdez 1990, Valdez and Williams 1993),
4. Desolation/Gray canyons, Utah (Holden and Stalnaker 1975, Tyus et al. 1982, Valdez and Clemmer 1982),
5. Yampa Canyon, Colorado (Karp and Tyus 1990), and
6. Marble/Grand canyons, Arizona (Kaeding and Zimmerman 1983).

The species has been extirpated from the following areas:

1. Flaming Gorge, Colorado (Gaufin et al. 1960),
2. Lodore Canyon, Utah/Colorado (Holden and Stalnaker 1975),
3. Whirlpool Canyon, Utah (Holden and Stalnaker 1975),
4. Split Mountain Canyon, Utah (Holden and Stalnaker 1975), and
5. Narrow Canyon and lower Cataract Canyon (Valdez 1990, Valdez and Williams 1993).

Small numbers of humpback chub were also reported from Moab Canyon, Utah (Taba et al. 1965, Valdez and Clemmer 1982), and from Debeque Canyon, Colorado (G. Kidd, per. comm., Valdez and Clemmer 1982), but populations were not reported from these areas, and the cause for their disappearance is unknown.

While the distribution and abundance of humpback chub were not well known when Glen Canyon Dam was completed in 1963, predam records and current distribution show that this relatively sedentary species was probably found in most canyon-bound regions. Potential habitat between the confluence of the Green and Colorado rivers and Grand Wash included 535 km in four canyons (Cataract, Narrow, Marble, and Grand). The species probably occurred throughout 66 km of Cataract Canyon (confluence of Green and Colorado rivers to Sheep Canyon), which Dellenbaugh (1908) "*...credited with forty-one miles, and in which I counted sixty-two rapids*

Distribution of fishes in Glen and Grand Canyons (1990 - 1991)

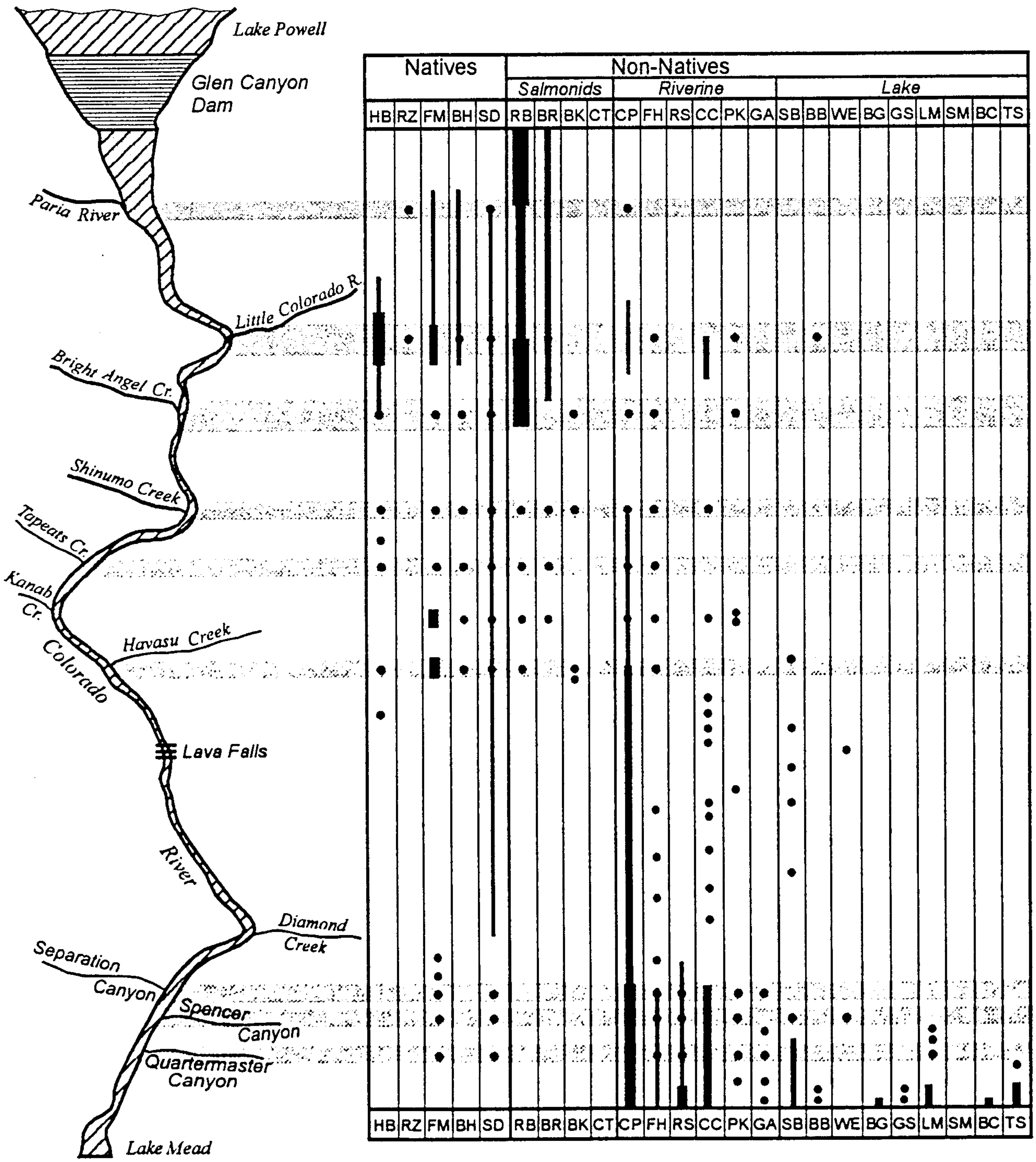

Fig. 10-2. Longitudinal occurrence of fishes from Glen Canyon Dam to Lake Mead. Approximate relative abundance from selected areas is indicated by band width. See Table 5-3 for species codes.

and cataracts...", and 14 km of Narrow Canyon (Sheep Canyon to the Dirty Devil River).

Historic photographs and accounts (Dellenbaugh 1908, Stephens and Shoemaker 1987) indicate that Glen Canyon (Dirty Devil River to Paria River) was a gentle alluvial region of river not likely suited to large numbers of humpback chub. Further downstream, the Grand Canyon with its two subdivisions and a combined length of 455 km (283 mi) (Dellenbaugh 1908) probably contained suitable habitat in most reaches. The two subdivisions of Grand Canyon include 99 km of Marble Canyon (Paria River to Little Colorado River) and 356 km of Grand Canyon (Little Colorado River to Grand Wash). Humpback chub were never historically reported downstream of Grand Wash (Minckley 1979), but may have occurred locally in canyon regions.

Of 535 km of potential humpback chub habitat (80 km in Cataract and Narrow canyons, and 455 km in Marble and Grand canyons), the first reduction of 70 km (13%) occurred as a result of inundation and sedimentation of lower Grand Canyon by Lake Mead following construction of Hoover Dam in 1935 (Table 10-1). Predaceous and competing non-native fish introduced into Lake Mead added to the impact of habitat modification. The second habitat reduction of 52 km (10%) occurred as a result of inundation and sedimentation of Narrow Canyon and lower Cataract Canyon by Lake Powell following construction of Glen Canyon Dam in 1963. This left 28 km of occupied habitat in upper Cataract Canyon, from the confluence of the Green and Colorado rivers to Imperial Canyon (Valdez 1990, Valdez and Williams 1993). Humpback chub found in Lake Powell in the early 1970s (Holden and Stalnaker 1970) were probably remnants of the Cataract Canyon and Narrow Canyon population. The third reduction of 77 km (14%) was the result of operations of Glen Canyon Dam (e.g., cold releases, altered flow regimes). Non-native fishes were also expanding in distribution and abundance and exerting increasingly competitive and predaceous forces on native species.

Hence, by the time Glen Canyon Dam was completed in 1963, the habitat of humpback chub in this region of the basin had already been reduced by about 13% as a result of construction of Hoover Dam in 1935 and subsequent filling of Lake Mead. The effects of land-use practices, non-native species, and other water diversions on the native fishes were insidious and probably contributed substantially to decreased distribution and abundance but these effects remain largely unmeasured. Habitat changes from sedimentation and large numbers of predators reduced presumed distribution in Grand Canyon (455 km from Paria River to Grand Wash) by an additional 16% to 384 km (Paria River to Separation Canyon). Following construction, humpback chub were reported from the base of the dam in the early 1970s, and

Table 10-1. Loss of potential humpback chub habitat between the confluence of the Green and Colorado rivers, UT and Grand Wash, AZ.

Region Description	Distance Km (%)	Habitat Lost		Habitat Remaining	
		Description	Km (%)	Description	Km (%)
Cataract Cyn.[a]	66 (12%)	Lower Canyon	38 (7%)	Upper Canyon	28 (5%)
Narrow Cyn.	14 (3%)	All	14 (3%)	None	(0%)
Marble Cyn.	99 (19%)	Paria River - Shinumo Wash	47 (9%)	Shinumo-LCR	52 (10%)
Grand Cyn.[bc]	356 (66%)	Granite Springs Cyn.-Grand Wash	100 (18%)	LCR - Granite Springs	256 (48%)
Totals:	**535 (100%)**		**199 (37%)**		**336 (63%)**

[a]Lower Cataract Canyon (38 km) and all of Narrow Canyon (14 km) inundated by Lake Powell after Glen Canyon Dam was completed in 1963.
[b]Lower 70 km (Separation Cyn. to Grand Wash) inundated by Lake Mead after Hoover Dam was completed in 1935.
[c]Paria River to Shinumo Wash (47 km) and Granite Springs Canyon to Separation Canyon (30 km) eliminated through Glen Canyon Dam operations.

presumed to be distributed downstream to Separation Canyon. The distribution of species in Grand Canyon was further constricted as Lake Powell filled and downstream dam releases became increasingly colder (starting about 1970). These changes in thermal regime precluded mainstem reproduction by native fishes, altered food supplies, possibly transported some individuals downstream, and increased predation and competition by non-native salmonids. Humpback chub reported from the base of the dam in the early 1970s were probably relict adults that were eventually extirpated by either high densities of predaceous rainbow trout of up to 7 kg, by high floods in 1983-85, or by natural attrition.

The present distribution of humpback chub in Grand Canyon is 308 km (Shinumo Wash to Granite Springs Canyon), a 32% reduction from a total of 455 km. Also, of the presumed habitat of 535 km historically occupied by humpback chub downstream of the confluence of the Colorado and Green rivers in Utah (i.e.,Cataract, Narrow, Marble, and Grand canyons), the species presently remains in 336 km (i.e., 28 km in upper Cataract Canyon and 308 km in Grand Canyon), for a 37% reduction in presumed habitat. Although one adult was captured near Maxson Canyon (RM 253.2) (Valdez 1994), this lower region of Grand Canyon is not considered to be consistently occupied by the species.

Although the distribution of humpback chub in the Colorado River in Grand Canyon has been reduced by about 32%, reduction in numbers of fish has probably been greater, primarily because of the absence of significant mainstem reproduction, low survival and recruitment, depleted food resources, cold temperatures, non-native fishes, and the long history of basin-wide land use practices. Cold dam releases of 7.5-10°C have severely limited mainstem reproduction and compressed distribution of humpback chub primarily to regions of the mainstem associated with warm tributaries and warm springs. Changes in flow regimes and sediment loads may have reshaped river habitat and contracted longitudinal as well as local fish distribution and abundance.

During 1990-93, humpback chub were found as nine aggregations associated with discrete geomorphic features, warm tributaries, or warm mainstem springs. The largest aggregation, at the LCR inflow (RM 57.0-65.4), was associated with a warm tributary and distinct mainstem geomorphology characterized by a wide channel and large numbers of debris fans with associated recirculating eddies. The next largest aggregations were 81 and 98 km downstream of the LCR in Stephen Aisle (RM 114.9-120.1) and Middle Granite Gorge (RM 126.1-129.0). These aggregations were associated with the same geologic strata and geomorphic characteristics as the LCR aggregation, but these occurred in the absence of a warm tributary. Three other smaller aggregations were at tributary inflows, including Bright Angel Creek, Shinumo Creek, and Havasu Creek, and two were near warm springs, Fence Fault Springs and Pumpkin Spring. One aggregation was immediately downstream of the LCRI aggregation and consisted primarily of young fish from the LCR. Total numbers of adults in the mainstem range from 3,300 to 3,800, while numbers of subadults may be as high as 3 million in years of high reproductive success.

The 30-Mile aggregation consisted of about 40-60 large adults considered relicts from about the inception of cold releases following dam construction. Since these fish are about 50 km upstream of the only reproducing population at the LCR, significant recruitment from the LCR is unlikely. Assuming the fish at 30-mile are progeny of the last successful mainstem reproduction shortly after dam construction, minimum age of individuals is probably about 25 years; the last year in which average water temperature at Lees Ferry exceeded minimum spawning and incubation temperature of 16°C was 1970. Fish in this aggregation could be close to maximum longevity for the species; Hendrickson (1993) found a maximum of 23 annular rings on lapilli of humpback chub examined from the LCR. The fish in the 30-Mile aggregation may represent the last remaining exclusively mainstem genotype in Grand Canyon and may require immediate management action (See Management Options).

Habitat

Channel geomorphic changes, and hence fish habitat changes, in the Colorado River in Grand Canyon have been dramatic since completion of Glen Canyon Dam in 1963. Nearly 90% of the sediment load of the Colorado and San Juan rivers is retained in Lake Powell, and the river below the dam continues to scour sediments from the channel. Most large sand bars and sand margins have been eroded, exposing cobble and boulder bed surfaces and shorelines. The most dramatic change has been the reduction of sand deposited by some large recirculating eddies, resulting in some eddy complexes as open water features with reduced velocity and associated sand bars of characteristic origin, structure, and evolution (Rubin et al. 1990). As a result of these geomorphic changes and reduced spring flows, shoreline vegetation has become established on sand bars and irregular shorelines, providing fish with a habitat type that, predam, occurred only during peak runoff. These vegetated shorelines may be the most productive shoreline habitats now available to the fish.

Changes in fish habitat have been dramatic as a result of these geomorphic changes and may help to explain present fish distribution and abundance. Cataract Canyon, like Grand Canyon, is an eddy-dominated system, with occurrence of expansion zones below debris fans and provides a reasonable model of pre-dam conditions in a similar canyon. Historic aerial photographs of Grand Canyon (J. Schmidt, USU, pers. comm.) show that, like Cataract Canyon and Desolation/Gray canyons of today, the eddy expansion zones were largely filled with sediment and sand, and prominent sand bars had numerous small scour channels. These photographs also show substantial shoreline sand deposits, and midchannel sand islands associated with wide channel areas. In Cataract Canyon and Desolation/Gray canyons, where channel geomorphology most closely resembles historic conditions, adult humpback chub are found in a variety of habitats, associated primarily with talus shorelines, and small and large recirculating eddies (Valdez 1990, Valdez et al. 1993, Karp and Tyus 1990). The present distribution of humpback chub in Cataract Canyon indicates a more dispersed habitat and food supply than found in present Grand Canyon.

The high degree of selection by adult humpback chub for large recirculating eddies in Grand Canyon appears to be a manifestation of dramatic channel geomorphic changes, reduced allochthonous drift, high base flows, cold water temperature, and altered food production in the canyon from heterotrophy to autotrophy. We hypothesize that eddies are selected habitats in Grand Canyon because they provide low-velocity feeding and resting sites that entrain drifting material. While removal of sediments from Grand Canyon has reduced available sand deposits and drifting allochthonous food material, development of these large, open recirculation zones has served as effective energy traps for fish. The change from heterotrophy to autotrophy, as a result of coldwater releases, has also restricted production to photic zones, greatly reducing benthic macroinvertebrates with distance downstream of the dam (Blinn et al. 1994) where turbidity is persistent. High base flows have further restricted adults to these habitats by decreasing the availability of small shoreline eddies and increasing velocities along deepened shorelines. Swimming ability of juveniles, and possibly of adults, has been reduced by persistence of cold water temperatures, hence, limiting useable habitat to low-velocity areas.

Subadult shoreline habitat has also undergone dramatic changes. Irregular shorelines such as those commonly used by subadults in other populations are common in Grand Canyon, but we hypothesize that young chubs are not widespread because high base flows and cold temperatures produce marginal conditions for these young fish. While some shoreline habitats are used by subadults in Grand Canyon, coldwater releases have resulted in high use of warmer eddy return channels (i.e., backwaters) (Arizona Game and Fish Department 1993). Channel geomorphology of other canyon areas occupied by humpback chub indicates a frequency of 0.6 backwaters (Westwater Canyon) to 0.7 backwaters (Cataract Canyon) per mile at base flow, suggesting far less availability of this habitat in predam Grand Canyon than under present conditions (i.e., 3.2 backwaters per mile, RM 57-65.4). This increased availability may be related to greater circulation in the large eddy complexes that has maintained a higher frequency of eddy return channels (i.e., backwaters).

The instability of backwaters under fluctuating flows in Grand Canyon probably precludes persistent occupation by subadults. Significantly higher catch rates indicated selection for vegetated banks, talus, and debris fans over cobble bars, sand banks, and bedrock. Selected shoreline types were most commonly found in reaches associated with Muav limestone, Bright Angel shale, Tapeats sandstone, and members of the Unkar group, reaches that were also selected by adults. Although habitat parameters within all six shoreline types indicate that these were suitable for depth and velocity, comparison of swimming ability of juveniles from laboratory studies (Bulkley et al. 1982; time to fatigue of juveniles was reduced by 98% for swim tests at 20°C and 14°C) indicate that at mainstem temperatures of about 10°C, juvenile humpback chub are able to maintain their position only under stable flows in vegetated banks, talus, and debris fans. These shoreline types have the highest amount of cover and maintain interstitial spaces over a wider range of flows, offering more consistent and contiguous cover for the fish.

While this phenomenon may explain selection for these shorelines, the dramatic decrease in densities of young chubs in their first year of life is attributed to a combination of factors. We hypothesize that cold mainstem temperatures restrict swimming ability of juveniles and thus, use of shorelines. Daily fluctuating flows may displace juveniles from sheltered shorelines, making them more susceptible to predation. Also, food availability along these shorelines may be limited, particularly in more downstream reaches, forcing fish to seek more lucrative food supplies.

In steep, narrow, vertical canyon regions, such as downstream of Hance Rapid, shoreline complexity is reduced, and there is less habitat for subadults to rest and escape predators. This area is also inhabited by large numbers of brown trout, the most significant predator of humpback chub in Grand Canyon. High mortality of subadult humpback chub may occur in this area as a result of the combination of inadequate escape cover, cold summer water temperature, large numbers of coldwater sight predators, and low littoral invertebrate production.

Movement

Although construction of Glen Canyon Dam physically separated humpback chub in Cataract Canyon and Narrow Canyon from fish in Marble Canyon and Grand Canyon, the presence of the dam probably did not directly impeded long-range movement of humpback chub in the way that mainstem dams have blocked long-range migration of sympatric potomodrous species, such as Colorado squawfish (Tyus 1984, 1990), and possibly razorback sucker and bonytail. The humpback chub is a relatively sedentary riverine species, with strong spatial fidelity for specific areas within canyon-bound regions (Valdez and Clemmer 1982, Kaeding et al. 1990). The long-term effect of isolation of populations on genetic diversity is recognized, but the issue is not addressed in this report.

Spatial fidelity by adult humpback chub was reported in Black Rocks (Valdez and Clemmer 1982, Kaeding et al. 1990), Yampa Canyon (Karp and Tyus 1990), Cataract Canyon (Valdez 1990), and was indicated for Westwater Canyon and Desolation/Gray canyons (Chart 1995). Radio-tagged adults and PIT-tagged adults in Black Rocks, Colorado, moved an average of less than 2 km from first to last contact over periods of 3 months to 3 years (net displacement) in each of two separate studies (Valdez and Clemmer 1982, Kaeding et al. 1990). This investigation found a similar pattern of spatial fidelity in Grand Canyon; average net displacement of radio-tagged adults (n=69) and PIT-tagged adults (n=238) was 1.49 km and 0.99 km, respectively. However, mean gross displacement (average of sum of all movements) of radio-tagged adults in Grand Canyon of 5.13 km was much greater than 1.64 km reported in Black Rocks, indicating that annual spawning migrations of mainstem adults to the LCR account for greater long-range movement in Grand Canyon.

Home range of the LCR/mainstem population in Grand Canyon was defined as 13.5 km in the mainstem and 14.9 km in the LCR for a total of 28.4 km. We could not determine if greater movement by Grand Canyon fish to reach spawning locations in the LCR was the direct result of dam operations. The physiological condition of the fish and repeated annual migrations suggest no detrimental effect from this nuptual behavior and underscore the importance of the LCR to the mainstem spawners.

Despite greater long-range movement by the Grand Canyon population for spawning, movement of adults in the mainstem not associated with spawning was consistently low and comparable to adult movement in other populations. There was no significant exchange of adults among the nine aggregations found in Grand Canyon. Only 2 of 280 adults (0.7%) recaptured (1,524 marked) from the LCRI aggregation moved outside of the defined home range; both moved downstream. Movements of individual adults outside of population centers have been reported between the Black Rocks and Westwater Canyon populations located about 20 km apart; two were reported by Valdez and Clemmer (1982) and two by Kaeding et al. (1990). These "sallies", or sudden and extended movements from a home area by an otherwise sedentary species, are reported in other animal populations and may be important in the population dynamics of species in dispersed aggregations (Goldwasser el al. 1994).

Although long-range movement of adults has apparently not been affected by the dam, local movement or activity has been affected by dam operations, i.e., flow magnitudes, ramping rates, and reduced frequency and level of turbidity. The proportion of times fish moved (P_m) was significantly higher when change in flow rate was greater than 300 cfs/hr at flow magnitude of 10,000 cfs or greater. High magnitude or sudden change in flow rate apparently altered hydraulic characteristics (most likely velocity), resulting in movement. While the energy debt of this increased activity was unknown, high condition factor (Kn) of adults indicated little negative physiological effect.

High water clarity (i.e., low turbidity, NTU<30) significantly reduced near-surface activity, indicating that adults remained in deeper water possibly as security from predators. Conversely, significantly greater activity during high turbidity (NTU>30) was attributed to use of turbidity as cover or increased feeding activity in response to greater food availability in drift. Similarly, subadults may use high turbidity for cover during resting and feeding. In the postdam era of greater water clarity, increased shoreline vegetation or greater exposure of talus may compensate subadults for less turbidity which provided cover in the predam era.

Despite the sedentary nature of humpback chub, the behavioral transition of subadults to adults is not understood. Humpback chub apparently imprint to specific sites, but the age at which this imprinting occurs is unknown. Greater long-range movement was observed for subadults than for adults during this investigation, indicating that spatial imprinting may not occur until adulthood.

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.

Age And Growth

Growth rate of subadult humpback chub was greater in the LCR than in the mainstem, but appeared to be higher for adults in the mainstem. Average 30-day growth rate of 10.30 mm (from scale back-calculations) for first year LCR fish was comparable to 10.63 mm reported for laboratory fish at 20°C (Lupher and Clarkson 1994). Apparently growth rate in the LCR was greatly reduced as fish reached maturity. Average monthly growth rates in the LCR were 1.42 mm, 1.33 mm, and 1.08 mm for fish 150-200 mm TL, 200-250 mm TL, and 250-300 mm TL respectively, annual growth rate of LCR fish larger than 300 mm TL was less than 1 mm (Minckley 1992).

Growth rates of subadults in the mainstem were substantially lower at 4.00 mm per 30 days and compared to laboratory fish that grew at a monthly rate of 2.30 mm at 10°C (Lupher and Clarkson 1994). Greater growth by the wild fish was attributed to time spent in shallow shorelines and backwaters which were warmer than the mainstem. Monthly growth rates of fish in the mainstem, although reduced as the fish reached maturity, were higher than rates of fish of comparable size in the LCR; 2.25 mm , 2.79 mm , 2.50 mm for mainstem fish 150-200 mm TL, 200-250 mm, and 250-300 mm TL, respectively. Monthly growth rate of mainstem fish larger than 300 mm TL was about 1.2 mm. Hence, although cold dam releases have slowed subadult growth, adults appear to have higher growth rates in the mainstem than in the LCR, possibly because of greater space and food availability. As a comparison, average monthly growth rates reported for recaptured PIT-tagged humpback chub from Westwater Canyon, Utah were 1.08 mm and 1.35 mm for fish 200-250 mm TL and 250-300 mm TL (T. Chart, pers. comm., Utah Division of Wildlife Resources). Growth rates of humpback chub from Westwater Canyon are similar to growth rates of fish from the LCR, and suggest that growth rates of mainstem Grand Canyon fish are about double those of other populations. Hence, while cold dam releases have precluded successful mainstem reproduction, conditions in Grand Canyon (e.g., more stable year-around flows, regular food supplies from fluctuating flows, etc.) may be enhancing growth. In addition, relatively high growth rates and condition factors indicate that the population of adults in the mainstem may be well below the carrying capacity.

Food Habits

The predam Colorado River in Grand Canyon probably contained a large variety of macroinvertebrates similar to those communities presently found in Cataract Canyon; areas of loose cobble or shoreline talus are pockets of high macroinvertebrate densities, often supporting relatively high fish densities. These islands of high productivity are associated with channel structure that provide cover from predators, low-velocity areas for resting, and food for fishes. This island phenomenon also describes the coincidental longitudinal occurrence of roundtail chub with rock spills or debris flows in otherwise alluvial regions of the Colorado and Green rivers above their confluence (Valdez and Williams 1993). These isolated debris fans often abound with chironomids, simuliids, odonates, plecopterans, ephemeropterans, and megalopterans (D. Shiozawa, Brigham Young University, pers. comm.)--macroinvertebrate species that have largely been excluded from Grand Canyon by cold water releases.

In the historic river system, we believe that these islands of high production provided fish with a reliable supply of food, supplemented periodically by terrestrial and aquatic insects, seeds, and detritus washed into the river by spring runoff, summer rainstorms, or periodic winter melt events. Late summer mayfly hatches, grasshopper infestations, or migrations of Mormon crickets (Tyus and Minckley 1988) also provided the fish with a high protein source. Although this floatsom accumulated in eddies, the material was typically distributed throughout the channel and was probably available to the fish in a variety of habitats. A complete inventory of invertebrates was never conducted in Grand Canyon prior to dam construction, but collections from other mainstem areas in the basin (Pearson 1967, L. Stevens, NPS, pers. comm.) indicate that the variety of organisms was much greater predam than postdam.

Presently, the mainstem Colorado River in Grand Canyon has a low diversity of nearctic aquatic macroinvertebrates dominated by simuliids, chironomids, and amphipods (Gammarus lacustris). These species have life cycles that are completed under the existing thermal regimes of the mainstem. The numbers of macroinvertebrates decrease longitudinally downstream, such that downstream of Havasu Creek, there are low benthic standing crops (Blinn et al. 1994). It appears from this reduction in downstream production and entrapment of upper basin detritus in Lake Powell that food supplies for native fishes are significantly reduced from predam conditions, despite significantly higher autotrophic production immediately downstream of Glen Canyon Dam.

Reduced shoreline production and less available detritus have probably increased the importance of recirculating eddies as food entrainment centers. Most adult humpback chub were captured or located in these eddy complexes, and comparisons of gut contents with drift material showed approximately equal proportions of items, except for simuliids. Adult humpback chub in the mainstem ate primarily simuliids (black flies), Gammarus lacustris (freshwater shrimp), and chironomids (midges). Seasonal variation reflected greater availability of one or more groups. Greater proportion of terrestrial invertebrates in fish from Middle Granite Gorge than from the LCR inflow indicated less availability of aquatic forms and greater importance of terrestrials to downstream aggregations.

The mechanism for feeding was not determined, but comparison of drift with diet did not coincide and indicated that the fish were probably feeding on both drift and benthos. We believe that adult humpback chub aggregate in large recirculating eddies where large amounts of food are entrained, and much is eventually deposit with sediments. A midwater soaring behavior suggests a low-energy feeding strategy on drift, and deeper forays suggest foraging on benthic materials. The occurrence of large numbers of simuliid larvae and pupae in individual fish also suggests foraging on submerged woody debris, where immature black flies occur attached in great numbers (L. Stevens, NPS, pers. comm.). Adults were also observed feeding at night on invertebrates (i.e., Gammarus, black flies, midges) trapped in small sand riffles on the lee side of reattachment bars.

Greatest numbers and volumes of drifting macroinvertebrates occurred during down-ramp (decreasing flows), indicating that food availability varied daily, and could have prompted fish to feed more frequently during these periods. No evidence was found of feeding timed to down-ramp, but typically humpback chub appeared to be most active during crepuscular periods or in high turbidity; a behavior pattern that could be keyed to flow patterns or time of day. It is noted that activity by fish in the LCRI aggregation was greatest in the evening, which was usually during decreasing flows caused by down-ramp. Hence, the increased invertebrate drift associated with down-ramp may be coincidentally timed at the LCR area for dusk, a time when fish are normally most active.

Food appears to be a limiting factor for native fishes downstream of Stephen Aisle. Low instream production from persistent sediment loads and high non-native fish biomass may be limiting native fish biomass; a greater occurrence of terrestrial invertebrates in diets of humpback chub indicates low availability of food of aquatic origin.

Today, nearly 70% of the benthic standing crop biomass found in 360 km of river between Glen Canyon Dam and Diamond Creek occurs in 25 km below the dam (Blinn et al. 1994). The primary algae produced in this subreach (Cladophora glomerata) is transported very short distances before becoming pulverized by wave action and rapids. Epiphytic macroinvertebrates quickly drop from the algae, and are essentially unavailable to fishes at the main aggregations, between 43 and 343 km downstream of the dam. Food supplied to these downstream aggregations is probably primarily produced locally along shallow shorelines or in warm tributaries. The predam river probably supported small islands or "hot spots" of invertebrate production along talus slopes, in warm backwaters, or on woody debris. These areas provided the fish with ongoing food supplies supplemented by large but unpredictable influxes of food.

Humpback chub evolved in the muddy Colorado River and possess a highly sensitive lateral line system to detect minute movements of struggling insects many meters away, and a refined neuromast system (Muth 1990) to detect even minor chemical odors. Turbid conditions and high turbulent flows thus advantage this species over non-native species during feeding.

Reproduction

Cold hypolimnetic releases from Glen Canyon Dam since the early 1970's have dramatically altered river temperatures from a maximum predam range of 25 to 29°C at Lees Ferry to a postdam maximum of about 12°C (Kubly 1990). These changes have precluded most mainstem reproduction by warmwater native fishes, including humpback chub, razorback sucker, flannelmouth sucker, bluehead sucker, and speckled dace. These species require 16-24°C for spawning, egg incubation, and larval survival. Longitudinal warming of about 1°C/51 km provides maximum annual temperatures of about 12°C at the upper end of the canyon and about 16°C at the lower end. Only warm tributaries, tributary inflows, and warm mainstem springs provide adequate thermal conditions for reproduction, although persistence and stability of these local tepid habitats can vary dramatically with changes in river flow. Spawning by humpback chub is well known from the LCR, and suspected in other major tributaries (e.g., Bright Angel Creek, Shinumo Creek, Kanab Creek) in Grand Canyon (Maddux et al. 1987).

Despite mainstem water temperatures that vary by only about 2-4°C from winter (8-10°C) to summer (10-12°C), simultaneous movement and aggregation of mainstem adults from above and below the LCR inflow suggests that pre-spawning cues are not related to LCR water quality or temperature. The absence of high spring flows and lack of warmer temperatures indicates that gonadal maturation is prompted by increased photoperiod; temperature increase of 1°C from winter to spawning time in March and April may be too subtle to cue gondal development. However, once the fish are staged at the inflow, ascent into the LCR is apparently related to flow volume, water clarity, and water temperature of the LCR. Thus, although cold mainstem temperatures have precluded mainstem reproduction by humpback chub, gonadal maturation appears normal and timed to correspond to either suitable LCR conditions (March-May) or historic mainstem conditions (May-July).

Several investigators since the early 1970s have reported young humpback chub in areas substantial distances upstream or downstream of the LCR inflow, giving rise to the hypothesis that mainstem reproduction is occurring, most likely in local tepid environments. During 1970-76, individual juveniles of unknown length were captured by Suttkus et al. (1976) at RM 41 and RM 44, at approximately the same location that AGF captured 20 humpback chub (range, 20-50 mm TL) in a backwater near the Eminence Break Fault (RM 44.3), and below President Harding Rapid; 3 were caught in July, 3 in September, and 14 in October (Arizona Game and Fish Department 1994). These findings suggest past and recent spawning attempts by humpback chub, probably in springs in the vicinity of Fence Fault (30-Mile area). It is unlikely that these young fish originated from the Paria River, since adult humpback chub have not been reported in that tributary, and a large number of young would be necessary to supply a distant backwater with 20 individuals, under normal dispersal patterns where numbers of fish become more diffuse with distance downstream.

Between 1984 and 1989, AGF (Kubly 1990) captured 5 juvenile humpback chub (range, 57-84 mm TL) in the mouth or mainstem of Kanab Creek, and a single specimen (15 mm TL) was captured in a backwater at RM 166. In June 1993, AGF captured 12 juveniles (range, 14-43 mm TL) between RM 108.6 (mouth of Shinumo Creek) and RM 193.9 (Boulder Wash) (AGF, unpublished data, 1993 Trip Reports). Other records of juveniles captured in the mainstem suggest tributary spawning, but can also be explained as movement of individuals from the LCR. Suttkus et al. (1976) captured juveniles at RM 61.5, RM 69, RM 71, and RM 108.7, all of which probably originated from the LCR. More recently, Maddux et al (1987) reported large numbers of juveniles downstream of the LCR inflow, but the fish captured from RM 30 to RM 61 were all adults. Of the fish captured downstream of the LCR, as far as RM 217, the majority were juveniles as small as 32 mm TL. There was no distinct pattern in the distribution of these fish to suggest mainstem or tributary reproduction and all of these fish probably originated in the LCR and were transported downstream by the higher flows experienced during that study (See Chapter 3 - HYDROLOGY).

Most investigators have reported few YOY or juveniles upstream of the LCR confluence, indicating that young LCR fish disperse primarily downstream of the inflow. Kaeding and Zimmerman (1983) did not collect chub smaller than 145 mm TL in the mainstem upstream of the LCR in October and November of 1980, and April, May, October, and November of 1981. We found only three juveniles upstream of the LCR confluence, all within 0.5 km.

The only definitive evidence of mainstem reproduction during this investigation was the discovery of about 100 post-larval humpback chub (14 captured, range, 18-31 mm TL) in a spring plume at RM 30.8 on July 12, 1994 (Valdez and Masslich 1995). Water temperature at the source of the spring was relatively constant at 21.5°C, compared to 10°C in the adjacent main channel. The fish were in a plume with a temperature of 15-19°C. These young fish belonged to the 1994 year class, and probably hatched from eggs deposited in the warm spring plume, since mainstem water temperature was too cold for survival of eggs or larvae (Hamman 1982, Marsh 1985). These fish were about 36 days old (hatched about June 8, 1994), based on age to length relationships of larvae and post-larvae (Muth 1990). Assuming an incubation time of less than 10 days, the timing of spawning is consistent with peak spawning readiness displayed by mainstem fish away form the LCRI aggregation (i.e., May - July).

It is unlikely that larval humpback chub could survive the thermal shock of a transition from a spring plume of 20°C to a mainstem temperature of 10°C. Sufficient size and temperature of spring plumes must persist under various mainstem flows to allow fish to age and acclimate to greater thermal tolerance. If young fish reach sufficient size to survive the thermal transition (i.e., about 50 mm TL), their chances of survival may still be low because of the large numbers of mainstem predators (i.e., rainbow trout and brown trout) and lack of suitable shoreline habitat for nearly 20 km downstream. Nevertheless, the value and stability of these spring plumes as spawning and nursery areas appear to depend on mainstem flow magnitude and range of fluctuations created by dam operations.

The elevation of Spring No. 5 (where YOY humpback chub were found in July 1994) and associated crevices and cover indicate that flows on the order of 10,000 - 15,000 cfs probably provide the most stable thermal plume (which is entrained by a shoreline eddy) and maximum crevice and overhead cover for eggs and larvae. Mainstem flows of less than about 10,000 cfs are insufficient to cover the crevices, and the size of the shoreline eddy that entrains the thermal plume is substantially reduced at these lower flows, allowing the warm water to be quickly diluted by the colder mainstem. Hence, the operation of Glen Canyon Dam is vital to continued spawning attempts and success in this Fence Fault spring. Further monitoring of fish in the eight major springs in the area is needed. Also, relationships of flow stage to plume dynamics and cover need to be described for each spring.

Additional spawning attempts may be occurring in other springs associated with Fence Fault or in localized thermal pockets along the river bed. Huntoon (1981) reported eight warm shoreline springs associated with Fence Fault, between RM 30 and RM 34.5 with possible subriverine connection between springs on opposite shores. Springs were not located downstream of RM 34.5 despite numerous fractures associated with Eminence Break (RM 44.0) and the intervening area known as Eminence Graben. Recent surveys with thermal infrared (FLIR, Holroyd 1995) may be useful in locating additional springs.

Only the two lowermost springs of the Fence Fault complex are located within critical habitat designated for humpback chub in Grand Canyon. Protection of these springs may be vital to conserving the last recognizable mainstem stock of humpback chub in Grand Canyon. This topic is discussed under the Critical Habitat section of this chapter.

Past and present collection of young humpback chub in the vicinity of Fence Fault indicates that spawning occurs in the associated warm springs in mid to late summer. These results also indicate that mainstem fish away from the LCRI aggregation are developing mature and fertile gametes, despite cold mainstem temperatures, but final maturation and spawning are triggered by the warm temperature of the springs. Recognizing this reproductive potential is an important element in evaluating the feasibility of a second population of humpback chub in Grand Canyon.

There is presently no evidence to indicate that humpback chub spawn in backwaters or flooded bottomlands (e.g., Cardenas) either in Grand Canyon or other regions of the basin. The species is known to spawn primarily over rock substrate in moving water (Hamman 1982).

Young humpback chub captured downstream of the LCR during this investigation did not occur in a particular pattern to suggest mainstem spawning at particular locations. Of 4,503 subadults (≤200 mm TL) captured, the smallest was 23 mm TL, but only nine (0.3%) were smaller than 30 mm TL (except for 14 post-larvae, range, 18-31 mm TL, captured at RM 3018 in 1994). Most young humpback chub were captured near the LCR inflow, but some were captured as far downstream as the Shinumo Creek area (RM 119.0-129.0) and at Whitmore Wash (RM 187.6). Some spawning may be occurring in lower reaches of warm tributaries, but other than the post-larval fish found at the spring at RM 30.8, all fish captured in the mainstem during 1990-93 could have originated from the LCR and dispersed to any area downstream within days. Assuming average transport time of about 1.1 to 3.6 km/hr (0.3-1.0 m/sec, Graf 1995), an object moved by currents could be transported 265 km from the LCR (RM 61.3) to Diamond Creek (RM 226.0) in about 241 to 74 hr.

Adult humpback chub in the mainstem displayed spawning characteristics (i.e., expression of milt or eggs, tuberculation, coloration) during two time periods. The majority of adults in the LCRI aggregation reached the peak of spawning readiness in March, consistent with LCR temperatures, while adults in other aggregations peaked in May, consistent with historic mainstem temperatures. Of 48 adults in spawning condition outside of the LCRI aggregation, the greatest numbers were in the MGG aggregation (n=23) and 30-Mile aggregation (n=7). Also, 15 adults with spawning characteristics were captured near tributaries, including four within 0.3 mi of Clear Creek, one within 0.3 mi of Bright Angel Creek, five within 0.6 mi of Shinumo Creek, and five within 0.9 mi of Havasu Creek. This evidence supports the hypothesis by Kaeding and Zimmerman (1983) that year-round low mainstem temperatures do not inhibit gonadal maturation, but preclude survival of embryos. It also suggests that fish in the LCRI aggregation historically spawned early or these fish have shifted timing of spawning readiness consistent with temperatures of the LCR, while other mainstem fish continue to reach spawning readiness two months later, as with other basin populations and more in line with historic temperatures. Hence, mainstem adults spawning in the LCR appear to respond to photoperiod for gonadal maturation and the warm LCR as the trigger for spawning, while other adults away from the LCR may be responding to photoperiod or a small warming in the mainstem of 2-4°C.

Adults captured in the mainstem were in spawning condition from March through July at maximum water temperatures of 10-14°C, a range that is marginal for survival of eggs and larvae. Ripe humpback chub were reported at 16°C from Cataract Canyon, Utah, in June 1988 (Valdez and Williams 1993), and at 11.5°C from Black Rocks, Colorado, in June 1980 (Valdez and Clemmer 1982), where Kaeding et al. (1986) also reported spawning readiness at 13-17°C in June 1983 and at 15-23°C in July 1984.

Reports of spawning by humpback chub in the LCR were at water temperatures of 16-20°C (Suttkus and Clemmer 1977, Carothers and Minckley 1981, Kaeding and Zimmerman 1983). Hatching success under laboratory conditions 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 at the same respective temperatures was 15%, 91%, 95%, and 99% (Hamman 1982). Hence, although hatching success was highest at 19-20°C, larval survival was highest at warmer temperatures of 21-22°C.

Survival

Survival rates are difficult to determine for any fish species, particularly in a large open riverine system such as the Colorado River. Although the survival estimates presented in this chapter have sizable variance, these statistics will provide empirical data for input to population models. Such models may provide insights into the accuracy of these survival estimates.

We begin by calculating the numbers of eggs potentially deposited by mainstem females during spawning in the LCR. Assuming half of about 3,500 adults estimated in the LCRI aggregation were females, and each carried approximately 2,500 eggs, the total number of eggs deposited in a year is 4.37 million (1,750 females x 2,500 eggs/female). In order for the estimated 3,500 adults in the aggregation to be replaced, an average of two fish from each female during her lifetime would need to survive to median adult age.

The numbers of young hatching and surviving in the LCR are unknown, as are the numbers descending into the mainstem. In the mainstem, shoreline densities of subadults from seining for 24.6 km from the LCR (RM 61.3) to Hance Rapid (RM 76.6) ranged from about 1 to 3.5/100 m^2 in 1991 and 1992, and up to about 13/100 m^2 in 1993. This was equivalent to approximately 246,000 to 738,000 subadults in 1991 and 1992, and up to 3,918,000 subadults in 1993 based on a 5-m wide strip along each shoreline. For the 6.6 km between the LCR inflow (RM 61.3) and Lava Canyon (RM 65.4), estimated numbers of subadults for 1991, 1992, and 1993 were 65,980, 230,930, and 857,750 respectively. The lack of upstream movement of fish from below Lava Canyon indicates that subadults that descend downstream of Lava Canyon Rapid are lost as potential recruits of the LCR population. Roughly 73% of subadults were captured below Lava Canyon Rapid and may represent an estimate of subadults descending the LCR lost from the population due to extensive movement.

Decreases in densities (electrofishing catch rates) of subadults in the mainstem, between the LCR inflow (RM 61.3) and Lava Canyon (RM 65.4) in 1991 and 1992, indicated survival rates of 0.827 for 1 month, 0.102 for 6 months, and 0.097 for 1 year. At a 3-year survival rate of about 0.001, only about 66, 231, and 858 subadults would be expected to survive and recruit to adults from the LCR inflow to Lava Canyon in years like 1991, 1992, and 1993.

Average annual survival of adults (≥200 mm TL) was estimated to be about 0.755. Although survival for this species has not been previously reported, this rate appeared low for a long-lived fish (>25 years) (Ricker 1975, Carlander 1969). A 0.755 annual survival rate and concomitant 0.245 annual mortality rate translates to about 860 adults lost annually from the estimated LCR inflow population of about 3,500 adults. Hence, survival of subadults might replace about 8% (66÷860), 27% (231÷860), and 100% (858÷860) of average annual adult mortality. At the annual rates of subadult survival of 0.1 and mean numbers of subadults seen in 1991, 1992, and 1993, recruitment would not replace adult losses and the decreasing mainstem adult population would be expected to equilibrate at a much lower level in less than 10 years. Population estimates during this investigation showed a relatively stable adult population, indicating another source of recruitment such as adults directly from the LCR. Length-frequency analysis indicates that many young adults (i.e., 250 - 350 mm TL) descend from the LCR to the mainstem and could be the principal source of recruitment to the mainstem component. Lower annual survival rates for subadults observed in 1993 (<0.003%) would mean substantially less replacement of adults than was estimated using rates for 1991 and 1992.

Although it was difficult to directly relate survival of humpback chub to environmental influences, several possible mortality factors are identified for adults, including predation, starvation, diseases, parasites, and handling by scientists. Predation on humpback chub has been documented for rainbow trout (P. Marsh, ASU, pers. comm), brown trout, and channel catfish, and suspected for striped bass. Avian predators such as bald eagles and ospreys could also take small number of adults; an osprey was observed taking one adult humpback chub near the LCR inflow (Wasowicz and Yard 1993) and osprey were suspected of taking a second adult within a 5-month period. The numbers of adult humpback chub taken by these predators was undetermined, but even predation by a small percentage of a large predator population can significantly reduce a prey population.

Evidence of starvation was not noted for adult humpback chub during this investigation. Most individuals handled seemed to be healthy and robust as indicated by high relative condition factors. Diseases and parasites may account for some deaths of adults, although fish handled during this investigation were relatively free of apparent pathogens (<1% had L. cyprinacea and about 4% had Asian tapeworms). Although difficult to evaluate, Asian tapeworms may become a significant mortality factor for humpback chub with increased incidence of the parasite and exposure to warm water.

The causes of subadult mortality are probably linked to food supplies, habitat availability and stability, and predation. Emaciated subadults were captured in late summer indicating local food shortages. Also, the dramatic decrease in density of subadults seen between September and November of 1993, and to a lesser degree during the same period in 1991 and 1992, may be related to the change in operation from high volume to low volume release months (See Chapter 3 - HYDROLOGY). This change in operation reduces average releases from about 15,000 cfs to about 10,000 cfs, hence the amount of available shoreline vegetation and cover for the fish may be dramatically reduced, increasing the susceptibility of these young fish to predation. This fall season is also the time of year of highest feeding activity by brown trout, the most significant predator of humpback chub in Grand Canyon.

About 0.2% of 6,294 (3 adults and 11 subadults) humpback chub handled by B/W during 1990-93 died as a result of injuries from sampling or handling, and an equal number may have died following release from post-handling infection or stress. Thus perhaps as many as 30 humpback chub died from handling during this investigation or about 10 fish per year.

Interactions With Other Species

Possible interactions between humpback chub and sympatric fishes included predation, competition, and as vectors for diseases and parasites. Of 15 fish species captured between Lees Ferry and Diamond Creek during 1990-93, only 4 were native and 11 were non-natives. Humpback chub were caught in direct association (same sample effort) with 10 of the 11 non-native species and with all 3 native species. The most commonly associated species with adult humpback chub were rainbow trout and flannelmouth sucker, while common associates with subadults along shorelines were rainbow trout, speckled dace, fathead minnow, and carp. Channel catfish were not commonly captured in the mainstem, but these fish were probably present in greater numbers than reflected in sampling gears.

The most common and significant predator of humpback chub was the brown trout; 10.4% of adults each contained an average of 2.0 humpback chub. It was determined that 3,000 adult brown trout were capable of consuming 227,760 humpback chub annually as large as 340 mm TL. It was also calculated that if 1.5% of adult rainbow trout each ate 1.0 humpback chub daily, 5,000 adults could annually consume about 27,373 humpback chub up to 261 mm TL. Channel catfish, at a predation rate of 1.5%, and an estimate of 500 adults, could consume up to 2,738 humpback chub annually, as large as 165 mm TL. Thus, brown trout, rainbow trout, and channel catfish can potentially consume an estimated 250,000 humpback chub annually. Predation of native fishes in Grand Canyon by brown trout is of particular concern, since it appears that brown trout are increasing in abundance in the Bright Angel area. The proportion of brown trout to rainbow trout at Bright Angel Creek in 1980 was one in ten (Usher et al. 1984), but results of this investigation suggest that this proportion has been reversed.

Flannelmouth suckers and bluehead suckers were found in lower numbers than humpback chub, and few young fish were caught, indicating low reproductive success or survival of eggs or larvae. Weiss (1993) reported large numbers of flannelmouth suckers in spawning readiness in the Paria River, but reported no larvae. If the behavior of young flannelmouth suckers in the upper basin (Valdez et al. 1985) is an indication of behavior in Grand Canyon, large numbers of drifting mesolarvae and metalarvae (young less than 2 weeks of age) would be expected over relatively short time periods. These life stages are highly susceptible to thermal shock, and the majority are probably succumbing to changes in temperature during dispersal from warm tributaries such as Kanab Creek, Shinumo Creek, and the Paria River to the cold mainstem. Those surviving the transition may exhibit erratic swimming behavior that often elicits predator responses, suggesting that the majority of larval fishes reaching the mainstem die from either thermal shock or predation.

Individuals of all species, but particularly the larger predators and scavengers (i.e., channel catfish, carp, black bullhead, green sunfish) seem to be able to detect even relatively minute particles of food in the river. Although human food remains are not a major component of organic matter in the system, the higher incidence of occurrence in stomach of these non-natives indicates highly developed sensory systems in these fish and a high capacity for competition.

DIRP Hypotheses

Three hypotheses were identified in the Draft Integrated Research Plan (DIRP) and presented in Chapter 1 of this report relative to the effects of Glen Canyon Dam operations on native fishes. The following is a restatement of those hypotheses and a discussion of our findings with respect to each hypothesis.

Hypothesis 6.1: "There is no significant relationship between the population dynamics (including short-term abundance of early life stages and potential predation relationships) of native (especially the humpback chub) and introduced fish species in the mainstem Colorado, including mainstem backwaters and the confluence of the Little Colorado, and the magnitude of fluctuations, minimum discharges and rates of change of fluctuating discharges."

This general hypothesis was developed before interim flows were implemented in August 1991, and reflects the concern for high and low flow magnitude with high daily fluctuating discharges characteristic of dam operations under full power plant capacity; i.e., minimum discharges of 1,000 cfs or 5,000 cfs, and maximum discharge of 31,500 cfs, with unrestricted ramping rates, as seen from October 1986 to June 1990. This investigation did not witness this operating scenario; instead research flows were in effect during the first 10 months of the study (October 1, 1990 - July 31, 1991), and interim flows were effective during the remaining 28 months (August 1, 1991 - November 30, 1993). Nevertheless, information gathered during this investigation provided insight into this hypothesis and the following two sequential hypotheses (i.e., Ho:6.1a and Ho:6.1b):

Hypothesis 6.1a: "There is no significant relationship between population dynamics of native and introduced fish species in the mainstem Colorado, including backwaters and tributaries, and the magnitude of discharge fluctuations."

The effect of the magnitude of discharge fluctuations on fish population dynamics is a general hypothesis that logically leads to a series of sequential and parallel hypotheses, each dealing with effects on different life history aspects of the various fish species. This investigation addressed some of these hypotheses as applied to humpback chub.

We identified significantly greater local movement by adult humpback chub at highest magnitude of discharges; the proportion of times fish moved was significantly higher ($P<0.00001$) at flows above than below 10,000 cfs. The greatest movement occurred during periods when flow was increasing or decreasing, and not during the period in which flow was steady at highest magnitude. This movement was significantly higher ($P<0.00005$) when ramping rates were greater than 300 cfs/hr at flows above 10,000 cfs. Movement was also greater, but not significant, at ramping rates greater than 300 cfs/hr at flows below 10,000 cfs.

We also noted that average ramping rates at the USGS gage above the LCR confluence during research flows were 886 cfs/hr and average rates during interim flows were 378 cfs/hr. Proportion of times adult humpback chub moved was significantly greater ($P=0.023$) during research flows than during interim flows.

We believe that greater movement by adult humpback chub during high ramping rates at highest flow magnitudes were either (1) in response to changes in local hydraulics (i.e., velocity, current direction, water depth) forcing fish to find new microhabitat positions, or (2) from increased feeding activity as a result of increased material drifting in the river during increasing flows (significantly more Cladophora) or decreasing flows (significantly more macroinvertebrates). High relative condition factors of most adults handled in the mainstem suggest that this increased activity was not an energetic deficit to the fish, and may have been a response by fish to find microhabitats best suited as low-velocity resting and food entrainment areas. We did not view the magnitude of discharge fluctuations observed during interim flows (i.e., 8,000 cfs to 20,000 cfs) as energetically detrimental to adult humpback chub.

While high magnitude of discharge fluctuations may have not detrimentally affected bioenergetics of adult humpback chub, other life history aspects may have been affected. Although we determined from bathymetry of the LCR inflow that fish movement through the inflow was not limited by base LCR flow (i.e., 230 cfs) and low mainstem flow (i.e., 5,000 cfs), high and low magnitude of discharges likely affected YOY and juvenile humpback chub. Bathymetry and temperature isopleths at different flows revealed a highly dynamic thermal plume from the LCR depending on mainstem flows. 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.

We also tested the hypothesis that high magnitude of discharge fluctuations did not significantly affect shoreline habitat of subadult humpback chub. While the magnitude of fluctuations observed during interim flows (i.e., 8,000 cfs to 20,000 cfs) did not significantly change the composition of shoreline type or shoreline complexity, the densities of subadults along shorelines decreased dramatically from peak levels in mid-summer to low levels the following spring. We estimated 10% annual survival of subadults, and attributed loss of fish to habitat changes and downstream transport, predation, food availability, and parasites and diseases. We further hypothesized that fluctuating flows destabilized shorelines and, combined with cold temperatures, displaced and transported young fish downstream into less desirable habitats with high predator loads. 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°C compared to 14°C (Bulkley et al. 1982). This hypothesis needs to be more fully tested by monitoring densities and locations of subadults, evaluating predation levels by non-natives, and conducting laboratory swimming performance experiments with YOY (range, 50-100 mm TL), juveniles (range, 100-200 mm TL), and adults (>200 mm TL).

Clearly, these sequential hypotheses address only some life history aspects of humpback chub. Many other life history aspects and ecosystem components affected by magnitude of discharge fluctuations remain to be addressed. There are presently substantial volumes of information and data available by which to make these evaluations. This information can only come to bear if researchers assimilate their respective data bases and reports to facilitate an integration of existing information.

Hypothesis 6.1b: "There is no significant relationship between population dynamics of native and introduced fish species in the mainstem Colorado, including backwaters and tributaries, and the magnitude of minimum discharges."

The magnitude of minimum flows under interim flows (i.e., daytime minimum of 8,000 and nighttime minimum of 5,000 cfs) is generally higher than the lowest mean daily flow of 5,000 cfs (January) during predam flows. Although this higher magnitude of minimum discharges does not appear to be significant, the reduced swimming ability of subadult humpback chub in cold water suggests that greater volume flows provide fewer low-velocity areas and may substantially restrict suitable subadult habitat throughout Grand Canyon. Minimum release patterns are inconsistent with predam patterns of low flow, which usually occurred concurrent with lowest temperatures in November through February. This was a time when humpback chub were 5-8 months old and more tolerant to low temperature. Under existing flow and temperature scenarios, low and high flows occur monthly at relatively constant cold temperatures and during spring, summer, and fall months when newly-hatched fish are small and metabolic rates were historically high.

MANAGEMENT OPTIONS

Flow Management

Stratigraphic records and historic flow patterns show that the Colorado River in Grand Canyon was highly variable with respect to flow magnitude, temperature, and sediment loads. These are conditions to which a small assemblage of fish adapted over a period of about 3 million years. This variability in seasonal and annual flow patterns and seasonal temperature was important in maintaining the structure and function of the aquatic ecosystem (Clarkson et al. 1994). Changes in hydrology and water quality brought about by the operation of Glen Canyon Dam have changed many structural and functional relationships of this system. While returning the ecosystem to its historic condition is not possible, maintaining and restoring some structure and function is essential to conserving the native fishes. Flow as well as non-flow alternatives should be identified and explored.

High Spring Releases

A large, but unspecified release of water from Glen Canyon Dam in spring has been identified by the Service as a favorable operational aspect for native fishes. A high spring release of 31,500 cfs (power plant capacity) would be too low to provide much benefit to native fishes. Higher velocities in recirculating eddies would probably remove lighter sediments from eddy return channels (i.e., backwaters) but the capacity of backwaters is not expected to change substantially. High cold releases would likely transport some young humpback chub and less-resistant non-native species downstream.

A spring release of 48,200 cfs (powerplant plus outlet works) would probably top debris fans and rearrange sand deposits in recirculating eddies, effectively reshaping reattachment bars and eddy return channels. This flow would be expected to displace many non-natives from the system, but 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 warmwater species is significantly reduced at colder temperatures. Sufficiently low ramping rates may reduce the risk of transporting young chubs 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.

Steady Summer Flows

A steady summer release of unspecified amount has been identified by the Service as one possible operational scenario to enhance survival of young humpback chub in the mainstem. Steady flows would presumably stabilize water levels in nursery backwaters, allowing them to warm and increase in productivity. This stabilized water level would presumably benefit humpback chub, flannelmouth suckers, bluehead suckers, and speckled dace by providing permanence in nursery habitat and enhancing growth through warmer water and higher in situ food production.

The level at which to stabilize this flow may be difficult to determine because the elevation of the reattachment sand bars 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 sand bar formation and elevation, such that steady flows may maximize backwater habitat in some reaches of the canyon, but not in others. The relationships between reattachment bars and eddy return channel elevations, as affected by antecedent flows, need to be determined for all presumed nursery regions in Grand Canyon.

Assuming that a steady flow can be identified to optimize backwater habitat, the stable, warm environments produced are likely to also attract large numbers of non-native species. Fathead minnows, carp, mosquitofish, plains killifish, green sunfish, and channel catfish are known to spawn in similar quiet habitats in other river systems (Pflieger 1975), and would be expected to reproduce in these areas as well. A high spring release (See previous section) may inundate these backwaters and transport these non-native fish from the system, but it would not occur for about 6 months after the steady release. Assuming non-native fish reproduced during the steady summer flow, their young could be of sufficient size and temperature-acclimated to resist some of the effects of a high spring release.

A steady release from the dam is likely to result in increased water clarity in the absence of tributary floods. High water clarity is likely to significantly affect behavior of humpback chub and increase the likelihood for predation. Adult humpback chub were less active during high water clarity (NTU<30), especially in the daytime, indicating that the fish used turbidity as a cover element and probably fed on a greater availability of drifting food items during fluctuating releases. The likelihood of predation on subadults along shorelines is also greater under high water clarity.

Selective Withdrawal

Selective withdrawal is identified as an element common to all the alternatives of the Glen Canyon Dam Final EIS (U.S. Department of Interior 1995). While the engineering, technological feasibility, and cost of this element are being evaluated, little is known of the biological impact of releasing warmer water into the Colorado River in Grand Canyon.

Modifying the penstocks of Glen Canyon Dam to withdraw warmer, epilimnetic water from Lake Powell would increase the temperature of the Colorado River in Grand Canyon, resulting in beneficial effects to some aspects of the aquatic ecosystem and detrimental effects to others. Ultimately, the decision to implement a selective withdrawal structure, and the design of its operation, will have to weigh possible benefits and risks for all canyon resources.

Possible benefits to fishes include:

- mainstem reproduction by native warmwater fishes,
- increased primary production,
- increased secondary production and invertebrate species diversity,
- reduced numbers of coldwater predators and competitors (i.e., rainbow trout) in downstream habitats occupied by native fishes,
- higher growth rates for warmwater fishes,
- higher growth rates for trout in the tailwater fishery,
- warm nursery backwaters, and
- reduced thermal shock for larval fish dispersing from tributaries.

Possible detriments to fishes include:

- mainstem reproduction by nonnative warmwater fishes,
- invasion by new nonnative warmwater species,

- altered algal and diatom composition and communities, possibly from pedicled (upright) forms to sessile (adnate) forms, less available to predaceous macroinvertebrates (Blinn et al. 1989),
- increased incident of fish parasites, including Asian tapeworm and parasitic copepods,
- altered macroinvertebrate species composition and abundance, and
- reduced downstream populations of rainbow trout (e.g., Nankoweap Creek, Bright Angel Creek).

Temperature Requirements of Fishes

Three analyses of temperature requirements of the fish species in Grand Canyon were recently conducted (Valdez et al. 1992, Haden 1992, Lechleitner 1992) to evaluate possible effects of selective withdrawal. Lechleitner (1992) presented thermal requirements and tolerances of fish species (Fig. 10-3, Fig. 10-4, and Fig. 10-5), as well as other aquatic organisms below Glen Canyon Dam.

No information is available to identify upper lethal,lower lethal, temperatures for the native species. The wide range of historic temperatures of the Colorado River suggests that adults of the native mainstem species can survive ranges of 0-30°C.

Upper lethal temperatures for rainbow trout, cutthroat trout, and brown trout are 25°C, 23°C, and 24°C, respectively, which are suitable upper limits for spawning by the native Colorado River fishes, indicating that thermal regulation to favor native fishes could be detrimental to salmonids in downstream reaches. It is also noted that optimum growth for rainbow and cutthroat trout occurs at 12-17°C and at 10-16°C for brown trout.

The range of suitable spawning temperatures for the warmwater non-native species are similar to those of the native species. Red shiner and fathead minnow are capable of successful reproduction at a wide range of temperatures of 15-30°C, while carp require 20-26°C. Channel catfish have a slightly higher spawning requirement of 23-29°C, similar to

Lethal and Optimum Growth Temperatures for Colorado River Fishes

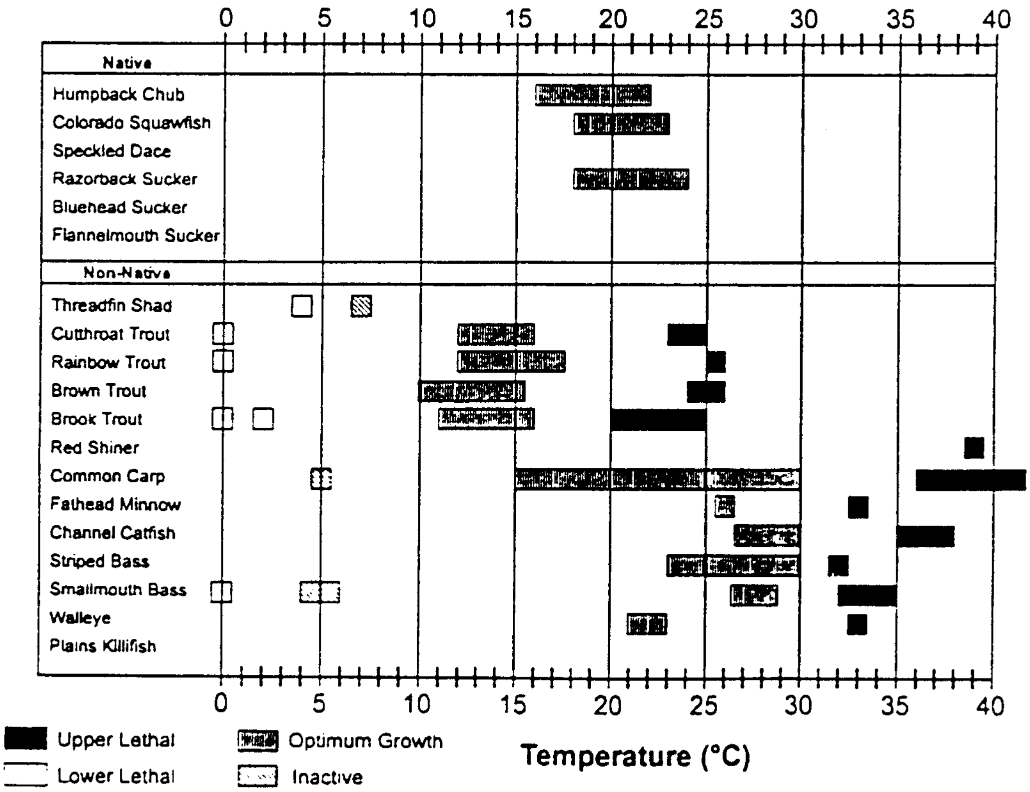

Fig. 10-3. Lethal and optimum growth temperature for Colorado River fishes. From Lechleitner (1992).

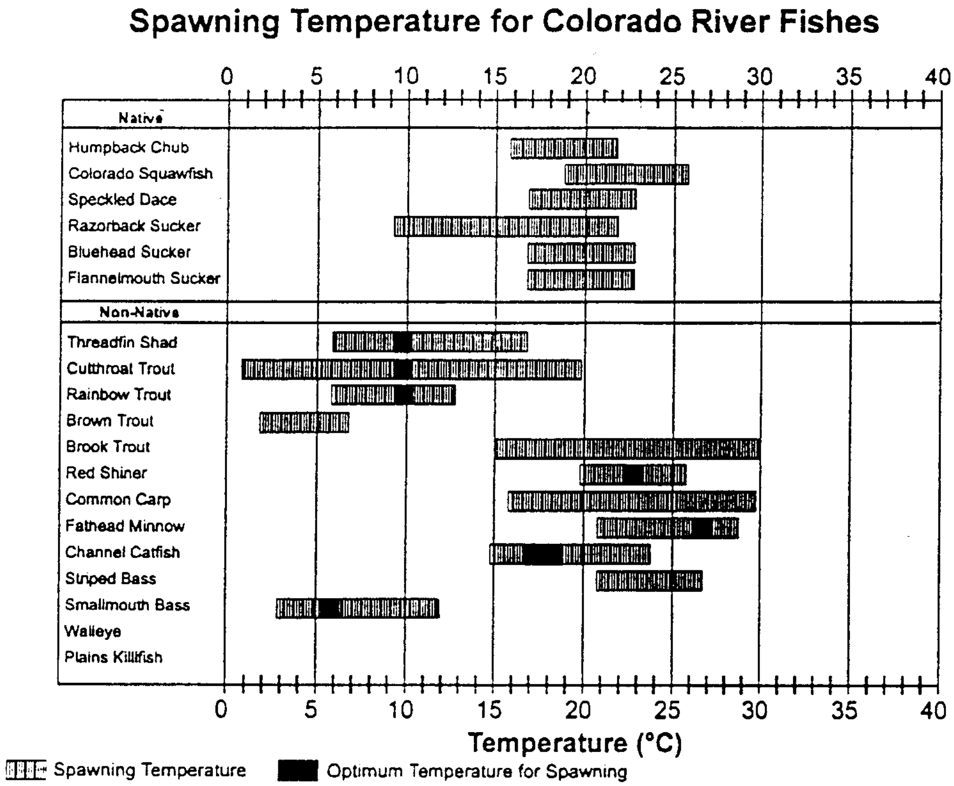

Fig. 10-4. Spawning temperature for Colorado River fishes. From Lechleitner (1992).

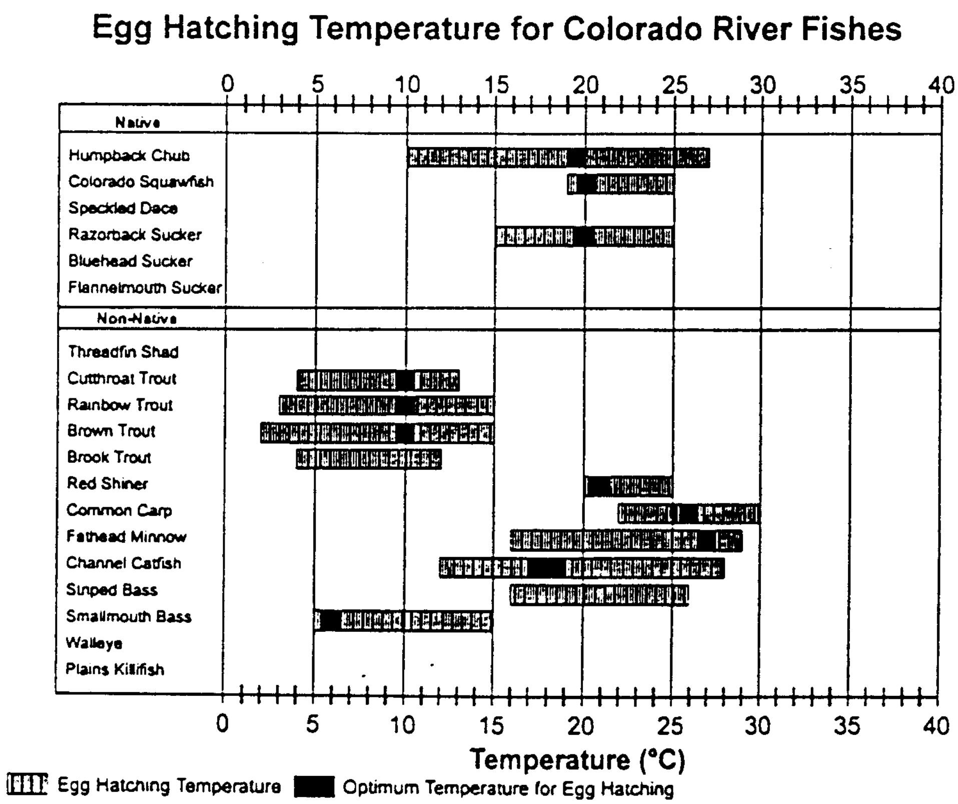

Fig. 10-5. Egg hatching temperature for Colorado River fishes. From Lechleitner (1992).

that of largemouth bass. Suitable spawning temperature for striped bass is 15-24°C, while that of walleye is much colder at 3-12°C, although some strains are capable of spawning in warmer conditions.

Suitable spawning and egg incubation temperature range for humpback chub is 16-22°C (Hamman 1982), with an optimum of 19-20°C (Marsh and Pisano 1985). Reduced survival and significantly higher incidence of physical anomalies were reported at 15°C and 25°C. Hatching success and survival of larvae was less than 15% at temperatures of less than 16°C, and no hatching occurred at temperatures of less than 12°C (Hamman 1982). Suitable egg incubation temperature for razorback suckers is 15-25°C, with an optimum of about 20°C. Maddux and Kepner (1988) reported bluehead suckers spawning in Kanab Creek at temperatures of 18.2°C to 24.6°C. Suitable spawning temperature for flannelmouth suckers is probably similar to that of bluehead suckers.

Suitable spawning and egg incubation temperatures for flannelmouth sucker, bluehead sucker, and speckled dace were 17-23°C. Only razorback suckers demonstrated an ability to spawn and successfully incubate at temperatures as low as 10°C and as high as 22°C.

The present thermal regime of the Colorado River in Grand Canyon does not reach the optimum spawning temperature for humpback chub of 19-20°C (Hamman 1982, Marsh and Pisano 1985). The existing thermal regime reaches the lower range of suitable spawning temperature of 16°C below Diamond Creek only during the months of July and August. The remainder of the year, the temperature of the Colorado River in this region is too cold for successful spawning, hatching, and survival of humpback chub. Some very localized reproduction may be occurring in the mainstem, most likely at tributary or spring inflows, but the numbers of young fish produced and surviving is probably insignificant to the continued existence of the species in Grand Canyon.

Clearly, spawning by humpback chub in the LCR is timed to occur when temperatures of that tributary are within the suitable range of 16-22°C, from April through May (Fig. 10-6). Kaeding and Zimmerman (1983) reported that mean female gonadosomatic indices and ovary diameters of humpback chub in the LCR, mainstem, and LCR inflow were highest between early February and late April 1980,

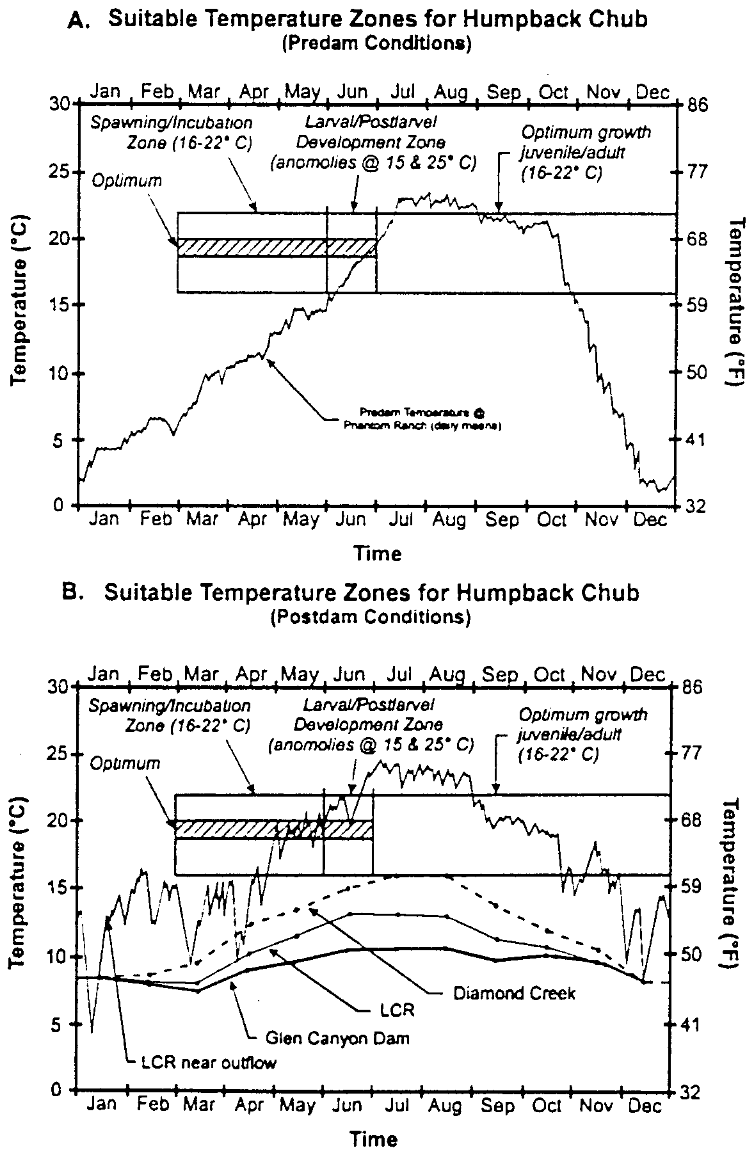

Fig. 10-6. Suitable and optimal temperature range for spawning by humpback chub compared to predam temperature of the Colorado River at Phantom Ranch (A), and the temperature of the LCR and postdam Colorado River at Glen Canyon Dam, LCR, and Diamond Creek (B). Spawning, egg incubation, and larval development periods are shown for present LCRI aggregation.

indicating that most spawning probably occurred in March, April, and May.

If humpback chub were spawning in the mainstem prior to Glen Canyon Dam--as they presently do in all other populations in the basin--that activity would have had to occur when temperatures were suitable, most likely from late May to early July (Fig. 10-6). One of three explanations accounts for the disparity in timing between predam and present spawning events:

1. Humpback chub in Grand Canyon did not spawn in the mainstem prior to Glen Canyon Dam, only in the LCR; an unlikely scenario considering all other populations spawn in similar mainstem conditions.

2. Cold releases forced mainstem spawners to switch to an earlier spawning mode and ascend the LCR to coincide with temperatures of that tributary; a possible scenario considering many fish species are capable of switching spawning times under changed environmental conditions, e.g., temperature, photoperiod.

3. Two population components existed in Grand Canyon--one spawned in the mainstem, and one in the LCR. The mainstem component experienced unsuccessful reproductive efforts following Glen Canyon Dam and few if any individuals remain; this is the most likely scenario and an important consideration for a second population in the mainstem if unique genetic stocks exist.

The third explanation presented above appears the most plausible, based on length characteristics and movement patterns of fish in the mainstem and LCR. It appears that the present population is based in the LCR with some small and large individuals using the mainstem. Predam relicts probably occur at 30-Mile and perhaps in other regions of the canyon.

Temperature Effects on Non-Native Fishes

The most significant concern for warming the temperature of the Colorado River in Grand Canyon is the possible invasion by predaceous and competing non-native fish species that presently occur upstream in Lake Powell, downstream in Lake Mead, and in several tributaries throughout Grand Canyon. The response by non-native fishes must be considered in every management option evaluated. A definitive evaluation cannot possibly be presented in the confines of this treatise, nor is it possible with existing information to evaluate possible responses by the fish. Kaeding and Osmundson (1988) proposed that because Colorado squawfish were restricted by dams to the cooler upper basin, their growth rates and life history functions were affected. Similar effects may be expected in Grand Canyon.

Warming releases from Glen Canyon Dam is likely to change the distribution and abundance of some species of fish. The distribution of rainbow trout is likely to be compressed upstream, with fewer numbers expected below the LCR, particularly in summer. Brown trout are not expected to change their distribution, although greater numbers may move upstream from the area of the Bright Angel Creek inflow into the area of the LCR inflow. Brown trout appear to be spatially allied to their spawning habitat in Bright Angel Creek, and this species is not likely to take up residence near the LCR, where suitable spawning streams are absent. However, warmer mainstem temperature may result in greater mainstem reproduction by these salmonids, and should increase their growth rates, especially in the tailwater fishery.

Thermal regulation in Grand Canyon is likely to benefit the tailwater trout fishery by providing more optimal temperatures for growth by rainbow trout, cutthroat trout, brook trout, and brown trout. However, downstream populations of trout would be detrimentally affected by above-optimum temperatures, thus reducing downstream distribution and abundance of trout, which in turn would reduce competition and predation with native species.

Under thermal augmentation, the suitable spawning temperature for channel catfish of 21-29°C would occur only in the lowermost reaches of the canyon, and only in June, July, and August. Still, optimum growth temperature of 26-30°C is not likely to occur under the described thermal regulation scenario. Another species of equal concern is the carp, which can detect and consume large numbers of recently-deposited eggs. This species is likely to have suitable spawning temperatures in the mainstem under the described scenario, but since carp require vegetation or structure for attaching their eggs, their spawning sites are likely to be limited to warm quiescent areas such as flooded lowlands or stable backwaters. These features are likely to be available to carp under flow management scenarios that favor long-term stability of backwaters, even in the absence of a selective withdrawal structure. The effect of carp on native fishes is expected to be insignificant since most native species deposit their eggs in deep, swift cobble where the eggs drop into protected crevices, removed from the suction feeding mode of the carp.

The small numbers of fathead minnows that occur in Grand Canyon could be expected to increase in abundance and distribution with warmer flows, but because of the inability of this species to tolerate even moderate current and riverine conditions, its numbers could be controlled with flow management. Flows that inundate warm, quiet backwaters would force these fish into the colder, swifter mainstem, where their chances of survival are reduced.

Considerable evidence indicates that red shiners may outcompete and exclude other species (Ruppert et al. 1993), although the mechanisms are not fully understood. Like fathead minnows, red shiners experienced dramatic decreases in density in the upper basin during the high flows of 1983-86 (Valdez and Williams 1993), but red shiners are more tolerant to current and riverine conditions. W.L. Minckley (ASU, pers. comm.) reported that red shiners were common in the Colorado River in Grand Canyon Dam prior to the coldwater releases, suggesting that the species was excluded from the region by temperature alone. However, it should also be noted that high fluctuating releases from the dam prevented stable backwaters, the primary habitat for this species in the upper basin. Another consideration is the rate of invasion by a small cyprinid like the red shiner into the high velocity Colorado River in Grand Canyon. The species is presently common as far upstream as Bridge Canyon (404 km downstream of the dam) and spawns primarily in the tributaries of that reach, i.e. Separation Canyon, Spencer Canyon, Lost Canyon, Quartermaster Canyon (Valdez et al. 1995). The most likely mode of invasion would be establishment of spawning populations in tributaries upstream of Bridge Canyon, although the absence of perennial tributaries for 111 km between Diamond Creek and Havasu Creek could impede invasion (Valdez et al. 1995).

Plains killifish and mosquitofish would not be expected to increase in great numbers in the mainstem as a result of thermal augmentation, primarily because these species are tributary inhabitants and fare poorly in high velocity lotic environs.

Of the species that presently inhabit Lake Mead and Lake Powell, only striped bass have been found in any numbers in Grand Canyon; 39 were captured during 1991-93, during spawning ascents between May and July. Individuals have not been captured at other times of the year indicating that the fish presently move into the canyon only to spawn, and are present in other seasons only as far upstream as Bridge Canyon. Most of the striped bass examined had empty stomachs indicating fasting during these spawning ascents, which is typical for the species. Thermal augmentation may allow for greater numbers of striped bass to ascend into Grand Canyon, but it is unlikely that these would become resident any further upstream than their current distribution. Mainstem temperatures do not presently appear to be limiting the fish since temperatures at Bridge Canyon are similar to those of the river as far upstream as Havasu Creek. It is likely that stream velocity and the absence of deep lentic habitat limits the upstream distribution of striped bass in Grand Canyon, and not the coldwater dam releases. Similarly, walleyes, although highly predaceous, are not expected to invade the Grand Canyon under selective withdrawal, since present releases already provide optimum spawning temperature for the species.

Other lentic fish species that pose a possible threat to natives in Grand Canyon are black bullhead, green sunfish, smallmouth bass, and largemouth bass. Except for smallmouth bass, these species are relatively weak swimmers and unlikely to gain access into the Grand Canyon in large numbers. Black bullhead, green sunfish and largemouth bass rarely occur in the main river channel in the upper basin, and rely almost exclusively on backwaters and flood bottomlands. These species can be highly predaceous if they gain access to backwaters. Smallmouth bass, on the other hand, are small stream inhabitats that could invade the mainstem, and may become established particularly near tributary mouths. The other lentic species in Lake Mead--bluegill, black crappie, and threadfin shad--are apparently intolerant of swift riverine conditions, and would not be expected to invade the Grand Canyon under selective withdrawal.

Another species of concern is the flathead catfish (Pylodictis olivaris), a species that is common and a voracious predator in many tributaries and the mainstem of the Colorado River below Hoover Dam (W.L. Minckley, ASU, pers. comm.). It is presently found downstream of Hoover Dam and has not been reported from Lake Mead, although conditions in the reservoir are probably suitable for survival and possibly reproduction. This species usually spawns at 24-28°C (Carlander 1969) and prefers warmer temperatures and more quiescent flooded bottomlands than are available in Grand Canyon.

Temperature Effects on Parasites

Two species of fish parasites are of particular concern in Grand Canyon. Recently, the Asian tapeworm (Bothriocephalus acheilognathi) was reported from the intestine of humpback chub in Grand Canyon (Angradi et al. 1992). The degree of infestation in the population is unknown, but 80% of young humpback chub (range, 13-35 mm TL) examined in 1990 by AGF had tapeworms. The absence of tapeworms from humpback chub in 1989 (Angradi et al. 1992) suggests that this parasite only recently entered the region, or that the parasite had not proliferated for lack of suitable conditions.

A literature review of this parasite was done by Lechleitner (1992). The Asian tapeworm was introduced into the United States in grass carp (Ctenopharyngodon idella) in the 1970s and is well established in the southeastern U.S. (Granath and Esch 1983). The life cycle begins with operculate eggs shed into the water via feces from an infected fish. A motile coracidium emerges after a period of development (96 hr at 20°C). Coracidia are ingested by cyclopoid copepods and develop into a procercoid stage, which in turn are ingested by a fish host where the cestode matures into an adult in the intestine. Asian tapeworms lack host specificity and have been found in fathead minnows, red shiner, and mosquitofish. Egg maturation occurs between 25°C and 30°C, although highest densities of worms occurred at 20°C (Hoffman 1980). This information suggests that egg maturation could occur in the mainstem if thermal augmentation raised ambient temperature to 20°C. Increased production of this parasite could infect greater numbers of fish in the mainstem, assuming the host-specific copepods are also present.

The second parasite of concern is the parasitic copepoda, Lernaea cyprinacea, or anchor worm. Its life cycle begins when attached females shed eggs that develop into two motile phases (nauplia and metanauplia), and the copepoda parasitic phase, which penetrates the tissue of the fish and anchors externally (Marcogliese 1991). Females mature as they remain attached to the fish, and eggs are shed into the surrounding water. There is no intermediate host. Temperature affects the rate of development of all stages of L. cyprinacea. Naupliar development fails to proceed below 20°C (Shields and Tidd 1968). The critical low temperature for development and penetration is believed to be between 15°C and 20°C, and egg production does not appear to occur at temperatures of less than 24°C. This information suggests that naupliar development could occur in the mainstem if thermal augmentation raised temperature to 20°C. However, this parasite would not be expected to proliferate in the mainstem because swift currents could reduce low-velocity regions needed for attachment, although enhancement of stable backwaters would produce a suitable environment for this parasite to spread.

Lernaea cyprinacea is common on native and non-native fishes in the Upper Colorado River Basin. Infestations of Colorado squawfish, razorback suckers, and humpback chub are common, with highest numbers of individual parasites in fish from backwaters and warm flooded bottomlands (Valdez et al. 1982, Tyus et al. 1982). The effect of anchor worms on fishes in the upper basin is unknown, but does not appear to lead to significant numbers of fish mortalities.

Sediment Augmentation

Sediment augmentation is identified as an element common to all alternatives of the Glen Canyon Dam Final EIS (U.S. Department of Interior 1995). While the engineering and technological feasibility of this element remains to be evaluated, little is known of the biological impact of added sediment to the aquatic ecosystem in Grand Canyon. This investigation identified a relationship between turbidity (suspended sediment) and fish behavior that provides some insight into the importance of this element to native fishes.

Adult humpback chub were significantly more active during higher levels of turbidity (NTU>30) and at night than during high water clarity. These results indicate that the species uses turbidity as a cover element for foraging and possibly as escape from predators. Presumably, prolonged periods of high water clarity could impede daytime feeding activity and place individuals at greater risk of predation. Most fish examined during this investigation appeared robust and healthy, with high relative condition factors for all aggregations, indicating that feeding was not being significantly impaired by current dam operations.

Water clarity also seemed to affect use by subadults of certain shoreline habitats. Incidental observations suggest that higher densities of young humpback chub were found along shorelines during high turbidity or at night. Such observations also indicate similar use of backwaters. The effects of these relationships on condition of these young fish were not evaluated.

Frequency and magnitude of turbidity above and below the LCR also had a substantial effect on the abundance of rainbow trout. Densities of trout decrease significantly from 1992 to 1993, following high, turbid, and persistent floods from the LCR in spring and summer. We attribute this reduction to the inability of rainbow trout to feed in high turbidity (NTU>30), resulting in starvation or movement to other areas. Hence, increased frequency of turbidity in the mainstem is likely to decrease predation by sight feeders (e.g., rainbow trout, brown trout).

Removal of substantial sediment from the system has also depleted sand bars in eddy complexes and along shoreline margins. Sediment augmentation could supplement these depleted sand supplies, but the benefit to fish habitat is unknown until geomorphic effects are fully evaluated. Since the present system is primarily autotrophic, added sediment could significantly reduce primary production.

Non-Native Fish Management

Non-native fishes are the single most important factor limiting management alternatives for native fishes in Grand Canyon, and they may be the most important factor limiting native fish populations (Minckley 1991). Fourteen non-native species are presently sympatric with humpback chub in Grand Canyon that can be classified as known or potential predators, competitors, and agents for parasites and diseases. Known predators include brown trout, rainbow trout, and channel catfish. Striped bass, green sunfish, brook trout, black bullhead, and walleye occur in small numbers and probably have an insignificant predator impact. Carp may also be significant predators of incubating eggs in the LCR and warm springs, and small cyprinids, such as fathead minnows and red shiners are known predators of early life stages of native species (Rupert et al. 1993, Douglas et al. 1994, Gregory and Deacon 1994).

We estimate that brown trout, rainbow trout, and channel catfish may consume approximately 250,000 young humpback chub annually. Most of this predation occurs between the LCR (RM 61.3) and Bright Angel Creek (RM 87.7), in the area where the species are sympatric and humpback chub occur in highest densities. An examination of rainbow trout in 1992 and 1993 for coded wire nose tags used by AGF to mark fish released in the tailwater fishery between Glen Canyon Dam and Lees Ferry, showed that of about 151,000 marked rainbow trout released in 1992 and 1993, only 3 were captured downstream of Lees Ferry (RM 2.9, 3.2, 3.2). These findings indicate that rainbow trout found in downstream reaches, sympatric with humpback chub, are probably the progeny of local natural reproduction from tributaries such as Nankoweap Creek, Clear Creek, Bright Angel Creek, Shinumo Creek, Tapeats Creek, Deer Creek, and Havasu Creek, and not from the tailwater fishery. In the area of highest predation (i.e., LCR to Bright Angel Creek), rainbow trout probably originate primarily from Nankoweap Creek, Clear Creek, and Bright Angel Creek, and possibly from mainstem spawning near these tributaries. Brown trout are not presently stocked in the system, and Bright Angel Creek is the primary spawning area for that species.

The third major predator of humpback chub in the system, channel catfish, are apparently primarily mainstem inhabitants that aggregate annually for spawning in warm tributaries, primarily the LCR. Researchers in the LCR have reported channel catfish in that tributary for many years, indicating that the species is also resident in that stream (Kaeding and Zimmerman 1983, Gorman et al.

1994). Channel catfish were not reported in recent surveys of the Paria River (Weiss 1993), Shinumo Creek, or Bright Angel Creek (Otis 1994).

A Non-Native Fish Management Plan is recommended to further evaluate effects of non-native fishes on native species. This plan should also evaluate the possibility of controlling non-native predators in the mainstem and tributaries. This plan should identify population centers of documented predators and determine spawning areas and places of origin for fish in high density chub areas. Possible control methods should be evaluated, and the likelihood of success determined. This plan should be reviewed and agreed to by all the resource agencies in Grand Canyon, and a direction with milestones and goals should be established so that numbers of predators and subadult humpback chub can be monitored by the long-term monitoring program. Sensitive areas need to be identified and addressed, such as the blueribbon tailwater trout fishery and the trout population at Nankoweap Creek that is an important winter food source for migrating bald eagles.

Small forms of non-natives such as fathead minnow and plains killifish cannot be mechanically controlled. These species do not presently affect native species significantly, but could become numerous with changed conditions, such as warmer mainstem temperatures from a selective withdrawal system. These species are relatively weak swimmers and inhabit low-velocity areas; fathead minnows thrive in flooded bottomlands and backwaters of the Mississippi and Missouri rivers, and are often the most resistant species to low oxygen, high temperature, and high turbidity (Pflieger 1975). Plains killifish are typically inhabitants of small to medium streams and prefer low velocity areas. These warmwater species are likely to become transported downstream and stressed with high flows that inundate sheltered shoreline habitats such as backwaters. These species are likely to remain in the system, since they inhabit many tributaries, and can readily resupply the mainstem.

Removal of adult non-natives from the system may avail more food for native fishes. Biomass estimates indicate that fish biomass in the mainstem is dominated by these alien species. If food is limiting, removing potential predators may also benefit native species by availing greater supplies of food.

Second Population of Humpback Chub

Conservation Measure 7 of the 1978 Biological Opinion identified the need to "Establish a second spawning population of humpback chub in the Grand Canyon". This element of recovery has several physical, chemical, and biological considerations that need to be weighed in order to evaluate the likelihood of success. We assume that existing conditions in Grand Canyon are unsuitable for fulfillment of life history requirements of the species in all areas, except for the LCR and adjacent mainstem. Although eight aggregations were found in the mainstem outside of the LCRI aggregation, none was considered a viable population; the only substantive evidence of reproduction was young from a warm spring near Fence Fault (RM 30.8). Reproduction may also be occurring in aggregations downstream of the LCR, but all mainstem reproduction appears to be insignificant for maintenance of populations. Nevertheless, aggregations of humpback chub in the mainstem have associated with environmental attributes that may provide a clue to factors that characterize the needs of a second population. Four factors presently limit establishment of a second population in Grand Canyon: (1) cold mainstem temperatures that prevent successful reproduction, (2) habitat arrangement, (3) non-native fishes, and (4) food availability. Other factors may also be important, and should be considered in more detailed integration studies.

Cold summer-time temperatures in the mainstem reach monthly maxima of 10-12°C in areas with known aggregations. These temperatures are known to limit survival of eggs and embryos (Hamman 1982, Marsh 1985), although normal gonadal maturation occurs (Kaeding and Zimmerman 1983), as indicated by tubercles, coloration, and expression of gametes during this study. Preferred temperature for eggs and larvae is 16-22°C. Hence, the association by six of nine aggregations with either warm springs (2) or warm tributaries (4) supports the hypothesis that temperature is one factor limiting establishment of a second population. It is important to note that cold summer temperatures may limit growth of individuals and possibly affect reproductive potential and survival. Cold temperatures may also be limiting swimming ability, especially of subadults (Bulkley et al. 1982), possibly restricting useable habitats to those areas of lowest velocity. If temperature alone were limiting the distribution and abundance of the native warmwater fishes, increasingly greater numbers of humpback chub would be expected downstream of Glen Canyon Dam. Instead, the fish are distributed in clumped fashion with greatest numbers about 125 km downstream of the dam

The second factor associated with four mainstem aggregations was a unique channel geomorphology consisting of high frequencies of debris fans and associated recirculating eddies. Adults selected eddy habitat disproportionate to their occurrence; 88% were captured and 74% were radio-contacted in eddies, which composed only 21% of surface habitat area. This habitat selection appeared to be driven by use of low-velocity vortices in eddies that entrained and deposited large volumes of drifting food, providing individuals with an opportunity to employ an energy efficient feeding strategy. Although thermal influence (i.e., warm springs, warm tributaries) accounted for greater numbers of aggregations, three aggregations, including the two largest aggregations (LCR Inflow and Middle Granite Gorge) were associated with a high frequency of debris fans and recirculating eddies.

The combination of temperature and habitat requirements help to explain the relative success and size of the LCR population. The warm LCR is sufficiently large to accommodate spawning and nursery requirements, but it is the combination of this warm tributary and the presence of large eddies in the adjacent mainstem reach that support a larger adult population than the LCR could independently support. Adults from this aggregation were distributed approximately evenly upstream (6.9 km) and downstream (6.6 km) of the LCR inflow, with approximately even numbers of adults captured upstream (771) and downstream (779). This distribution of adults suggests a reliance on the LCR for spawning, nursing, and early maturation. However, use of areas upstream of the LCR indicates independence of that tributary for other life functions of adults.

Selection for large recirculating eddies suggests that this habitat component is important to this aggregation, and the lack of a similar habitat complex in mainstem areas adjacent to other tributaries (e.g., Bright Angel, Shinumo, Tapeats, Kanab, Havasu) may explain the low numbers of adult humpback chub associated with those inflows. If the LCR was located in a more confined area of Grand Canyon, the lack of mainstem habitat could greatly limit the population.

The third factor that may be limiting humpback chub populations in Grand Canyon is food availability, particularly in downstream reaches. Assuming that the association with channel geomorphology partly explains the longitudinal distribution of humpback chub in Grand Canyon, we would expect to find aggregations in the area where the combination of Muav limestone, Bright Angel shale, and Tapeats sandstone reappears along the shoreline between RM 175 and RM 225. Although one small aggregation (4-5 adults) was found near Pumpkin Spring (RM 212.5-213.2), the fish seemed to be associated with a thermal source. Low numbers of humpback chub--and other fishes--and low primary and secondary production (Blinn et al. 1994) in this western-most reach of Grand Canyon leads us to the hypothesis that food is limiting fish densities in this otherwise suitable habitat. Production in this area is low because cold summer temperatures have disrupted life cycles of native invertebrates, total drift volume has been reduced by impoundment, and persistent turbidity limits photosynthesis in what has been converted from a heterotrophic to an autotrophic system. Food in the lower reaches of Grand Canyon appears to be limited along shoreline areas, where the greatest effect is to subadults. The apparent shift in food production from rocky shorelines and riffles to vegetated shorelines needs to be better documented.

The fourth factor that may limit humpback chub populations in Grand Canyon is the presence of non-native fishes. This is an underlying biological element whose effects have been difficult to quantify in terms of predation, competition, and disease vectors. The close association between native fishes and non-native species in the mainstem implicitly identifies alien species as a limiting factor. This investigation identified brown trout as significant predators of humpback chub, and others have identified channel catfish (C.O. Minckley, ASU, pers. comm.) and rainbow trout (P. Marsh, ASU, pers. comm.) as major predators in the system. Estimates of fish biomass show that throughout the canyon, non-native species dominate biomass and may be outcompeting natives for food supplies. We also recognize the introduction and dispersion of the Asian tapeworm and a parasitic copepod throughout the humpback chub population. Although one of these effects may not alone restrict fish from beginning a spawning population, their synergistic effect, combined with other affected elements of the aquatic ecosystem, interfere with certain life history requirements of the species. Presently, turbidity, temperature, and flow are the principal agents controlling non-native fishes.

The likelihood of a second spawning population in Grand Canyon is probably greatest with one of the eight existing aggregations (other than the LCRI aggregation), assuming that operations can address the four factors identified above. Although young humpback chub were found in a spring at RM 30.8, this warm habitat is presently too limited to allow for significant reproduction and survival of eggs and larvae. At maximum temperature of 15°C from a selective withdrawal structure and a longitudinal increase of 1°C, mainstem spawning may be possible in June or July, but maximum temperature of 16°C would be equal to the minimum requirement for the species. In the absence of temperature modification, chances of survival of young and significant recruitment are very limited. While the more stable interim flows have stabilized springs and made successful reproduction possible, reproductive success is probably not significant enough to make this a self-sustaining population.

Warmed releases are also not likely to enhance aggregations at Bright Angel Creek, Shinumo Creek, Kanab Creek, or Havasu Creek, primarily because of a lack of adequate adult habitat in proximate mainstem areas. The greatest likelihood for a second population of humpback chub in Grand Canyon is in Middle Granite Gorge, which is presently occupied by a small aggregation, and in the lower canyon between RM 175 and RM 225, where suitable habitat is largely unoccupied.

Genetics Management

Assuming the Grand Canyon population of humpback chub is most proximate to the region of speciation, the fish found between Glen Canyon Dam and Lake Mead may be the most representative genotype for the species. Although allozymes and mtDNA reveal evidence of historic introgressive hybridization in the Grand Canyon population (Dowling and DeMarais 1993), morphologic and meristic characteristics of individuals from the five other populations, and preliminary genetic analyses indicate a greater degree of hybridization in the upper basin stocks (Wydoski 1994, W. Starnes, Smithsonian Institute, pers. comm.). Hence, these fish warrant dedicated protection and possibly development of stocks in refugia. The fish near 30-Mile may represent the only recognizable predam relicts and the last remaining exclusively mainstem genotype in Grand Canyon. This aggregation contains an estimated 40-60 adults, and may require transfer of individuals or gametes to refugia. Development of a brood stock for this 30-Mile aggregation may be appropriate considering that the likely level of inbreeding with 50 adults may be as high as 2%. Assuming that the last year in which mainstem temperature was suitable for spawning was 1970, the youngest fish of this aggregation could be 25 years old, which may be approaching maximum longevity for the species.

This investigation provided strong evidence that the majority of humpback chub in Grand Canyon are recently linked to the LCR, with the exception of the 30-Mile aggregation. Mainstem population estimates, capture-recapture ratios, and characteristics of fish length distribution indicate that the LCR is the principal source of fish to the mainstem downstream of about RM 56. The majority of humpback chub now in the mainstem probably had their origin in the LCR, except for a few relict fish of historic mainstem origin, or small numbers of survivors from mainstem reproduction. Hence, we hypothesize that two behaviorally distinct stocks of fish remain in Grand Canyon; relicts of mainstem stocks at 30-Mile and possibly in some downstream areas, and the fish that historically continue to spawn in the LCR, with some individuals residing in the adjacent mainstem. Behavioral difference relate to differences in spawning times and length of migratory movements for spawning. It is uncertain whether these behavioral differences are genetically based. However after timing of spawning condition in adults in MGG, which are likely LCR spawned individuals, suggests that these differences are not genetic.

Critical Habitat

On March 21, 1994 the U.S. Fish and Wildlife Service (59 FR 13374) designated 3,168 km (1,980 mi) of the Colorado River as critical habitat for four species of endemic fishes: razorback sucker, Colorado squawfish, humpback chub, and bonytail. The Service designated seven reaches as critical habitat for humpback chub, for a total of 610 km (379 mi). This represents about 28% of the historic range of the species, and includes portions of the Colorado, Green, and Yampa rivers in the upper basin, and the Colorado and Little Colorado rivers in the lower basin. Critical habitat in the lower basin includes the Colorado River in Marble and Grand canyons, from Nautiloid Canyon (RM 34) to Granite Park (RM 208), and the lower 12.8 km of the LCR.

The Fence Fault spring (No. 5) in which we found post-larval humpback chub in July 1994 is located 5.1 km (3.2 mi) upstream of critical habitat (Valdez and Masslich In Review). We believe that this discovery warrants a 10-mi extension of critical habitat from RM 34 upstream to RM 24. Protection of the warm springs and associated habitat features of the Fence Fault spring complex may promote spawning and recruitment sufficient to maintain the aggregation until further management options are identified that will allow the aggregation to expand. It may be necessary to regulate river flows to maximize spawning habitat or to stabilize thermal plumes and enhance survival of young. Extension of critical habitat upstream to RM 24 is recommended to provide protection to the riverine area potentially used by fish associated with the Fence Fault springs between RM 30.0 and RM 34.5.

In determining critical habitat, the Service considered those physical, chemical, and biological attributes (i.e., "constituent elements") that are essential to species conservation. The primary constituent elements determined necessary for survival and recovery of the species include, but are not limited to, water, physical habitat, and the biological environment.

Water. This constituent element includes the quantity of water of sufficient quality (i.e., temperature, dissolved oxygen, lack of contaminants, nutrients, turbidity, etc.) that is delivered to a specific location in accordance with a hydrologic regime that is required for the particular life stage for each species (Maddux et al. 1993).

The volume and pattern of flow in Grand Canyon are controlled by releases from Glen Canyon Dam. Daily fluctuations are based on hydropower generation and weekly and monthly releases by compact requirements, instead of natural seasonal extremes of high spring runoff and low summer flows. Since August 1, 1991, dam operations have been under interim flow criteria, which have substantially reduced daily fluctuations from maximum vertical stage changes of 1.2 m to 0.6 m at the area occupied by the main population of humpback chub near the LCR inflow (RM 61.3). While this reduction in daily fluctuations has stabilized shoreline water depths and velocities, maintenance of cold year-around temperatures (8-12°C) in areas of critical habitat have reduced swimming ability of subadults, greatly increasing the probability of downstream dispersal and risk of predation by brown trout, rainbow trout, channel catfish, and possibly striped bass. Reduced fluctuations may enhance backwater formation and persistence, but use of this habitat appears to be greatly influenced by water clarity and time of day.

The presence of Glen Canyon Dam will continue to have inherent effects on critical habitat of humpback chub, primarily related to water quality (i.e., reduced sediment, dissolved organics, retention of allochthonous material, temperature). Other water quality parameters, such as dissolved oxygen, conductivity, TDS, and pH appear to remain within a suitable range for the species. Also, no evidence of contaminants was found during this investigation.

Physical Habitat. Physical habitat includes areas of the Colorado River system that are inhabited by fish or potentially habitable for use in spawning, nursery, feeding, and rearing, or corridors between these areas. In addition to river channels, these areas include bottomlands, side channels, secondary channels, oxbows, backwaters, and other areas in the 100-year floodplain, which when inundated provide spawning, nursery, feeding and rearing habitats, or access to these habitats (Maddux et al. 1993).

Habitats in the Colorado River in Grand Canyon potentially suitable for spawning, nursing, feeding, and rearing have all been impacted by the presence and operation of Glen Canyon Dam. Temperature has been the largest deterrent to mainstem spawning, and most successful reproduction occurs in tributaries; some reproduction occurs in warm springs, but recruitment is probably limited.

Nursery areas are also impacted by cold temperatures (i.e., young fish are susceptible to thermal shock), reduced sediment (shallow sheltered sand/silt habitats have been reduced), and daily fluctuations (destabilized shorelines and reduced shoreline production).

The effect of Glen Canyon Dam on physical fish habitat is not well understood. Removal of sediments in Lake Powell and scouring by clear releases below the dam have dramatically altered the sediment budget in Grand Canyon, possibly affecting fish habitat. Selection by adult humpback chub for areas with a high frequency of recirculating eddies suggests the need to better understand these geomorphic relationships to fish habitat.

Since Grand Canyon is a relatively narrow canyon-bound region, contained throughout most of the 400 km from Glen Canyon Dam to Lake Mead, there are few bottomlands, side channels, or secondary channels, and no oxbows which could be inundated by high flows, compared to more alluvial regions. While it is not known if these habitats are critical to the species, certainly tributary inflows impounded by high spring flows potentially impact all native fishes; e.g., humpback chub were first reported by Kolb and Kolb (1914) in an apparent prespawning aggregation at the LCR inflow during high mainstem flow. The effect of eliminating this impounding is unknown.

Biological Environment. The biological environment includes food supply, predation, and competition as important elements and components of this constituent element. Food supply is a function of nutrient supply, productivity, and the availability of food items to each life stage of the species. Predation, although considered a normal component of this environment, may be out of balance due to introduced fish species in some areas. This may also be true of competition, particularly from nonnative fish species (Maddux et al. 1993).

The form of nutrients delivered through Grand Canyon has been dramatically altered by Glen Canyon Dam. The combination of sediment retention in Lake Powell and clear hypolimnetic releases have transformed the river below the dam from a heterotrophic to an autotrophic system. While nearly 70% of production between Glen Canyon Dam and Lake Mead occurs in a 25-km reach below the dam (where phototrophic production is high), production, and thus food availability decreased dramatically downstream, particularly below the LCR (Blinn et al. 1994). Reduced productivity and food availability in downstream reaches have apparently restricted invasion by humpback chub into reaches of suitable habitat, located 320-370 km downstream of the dam.

The area of the Colorado River designated as critical habitat does not encompass the area of highest potential food production and source of dissolved organics to occupied areas downstream. Although the Colorado River in Grand Canyon is highly regulated and the ecosystem modified, highest levels of primary and secondary production occur in the 25 km below the dam, well above the upper end of critical habitat. Delivery of allochthonous food resources to aggregations of fish is one important source of food that the fish relied upon in predam conditions.

The area designated as critical habitat for humpback chub is dominated in numbers and biomass by nonnative fishes, specifically rainbow trout upstream of the LCR inflow, and carp in downstream reaches. Present dam operations provide temperature and water quality conditions most amenable to trout, although the temperature range of 8-10°C in the tailrace is below optimal preferred temperature of rainbow trout and cutthroat trout (12-17°C), and brown trout (12-16°C). Higher levels and frequency of turbidity in downstream reaches, particularly below the LCR, may have reduced salmonid numbers in these areas. On the other hand, the cold temperatures are below suitable range for red shiner and fathead minnow (15-30°C), carp (20-26°C), channel catfish (23-29°C), and striped bass (15-24°C), greatly reducing spawning potential and numbers of these species in the canyon.

Although most nonnative fishes have been provided with marginal temperatures, coldwater species (i.e., rainbow trout and brown trout), and warmwater species (i.e., channel catfish and striped bass) continue to be potential predators and competitors. Also, warmwater cyprinids in occupied habitat (i.e., fathead minnows) and in adjacent warmer waters in Lake Powell and Lake Mead are potential competitors.

RECOMMENDATIONS

1. Integrate LCR and Mainstem Data: Much valuable information on the aquatic ecosystem in Grand Canyon has been collected in the past 10 years, but the value of this information is not entirely apparent because it presently lacks integration. Analyses and interpretation of data collected in past and ongoing investigations of fishes, macroinvertebrates, primary and secondary production, water quality, and geomorphology need to be conducted, and possible linkages identified to test hypotheses presented in the Draft Integrated Research Plan. This information also needs to be integrated and further analyzed to better define future core research and long-term monitoring strategies. An assimilation of information will help researchers develop better scopes of work that can use existing information, minimize repetitive data collection, and develop more directed hypotheses that address cause and effects of operations. The framework for a Grand Canyon Fisheries Integrated (GCFIN, Brown et al. 1995) database has been developed (Supplement No. IV).

2. Develop a Population Model: 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).

3. Integrate Geomorphology with Fish Habitat: This investigation has developed the hypothesis that channel geomorphology determines hydraulic patterns that form fish habitat, and thus drives selection by humpback chub for canyon regions and specific reaches within those regions. 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.

4. Develop a Non-Native Fish Management Plan: This plan should be composed of two phases, (1) further evaluation of predation on native fishes, and (2) evaluation of possible control methods. 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 to RM 90; 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 affect 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 need 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.

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 blueribbon 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.

5. Develop A Genetics Management Plan: A genetics management plan is needed for all native fishes in Grand Canyon. Decisions need to be made regarding the need to move certain fish to refugia for procurement of gametes and for development of experimental material (e.g., fish for temperature-swimming performed experiments).

   A meeting of agencies and researchers is recommended to determine if the fish at 30-Mile are genetically unique and need to be taken to a hatchery for procurement of genetic material. Fish need to be captured for obtaining muscle tissue to determine if genetic differences exist with other mainstem fish. Special techniques, such as DNA fingerprinting (Gross et al. 1994) may need to be employed to distinguish subtle differences.

6. Evaluate EIS Elements: 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).

7. Conduct Swimming Performance Experiments: 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°C, 12°C, 15°C, and 20°C. Acclimation temperature should be comparable to warm LCR waters (e.g., 20°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.

8. Develop Depth and Velocity Isopleths of the River Channel: Understanding the relationship between river depth, velocity patterns, and channel geomorphology is critical 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.

9. Determine 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 stairstep 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.

10. Identify Sources of Primary and Secondary Production: 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 eddy return channels (i.e., backwaters), 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.

11. Develop and Implement a Long-Term Monitoring Program: A well-designed plan to monitor various attributes of the humpback chub population in Grand Canyon is vital to understanding the response by this species to continued interim flows, the preferred EIS alternative, or to other dam management scenarios that may be implemented. The plan should focus on densities and patterns in densities of subadult and adult humpback chub. The results of this investigation indicate a vital link between the LCR and mainstem fish such that an important source of recruitment to the mainstem is small adults from the LCR.

12. Develop a Temperature Model: 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.

13. Extend Critical Habitat Designation: We recommend that the U.S. Fish and Wildlife Service consider extending critical habitat designation for humpback chub in Grand Canyon by a distance of 10 miles, from its present upstream extent at RM 34 (Nautaloid Canyon) to RM 24. This extension would allow inclusion of the Fence Fault Springs (RM 30-34.5) as well as Cove Springs (RM 25.5), and the mainstem Colorado River in the area most likely used by the 30-Mile aggregation of humpback chub.

14. Identify Mainstem Flow Needs for 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.

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Glossary of Terms

Abiotic - Relating to inanimate processes; caused by non-living entities.

Active gears - Mobile sampling gears used to capture fish (e.g., seines, electrofishing, angling).

Adult - A fully developed, sexually mature individual (i.e., humpback chub ≥200 mm TL).

Age categories - A developmental or temporal delineation of a population of fish; includes larvae, YOY, juvenile and adult.

Age group - Fish are categorized by number of annular rings on scales or bony structures, i.e. 0, I, II, III, etc. where age 0 fish are less than one year of age, and age I fish have completed one year of life.

Aggregation - A longitudinally-isolated group of fish with no significant exchange of individuals between groups.

Allometric Growth - A change in relationship of weight to length during growth of a fish.

Arithmetic mean CPE (AM_{CPE}) - Average catch rate as number of fish captured by time or area.

Average proportion of fish located (APFC) - The ratio of number of radio-tagged fish located by surveillance within a specific river reach to the number of radio-tagged fish expected to be located within the reach. Also, the ratio of number of contacts with a radio-tagged fish by a remote telemetry station within a specific time period to the number of possible contacts with the fish during the same time period.

Biotic - Relating to life; caused by living beings.

Carlin tag - An oval disc-shaped external plastic tag inscribed with a unique number and generally attached near the base of the dorsal fin of a fish.

Catch rate - An index of fish abundance; the number of fish captured with a given gear type for a given period of time or area.

Circulus - A growth ring on the scales or other bony parts of a fish.

Cohort - A group of fish hatched during the same time; often synonymous with year class.

Coloration - First stage of sexual maturity where male or female fish assume nuptial colors.

Copepod - Any minute crustacean of the subclass Copepoda.

Crepuscular - Twilight period (i.e., one hour before and after dawn or dusk).

Critical Habitat - A specific designation of primary constituent elements necessary for the survival of a species, as defined under The Endangered Species Act of 1973, as amended.

Cyprinids - Any of numerous freshwater fishes of the family Cyprinidae, which include minnows, carp, and shiners.

Day - The period extending from sunrise to sunset.

Diel patterns - Patterns of activity corresponding with night and day.

Directional remote telemetry data - Telemetry data collected by a remote station equipped with a directional (Yagi) antenna.

Emigration - Movement from place of residence.

Endemic - Occurring only at a specific or particular locality, i.e., a specific river basin.

Extinction depth - The water depth (4.5 m) at which signals from radio transmitters can not be detected from a distance of 50 m on the surface.

Falcate - Large and fan-like, as in the fins of some fish.

Fecundity - The potential reproductive capacity of a fish measured as numbers of eggs produced per female.

Floy tag - A elongated, tubular (spaghetti shaped) external tag inscribed with a unique number and generally attached near the base of the dorsal fin of a fish.

Gametes - A germ cell possessing the haploid number of chromosomes; especially a mature sperm or egg capable of participation in fertilization.

Geometric mean CPE (GM_{CPE}) - Catch rate for each sample (number of fish by effort), plus one, transformed to a natural logarithm, averaged, and calculated as the antilog of the average.

Gravid - Female fish with mature or maturing eggs prior to spawning.

Gross displacement - Cumulative distance between successive contacts or recapture points for an individual fish.

Horizontal movement - Two-dimensional movement of a radio-tagged fish upstream or downstream and towards or away from shore.

Hypolimnetic - Lower stratum of lake water lying below the thermocline, characterized by cold temperatures and low oxygen levels.

Hypural plate - Fusion of several vertebral elements that mark the tail end of the skeletal portion of fish -- the last bony substance near the end of the caudal peduncle.

Ichthyofauna - Assemblages of fish species.

Ichthyocyde - A chemical that is used to kill fish.

Isometric Growth - Consistent relationship of weight to length increase of a fish.

Juvenile - An immature fish greater than 1 year of age.

Karstic - Associated with limestone fissures or caves.

Lacustrine - Of or pertaining to a lake, living or growing in a lake.

Larvae - The period of development of a fish from hatching to complete development of fins.

Lateral Line - Line formed by a series of scales with openings (pores) extending along the side of the body of a fish; serves to detect vibrations in the water.

Littoral - Relating to the shoreline or shallow region of a body of water.

Local movement or activity - Movement of fish within a macrohabitat (e.g., eddy, pool, run) or small habitat complex and depicted as horizontal movement in meters.

Long-range movement - Movement of fish between large habitat complexes or different river reaches.

Macrohabitat - Large hydraulic units that describe areas used by fish, e.g., eddies, runs, riffles, pools, backwaters.

Magnitude of flow change - The change in flow from lowest to highest volume (cubic feet per second) during a daily flow cycle.

Metapopulation - Ecological concept referring to a connection of groups of reproducing individuals or populations.

Microhabitat - The sum of hydraulic and physical factors that immediately surround a fish, e.g., water depth, velocity, cover, substrate.

Milt - Sex product of male fish including sperm and seminal fluid.

Moribund - At the point of death; about to die.

Motile coracidium - Early life stage of a tapeworm.

Nauplii - (In many Crustaceans) a larval form with three pairs of appendages and a single median eye, occurring usually as the first stage of development after leaving the egg.

Near-surface activity - Radio-tagged fish located within 4.5 m of the water surface (radio-signal extinction depth).

Necrosis - Death of a circumscribed piece of tissue or of an organ.

Net displacement - The horizontal distance from release site to last contact or recapture site for an individual fish.

Non-spawning season - June through January for humpback chub in Grand Canyon.

Nuptial - Of or relating to the spawning act of fish.

Observation block - A subset of an extended observation period that represents the period of time between successive locations of a radio-tagged fish.

Omni-directional searching - Tracking radio-tagged fish with a receiver and antenna capable of searching multiple direction (i.e., 360°) in contrast to directional searching with an antenna capable of identifying the direction of the radio signal.

Omnivorous - Capable of consuming plants and animals, including macroinvertebrates and fish.

Opportunistic feeder - Capable of feeding on available material.

Passive gears - Stationary fish sampling gear into which fish swim for capture (e.g., nets, traps).

Pectoral Fins - The forward-most pair of fins of a fish.

Peaking power - Use of hydropower to fulfill electrical power needs during highest demand periods.

Pelvic Fins - The rear-most pair of fins of a fish.

Piscivorous - Fish-eating.

PIT tag - A small, glass-encapsulated microchip (approximately the size of a grain of rice) coded with a unique 10 digit alpha-numeric sequence; the tag is injected intraperitoneally in fish and externally activated by an electro-magnetic scanner.

Pharyngeal arch- The last gill arch near the throat of a fish.

Pharyngeal teeth - Deciduous teeth of the pharyngeal arch, found in minnows and suckers.

Photoperiod - Interval in a 24-hr period during which an organism is exposed to sunlight.

Phototactic - The movement of an organism in response to a source of light.

Poisson - A probability distribution used to describe the occurrence of unlikely events in a large number of independent repeated trials.

Population - A reproducing self-sustaining aggregation.

Principal rays - All branched rays plus one unbranched ray on dorsal or anal fins of a fish.

Proportion of movement (Pm) - The ratio of observation blocks in which movement is observed to the total number of observation blocks.

Ramping rate - The rate of change in flow measured in cubic feet per second for a period of one hour.

Ripe - Describing stages of sexual maturity (i.e., colored, tubercled, or expressing eggs/milt).

Reach - A length of stream channel that is relatively uniform with respect to geomorphic characteristics.

Recruitment - Replacement of adults through growth and maturity of young individuals.

Region - A length of stream channel designating a major longitudinal area.

Sally - a brief and sudden trip from a home area.

Salmonids - Those fish that belong to the family Salmonidae, which include salmon, trout, and whitefishes.

Site - Place, position of something; or place where something happened.

Spawning season - February through May for humpback chub in Grand Canyon.

Staging area - Mainstem habitats near the confluence of the LCR used by congregations of humpback chub prior to ascent for spawning in the LCR.

Subadult - Immature fish, including young-of-year and juveniles.

Sub-reach - Portion on stream channel within a reach.

Surveillance telemetry - The act of searching a designated reach of river to locate fish with active radio transmitters. Conducted at least once daily during telemetry study.

Sympatric - Occupying the same or overlapping geographical areas without interbreeding.

Trammel net - Entanglement nets made of three panels.

Travertine - A buff-colored porous mineral formed in streams (especially hot springs) by deposition of calcium carbonate.

Tubercle - A small round projection (~ 1 mm in diameter) prominent on the head, fins, or body of a fish that usually develops during the spawning period.

Turbid - Water that is muddy due to sediment or other material suspended in the water column.

Urogenital papilla - External projection of the urinary and genital tracts.

Water year - Annual recorded hydrologic cycle, from October 1 of one calendar year through September 30 of the following calendar year.

Year class - A group of fish hatched in the same year e.g., 1990 year class

YOY - Young-of-the-year; fish less than 1 calendar year of age.

List of Abbreviations

A - Amperes

ACT - Aquatic Coordination Team

ADAP - Water quality data collection platform

ADU - adult

af - acre feet

AGF - Arizona Game and Fish Department

AM_{CPE} - Arithmetic mean catch-per-unit-effort

ANOVA - analysis of variance

APFC - average proportion of fish contacted

ASU - Arizona State University

ATS - Advanced Telemetry Systems

B/W - BIO/WEST

°C - Degrees celsius

cfs - Cubic feet per second

C.I. - confidence interval

cm - centimeters

CPE - Catch per Effort

CPS - Complex Pulse System

df - degrees of freedom

DIRP - Draft Integrated Research Plan

DO - dissolved oxygen

EIS - Environmental Impact Statement

EPF - eggs per female

Fig - Figure

LSD - least significant difference

FL - fork length

FPN - A measure of trammel or gill net catch rate (No.fish/100 ft/100 hr)

FPH - A measure of electrofishing catch rate (No.fish/10 hr)

ft - feet

GCES - Glen Canyon Environmental Studies

GD - Gross displacement

GIS - Geographical Information System

GM_{CPE} - Geometric mean catch-per-unit-effort.

GPS - Global Positioning System

hr - hour

HSI - habitat suitability index

Hz - hertz

JEI - Johnson's Electivity Index

JUV - juvenile

Kn - relative condition factor

km - kilometer

LCR - Little Colorado River

LCRI - Little Colorado River Inflow

m - meter

maf - million acre feet

mm - millimeter

μS/cm - micro Siemens per centimeter

MD - Mean displacement

MGG - Middle Granite Gorge

mg/L - milligrams per liter

MHZ - megahertz

mi - mile

ML - maximum likelihood

MS-222 - tricaine methanesulfonate

No. - number

ND - Net displacement

NEF - Native Endangered Fish

NPS - National Park Service

NTU - nephelometric turbidity unit

OSHA - Occupational Safety and Health Administration

P - probability

pers. comm. - personal communication

pH - hydrogen ion concentration

RK - River kilometer

RM - River mile

S.D. - standard deviation

S.E. - standard error

sec - second

SL - standard length

TDS - total dissolved solids

TL - total length

UDWR - Utah Division of Wildlife Resources

USFWS - U.S. Fish and Wildlife Service

USGS - U.S. Geological Survey

WT - weight

V - volts

YOY - young-of-year

Table of Measurement Conversions

To Convert	Into	Multiply by
acres	hectares	0.40468564
Celsius (centigrade)	Fahrenheit	(C°x9/5)+32
centimeters	inches	0.3937008
cubic feet	cubic meters	0.028316847
cubic meters	cubic feet	35.31467
Fahrenheit	Celsius (centegrade)	5/9(F°-32)
feet	meters	0.3048
gallons (U.S. liquid)	liters	3.785412
grams	ounces (troy)	0.032150747
hectares	acres	2.471054
inches	centimeters	2.54
inches	millimeters	25.4
kilograms	pounds	2.2046226
kilometers	miles (statute)	0.6213712
liters	gallons (U.S. liquid)	0.26417205
meters	feet	3.2808399
meters	yards	1.093613298
miles (statute)	kilometers	1.609344
milliliters	ounces (U.S. fluid)	0.03381402
millimeters	inches	0.03937008
ounces (troy)	grams	31.1034768
ounces (U.S. fluid)	milliliters	29.57353
pounds	kilograms	0.45359237
square kilometers	square miles	0.38610216
square miles	square kilometers	2.58998811
yards	meters	0.9144