OBSERVATIONS ON THE BIOLOGY OF THE HUMPBACK CHUB IN THE COLORADO RIVER BASIN 1980-1990

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ABSTRACT

OBSERVATIONS ON THE HUMPBACK CHUB IN THE COLORADO RIVER BASIN, 1908-1990.

Charles O. Minckley

The humpback chub is listed as a federally endangered species primarily as the result of the impacts of hydroelectric dam operations and the introduction of nonnative fishes.

Geographic distribution of the humpback chub in the Colorado River basin is well documented, occurring in the major tributaries of the upper basin including the Green, White, Yampa and Little Snake Rivers. Currently there are five upper basin populations to include: the Green, Yampa, and Colorado river (at Black Rocks, Westwater Canyon and Cataract Canyon). In the lower basin distribution is from Glen Canyon Dam into Lake Mead. In Grand Canyon, the largest population occurs in the Little Colorado River although fish occur consistently at five other areas along the river corridor.

The habitats used by humpback chubs are similar throughout the basin, varying with the life stage. Generally, larvae and fry occupy shoreline backwater habitats in slowly moving water. Young-of-the-year chub occur in slow to moderately moving eddies and adjacent backwaters. Juveniles live in deeper water such as low-velocity eddies and backwaters <10 m deep. Adults are in deep eddies and backwaters, presumably including depths >10 m.

Adult humpback chubs are considered sedentary, occurring in canyon-bound reaches of the Colorado River Basin. However, there are exceptions when some individuals move further.

The diet of this species consists of a variety of aquatic and terrestrial invertebrates, and occasionally fish. Reproduction has been confirmed throughout the basin but spawning has not been observed. Humpback chub host several parasites but only two present potential threats, the anchorworm and Asian tapeworm. These parasites have been found in the lower basin and may have negative impacts in the future.

A recovery plan is in place for this species addressing the upper basin population. No specific plan is extant for the lower basin.

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Acknowledgments

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CHAPTER ONE: INTRODUCTION

This document addresses the biology of the humpback chub (*Gila cypha* Miller; Fig. 1), a cyprinid fish endemic to the Colorado River basin of western North America. Populations of this large minnow, along with those of three other members of a unique set of comparable "big-river" fishes, the bonytail chub, *Gila elegans* Baird & Girard; Colorado squawfish, *Ptychocheilus lucius* Girard; and razorback sucker, *Xyrauchen texanus* Abbott, declined as the river was subjected to human development for irrigation, flood control, power generation, and recreation. All four are of considerable scientific interest because of their unique morphologies, habitats, and habits. All are listed by the U.S. Government as endangered under the Endangered Species Act of 1973 (as amended; U.S. Fish and Wildlife [USFWS], 1983, 1986). Humpback chub and Colorado squawfish were among the first fishes to be so listed (USFWS, 1967a) followed by bonytail (USFWS 1980) and razorback sucker (USFWS 1991).

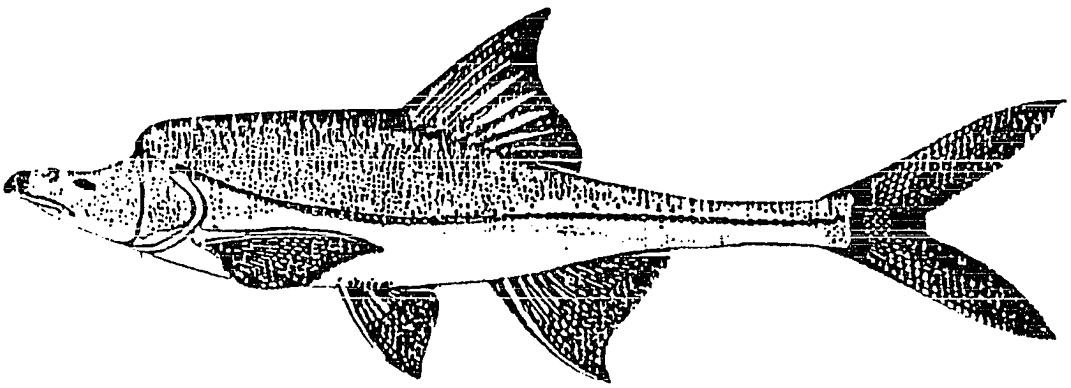


Figure 1. Illustration of the humpback chub, *Gila cypha.* Figure adapted from Miller (1946)

As result of the recognition and attendent requirements for federal attention, these fishes have been subject to one of the most extensive fishery research programs yet attempted in freshwater. Large amounts of data have been accumulated, much of which has yet to appear in the open literature. More than 350 references were cited, for example, in a recent review for the razorback sucker (W.L. Minckley et al.,

>90% were what is termed "gray" literature, defined by Collette (1990) as "...written information that is produced and distributed without adequate review." Of 250 articles pertaining to humpback chub cited here, >80% fall into that category.

Many workers in resource management agencies depend heavily on gray literature that is not only lacking in critical review but is not readily available to the general public, and which often presents preliminary and superficial interpretations of complex data sets (Wilbur, 1990). Such is the case for many reports on humpback chub. Annual reports for long-term studies have not been synthesized, abundance and distributional records are unquantified. Thus, critical data for formulation and implementation of management plans are obscured and remain generally unavailable.

The present work grew from the need to bring together diverse sources of data on humpback chubs and their habitats and set a baseline for present and future studies directed toward recovery throughout its range. My emphasis is, however, on chubs in the Grand Canyon region of Arizona, a major focus of Glen Canyon Environmental Studies, Bureau of Reclamation, which funded most research on the species in that area (Maddux et al., 1987; Douglas and Marsh, 1991; Kubly,

1990; Valdez 1990; Angradi et al., 1991).
Goals of the present effort were to: obtain copies of all "gray" and peer-reviewed literature possible on humpback chub and make them available at several permanent repositories; summarize available information and present an overview of the fishes biology; and examine the data collected from the Grand Canyon region between 1908 and 1990 relative to distribution, movements, condition, age and growth, reproduction, population size and other aspects of their life history.

Many investigators, at least in the past, used the common name "bonytail" for roundtail, humpback and bonytail chub, particularly for fish smaller than 100 mm TL. This precluded discussion of many reports and publications. With few exceptions, only those accounts which definitely mention humpbacked forms or "humpback chub" specifically were used here.

The first goal was achieved by deposition of photocopies of literature dealing with humpback chub in: the Office of Glen Canyon Environmental Studies, U.S. Bureau of Reclamation, Flagstaff, AZ; Special Collections, Cline Library, Northern Arizona University, Flagstaff; Special Collections, Hayden Library, Arizona State University, Tempe; and at the Parker Fishery Resource Office, U.S. Fish and Wildlife

Service, Parker, AZ. Copies of specific articles or the complete collection may either be used at those institutions or obtained at cost upon request.

The second goal is in part accomplished in Chapters Two and Three, the first of which deals with original discovery and description of the humpback chub; a general description of the Colorado River basin to which it is endemic, from both the historical and present-day perspectives; and a review of ichthyological exploration and description of the fish fauna of this vast and complex basin, especially that of the Colorado River.

Chapter Three pertains to the Upper Basin and presents biological information on humpback chub by summarizing past and present geographic and ecological distribution and presenting syntheses of information on distribution, movements, age and growth, food habits, reproduction, parasites, and condition factors. Chapter Four presents similar information for the Lower Basin. As noted before, I deal with accounts of this species and research between 1908 and 1990. Projects commenced and literature on this species that appeared or was in press after 1990 are generally not included. Emphasis is on distribution, movements, reproduction, and age and growth since my personal research in the Grand Canyon region was mostly concerned with those aspects of humpback chub biology.

Chapter Five presents a summary and recommendations for future protection and management of this endangered species. Suggestions are made of ways to implement recommendations.

Materials and Methods

Information Retrieval

My survey for information on humpback chubs began by contacting federal and state agencies, private individuals, and organizations conducting research on humpback chub and its habitat (Table 1). Extant bibliographies were referenced (e.g., Hoover & Langlois, 1977; Ecology Consultants Incorporated, 1977; Wydoski et al., 1980; Haynes & Hamilton, 1986; Miller & Hubert, 1990)and examined for additional information and references, which was requested. No computer search was conducted as most information was gray literature not identifiable in that manner.

Collecting Techniques

Between 1975 - 1980, access to Grand Canyon was accomplished in several ways. Between 1975 - 1979, eight river trips were made with the Museum of Northern Arizona (MNA). In 1977 the upper 14 miles, of the

Table 1
Organizations/individuals contacted for references the humpback chub in the Colorado River Basin.

Arizona Game and Fish Department
- Mr. Dennis Kubly, Phoenix
- Mr. Robert Clarkson, Phoenix
- Mr. Jerry Landye, Page Springs
- Mr. Bill Silvy, Phoenix
- Mr. Kirk Young, Phoenix

Arizona State University, Tempe
- Dr. Mike Douglas
- Dr. Paul Marsh
- Dr. Wendell Minckley
- Librarian, Hayden Library
- Librarian, Nobel Science Library

BIO/WEST, Incorporated, Logan
- Dr. Paul Holden
- Dr. Richard Valdez

Colorado Division of Wildlife, Denver
- Editor, *Colorado Outdoors*
- Mr. Jim Bennet
- Mr. Dave Langlois

Colorado State University, Ft Collins
- Dr. C.A. Carlson
- Dr. Kevin Bestgen
- Dr. Darryl Snyder
- Librarian

National Park Service, Arizona
- Mr. John Ray, Grand Canyon
- Mr. Mark Law, Grand Canyon
- Dr. Larry Stevens, Flagstaff

Northern Arizona University
- Librarian, Cline Library

(Table 1, continued).

University of Nevada, Las Vegas
Dr. Jim Deacon

University of New Mexico, Albuquerque
Dr. Steve Platania

University of Utah, Salt Lake City
Librarian

U.S. Bureau of Land Management
Dr. Jack Williams, Idaho
Librarian, Fort Collins
Librarian, Lakewood

U.S. Bureau of Reclamation
Mr. Gordan Mueller, Fort Collins
Mr. Dave Wegner, Flagstaff
Mr. Bob Williams, Salt Lake City
Librarian, Salt Lake City

U.S. Corps of Engineers, Sacramento

Utah Division of Wildlife
Mr. Wayne Gustaveson, Page
Mr. Henry Maddux, Salt Lake City
Mr. Miles Moretti, Price
Mr. Randy Radant, Salt Lake City
Librarian, Salt Lake City

U.S. Fish and Wildlife Service
Mr. Jerry Burton, Albuquerque
Mr. Frank Baucom, Phoenix
Mr. George Divine, Albuquerque
Mr. Roger Hamman, Dexter
Mr. Buddy Jensen, Dexter
Mr. Lynn Kaeding, Grand Junction
Ms. Cathy Karp, Ft. Collins
Mr. Lyle Miller, Willow Beach
Mr. Frank Pfeiffer, Grand Junction
Ms. Cindy Ramotnik, Ft. Collins
Mr. Larry Shanks, Denver
Dr. Harold Tyus, Ft. Collins
Dr. Holt Williamson, Denver
Interlibrary Loan Service, Salt Lake City
Utah Fishery cooperative Unit, Logan
Fish and Wildlife Reference Service, Bethesda

Wyoming Game and Fish Department, Cheyenne

Little Colorado River from Blue Springs to the confluence was surveyed in a grant funded by the Office of Endangered Species, Albuquerque. Additionally, between 1987-1990 month-long research trips were conducted in the Little Colorado River funded by the Arizona Game and Fish Department (AGFD).

Fish were sampled using a variety of methods. Samples were taken using trammel, gill and fyke nets, seining, and electrofishing. In the mainstream Colorado two trammel nets, 91.5 m x 2.5 m with a 4 cm outer wall and a 3.8 cm inner wall, were set in the Colorado River near each nights camp. Confluence areas were fished with fyke nets with dimensions of 4 m X 1 m X 14 mm mesh. Experimental gill nets, 45.7 m X 1.5 m with mesh sizes of 2.5, 3.8, 5.0, and 6.4 cm were used during helicopter based operations into the Little Colorado. Tributaries were sampled by seining the lower 200 m of stream. Seine dimensions were 6m X 2 m X 25 mm. The mainstream Colorado River was also seined where feasible. Electrofishing was also used along cliffs and boulder shorelines, near tributaries, and occasionally near inflowing springs (Carothers & Minckley, 1981). Electrofishing was done during the daytime.

Beginning in 1987, four major collecting efforts were fielded between 1987 and 1990 into the lower

Little Colorado River in the periods 7-31 May 1987, 2-31 May 1988, 1-31 May 1989, and 16 April to 16 May 1990. Access into and out of the area by research personnel was on foot. In 1987-1988, collecting gear was transported the area by commercial river companies (e.g., Canyoneers Inc., Expeditions, and Grand Canyon Expeditions). A Jet Ranger helicopter was provided by Glen Canyon Environmental Studies (GCES) in 1989 and 1990 to transport collecting gear to the Salt Trail sampling station 10 km upstream from the Little Colorado River-Colorado River confluence.

In 1987 permanent net sets were established from the confluence upstream to 1.2 km. Nets consisted of 9 hoop and 2 trammel net sets. Additionally, experimental gill nets were drifted at the mouth and varying distances upstream from the confluence in the Little Colorado River during those years. During week three of each year these core nets were supplemented by sets made by AGFD personnel who spent several days at the confluence, and the number of sets would be increased up to 20 nets. Net dimensions were as previously presented. In 1989, an additional station, the Salt Trail Camp, was established in the Little Colorado River 10 km above the confluence and nets were deployed 1.8 km downstream and 4.8 km upstream from that point. During 1989-90 additional net stations were established between the confluence and the Salt Trail Canyon at 3.2, 4.8, 6.4, and 6.5 km. Therefore in 1989-90, the core of 11 nets were set at the confluence, 6 hoop nets between 3.2 and 10 km and 8 nets (7 hoop and a trammel) were set between 10 and 14.8 km. The last 14 were also core sets, in place continuously. Seining and bait fishing were also used to varying degrees in all years.

Confluence hoop nets were run approximately every 12 hours while trammel nets were run every 6 hours. Nets from 3.2 to 6.5 km were run every 3.0 days as were those from 9.1 to 10 km. Hoop nets from 10 to 11 km were run on a 12-hour basis and the trammel net every six hours. Hoop nets from 11 to 14.8 km were run every 3.0 days. Many times nets were pulled for repair or replacement, general cleaning, or (less frequently) not run due to inclement weather. Trammel nets were pulled whenever personnel vacated the area for >24 hours. All fish were weighed in grams (gms) and total lengths (TL) were measured to the nearest millimeter. All humpback chub were sexed, when possible, and reproductive condition noted. Unintentional mortalities or fish intentionally taken were skeletonized or preserved and placed in the Collection of Fishes, Arizona State University (ASU). Piscivorous non-native fishes were sacrificed for stomach analysis.

Tagging

Humpback chub >150 mm in TL were tagged using two methods during this research. In 1987-1989 they were were tagged exclusively with Carlin fingerling tags which were used to a lesser extent in 1989-90. Tag colors were yellow, red, orange and blue for 1987, 1988, 1989 and 1990, respectively. The consecutively numbered tags were sewn into the body ventral to the dorsal fin, secured with an overhand knot on the other side of the fin, treated with antibacterial agent (Betadine), and released at the capture site. During 1989-90, humpback chubs were tagged with Passively Induced Transponders (PIT tags) which were injected interperitoneally just posterior to insertion of the pelvic fins. The area was treated prior to and after injection with betadine, as was the syringe prior to inserting the tag. Tag numbers, consisting of a 10-digit combination of letters and numbers (e.g.,7F7F123456), were read prior to injection. The tag is activated and read by an electronic scanner, but is otherwise inert and non-transmitting. Life expectancy of a PIT tag is a minimum of 10 years. PIT tags were developed for salmonid research (Prentice, et al., 1985). This was the first use known on a wild population of an endangered species.

Population Estimates.

Population estimates were made using the formula N = MC/R where M equals the number of marked fish, C equals the total sample size, and R is the number of recaptures (Ricker, 1971). Estimates were made for all fish >150 mm TL from the confluence upstream 1.5 km. One standard error was calculated for each estimate.

Calculated Hatching Dates

Calculated hatching dates for humpback chubs were estimated for the Little Colorado and Colorado river, using back-calculated standard lengths (SL) of young-of-the-year (yoy) chubs. To do this, a predictive equation developed by Muth (1990) was used, where Y = 7.284340.0280X. The calculated hatching date of the chub equals Y while X represents SL of wild fish for which an estimated time of hatching is desired. Once field-collected larvae or yoy juveniles are identified, approximate age in days after hatching may be calculated by substituting SL measurements for Y. Standard length of field-collected fish must fall within the length range from which the equation was developed for calculations to be valid. Reported egg-incubation times may then be added (possibly using a mean or median value) to calculate post-hatching age. An estimated date at which individual young were spawned (e.g., date at egg deposition and fertilization) may also be back-calculated from date of capture. Predicted dates at which individual young were spawned may be aggregated in a frequency distribution to demonstrate beginning and ending spawning dates and peak spawning periods.

To better define hatching dates in the Colorado River the river was partitioned into three reaches. Those reaches in river mile were: I, 62-83; II, 83-160; IV, > RM 160.

These data may then be compared with river discharge, temperature regimes, or other factors, to help describe physical conditions during spawning. The procedure assumes that growth and incubation time are similar for both wild and cultured young, which may or may not be valid depending on rearing conditions. Accordingly, back-calculated spawning dates must be considered estimates and should be substantiated by observations of adults in reproductive condition or other direct evidence of reproduction (Nessler et al., 1988).

Age and Growth

Age-growth data for field-collected specimens was estimated using length-frequency data expressed as four size classes and by opercle aging techniques. Four size classes were used and included: class I, <120 mm; II, 121-150 mm; III, 151-220 mm, and older fish > 220 mm. The opercle method is based on the assumption of regular increases in number of annuli and a highly significant positive correlation ($r = 0.956$, $P<0.01$) between TL and opercle size. The linear relationship described by the equation $OR = -0.734 + 0.055$ TL (mm), where OR = opercle radius (mm) indicates isometric growth of the opercle relative to TL (Carlander, 1969). The opercle method was further validated by close agreement between modes of length-frequency distributions for small fish and mean lengths estimated from opercles.

When determining annual and daily growth six size classes of fish were used. These were: class I, <120 mm; II, 121-150; III, 151-200; IV, 210-220; V, 221-240; VI, 241-250; VI, >250.

Condition Factors

Condition factors are a means to describe the well-being of fishes as a measure of "plumpness." A condition factor ranges in cyprinids from 1.0 to 3.0, with 3.0 representing a best possible "score" for an individual (Carlander 1969). The formula used to compute this factor was $K = W10^5/L^3$ where W weight divided by 10^5, a factor which brings the value of K near unity and L = length cubed. Both length and weight are affected by several things, including sex, shape, and size of fish, its robustness, and time of year.

Mainstream river mile (RM) designations follow Belknap (1965, 1969) and Evans (1974). The metric system is used for all other measurements.

CHAPTER TWO: FISHES OF THE COLORADO RIVER BASIN.

The ichthyofauna of the American Southwest includes 334 species in 69 families (Miller, 1959, W.L. Minckley et al., 1986). A majority of families (60) are marine dispersants which enter freshwater during some part of their life cycle or are marine in origin but now restricted to freshwater. The remainder are termed primary or secondary division freshwater fishes (Myers, 1938, Darlington, 1957), the first of which are restricted entirely to freshwaters for their complete life cycles. Secondary fishes are also generally restricted to freshwater habitats, but are salt tolerant, capable of crossing marine or brackish barriers. Twenty-one of 34 (62%) primary and secondary division freshwater fishes are endemic to the Colorado River basin, which is the highest species-level endemism of any of seven major drainages present in coterminous western North America (Miller, 1959, W.L. Minckley et al., 1986).

History of Colorado River Basin Icthyology

Pre-1900

As summarized by W.L.Minckley & Douglas (1991), several of the "big river" species of Colorado River fishes were described prior to 1860, e.g., bonytail and roundtail chub (*Gila robusta,* Baird & Girard, 1853a-c), flannelmouth sucker (*Catostomous latipinnis,* Baird & Girard, 1854), and Colorado squawfish (*Ptychochielus lucius,* Girard, 1857a-c, 1858, 1859). Descriptions continued with razorback sucker (*Xyrauchen texanus,* Abbott, 1860), as well as new salmonids and cyprinids described by Cope (1871, 1874) and Cope and Yarrow (1875). An early review of Girard's fish descriptions was provided by Jordan (1878, 1886, 1891a), who also reported new collections from the upper Colorado River in Colorado and Utah (Jordan, 1891b). Others included those by Kirsch (1889) for the Gila River, AZ and Gilbert (1893) for pluvial White River, Nevada. Gilbert & Scofield (1898) published on collections from the lower basin, and Snyder (1915) reported on surveys made by E. A. Mearns in Gulf of California, Mexico during the 1890's. Rutter (1896, 1907) also provided comments on fishes of the Pacific slope and Sacramento-San Joaquin basin.

Post-1900

Interest in fishes of the American Southwest waned around the turn of the century. F. W. Chamberlain made an important collection in southern Arizona in 1904 that is not yet fully reported in the literature (Miller, 1961; W.L. Minckley, 1973; W.L. Minckley et al., 1986). Ellis (1914) then published "The Fishes of Colorado," ending active ichthyological research in the Colorado River basin until the early 1930's.

Activity again increased when V. M. Tanner (1932, 1936) began to report on his work in Utah and Nevada. During the same decade, C. L Hubbs began research on Colorado River fishes (Hubbs, 1932, 1953, 1954, 1955; Hubbs & Miller, 1941, 1948a, b; Hubbs et al., 1943, 1979), which was continued and expanded by R. R. Miller (1943, 1944, 1946, 1950, 1952, 1959, 1961, 1963a, b; 1972a, b; Miller & Winn, 1951; Winn & Miller, 1954; Miller & Hubbs, 1960). Dill (1944) reported on fishes from the lower Colorado mainstream, and additional historic information was provided by Evermann (1916), Moffett (1942), Wallis (1951), and Walker (1961).

More recent works summarizing information on fishes of various states and regions included those of Beckman (1952, 1963), Everhart & Seaman (1971), Sutton (1976) and Woodling (1985) for Colorado; Simon & Simon (1939), Simon (1946), and Baxter & Simon (1970) for Wyoming; Sigler & Miller (1963) for Utah; LaRivers

(1952, 1962), LaRivers & Trelease (1952) and Deacon & Williams (1984) for Nevada; Koster (1957) and Sublette et al., (1990) for New Mexico; Miller & Lowe (1964) and W.L. Minckley (1971, 1973) for AZ; Evermann & Clark (1931), Shapovalov (1941), Shapovalov & Dill (1950), Shapovalov et al., (1959), Moyle (1976) and Hubbs et al., (1979) for California, and Follett (1961) and Castro-Aguirre (1978) for the Colorado River Delta, Mexico. Papers published since 1968 have dealt more with conservation status, life-history data and the increasing rarity of the various species (Colorado Division of Wildlife, 1989; Deacon 1968b; Deacon and Minckley, 1974; Johnson, 1976a, b; Brooks, 1985; Johnson and Jensen, 1991; W.L. Minckley & Deacon, 1968; Miller, 1972a; W.L. Minckley, 1973, 1983, 1985, 1991; Williams et al., 1985, 1989; Pister, 1974, 1976, 1981; Deacon, 1979; Deacon et al., 1979; Johnson & Rinne, 1982; Lee et.al., 1980; Miller, 1977; Miller et al., 1989; W.L. Minckley & Gustafson, 1982; Kaeding & Zimmerman, 1983; Kaeding et al., 1990; Tyus & Karp, 1991; Tyus, 1991).

Discovery and Description of *Gila cypha*.

The humpback chub was the last of the Colorado's "big-river" fishes described and thus the last known to the scientific community. The original description by

Miller (1946) is as follows:

Diagnosis. A strongly compressed *Gila* with...sides of...body slightly convex and...a prominent abrupt hump over the occiput; body almost entirely devoid of scales (except for about 80 in lateral line) which have basal radii; fins expansive, falcate; snout fleshy; mouth inferior; eye very small.

Holotype. The holotype (U.S.N.M. no 131839) is a specimen about 305 mm in standard length and was taken by N.N. Dodge near Phantom Ranch in the western end of Grand Canyon National Park, Arizona. It was caught in swift water on hook and line, presumably in the nearby Colorado River at or near the mouth of Bright Angel Creek....

Description. The following description is of the holotype. Fin rays: Dorsal iii, 9, the first full-length ray unbranched and preceded by 3 graduated, rudimentary rays, the first one very small; anal iii, 11, the first full-length ray unbranched and preceded by 3 graduated, rudimentary rays; pectoral rays, 18 in each fin; pelvic rays 9 in each fin; principal caudal rays 20, 18 branched plus a full-length unbranched ray above and below. Scales in lateral line about 80, embedded and only slightly imbricated anteriorly and becoming more embedded and less imbricated posteriorly until those on the caudal peduncle are scarcely evident....Scales above the peduncle are scarcely evident....Scales above the lateral line deeply embedded and, for the most part, completely isolated from one another, not evident above the level of the base of the nuchal hump. Scales below the lateral line similar to those above, not evident below the base of the pectoral fin except in the region behind the pectoral fin. Back, breast, and belly completely devoid of scales. Dorsal and ventral surfaces of caudal peduncle completely smooth and scaleless, about three or four irregular rows of embedded scales above and below the lateral line anteriorly which taper off to only one or two such rows above and below the lateral line posteriorly....Total gill rakers nine on the left side, 11 on the right, short and dimorphic; those (two or three) on the upper limb and the one at the angle of the arch are slender, pointed, and curved at the tip, whereas those on the lower limb are shorter and thicker and all but the most anterior ones are variously forked. All the rakers are attached anteriorly to the gill arch by a broad membrane. Pseudobranchiae weakly developed....

Dental formula 2, 5-4, 1?, three teeth missing from the right arch, with the definite possibility that there is also one tooth missing from the lesser row of this arch (if so, the formula would be 2, 5-5, 2 as usual in Gila. The teeth in the main row are thick, especially toward the base, bluntly pointed, with a weak grinding surface on the first two. No doubt the teeth were modified during the lifetime of the fish, as is characteristic in cyprinid fishes. The only tooth remaining on the lesser row (right arch) is well developed, conical, and bluntly pointed.

In coloration the holotype of *Gila cypha* is brownish--pinkish brown on the sides and belly and yellowish brown along the back. On close examination most of the head, back, and sides above the level of the lateral line are densely covered with dark puncticulations: these extend below the lateral line in the region above and behind the pectoral base and near the base of the caudal fin. The same pigmentation occurs near the base of the first pectoral ray...and also near the bases of the interradial membranes of the dorsal and caudal fins.

The following measurements were stepped off with a pair of precision dividers under a magnification of about 2.5 times. Body depth in standard length, 4.25; head length in standard length, 4.1; head depth in head length, 1.5; head width in head length, 12.7; length of caudal peduncle in head length, 4.8, in base of dorsal, 2.8; length of snout in head length, about 2.7; eye in head, about 13.0, in least depth of caudal peduncle, about 3.0: dorsal and anal bases equal; length of pectoral almost equal to that of head;length of pelvic 1.4 in head length; length of longer (upper) caudal lobe much greater than head length and about 3.3 in standard length...

Etymology. The specific name *cypha*, suggested by Dr. Carl L. Hubbs, is from the Greek.., meaning hump-backed, in reference to the striking nuchal hump.

General Distribution and Status.

A fish fossil closely resembling *G. cypha* is known from the Miocene Bidahochi formation in northern AZ (Uyeno 1961; Uyeno & Miller, 1965), indicating the presence in what is now the Colorado River basin of a congener >6.5 million years ago (mya). The earliest published archaeological record is from Stanton's Cave at River Mile (RM) 30 in Grand Canyon. The remains were dated at 4000 BP and were associated with Indian artifacts and flood deposits (Euler, 1978; Miller, 1963c; Miller & Smith, 1984). Remains of the humpback chub were also present at an Amerind site in Catclaw Cave, AZ, 15 miles downstream from Hoover Dam (Miller, 1955).

The humpback chub was not known outside the Grand Canyon area until 1950, when it was collected from Hideout Canyon on the Green River (W F. Sigler, in Holden, 1968; Holden & Stalnaker, 1970). The first specific account of the fish in the upper Colorado basin was by Sigler and Miller (1963). Miller & Lowe (1964, 1967) included it in their list of the fishes of AZ. Miller (1963b, 1964a, b) presented the first arguments for conservation of this unique cyprinid, and additional papers followed which dealt with its geographic range, ecology, and proposed listing as an endangered species (see below). It was listed as a federally endangered species on 11 March 1967 (USFWS, 1967a).

Several early works dealing with identification, status, general biology and taxonomy pertaining to the lower basin population of *G. cypha* included: Miller &

Lowe (1964), Bradley & Deacon (1967), Cole (1968), Holden & Stalnaker (1970), Rinne & Minckley (1970) and W.L. Minckley (1973). Later three studies dealing specifically with the Little Colorado River population produced a number of reports. Suttkus & Clemmer (1977) summarized early collections and knowledge of life history, morphology, and taxonomy. Carothers & Minckley (1981) and Kaeding & Zimmerman (1981, 1982, 1983), described foods, movement, age, and reproductive cycle.

Taxonomy, distribution, movement, food habits, and reproduction of the humpback chub in the upper Colorado River basin was addressed by: Vanicek et al., (1970), Holden et al., (1974), Holden & Stalnaker (1975a, b), Tyus et al., (1982a, b), Valdez & Clemmer (1982), Tyus & Minckley (1988), Douglas et al., (1989), and Kaeding et al., (1990).

A number of additional of articles (Hamman, 1981a, b, 1982a, b; Berry, 1984; Berry & Pimenthal, 1985; Marsh, 1985; Rosenfeld 1983; Rosenfeld & Wilkinson, 1989; deal with other aspects of the life history of this species throughtout the basin.

Description of Habitat

Geologic History

The Colorado River basin was formed over a long period of time by complex actions including plate tectonics, periods of mountain building and vulcanism, and vast cycles of erosion. The diversified region through which it flows includes parts of three major physiographic provinces, the Rocky Mountains, Basin-and-Range, and Colorado Plateau. This brief summary of the development of the Colorado Plateau and the evolution of the Colorado River is from diverse sources (Lucchitta, 1972, 1984; Nations et al., 1982; Carlson & Muth, 1989; W.L. Minckley et al., 1986), which should be consulted for details.

Development of the basin began 60 to 65 mya in the Late Cretaceous and Early Tertiary. Distant interactions at that time between the Pacific and North American tectonic plates resulted in increased mountain building along what is known as the Laramide Structural Axis, in an area later to be mostly known as Montana, CO, WY, and southern Canada. Deformation continued into the Eocene (53 to 37 mya), resulting in an ancestral Rocky Mountains bounded on the west by a broad, uniformly elevated region extending from southern Mexico through what is now Basin-and-Range, north to Alaska. This was followed by regional uplift and a period of relative inactivity that resulted in broad erosional surfaces from Canada into Mexico by the Late Eocene to Early Oligocene over most of western North America.

During the Oligocene (37 to 23 mya), movements occurred again along the Laramide Axis, in a broad arc moving from east to west and arriving at the west coast of North America by Early Miocene (~23 mya). At almost the same time (beginning 29 mya), collision of the East Pacific Rise and North American Plate promoted shear and rotation of lithospheric subplates far inland. The Laramide Axis and Colorado Plateau remained relatively stable, although the Colorado Plateau rotated dextrally. New tectonism and faulting in surrounding regions commenced again around 27 mya. With opening of the Rio Grande Rift from southern CO south through NM and into Mexico, the Colorado Plateau was isolated on the west, south, and east by Pliocene times.

Evolution of the River.

By Miocene or earlier, a stream or stream system which began in WY and CO followed the approximate course of the present Colorado and San Juan rivers to enter what is now AZ from the northeast. This stream crossed the Kaibab Plateau through an area of low relief, flowing northwest or west-northwest through a broad valley cut in Mesozoic strata. This was the master stream of the area, to which an ancient Little Colorado River, Havasu Creek and other north- and northwest-flowing streams were tributary. A lower

Colorado drainage may not have existed at that time.

Destination of this ancestral Colorado River is unknown, as the area into which it flowed (on what was then the southwestern Colorado Plateau) had been deformed by basin-and-range faulting then covered with alluvium and volcanic rock. Such activities also resulted in widespread ponding along the ancestral upper Colorado drainage, although the master stream succeeded in continuing its course through the Kaibab-Coconino Uplift.

During or shortly after opening of the present Gulf of California 5.0 to 6.0 mya another stream began to develop through the southern Basin-and-Range Province approximately along the present course of the lowermost Colorado River. It eroded headward, integrating interior drainages to cut through lower Grand Wash Cliffs via a southwest-facing scarp of the upper Grand Wash Cliffs. This scarp and the strike valley at its foot concentrated runoff from a large area to the south, forming a major headwater for what was to be the lower Colorado River. The drainage continued to erode rapidly headward, intersecting the north-trending Hurricane fault that deflected its headward progress. Between that point and the Kaibab upwarp it captured the upper Colorado watershed and the present system assumed its present course <6 mya.

Finally, about 0.6 mya, a linkage with the Mississippi drainage was severed and the uppermost Green River began to flow southward to complete the present Colorado River system (Hanson, 1985).

Colorado River Basin Today.

The present Colorado River basin encompasses ~650,000 square kilometers (km^2) of western North America (W.L. Minckley et al., 1986). It includes about a twelfth of the surface area of the contiguous United States (Carlson & Carlson, 1982, Carlson & Muth, 1989) that varies in elevation from below sea level to >4000 meters (m). Beginning in the Never Summer Range of Rocky Mountain National Park, CO, the stream flows ~2320 km to enter the Gulf of California in northwestern Mexico. The Green River, the largest tributary of the Colorado, originates in the Wind River Range of southwestern WY and joins the mainstream in Canyonlands National Park, UT. The Colorado River thus collects water from the states of AZ, CA, CO, NM, NV and WY. The Mexican states of Sonora (SON) and Baja California del Norte also contribute.

The Colorado River watershed has been divided into "upper" and "lower" political units for purposes of water management (Fig. 2). The upper basin is defined in the "Upper Colorado River Basin Compact" as "Those parts of the states of Arizona, Colorado, New Mexico, Utah, and Wyoming within and from which waters naturally drain into the Colorado System above Lee's Ferry, Arizona (Miller and Hubert, 1990).

The "upper basin" (283,600 km^2) thus consists of the Green, upper-mainstream Colorado, and San Juan subbasins draining western CO, southwestern WY, eastern UT, northwestern NM, and northeastern AZ. This region encompasses part of the Colorado Plateau as well as portions of the middle and southern Rocky Mountains and Wyoming Basins (Carlson & Carlson, 1982). Its Green River subbasin drains 115,773 km^2 of WY, CO, and UT. Headwaters are in the Wind River Range of western WY at almost 4270 m elevation. Major tributaries include the Yampa, Duchesne, White, Price and San Rafael rivers.

The upper Colorado River subbasin (68,625 km^2) is defined as the ~450-km-long Colorado (formerly Grand) River above its confluence with the Green and draining parts of CO and UT. It begins on the west slope of Mount Richthofen at the Continental Divide in CO, and flows southwest. Major tributaries are the Roaring Fork, Gunnison and Dolores rivers (W.L. Minckley et al., 1986). The San Juan subbasin drains ~99,200 km^2 of CO, UT, NM, and AZ. It begins on the southern

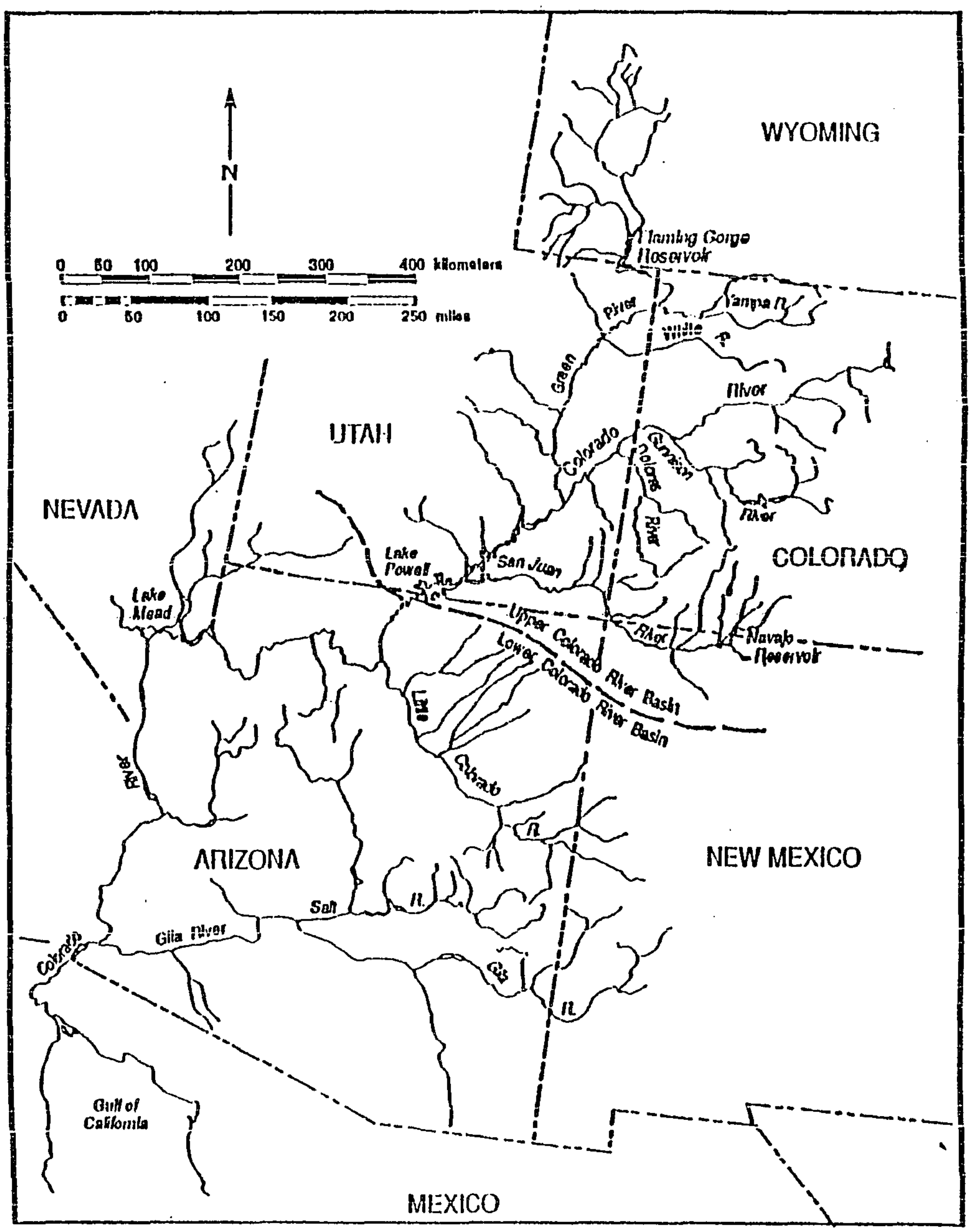


Figure 2. Map of the Colorado River Basin illustrating the boundary between the Upper and Lower Colorado River basins

slopes of the San Juan Mountains of southwestern CO, flows southwest into NM, back through the southwestern corner of CO into UT, to enter the Colorado River in Lake Powell. Major tributaries include the Animas, Chaco, and Mancos rivers (W.L. Minckley et al., 1986).

CHAPTER THREE: THE UPPER COLORADO RIVER BASIN

The humpback chub was first brought to the attention of agencies in the upper Colorado River basin when the states of UT and WY and USFWS proposed a joint "rough-fish eradication" project on the Green River in 1961 (Binns, et al, 1963; Binns 1967; Andriano 1963; McDonald & Dotson, 1964). Despite opposition from private parties and USNPS personnel at Dinosaur National Monument, the project was implemented and fishes were eradicated by rotenone application in the target area and by mistake downstream into Dinosaur National Monument (Miller, 1963b, 1964; Regenthal, 1962). A major result of the project was an elevation of agency and public awareness of the plight of native fish species (Holden 1991).

The decade of the 1980's saw a marked increase in research on native fish with establishment of the Colorado River Fishery Project (CRFP) by the USFWS. Research teams were established to gather information on all aspects of the biology of the Colorado squawfish, humpback chub, bonytail, and razorback sucker (Miller et al., 1982d-f), with information to be used by federal agencies or federally funded projects to prevent or minimize adverse impacts to the species concerned. In addition to the CRFP, fish and wildlife agencies in CO, UT and WY became more active in management of federally listed species and developed nongame programs (Langlois, 1977; Oberholtzer, 1987). Federal and state agencies also stimulated and supported increased research by universities and private consulting groups.

This chapter reviews the results of these activities on the humpback chub. However, prior to beginning this process, some cautionary comments on the data are necessary. Distributional data are often considered absolute in quality, especially if documented with physical evidence such as photographs or preserved specimens. However, two major factors make distributional data for humpback chubs subject to question. First there has been much confusion, particularily in the upper basin, about the identity of various kinds of chubs in the Colorado River system. This has resulted in the use of imprecise common names, with the term "bonytail" generally applied by both technical and lay persons to all Colorado River chubs for a many years. Many records in non-technical writings such as diaries and trip accounts, cannot be used at the species level unless accompanied by sketches or photographs.

Furthermore, in the 1940's and 1950's both roundtail chub and bonytail were recognized as subspecies of *Gila robusta* (Miller, 1959), and the humpback chub had only recently been described (Miller 1946). Initially, the humpback chub did not enjoy general acceptance as a valid taxon. There was considerable resistance to accepting the newly described species as more than another variant of this complex of minnows (Holden, 1991). Several taxonomic studies (Holden & Stalnaker, 1970; Suttkus & Clemmer, 1977; Smith et al., 1979) that recognized roundtail chub, bonytail, and humpback chubs as full species continued to meet with skepticism, and even now specific status of the three Colorado River *Gila* is not resolved to the everyones satisfaction.

Reasons for this skepticism include difficulty in field identification, which continues to be a problem especially for young fish, resistance on the part of individual workers to accept the specific identity of the three morphological types, and the presence of some individual fish which clearly represent hybrids (Valdez, 1980; Tyus et al., 1986a, b; Douglas et al., 1989; Holden, 1991). Most current concern, however, revolves around whether or not humpback chubs are being genetically swamped by introgressive hybridization rather than whether they are a separate species.

Second, the remarkably difficult conditions for sampling the Colorado River basin's dangerous, canyon-bound rivers dictate in part when, where, and how collections are made. Random sampling is not evident with effort and collection sites concentrated where access or other factors are least threatening.

The second point is addressed as follows: based on experiences in the Grand Canyon, some distributional patterns for humpback chub in canyon-bound reaches of the Colorado basin may be more apparent than real. Distribution of sampling is clearly affected by the scheduling vagaries of river trips. A trip has a given number of days to travel through a canyon area and distance traveled is dictated by type and size of boat, means of propulsion, number of other trips on the river, total number of days permitted and amount of water released from Glen Canyon Dam. Most early surveys of Grand Canyon accompanied commercial trips and collected where possible. Sampling was by seine at camps selected to accommodate the downriver schedule rather than the collectors. Few stationary (trammel, gill, fyke) nets were set; appropriate boats were unavailable (highly mobile motorized craft came later) and time required to set and retrieve such gear interfered with down-river progress. Electrofishing, most profitably done at night, was impractical for logistic and safety reasons. Collecting in tributaries was minimal due to down-river schedules and the improbability of camping near a tributary. Thus, practical factors resulted in most collecting at camping beaches and other popular areas visited each trip. This is reflected in Grand Canyon in numerous samples at RM 27-31 (good campsites), RM 61.5 (Little Colorado River, (a well known locality for humpback chubs increasing the number of samples there) and at RM 64-71 (campsites). Phantom Ranch is at Bright Angel Creek (RM 87.5), while Shinumo (RM 108) and Havasu creeks (RM 156) also provide pleasant vistas and swimming. After Havasu Creek, most trips moved quickly downstream and exited the canyon in 2-3 days.

Some gaps may also be due to basic river logistics. In Grand Canyon an example is between RM 0 (Lee's Ferry) and RM 27, because rafting companies prefer to camp below the "Roaring Twenties" rapids (RM 20-27) to avoid difficulties with low water and the first "good" camping beaches are beyond RM 27. This is also true of a section from RM 221 to Pierce's Ferry (RM 285), where no collections of humpback chub were made for 36 years, in large part because most trips ended at Diamond Creek (RM 226). The reach between RM 220-226 was essentially never sampled, as activities were directed toward leaving the river the next day. Occasional surveys were made below Diamond Creek (McCall, 1980a; Carothers & Minckley, 1981; Deacon & Baker, 1983), but the reach never received intensive effort. Another factor was the location of rapids which made it difficult to stop and sample. Examples would be the "Roaring Twenties," Sockdolager to Grapevine (RMs 79-82) rapids, and "the Jewels" from Crystal to Serpentine rapids (RMs 98-106).

After 1980, with more emphasis placed on mainstream research, some river trips targeted previously slighted areas (Maddux et al., 1987). As a result, the number of known locales for humpback chub increased markedly. Nonetheless, many parts of the Colorado (such as RMs 0-27) had not yet been thoroughly surveyed by 1990, in part so that more intensive research could be carried out elsewhere (Kaeding & Zimmerman, 1983; Valdez, 1990; Valdez et al., 1992).

Geogaphic Distribution.

Despite these problems, the historic and current geographic distribution of humpback chub reflects both the topographic uniqueness of the Colorado River basin and the difficulties in conducting fisheries research in such a remote and inaccessible place (Fig. 3). Early (pre-1970) upper-basin records were either

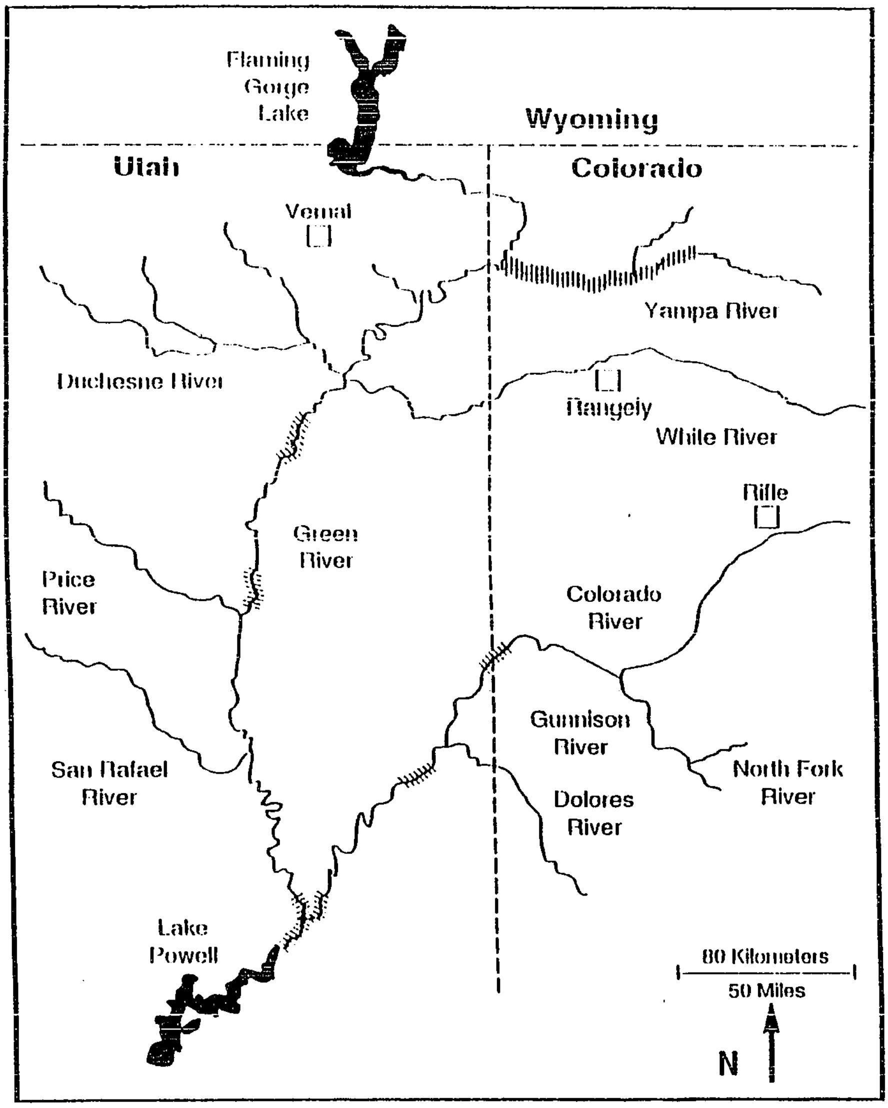


Figure 3. Distribution of the humpback chub in the Green, Yampa, White, Little Snake and Colorado rivers through 1990.

incidental from angling, or from the first attempts to collect in the more accessible areas (Gaufin et al., 1960; Woodbury, 1959, 1963; Flowers et al., 1960; Binns et al., 1963; Banks, 1964; MacDonald & Dotson, 1964; Holden, 1968, 1973; USFWS 1967b; Vanicek, 1967; Vanicek & Kramer, 1969). In later years (*e.g.* 1970-1980), increased funding enabled collecting in isolated habitats, although, systematic sampling remained sporadic.

The era from 1980-90 saw development of projects geared specifically to investigation of chubs and thus produced fisheries research in remote and inaccessible places (Miller et al., 1980, 1981, 1982a-g, 1983a, b; 1984; Archer et al., 1985) This trend, however, also initiated the practice of repeated returns to where humpback chubs were caught before; the impact of which on innovative, opportunistic data acquisition cannot be assessed. Despite or because of these operations, the geographic distribution of humpback chubs (Fig. 3) was soon well known in the upper basin. New localities were only occasionally reported (Haynes, 1980a, b; Wick et al., 1991).

Even with these intensified sampling efforts, humpback chubs were only taken regularly from the Yampa, Green, and Colorado rivers (Joseph 1978, Kidd 1977). Small samples or single individuals were caught from the Little Snake River (Wick et al., 1991, 1985a, b) and White River near Bonanza, UT (Taba et al., 1965; Sigler & Miller, 1963). Recent absence of the chub from the White River was confirmed by numerous additional surveys (Hill & Burkhard, 1963, 1965, 1967; Baumann & Winget, 1975; Prewitt et al., 1976, 1977, 1978; Carlson et al., 1979; Holden & Shelby, 1979; Harper & Tyus, 1982; Lanigan & Berry, 1981; USBLM, 1982; Martinez, 1986). It was never reported from the San Rafael River (McAda et al., 1980); no data are available for Price River.

Nothing construed as humpback chub was ever captured from the Green River basin of WY, either historically (Cope, 1871; Simon & Simon, 1939; Simon, 1946; Kanely et al., 1955) or recently (Baxter & Simon, 1970; Binns et al., 1967; Binns 1963; Oberholtzer, 1987; Marsh et al., 1991). Categorical statements of presence or absence should, however, be tempered with caution (Oberholtzer, 1987), as indicated by its capture in the Little Snake River of CO (Wick et al., 1991).

Distribution in Upper Basin Rivers.

Green River

The first collection from the Green River, UT, was by "....W. Sigler [who] collected "over a hundred" in the Flaming Gorge Basin in 1950 [in Holden, 1973, p. 21]." No specimens were retained for positive identification. Additional specimens were taken near Hideout Canyon in 1959 (Sigler & Miller, 1963; Smith, 1959, 1960; Smith et al., 1959), a locale now inundated by Flaming Gorge Reservoir. Bosley (1960), in discussing those collections, stated

"There appears....to be a change in the physical characteristics of this fish in the extreme lower section of the study area, from Flaming Gorge downstream. Many of the fish taken in this section of the Green River had a very pronounced humpback. In one gill net set made in this area, the incidence of humpback ran over 66% of the total bonytails taken."

Judging from his narrative and associated photograph, several were humpback chubs. One humpback chub was reported from Echo Park (RM 225) in 1961 (Hagen, 1961; Hagen & Banks, 1963) and two others from Split Mountain Canyon (RM 200) in 1962 (Azevedo, 1962a). Banks (1964) made it clear there were three types of *Gila* present in collections from Green River in 1961-62 (roundtail, humpback, bonytail), although all were called "bonytails." Other preimpoundment surveys (McDonald & Dotson, 1964; Azevedo, 1962b, c; 1963; Binns et al., 1963) reported no humpback chubs nor mentioned a humpbacked morphology. As discussed by Holden (1991), accounts of these early upper basin samples illustrate the difficulty researchers experienced in identifying the fish and exemplify a fairly common phenomenon of the time. Many fishery biologists either did not identify similar or poorly known nongame species, especially closely related minnows or suckers, or else misidentified them.

Subsequent sampling of the upper Green River indicated that an attempted eradication of "rough fish" from 712 km of stream before closure of Flaming Gorge Dam (Holden 1991), coupled with changes due to later dam operations, likely extirpated humpback chub in that reach (Anonymous, 1962; Andriano, 1963; Binns et al., 1963; Dexter, 1965). No humpback chub has been taken from the Green above its confluence with the Yampa River since that impoundment was formed (Vanicek & Kramer, 1969; Vanicek et al., 1970; Holden, 1973; Stalnaker & Holden, 1973; Holden & Stalnaker, 1975a, b; Tyus et al., 1980, 1982a, b, 1986a, b; Miller et al., 1982a-g). They were either destroyed by poison, excluded by low water temperatures following closure of the dam, or eliminated by other factors. Three humpback chub were nonetheless caught in Echo Park (junction of the Green and Yampa rivers) shortly after closure of the dam (Franklin, 1963), indicating some survival, or recolonization after rotenone passed through the reach. A relatively long period with no sampling resulted in no records from the upper Green River from 1964 through 1978 (Miller et al., 1982d, e).

Between 1979 and 1985, about 25% of all *Gila* specimens taken in revived research on the upper Green River were identified as humpback chubs (Tyus et al., 1986a, b; Valdez and Masslich, 1989); the remainder were considered roundtail chubs or humpback X roundtail hybrids. Unfortunately, many data were reported for *Gila* species, and therefore cannot be sorted out. Fish identified as humpback chub were nonetheless taken in Echo Park and Whirlpool Canyon in Dinosaur National Monument, and from Cross Mountain, Gray, Gunnison Butte, and Labyrinth Canyons downstream on the Green (Stalnaker & Holden, 1973; Holden & Stalnaker, 1975b; Seethaler et al., 1976; Holden, 1977a, b; Ecology Consultants Inc., 1978; Haynes, 1981; Holden & Crist, 1981; Miller et al., 1982d-f; Tyus et al., 1982a, b, 1985, 1987; Kaeding et al., 1986; Karp & Tyus, 1991). Two concentrations of humpback chub were ultimately identified in the Green River basin, near the confluence of the Yampa and Green Rivers (Echo Park) and in the Green River at the Gray Canyon area some 125 RM downstream (Holden & Stalnaker, 1975a, b; Miller et al., 1982d-f; Tyus et al., 1982a, b). Moretti (1989) also documented humpback chub from Gray Canyon between 1987 and 1989.

Yampa River

Banks (1964) collected numerous "bonytails" from the lower 20 km of the Yampa River in 1961-62. Although not specifically mentioned, humpback chubs were undoubtedly included as suggested by Miller (1963, 1964) in his discussions of fishes of Dinosaur National Monument. Holden (1973) reported humpback chub rare in the lower Yampa, collecting only 26 specimens in the vicinity of Echo Park between 1967 and 1971. Two were recorded from the Yampa by Miller et al., (1982e-g), and numerous incidental collections were reported during 1978 and 1987 (Seethaler et al., 1976; Langlois et al., 1978, 1979; Carlson et al., 1979; Behnke & Benson, 1980; Holden, 1980; Holden & Crist, 1981; Miller et al., 1982e-g; McNatt and Skates, 1985; Rose and Hamill 1988; Tyus et al., 1986a, b; 1987; Kaeding, et al., 1986). During 1986 and 1989, humpback chubs were found only in whitewater reaches of this area. Tyus & Karp (1991) sampled 70 km of the Yampa between Deerlodge to Echo Park and caught the fish only in the vicinity of Big Joe and Warm Spring rapids. Most (85% of 113 adults) were from the upper 43 km of Yampa Canyon; the remaining 15% were from the lower Yampa.

Colorado River

Humpback chub have been collected from four areas on the Colorado River (Fig. 3). These include the Black Rock reach near Grand Junction, Westwater Canyon, a short distance downstream, Cataract Canyon, at the headwaters of Lake Powell, and Lake Powell (Valdez and Clemmer 1982; Valdez 1984, 1987, 1988, 1990; Valdez and Masslich, 1989). All of these areas are canyon-bound and contain rapids.

Other Upper Basin Rivers

Humpback chubs have never been caught from the Gunnison or Dolores rivers despite several surveys (Kinnear, 1966; Langlois et al., 1978, 1979; Miller et al., 1982d-f; Valdez et al., 1982; U.S. Army Corp of Engineers, 1986). Neither have any been taken from the San Juan (Koster, 1954; Sublette, 1977; VTN Inc., 1981; Sublette et al., 1990) or Escalante Rivers (Holden & Irvine, 1975).

Upper Basin Habitat Use

Some of the most detailed data on habitat use by chubs was provided by Holden (1978), Tyus et al., (1980, 1982a, b) and Valdez et al., (1987), for sites in the upper Green River basin. Unfortunately, humpback and roundtail chubs were not separated, implying that conclusions applied as well to one species as the other. Adult *Gila* species (>260 mm TL) occurred almost exclusively in eddy and shoreline habitats over sand/silt substrate; only a few were taken from runs. Water velocities averaged 0.3 meters per second (m/s) and depth averaged 1.3 m, while ranging up to 1.5 m.

Juveniles (60-259 mm TL) generally inhabited shoreline and backwater habitats but also occurred in runs and eddies. They were generally collected over sand and silt substrates near boulders. Mean water velocity was 0.2 m/s, and ranged up to 0.3 m/s. YOY *Gila* species (<60 mm TL) were in a variety of habitats although they occurred mostly in backwaters, along shorelines, and in runs with sand and silt substrates. Velocities in these habitats varied from 0-0.3 m/s, depth varied from 0.2 to 1.2 m with a mean of 0.4 m.

In the Yampa River more recent data were recorded by Wick et.al.,(1991) from the lower 10 km of the Yampa River, where patterns of habitat use were similar to those in the Green River. Humpback chubs were generally in shoreline eddies downstream from large boulders and rapids, in smaller eddies near shoreline runs, and in pockets adjacent to sheer canyon walls. The substrate was sand and boulder, with an average water depth of about 1.3 m. Juvenile humpback chubs

(<228 mm TL) were captured most often in rocky shoreline runs and eddies (Tyus et al., 1980, 1982a, b; Tyus & Karp, 1991; Miller & Hubert, 1990; Wick, 1991).

The two areas of fish concentration in the Yampa River, in upper Yampa Canyon and near the confluence of the Yampa and Green (Fig. 3), differ in a number of ways. The upper reach is an area of moderately steep gradient where rocky runs, riffles, and rapids predominate (Tyus & Karp, 1989; Seethaler et al., 1976). Downstream the river is less precipitous. Side channels are present as well as eddies from adjacent areas with water up to 5.0 m in depth (Seethaler et al., 1976).

In the upper Colorado River subbasin, adult humpback chubs at Black Rocks were studied by radiotelemetry, providing different kinds of data on habitat use. The fish exhibited a variety of vertical movements, generally occupying shallow shorelines at dawn and evening, deeper water in mid-morning and mid-afternoon, and the deep mid-channel at midnight and midday. They occupied depths of 0.7-15.3 m (mean, 4.7 m) and velocities of 0.38-0.6 centimeters per second (average, 0.49 cm/s) over sand and bedrock substrates (Valdez et. al., 1982).

Humpback chub also occur in Cataract Canyon above Lake Powell and in the headwaters of that reservoir

(Tyus et al., 1986a, b: Valdez 1985, 1987, 1988, 1991; Valdez and Clemmer 1982; Valdez and Williams 1986, 1987; Valdez et al., 1982a, b, 1986). In Cataract Canyon, adults and juveniles suspected to be this species were in eddies and to a lesser extent along boulder and talus shorelines. Larvae and YOY occurred in backwaters, along shorelines and in isolated pools (Valdez 1990). Concentrations occur in three areas within this reach, including: the head of Cataract Canyon, between RM 205 to 208, and immediately above the inflow to Lake Powell (RM 201; Valdez 1990).

Humpback and bonytail chubs were both reported from Lake Powell shortly after its impoundment (Holden and Stalnaker 1967; Stone and Miller 1966; Stone et al., 1965; Suttkus and Clemmer 1977; Tyus et al., 1986b) and as recently as 1980 in the *Lake Powell Chronicle*. In that article, a photograph of the fish distinctly shows an overhanging snout, characteristic of both humpback and bonytail chubs; however, the caudal peduncle is too thick for a bonytail and I consider it a humpback chub.

It is entirely possible that both humpback chub and bonytail persist in Lake Powell, much as bonytail remain in Lake Mohave, Az.-Nv. (W.L. Minckley et al., 1986). This is supported by numerous reports of "bonytails" or "Colorado chubs" taken over the years by

Utah Division of Wildlife personnel during research on Lake Powell (Hepworth et al, 1975, 1977, 1978; Stone et al., 1965; Stone and Miller 1965, 1966) and the Lake Powell Chronicle article, which states ". . . a half dozen a year are taken. . . ". Furthermore, a source of recruitment for humpback chub in Lake Powell exists in the upper Lake Powell-Cataract populations (Valdez 1990),which makes it even more likely this fish persists in the reservoir. Finally, the relict population of bonytail, like the humpback chub a long-lived species, in Lake Mohave has survived for decades in the absence of successful reproduction(W.L. Minckley et al., 1991 ; USFWS 1989b, c).

Life History Information, Upper Basin.

Movement

There is little information on long-term and short-term movements of native fishes in the Colorado River basin. Colorado squawfish and razorback sucker have been subjects of long-term movement studies in the Green River using both Carlin and implanted radio tags (Miller et al., 1982d-e, 1991; Tyus et al., 1986a; Tyus, 1991). Scattered data are also available on movements of flannelmouth sucker (McCall, 1980, 1981; McAda, 1977; Carothers & Minckley,1981), roundtail chub (Valdez et al., 1982a, b), bonytail (F. Pfeiffer, USFW pers. comm.) and humpback chub (reviewed below).

Tagging and radiotracking programs have been conducted in the Colorado River at Black Rocks near Grand Junction, CO (Valdez & Nelson, 1982). Humpback chubs were marked with external Floy and Carlin tags and by radiotagging (Valdez et al., 1981; Tyus et al., 1982a, b; 1987; Miller et al., 1982e-g; Archer et al., 1985; Kaeding et al., 1986). Seven percent (n=16) of the 218 fish marked in 1980-81 were recaptured, fifteen were taken <0.8 km from their release site. The single exception moved from Westwater Canyon upstream 23 km to the Black Rocks area over 232 days.

Radio transmitters were again implanted in Black Rocks chubs in 1983 (N = 10) and 1984 (N = 13). In 1983 one remained at its release location, two exhibited limited movement (average, 0.3 km) near their release locations, and the fourth moved 1.6 km downstream outside the Black Rocks reach. Contact was lost almost immediately with the other six fish and no data was recorded (Archer et al., 1985).

In 1984, chub movement was almost entirely restricted to Black Rocks, with 8 of 13 fish staying there. Two moved 14 and 4.6 km downstream, respectively, then returned to their original capture site. The remaining three moved downstream, with one traveling 13 km over 75 days. Net downstream movement averaged 0.3 km during both years, while upstream movement averaged 0.3 and 2.0 km in 1983 and 1984, respectively (Archer et al., 1985).

During 1983-84, Archer et al., (1985) recaptured 57 chubs previously marked with Carlin tags. Most were tagged during 1983 and 1984 (46% and 31%, respectively); the remainder (11% and 12%) had been tagged earlier (1979-82; Valdez & Mangan 1980a, b). Recapture locations were 0.0 to 13.5 km from site of tagging, averaging 1.1 km. Most were recaptured within 0.2 km of their point of initial tag and release. Two, taken in 1983 and 1984, were tagged in Westwater Canyon in 1980 some 23 km downstream (Archer et al., 1985).

Kaeding et al., (1986) radio-implanted 10 Black Rock humpback chubs in 1985 and observed movement almost entirely restricted to the reach. Seven of 10 fish remained while three made sporadic downstream movements. Two moved downstream immediately after implantation to remain outside the reach from 1 to 5 weeks before returning to near their respective tagging sites. A third left the area after six weeks and was last contacted 1.6 km downstream, the farthest movement observed in 1985. Additional information was obtained in 1985 through recapture of seven Carlin-tagged fish all from the Black Rocks area. All were recaptured 0.0 to 0.9 km (average, 0.3 km) from the original tagging sites (Kaeding et al. 1986).

Upper basin humpback chubs thus appear to be sedentary (Tyus et al., 1982a, b; Valdez & Clemmer, 1982; Archer et al., 1985; Kaeding et al., 1986). Thirteen fish moved an average distance of 1.2 km, with most retaken at or near the site of original capture. Three individuals did, however, move 23 km upstream to Westwater and other movements of up to 14 km were recorded. This apparent lack of movement was thought related to habitat preference for canyon-bound reaches (Miller et al., 1982d-f; Valdez et al., 1982a, b; Archer et al., 1985; Kaeding et al., 1986).

Food Habits

Adult humpback chubs in the upper basin consume mostly invertebrates (Miller et al., 1982d). Adults have repeatedly been observed feeding at the surface. Holden (1968) watched humpback chubs feeding on floating materials in a swift run in Desolation Canyon (Green River) in 1967 and Armantrout saw surface feeding in an eddy in upper Desolation Canyon in 1976 (Joseph et al., 1977). Humpback chub have also been observed feeding on emerging mayflies (Ephemeroptera) in Westwater Canyon (Valdez 1982a). Adult roundtail chub or humpback chub also have been seen feeding on floating Mormon crickets (*Anabrus simplex*) and both species were readily captured on cricket-baited hooks in the Yampa River (Tyus & Minckley, 1988).

No specific information is available on foods of smaller size classes of humpback chub in the upper basin. Young-of-the-year *Gila* species from the Colorado River ate ephemopterans and dipteran larvae, while stomachs of juveniles contained diverse invertebrate remains (Jacobi & Jacobi, 1982; Miller et al., 1982e) and rarely fishes (Grabowski & Hiebert 1989).

Age and Growth

The Cataract Canyon population is the only upper basin stock of humpback chubs yet investigated for age and growth (Valdez, 1990). Scales of 23 fish were examined to estimate lengths at annulus formations. Average lengths at each annulus estimated by back calculation were 50, 100, 144, 200, 251, and 355 mm for age classes 0 through V respectively. These data, when compared to those of Kaeding & Zimmerman (1983) from the Little Colorado River, indicate fish from Cataract Canyon grew slower. Holden (1977) considered humpback chubs <70 mm TL from the Green River as YOY (age class 0). Those varying up to 150 mm were considered juveniles, while chubs >200 mm were classed as adults, as a majority that size-class were sexually mature.

Reproduction

Although spawning (oviposition and fertilization) by humpback chub has not been observed, its occurrence and timing are indirectly documented by records for ripe adults, occurrences of larvae <15 mm TL and appearance of other sizes of YOY. In the upper Colorado River basin, spawning readiness or reproduction has been documented in these ways in the Green, Colorado (Black Rocks and Cataract canyons), and Yampa rivers (Rose, 1984; Burdick and Kaeding 1984, 1985; Miller et al., 1982d-f; Valdez et al., 1982a, b, 1986; Archer et al., 1985; Tyus et al., 1982a, b; Valdez & Williams, 1986, 1987; Tyus et al., 1986a, b; Valdez, 1987, 1988, 1990; Karp & Tyus, 1989; Tyus & Karp, 1989). In the Green River, a running ripe male was taken in Gray Canyon in 1985 (Tyus et al., 1987). Prior to that several fish referred to *Gila* species were taken in 1980-81 at lower Coal Creek Rapid in Desolation Canyon. Several males displayed secondary sexual characters (tubercules); a female was gravid and six males exuded milt. Both humpback and roundtail chub were represented (Tyus et al., 1982).

Karp & Tyus (1990) summarized reproductive data on 39 Yampa River humpback chubs (21 ripe, 18 tuberculate) taken from shoreline eddies in Whirlpool Canyon. No behavioral observation was made due to high turbidity.

Ripe males had some orange on lower sides of the heads, opercles, abdomens, and paired and anal fin-bases. Although both sexes had light tuberculation on the nuchal humps, opercles, and parts of the head and paired fins, it was clearly heavier on males. They were captured following highest spring discharges during mid-May to late June 1987-1989 at water temperatures varying from 14.5 and 23.0°C (average, 19.9°C); Tyus and Karp (1989).

Ripe individuals were collected from the Black Rocks population in June 1980 and May 1981 (Valdez et al., 1982a, b). It appeared that spawning in 1980 was between 2 and 15 June at water temperatures of 11.5 to 16.0°C as discharge was decreasing from 733 to 605 m3/s. Three weeks later, most females were spent. In 1981, spawning probably occurred between May 15 and 25 at water temperatures of 16 to 16.5°C(when gravid females were observed) and as flows were again decreasing, from 141 to 85 m3/s (Valdez et al., 1982a, b). Ripe chubs were taken along discontinuous sand beaches between protruding rock pillars at depths of up to 3.8 m and velocities of 0.15 to 3.0 m/s. Spawning was thought to occur on submerged gravel bars in the vicinity of the collection site (Valdez & Clemmer 1982). Archer et al., (1985) reported possible reproduction in the same area in 1983 at water temperatures between 13 and 17°C and discharge declining from 2101 to 1051 m3/s. Spawning was suggested later in 1984, when flows were declining from 600 to 386 m3/s and at water temperatures of 21 to 23 C° (Archer et al., 1985). During both these years, spawning areas were thought to be along shorelines adjacent to eddies and rubble substrates. Male chubs expressed milt earlier in the season and over a longer time-interval than females yielded ova. The highest within-sample percentages (75 to 100%, N=88 fish) of male humpback chub expressing milt was in June and July of both years. Females with expressible ova were captured during only a week each year, in late June 1983 and mid-July in 1984.

Presence and intensity of tuberculation has not proven reliable for precisely estimating spawning times. Males usually develop tubercles first on the pectoral fins, followed by development on the body. In May-June 1984-85, both male and female chubs exhibited tuberculate fins, a month or more before probable time of spawning. Body tubercles persisted on some fish into late July (Archer et al., 1985). Females usually have less development of tubercles than males, and marked differences between the sexes was described by Suttkus and Clemmer (1977).

Expressed milt by males has relatively little application as a definitive indicator of spawning time (Archer et al., 1985). Presence of expressible ova was, however, the best indication that spawning was occurring or recently occurred, as ova can be voided only after ovulation. Occurrence of expressible ova was correlated with a higher gonadal somatic index (GSI; Archer et al., 1985).

Capture of five adults in spawning condition and later collection of six YOY humpback chubs in the spring 1984 indicated reproduction in or near Cataract Canyon (Valdez, 1985). Between 1986-89, a 14-km reach (RM 200-215), yielded 8 larvae and 18 young-of-year in July and August, suggesting a likely spawning site (Valdez, 1990). The area was made up of talus shorelines with cobble/gravel bars that were considered suitable spawning habitat.

Artifical Propagation

Humpback chubs (adults and/or fertilized ova) have been removed from Black Rocks three times for a hatchery propagation program (Jensen, 1982). The initial retrieval was of 18,000 fertilized eggs, obtained in May 1980 and placed at Willow Beach National Fish Hatchery , AZ (Valdez et al., 1982a, b). Most resulting progeny were used in experiments on swimming speeds, effects of turbidity, and tolerance to various pesticides (Bulkley et al., 1982; Miller et al., 1982c-e). The remainder was stocked into Cataract Canyon just above Rapid 11 in December 1981, a site chosen due to ease of access. The 7,600 fish were 1.5 years old and marked with coded nose tags. To date (Valdez, 1990), none has been recovered. A second removal of fish for hybridization experiments and potential broodstock was accomplished in 1981 (Hamman, 1982). A third and final removal from nature occurred in January, 1991, when 20 adults were placed at Dexter National Fish Hatchery and Technology Center (Frank Pfeiffer, USFWS, pers. comm.) to maintain a genetic "buffer" against possible loss of the natural populations. Those fish have since expired (B. L. Jensen, USFWS, pers. comm.).

Parasitism

Flagg (1980,1982), surveyed endangered fishes in the Colorado River Basin. Parasites recorded from humpback chubs in the upper basin are the anchorworm *Learnea sp*. and a leech, *Myzobdella moorei*. Nonlethal infections of protozoa, bacteria and fungi also are known (Hagen & Banks, 1963; Flagg, 1980; Miller et al., 1982d-g).

Condition Factors

Condition factors computed for humpback chubs from the Black Rock reach of the Colorado River during 1984-85 varied from 0.8-1.2 (Archer et al., 1985).

Upper Basin Recovery Actions.

The first recovery plan for humpback chub was approved in 1979 (USFWS 1979) and has been revised twice (USFWS 1984; 1990a). The decline of this species has been attributed to: stream alterations due to irrigation development, water-storage/hydroelectric dams, drying of stream channels, and channelization; competition with and predation by introduced non-native fishes; hybridization with other *Gila sp.*, and other factors such as cold water temperatures impacting reproduction or possible effects of parasites.

The goal of the current recovery plan is protection or restoration of five self-sustaining populations and their habitat. Downlisting, e.g., upgrading its status from endangered to threatened, is to occur when five, viable, self-sustaining populations have been located or re-established. Delisting would indicate the species was recovered and no longer in jeopardy of dramatic population decline back to threatened or endangered status. Such will be considered when five viable, self-sustaining populations and their habitats are fully protected.

Actions deemed necessary to achieve recovery of this species (USFWS 1990a) include: resolve taxonomic problems in Colorado River basin *Gila*; identify and define humpback chub populations; implement monitoring programs to determine the status and trends of humpback chub populations; investigate life history and ecological requirements; protect populations and their habitats; assess potential reintroduction or augmentation sites and stocking when deemed necessary and feasible; promote and encourage improved communication and information dissemination; and determine biological criteria/objectives for downlisting and delisting.

To date, several of the recommended actions have been implemented for humpback chub. Currently, a major taxonomic study which is underway to clarify status of various *Gila* in the Colorado River basin and identify areas of hybridization (Starnes, 1990a-b). Distribution of the species is well documented; reproduction and successful recruitment has been confirmed in three populations; and estimates of age distributions have been made in one.

The current plan is for humpback chubs to be deemed recovered, along with bonytail, Colorado squawfish and razorback sucker through a "Recovery

Implementation Program for Endangered Fish Species in the Upper Colorado River Basin" (USFWS, 1987a, 1988, 1989c, 1990b; Wydoski & Hamill 1991). This program identifies specific tasks and strategies to be applied toward achieving recovery for upper basin populations of these fishes by the year 2003. The lower basin populations will then be addressed.

CHAPTER FOUR: THE LOWER COLORADO RIVER BASIN

The following chapter provides information on the lower basin population of the humpback chub. It presents a summary of ichthyological research in Grand Canyon through 1990, provides information on geographic distribution, habitat use, and factors influencing distribution and abundance of this species in Grand Canyon. Furthermore it provides insight into the effects of Glen Canyon Dam on this fish, the impact of introduced fishes and presents information on various life history aspects of this species.

The "lower basin" as politically defined (Miller & Hubert, 1990) includes rivers in AZ, CA, NM, NV, and UT "whose waters naturally drain into the system below Lee's Ferry," including the Little Colorado, Virgin, Bill Williams, and Gila river subbasins. The lower basin is 348,400 km^2 in area including parts of the Colorado Plateau and Basin-and-Range physiographic provinces.

The largest subbasin (145,000 km^2) is that of the Gila River, draining Basin-and-Range terrain of southern and central AZ, southwestern NM, and northern

Sonora, Mexico. It is bounded on the north by the Little Colorado, Colorado, and Bill Williams river basins. East are the Mimbres and Rio Grande basins. The Gila abuts on the south on several Mexican drainages that flow south and west, including the Sonoyta, Magdalena, and Yaqui drainages and enters the Colorado near Yuma, AZ.

The Little Colorado River subbasin begins in the White Mountains of AZ and drains 69,139 km^2 of northeastern AZ and northwestern NM. It is bounded on the north by the San Juan, east by the Rio Grande, west by the Colorado, and south by the Gila. This river flows entirely on the Colorado Plateau and has two major tributaries, the Zuni and Puerco rivers. It enters the Colorado 61.5 miles below Lee's Ferry to form the demarcation between Marble and Grand canyons (W.L. Minckley et al., 1986).

The last two subbasins are considerably smaller. The Virgin River (~28,500 km^2) enters AZ from the north, draining the southwestern Colorado Plateau escarpment and Basin and Range. The headwaters are in southwestern UT and the Pluvial White River of eastern NV. The river presently enters the Colorado River in Lake Mead. The smallest subbasin (14,000 km^2) is the Bill Williams River, located entirely within the Basin-and-Range Province, north and west of the Gila

River subbasin, and now entering the Colorado River in Lake Havasu (W.L. Minckley et al.,1986).

Summary of Ichthyological Research in the Grand Canyon Region.

Icthyological research within Grand Canyon was limited prior to 1970 due to the difficulties in accessing the area. Early collections were made by GCNP personnel or by anglers who gave their catches to them for identification. This included a collection of speckled dace from Pipe Creek in 1937 (mistakenly called *Tiaroga cobitus*, the loach minnow). Several fish were preserved from Bright Angel Creek including: a razorback sucker (1944), the type specimens of humpback chubs (1944) and a small number of bluehead and flannelmouth suckers (1950-1960). Additionally, a brook trout from Clear Creek (1944) and a channel catfish from the mainstream (1940's) were preserved in the fish collection at GCNP. This collection was transferred to the icthyological collection at Arizona State University in 1978. Dr. R.R. Miller made a whirlwind trip down the Bright Angel Trail in 1968 (pers comm) collecting speckled dace, bluehead and flannelmouth suckers on that trip. Four humpback chubs were taken from Spencer Creek by Wallis (1955) while Carothers and Aitchison (1972) examined the effect of carbon dioxide on speckled dace in the Little Colorado

River.

Collections made in the mainstream began in 1968 with a trip by R.R. Miller through Grand Canyon. The 1970's saw numerous collecting trips through the Grand Canyon as summarized in Miller (1975a, b); Suttkus et al (1977), Suttkus and Clemmer 1978; C.O. Minckley and Blinn (1975). Additionally, during this time, C.O. Minckley (1978c) concentrated on Bright Angel, Pipe and Phantom Creeks. The AGFD was also actively working between Lee's Ferry and Glen Canyon Dam developing their trout management plan for that area (see J. Stone 1964a, b; 1965a, b; 1966a, b; 1967a, b; 1968, 1969, 1971, 1972; Stone and Burce, 1971; Stone and Queenan, 1967, Stone and Rathbun, 1968, 1971). Funding for these projects were primarily from GCNP and AGFD. In 1978, MNA began a series of trips to determine status of the genus *Gila* in Grand Canyon, funded by the GCNP. In 1979-1980 MNA conducted studies to determine the life histories of fish in Grand Canyon, an effort funded by the Boulder City Office of the Bureau of Reclamation (Carothers and Minckley, 1981). That same year (1980) the Colorado River Fishes Project established an office in Flagstaff and began research on the humpback chub in Grand Canyon. As this project phased out, the beginning of GCES program, Phase I began (1981). This funded work by AGFD on the mainstream (see Maddux et al., 1985). At the same time, the nongame branch of AGFD contracted with C.O. Minckley to initiate an annual month long monitoring program in the Little Colorado in 1987 which continues to date. At this time (1996), GCES has developed into a multi-faceted program, and is now developing a interim monitoring plan for the Grand Canyon region. A direct result of GCES Phase II was four major projects on humpback chub. This included: research in the Little Colorado River by Arizona State University and the Navajo Natural Heritage Program to determine population size and movement characteristics of humpback chubs <15 cm between 1990-1994 (Marsh and Douglas 1996); Radio-telemetry studies and life history aspects of the mainstream population by BIO/WEST (see Valdez and Ryel 1995); habitat investigations in the Little Colorado River by the USFWS (Gorman, 1995). Studies by AGFD on larval humpback chub and other native fishes in this region (Robinson, 1996). These more recent studies are not addressed in this text as they are outside the scope of this work.

The following projects are the source of the data I used to develop this document:

1975 - Two fishery survey trips through Grand Canyon for Northern Arizona University (C.O. Minckley & Blinn 1975); 1975-1976, Surveys of Bright Angel, Pipe and

Phantom creeks, conducting basic life history studies of the fish; 1977 - Surveyed Little Colorado River from Blue Springs downstream, funded by Office Of Endangered Species (C.O. Minckley, 1977b); 1978-1979 - River monitoring project to determine the status of the Genus *Gila* in Grand Canyon. Funded by GCNP through MNA; 1979-1980 - Study to determine the life histories of fishes in Grand Canyon, funded by U.S. Bureau of Reclamation, Boulder City, through MNA; 1987-1990 - Established monitoring project for humpback chub in Little Colorado River for AGFD. Additional data for larval hatching dates was developed from information provided by AGFD.

Geographic Distribution

Extant lower basin populations of humpback chub occur in the Colorado River and its tributaries between Glen Canyon and Hoover Dams. The earliest record of humpback chub from the lower basin is from Stanton's Cave (RM 30),an archeological site in Marble Canyon, AZ. Skeletal remains were associated with bones of other Colorado big-river fishes and Indian artifacts (Euler, 1978; Miller, 1984; Miller & Smith, 1984). Fish bones referred to *Gila* are associated with an archeological site at RM 136 in Grand Canyon (Jones, 1985); humpback chub is likely represented in that material. Humpback chub bones were also present in the now-inundated Catclaw Cave (Miller, 1955), 14 miles below Hoover Dam, AZ-NV. An additional report of humpback chub from the lower Colorado River by USFWS (1980b, 1981) from Blake (1864) is referable to bonytail based on my examination of a sketch present in the unpublished diary.

Remains referred to humpback chub were also reported by Olsen (1976) from an Amerind site along the Gila River south of Phoenix. It is unlikely that the species occurred anywhere near that locale, W.L. Minckley, (1976) referred different material he examined from the same site to bonytail.

Humpback chub were eaten by early river runners, resulting in the first published account of the species. In May 1908, when the Kolb brothers (Kolb, 1914; Kolb & Kolb, 1914) hiked into the Little Colorado River and camped, they heard a noise:

"Then Emery [Kolb] discovered what it was. 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. They are otherwise known as Gila Elegans, or Gila Trout, but 'bony tail' describes them very well. The Colorado is full of them; so are many other muddy streams of the Southwest. They seldom exceed 16 inches in length, and are silvery white in color. With a small flat head somewhat like a pike, the body swells behind it to a large hump [Kolb and Kolb, 1914]."

Published photographs of the fish (USDI, 1987) show they were humpback chub.

Historic (1942-70) and current distributions of humpback chub (1980-91) downstream from Glen Canyon Dam are summarized in Appendix A and Figure 4. Records existed in 1940-70 from Glen Canyon Dam to Spencer Creek, some 246 RM downstream. Just after closure of the dam in 1963, chubs were commonly taken above Lee's Ferry (Stone, 1964a, b). I found no records for that reach after 1971 (Rathburn, 1970; Stone & Bruce, 1971; Stone, 1972; Persons et al., 1985; Kubly, 1990; Maddux et al., 1987). During the 1970's, the most upstream collection locality known was at RM 19.5 (Carothers & Minckley, 1981). Several were collected, however, from the Colorado River at RM 27 and 30-32, at the Little Colorado River (RM 61.5), and from RM 64-71.

Additional localities in that period were in or near Bright Angel (RM 87.5), Shinumo (RM 108.5), Kanab (RM 144.5), and Havasu creeks (RM 157). The furthest downstream locality reported in 1979 was at RM 194, where a passenger on a commercial river trip caught a humpback chub while angling (M. Walker, OARS Inc., pers. comm.). Thus, known localities prior to 1979 were few and concentrated at some ten sites (Fig. 4). This distribution changed markedly in the 1980's when surveys documented an essentially continuous distribution from RM 8 to RM 220 (Appendix A; Fig. 4;

Maddux et al.,1987). The fish taken at RM 8.0 was by angling (Dan Pearson, Flagstaff, pers. comm.). A concentration of fish was apparent from RM 52 to 72, the reach of most intensive research in and near the Little Colorado River (Kaeding & Zimmerman, 1981, 1982, 1983). Humpback chubs were consistently taken at Bright Angel, Havasu, Shinumo and Kanab creeks, as well as at other Colorado River localities (Appendix A; Maddux et al., 1987).

Lower Basin Habitat Use.

Historically runoff from snowmelt on high mountains of the upper basin resulted in maximum discharges during spring and early summer (W.L. Minckley, 1991). Low water conditions predominated in late summer through winter. In the lower basin, a bimodal pattern of winter rains and late summer monsoons prevailed, some flooding also occurred in summer.

The Colorado River and its major tributaries flow alternatively through broad aggraded valleys and deep or shallow intervening canyons. In the former, runs and riffles are common in braided channels cut in sand and gravel, and pools or pool-like habitat occurs along cut banks and near downed trees and other channel

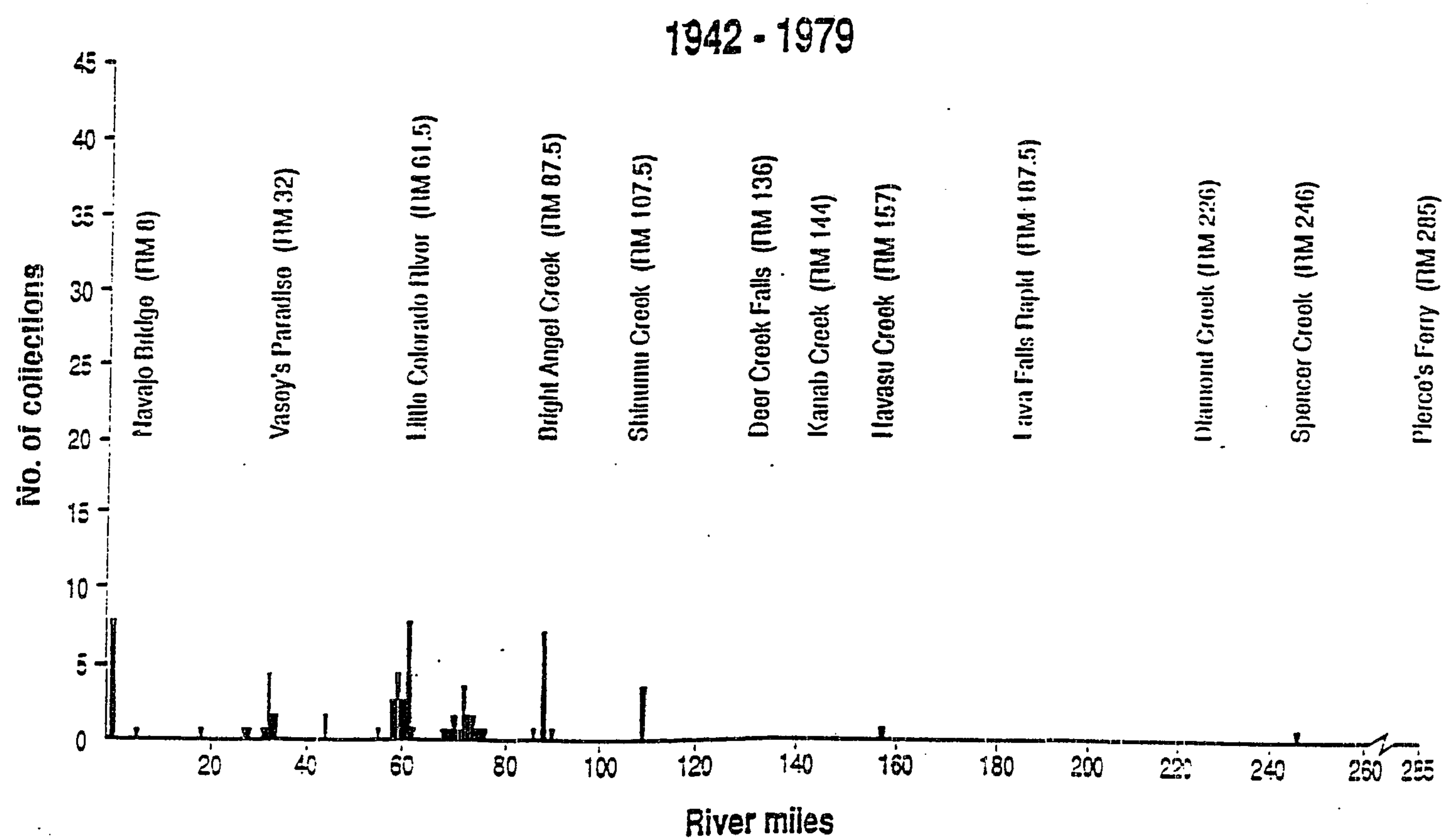
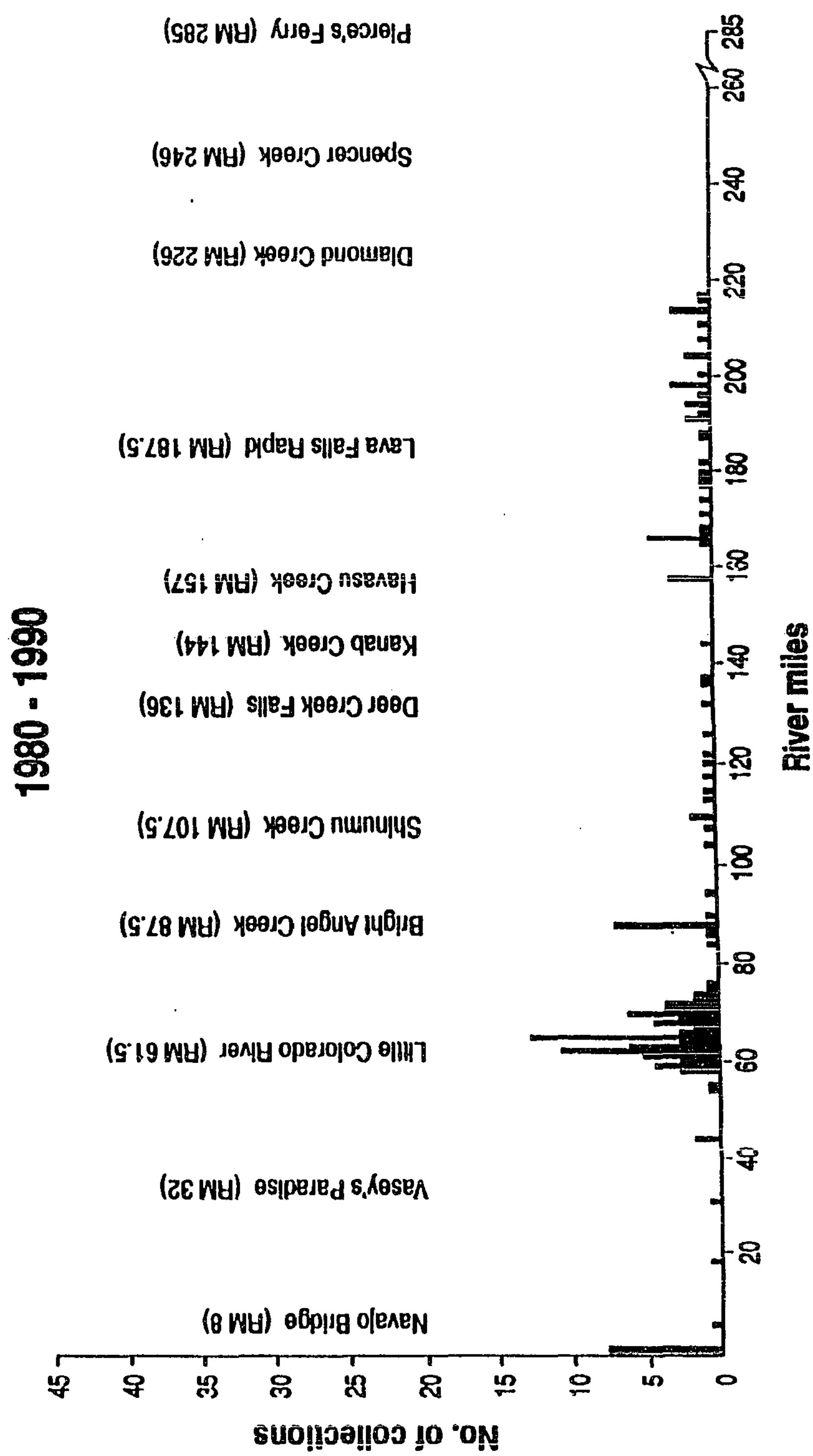


Figure 4. Diagram illustrating distribution and collecting localities of humpback chub from the Colorado River mainstream between Glen Canyon Dam and Davis Dam, 1942-1990.



(Figure 4, continued).

obstructions. In canyons, dangerous rapids form as the result of bedrock debris, rockfalls from canyon walls, or debris flows carried in from tributaries (Leopold, 1969; Dolen et al., 1978). Between rapids are large deep pools where strong currents flow unobstructed.

The river's variability in discharge and sediment loads are marked. During a 40-year pre-dam period, discharge at Yuma, AZ, varied over five orders of magnitude, from 0.5 to 7,100 cubic meters per second (m3/s), and volume of sediment moved through Grand Canyon between 1922 and 1935 was estimated between 44.5 to 455 million metric tons per year (Howard, 1947; Howard & Dolan, 1981).

Turbulent floods result in differential sorting of sediments and formation of sand, gravel, and rubble bars that are later exposed and dissected at low water. High discharges also provided access for fishes to tributaries by inundating confluence areas and alluvial barriers, as well as supplying massive quantities of allochthonous organic material to support productivity of the river (Dolan et al., 1974, 1978).

In areas of bars, tributary confluences, and other obstructions, large eddies and backwaters form and became sites where invertebrate communities developed. Such places also provided refuge from extreme discharges for all sizes of fish. The longer eddies and backwaters persisted, the more fish using them could grow before entering the channel, giving them an advantage in avoiding predators. Also, as ambient temperatures increased in quieter waters so did productivity, creating food-enriched nurseries for YOY. Today's backwaters and ponded tributaries still serve this function (W.L. Minckley, 1991; C.O. Minckley, 1975, 1978a, c)

Although habits of endemic fishes in the historic Colorado River are largely unknown, studies in recent years in the human-modified basin provide some insights into their biology (Carothers & Minckley, 1981; Miller et al., 1982a; W.L. Minckley, 1991; Kaeding & Zimmerman, 1983; Tyus & Karp, 1991). Under pre-dam conditions, most fishes of the Colorado River probably occupied valley reaches. Canyons would have been most densely populated in wider places near tributary mouths. During low flow, chubs and other indigenous fishes may have moved into canyons to avoid declining water levels or high summer water temperatures, as in other southwestern systems (Siebert, 1980).

Species of big-river fishes were almost certainly segregated by habitat (W.L. Minckley, 1991). The large, piscivorous squawfish occupied quiet places along shore, often near overhead cover or in areas between boulders. Flannelmouth suckers stayed on the bottom in deep, quiet places along shore, feeding on invertebrates in eddies and along shorelines of pools and riffles. Bluehead suckers also lived in pools, except when moving into shallow areas to graze on algae (W.L. Minckley, 1991). Razorback suckers occupied near-bottom space, most likely in open, flowing channels, but also in backwaters and eddies, feeding on plankton and detritus (W.L. Minckley, et al., 1991). Bonytails may have remained mostly in the water column in the channel while only humpback chub lived in deep pools and eddies of whitewater canyons (W.L. Minckley et al., 1991). The roundtail chub most likely occupied transition zones between canyon-bound and valley reaches in the upper basin; it was rare or essentially absent in the lower Colorado River. Speckled dace, *Rhinichthys osculus* another small native minnow, lived near bottom along shorelines, in riffles, and in tributaries and their confluences with the river (W.L. Minckley, 1973, 1991).

Taming of the Colorado River began in 1935 with closure of Hoover Dam to form Lake Mead. Changes in fish species composition were quickly noticed below Hoover Dam (Dill, 1944) and in Lake Mead where populations of introduced centrachids and ictalurids rapidly increased (Jonez et al., 1951, Jonez & Summer, 1954). The reservoir provided a source for colonization by newly introduced centrachids and a refuge for non-native fishes flushed from upstream canyons by scouring flows. Lake Mead also inundated several rapids, enhancing upstream dispersal by alien species whose progress might be inhibited by swift water.

As with most Western reservoirs, Lake Mead soon filled with lentic-adapted, non-native species (Table 2; Jonez et al., 1951; Kimsey, 1958; Nicola, 1979; W.L. Minckley, 1991). Not only were they inadvertently stocked, but a variety of baitfishes used and released by anglers exacerbated the problem of introduction of foreign species into the Colorado system (Miller, 1952; Kimsey et al., 1957; USFWS, 1980b, 1981). By the 1960's, indigenous fishes of the Colorado River downstream from Hoover Dam had been largely replaced by non-indigenous forms (Miller, 1961; W.L. Minckley, 1973, 1973, 1985, 1991) and decline of the native fish fauna in Grand Canyon was well underway.

Colorado River

Adult humpback chubs were collected from the Colorado River in the Grand Canyon region mostly in large eddies whose configurations varied with river stage. Substrates were generally sand or sand-boulder and depths varied from 4.0 to >10 m (Deacon, 1968a;

Table 2.
List of fishes reported from the Colorado River and Lake Mead. (Species list developed from Jonez et al., 1951, Jonez and Sumner 1954, Carothers and Minckley 1981, and W.L. Minckley, 1973).

Family: Clupeidae:
Threadfin Shad, *Dorosoma pentenese*

Family Anguillidae
Freshwater Eel, *Anguilla sp.*

Family Salmonidae:
Rainbow Trout, *Onchorhychus mykiss*
Silver Salmon, *O. kisutch*
Brown Trout, *Salmo trutta*
Cutthroat Trout, *S. clarki*
Brook Trout, *Salvelinus fontinalis*

Family: Cyprinidae
Carp, *Cyprinus carpio*
Goldfish, *Carassius auratus*
Red Shiner, *Cyprinella lutrensis*
Redside Shiner, *Richardsonius balteatus*
Fathead Minnow, *Pimephales promelas*
Virgin River Spinedace, *Lepidomeda mollispinis*
Humpback Chub, *Gila cypha**
Bonytail Chub, *G. elegans**
Roundtail Chub, *G. robusta**
Speckled Dace, *Rhinichthys osculus**
Colorado River Squawfish, *Ptychocheilus lucius**
Golden Shiner, *Notemigonus chrysoleucus*

Family Catostomidae:
Flannelmouth Sucker, *Catostomous latipinnis**
Bluehead Sucker, *Pantosteus discobolus**
Razorback Sucker, *Xyrauchen texanus**

Family Ictaluridae:
Channel Catfish, *Ictalurus punctatus*
Black Bullhead, *I. melas*

(Table 2. continued).

Family Cyprinodontidae:
Plains Killifish, *Fundulus zebrinus*

Family Poeciliidae:
Mosquitofish, *Gambusia affinis*

Family Percichthyidae:
Striped Bass, *Morone saxitalis*

Family Centrarchidae:
Largemouth Bass, *Micropterus salmoides*
Bluegill Sunfish, *Lepomis macrochirus*
Green Sunfish, *L. cyanellus*

Family Percidae:
Walleye, *Stizostedion v. vitreum*

*Native to Colorado River system.

Carothers & Minckley, 1981; Maddux et al., 1987). Collections of smaller chubs (>120 mm) prior to 1980 found small numbers (e.g., one or two) in water ranging from 1.0 to 1.3 m deep over sand-rubble or sand-silt substrate (Suttkus et al., 1976; Suttkus & Clemmer, 1977, 1979). Water temperatures varied from 10.5 to 17.0°C. Current varied from none to 1.5 m/sec. Several of these fish were taken at night (Deacon, 1968a; Clemmer, 1976, 1981, 1982; Suttkus & Clemmer, 1976). In one instance, a YOY was taken from a backwater at Granite Rapid in water <1.0 m deep and varying from 12 to 14°C (C.O. Minckley, 1979a,b-d). In more recent years, numerous YOY have been taken from sandy runs and backwaters. Juvenile chubs have also been found in backwaters during spring, summer, and autumn, when water temperatures were higher than those of the adjacent Colorado River (Kubly, 1990; Maddux et al., 1987; USFWS, 1981).

Grand Canyon Tributaries

Repeated reference to collection of humpback chubs in tributaries of the lower basin must be qualified, as it implies occurrences in such habitats far more commonly than is actually the case. To my knowledge, with exception of the Little Colorado River and Spencer Creek, most records from tributaries were in fact from the Colorado in immediate areas of tributary confluences or the Colorado within 500 m of a tributary mouth. Confluence is defined as the point where an inflowing stream meets a larger tributary.

Other than seeps, there are 27 creeks and springs entering the Colorado River within the Grand Canyon region, and they may be separated into either high or low-gradient. High gradient systems are characterized by distinctive water sources, water chemistry, discharges, substrates, and invertebrate faunas. Larger examples include Clear, Bright Angel, Shinumo, Tapeats, and Havasu creeks. All have large, permanent spring-fed sources a number of kilometers from the river and are perennial. Discharges vary from 1.0 to 8.0 m^3/s at baseflow (Johnson & Sanderson, 1968; Cole & Kubly, 1976; Carothers & Minckley, 1981). Substrates consist of fine mud to gravel, cobble, and boulders. The streams are generally <10 m wide with depths occasionally to 3 meters. Stream morphology is characterized as pool-riffle, with occasional barrier falls.

Fishes from the Colorado River can have difficulty entering high-gradient tributaries. In addition to occasional barrier falls, tributary mouths often have thick alluvial fans of coarse gravels and boulders. At low flow, the streams often percolate into these fans and enter the river underground, or lower parts of their channels become braided and shallow, forming a precipitous barrier to entry. Under present conditions of fluctuating discharge and fluctuating water levels in the Colorado River these small deltas may alternate between passable and dry.

Invertebrate faunas of high gradient streams are generally dominated by dipterans (mostly Simuliidae), Ephemoptera, and Trichoptera (C.O. Minckley, 1978a,b; Carothers & Minckley, 1981; Hofknecht, 1983). Water temperatures range from 7.0-23.0^{0}C and reflect ambient air temperatures as well as effects of shading by canyon walls. Conductivities range from 100-795 micromhos/cm (um/cm) and pH from 7.9-8.8. These systems, with exception of Havasu Creek, are termed dolomitic streams, high in magnesium and calcium carbonate and low in nitrogen and phosporus (Cole & Kubly, 1976). Havasu Creek is classed as an impure dolomitic stream, as it is relatively high in silica.

Humpback chubs have been recorded in or near several high-gradient tributaries, particularly Bright Angel Creek (Appendix A, Fig. 4). Records from the latter include the holotype taken in 1942 and another caught by angling in 1968 (Miller, 1946; GCNP, 1968). Adults were also netted at the confluence in September 1984, and others were taken by angling in autumn-winter

1987 (Mark Law, pers. comm.; Maddux et al., 1987).

Humpback chubs are also frequently caught at Shinumo Creek (RM 108.5), where adults and YOY, respectively, were recorded in August and September of 1975 (Suttkus & Clemmer, 1976, 1977). There are several collections of humpback chub from Shinumo Creek including those of: Maddux et al., (1987) and Kubly (1990). Carothers & Minckley (1981) collected an adult from the river immediately above the Shinumo confluence as well as a single chub taken from the Colorado River near the confluence of Stone Creek (RM 132) in 1979.

Examples of low-gradient streams entering the Colorado River in the Grand Canyon region include Kanab Creek and the Paria and Little Colorado rivers. The most common substrates are mud or mud-sand, and they vary substantially in width, with the Little Colorado being the largest (>30 m wide) while both Paria River and Kanab Creek are generally <10 m. Springs are the sources of baseflow. Deltas of low-gradient streams consist of broad deposits of coarse sediments carried in by major flooding that are typically incised by the stream to form a discrete channel. Fine sediments accumulate so that mud flats and bars may block the channel at low flow. Again, with fluctuating flows in the Colorado, alternating inundation and desiccation exacerbate the problem of access for fishes.

The invertebrate fauna of low-gradient systems is dominated by dipterans, generally Chironomidae (Carothers & Minckley, 1981). As with high-gradient tributaries, water temperatures reflect ambient air temperature and shading by canyon walls, ranging from 9.0 to 33.5°C. Conductivities are from 377 to 6100 um/cm and pH from 7.7-9.0, depending on the tributary. In many, flow ceases or is markedly reduced in summer near the mouth, as baseflow is not sufficient to replace water lost to evaporation.

Humpback chub have been taken in and near these low-gradient tributaries. In June 1984 and May 1989, small numbers of YOY were seined from or near Kanab Creek (RM 144.5; Maddux et al., 1987; Kubly, 1990). I received a written report (J. Hendricks, OARS Inc., pers. comm.) of an adult caught at Havasu Creek (RM 157) by an angler in spring 1978. Additional fish were netted near Havasu Creek in 1987, 1989, and 1990 (Maddux et al., 1987; Kubly, 1990). Spencer Creek (RM 246) is the most downstream record site, where four chubs were taken 1.0 km upstream from its confluence with the Colorado by Wallis (1955).

Although YOY are taken in tributaries, their appearance is sporadic at best outside the Little Colorado River. During 13 surveys between 1975 and 1979, the lower reaches of all Grand Canyon tributaries were seined for fishes and no humpback chubs were taken (C.O. Minckley & Blinn, 1976; Carothers & Minckley, 1981). During monthly surveys of Pipe, Bright Angel, and Phantom creeks over a 13-month period, no humpback chubs were taken (C.O. Minckley, 1975, 1978c). Previous collectors have also consistently surveyed streams in Grand Canyon (e.g., Miller, 1975a, b; Holden & Stalnaker, 1976; Suttkus & Clemmer, 1976; J. N. Rinne, pers. comm.) and have seldom taken chubs outside the Little Colorado River.

Little Colorado River

C.O. Minckley,(1977b) first documented presence of humpback chub outside of the confluence zone, collecting it 7 miles upstream from the mouth. Later, Kaeding & Zimmerman (1983) found the species 9 miles above the confluence area, an upstream record that has not yet been exceeded (Fig. 5).

Dominant substrates in the Little Colorado River are mud, sand, or a composite of mud and sand (Kaeding & Zimmerman, 1983, C.O. Minckley, 1988a, b; 1989 a-c; 1990a-c), often covered by a variably thickened and consolidated layer of travertine. Travertine dams and other structures are developed by carbonate rich waters de-gassing through physical, chemical, and biological

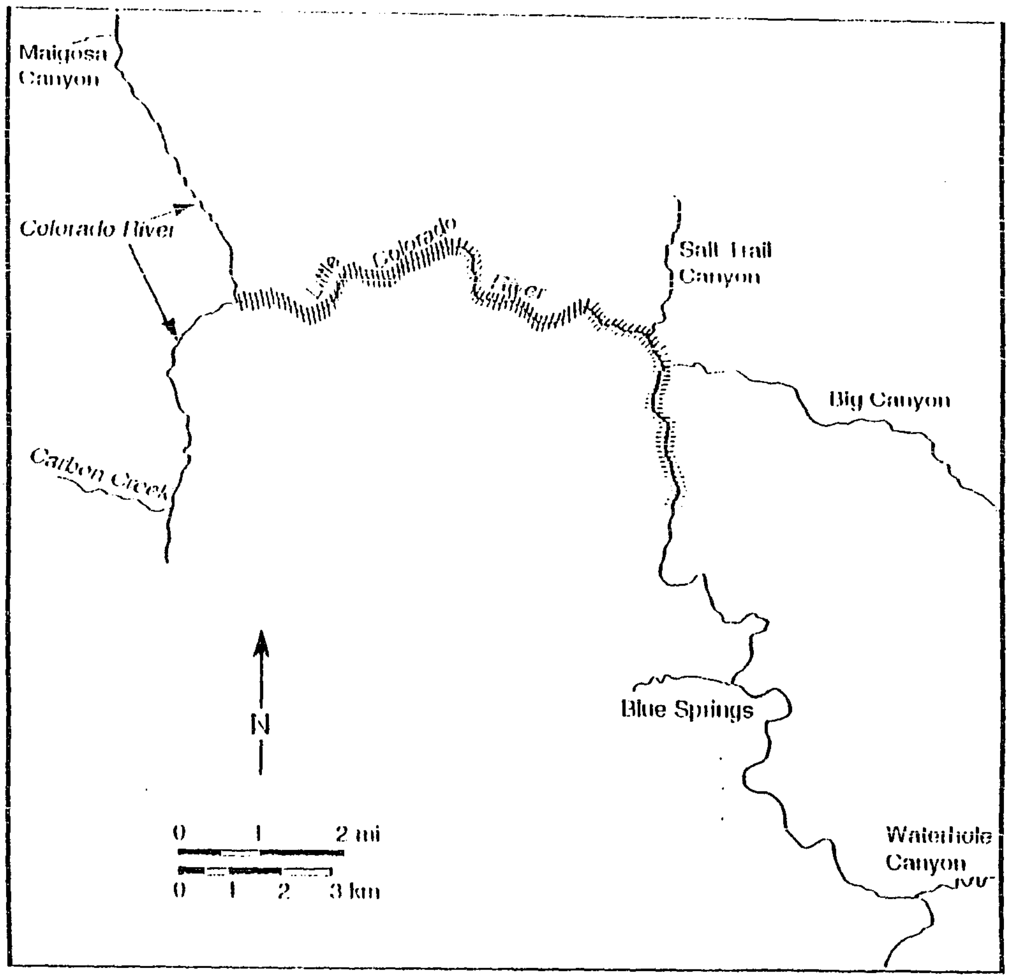


Figure 5. Distribution of the humpback chub in the Little Colorado River, 1908-1990.

action, and depositing calcium carbonate on the stream bottom and other surfaces. Colloidal carbonates also form in the water column, giving the Little Colorado River its characteristic chalk-blue coloration.

Humpback chub fry (7-20 mm TL) live in shallow areas with reduced or no current. They frequent areas of shade, utilizing undercut banks, structure represented by variations in substrate, and submerged or riparian vegetation such as poolmat (*Zannichellia palustris)*, tamerix (*Tamerix pentandra)*, cattail *(Typha domingensis, T. latofolia)* or common reed (*Phragmites communis*). They are active, reacting quickly to stimuli such as shadows or objects dropped in their vicinity, and generally remain near the bottom unless inspecting floating materials (C.O. Minckley 1978b). Valdez (1989) observed post larval humpback chubs in water from 0.4-1.2 m deep over boulder/silt substrates at velocities of 0-0.3 m/sec.

Larger fish (up to 100 mm TL) begin to avoid shallow places, generally occurring in water greater than a meter deep. In July of 1978, several hundred were taken from pools and riffles below small travertine dams and in deeper runs near Big Canyon (C.O. Minckley, 1978b; Carothers and Minckley,1989). These areas varied from 0.1-1.5 m deep. Many of these larger fish frequented overhanging banks and areas of cover provided by riparian vegetation and were generally in mixed schools with flannelmouth and bluehead suckers of similar lengths (C.O. Minckley, 1978a, b).

As chubs increase in size (>100 mm TL) they move into even deeper water (C.O. Minckley,1989a-c, 1990a, b). Such dispersal from littoral areas may have several benefits. Larger fish may be unable to survive on diatom and small invertebrate foods found in littoral areas. Furthermore stranding and desiccation in isolated pools is clearly avoided by moving offshore and has been observed. Additionally, fish in deeper water are less susceptible to avian predators such as the great blue heron (*Ardea herodias*), cattle egret (*Bubulcus ibis*), belted kingfisher (*Megaceryle alcyon*), golden eagle (*Aquila chrysaetos)*, and bald eagles *(Haliaeetus leucocephalus)* which frequent the area.

Humpback chubs up to 150 mm TL occur in single-species schools of similarly sized fish. Fish of this size were taken at all depths (to >3.0 m) in slow-moving runs as well as in pool habitats and slower, protected areas, such as behind large boulders.

Large chubs, >150 mm TL, inhabit all but the shallowest habitats. They were observed and collected in deep water adjacent to undercut banks, behind boulders, and in pools. They also associate in daytime with shade and overhanging riparian vegetation. All sizes of humpback chubs are more susceptible to being collected at night and during times of higher turbidity (C.O. Minckley, 1979a, 1988a, b; C.O. Minckley et al., 1980; Carothers & Minckley,1981; Kaeding & Zimmerman, 1983; Brooks & Minckley, 1984; Kubly, 1990).

Apparent abundance of chubs in the Little Colorado River changes dramatically with seasons. Based on catch rates, more are present in summer than other times of the year. Numbers decline in autumn and continue to drop into winter, then again increase in spring (Carothers & Minckley, 1981; Kaeding & Zimmerman, 1983). It is yet to be determined if the pattern is due to movement into the Colorado River in autumn or winter and back into the Little Colorado in spring and summer, or reflects less local movement of resident fish resulting in lower catch rates in passive nets in colder times of the year.

Factors Influencing Distribution and Abundance in Grand Canyon

Effects of Introduced Fishes

Alien fishes may prey on, compete with, or introduce foreign parasites to native species. Principal non-natives introduced in the region include trouts, minnows, sunfishes, and catfishes. All are potential predators on humpback chub, although direct demonstration of predation is rare (Calhoun 1960). Channel catfish (*Ictalurus punctatus*), striped bass (*Morone saxitalis*) and various trouts (mostly rainbow trout, *(Onchorhynchus mykiss)*, and brown trout, *Salmo trutta*) are known piscivores that co-occur with humpback chubs in Grand Canyon.

Channel catfish were already in the lower Colorado River basin by the late 1800's and reported from the inner Grand Canyon by 1909 (Miller & Lowe, 1967; Carothers & Minckley, 1981). Prior to impoundment of Lake Powell there was a fishery for the species at Lee's Ferry (Stone, 1964) which persisted several years after closure of Glen Canyon Dam (Bancroft & Sylvester 1978; McCall, 1980a, 1981). Channel catfish are currently present throughout the reach from Lee's Ferry to Diamond Creek and below, appearing most concentrated near low-gradient tributaries and increasing in numbers toward Lake Mead (Carothers & Minckley, 1981; Kaeding & Zimmerman, 1983). Channel catfish are common in the lower Little Colorado River (C.O. Minckley, 1988a, b; 1989a-c, 1990a, b).

The channel catfish, a known piscivore (see Carlander 1969), are suspected to exert negative impacts on native fishes and may represent the longest continuous threat by an introduced species to chubs in the Grand Canyon region. Humpback chubs were taken at least five times from stomachs of an estimated 200 channel catfish (Maddux et al., 1987; C.O. Minckley, 1987, 1988a, b,1989 a-c, 1990a, b). This small number of humpback chubs occurring in stomachs is thought to be an underestimation as many times, catfish stomachs were empty as the fish had been in nets for several hours allowing digestion or reguritation of stomach contents. Other food items in catfish stomachs were scuds (*Gammarus lacustris*), fishes, and blackfly larvae (Simuliidae) and the green alga *Cladophora glomerata*. Other fishes found in stomachs included flannelmouth suckers, bluehead suckers, and speckled dace.

Attempted predation is further documented from bite scars on chubs (C.O. Minckley, 1978a, b, 1979b-d; Kaeding & Zimmerman, 1983; C.O. Minckley, et al., 1981), a characteristic, horseshoe-shaped scar identical in shape to channel catfish jaws. Fresh bites have been observed on chubs caught along with catfish in hoop nets and entangled near channel catfish in trammel nets, leaving little doubt as to their origin.

Striped bass are well established both in lakes Mead and Powell, where, they were stocked in 1969 and 1974, respectively (Gustaveson et al., 1979; McCall, 1980a), and have subsequently moved into the Grand

Canyon. McCall (1980a) reported striped bass as far upstream as Surprise Canyon (RM 260), while Suttkus & Clemmer (1979) documented the species at RM 250 in 1978. Carothers & Minckley (1981) found them upstream to Separation Rapid (RM 240) in 1977-1979. In 1980, a striped bass skeleton was also found at Kanab Creek (RM 144; Clemmer, 1981).

Striped bass were reported below Glen Canyon dam in 1980 (McCall, 1981) where a dead individual was found 12 km below the dam. After Lake Powell reached capacity in June 1980, the fish could enter the river with surface water flowing through outlet pipes over the dam, a fact later documented by fishermen's reports and creel records of both striped bass and walleye (*Stizostedion vitreum*) in the reach between Glen Canyon Dam and Lee's Ferry (McCall, 1980b). Several walleye were also observed during diving surveys after high water in 1983 in the reach above Lee's Ferry (W. L. Montgomery, pers. comm.).

Following collection of striped bass at the confluence of the Little Colorado and Colorado in May 1990 (C.O. Minckley, 1990a, b), I interviewed 11 commercial boatmen, five of whom attested to catching striped bass "at will" below Havasu Creek (RM 156) and upstream as far as 24.5-mile rapid, 37 miles above the Little Colorado River. Further interviews provided additional records of striped bass catches near Bright Angel Creek (RM 87.5), Dubendorff Rapid (RM 144), and in particular of seven from the confluence area of the Little Colorado in 1990. The remaining fish ranged between 180-500 mm TL.

Although humpback chubs have not yet been recorded in a striped bass stomach, this large species has proven to be a major piscivore in Colorado River reservoirs, where it decimated threadfin shad (*Dorosoma petenense*) a very few years after introduction (Edwards 1974; McCall, 1980a; Jordan, 1981; Baker & Paulson, 1983; W.L. Minckley, 1985, 1991; Maddux et al., 1987; Gustavson et al., 1979).

The full impact of this efficient predator may not yet be realized in Grand Canyon National Park. Populations of bass might be maintained both by limited reproduction in the Little Colorado River and recruitment from lakes Mead and Powell. Striped bass could ultimately be limited by available food, as suggested by McCall (1980a), but in the interim could decimate fishes like the humpback chub whose refuge is the warm, saline Little Colorado River.

Striped bass incursions followed by many years the active introduction of trouts into the Grand Canyon. Trout stocking began in 1919, and in 1924 rainbow, brown, brook (*Salvelinus fontinalis*), and cutthroat trout (*O. clarki*) were present (McKee, 1930; Brooks, 1931; Williamson & Tyler, 1932; Carothers & Minckley, 1981; W.L. Minckley, 1991). By 1932, naturalized populations of rainbow and brown trouts existed in Bright Angel and Tapeats creeks (Williamson & Tyler, 1932).

A possible long-term effect of these introductions may be inferred from observations made on Bright Angel, Pipe, and Phantom creeks (C.O. Minckley, 1978c). During September-March of 1975-76, when rainbow trout spawned in those streams, native fishes were absent or secretive as none were collected. Native fishes spawned in late April-early June, after most adult trout had departed. At that time, the tributaries were dominated by natives. In summer, the tributaries served as nursery areas for all species, including trouts.

Apparent differential use of tributaries by native and introduced fishes may either result from seasonal exclusion of natives from tributaries by aggressive spawning activities and predation by trout, or from movement by native fish into preferred (warmer) winter temperatures of the Colorado River. Rainbow trout feed mostly on invertebrates (McAfee, 1966; Jordan, 1981; Maddux et al., 1987), but often become piscivorous when large (Crossman, 1959; McAfee, 1966; Sigler, 1983;

Beauchamp, 1990; Swartzman, G.L., and D.A. Beauchamp. 1990).

One humpback chub (est. 100 mm TL) was found in a rainbow trout caught in the Colorado River near its confluence with the Little Colorado River in the summer of 1990 (A. Leweka, USFWS, pers. comm.). This record is thought to under represent predation by trout on humpback chub as trout were rarely taken in the Little Colorado River proper. Rainbow trout predation has been implicated, in declines of the federally threatened Little Colorado spinedace, *Lepidomeda vittata* in smaller stream systems (Blinn & Runck, 1990, 1993). Further, large humpback chubs in the Colorado River could be displaced by trouts, which seem to occupy similar habitats in larger streams.

Prior to closure of Glen Canyon Dam, the Colorado River was unsuitable for trout due to high summer temperatures, sporadic flooding, and periodically elevated turbidity. Trouts were restricted to tributaries in warmer times, entered the Colorado in winter and spring, where populations were probably minuscule compared with those established after dam closure when the river was changed from turbid, abrasive, and warm; to clear and cold. Coincident with closure of Glen Canyon Dam in 1962, introductions of trout at Lee's Ferry were commenced by AGFD, resulting in ~1.7 million being stocked by 1986. Of these 62% were rainbow, 32% brook, and 6% cutthroat trout. Additionally, 20,000 coho salmon (*Oncorhynchus kisutch*) were stocked in 1971 (Carothers & Minckley, 1981; Maddux et al., 1987). Naturalized salmonids in the "tributary corridor" (RMS 85-140) probably responded to lowered water temperatures after dam closure by moving into the altered Colorado, where they suddenly could thrive year around. By autumn 1975, spawning runs of trout were using all accessible tributaries in Grand Canyon National Park (C.O. Minckley, 1978c).

A number of other non-native species may threaten chub populations. Fathead minnow (*Pimephales promelas)*, red shiner (*Cyprinella lutrensis*), green sunfish (*Lepomis cyanellus*), common carp (*Cyprinus carpio*), and others can affect recruitment by eating eggs and early life stages. In Lake Mohave, AZ-NV, carp and channel catfish patrol razorback sucker spawning beds and devour eggs as they are deposited (W.L. Minckley, et al., 1990). Jonez & Sumner (1954) also observed carp presumably feeding on eggs of bonytail in Lake Mohave. Carp concentrate in the lowermost 1.2 km of the Little Colorado River when humpback chubs are concentrated for spawning (pers. obs.), and could be feeding on eggs and fry. Humpback chubs are piscivorous also and undoubtedly consume conspecifics.

In addition to direct effects, salmonid, centrarchid, and ictalurid fishes are aggressive when compared with most cyprinids, especially when defending spawning sites, nests, or young (Carlander, 1969, 1975). Such behavior could force humpback chubs from preferred habitat and expose them to increased risk of predation or the vagaries of habitats for which they were not suited. If excluded from backwaters, for instance, small chubs could be forced from preferred microhabitats, which in Grand Canyon can be up to 10 C° warmer and higher in dissolved oxygen and contain more invertebrate foods than the Colorado River (Kubly, 1990; Maddux et al., 1987).

Impacts of Glen Canyon Dam

Despite the impact of introduced fishes which appeared and expanded their ranges in the early 1900's, native fishes remained in the pre-dam Colorado River long past that time. One key to survival was their adaptation to the big-river environment, particularly the warm water temperatures (>16 °C) necessary for reproduction. Colorado squawfish ran to the base of Grand Falls, Little Colorado River in 1936 (Miller, 1963a), and were recorded once in a creel census from the Lees Ferry area in 1962 (Stone, 1964). Several species also persisted briefly in the post-dam environment, with the last known squawfish taken by angling at Havasu Creek in 1972. Bonytail also lived above Lee's Ferry until 1971, as did humpback and roundtail chub. Even today, razorback suckers persist, as do a number of other native fishes, in GCNP (Miller, 1975a; Carothers & Minckley,1981; W.L. Minckley, 1991).

Before closure of Glen Canyon Dam, Colorado River water temperatures varied with ambient climatic temperatures and the influence of snowmelt (Kubly and Cole 1979). The river was low in discharge and variably cold in winter, warmed slowly because of high-volume snowmelt runoff in spring and early summer, reached its maximum temperature in late summer, and cooled in fall. With start of dam operations, the pattern was disrupted due to releases of cold hypolimnic water from Lake Powell. Colorado River water temperatures in summer were reduced from pre-dam highs and lows of 29.5^{0}C and 0^{0}C, respectively, to a constant post-dam temperature of ~10°C (Kubly & Cole, 1979).

The first time hypolimnetic temperatures prevailed throughout a year may have had a dramatic impact on native fishes, as their reproduction and survival of young is generally most successful between 16 and 18°C

(Hamman, 1981, 1982a, b; Bulkley & Pimentel 1985; Marsh, 1985). Both eggs and larvae would have been exposed to temperatures in the Colorado River which would slow or stop development and slow growth of those which hatched.

Neither eggs or larvae of humpback chub were collected in the 122 km reach from Glen Canyon Dam to the Little Colorado River during my studies, although ripe adults were found occasionally (C.O. Minckley, 1978a, b; 1979b, c;1980a, b; 1987; 1988a, b; 1989a, c; 1990a, b; Carothers & Minckley, 1981; Kaeding & Zimmerman, 1983). One small individual (37.5 mm SL) was taken above the Little Colorado (RM 44) in 1970 (Suttkus & Clemmer, 1977). Ripe adults were also taken at Shinumo Creek (RM 108.5; Suttkus & Clemmer, 1977). Apparent lack of recruitment above the Little Colorado River reflects the loss of fish once present in the Lee's Ferry reach, where they were relatively common until 1971 (Stone & Bruce 1971) and after which they disappeared (Stone, 1972; Bancroft & Sylvester, 1978; Bancroft 1979; McCall, 1980b, 1981; Maddux et al., 1987; Kubly, 1990).

This pattern of absence below a major hydroelectric dam is similar to that observed below Flaming Gorge Reservoir in UT-WY (Varley et al., 1971). Collections shortly before impoundment of that reservoir (and prior to rotenone application; Holden, 1991) included humpback chubs, but none has been taken since in the 110 km from the dam to confluence of the Yampa River. Although the fish eradication project reduced native populations, many believe that cold water temperatures precluded subsequent recruitment by suppressing reproduction by fish that survived or reinvaded the area, thus exerting greater impact than the eradication efforts (Holden, 1968, 1970, 1991; Holden & Stalnaker, 1970).

This was supported in 1981 when intake elevations of the penstocks in Flaming Gorge Reservoir were raised, thereby increasing temperatures of water released. This, combined with ameliorating effects of warm inflows from Yampa River, allowed the Green River to return to pre-dam temperatures below its confluence with the Yampa. Colorado River squawfish responded to that change and successfully spawned for the first time since 1968, although humpback chub apparently did not (Holden & Crist, 1981).

An additional impact may be realized when cold water temperature is combined with fluctuating water levels. This is well illustrated in the lower Paria River near Lee's Ferry. The lower 100 m of the Paria is ~30 m wide, with a mud-sand substrate. Under baseflows and low Colorado River water levels, this area is a mud flat with a small channel 5.0 cm deep and 1.0 m wide. When impounded by high discharges in the Colorado River, depth and width vary but may reach 3.0 and 100 m, respectively. Native fishes (e.g., flannelmouth suckers) spawn here in an environment that, over a 24 hour period is alternatively dry and then contains water. Any eggs deposited in this reach would be desicated when the area was dewatered. When water levels remain high due to high Colorado River discharge, eggs are exposed to lower-than-optimum temperatures for development. This regime may be repeated daily throughout Grand Canyon National Park, where the lower reaches of many tributaries are alternatively exposed to drying and flooding.

Life History Observations, Lower Basin

Movement

In the lower basin, chub movements were studied using external Floy, Carlin, radio and internally placed PIT tags (C.O. Minckley, 1988a, 1989b, 1990a; Hendrickson & Kubly, 1990). Radiotagging studies have also been initiated (Valdez, 1991), but are not reviewed here. Humpback chubs were first Carlin tagged in Grand Canyon in 1978; 223 were tagged, none was recovered (Carothers and Minckley, 1981). Research continued in 1980-81 (Kaeding & Zimmerman, 1983; Miller et al., 1982d-f), when 675 chubs were tagged in the lower 16 km of the Little Colorado and 45 in the Colorado River between Lee's Ferry and Diamond Creek. Thirty from the Little Colorado River and two from the mainstream were later recaptured. Recaptured fish tagged in 1980-81 exhibited movement of up to 17.1 km. Thirteen of 32 were recaptured within 0.3 km of point of release, the remaining 19 had moved an average of 3.8 km.

Arizona Game and Fish Department initiated a Grand Canyon study on chub movements in 1984. Of 1009 fish tagged in the Little Colorado River, 41 were recaptured by 1989. Thirty-six were retaken within 0.2 km of their tagging site, and the greatest movement was 10 km. Six tagged in the Colorado River and recaptured in the Little Colorado River had moved 0.2-10.0 km (average, 0.5 km; Maddux et al., 1987).

Tagging studies by AGFD were continued in May of 1987-89 and April-May 1990 (C.O. Minckley, 1988, 1989, 1990). In 1987, 562 chubs were tagged, 542 (96%) within 0.1 km of the Little Colorado confluence. The remaining 20 were tagged 5.8 km upstream in the Little Colorado. A total of 67 fish were recaptured within 0.6 km of their original capture site. The greatest movement observed was 0.6 km (C.O. Minckley, 1988a).

In 1988, 723 chubs were tagged at the confluence;

17% (120 fish) were recaptured in the lowermost 0.3 km of the Little Colorado. Maximum upstream movement was 9.3 km and maximum downstream movement was 2.9 for two fish. Several fish were also recaptured that had been tagged in previous years. All were recaptured in the Little Colorado River and had been originally tagged there, with the exception of one which was from the Colorado River (C.O. Minckley, 1989a).

A total of 771 chubs was tagged in 1989, of these, 11 percent (n=85) were recaptured. All were retaken in the vicinity of their original capture with the exception of three. One of these moved 2.4 km in 5 days while the remainin two were collected 10 km downstream.

In 1990, five hundred humpback chubs were tagged. Sixty-five (15%) were recaptured. Movement by recaptured fish was limited to <600 m with exception of two individuals who moved upstream 2.2 and 3.7 km respectively.

All movement data were then combined and summarized based on all fish tagged from 1978 through 1990 (Carothers & Minckley, 1981; Kaeding & Zimmerman, 1983; Maddux et al., 1987; C.O. Minckley, 1988a, 1989a 1990a. Data on multiple recaptures of individuals (e.g., individuals recaptured two or more times) illustrate movement patterns as well as considerable fidelity of individual humpback chubs to the Little Colorado River.

Between 1987 and 1990, 358 individual chubs tagged during the same years were recaptured more than once. Mean distance moved between recaptures was 0.43 km (range 0.0-8.7 km). Only seven fish moved between the Little Colorado River and Colorado River. Of these, six were tagged in the Colorado River between 4.8 km above the confluence to 11.3 km below. Five were retaken within 0.1 km of the mouth of the Little Colorado. One fish tagged in a Colorado River backwater 11.3 km downstream of the confluence on 22 May 1987 and recaptured 0.6 km upstream in the Little Colorado River on 24 May 1987 having moved ~12 km in two days. The remaining fish was tagged at the confluence and taken <0.5 km upstream in the Colorado River shortly afterward (Kubly 1990).

Age and Growth

Estimations of age and growth by length-frequency methods was first applied to humpback chub in 1977 (C.O. Minckley, 1977c); standard aging techniques were not used to verify age of fish in the various size classes due to their endangered status. Size classes predicted to represent age classes I through III and older were present. Size classes used were: class I,

<120 mm; II, 121-150mm; III, 151-220; IV, >220 mm, older fish.

Length-frequency histograms for monthly collections at the confluence and the Salt Trail are summarized in figures 6 and 7. At the confluence smaller numbers of size class I humpback chubs were collected in 1987-1988 than during 1989-1990, with collections generally dominated by fishes in size class IV or larger. At the Salt Trail few size class I fish were taken, with samples being dominated by size classes II-III during both years of record. Larger fish (size class IV) were also well represented.

In the lower basin, growth rates of humpback chub from presumed annular rings on opercles were first calculated by Usher (1981). Age-class 0 chubs varied from 89.5 to 92.2 mm TL at the first annulus; by January-February 1978, fish spawned in Spring 1977 had achieved up to 75 mm TL; year-class 0 fish spawned in 1978 approached 80 mm TL by September-October of that year. Mean annual growth increment for year-class II was 39.7 mm, and mean annual growth in years III-IV varied between 46.6 and 30.4 mm. Fish in their ninth year of life exhibited an estimated mean annual growth increment of 18.6mm (Usher, 1981). Four age-classes,

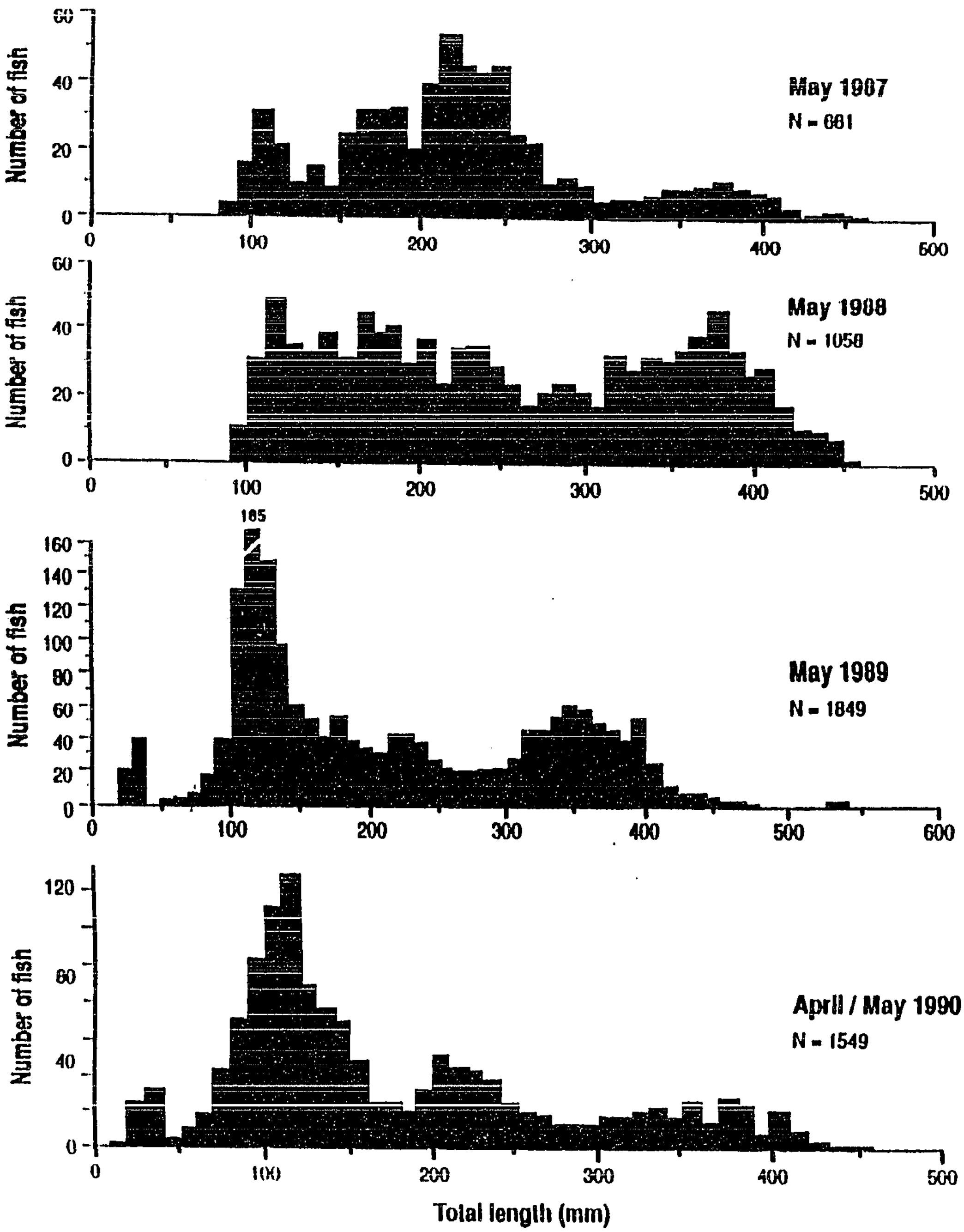


Figure 6. Length-frequency histograms for all confluence collections made during May 1987 and April-May 1990.

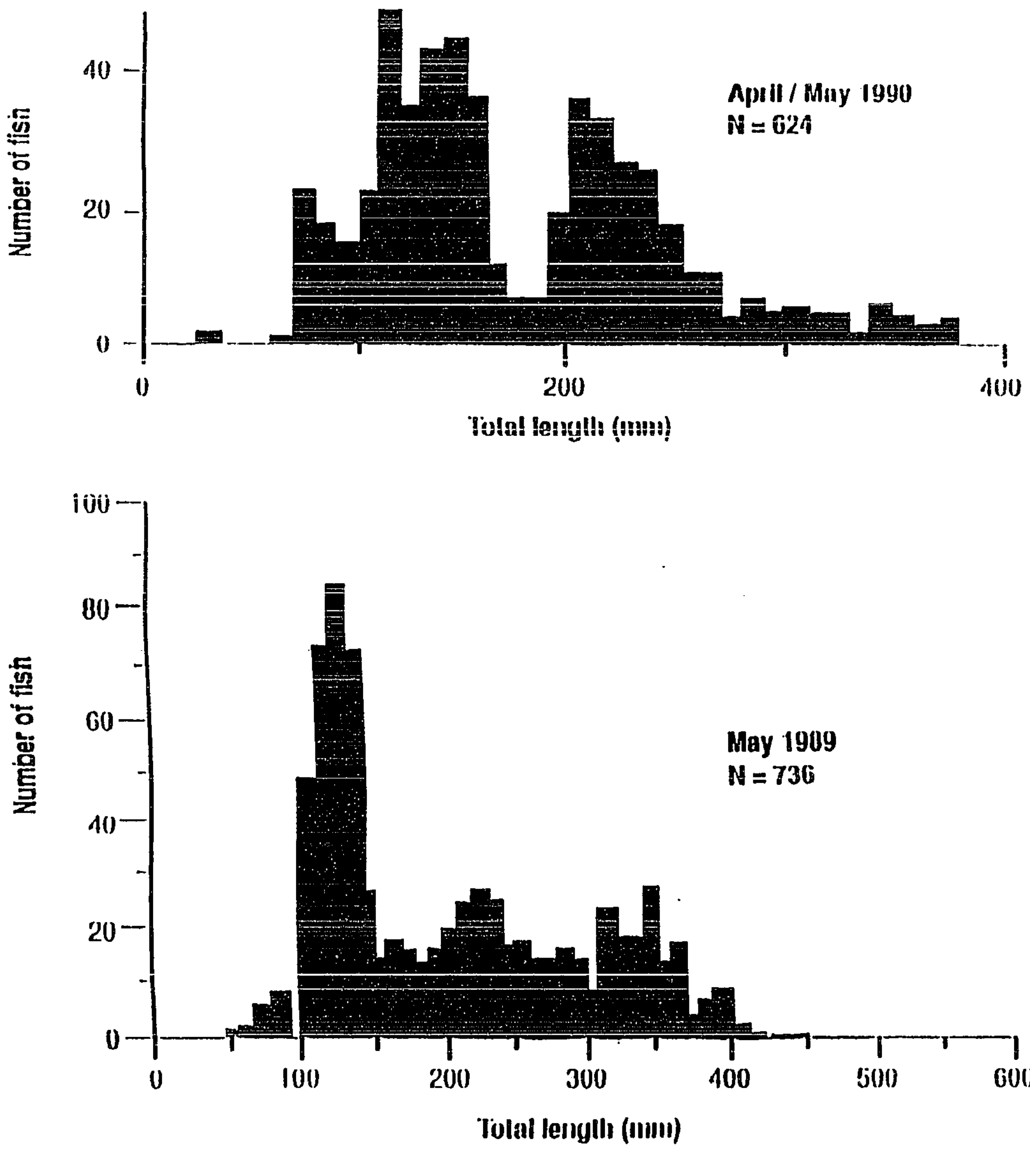


Figure 7. Length-frequency histograms for all salt trail collections made during May 1989 and April-May 1990.

IV, V, VI, and IX, were represented in these older fish. The largest chub was nine years old and measured 380 mm TL. As the sample size was small (n=10) representing one fish from 1972 and 9 unintentional mortalities taken between 1978-1980, caution should be applied when drawing conclusions from these results. Kaeding and Zimmerman (1983) found annuli on scales and used them as indicators of age in humpback chubs from the Grand Canyon region. Observed annuli correlated with length-frequency distributions for fish up to 3 years old and 250-300 mm TL. New annuli were observed on a few scales collected in February, but were present on most scales in May. The first annulus formed when fish reached a length of ~100 mm at a year of age. The greatest increase in length was during the first three years of life, to TL of 250-300 mm.

Age-and-growth characteristics of humpback chub were similar from the Little Colorado River and the Little Colorado-Colorado confluence (Kaeding & Zimmerman, 1983). New annuli were evident on many scales in April-May 1981, and crowded circuli were evident at scale margins in October-November 1980 and 1981. They nonetheless thought age estimates of chubs from the Colorado River were unreliable because some formed annuli near the end of their first year of life whereas others apparently did not. Supporting evidence was from fish in a well-defined 38-mm to 107-mm size-class collected in April-May. Kaeding & Zimmerman (1983) considered all the fish yearlings, too large to be age class 0 on the dates of collection. Poor growth in Colorado River chubs was attributed to consistently low water temperatures.

Studies of growth using otoliths are ongoing and age estimates to date are highly preliminary (D. A. Hendrickson, University of Texas, pers. comm.). Available data suggest, however, more old individuals in the population than expected. Daily growth increments are clearly discernible in lapilli (an inner ear bone) of younger fish (to at least three years), and growing season for the few specimens analyzed thus far is 180-190 days. Age 1+ and 2+ year-old chubs captured on the 17 and 24 May 1989 had been growing for 78 and 100 consecutive days, respectively. Lengths of previous growing seasons for these fish were 180 (1+ fish), and ~185 (2+ fish) days. Correlation between TL and age appeared weak, with extensive variation in body size at a given age.

Observations on actual growth were made based on tag-recapture information collected in 1985 and 1990 (Maddux et al., 1987; C.O. Minckley, 1988a, 1989a, 1990a). Fish were separated into six size-groups varying from <150 mm to >400 mm TL for ease of manipulation; categories were not intended to approximate age classes.

Between 1985 and 1990, 358 adult humpback chubs were caught more than once. Between-year growth analysis included 73 fish. Mean TL at capture was 301 mm (151 to 468) and mean length at recapture was 320 mm (182 to 469). Average growth was thus 19 mm (0.0 to 143 mm). Average and annual growth rates were 0.037 mm per day, 1.1 mm per month, and 13.5 mm per year. On a size-category basis (73 fish), mean increase in TL varied from 23 mm (group I) to 2.5 mm (group VI). The first three size-groups exhibited the greatest increases in size both daily and annually (Fig. 8). Larger (presumably older) fish grew more slowly.

Reproduction

Information on reproduction by Little Colorado River humpback chubs includes data on sexual dimorphism, secondary sexual characters (breeding colors, tubercles), size of ova and GSI, sex ratios, numbers of ripe fish at various times of year, and presence-absence data for fry and YOY. Standard lengths (SL) of fry (<50 mm) may also be used to suggest when spawning has occurred by back-calculation to presumptive hatching dates (Muth, 1990). Artificial propagation techniques have also been developed.

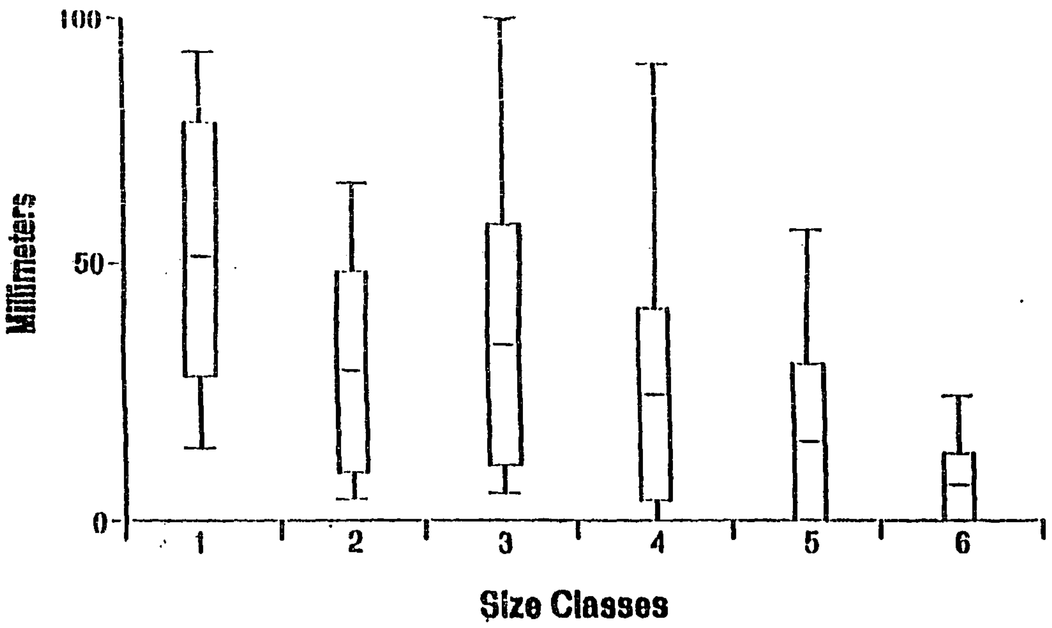


Figure 8. Illustration of growth per day (mm) in six size classes of humpback chub collected from the Little Colorado River between 1987-1990.

it projects ventrally, its tip visible (Suttkus & Clemmer, 1977). Using these structural differences, fish >150 mm TL may be reliably sexed by inverting the fish and pressing on the ventral surface immediately in front of the vent. In males, the urogenital paipllae moves to project forward. In females, there is little or no movement of the structure (C.O. Minckley, original data). Documentation of this method was confirmed by ripe individuals which expressed gametes when examined. Breeding colors in humpback chub were first described from preserved specimens (Suttkus & Clemmer, 1977), which exhibited orange coloration on their vents and on the bases of paired fins. Subsequent observations by C.O. Minckley (1988a) of living chubs revealed male fish red or reddened ventro-laterally from the lateral line along the entire length of the body, excluding the milk-white belly. Reddening was intense and most concentrated at the fin bases, from which it diffused outward toward the fin tips. Observations on breeding colors of large numbers of chubs revealed marked variation from orange to red-orange to crimson red.

In April 1981, 79% (15) of males 200-250 mm TL and 74% (35) of those 250-300 mm TL from the Little Colorado River expressed milt. The smallest ripe male was 205 mm TL (Kaeding & Zimmerman, 1983). GSI of both sexes fluctuated similarly, increasing or decreasing at the same time of year. Mean ova diameters also decreased as mean GSI decreased. GSI values increased markedly in both sexes between December and April, followed by a sharp decline in April-May, indicating that spawning had occurred (Kaeding & Zimmerman, 1983). The small numbers of ripe or gravid females studied (<10) added little to knowledge of when most spawning occurred. The main reproductive period may also have been missed, explaining the small numbers of ripe females.

In the lower basin, sixteen mature fish were sacrificed in 1983 (Kaeding & Zimmerman 1983) to determine GSI values. In late June, two females had high GSI (20%), while the third was considerably lower (5.0%) and appeared post-reproductive. Based on 10 individuals, female GSI's continued to decline over the following three weeks. The pattern in males >250 mm TL was essentially identical.

Relatively few ripe females at a given time, large variation in TL of year class 0, and possibly extended spawning periods (see below) may indicate production of several clutches of eggs by a given female. Such patterns are common in marine fishes and have also been documented in cyprinids and percids (Gale 1986; Gale & Buynak, 1978; Gale & Gale, 1979; Heins & Rabito, 1986;

Gale, 1986). Repeated spawning may allow increased numbers of eggs, allow spawning to be delayed until optimal conditions exist, allow repeated use of spawning sites, and possibly result in less competition among larvae and thereby reduce mortality (Heins & Rabito 1986). Spawning by several members of the Genus *Gila* has been reported in riffle-pool or pool habitats over gravel or sandy-rocky substrates (Graham, 1961; Vanicek & Kramer, 1967; W.L. Minckley, 1973; Neve, 1976). In roundtail chub and bonytail several males escort or swarm around a female while presumably fertilizing eggs (Jonez & Summer, 1954; Neve, 1976). Such "mobbing" behavior is suggested in humpback chub by several observations of large numbers of ripe males (>50) captured in a single net containing one ripe female (C.O. Minckley, original data). Preferred spawning substrate is similarly unknown, but the eggs are adhesive and the fish have spawned in areas of current in hatchery raceways (Hamman, 1982a-b), suggesting they may reproduce in areas with current in the wild. Larvae would presumably remain in the substrate or move to lower-velocity areas shortly after hatching.

The best indicator of successful spawning is the presence of fish <25 mm TL. Using this criterion, spawning times in the Little Colorado River have been proposed to include June-July (Suttkus & Clemmer, 1977), March-June (C.O. Minckley et al., 1980; Carothers & Minckley, 1981) and April-May (Kaeding & Zimmerman, 1983). In an attempt to better estimate spawning times, hatching dates were computed using a formula based on laboratory-spawned fish and developed first for Colorado squawfish and later for humpback chubs (Haynes & Muth, 1982, 1983, 1984, 1985; Haynes et al., 1982, 1983a, b; 1985; Muth, 1990). Spawning dates precede hatching dates by 5 to 7 days at 14-17 C° and by 7 to 14 days at <12 C° (Hammon, 1981; Marsh, 1985). Estimation of hatching times are presumed to be 1-2 weeks shorter in the warm Little Colorado River than the cold Colorado River. Also, computed dates are based on when collections were made and not the earliest or latest date of spawning in a given year, e.g., the apparent lack of an extended spawning season in 1987 reflects absence of small fish in collections, not necessarily the absence of small fish. Computed hatching dates are presented in Table 3. Based on these calculations, humpback chubs reproduced at varying times over a twelve year period in the Little Colorado River. Estimated times were from early from early February into October (Fig. 9), longer than apparent suggested times of spawning (March through June), based on adult reproductive characters.

Table 3.
Calculated hatching dates for the humpback chub in the Little Colorado River. Dates correspond to Figure 10.

Year	Calculated Hatching Dates	Year	Calculated Hatching Dates
1978:	A: April 25-30	1985	A: April 15-30
	B: May 1-31		B: May 1-29
	C: June 1-3		C: June 1-3
	D: July 27-4 August		
		1986	A: March 27
1979	A: May 7-25		B: April 7-19
	B: August 10-13		
		1987	A: March 31
1981	A: March 28-31		B: April 1-8
	B: May 2-5		
	C: June 1-29	1989	A: March 3-31
	D: July 29-31		B: April 1-30
	E: August 1-15		C: May 1-8
1984	A: February 8		
	B: April 19-25		
	C: May 1-2		
	D: June 25		

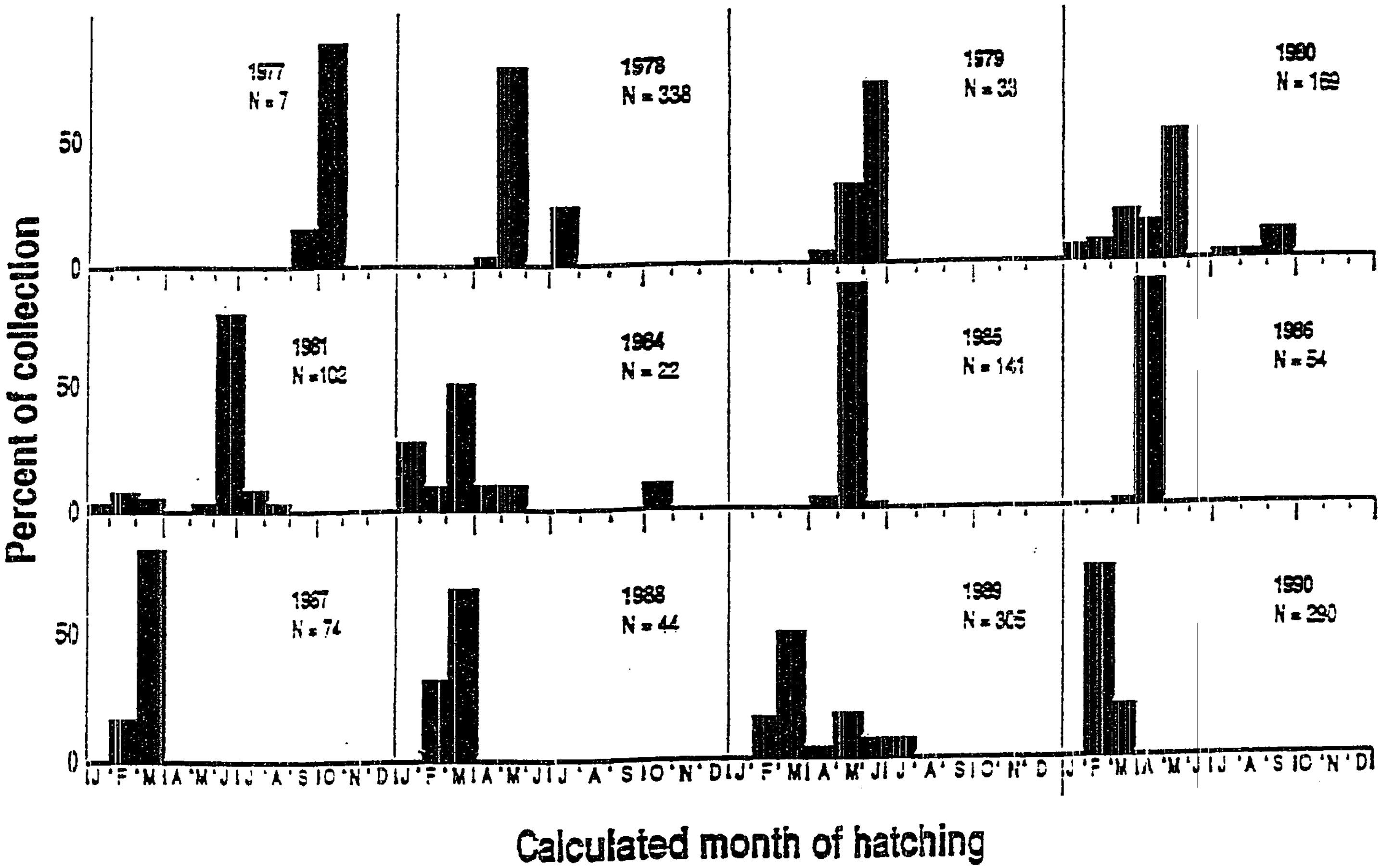


Figure 9. Calculated hatching dates for humpback chubs collected from the Little Colorado River confluence area over a twelve year period.

The most important cues for initiation of spawning are probably water temperatures and photoperiod. When the Little Colorado River is not in flood, Blue Springs provides a warm, constant-temperature source (21 ^{0}C) influenced downstream by solar radiation. In years of limited runoff from snowmelt or other sources, spawning may be early because of warm water from Blue Springs. In years of high or sustained flooding, spawning may be delayed due to colder water temperatures, high turbidities, and increased turbulence. In 1987, the Little Colorado flooded and spawning appeared to occur in March. In 1990, no flooding occurred and spawning was likely in early February.

Timing of peak discharge, suggested to influence spawning by upper basin humpback chubs, does not appear to be a factor in the Little Colorado River. Computed hatching dates were plotted at a variety of discharges; and no relationships between hatching dates and discharges were evident (Fig. 10). Success of a year class in the Little Colorado River during a year of no flooding, may nonetheless be more successful than one appearing during extended flooding. Water temperatures in the Little Colorado River during the Spring spring 1987-90 varied between 16 and 21^{0}C, reaching 23-25°C in May. In 1987 and 1988, the river experienced moderate but extended flooding, discharging

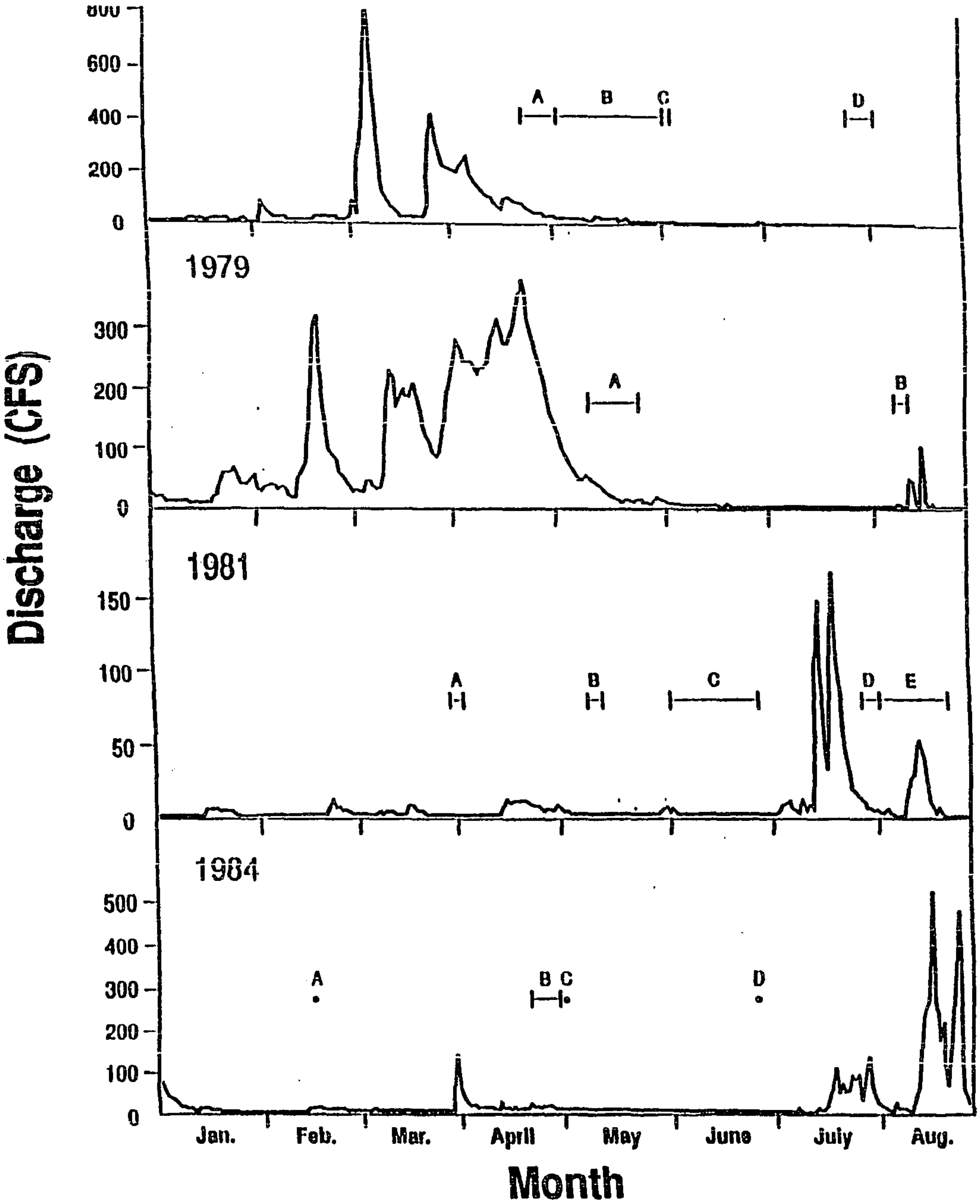
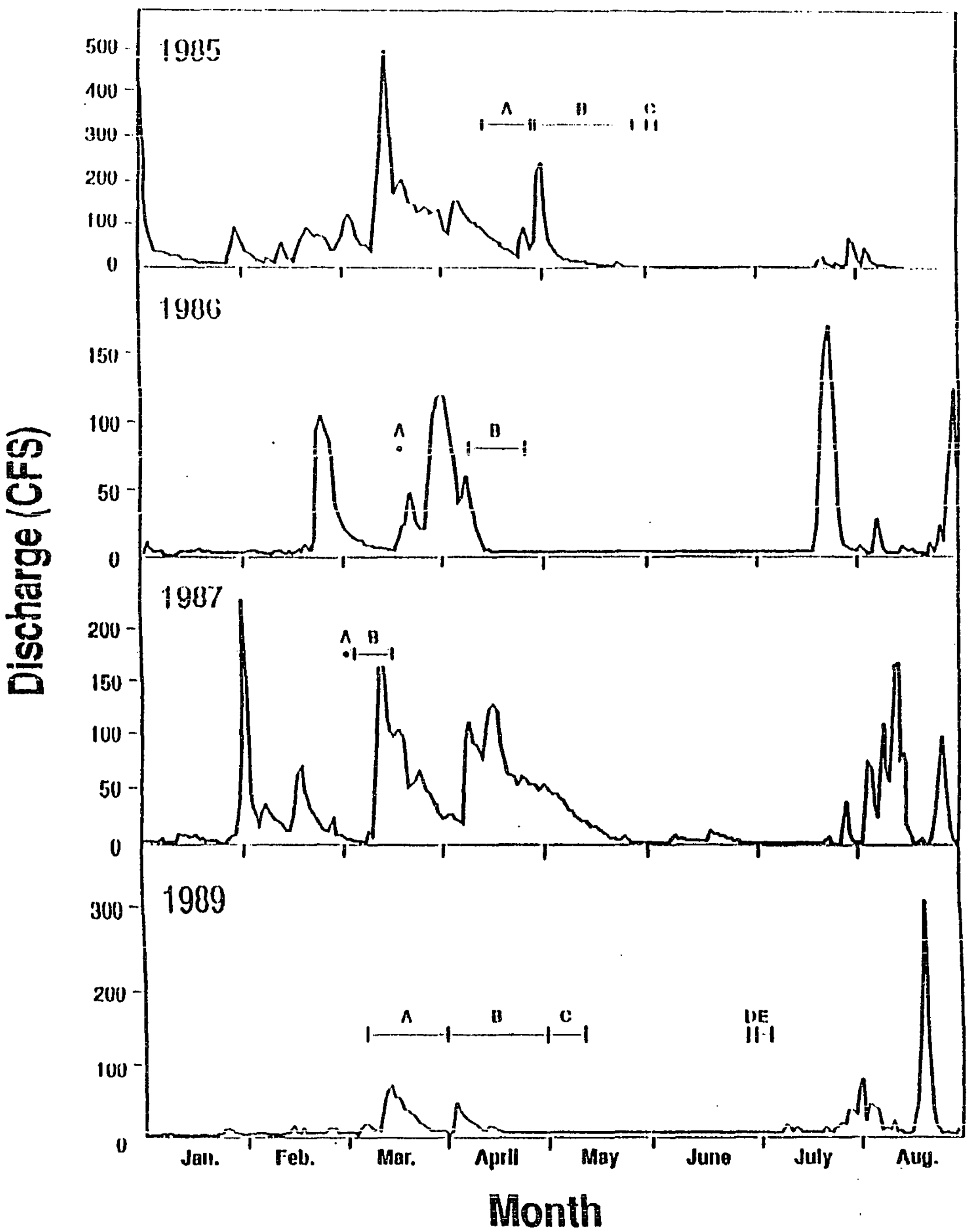


Figure 10. Calculated hatching dates for humpback chubs collected from the Little Colorado River plotted with the hydrograph for the year of collection.



(Figure 10. continued).

11.33 to 18.41 m^3/s, respectively (baseflow is 6.26 m3/s; Johnson & Sanderson, 1968). In 1989-90 the river remained at baseflow except for two brief spates in 1990; water temperatures exceeded 21^{0}C essentially every afternoon.

In absence of extreme flows, the Little Colorado represents a productive, nursery area for small fishes, with warm temperatures and abundant foods. This may have been the case in July 1978, when hundreds of fish <100 mm in TL were encountered near Big Canyon, 6 miles upstream from the confluence (Carothers Minckley, 1981). In years with flooding, the numbers of smaller fish taken was much lower suggesting that there were fewer smaller fish in the population at that time (C.O. Minckley 1988a, 1989a 1990a).

Early life-history stages of humpback chub have been collected far more infrequently from the Colorado River than the Little Colorado, presumably because cold water temperatures preclude most successful reproduction. Two possible and not mutually exclusive explanations for larvae and juveniles that have been taken in this environment are spawning in tributaries after which young drift or move to the river, or reproduction in the river itself (Suttkus & Clemmer, 1976, 1977, 1979; C.O. Minckley et al., 1980; Carothers & Minckley, 1981; Maddux et al., 1987; Kubly, 1990).

Mainstream reproduction is suggested by the humpback chubs examined by Suttkus & Clemmer (1977) all appeared to have fully developed testes, but ovum diameters varied from small and granular (1.0-1.2 mm) to larger (1.4-2.2 mm). Additionally, in April 1978 two tuberculate, ripe males and a gravid female were taken at Tiger Wash (RM 27; C.O. Minckley, 19878a, b). A few days later another ripe male was taken at RM 70. Furthermore another male with strong nuptial tubercles and running milt was collected in a Colorado River backwater in May 1981 (Kaeding & Zimmerman, 1983). GSI of chubs from the Colorado River increased in spring as in the Little Colorado (Kaeding & Zimmerman, 1983). These collections of reproductive individuals suggest that spawning is possible in mainstream chub. A YOY chub (37.5 mm SL) was taken above the Little Colorado in 1970 at RM 44 (Suttkus & Clemmer 1976) and must have represented mainstream reproduction, as no tributaries are near that locale. No successful reproduction or recruitment upstream of the Little Colorado was detected between that collection and 1990.

Laboratory studies examining the impact of lower water temperatures on eggs and larvae of humpback chub, suggest that hatching and successful larval development at current Colorado River temperatures are unlikely (Bulkley et al., 1981; Hamman, 1982; Kaeding &

Zimmerman, 1983; Marsh, 1985; Valdez et al., 1991).

Effects of low incubation temperatures on hatching success of humpback chubs were experimentally examined by Marsh (1985) to evaluate potential impacts of cold hypolimnetireservoir releases on reproductive success. Eggs were spawned and fertilized at 18°C and embryos incubated at 5, 10, 15, 20, 25, and 30°C. Total mortality of embryos occurred in 12 to 96 hours at 5, 10, and 30°C. Survival and percentage hatch were highest at 15 and 25, but spinal or other anomalies were more frequent at 15 and 25°C than at 20°C. Development rates were similar at all temperatures. Optimal temperatures for development and hatching near 20 °C; reproduction may thus be limited in the wild by low water temperatures, although successful hatching is not precluded (Marsh, 1985).

Acute temperature preferendum was measured by Miller et al., (1982) for humpback chubs acclimated to 14, 20, and 26°C. The temperature preferendum is defined as that temperature toward which a fish will remain regardless of previous thermal history and at which acclimation and preferred temperature are equal (Fry, 1947). It is generally assumed to be an innate and species-specific measure of thermal behavior. Humpback chubs acclimated at 20°C selected higher temperatures than did those acclimated at 14°C. Those acclimated at 26°C selected temperatures lower than those of 20°C chubs and much lower than would be predicted based on other fishes. Differences in temperatures selected acclimated to the three temperatures were not, however, statistically significant (Miller et al., 1982b, c).

Small numbers of chubs (<29 mm SL) were taken in the Colorado River over a eight year period (Suttkus & Clemmer 1976, 1977; Suttkus et al., 1976, Maddux et al., 1987; Kubly 1990). Additionally, collections of fish <50 mm SL by AGFD suggest that spawning in the Colorado River may still occur.

Figures 11-13 present computed hatching dates for fish taken by AGFD from the Colorado River over a ten year period (1980-1990). The data are separated into three reaches. Data are not presented for Reach I (RM 62-83) initially, due to the small number of fish taken (n=11). Based on these data, chubs hatched as early as February (1981) and as late as October (1984) in reach II (RM 84-160). Hatching during May occurred during seven of the eight years and also during June and August during three years (Fig. 11). In Reach III (> RM 160) hatching occurred in March, April or May and between May through August for the largest sample of fish (N = 44; Fig 12) several miles below inflow of any

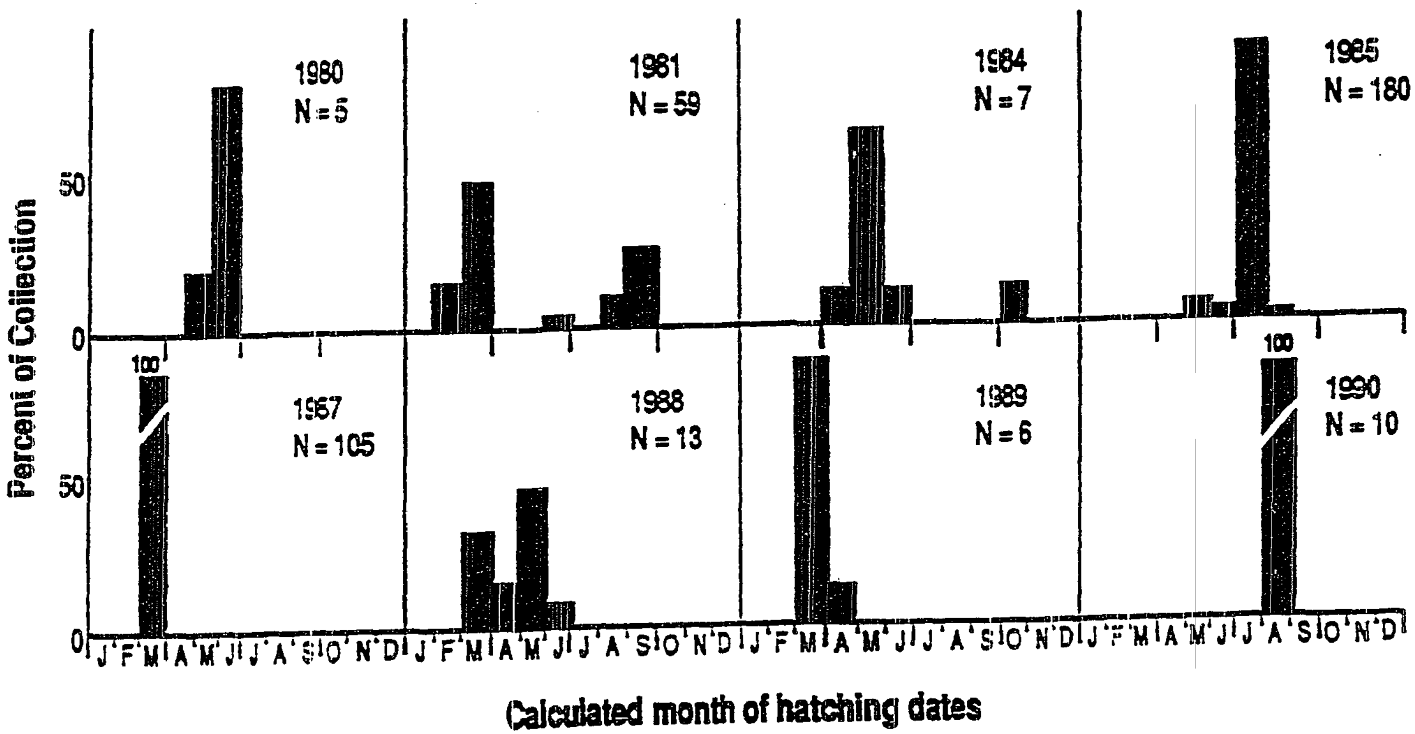


Figure 11. Calculated hatching dates for humpbck chubs collected from Region II (RM 84-160) of the Colorado River during a eight year period.

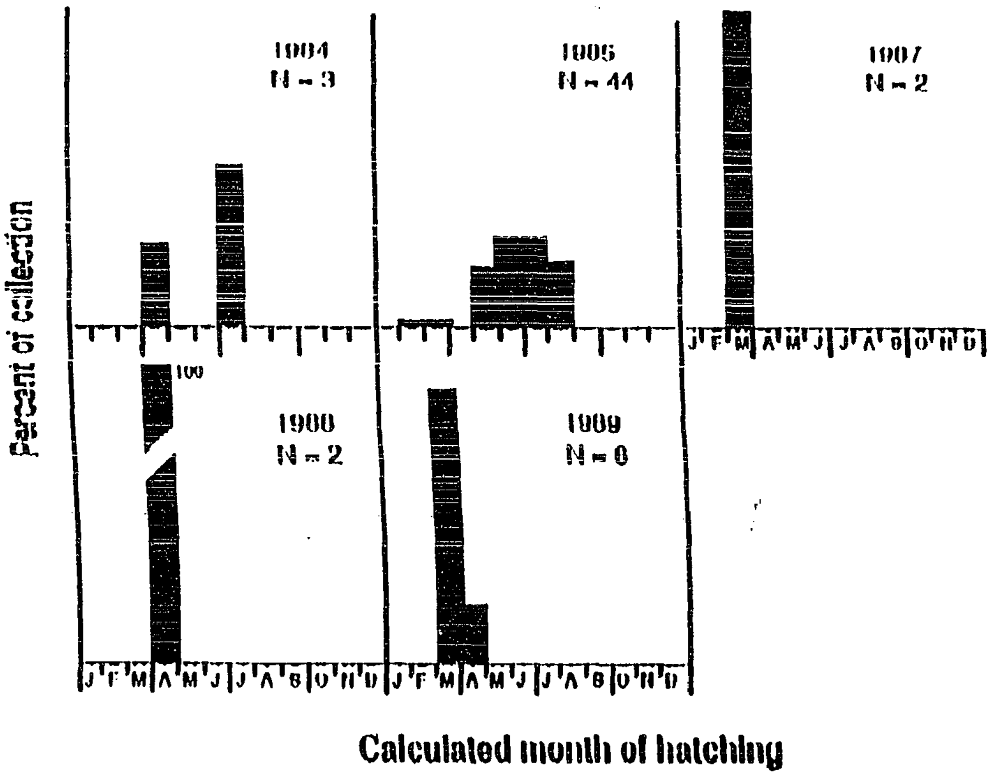


Figure 12. Calculated hatching dates for humpback chubs collected from Region III (RM 84-160) of the Colorado River during a five year period.

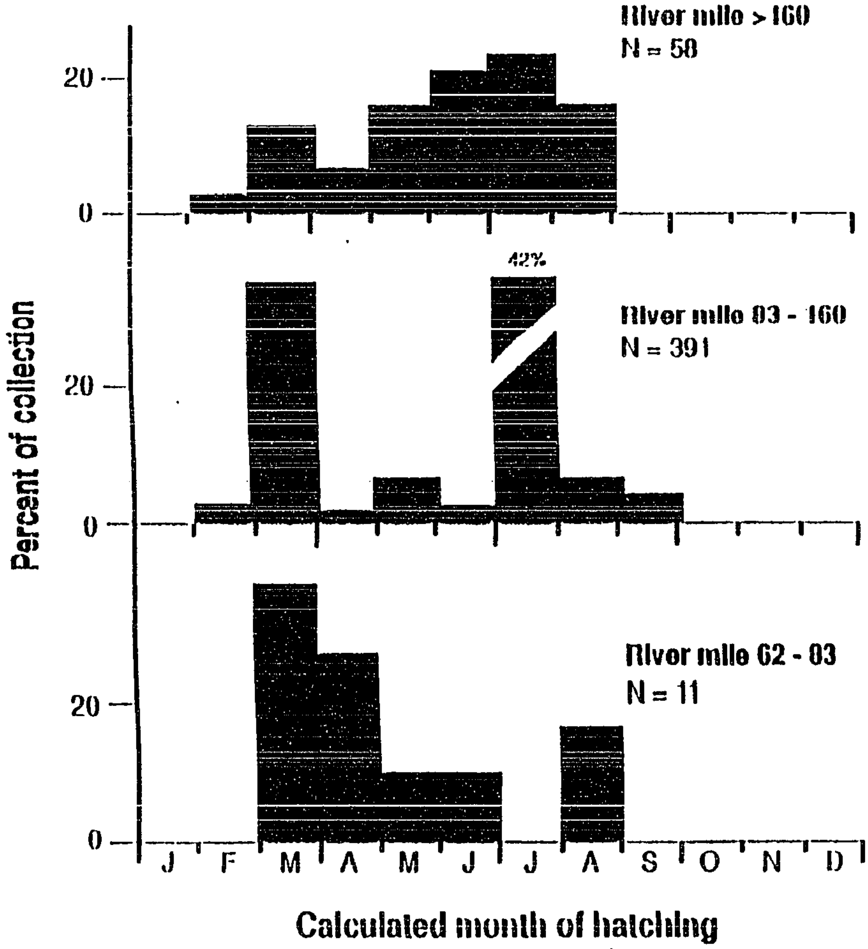


Figure 13. Combined calculated hatching dates for humpback chub taken from three regions of the Colorado River over a ten year period.

tributary. Below Reach II and particularly in Reach III, Grand Canyon is wider than upstream. Shallow places exist along sloping beaches where water is warmed by insolation to temperatures as high as 23 C° (Maddux et al., 1987). Many suggested hatching dates were in June or later, the warmest time of year in lower Grand Canyon. Numbers of YOY caught have not been large, but their presence suggests limited recruitment far removed from major upstream tributaries.

When combining the various years within the river reaches, hatching occurred from May - August in Reach I; February - September in Reach II and from February - August in Reach III. In reaches II and III more hatching occurred during the summer than in the spring (Fig. 14). Further combining and comparing all samples from the respective systems (Fig. 14), hatching occurred from January through October and February into December respectively. Hatching occurred most frequently in March and May, and March and July in the Little Colorado and Colorado rivers, respectively.

Artificial Propagation.

Culture of humpback chubs was first accomplished in 1981 by personnel at Willow Beach National Fish Hatchery, AZ. Their program was designed to determine

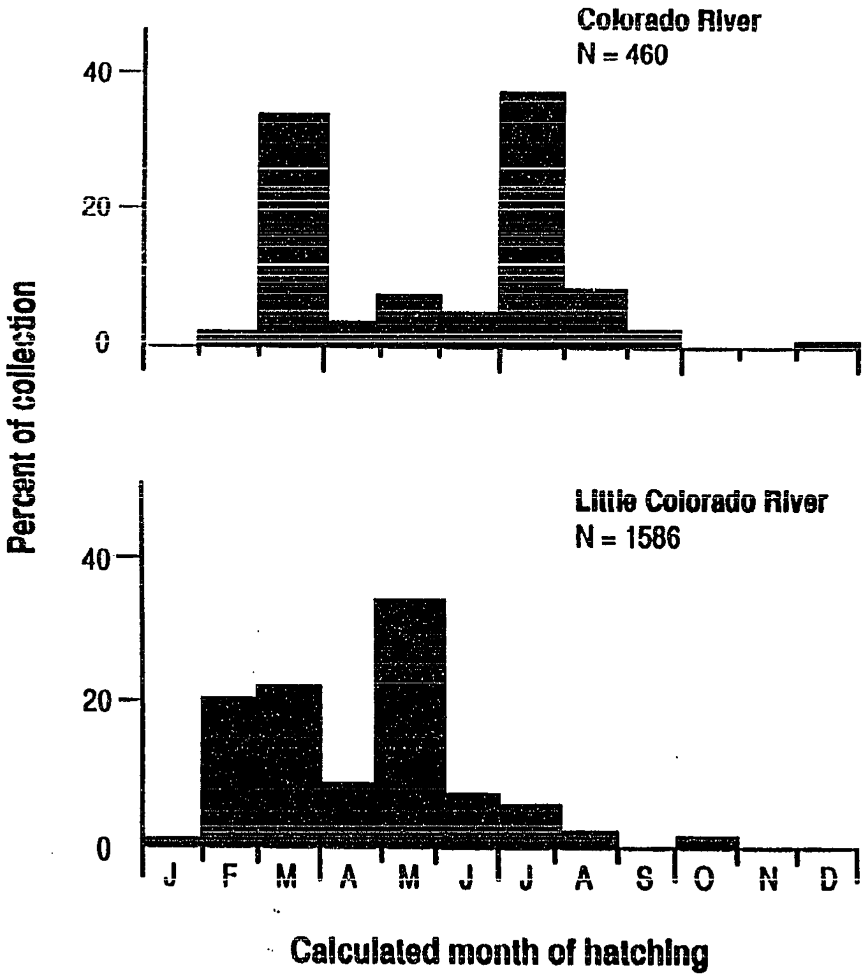


Figure 14. Combined calculated hatching dates for humpback chub taken from the Little Colorado River over a twelve year period and the Colorado River over a ten year period.

spawning habits and early life-history stages. The first objective was to induce captive adults to spawn in a hatchery situation and rear progeny for laboratory purposes. The second objective was to produce known hybrids between species of *Gila* of the Colorado River basin for future taxonomic assessment (Miller et al., 1982). The following account of procedures used and results are from Hamman (1981, 1982).

Broodstock consisted of 14 adults from Little Colorado River and 16 from the Colorado River at Black Rocks. Little Colorado River fish were captured by various workers on 17 May 1978, 17 October 1979, and 13 June 1980 near the Little Colorado-Colorado confluence. Black Rocks fish were caught 5 November 1979 near Grand Junction, CO, by Colorado River Fishery Project personnel.

Semi-natural and induced spawning was accomplished using using fish from the Little Colorado River (9 females, 5 males). The fish were placed in two concrete raceways connected to allow water recirculation, obtain warmer water, and produce current. Two layers of spawning substrate were placed in the upper 10 m of one raceway. A bottom layer consisted of boulders (30-40 cm diameter) and a top layer was cobble (4-10 cm). Water depth over the substrate varied from 10-76 cm. Spawning was induced by intraperitoneal injections of 4.0 mg acetone-dried common carp pituitary per kg of chub body weight (Hamman, 1981). Adults were allowed to spawn on the substrate and removed when eggs began to hatch. Actual spawning was not observed due to turbidity caused by a plankton bloom (R. Hamman, USFWS, pers. comm.).

Males allowed to semi-naturally spawn exhibited orange to red-orange breeding colors on their ventral surfaces and paired fins. Spawning females were light orange on the sides and at the bases of the paired fins and anal fin. Females were larger than males, and both sexes had fine tubercles on the head, opercles, and paired fins. Males produced milt without injection; however, no eggs could be expressed from females until after hormone injection.

Spawning occurred within 24 hours of a first injection. Eggs were deposited over an area of 1.0 by 2.4 m in water depths of 35 to 45 cm; water temperatures were 16 to 20^{0}C. An estimated 30,000 eggs were produced by nine females. Egg varied from 2.6 to 2.9 mm in diameter (average. 2.8). They adhered to the cobble and were allowed to hatch in situ, a process that was completed 168 hours (7 days) after fertilization. Newly hatched fry averaged 7.1 mm TL. Fry (estimated at 23,490) were cultured in the raceways in which they were spawned.

Fish artificially spawned were injected and placed in a holding tank at 21-22 C° until they could be manually stripped, usually ~20 hours after injection. When eggs could be expressed, a female was stripped and her entire complement of eggs was fertilized with milt from one male. After 50 minutes of water hardening they were poured on screen trays, covered with hardware cloth, and placed in aluminum troughs slanted at a 30-degree angle against incoming water. Egg diameters after water hardening varied from 2.6 to 2.8 mm (2.7 mm), with 51 to 58 eggs per milliliter (average, 55). Total fecundity of eight females was 20,185 eggs (average, 2,523 per female) or 5,262 eggs/kg body weight. Eggs were placed in temperatures of 21-22°C, 16-17°C, and 12-13°C. Hatching began at 102, 167, and 340 hours, and was completed at 146, 266, and 475 hours, respectively. Fry averaged 6.9 mm TL at hatching, and were moved from trays to raceways for culture 72-168 hrs after hatching.

Fry were active and fed near the surface during the first two weeks in raceways. Schooling behavior was observed from the onset of culture. As zooplankton numbers in raceways declined, dry commercial trout starter was fed 4 or 5 times a day. On day 56 after hatching, fry spawned semi-naturally had a mean TL of 36.9 mm; artificially spawned fish were 47.5 mm TL.

The fish had increased 5- to 7-fold in TL.

In addition to successful propagation of humpback chubs, a hybrid humpback chub X bonytail was produced by artificial means at Willow Beach National Fish Hatchery, AZ (Hamman, 1981, 1982). These were preserved and are stored at ASU for future use for taxonomic purposes.

Food Habits

Data from actual stomach analyses of chubs in the lower basin are limited. Adults collected below Glen Canyon Dam in the 1960's fed primarily on planktonic crustaceans, apparently from Lake Powell (W.L. Minckley, 1973). Three YOY humpback chub examined from the Little Colorado River in 1979 contained dipterans of the families Chironomidae and Dolichipoidae (Jordan, 1981). Kaeding & Zimmerman (1981, 1982, 1983) also found immature dipterans (chironomids, simuliids) as the most commonly eaten. Ten other groups of invertebrates were also present in the diet, as was fathead minnow. Stomachs of fish from the Colorado River contained more food materials than did fish from the Little Colorado. The most common items were algae (77%), invertebrates (9%) and fishes (8%) (Kubly, 1990).

Foraging behavior was observed in the Little

Colorado River numerous times in summer 1980 (C.O. Minckley, 1980a, b) and subsequent years. In one instance, adults at the confluence of the Little Colorado River took materials, including drifting *Cladophora glomerata*, from both bottom and surface. In 1978, YOY humpback chubs were observed from less than a meter away several times in the Little Colorado. The fish foraged much like adults, actively inspecting and taking materials, most probably epipelic and epilithic diatoms and small invertebrates, from the bottom, midwater, and surface.

During summer 1980, a school of chubs (which consisted of 15 fish >200 mm TL) was attracted into a pool using prepared sandwich spread, which they readily consumed from the surface, midwater, and bottom (C.O. Minckley, 1980a-b). On several occasions, individuals in the school jumped from the water in an attempt to obtain food; however, they ignored a canyon tree frog (*Hyla arenicolor*) presented as a potential food item, floating above them.

Affects of Parasites

An additional problem for native fishes may be non-native parasites brought to the area along with alien fishes. Although not yet perceived as a major factor in Grand Canyon, the potential exists for considerable impact (Amin 1969a, b; Carothers & Minckley, 1981; Kaeding & Zimmerman, 1983). For example, parasitism can cause reduced growth rate and egg production, poor swimming performance, and aberrant behavior (Davis 1947, Dogiel, 1958, Hoffman, 1967; Heckmann et al., 1986). Anchorworm parasite, *Learnea cyprinaceacea,* a copepod, infests the Virgin chub (*G. seminuda*) in the Moapa River, NV (Wilson, 1966) and the roundtail chub in the Verde River, AZ (James, 1968). It may be a potential problem in the Little Colorado River, where the incidence of infestation in humpback chub varies seasonally from 0 to 55% (C.O. Minckley, 1979b, c; 1988a, b; 1989a-c; 1990a, b; Carothers & Minckley, 1981; Kaeding & Zimmerman 1983).

The Asian tapeworm (*Bothriocephalus acheilognathi*), was recently recorded from chubs taken at the Salt Trail on the Little Colorado in May 1990 (C.O. Minckley, 1990a-b). The cestode was in the stomach and upper intestine of three infected individuals also has potential for negative impacts (C.O. Minckley, 1990a, b; J.J. Landye USFWS, pers. com.). This parasite is of concern throughout the country because of its large adult size and high infection rate, particularly in previously unexposed populations (Heckmann et al., 1986). It has recently been reported in four endemic fishes of the Virgin

River and also in golden shiner (*Notemigonus crysoleucus*), fathead minnows, red shiner, and Colorado squawfish from other parts of the region (Hoffman, 1976, 1983; Heckmann, et al., 1986).

Philometra sp., a nematode, was taken from the body cavity of a single specimen (Flagg, 1980). In addition, a fungus, 6 protozoans, and 13 bacteria have been reported from hatchery stock of humpback chubs (Flagg, 1980). One bacterium, *Aeromonas hydrophila,* was also present in wild-caught fish (Flagg, 1980; Kaeding & Zimmerman 1982, 1983).

Total Dissolved Solids

Juveniles of humpback chub are also subjected to a gradient of total dissolved solids between the Colorado and Little Colorado Rivers. To determine preferred or avoided concentrations studies were conducted to determine preferences if any. It was found that perferred concentrations were generally <1,000- 2,500 milligrams/liter and avoidance was recorded at concentrations >5,100 mg/l. Humpback chubs thus selected concentrations similar to those in the natural waters they inhabit (Miller et al., 1982d-f; Prewitt et al., 1976, 1977, 1982; Pimentel & Bulkley, 1983).

Swimming Velocity

Thomas et al., (1984) determined swimming ability of humpback chubs in a stamina tunnel. Swimming speeds of fishes are usually defined as burst speed (darting for a few seconds at 8 to 12 body lengths/s), or sustained speed (swimming for several minutes at 4 to 7 body lengths/s). Chubs were tested at various water velocities at 14, 20, and 26^{0}C They could swim for about 2.0 hours at 0.32 m/s, but for only a few minutes at 0.78 m/s. Swimming ability was positively and significantly related to temperature. Larger fish (>134 mm TL) performed significantly better (i.e., swam longer and faster; P <0.05), than did smaller fish (<73 mm TL).

Hematological Factors

Pimental & Bulkley (1983) performed hematological analysis. Parameters determined included glucose, chloride, hematocrit, and red and white blood-cell counts, and white blood-cell differentials. Hematocrit of juvenile humpback chub average 30%, hemoglobin averaged 7.2 f/100 ml, and red blood cells numbered 1.92 x 10 6/mm3. Leucocytes numbered 52.5 x 103/mm3; thrombocytes were the most abundant cell (62.4%), followed by lymphocytes (33.4%), and granulocytes (3.5%). Less than 1.0% of all white blood cells were identified as hemoblasts or macrophages (Miller et al., 1982d-f; Pimentel & Bulkley, 1983).

Condition Factors

Mean condition factors for six size-classes of chubs from the Little Colorado are compared for two seasons in Figure 17. Male conditions varied from 0.64 to 0.85 for January-April (season I) and from 0.42 to 0.72 for May-December (season II). Females varied from 0.71 to 0.80 and 0.4 to 0.75, respectively (Fig. 15). No significant differences existed between sexes and seasons for size-classes I or VI. Size classes II, III, IV, and V, however, showed significant differences between seasons for both sexes. Each was in better condition in winter-early spring than in late spring-winter. Reasons for these differences are likely related to reproductive cycle with expanded gonads in winter-early spring influencing plumpness of fish. Fish in size-classes I and VI did not differ significantly and may represent non-reproductive states. This is particularly true with size-class I except in rare instances of reproduction by small (young) individuals.

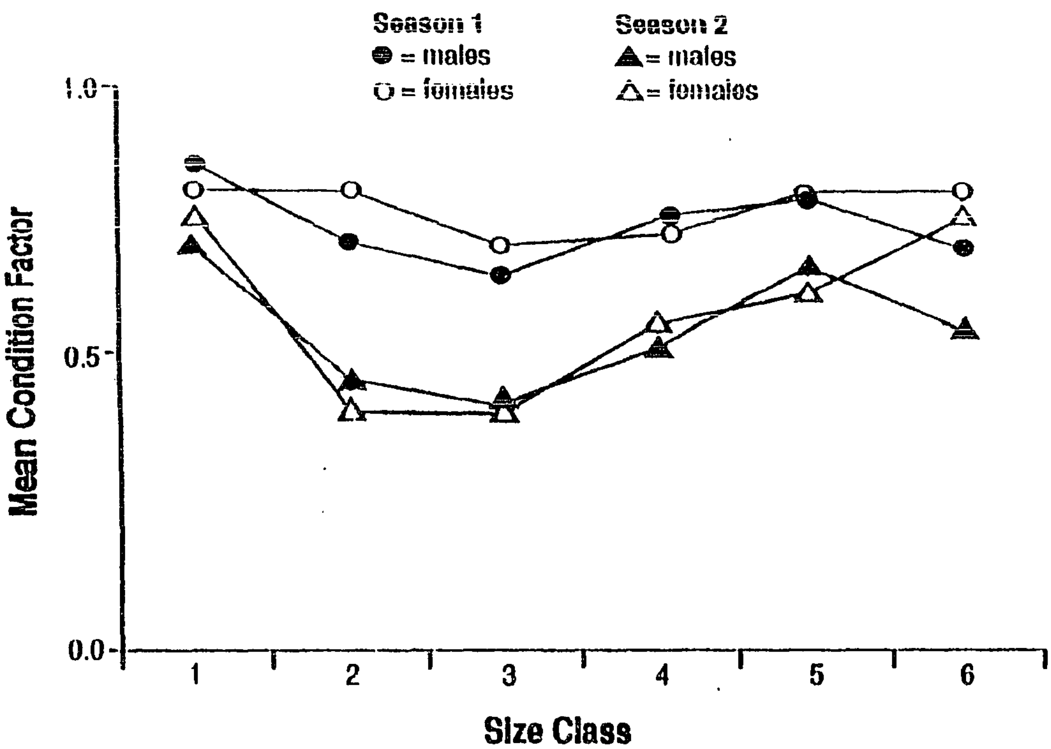


Figure 15. Illustrating condition factors for male and female humpback chubs from the Little Colorado River during 1987-1990 for two seasons. Season I (January-May), Season II (June-December).

Population Estimates

Data on tagged humpback chubs were used for estimation of population size in the lower 1.5 km of the Little Colorado River, just above its confluence with the Colorado mainstream. The Peterson (single census) method was applied, based on tagged fish recaptured during springtimes of 1987 through 1990, even though the population was not closed during this four year period.

A total of 3878 chubs was marked with Carlin, Floy, and PIT tags over the period. Population estimates for fish >150 mm TL varied from 5712 to 6747 (standard errors from 407 to 899, Table 13). Kaeding & Zimmerman (1982), using data collected throughout the year, presented a comparable "ball park" figure of 7000 to 8000 chubs >200 mm TL, in their study area, which included a larger proportion of the confluence area than mine, but was centered there. They used multiple census methods (e.g., Schnable, Modified Schnable, and Schumacher/Eschmeyer), acknowledging that many assumptions implicit for application of the methods were violated.

Population estimates are subject to numerous limitations. Assumptions to be satisfied for the Peterson Method, for example, are that mortality is zero (low), recaptures represent a single second sample, and marked and unmarked fish mix randomly and are equally vulnerable to capture (Ricker, 1975). Since no independent evidence of population-wide mortality rates exist for this long-lived minnow, an assumption of low mortality may be reasonable. That recaptures represent a single second sample is violated because time-series data were integrated into the single-census model, failing to account for both numbers taken and recaptures increasing with each additional sample and resulting in over-estimation of population size. Random mixing of marked fish with the general population in the Little Colorado also is assumed but not demonstrated. Sampling was biased for the time of year when chubs congregate before and during spawning, and the percentage participating in the aggregation is unknown. Individuals may not spawn annually, and an unknown number may be unavailable to sampling any given year. Other broader sources of error also exist (e.g., differential mortality of marked and unmarked fish, differential vulnerability to capture, and effects of sample size on estimates.

Lower Basin Recovery Efforts

There is no specific plan for lower basin populations. Several actions have been taken, however to benefit the species. After passage of the

Endangered Species Act, the state of AZ placed it in their Category 1 (AGFD 1988). The USNPS, Grand Canyon National Park (Anonymous, 1979; Robinson, 1980), prohibited angling in an area 0.8 km upstream and downstream from the confluence of the Little Colorado River with the Colorado and upstream in the former to the Park boundary. The action was taken to protect the concentration of humpback chubs in that area.

Removal of specimens from the Little Colorado to establish broodstock and maintain fish as a buffer against manmade or natural perturbations that might destroy the natural population has occurred. Initially accomplished in 1978, chubs were removed again in 1979, 1980, 1984, and 1985. In AZ, fish have been maintained at Willow Beach National Fish Hatchery and the AGFD Page Springs Hatchery. Stocks were later moved to Dexter National Fish Hatchery and Technology Center, Dexter, NM, a facility specializing in maintenance of threatened and endangered fishes. Although hybrid combinations were produced (Hamman 1981) for experimental purposes, no broodstock or ex situ population exists today. The fish all succumbed to natural or man-caused events.

CHAPTER FIVE: SUMMARY AND RECOMMENDATIONS.

The following recommendations are made and pertain only to the lower basin population of humpback chub. They are made without regard to the political realities which govern the fate of this species and focus on ways to prevent the extinction and maintain the current population in Grand Canyon. They were developed using much of the material presented in this document but also from disscusions through time with other native fish biologists concerned with this resource. As a result, they may seem unrelated to the material which has been presented here but in fact they are, and represent current research efforts and philosophies. These recommendations also incorporate new plans or techniques developed after 1990 (C.O. Minckley 1995), to more realistically present recommendations for this species. They are not meant to reflect the position or ideas of any of the institutions, agencies or individuals that I have been involved with during my time in Grand Canyon.

Recommendations:

1. Develop a comprehensive lower basin management plan for the Big River Fishes specifically addressing the Lower Colorado Basin and in this case the humpback chub.

2. Adapt the strategies suggested in C.O. Minckley (1995) to prevent the extinction and maintain the population of this species. This would at a minimum include:

A. Development of isolated habitats to rear fish produced in a genetically sound way to supplement the more isolated remanent populations in Grand Canyon. These habitats could include two types of facilities including:

In canyon facilities at:

A. South Canyon - develop Buck's Farm creek as a rearing area.

B. Bright Angel Creek - Develop ponds in this area to raise humpback chubs or use commercial fish farms to raise fish or;

C. Shinumo Creek - Develop the confluence area of Shinumo Creek as a growout site for fish produced in that stream.

D. Havasu Creek - In cooperation with the Havasupai Tribe, develop facilities at Supai to introduce humpback chubs into Havasu Creek and thus eventually the Colorado River.

Outside canyon facilities at:

A. Southwest Technology Center, Dexter, New Mexico.

B. Develop a large reservoir holding facility on lands owned by the National Park Service or the Navajo Nation to maintain a large number of humpback chubs for protection of the species against catastrophic loss as well as a source for fish for repatriation into the Grand Canyon region.

3. To further protect the species initiate a program in cooperation with Arizona Game and Fish Department, Grand Canyon National Park and the

Navajo, Havasupai and Hualapai Nations to exclude introduced species from the Colorado River and its tributaries between Lees Ferry and Lake Mead. This could be implemented in the following ways:

A. Using physical barriers, deny trout access to spawning streams between Lees Ferry and Diamond Creek.

B. Annually, electrofish all trout producing streams in Grand Canyon to remove trout which avoided the barriers.

C. Stipulate that all introduced fishes taken in future fishery investigations be destroyed, particularily brown trout, channel catfish and striped bass.

4. Continue the current program instituted by AGFD of a no limit creel on the numbers of introduced fishes caught by anglers below Lees Ferry.

5. Establish a multi-agency biological station at Phantom Ranch to continue aquatic investigations on the region. This would be an ideal location due to the amount of information known on Bright Angel Creek, the presence of electrical power, phones, laboratory facilities, and housing for research personnel. Such a facility would also prove invaluable if developed as a humpback chub rearing facility.

6. Continue monitoring the Little Colorado River population of humpback chub for basic life history information through the formation of a multiagency team. This could be done in the following manner:

A. Collect the population biannually, once in the Spring and then Late Summer. These efforts would be designed to determine:

1. The size classes of fish present for a given year to see if any marked change had occurred in the distribution of the various size classes in the population.

2. Determine reproductive success and the potential recruitment into the mainstream of a given year.

Summary

Geographic distribution of the humpback chub in the Colorado River basin is well documented. This species originally occurred from the upper Green River just upstream from the present Flaming Gorge Reservoir downstream to its confluence with the Colorado River. It was taken in the Colorado River mainstream from above Grand Junction downstream to just below Hoover Dam in the lower basin. It also occurs in several major tributaries, including the Yampa and Little Snake rivers in the upper basin and the Little Colorado River in Grand Canyon.

Based on recent records, it is apparent there is a relatively large, essentially population of humpback chubs in the Colorado River in Grand Canyon (Appendix , Fig. 5). Despite lack of recent records above Lee's Ferry, I consider the present distribution still to include the entire reach from Glen Canyon Dam downstream into upper Lake Mead, where they must sporadically also occur, as in Lake Powell. There is an obvious concentration in the Little Colorado River and its immediate vicinity. Chubs have also been consistently collected in or near four major tributaries in Grand Canyon National Park, and from one section of the Colorado River (RM 27-31).

Increased collecting of backwaters in the 1985-90 demonstrated the presence of both adults and smaller fish at numerous sites (Maddux et al., 1987; Kubly, 1990; Valdez 1990). Smaller fish at downstream sites may recruit from the Little Colorado River, other tributaries, or from the Colorado itself.

In these systems, numerous habitats exist that are used by humpback chubs to varying degrees depending on life stage. Reproduction has not been observed, so spawning substrates/sites have not been documented. Substrates suggested include gravel, gravel-cobble, and boulder in the upper basin to travertine dams, gravel, and rubble to sandy shoal areas along the lower mainstream within Grand Canyon. In hatchery raceways the fish spawned over cobble-gravel.

Observations in the upper basin have shown that fry (<20 mm TL) occupy shoreline backwater habitat in slowly moving water. Fish of this size in the lower basin are in slow-moving habitat along edges of the Little Colorado, generally in water <0.5 m deep. They also frequent shade and use available cover such as boulders, undercut banks, riparian and emergent aquatic vegetation.

Young-of-year humpback chubs in the upper basin occur in slow to moderately moving eddies and adjacent backwaters. They frequent backwaters in the Black

Rocks and Cataract Canyon reaches of the Colorado River. In the lower basin, these fish are more often in backwaters and adjacent eddies of the Colorado River. Young-of-the-year in the Little Colorado River are in almost all habitats in the system, including pools, behind various structures (e.g., boulders, travertine dams), and elsewhere. Their ecologic distribution reflects a considerable plasticity in habitat use.

Juvenile chubs live in deeper water habitats. Upper basin distribution has been characterized as low-velocity eddies. They also live in backwaters varying to >1.0 m deep. Lower basin studies show similar patterns, particularly in the Little Colorado River, where they occur in deeper waters throughout the system. Apparent ecological distribution in the lower Colorado River mainstream is in eddies and backwaters, perhaps in part reflecting collecting difficulties rather than absence of the fish in other habitats.

Adults are in deep eddies and backwaters wherever they occur, presumably including depths of >10 m that cannot be sampled by conventional means. Unidentified fish have been documented to depths of >25 m by side-scan sonar in the Grand Canyon region (C. O. Minckley, orig. data).

Humpback chubs were considered sedentary based on movement data of fish carrying both external and internal tags in the Black Rocks reach of the upper Colorado River. Based on tag returns, behavior appears similar in the Little Colorado River where a majority of fish appear sedentary, although a small percentage moved within the system as well as between the Little Colorado and Colorado rivers.

There is little information on food habits based on actual examination of stomachs. Dipterans, amphipods, the green alga *Cladophora glomerata*, and occasional fishes have been found. Anecdotal accounts indicate feeding on terrestrial invertebrates, mayflies, algae and commercial grocery items placed in the river by humans.

Several ectoparasites and endoparasites have been recorded from humpback chub. Two represent potential threats. Anchorworm can, under certain conditions, decimate fishes in natural situations and the potential for this exists in the Little Colorado population. The second, Asian tapeworm, presents a more insidious threat as an internal worm is not so readily detected.

Recommendations were also made suggesting ways to prevent the extinctions while maintaining the lower basin population of humpback chub.

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APPENDIX A

LIST OF COLLECTING LOCALITIES, OF HUMPBACK CHUB ARRANGED BY RIVER MILE (RM) FROM GLEN CANYON DAM TO THE MEXICAN BORDER, 1908-1990.

Date	Locality	Reference
1981	Lee's Ferry, RM 0.0,	*MNA collections
1963	Lee's Ferry,	*ASU collections
1967	Glen Canyon Damsite,	Holden and Stalnaker 1970
1970	"	
1964	100m below Glen Canyon Dam,	Stone 1964
1965	"	"
1966	"	"
1967	"	"
1968	"	, Stone and Rathburn
1968		
1969	"	"
1969		
1985	RM 8.0,	Dan Pearson, pers. comm. 1991 to COM
1980	RM 17.8,	Kaeding and Zimmerman 1983
1978	RM 19.5,	Carothers and Minckley 1981
1977	RM 27.0,	Minckley 1977b
1978	RM 27.0,	Carothers and Minckley 1981
1984	RM 31.0,	Maddux et al., 1987
1985	RM 31.0,	Maddux et al., 1987
1971	RM 31.5,	MNA collections, 1971
1971	RM 31.9,	MNA collections, 1971
BP*	RM 32.0,	Euler 1978, Miller and Smith 1984
1968	" ,	Miller and Smith 1968, 1969
1969	" ,	Miller 1968
1978	RM 33.0,	Carothers and Minckley, 1981
1984	RM 34.0,	Maddux et al., 1987
1970	RM 44.0,	Suttkus et al., 1976, Suttkus and Clemmer 1977
1971	RM 44,	MNA collections, 1971
1981	RM 52.8,	Kaeding and Zimmerman 1983
1981	RM 53.2,	Kaeding and Zimmerman 1983
1978	RM 55.0,	Carothers and Minckley 1981
1981	RM 57.1,	Kaeding and Zimmerman 1983
1981	RM 58.0,	"
1981	RM 58.2,	"
1981	RM 58.7,	"
1981	RM 58.9,	"
1981	RM 59.0,	"
1985	RM 59.0,	Maddux et al., 1987
1981	RM 59.3,	Kaeding and Zimmerman 1983
1981	RM 59.4,	"
1984	RM 60.0,	Maddux et al., 1987
1980	RM 60.5,	Kaeding and Zimmerman 1983

(Appendix A. continued.)

1980	RM 60.6,	"
1980	RM 60.8,	"
1980	RM 60.9,	"
1981	RM 60.9,	"
1984	RM 61.0,	Maddux et al., 1983
1980	RM 61.1,	Kaeding and Zimmerman 1983
1981	RM 61.1,	"
1981	RM 61.2,	"
1981	RM 61.3,	"
1980	RM 61.4,	"
1981	RM " ,	"
1989	RM " ,	Kubly, 1990
1984	RM " ,	Maddux et al., 1987
1986	RM " ,	"
1968	RM 61.5,	Miller 1968
1975	" ,	Suttkus et al., 1976
1975	" ,	Minckley and Blinn 1976
1976	" ,	Suttkus and Clemmer 1977
1977	" ,	Minckley 1977b, 1978
1978	" ,	Carothers and Minckley 1981
1979	" ,	"
1981	RM 61.9,	Kaeding and Zimmerman 1983
1984	RM 62.0,	Maddux et al., 1987
1981	RM 62.2,	Kaeding and Zimmerman 1983
1981	RM 62.5,	Kaeding and Zimmerman 1983
1985	RM " ,	Maddux et al., 1987
1981	RM 62.6,	Kaeding and Zimmerman 1983
1981	RM 62.7,	"
1968	RM 63.0,	Miller and Smith 1968
1975	RM 63.0,	Miller 1975
1975	RM 63.0,	Minckley and Blinn 1976
1985	RM 63.5,	Maddux et al., 1987
1981	RM 63.6,	Kaeding and Zimmerman 1983
1985	RM 64.0,	Maddux et al., 1987
1985	RM 64.1,	"
1981	RM 64.2,	Kaeding and Zimmerman 1983
1985	RM 64.3,	Maddux et al., 1987
1968	RM 64.5,	Miller 1968
1981	RM " ,	Kaeding and Zimmerman 1983
1985	RM " ,	Maddux et al., 1987
1980	RM 64.6,	Kaeding and Zimmerman 1983
1981	"	,
1980	RM 64.7,	
1981	RM " ,	"
1980	RM 64.8,	"
1980	RM 64.9,	"
1981	RM " ,	"
1985	RM 65.0,	Maddux et al., 1987
1985	RM 65.2,	"
1985	RM 65.5,	"

(Appendix A, continued).

1988 RM 65.6, Kubly 1990
1985 RM 66.3, Maddux et al., 1987
1985 RM 66.8, Kaeding and Zimmerman 1983
1988 RM 67.8, Kubly 1990
1981 RM 67.9, Kaeding and Zimmerman 1983
1988 " , Kubly 1990
1981 RM 68.0, Kaeding and Zimmerman 1983
1987 " , Maddux et al., 1987
1981 RM 68.2, Kaeding and Zimmerman 1983
1981 RM 68.3, "
1975 RM 69.0, Suttkus et al., 1976
1981 RM 69.1, Kaeding and Zimmerman 1983
1981 RM 69.3, "
1987 RM 69.5, Maddux et al., 1987
1981 RM 69.9, Kaeding and Zimmerman 1983
1977 RM 69.9, Minckley 1977b
1981 RM 70.1, Kaeding and Zimmerman 1983
1987 RM 71.0, Maddux et al., 1987
1975 " , Suttkus et al., 1976, Suttkus and Clemmer 1977
1981 RM 71.1, Kaeding and Zimmerman 1983
1989 RM 72.1, Kubly 1990
1981 RM 71.4, Kaeding and Zimmerman 1983
1979 RM 72.0, Carothers and Minckley 1981
1989 RM 72.3, Kubly 1990
1984 RM 73.0, Maddux et al., 1987
1985 RM 73.5, "
1985 RM 74.0, "
1985 RM 75.0, "
1985 RM 76.0, "
1985 RM 84.0, "
1984 RM 86.0, "
1942 Vicinity of Bright Angel Creek (RM 87.5), Miller 1946
1944 " , Grand Canyon National Park records
1954 " , "
1968 " , "
1987 " , Mark Law, Grand Canyon National Park
1984 Vicinity of Bright Angel Creek (RM 87.5) Maddux et al.,
1990 Vicinity of Bright Angel Creek (RM 87.5) Valdez 1990
1979 RM 90.0, Carothers and Minckley 1981
1984 RM 94.0, Maddux et al., 1987
1986 RM 104.0, "
1984 RM 107.0, "
1975 Shinumo Creek (108.5), Suttkus et al., 1976, Suttkus Clemmer 1977
1978 Shinumo Creek (108.5), Carothers and Minckley 1981

(Appendix A, continued).

1984 " , Maddux et al., 1987
1986 RM 109.0, Maddux et al., 1987
1985 " , "
1984 RM 112.0, "
1985 RM 114.0, "
1985 RM 117.0, "
1978 RM 132.0, Carothers and Minckley 1981
1985 RM 136.0, Maddux et al., 1987
1985 RM 136.5, "
1989 Kanab Creek (RM 143.5), Kubly 1990
1979 Havasu Creek (RM 157.0), Carothers and Minckley
1981 "
1987 " , Maddux et al., 1987
1988 " "
1985 RM 165.0, Maddux et al., 1987
1985 RM 165.1, "
1985 RM 165.4, "
1985 RM 165.5, "
1985 RM 165.6, "
1985 RM 165.6, "
1985 RM 166.3, "
1989 RM 167.5, Kubly 1990
1985 RM 171.0, Maddux et al., 1987
1985 RM 174.0, "
1985 RM 176.5, "
1985 RM 178.0, "
1985 RM 178.5, "
1968 RM 179.1, Miller and Smith 1968
1985 RM 182.0, Maddux et al., 1987
1986 RM 187.0, "
1987 RM 187.5, "
1985 RM 190.5, "
1985 RM 191.0,
1985 RM 192.0, "
1978 RM 194.0, Carothers and Minckley 1981
1985 " , Maddux et al., 1987
1985 RM 196.0, "
1985 RM 197.5, "
RM 197.8, "
1987 RM 198.0, "
1987 RM 200.0, "
1985 RM 203.2, Maddux et al., 1987
1985 RM 204.0, "
1985 RM 208.0, "
1985 RM 211.0, "
1985 RM 213.5, "
1984 RM 214.0, "
1985 " , "
1985 RM 216.0, "
1985 RM 217.0, "

(Appendix A, continued).

1955 RM 246.0, Miller 1955
1955 Catclaw Cave Site below Hoover Dam, Miller 1955

APPENDIX B

BIOGRAPHICAL INFORMATION

Name of Author: Charles O. Minckley

Place of Birth: Ottawa, Kansas

Date of Birth: 11 October 1945

Educational Degrees Awarded

University of Nevada, Las Vegas, M.S. 1970
Kansas State University, B.S. 1968

Professional Positions Held

Biologist, Museum of Northern Arizona, Flagstaff, Arizona, 1977-1981.

Biologist, Center for Environmental Studies, Tempe, Arizona 1990-1992.

Fisheries Biologist, U.S. Fish and Wildlife Service, Parker, Arizona. 1992 to present.

Professional and Honor Socities

American Fisheries Society
American Society of Icthyologists and Herpetologists
American Society of Southwestern Naturalists
Society of Conservation Biologists
Desert Fishes Council
Sigma Xi

Scholarly Publications

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