TRANSACTIONS of the AMERICAN FISHERIES SOCIETY

September 1983

VOLUME 112

NUMBER 5

Transactions of the American Fisheries Society 112:577–594, 1983

Life History and Ecology of the Humpback Chub in the Little Colorado and Colorado Rivers of the Grand Canyon

LYNN R. KAEDING[1] AND MARIAN A. ZIMMERMAN[2]

United States Fish and Wildlife Service, Colorado River Fishery Project
Flagstaff, Arizona

Abstract

Humpback chubs *Gila cypha* in the Little Colorado River, a warm saline tributary to the Colorado River, grew rapidly to about 250–300 mm total length at 3 years of age, the onset of reproductive maturity for female fish. Fish spawned in April or May; annual reproductive success was greatest when spawning coincided with seasonal river runoff. Meristic characters of humpback chubs from the upper 8 km of the river differed from those of fish from the adjacent lower 5-km river reach, and suggested that some genes of bonytail *Gila elegans* may occur in the latter population. Use of the physical habitat by age-0 and juvenile humpback chubs was affected by light intensity; shallow littoral areas were used during darkness, but during daylight only when the water was turbid. No evidence of humpback chub reproduction was found in the Colorado River part of the study area; small humpback chubs collected there resulted from spawning in the Little Colorado River. Year-round low temperatures in the Colorado River (the tailwater of Glen Canyon Dam) did not inhibit seasonal gonadal maturation of humpback chubs; however, laboratory studies have indicated that such low temperatures result in nearly complete mortality of embryonic and larval humpback chubs. The recapture of tagged fish, seasonal changes in rates of capture of adults from the Little Colorado River, and the distribution of adult humpback chubs in the Colorado River near its confluence with the Little Colorado River supported the hypothesis that some adult fish from the Colorado River enter the Little Colorado River to spawn. Stomach contents from humpback chubs were dominated numerically by immature Chironomidae and Simuliidae. *Lernaea cyprinacea* was the most conspicuous metazoan parasite of humpback chubs in the Little Colorado River but was rarely found on fish in the Colorado River. Persistence of the humpback chub in the Little Colorado River could be attributable, in part, to the unsuitability of that environment, and that of the Colorado River, for potential competitor or predator species in the drainage. Introduction to the Little Colorado River of such a species that might prosper under the physicochemical conditions of the river could have a devastating effect on the humpback chub in the Grand Canyon.

Received November 24, 1982 Accepted June 1, 1983

The historic fish community of the warmer reaches of the Colorado and Green rivers consisted largely of endemic species, several of which are now formally designated as endangered or are considered rare because alteration of the aquatic environment has greatly reduced their numbers (Miller 1961; Minckley and Deacon 1968; Holden and Stalnaker 1975). The loss of habitat for some native fishes of the Colorado River drainage coincided with the closure of Flaming Gorge Dam on the Green River (Van-

[1] Present address: United States Fish and Wildlife Service, 551 25½ Road, Grand Junction, Colorado 81505.

[2] Present address: United States Fish and Wildlife Service, 605 West 4th Avenue, Room G81, Anchorage, Alaska 99501.

icek and Kramer 1969; Vanicek et al. 1970; Holden and Stalnaker 1975). The dam discharged hypolimnetic water from the reservoir and temperatures in the tailwater remained low throughout the year. Lower tailwater temperatures and the loss of lotic habitat in the reservoir presumably eliminated reproduction by some native fishes and led to their eventual extinction in that region.

Although comprehensive surveys of the fishes of the 400-km Colorado River reach that includes the Grand Canyon did not begin until several years after the 1963 closure of Glen Canyon Dam upstream, results of these investigations suggested that dam operation affected native fishes in much the same way as it affected them below Flaming Gorge Dam. Researchers in the Grand Canyon failed to collect the Colorado squawfish *Ptychocheilus lucius*, razorback sucker *Xyrauchen texanus*, or bonytail *Gila elegans*, although these species probably once occurred there. A few humpback chubs *Gila cypha* were found, however. They were most abundant, and apparently reproduced, near the confluence with the Little Colorado River, a small though significant tributary (Minckley and Blinn 1976; Suttkus and Clemmer 1979; Minckley et al. 1980). In the present report, we describe the life history and ecology of the humpback chub near the confluence of the Little Colorado and Colorado rivers in the Grand Canyon.

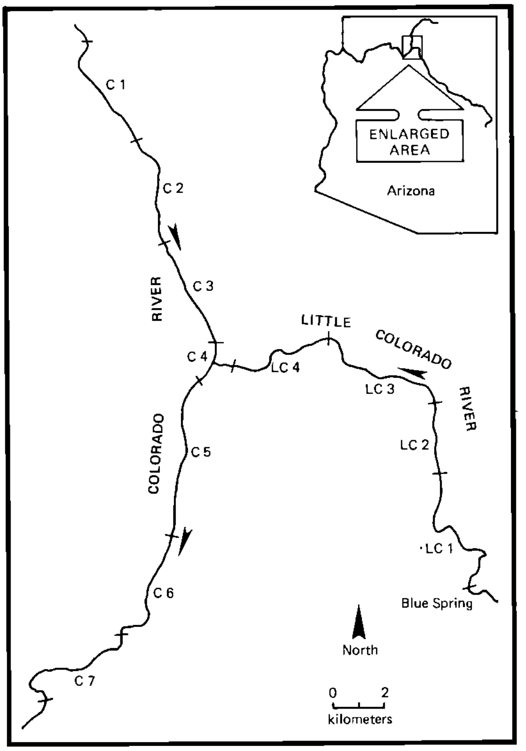


FIGURE 1.—*Study area showing locations of sampling reaches in the Colorado River (C 1–7) and Little Colorado River (LC 1–4). Arrows along the rivers denote directions of flow.*

Methods

Study Area and Sampling Scheme

The study area included 32 km of the Colorado River, and 20 km of the Little Colorado River to Blue Spring, the farthest upstream source of perennial water for the Little Colorado within the Grand Canyon (Fig. 1). The rivers were divided into reaches about 5 km long, except the confluence (reach C 4) included both rivers and totaled 3 km. Sampling at LC 1, the most upstream reach of the Little Colorado, was stopped after intensive collecting efforts in May and July 1980 yielded no humpback chubs.

Before each sampling trip, we randomly selected one 0.5–1-km-long sampling site within each reach, using large-scale aerial photographs. Seven quantitative sampling trips were made along the Little Colorado, and three semiannual quantitative trips along the Colorado, in 2 years; however, only two Little Colorado reaches were sampled during some trips. Aerial photographs were used on the ground to accurately identify the locations of individual collection areas. Sampling was stratified by three diel periods: morning, afternoon, and night (darkness). Sampling at each site usually continued for 2 days.

Physicochemical and Biological Measurements

River cross sections were measured manually in the Little Colorado and electronically in the Colorado. Chemical analyses of the water were performed in the field between 1000 and 1400 hours. Continuously recording thermometers were placed in the Little Colorado at two locations, 5 and 13 km above the confluence of the rivers, and in the Colorado at the United States Geological Survey gauge 23 km below the study area. Temperatures at the gauge were representative of those in the study area; Cole and Kubly (1976) showed that water temperature in the Colorado increases no more than

0.3 C over a reach of this length in the Grand Canyon. Mean daily temperature was computed as a mean of the maximum and minimum readings in the 24-hour period starting at midnight. Mean daily temperatures for each month were averaged within six periods; the first five consisted of 5 days each and the sixth contained the remaining days of the month. We equated discharge of the Colorado at the gauge with relative water-surface elevation at a reference point in the confluence reach using a relationship estimated by the United States Bureau of Reclamation. These data were then summarized in the same manner as were temperatures. Data on Colorado River temperature and discharge that predate our study were taken from published reports of measurements made at the gauge.

Quantitative fishing gears were minnow traps (45 × 23 cm, 6-mm hardware cloth), seines (9.1 × 1.8 m, 3-mm mesh), and trammel nets (45.7 × 1.8 m, 2.5-cm-mesh wall, 25.4-cm-mesh trammel). The time spent fishing each gear and the area swept by seines were recorded. Total fishing effort by each quantitative gear was about equal among sampling sites within rivers. Qualitative sampling was performed with fine-mesh hand nets, gill nets of various sizes, and electrofishing gear in the Colorado.

Fish collected were weighed (g) and measured to total length (mm). Humpback chubs were examined grossly for ectoparasites and external characteristics of seasonal reproductive development. Dorsal and anal fin-ray counts are among several morphomeristic characters used to taxonomically separate the humpback chub, bonytail and roundtail chub *Gila robusta* (Miller 1946; Holden and Stalnaker 1970). Later analyses were limited to humpback chubs longer than 100 mm, a size that resulted in no disagreement over fin-ray counts among workers. Scales used for age estimation were plucked from the caudal peduncle above the lateral line. A numbered Carlin tag was attached to humpback chubs longer than 200 mm before the fish were released.

Although external urogenital characteristics almost always proved accurate for selecting female humpback chubs for later laboratory analyses of gonad development, we selected only fish for which these were pronounced (Suttkus and Clemmer 1977). Sex determinations in the field were sometimes questionable, particularly after the spawning season. Therefore, we made no attempt to separate sexes in analyses other than those of gonad development.

Seasonal gonad development of females was followed with gonadosomatic indices (100·gonad weight/whole-body weight) and mean ovum diameters from mature fish (longer than 255 mm). Gonads were excised in the field, preserved in Bouin's fixative, and weighed to the nearest 0.1 g in the laboratory. Maximum diameters of 20 of the largest ova were measured with an ocular micrometer. Histological analyses of gonads were made at the Bozeman (Montana) Fish Cultural Development Center of the United States Fish and Wildlife Service (USFWS). Contents of digestive tracts from sacrificed fish and fish killed accidentally were examined for food items. Tissues from fish killed and microbiological cultures from fish having external symptoms of disease were sent to the Fish Disease Control Center (USFWS), Fort Morgan, Colorado, for routine pathological analyses.

Catch per unit of fishing effort (C/f) was calculated for humpback chubs in three broad age categories, but no age distinctions were made for other species. Length frequency was effective in identifying age-0 humpback chubs, and juvenile and adult fish were arbitrarily separated at a length of 200 mm. The C/f was calculated as fish per trap-night in minnow traps, fish per 100 m^2 swept by seines, and fish per hour in trammel nets. When preliminary analyses revealed that catch rate in seines differed significantly between daylight and darkness, these data were stratified on that basis. Because trammel nets in the Little Colorado were checked every 1 to 2 hours and fished much of the day and night, but those in the Colorado were fished unattended overnight only, the Little Colorado River data provided resolution of differences in C/f among diel periods not possible with data from the Colorado. After preliminary analyses, trammel-net data from the Little Colorado were stratified into three periods: daylight, sunset (sundown ± 3 hours), and darkness.

The C/f was averaged within gear, river reaches, sampling trips, diel periods, and occasionally age categories of humpback chubs.[3]

---

[3] The full tables containing mean C/f data for all species collected during the study can be obtained from the senior author.

TABLE 1.—*Range of physicochemical characteristics measured in the Little Colorado River, the confluence, and the Colorado River. Number of observations (cross sections or chemical determinations) is given in parentheses.*

Reach	Width (m)	Mean depth (m)	Maximum depth (m)	Dissolved oxygen (mg/liter)	Conductivity (μmho/cm, 25 C)	Salinity (‰)	Turbidity (formazin units)	pH
				Little Colorado				
LC 1				2–8(4)	4,161–5,161(3)	2.1–3.3(3)		
LC 2	18.0–35.1(5)	1.0–1.5(5)	1.4–2.6(5)	7–10(9)	3,772–6,017(9)	2.0–3.1(7)	12–16(2)	7.6–8.0(4)
LC 3	29.3–50.0(4)	0.5–0.9(4)	1.0–1.2(4)	8–10(8)	3,973–5,012(9)	2.0–3.5(9)	0–7(4)	7.3–7.7(4)
LC 4	20.1–27.4(4)	0.7–0.9(4)	1.0–1.7(4)	8–10(7)	3,548–6,018(6)	1.7–3.0(6)	2–7(4)	7.5–8.2(5)
				Confluence				
C 4	75.6–132.0(9)[a]	4.9–9.1(6)[a]	6.1–13.7(6)[a]	7–11(12)	503–4,990(18)	0.1–3.1(17)	0–310(9)	8.1–8.5(5)
				Colorado				
C 1	81.2–205.6(9)	3.3–8.5(9)	4.6–15.2(9)	10–11(5)	567–1,160(6)	0.0–0.4(6)	0–10(5)	7.5–8.0(3)
C 2	77.7–193.5(9)	4.0–8.3(9)	5.2–17.1(9)	9–10(6)	483–787(6)	0.1–0.4(6)	2–36(5)	7.1–7.8(2)
C 3	51.1–132.8(9)	4.3–6.4(9)	4.6–11.9(9)	10–11(7)	397–787(7)	0.1–0.5(6)	0–5(3)	7.9–8.0(2)
C 5	71.5–190.6(9)	4.0–11.3(9)	4.9–18.6(9)	9–11(5)	436–920(5)	0.2(5)	0–10(5)	8.0(2)
C 6	65.2–124.6(9)	3.8–6.5(9)	6.4–10.4(9)	9–11(5)	534–778(6)	0.1–0.4(6)	2–5(4)	7.5–7.8(2)
C 7	83.2–192.8(9)	3.4–7.1(8)	5.5–9.8(8)	9–11(6)	551–778(7)	0.1–0.5(7)	4–60(4)	7.9–8.0(2)

[a] All these measurements were taken in the Colorado River.

Resulting mean values of C/f then were examined for relationships with seasons, river reaches, and diel periods. Because humpback chubs differed greatly in vulnerability to capture between rivers, statistical analyses of catch data were made within rivers only. Linear-regression analyses were used to test for relationships between mean C/f for humpback chubs and individual sympatric species within rivers. These analyses were made within quantitative gear types, and between quantitative gears fished simultaneously.

Results and Discussion

Physicochemistry

The physicochemical characteristics of the reaches differed markedly between rivers, but little within rivers (Table 1). Dissolved oxygen concentration was near saturation except in upstream areas of LC 1, where carbon dioxide concentrations were high in spring discharges. Equilibration of dissolved gases with the atmosphere results in considerable precipitation of travertine ($CaCO_3$) at LC 2 and lower LC 1 (Cooley et al. 1969), where a rocklike accumulation 8 mm thick was found on the thermograph after it had been in the river for 3.5 months. A particularly large travertine dam marked the boundary between LC 1 and LC 2, and LC 2–4 contained numerous travertine dams 0.1 to 2 m high. The height of the dams affected the depth and length of intervening pools, as indicated by the following percentages of the thalweg consisting of pool habitat: LC 2, 70%; LC 3, 54%; LC 4, 34%.

Sodium chloride contributes greatly to the high specific conductance and salinity of the Little Colorado (Cooley et al. 1969). Because the volume of the Little Colorado is relatively small (about 5% that of the Colorado), the river has little effect on the physicochemical characteristics of the Colorado, although in flood the Little Colorado greatly increases turbidity in the Colorado (Cole and Kubly 1976). Only one turbidity measurement (from C 4) was taken during a flood in the Little Colorado.

Mean water temperatures were about 9 C warmer in the Little Colorado (specifically at reach LC 4) than in the Colorado throughout the year (Fig. 2). Unlike river temperatures before dam construction, Colorado River temperatures varied little annually within the study area. Relative Colorado River water-surface elevation fluctuated 0.6 to 1.9 m within 5-day periods, whereas little short-term variation occurred before Glen Canyon Dam was constructed (see Dolan et al. 1974).

Age and Growth

Scale annuli were useful indicators of age of Little Colorado River humpback chubs; annuli correlated directly with modes in length-fre-

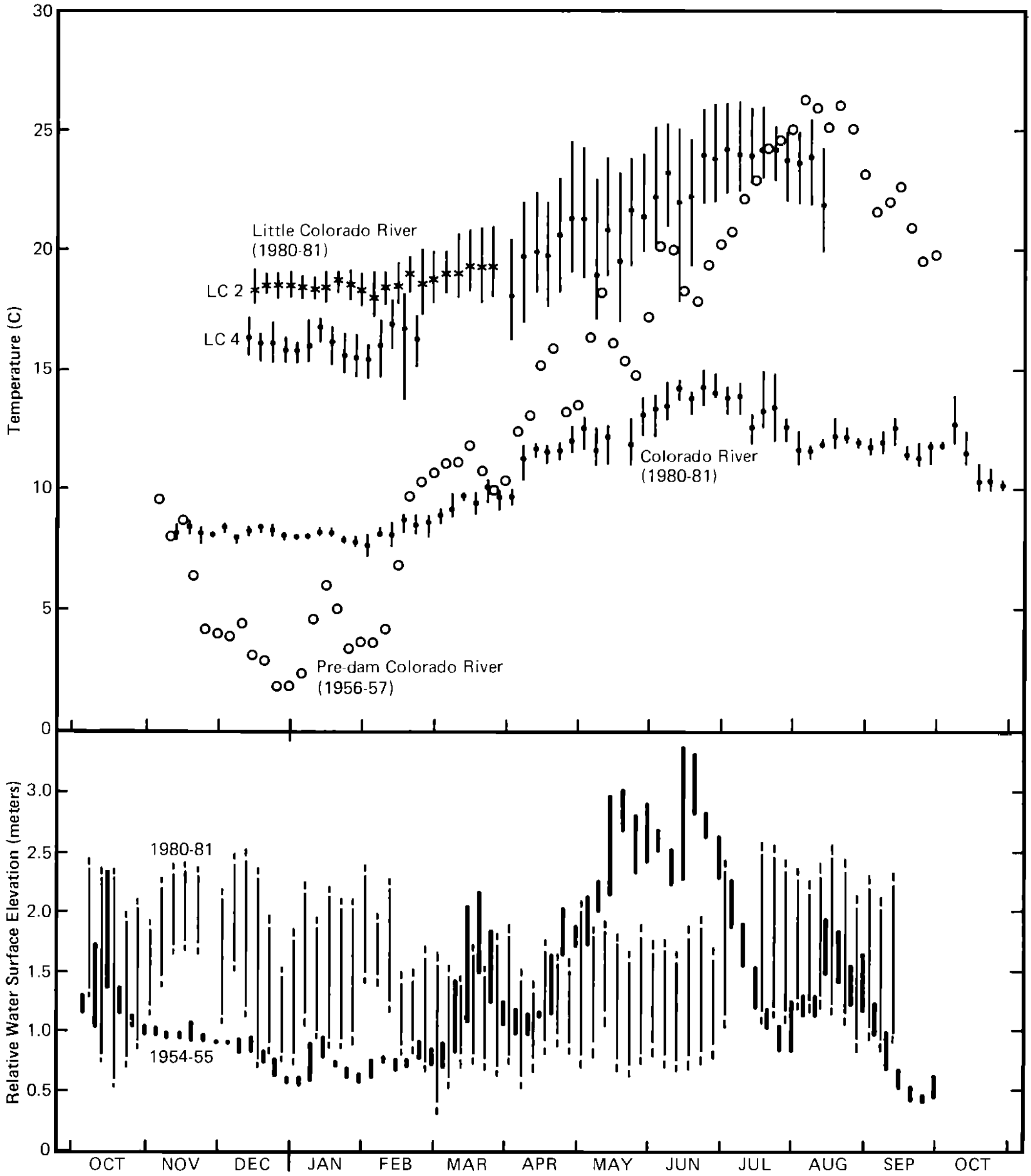
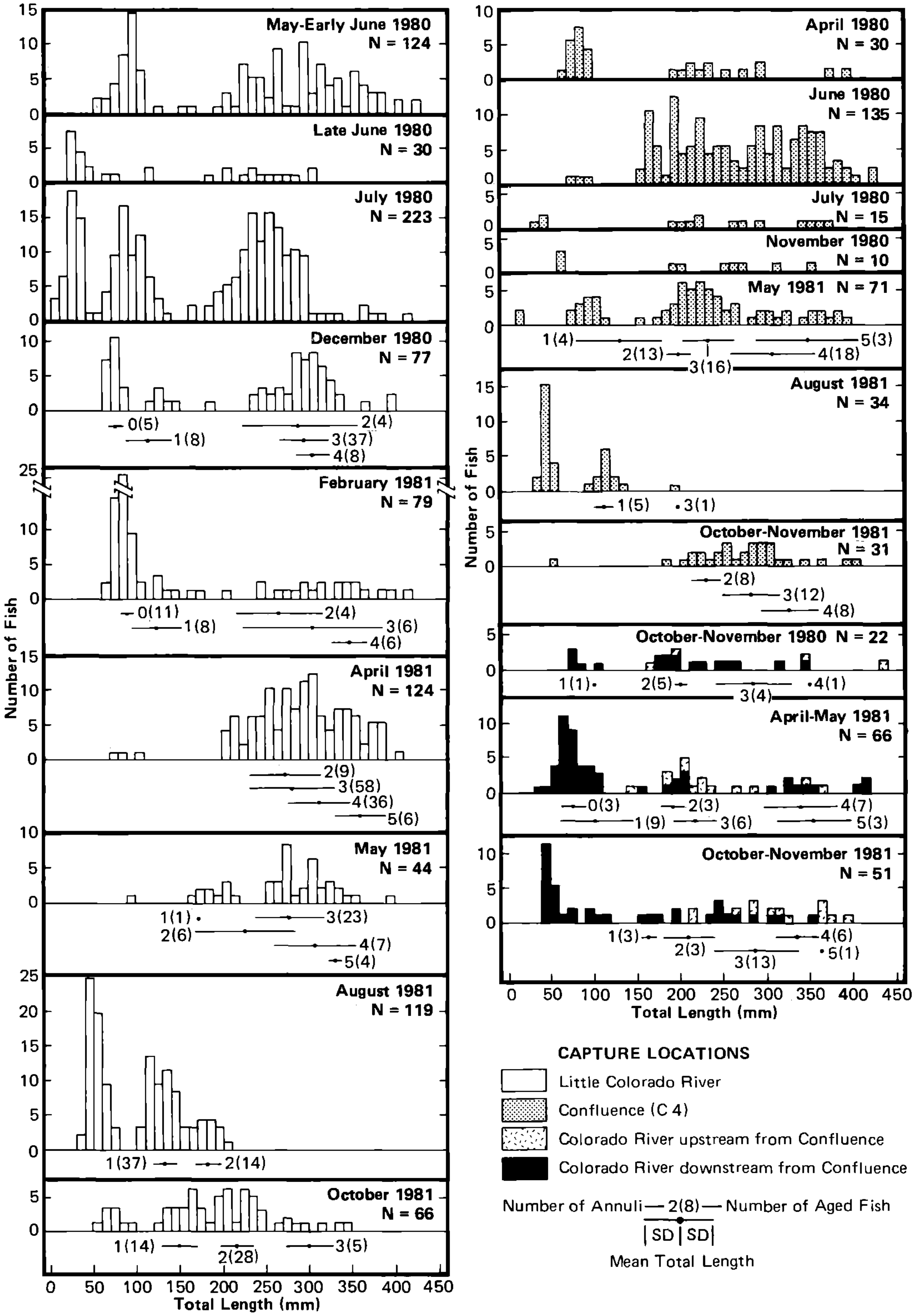


FIGURE 2.—*Chronologies of Little Colorado River and Colorado River 5-day mean water temperatures (above) and of Colorado River surface elevations (below). Vertical bars are ranges. Data for 1980–1981 are from the present study; 1954–1957 data predate construction of Glen Canyon Dam on the Colorado River upstream of Grand Canyon.*

quency distributions for fish up to about 3 years old and 250–300 mm long (Fig. 3). New annuli were observed on few scales collected in February but were present on most scales in May. There was no evidence of the formation of false checks. The first annulus formed when fish reached a length of about 100 mm and an age of 1 year. The annual increase in length of Little Colorado River humpback chubs was largest during the first 3 years of life, to a total length of 250–300 mm. Age-and-growth characteristics of humpback chubs in the Little Colorado and at the confluence of the rivers (C 4) were similar.


May-Early June 1980
N = 124
Late June 1980
N = 30
July 1980
N = 223
December 1980
N = 77
0(5)
1(8)
2(4)
3(37)
4(8)
February 1981
N = 79
0(11)
1(8)
2(4)
3(6)
4(6)
April 1981
N = 124
2(9)
3(58)
4(36)
5(6)
May 1981
N = 44
1(1)
2(6)
3(23)
4(7)
5(4)
August 1981
N = 119
1(37)
2(14)
October 1981
N = 66
1(14)
2(28)
3(5)
Number of Fish
Total Length (mm)
April 1980
N = 30
June 1980
N = 135
July 1980
N = 15
November 1980
N = 10
May 1981 N = 71
1(4)
2(13)
3(16)
4(18)
5(3)
August 1981
N = 34
1(5)
3(1)
October-November 1981
N = 31
2(8)
3(12)
4(8)
October-November 1980 N = 22
1(1)
2(5)
3(4)
4(1)
April-May 1981
N = 66
0(3)
1(9)
2(3)
3(6)
4(7)
5(3)
October-November 1981
N = 51
1(3)
2(3)
3(13)
4(6)
5(1)
Number of Fish
Total Length (mm)
CAPTURE LOCATIONS
Little Colorado River
Confluence (C 4)
Colorado River upstream from Confluence
Colorado River downstream from Confluence
Number of Annuli — 2(8) — Number of Aged Fish
SD | SD
Mean Total Length

An annual growth cycle of humpback chubs in the Colorado was indicated by scale characteristics. New annuli were evident on many scales in April–May 1981, and crowded circuli were found at scale margins in October–November 1980 and 1981. However, we believe that age estimates derived from the scales of humpback chubs from the Colorado are not reliable because some fish formed an annulus near the end of their first year of life whereas other fish did not. Evidence supporting this belief is provided by fish from the well-defined 38–107 mm length class collected from the Colorado in April–May (Fig. 3). We believe that all of these humpback chubs were yearlings because they were too large to be age-0; the smallest fish was twice the length of the largest known age-0 fish collected concurrently (an 18-mm metalarva from the Little Colorado waters of C 4). Collected during the time of annulus formation, the small yearling fish would not have formed an annulus that year because the fish had yet to develop scales or had scales too small to show circuli, whereas the larger humpback chubs of this length class had developed scales that showed one clear new annulus. We attribute poor early growth of small Colorado River humpback chubs to low water temperatures.

Reproduction

The onset of female sexual maturity occurred at lengths of about 250 to 300 mm (Fig. 4). Fish of this length were about 3 years old in the Little Colorado but perhaps older in the Colorado. The sparse data from males killed accidentally suggest that the onset of male sexual maturity occurs at about the same lengths (Fig. 4). However, smaller mature males were seen in the field. Of the males collected in April 1981, 15 of 19 (79%) between 200 and 249 mm long and 26 of 35 (74%) between 250 and 300 mm long expressed milt when external pressure was applied. The smallest male with milt was 205 mm long.

Seasonal fluctuations in the gonadosomatic index and mean ovum diameter of humpback chubs from the Little Colorado were similar

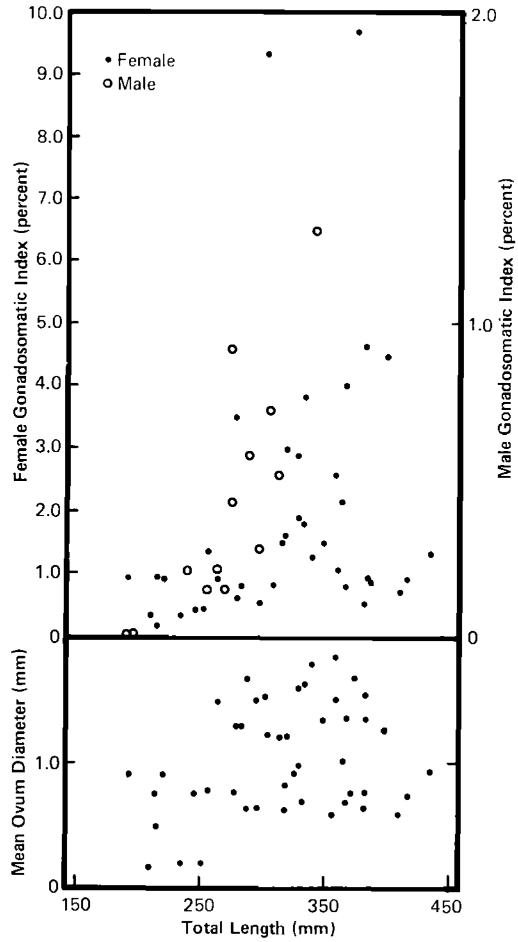


FIGURE 4.—*Relationships between gonadosomatic index (100·gonad weight/whole-body weight) and fish length, and between mean ovum diameter and fish length, for humpback chubs from the Little Colorado and Colorado rivers.*

(Fig. 5). Gonad development in preparation for spawning was rapid between December and February–April; sharp declines in indices during April–May indicated that spawning had occurred during this period. Seasonal gonad development of Little Colorado River males longer than 250 mm paralleled that of females. Milt was expressed from 25% of 12 males in Feb-

←

FIGURE 3.—*Length-frequency distributions for humpback chubs collected from the Little Colorado River, confluence, and Colorado River. Results of analyses of annuli on scales from humpback chubs are given below respective length-frequency distributions.*

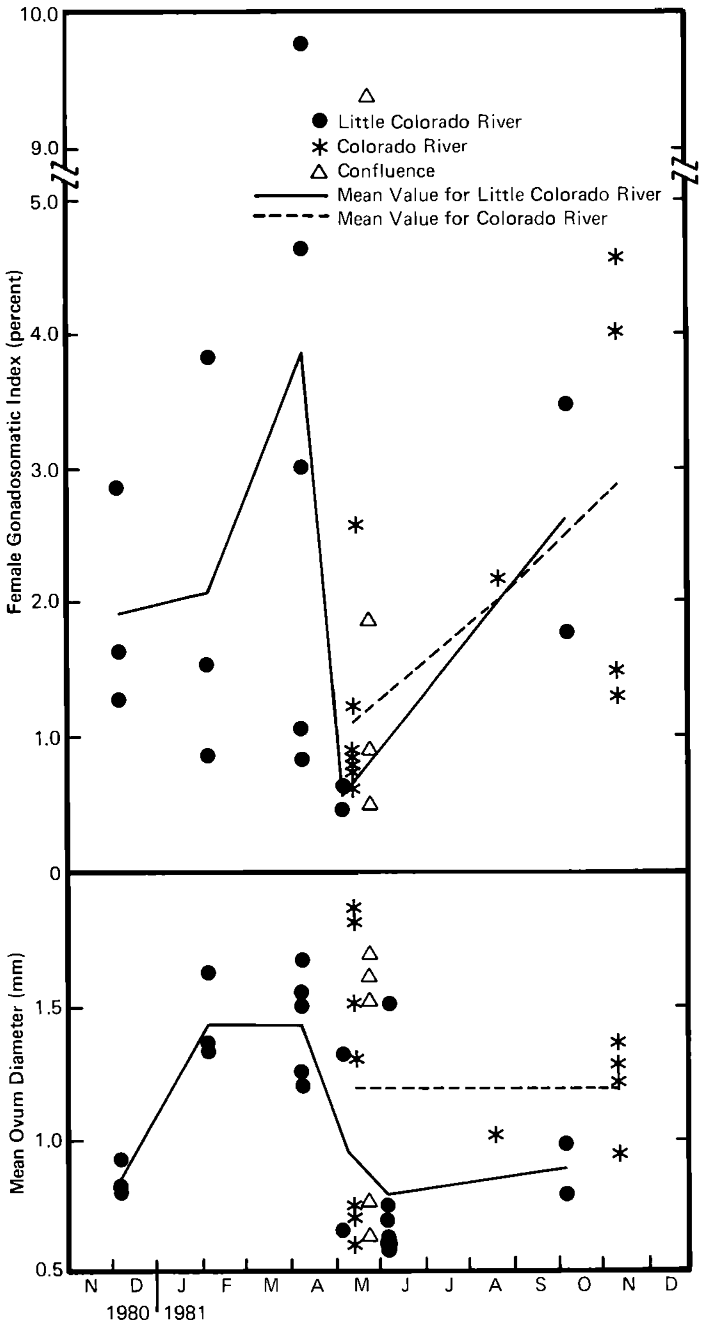


FIGURE 5.—*Seasonal changes in female gonadosomatic index (100·ovary weight/whole-body weight) and mean ovum diameter for humpback chubs from the Little Colorado River, confluence, and Colorado River. Six specimens collected in June 1980 are included in the data for mean ovum diameter.*

ruary, 74% of 57 in April, and 17% of 23 in May. Nuptial tubercles were observed on 50, 23, and 22% of the fish in these respective samples.

Observations on growth rate of humpback chubs spawned and raised in a hatchery (Hamman 1982) indicated that fish 14–18 mm long from the Little Colorado River part of the confluence (C 4) in May 1981 (Fig. 3) probably resulted from spawning 2 or 3 weeks earlier. Humpback chubs from the Little Colorado, Colorado, and the confluence exhibited post-ovulatory characteristics of low gonadosomatic indices in May, and some large residual ova. Gonad-development stage appeared similar in histological preparations from these concurrent collections (Charlie Smith, Fish Cultural Development Center, USFWS, Bozeman, Montana, personal communication). These data suggest that female humpback chubs undergo seasonal gonad development in the Colorado and may spawn there. This observation was not unexpected. Temperatures of the Colorado during the period of rapid seasonal gonad development are similar to those present before Glen Canyon Dam was constructed (Fig. 2). We found one male humpback chub with nuptial tubercles and running milt among eight humpback chubs collected in an overnight set of a trammel net in a Colorado River (C 3) backwater in May 1981.

Although humpback chubs might spawn in the Colorado, our data strongly suggest that spawning there does not result in the production of viable offspring and the recruitment of young fish to the population. No humpback chubs shorter than 145 mm were collected from the Colorado upstream from the confluence, even though mature fish were present in this river reach (Fig. 3). This distribution suggests that small humpback chubs in the Colorado resulted from spawning in the Little Colorado. This hypothesis is supported by results of recent thermal tolerance tests that showed temperatures like those of the Colorado River study area preclude appreciable reproduction of humpback chubs. Hamman (1982) found that at 12–13 C, only 12% of fertilized humpback chub eggs hatched after 340–475 hours of incubation and only 15% of these reached the feeding-larva stage in a controlled hatchery environment. When water temperature was maintained at 16–17 C, incubation time was about 167–266 hours; hatching success was 62%, and 91% of the embryos that hatched became feeding larvae. Humpback chub reproduction in the Colorado is made more improbable by the frequent water-level fluctuations (Fig. 2). A decline in water level would expose fertilized eggs deposited in shallow lentic areas—the only locations where the water might be warm enough to otherwise allow reproduction.

TABLE 2.—*Food organisms in the stomachs of humpback chubs collected from the Little Colorado and Colorado rivers. Data are mean percentages of the total number of organisms per sample, and mean frequencies (percent of stomachs) within samples for each food organism. A sample is the group of stomachs (including those that were empty) collected during a season (quarter-year). Ranges for samples are in parentheses. T = trace (<0.5%).*

Taxon or measure	Little Colorado (4 samples; 26 fish)	Colorado (2 samples; 18 fish)
Number of organisms per stomach	7 (3–14)	192 (49–336)
Chironomidae		
% numbers	36 (6–92)	28 (T–55)
% frequency	37 (20–50)	50 (11–89)
Simuliidae		
% numbers	22 (0–90)	71 (43–99)
% frequency	5 (0–20)	56 (33–78)
Other Diptera[a]		
% numbers	12 (0–36)	T (T)
% frequency	22 (0–50)	11 (11)
Trichoptera		
% numbers	18 (0–67)	T (T)
% frequency	16 (0–50)	6 (0–11)
Neuroptera		
% numbers	2 (0–10)	0
% frequency	7 (0–27)	0
Coleoptera		
% numbers	2 (0–6)	T (T)
% frequency	18 (0–50)	11 (11)
Gammarus		
% numbers	0	1 (T–2)
% frequency	0	22 (11–33)
Other[b]		
% numbers	7 (0–17)	T (T)
% frequency	35 (0–100)	11 (11)

[a] Ceratopogonidae, *Hemerodromia*, Ephydridae, *Limnophora*.

[b] Ephemeroptera, Orthoptera, Hymenoptera, Oligochaeta, Nematoda, *Pimephales promelas*.

Stomach Contents

Stomach contents from humpback chubs were numerically dominated by immature Chironomidae and Simuliidae (Table 2). Two fish from the Little Colorado contained fish remains, including a fathead minnow *Pimephales promelas* about 50 mm long. Although the amphipod *Gammarus* sp. was abundant in many littoral areas of the Colorado, it was relatively uncommon among the stomach contents. Twelve of the 26 humpback chub stomachs from the Little Colorado and 5 of the 18 stomachs from the Colorado were empty. A few fish were kept in holding pens 1–2 hours before they were killed; digestion or regurgitation while fish were in pens or trammel nets may in part account for the numbers of empty stomachs found. The large number of organisms in humpback chub stomachs from the Colorado suggests that food organisms might be more available in the Colorado than in the Little Colorado.

Pathogens

Thirteen species of bacteria, six protozoans, and the fungus *Saprolegnia*—all common fish pathogens—were identified in low incidence from humpback chubs (Rex Flagg, Fish Disease Control Center, USFWS, Fort Morgan, Colorado, personal communication). However, many adult humpback chubs collected from the confluence and from the lower Little Colorado during the 1981 spawning season showed acute signs of systemic *Aeromonas hydrophila* infection, including abundant petechia and poor physical condition.

Lernaea cyprinacea (Copepoda) was the most conspicuous metazoan parasite encountered. Infection incidence was highest in winter and lowest in spring in the Little Colorado and the confluence (C 4). Only six infected fish were collected from the Colorado (Table 3). The intensity of *L. cyprinacea* infection was below that reported where appreciable mortality of other host species has occurred (for example, Bauer 1959), but high infection incidence in small humpback chubs in the Little Colorado during December could result in mortality from secondary infection by other pathogens. Optimal temperatures for the development of *L. cyprinacea* are between 23 and 30 C; the life cycle cannot be completed below 14 C (Bauer 1959), near the maximum temperature found in the Colorado (Fig. 2). Thus, the capture of infected humpback chubs from the Colorado strongly suggests movement of the fish from the Little Colorado.

TABLE 3.—*Seasonal incidence of* Lernaea cyprinacea *infection of humpback chubs of three length categories from the Little Colorado River, the confluence, and the Colorado River. Data are given as number of fish examined/number infected (percent infected in parentheses).*

Length class	Little Colorado	Confluence	Colorado
	Winter (Dec)		
<100 mm	20/9 (45)		
100–200 mm	7/5 (71)		
>200 mm	50/25 (50)		
Total	77/39 (51)		
	Spring (Feb–May)		
<100 mm	50/4 (8)	11/1 (9)	34/0 (0)
100–200 mm	16/1 (6)	12/0 (0)	10/1 (10)
>200 mm	178/8 (4)	48/3 (6)	22/1 (5)
Total	244/13 (5)	71/4 (6)	66/2 (3)
	Summer (July–Aug)		
<100 mm	57/7 (12)	21/0 (0)	
100–200 mm	61/21 (34)	12/6 (50)	
>200 mm	1/0 (0)		
Total	119/28 (24)	33/6 (18)	
	Fall (Oct–Nov)		
<100 mm	9/1 (11)	4/1 (25)	21/1 (5)
100–200 mm	28/7 (25)	2/2 (100)	16/0 (0)
>200 mm	29/10 (34)	35/16 (46)	32/3 (9)
Total	66/18 (27)	41/19 (46)	69/4 (6)

No relationship between fish size and incidence of *L. cyprinacea* infection was apparent. Infection site on the exterior surface of the fish was usually near the fin base (buccal and opercular cavities were not regularly examined). Of 271 copepods seen, 32% were associated with the dorsal fin, 24% with the pelvic fins, 21% with the pectoral fins, 13% with the anal fin, 2% with the caudal fin, and 8% with other body parts. Mean intensity of infection was 1.7 copepods per infected fish; 63.6% of 162 infected fish hosted one parasite; the maximum number was seven.

Recapture of Tagged Humpback Chubs

Recaptures of tagged fish included 17 of 433 (3.9%) tagged in the Little Colorado, 13 of 242 (5.4%) tagged at the confluence (C 4), and two of 45 (4%) tagged in the Colorado. One fish was recaptured twice from the Little Colorado, 5 and 15 months after tagging. Recaptured fish at large from 1 day to 16 months were as much as 17.1 km from the point of release (Fig. 6). Thirteen recaptures, mostly from reaches LC

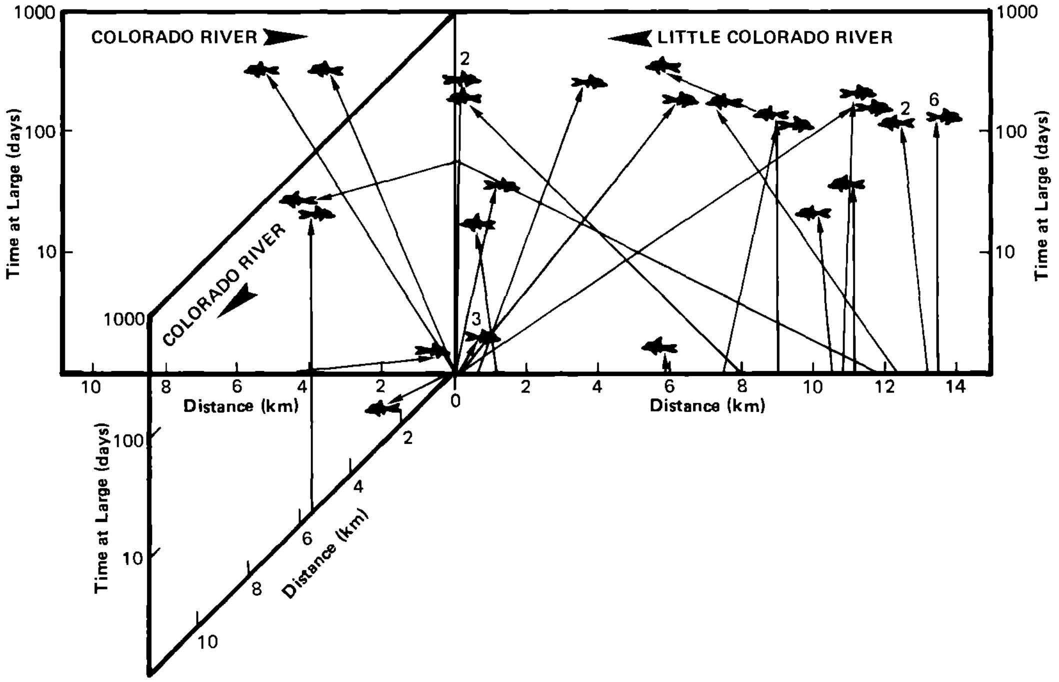


FIGURE 6.—*Diagrammatic representation of the study area, showing points of initial capture and subsequent recapture of tagged humpback chubs. Numbers designate multiple observations.*

2 and 3, were within 0.3 km of the release site; the remaining 19 fish recaptured were displaced an average of 3.8 km. No relationship was evident between time at large and displacement distance.

Tagging can induce stress and latent debilitation in fish due to handling, secondary infection, and the drag effect of the tag—problems that could result in downstream movement that would otherwise not occur. Although many humpback chubs were recaptured near their original tagging site, which suggests that the effect of tagging was not important, two fish were recaptured in poor condition 2–4 km downstream 1 or 2 days after release during the 1981 spawning season (Fig. 6). Fish experiencing adverse tagging effects seem unlikely to make significant upstream movements, however. Nine of 10 tagged humpback chubs that moved more than 0.3 km upstream had been tagged during the 1980 or 1981 spawning period (April–June). Seven were recaptured from the Little Colorado during that same or the next spawning season, whereas two were recovered from the Colorado upstream from the confluence after the spawning season. These recoveries suggest that movement of adult humpback chubs within the study area might be related largely to spawning, and that this movement might occur between rivers.

Analyses of Catch Statistics

Age-0 and Juvenile Fish

Minnow traps collected mostly age-0 humpback chubs, 80 ± 23 mm long (mean ± SD), whereas seines collected age-0 and juvenile fish 92 ± 46 mm long. Mean *C/f* by seine was higher during darkness than during daylight, except during three sampling trips (August and October 1981) when waters were turbid in the Little Colorado and at the confluence, and one (July 1980) when the water was clear in the Little Colorado but small humpback chubs might have been particularly abundant (Fig. 7). Although it may be speculated that humpback chubs eluded seines during daylight, water clarity in the Little Colorado and the Colorado readily allowed us to see that the number of fish escaping seines was trivial. Our data suggest that

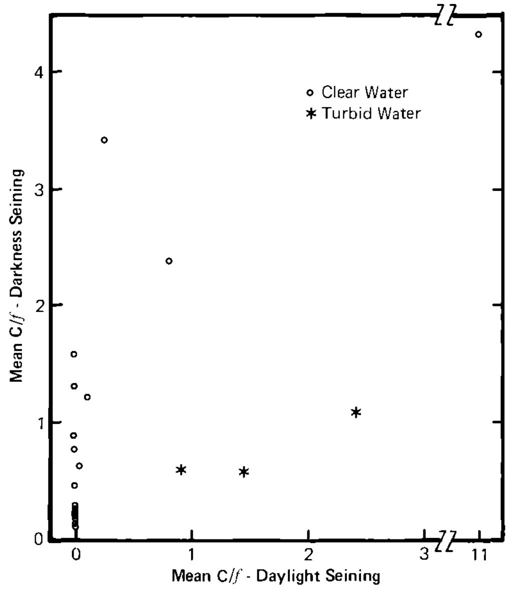


FIGURE 7.—*Relationships between mean catch rates by seine during darkness (2–14 seine hauls per mean; average 6.9) and during daylight (2–18; 9.8) for age-0 and juvenile humpback chubs in the Little Colorado River, confluence, and Colorado River, 1980–1981. Each data point gives the mean catch rates for the 2-day collection effort at a sampling site; efforts that yielded no humpback chubs in both diel periods are not included. Seven data points are included in the aggregation near the origin.*

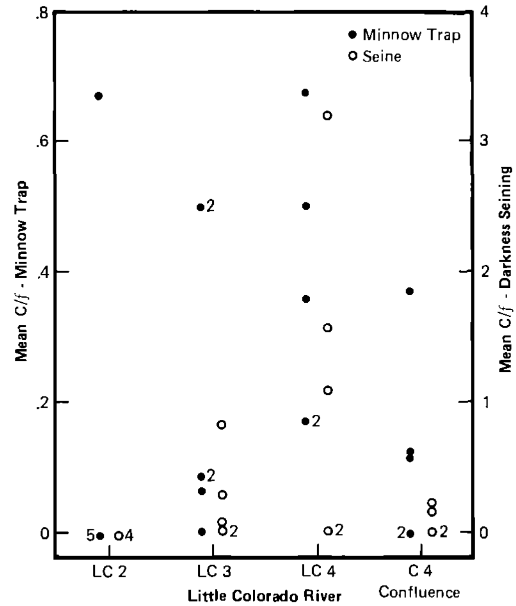


FIGURE 8.—*Mean catch rates for age-0 and juvenile humpback chubs collected by minnow traps and seines during darkness from reaches LC 2, 3, and 4 of the Little Colorado River and from the confluence of this tributary with the Colorado River, 1980–1981. Numbers designate multiple observations.*

humpback chubs avoid the clear, shallow water swept by our seines during daylight, a hypothesis supported by the occurrence of humpback chubs in these same littoral areas when the water is turbid.

Mean *C/f* for age-0 humpback chubs collected by minnow trap and by seine during darkness from the Little Colorado (data largely from 1981) increased with proximity to the confluence (Fig. 8). Although this relationship suggests that downstream reaches were most important for humpback chub reproduction in 1981, downstream drift or movement of small fish could account for this distribution. Data on seining during daylight for the postspawning period in 1980 and 1981 are more detailed than are the data for seining during darkness, and they provide evidence of differences in humpback chub reproductive success between years. Mean *C/f* for age-0 humpback chubs was appreciably higher in 1980 than in 1981; density was greatest at LC 2, where no age-0 humpback chubs were collected in 1981 (Table 4). Seasonal runoff coincident with spawning could significantly enhance humpback chub reproductive success in the Little Colorado, particularly in upstream regions. Seasonal runoff occurred during the spawning season in 1980 but not in 1981. Humpback chubs that spawned in hatchery raceways laid eggs that adhered to rock substrate where they were deposited (Hamman 1982). Runoff of the Little Colorado removes fine travertine sediments that could suffocate developing humpback chub embryos. Runoff also dilutes chemically concentrated spring waters, which otherwise might be harmful to embryos and larvae.

Adults

Of 504 humpback chubs averaging 278 ± 54 (SD) mm long collected in trammel nets, 93% were classified as adults. Higher catch rates during sunset and darkness than during daylight suggested that activity of the fish increased as light diminished, although avoidance of nets during daylight cannot be discounted. Many of

TABLE 4.—*Mean catch rates for age-0 humpback chubs collected by seine during daylight from the Little Colorado River and its confluence with the Colorado River.*

Date and measure	River and reach			
	Little Colorado			Confluence
	LC 2	LC 3	LC 4	C 4
July 1980				
Mean fish/100 m² (SD)	13.3 (2.3)	4.7 (1.6)	1.9 (0.4)	4.1 (0.6)
Total effort (m²)	574	1,324	1,344	266
August 1981				
Mean fish/100 m² (SD)	0.0 (0.0)	0.9 (0.1)	0.5 (0.1)	0.7 (0.1)
Total effort (m²)	1,678	2,644	2,306	2,538

the highest mean values of C/f were from LC 2 and 3; however, there was no consistent relationship between catch rate and river reach within the Little Colorado. Mean C/f from reaches LC 3 and 4 increased in all diel periods between February and April–May 1981 (Fig. 9), perhaps because vulnerability to capture was greater during the spawning period or because mature fish were moving from the Colorado into the Little Colorado to spawn.

The distribution of mean C/f from the reaches in the Colorado followed a bell-shaped curve about the confluence (Fig. 10). Adult humpback chubs from the Colorado are probably associated with the confluence because of the importance of the Little Colorado for reproduction.

Interspecific Associations

Fourteen fish species and one hybrid were found in the study area. Seines and minnow traps collected all ages of fathead minnows, speckled dace *Rhinichthys osculus*, and plains killifish *Fundulus zebrinus*, and age-0 and juveniles of other species that attain relatively large size at maturity. Adults of the species of large fish were collected most often by trammel net (Fig. 11).

No Colorado squawfish, razorback suckers, or bonytails were encountered. Nearly all fathead minnows, plains killifish, and juvenile bluehead suckers *Catostomus discobolus* in the Colorado were collected below the confluence, suggesting that they reproduce in the Little Colorado. Distributions for speckled dace and flannelmouth sucker *Catostomus latipinnis* suggested some reproduction in the Colorado or its tributaries upstream. Of the salmonids collected, 86% were rainbow trout *Salmo gairdneri*. Cutthroat trout *Salmo clarki*, hybrid rainbow trout × cutthroat trout, brown trout *Salmo trutta*, and brook trout *Salvelinus fontinalis* also were found.

Only a few redside shiners *Richardsonius balteatus*,[4] black bullheads *Ictalurus melas*, channel catfish *Ictalurus punctatus*, and common carp *Cyprinus carpio* were collected, although angling and electrofishing suggested that channel catfish and common carp are abundant in some areas of the Colorado. The small catch of these species prevented their inclusion in the graphic presentation (Fig. 11).

Although each of the species collected from the study area is a potential colonizer, only humpback chubs, speckled dace, bluehead suckers, and fathead minnows were found in the Little Colorado in large numbers. The large travertine dams separating LC 1 and 2 may have prevented upstream fish movement. Only speckled dace and fathead minnows lived in LC 1, and these species plus humpback chubs and bluehead suckers were found immediately downstream in LC 2. Species diversity in the Little Colorado increased with proximity to the confluence.

No significant linear relationships were found between mean C/f for humpback chubs and those for individual sympatric species, which suggests that the occurrence of another species does not significantly affect the relative abundance of humpback chubs within the study area. However, adult humpback chubs from the Little Colorado sometimes exhibited apparent channel catfish bite marks—similar crescent-

[4] This represents a range extension for redside shiner. Voucher specimens have been deposited in the museum at the USFWS National Fish and Wildlife Laboratory, 1300 Blue Spruce Drive, Fort Collins, Colorado, 80524.

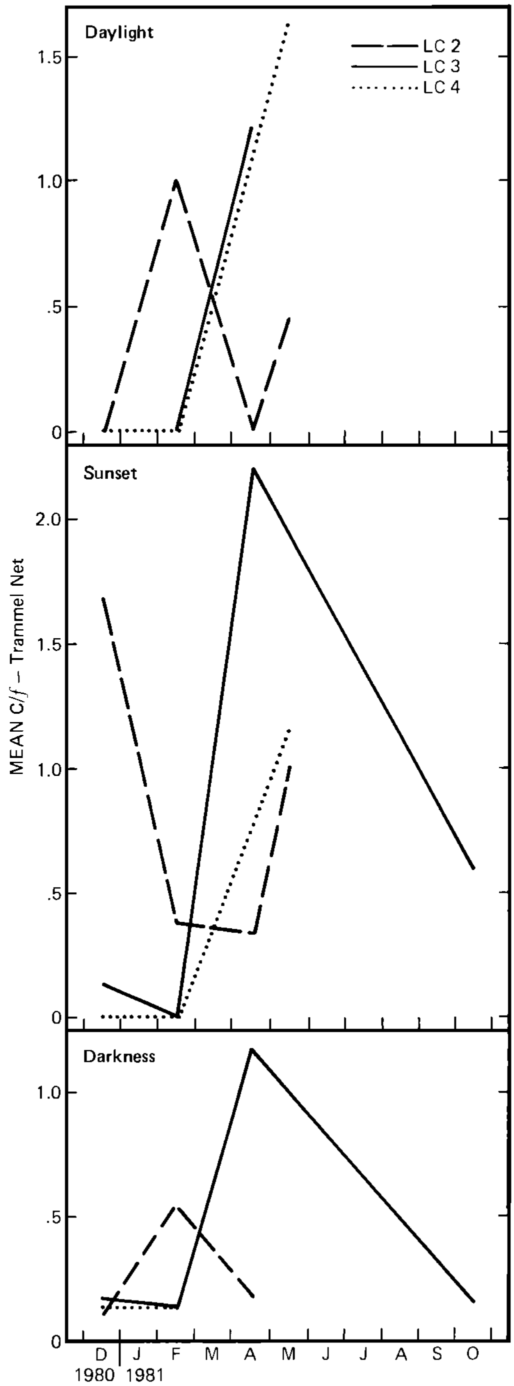


FIGURE 9.—*Mean catch rates for humpback chubs collected by trammel net during three diel periods from reaches LC 2, 3, and 4, Little Colorado River, 1980–1981. Inflection points indicate collection date.*

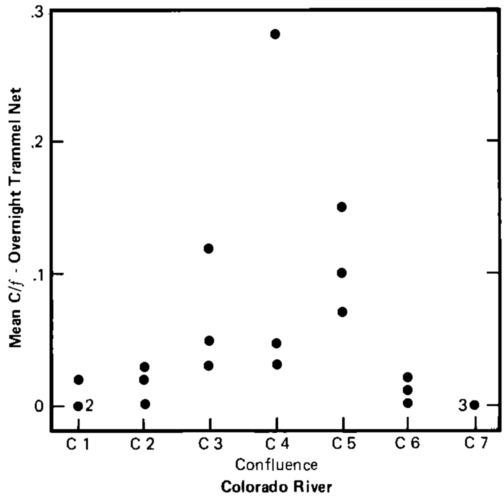


FIGURE 10.—*Mean catch rates for humpback chubs collected by trammel net fished overnight in the Colorado River and its confluence with the Little Colorado River, 1980–1981. Numbers designate multiple observations.*

shaped wounds on both sides of the body with various degrees of healing and infection. This observation suggests that channel catfish might be an important predator on humpback chubs in the Little Colorado. Humpback chubs and channel catfish were sometimes observed in shaded areas during daylight, particularly those areas under overhanging rock ledges where considerable opportunity for predation might exist.

Meristic Variation

None of the juvenile or adult humpback chubs handled in the field, or brought back to the laboratory for taxonomic analyses (Glenn Clemmer, National Fish and Wildlife Laboratory, USFWS, Fort Collins, Colorado, personal communication)[5] differed from published descriptions of *Gila cypha* from the Grand Canyon area (Suttkus and Clemmer 1977). Eight combinations of dorsal/anal fin-ray counts were found; the 9/10 combination characteristic of humpback chubs was most common (Table 5). However, pair-wise chi-square analyses demonstrated that combination frequencies from LC 4 and the confluence (C 4) differed significantly ($P <$

[5] All specimens have been deposited at the National Fish and Wildlife Laboratory (see footnote 4).

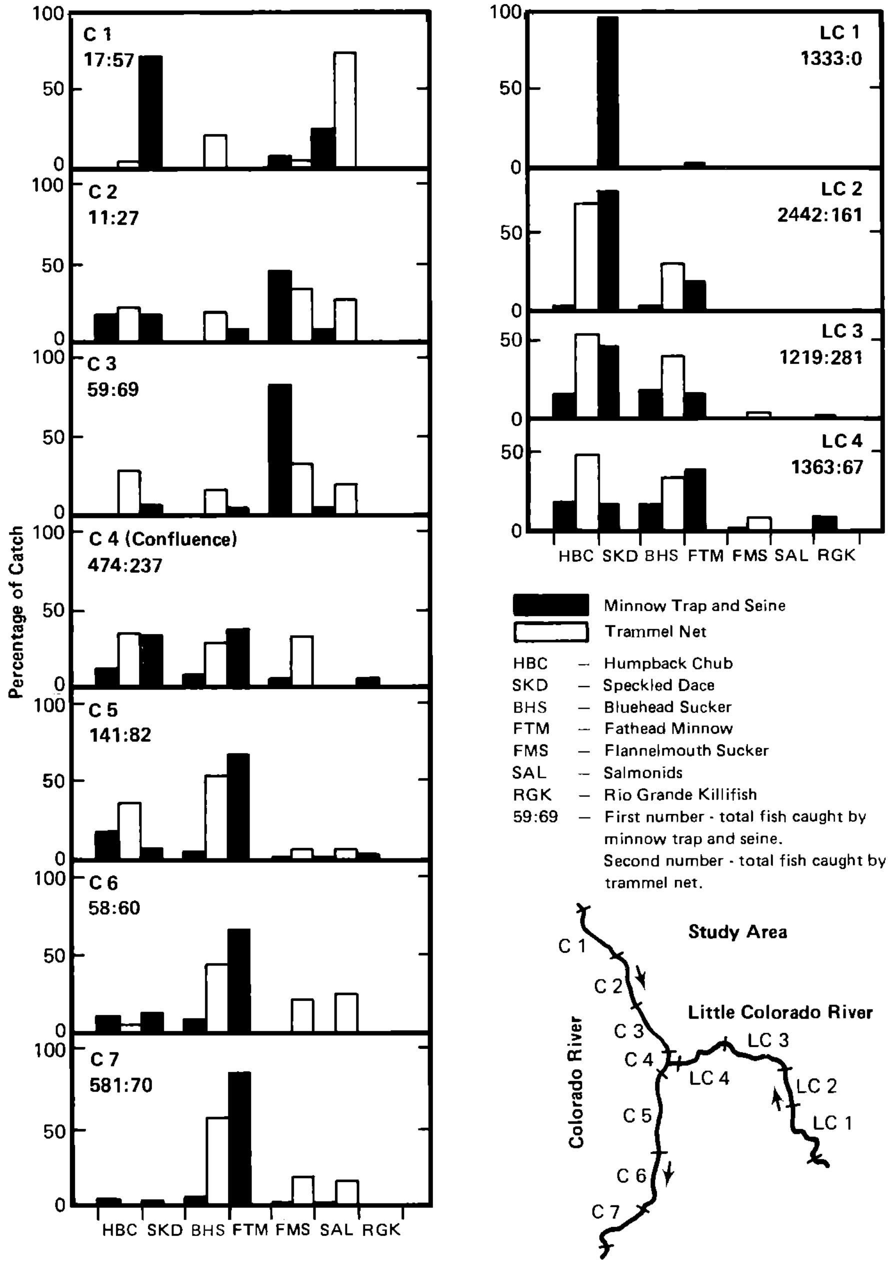


FIGURE 11.—*Relative abundance (percent) of the dominant species caught by minnow trap and seine, and by trammel net from Little Colorado River, confluence, and Colorado River reaches, 1980–1981.*

0.01) from those in LC 2 and LC 3. This difference was due to the high frequency of the 10/10 combination in LC 4 and the confluence. No differences were observed among Colorado River reaches, or between the total Colorado River sample and individual Little Colorado River reaches or the confluence; however, the total Colorado River sample was small.

Ecotypic variation can occur among populations in response to differences in their respec-

TABLE 5.—*Frequency (percent) of dorsal/anal fin-ray counts for humpback chubs longer than 100 mm collected from the Little Colorado River, confluence, and Colorado River.*

Reach	*N*	Dorsal/anal fin-ray counts							
		9/10	10/10	9/9	9/11	10/11	8/10	10/9	11/10
				Little Colorado					
LC 2	168	81.0	7.1	7.1	1.8	0	1.8	1.2	0
LC 3	296	80.4	7.1	7.4	2.0	2.0	0.7	0.3	0
LC 4	57	70.2	17.5	7.0	1.8	1.8	1.8	0	0
				Confluence					
C 4	216	67.6	16.7	7.4	3.2	3.2	0.9	0.5	0.5
				Colorado					
C 1	2	50.0	0	50.0	0	0	0	0	0
C 2	8	87.5	0	12.5	0	0	0	0	0
C 3	19	78.9	5.3	10.5	5.3	0	0	0	0
C 5	42	69.0	11.9	14.3	2.4	2.4	0	0	0
C 6	5	100.0	0	0	0	0	0	0	0
C 7	3	33.3	0	66.7	0	0	0	0	0
Total	816	75.7	10.4	8.1	2.3	1.8	1.0	0.5	0.1

tive physicochemical environments, and marked differences in physicochemical characteristics exist between the Little Colorado and the Colorado (Table 1; Fig. 2). Young humpback chubs that move from the Little Colorado into the cooler waters of the Colorado might form more fin rays than do humpback chubs that remain in the Little Colorado. Such relationships between temperature experienced by embryos and early larvae and the development of fin rays have been demonstrated for several fish species (Blaxter 1969). However, the nearly complete mortality of embryonic and larval humpback chubs at the temperatures of the Colorado (Hamman 1982) seems to us to preclude temperature-induced ecotypic variation as a possible explanation for the observed differences in ray counts. We believe that a more plausible hypothesis is suggested by the work of Holden and Stalnaker (1970). They found many *Gila* from the Colorado of Glen Canyon, about 100 km upstream from our study area, with morphologies that integraded between the humpback chub and the bonytail. Holden and Stalnaker speculated that the presence of these intergrade forms is an indication of incompete speciation and of subsequent interbreeding. The high frequency of the 10/10 ray-count combination—more characteristic of the bonytail than of the humpback chub (Miller 1946; Holden and Stalnaker 1970)—could indicate the occurrence of some bonytail genes in the humpback chub population from the lower Little Colorado.

Analysis

The Little Colorado immediately upstream of our study area was formerly a perennial stream. Colorado squawfish, bonytail, and roundtail chub are among the fishes that may have then occurred in the river as far upstream as Grand Falls, a barrier to upstream movement about 120 km above the confluence (Miller 1963; Smith et al. 1979). Changing land-use practices and water impoundments in the drainage led to seasonal dewatering of this reach of the Little Colorado River about the turn of the century (Miller 1961), and thereby reduced the region where perennial flow occurs to that of our study area. Seasonal dewatering of the upstream reach might have eliminated use of the Little Colorado by species other than those tolerant of its present physicochemical conditions.

The alteration of the Colorado River environment that resulted from closure of Glen Canyon Dam was too rapid for adaptation by species unable to persist under the new conditions. We believe that the humpback chub persisted, whereas other endemic species were eliminated, because a portion of the humpback chub population spawned in the Little Colorado. Because the modified Colorado River thermal regimen is not entirely unlike that of the past (Fig. 2), humpback chubs in the Colorado can undergo normal seasonal gonad development up to the point of spawning. However, we believe that significant reproductive success can occur only if mature fish enter the Little Colorado to spawn. Selection for development of such a spawning migration would be very strong, and our data suggest that some humpback chubs do move from the Colorado into the Little Colorado to spawn. The alteration of the Colorado River environment could have forced bonytails there to spawn in the lower Little Colorado; some interbreeding might then have occurred with humpback chubs before the bonytail stock was eliminated. Such hybridization between cyprinid species has been documented in other waters where environmental disturbance and the loss of reproductive habitat have occurred (see Gilbert 1961). There are evidently no chromosomal differences between the two species that would prevent gene exchange between humpback chub and bonytail populations, because fertile hybrids have been artificially produced in the hatchery. The humpback chub × bonytail hybrids produced by Hamman (1981) matured in the hatchery at 2 years of age and were introgressively crossed with parent stocks; hatching success, about 60% at 17 C, did not differ among the F_2 generations (Theophilus Inslee, Dexter National Fish Hatchery, USFWS, Dexter, New Mexico, personal communication).

Although the Little Colorado seems isolated from potential human-caused perturbations, perpetuation of this area as reproductive habitat for the humpback chub is not assured. Few species now live in the river, and competitive or predatory interactions may not have important effects on humpback chubs. The unsuitability of the Little Colorado and Colorado river environments for many of the fish species in the drainage could, in part, account for the persistence of humpback chubs in the Little Colorado. However, our collection of the redside shiner, a recent immigrant to the Colorado of the Grand Canyon, suggests that colonization of our study area by species for which this environment is favorable might not be complete. Introduction to the Little Colorado of such a species that might prosper under the physicochemical conditions of the river could have a devastating effect on the humpback chub in the Grand Canyon.

Acknowledgments

We thank the many individuals who helped with the study, particularly Flagstaff field station personnel including C. O. Minckley, Kim Sylvester, Mike Hurley, Wendy Ripp, Don King, and Alan Fredericksen, and the many persons who provided a ready source of field assistance. Project Leader Bill Miller and Assistant Project Leaders Don Archer and Joe Valentine provided valuable administrative and technical support. Glenn Clemmer and Darrel Snyder verified and provided identifications of fish species. Jerry and Donna Jacobi analyzed stomach contents of humpback chubs. Pathologic analyses were made by Rex Flagg. Charlie Smith performed the histologic work on humpback chub gonads. R. V. Bulkley, J. E. Johnson, and R. Pimentel commented on the manuscript.

Dean Blinn and H. E. Graham, Biology Department, Northern Arizona University, provided laboratory equipment and space. Norm Sharber designed and built the electrofishing boat and provided logistic support, as did Steve Carothers. Jim Walters, Grand Canyon National Park, as well as numerous other park personnel, provided assistance throughout the study. Mary P. Young prepared the illustrations.

Funding was provided largely by the United States Bureau of Reclamation; additional funds were provided by the National Park Service and the United States Fish and Wildlife Service. The Navajo and Hopi Indian Relocation Commission provided office equipment and space.

References

BAUER, O. N. 1959. Parasites of freshwater fish and the biological basis for their control. Bulletin of the State Scientific Research Institute of Lake and River Fisheries 49, Leningrad, Russia. Translated from the Russian: National Technical Information Service, OTS 61-31056, Springfield, Virginia, USA.

BLAXTER, J. H. S. 1969. Development: eggs and larvae. Pages 177–252 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume 3. Academic Press, New York, New York, USA.

COLE, G. A., AND D. M. KUBLY. 1976. Limnologic studies on the Colorado River from Lees Ferry to Diamond Creek. Colorado River Research Program, Grand Canyon National Park, Technical Report 8, Grand Canyon, Arizona, USA.

COOLEY, M. E., J. W. HARSHBARGER, J. P. AKERS, AND W. F. HARDT. 1969. Regional hydrology of the

Navajo Hopi Indian Reservations, Arizona, New Mexico, and Utah. United States Geological Survey, Professional Paper 521-A.

DOLAN, R., A. HOWARD, AND A. GALLENSON. 1974. Man's impact on the Colorado River in the Grand Canyon. American Scientist 62:392–401.

GILBERT, C. R. 1961. Hybridization versus intergradation: an inquiry into the relationship of two cyprinid fishes. Copeia 1961:181–192.

HAMMAN, R. L. 1981. Hybridization of three species of chub in a hatchery. Progressive Fish-Culturist 43:140–141.

HAMMAN, R. L. 1982. Spawning and culture of humpback chub. Progressive Fish-Culturist 44: 213–216.

HOLDEN, P. B., AND C. B. STALNAKER. 1970. Systematic studies of the cyprinid genus *Gila*, in the upper Colorado River basin. Copeia 1970:409–420.

HOLDEN, P. B., AND C. B. STALNAKER. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basins, 1967–1973. Transactions of the American Fisheries Society 104:217–231.

MILLER, R. R. 1946. *Gila cypha*, a remarkable new species of cyprinid fish from the Colorado River in Grand Canyon, Arizona. Journal of the Washington Academy of Sciences 36:409–415.

MILLER, R. R. 1961. Man and the changing fish fauna of the American southwest. Papers of the Michigan Academy of Science, Arts, and Letters 46: 365–404.

MILLER, R. R. 1963. Distribution, variation, and ecology of *Lepidomeda vittata*, a rare cyprinid fish endemic to eastern Arizona. Copeia 1963:1–5.

MINCKLEY, C. O., AND D. W. BLINN. 1976. Summer distribution and reproductive status of fish of the Colorado River in Grand Canyon National Park and vicinity, 1975. Colorado River Research Program, Grand Canyon National Park, Technical Report 14, Grand Canyon, Arizona, USA.

MINCKLEY, C. O., S. W. CAROTHERS, J. W. JORDAN, AND H. D. USHER. 1980. Observations on the humpback chub, *Gila cypha*, within the Colorado and Little Colorado rivers, Grand Canyon National Park, Arizona. United States National Park Service Transactions and Proceedings Series 8: 176–183.

MINCKLEY. W. L., AND J. E. DEACON. 1968. Southwestern fishes and the enigma of "endangered species." Science (Washington, District of Columbia) 159:1424–1432.

SMITH, G. R., R. R. MILLER, AND W. D. SABLE. 1979. Species relationships among fishes of the genus *Gila* in the upper Colorado River drainage. United States National Park Service Transactions and Proceedings Series 5:613–623.

SUTTKUS, R. D., AND G. H. CLEMMER. 1977. The humpback chub, *Gila cypha*, in the Grand Canyon area of the Colorado River. Occasional Papers Tulane Museum of Natural History 1, New Orleans, Louisiana, USA.

SUTTKUS, R. D., AND G. H. CLEMMER. 1979. Fishes of the Colorado River in Grand Canyon National Park. United States National Park Service Transactions and Proceedings Series 5:599–604.

VANICEK, C. D., AND R. H. KRAMER. 1969. Life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964–1966. Transactions of the American Fisheries Society 98:193–208.

VANICEK, C. D., R. H. KRAMER, AND D. R. FRANKLIN. 1970. Distribution of Green River fishes in Utah and Colorado following closure of Flaming Gorge Dam. Southwestern Naturalist 14:297–315.