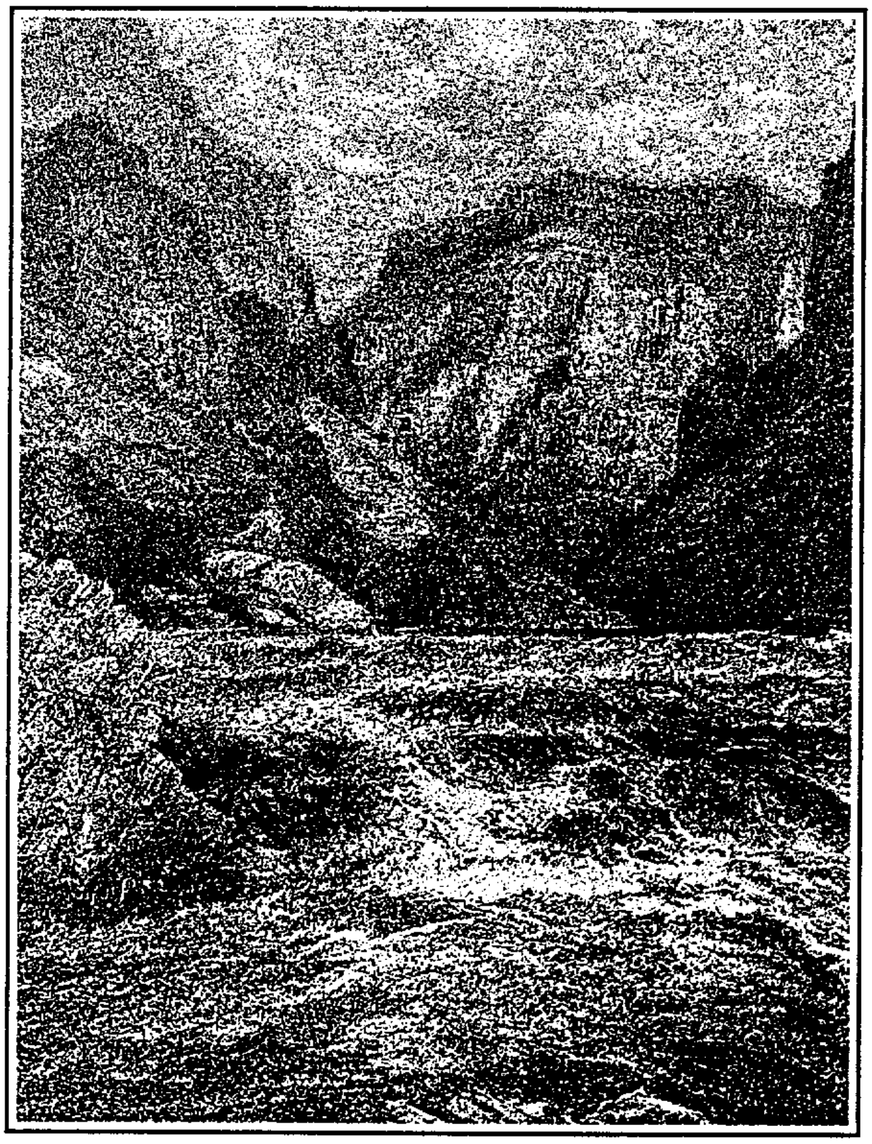
Life History and Ecology of the Humpback Chub (<u>Gila cypha</u>) in the Colorado River, Grand Canyon, Arizona

Executive Summary



Bureau of Reclamation

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Glen Canyon Environmental Studies

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Cover drawing from Powell (1875)

OVERVIEW

This Executive Summary accompanies the Final Report submitted by BIO/WEST, Inc. to Bureau of Reclamation for Contract No. 0-CS-40-09110. The Final Report is entitled Life History and Ecology of the Humpback Chub (Gila cypha) in the Colorado River, Grand Canyon, Arizona. This summary provides an overview of findings. The reader is referred to the Final Report for more detailed information. Also, six supplements to the Final Report are available, including a Data Collection Plan, Evaluation of Sampling Design, Photographic Record of Humpback Chub, Grand Canyon Fisheries Integrated Database, Development of a Population Model for Humpback Chub in Grand Canyon, and a Flow Routing Model. Copies of these reports can be obtained from BIO/WEST in Logan, Utah, or Glen Canyon Environmental Studies in Flagstaff, Arizona.

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EXECUTIVE SUMMARY

INTRODUCTION

The life history and ecology of the humpback chub (Gila cypha) in the Colorado River in Grand Canyon was studied from October 1990 through November 1993, as part of the Glen Canyon Environmental Studies (GCES). The purpose of the investigation was to describe the ecological requirements of the species and evaluate the effects of Glen Canyon Dam operations on the various life stages.. The objectives of the study were to describe and identify limiting factors to distribution, abundance, survivorship, movement, habitat, food habits, and reproductive capacity. Important biotic interactions and the life history schedule for the species were also described. This life history information was used to identify management options and recommendations for core research and monitoring with respect to dam operations. This investigation was designed to integrate with other companion studies and provide the framework for an integrated scientific report by GCES.

THE COLORADO RIVER

Preceding the summary of the life history of the humpback chub is a characterization of the changes to the Colorado River following the construction of Glen Canyon Dam, as a perspective of the physical and chemical changes to the aquatic ecosystem in Grand Canyon. The physical, chemical, and biological nature of the Colorado River in Grand Canyon was changed dramatically after it was impounded by Glen Canyon Dam in March of 1963. Since impoundment, water has been released through the dam under six operational scenarios, each with unique characteristics but all with common features. The dam eliminated spring floods and increased low base flows in late summer, fall, and winter. Daily fluctuations for hydropower generation became a normal feature of the hydrograph (Fig. 1), and flows of over 31,500 cfs and below 1,000 cfs were eliminated. Daily flows varied by as much as 30,000 cfs. Interim flows implemented in August 1991 decreased high flows to 20,000 cfs and increased lows to 5,000 cfs, with reduced daily fluctuations.

The physical and chemical nature of the river were also substantially altered by the dam, primarily from retention of sediments in Lake Powell and cold hypolimnetic releases. The predam temperature range at Lees Ferry of 2 to 26°C was modified to a range of 7 to 12°C, resulting in colder spring, summer, and fall temperatures, and warmer winter temperatures. This temperature pattern did not

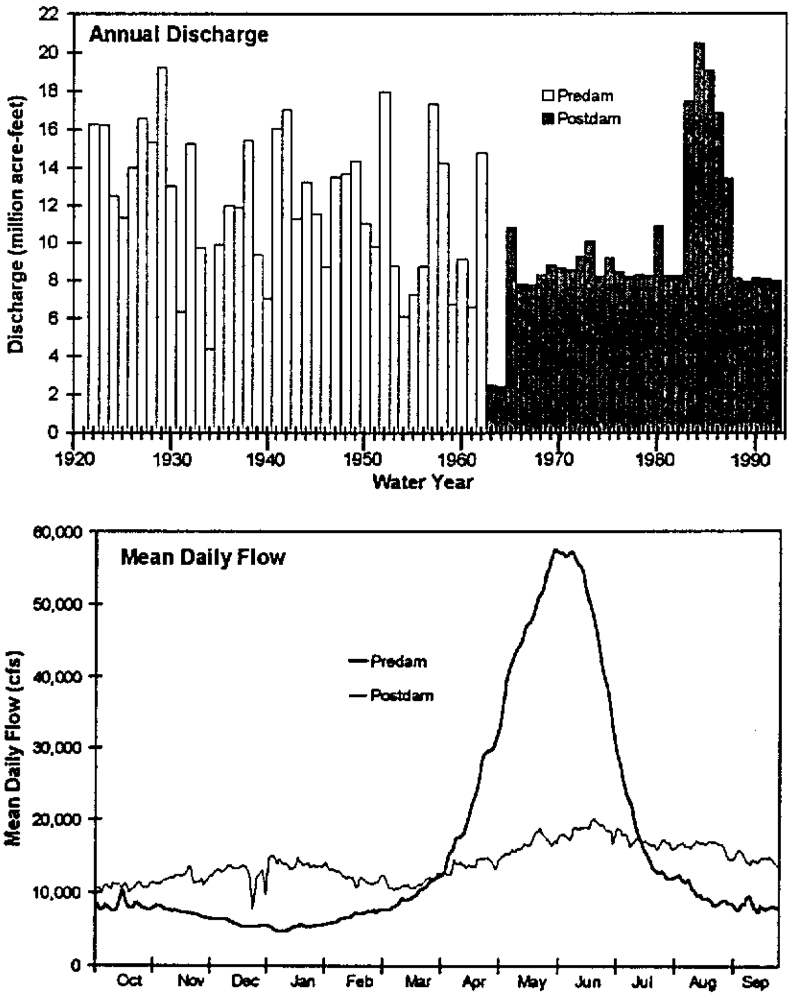


Fig. 1. Annual discharge (WY 1922-92) and mean daily predam (WY 1922-62) and postdam (WY 1965-92) flow of the Colorado River at Lees Ferry, AZ.

become fully evident until about 1970 (Fig. 2), when Lake Powell reached sufficient depth to stratify. Maximum longitudinal warming of the Colorado River below the dam now occurs in late summer at a rate of about 1°C/51 km.

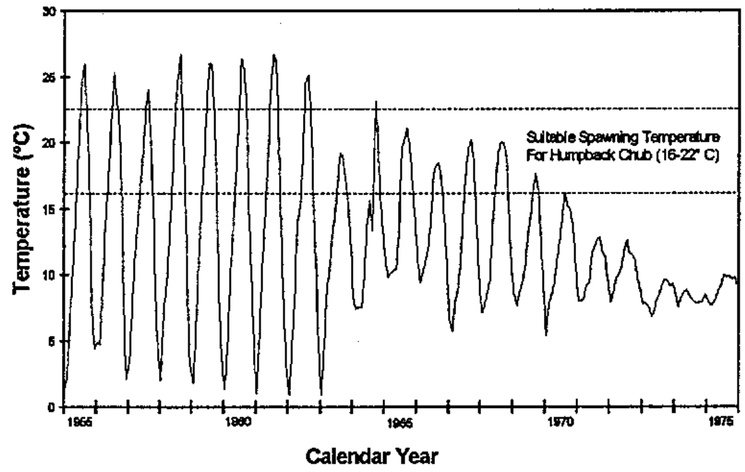


Fig. 2. Mean monthly water temperature at Lees Ferry following closure of Glen Canyon Dam and impoundment of Lake Powell on March 13, 1963. Monthly means are based on measurements at 15-min intervals. Suitable spawning temperature range for humpback chub is shown at 16-22°C.

Post dam sediment load of the Colorado River was reduced by about 90% from retention in Lake Powell, and removal of sediments through Grand Canyon has been substantial as a result of scouring and clear water releases. This has greatly reduced allochthonous material in the Colorado River in Grand Canyon and modified availability of aquatic food supplies, while converting the system from heterotrophic to autotrophic energy sources. Clear, cold releases probably eliminated many of the invertebrates native to the river, leaving only nearctic species. The degree and frequency of turbidity has been reduced and sediment replacement is now primarily from the Paria River and the Little Colorado River (LCR). Daily fluctuations maintain turbidity in the mainstem and a regular supply of food in the system. Water clarity is substantially increased when flows are low and constant (Fig. 3).

DISTRIBUTION

The present distribution of humpback chub in Grand Canyon is related to mainstem temperature, locations of warm tributaries and springs, occurrence of suitable adult habitat, and food availability. Humpback chub were found in 308 km of the mainstem Colorado River, from Shinumo Wash (RM 29) to Granite Springs Canyon (RM 220), as nine persistent aggregations in which 94% of 6,294 chubs (92% of YOY, 94% of juveniles and 98% of adults) were captured (Fig. 4). Four of these aggregations were associated with warm tributaries (LCR, Bright Angel Creek, Shinumo Creek, Havasu Creek), and two with warm springs (Fence Fault Springs, Pumpkin Spring), indicating that fish were attracted to thermal areas in the cold river. Four aggregations, including the two largest, were associated with unique geomorphic reaches (LCR, Lava to Hance, Stephan Aisle, Middle Granite Gorge), characterized by numerous debris fans and associated recirculating eddies.

Longitudinal warming in summer of 1°C/51 km increased mainstem temperature from an average of

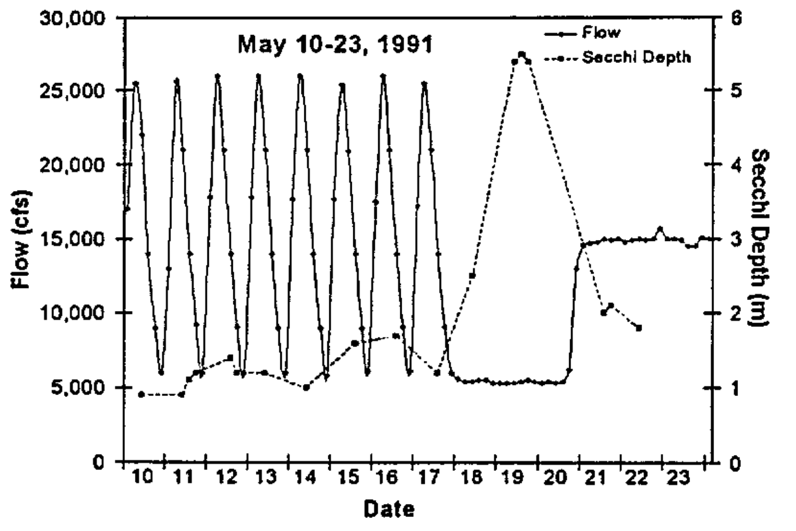


Fig. 3. Relationship of flow to Secchi depth during a transition of high fluctuating releases (7,000-25,000 cfs) to constant 5,000 cfs, May 10-23, 1991.

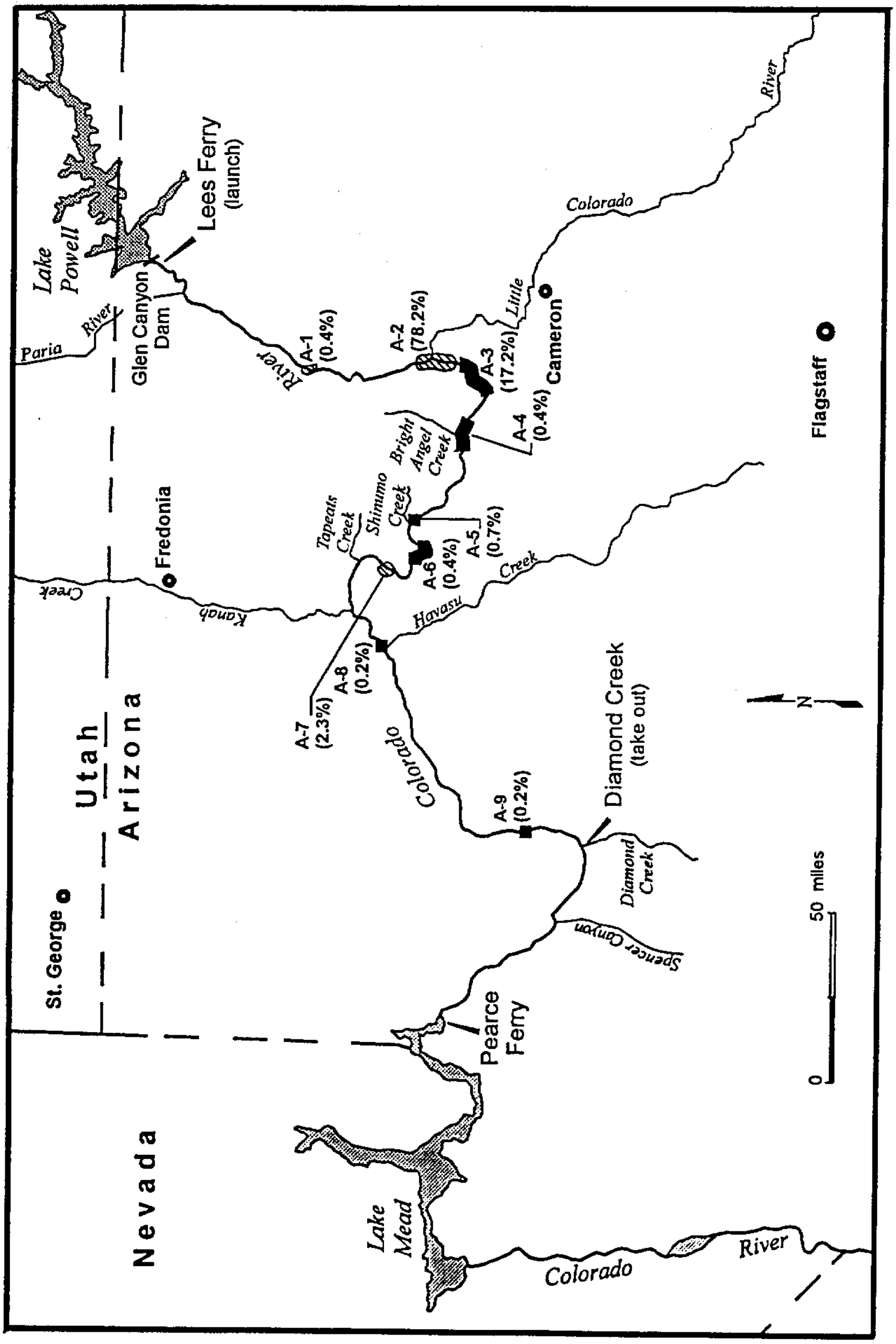


Fig.4. Locations (percentage of total captures of fish within these aggregations) of nine aggregations of humpback chub in the Colorado River in Grand Canyon.

8°C at the dam to 16°C at Diamond Creek. Despite the warming, the numbers of humpback chub--and other warmwater species--did not increase in a downstream direction. Suitable habitat was largely unoccupied in the lower reaches of Grand Canyon, apparently because of low food availability and competition from warmwater non-native fishes. These alien species dominated fish biomass and thus energy flow through the aquatic ecosystem (Fig. 5).

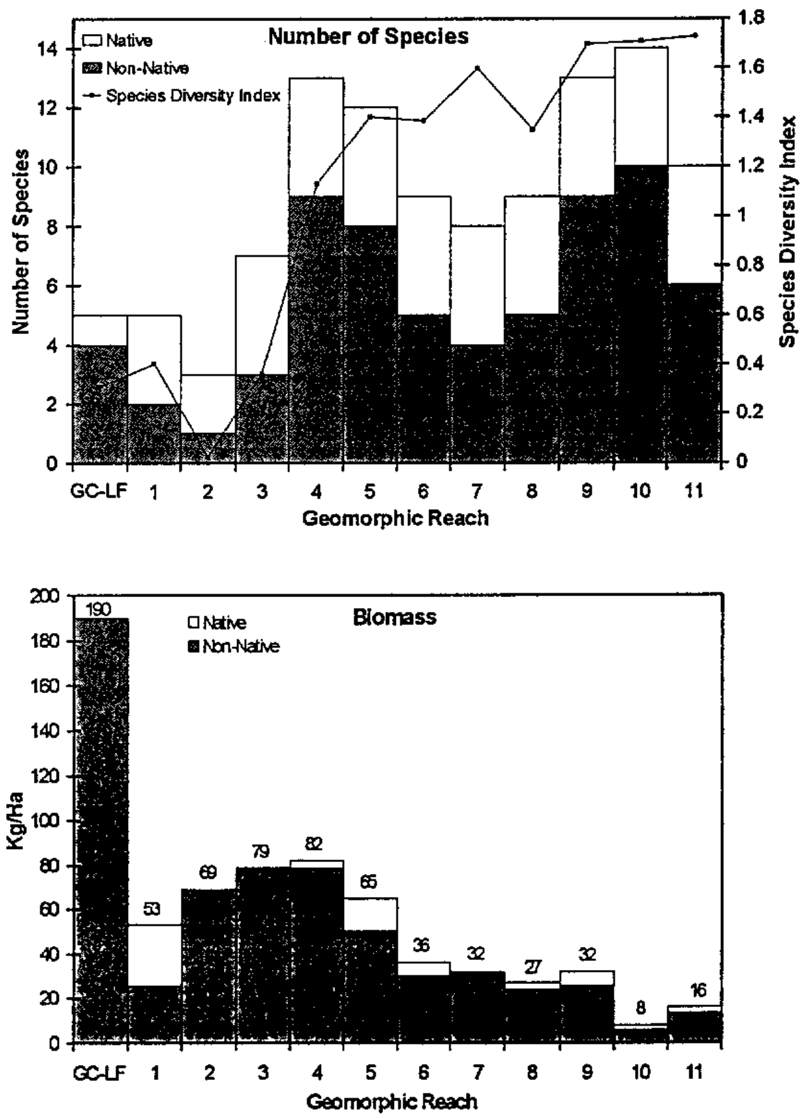


Fig. 5. Number of species, species diversity, and biomass of native and non-native fish species by geomorphic reach from Lees Ferry to Diamond Creek. Data for Glen Canyon Dam to Lees Ferry (GC-LF) from Arizona Game and Fish Department (1993).

The largest aggregation of humpback chub, and the major reproducing population in Grand Canyon, was located in the lower 14.9 km of the LCR and adjacent 13.5 km of the mainstem Colorado River (6.9 km upstream and 6.6 km downstream of the LCR inflow). This area supports the only self-sustaining population in the canyon and provides a profile of life history requirements for the species in Grand Canyon. The LCR is a warm tributary sufficiently large to contain ample habitat for spawning, nurseries for young, and maintenance of subadults and adults and it provides reliable food resources for fish. This food supply is supplemented by high volumes of terrestrial insects and allochthonous material during floods. The LCR provides suspended sediment to the mainstem that helps maintain fish habitat (i.e., sand deposits) and increases the frequency and duration of turbidity. Humpback chub appear to use turbidity as a cover element during feeding and possibly for protection from aquatic and avian predators.

The adjoining reach of the mainstem is equally important to this population in that it provides suitable subadult and adult habitat, greater living space than the LCR, and regular supplies of food produced locally and transported from upstream. The channel in this reach has a high frequency of debris fans and associated recirculating eddies, a habitat type selected by adults; 88% of adults captured and 74% of radio contacts were from these eddy complexes. Adults occupy low-velocity vortices in these eddies where food is entrained, and where adults may use a soaring behavior that enables them to feed with relatively little energy expenditure.

The present distribution of humpback chub in Grand Canyon is believed to be the remnant of a more dispersed historic distribution that probably extended 455 km, from the Paria River (RM 0) to Grand Wash (RM 283). As in other canyon regions (e.g., Desolation/Gray Canyon, Cataract Canyon, Westwater Canyon, Yampa Canyon), predam humpback chub in Grand Canyon probably spawned in the mainstem, and likely occurred in higher concentrations in areas of more suitable habitat or greater food supplies. Tributaries and tributary inflows were probably also used for spawning, and young remained close to hatching sites. Humpback chub were also believed to occur in canyon regions upstream of Grand Canyon, including 80 km in Narrow and Cataract canyons. Hence, historic distribution in this part of the basin probably extended about 535 km from the confluence of the Colorado and Green rivers, UT to Grand Wash, AZ, including all canyon regions except for Glen Canyon, which was a gentle alluvial reach uncharacteristic of humpback chub habitat.

Fish populations of the Colorado River have been affected in numerous ways by land use practices, water diversions, and non-native fishes starting in the late 1800s (Miller 1961). By the time Glen Canyon Dam was completed in 1963, the lower 70 km of Grand Canyon had been inundated and aggraded by Lake Mead as a result of construction of Hoover Dam in 1935. Lake Powell eventually inundated 52 km of potential habitat in Narrow Canyon and lower Cataract Canyon. Occupied habitat was reduced by an additional 77 km (Paria River to Shinumo Wash plus Granite Springs Canyon to Separation Canyon) following closure of Glen Canyon Dam in 1963. The combined effects of Lake Mead (13%), Lake Powell (10%), and Glen Canyon Dam operations (14%) have reduced 535 km of potential historic habitat by 199 km or 37%.

ABUNDANCE

The largest of nine aggregations in the Colorado River in Grand Canyon was the mainstem component of the LCR population, with about 3,500 adults (≥200 mm TL). The second largest aggregation was in Middle Granite Gorge with an estimated 98 adults. The other aggregations and estimated numbers of adults (N) included the Shinumo Creek inflow (N=57), 30-Mile (N=52), Havasu Creek inflow (N=13), and Pumpkin Spring (N=5). The combined estimates for the nine mainstem aggregations were about 3,300 to 3,800 adults. Since 98% of all humpback chub captured were in these nine aggregations, the estimated total numbers of adults in the mainstem were about 3,370 to 3,880 (95% C.I. = ± 25% of total).

The numbers of subadult humpback chub (<200 mm TL, 1-3 years of age) in the mainstem varied dramatically as young descended from the LCR annually in mid to late summer. Lowest densities of <1 fish/100 m² were usually found in late winter and early spring, and highest densities (3 fish/100 m² in 1991 and 1992 and up to 13 fish/100 m² in (1993) were found in mid to late summer, as young descended concurrent with monsoon floods from the LCR. Greatest numbers of subadults were usually found between the LCR inflow (RM 61.3) and Hance Rapid (RM 76.6), with dramatically fewer numbers downstream where shoreline habitat was limited and numbers of predaceous brown trout were higher. The estimated numbers of subadults in this 24.6 km subreach ranged from 246,000 (1/100 m²) to 738,000 (3/100 m²) individuals in years of lowest observed densities (1991 and 1992), and up to 3,198,000 (13/100 m²) in the year of highest observed density (1993). Subadults upstream of the LCR were rare, and densities downstream of Hance Rapid were much lower than in the subreach immediately below the LCR. Since 92% of all subadults captured were found in this 24.6-km subreach, the estimated peak number of subadults in the mainstem during 1991 and 1992 were 250,000-800,000 and numbers in 1993 may have reached 3,500,000 subadults.

SURVIVORSHIP

Survival of humpback chub in the mainstem is probably limited by cold temperatures, suitable habitat, food availability, and predation. Parasites are not believed to be a significant factor to survival in the mainstem, although an increased incidence of Asian tapeworms could affected the health of individual fish under stress. Cold mainstem temperatures likely induce thermal shock in many young fish descending from the LCR, causing death or aberrant behavior that can solicit predator response. Cold temperatures also significantly reduce swimming performance of young fish (Bulkley et al. 1982), restricting suitable habitat to low-velocity areas and limiting escape potential from cold-water predators. Subadult shoreline habitat is destabilized by fluctuating releases from Glen Canyon Dam, causing greater exposure of subadults to predation. Predation on subadult humpback chub in the mainstem could be substantial, and may be a primary factor limiting survival and recruitment of young.

Estimated annual survival of adult humpback chub was 0.755, but the 95% confidence intervals place this estimate as high as 0.896. Subadults in the mainstem, up to 3 years of age, had an estimated annual survival of about 0.100, and over 3 years only 1 in 1,000 fish survive to recruit as adults. Although the various sources of mortality were not quantified, marking studies indicate that movement to reaches downstream of the LCRI aggregation probably resulted in a permanent loss of individuals to the aggregation. Low estimated numbers of subadults surviving to adult in the mainstem suggest that recruitment may not be sufficient to offset mortality of adults. A smaller than expected number of younger adults (based on length-frequencies of adults captured) indicates that most of the recruitment of mainstem adults may be from the LCR and not from survival of younger chubs in the mainstem.

It was estimated that brown trout, rainbow trout, and channel catfish potentially consume about 250,000 subadult humpback chub annually in the 26.4-km subreach between the LCR and Bright Angel Creek. Surviving fish that are transported into the Inner Gorge probably have low survival because of limited shoreline habitat and high predator densities. Young humpback chub that descended downstream of Lava Rapid (RM 65.4) did not ascend this point to return to the LCRI aggregation, and hence, recruitment potential was lost from the LCR population.

MOVEMENT

Adult humpback chub in Grand Canyon exhibited strong spatial fidelity for specific river sites, similar to behavior observed in other populations. Average net displacement (distance from first to last radio contact or capture site) for radio-tagged and PIT-tagged adults in Grand Canyon was only 1.49 km and 0.99 km, respectively, which was similar to 0.8 km and 1.67 km, respectively for adults in the Black Rocks reach of the Upper Colorado River Basin (Valdez and Clemmer 1982). Average time of radio contact for radio-tagged fish and between captures of PIT-tagged fish was 93 days and 406 days respectively. Adults in Grand Canyon however, demonstrated greater gross displacement (sum of distances between radio contact sites) of 5.13 km compared to 1.64 km in Black Rocks, primarily as a result of spawning migrations from various mainstem locations into the LCR. Maximum round-trip distance traveled by an adult from the mainstem into the LCR for spawning was 40 km, although the only mainstem adults that migrated to the LCR were from within a 13.5-km subreach (RM 57 - RM 65.4). The majority of these fish returned to locations within 2 km of their premigration sites (Fig. 6).

The home range of the adult portion of the LCR Inflow (LCRI) aggregation was 28.4 km, including 13.5 km in the mainstem and 14.9 km in the LCR. Adults moved very little between aggregations, indicating that most adults throughout the canyon were associated with groups of fish at specific river locales. Of 1,524 adults captured in the LCRI aggregation (280 recaptured), only two were recaptured outside of the 13.5-km mainstem area in other downstream aggregations. Also, four subadults (>175 mm TL) were recaptured downstream of the LCRI aggregation in the adjacent aggregation.

Long-range movement and local activity of adults in the LCRI aggregation were greatest during spawning-related behavior from February through May. Adults moved to large local congregations in disjunct eddy complexes in February, then migrated to stage at the LCR inflow, prior to ascent into the LCR for spawning. Adults from upstream and downstream of the LCR moved simultaneously to the LCR inflow, suggesting that external reproductive stimuli, such as photoperiod, cued gonadal maturation and pre-spawning migrations. Remote radiotelemetry indicated an average residence time of about 17 days at the LCR inflow by staging adults, suggesting that the fish accumulated temperature degree days for gonadal maturation. This pre-spawning staging led to significantly higher catch rates of adults in this area in late January - March (Fig. 7). Adults ascended the LCR during decreasing LCR flows, increasing water temperatures, and decreasing turbidity, indicating that spawning ascent was cued by conditions in the LCR, while mainstem staging was cued by other factors such as photoperiod and slight seasonal mainstem warming.

Adults in the mainstem moved very little during non-spawning periods, in summer, fall, and winter (July-January), when local movement was primarily influenced by time of day, turbidity, flow magnitude,

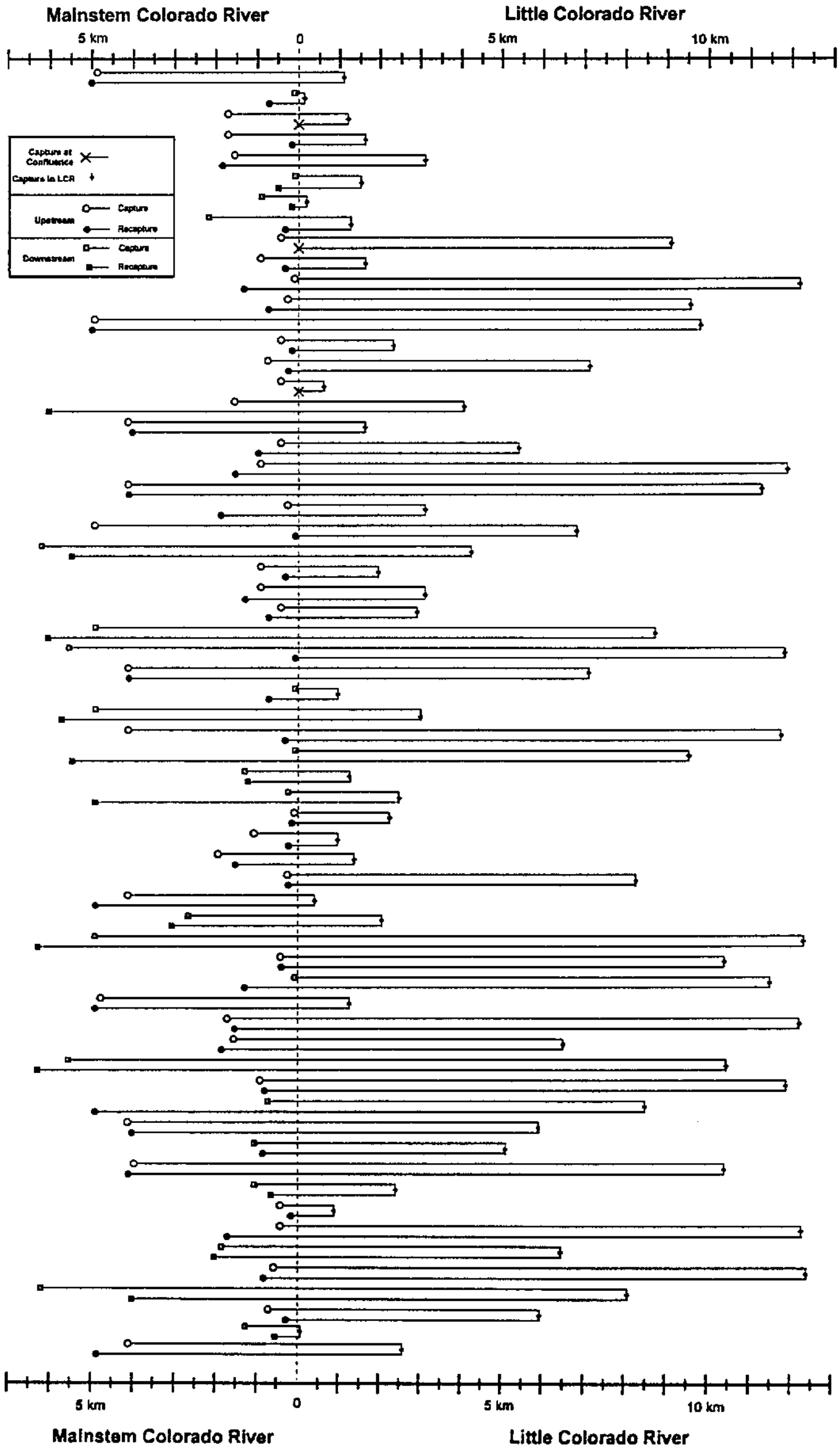


Fig. 6. Fidelity of 60 PIT-tagged humpback chub in the mainstem Colorado River following presumed spawning in the LCR, October 1990-November 1993.

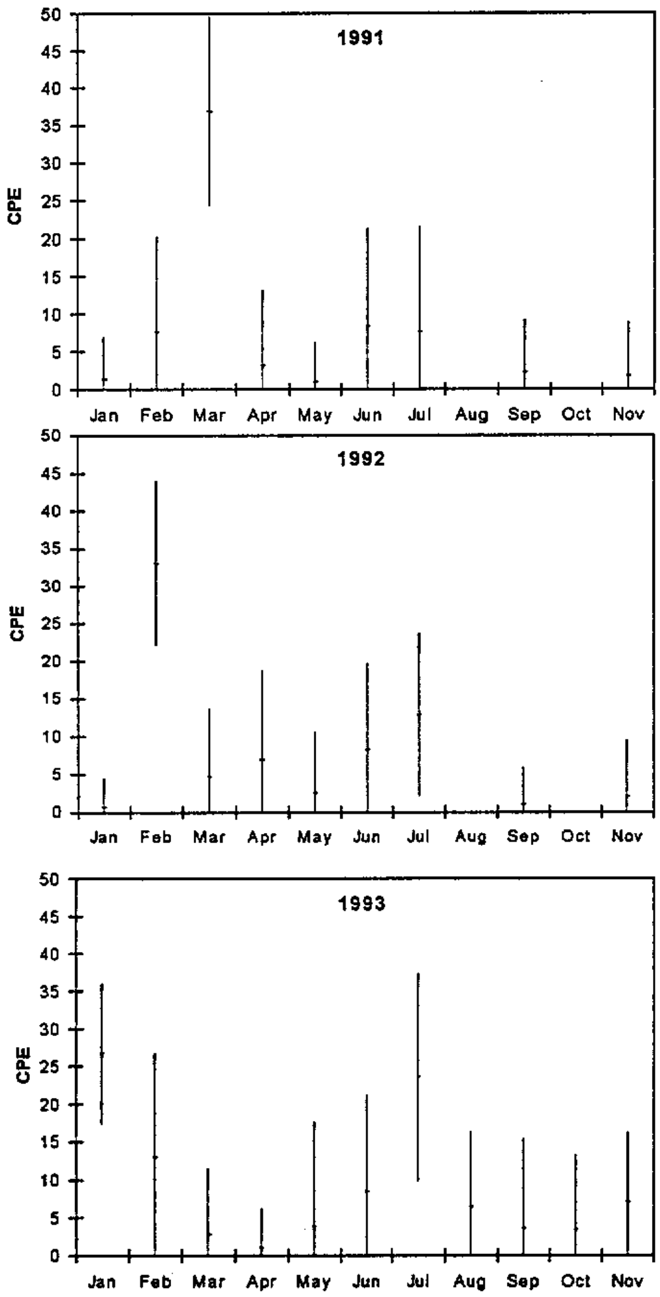


Fig. 7. Monthly geometric mean catch per effort, CPE (GM_{CPE} # fish/100 ft/100 hr) for adult humpback chub captured in nets within RM 60.0-61.9 (LCR Inflow), 1991-93. Standard error bars are shown.

and ramping rate. Adult radio-tagged humpback chub were more active and in shallower water at night and during the daytime when river turbidity was high (NTU>30). Adults used deep water (>4.5 m) more frequently during the day, particularly in clear water conditions. Catches of subadults indicate that this life stage exhibited similar photosensitivity. Movements during low light conditions were attributed to the use of turbidity as cover from predators and to increased feeding activity from increased loads of suspended and drifting material.

Movement by adults was greater during high magnitude discharges and during highest ramping rates, probably in response to changing river hydraulics or to increased drift food availability, or both. The proportion of times that adults moved was significantly greater when flows were above 10,000 cfs, although the greatest movement occurred during increasing flows or decreasing flows. Movement was reduced when flows stabilized at higher magnitudes (Fig. 8). The proportion of times adults moved was also greater when local ramping rates (measured at the nearby LCR USGS stream gage) were greater than 300 cfs/hr during a full range of flow magnitudes, although this movement was significantly greater only at flows above 10,000 cfs. The fish probably moved in response to changing hydraulic characteristics (e.g., water velocity, depth, current direction), as well as to increases in drift food items. Densities of drifting macroinvertebrates increased during descending flows and volume of Cladophora glomerata (dominant green algae) increased during ascending flows.

Movement of subadults (<200 mm TL) was attributed primarily to downstream dispersal resulting from unstable shoreline habitats and cold mainstem temperatures. This movement was deduced from reduced densities of subadults between the LCR (RM 61.3) and Hance Rapid (RM 76.6). We believe that this dispersal resulted from a combination of destabilized shoreline habitats (caused by daily flow regulation) and reduced swimming ability of young fish (caused by cold water temperatures); laboratory tests (Bulkley et al. 1982) showed a 98% reduction in fatigue time of juvenile humpback chub in 0.51 mps velocity water at 20°C (85 min) compared to water at 14°C (2 min). It was hypothesized that displacement of subadults from sheltered shorelines exposed these fish to predation, increased their energy expenditure in finding new habitat, and transported young into reaches with little shoreline habitat, such as the Inner Gorge. The combination of cold water

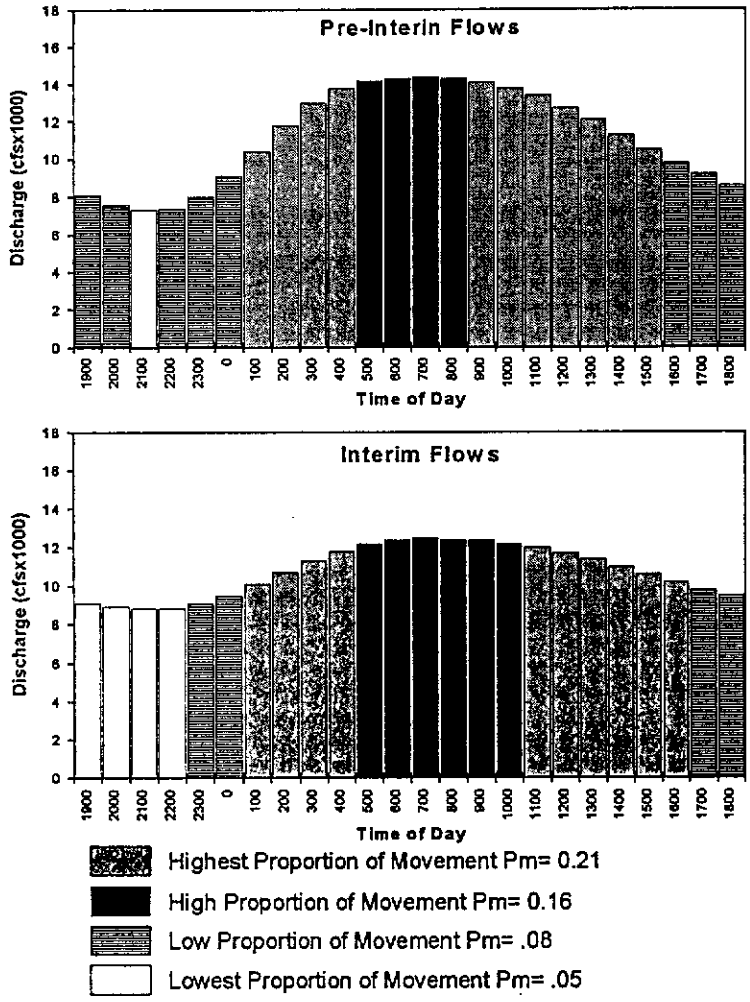


Fig. 8. Fraction of telemetry observation time blocks with horizonal movement of radio-tagged adult humpback chub in Region I during average research and interim flow cycles.

releases in spring, summer, and fall, and fluctuating flows from Glen Canyon Dam operations, with increased exposure to predation, were probably the primary causes leading to high mortality of young humpback chub in Grand Canyon. This effect was probably compounded in September and October when dam operations reduce releases from high to low volume, and shoreline cover (esp. vegetation) becomes stranded.

High relative condition factor for adults indicates that movement during high flows and high ramping rates was not energetically detrimental to adult humpback chub. Although this determination was made for flow ranges associated with interim flows (i.e., 8,000-20,000 cfs), similar effects were observed for higher flows under previous peaking power operations (i.e., 5,000-31,500 cfs). In addition, movement patterns of adults are not likely to substantially change until river flows overtop the debris fans that form the recirculating eddies used extensively by these fish. These high flows did not occur during this investigation.

Although the presence of Glen Canyon Dam probably did not impede movement of the sedentary humpback chub, it apparently affected the potomodromous Colorado squawfish (Tyus 1984, 1990), and possibly other native fishes. Subsequent dam operations have modified movement patterns, frequency of movement, and distance moved by humpback chub. These effects do not seem to be energetically detrimental to adults, but the combination of fluctuating flows, cold temperatures, and large numbers of non-native predators are probably the major factors leading to low survival of subadults.

HABITAT

Subadult humpback chub (<200 mm TL) used primarily shallow sheltered shorelines, while adults (≥200 mm TL) used primarily large recirculating eddies. The transition from shoreline to offshore habitat use began when the fish were about 1 year old and 100 mm TL, and was largely completed by the time the fish were 3 years old and about 200 mm TL, which is about the size of maturity (Fig. 9).

Significantly higher densities of subadults were captured with electrofishing along vegetated banks, talus, and debris fans of the six shoreline types compared. Selected shorelines had a greater degree of cover with more consistent low-velocity interstitial spaces than sand, bedrock, and cobble bars, and provided more stable habitat over the range of flows observed (i.e., 5,000-20,000 cfs). While shoreline velocities were within the range for YOY (0-0.30 m/sec) and juveniles (0-0.79 m/sec) found by Valdez et al (1990) in Blackrocks in 16-20°C water, the fish in Grand Canyon were constantly exposed to cold temperatures of 8-12°C and their swimming efficiency was likely reduced.

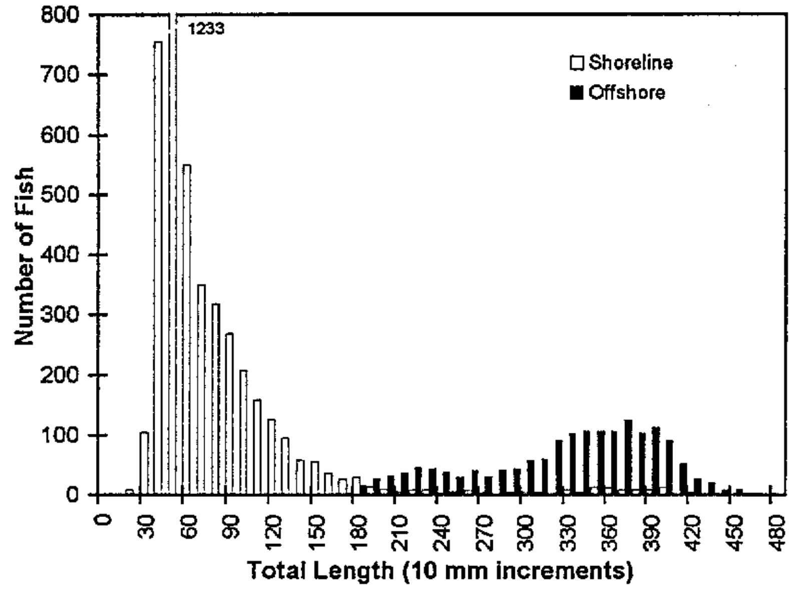


Fig. 9. Length-frequency distribution of humpback chub captured in shoreline habitats (with electrofishing, seines, minnow traps) and in offshore habitats (with gill nets, trammel nets) for 1991-93.

Hence, although shoreline habitats of the type selected by subadults appeared to be suitable and abundant in Grand Canyon, we hypothesize that use was reduced by the limited swimming ability of the young fish at cold temperatures, and by the destabilizing effect of fluctuating dam releases. Greater use of vegetated shorelines was attributed to reduced velocities, high cover value, and relatively high food production among tamarisk, willows, sedges, and other riperian vegetative types. This vegetative cover, which was absent under predam conditions, except during high runoff or flood flows, may be used by the fish in the absence of high constant turbidity as cover from predators and to avoid high light levels.

Nearshore velocities along cobble bars and bedrock exceeded the range of maximum cruising speed of YOY humpback chub (range, 30-100 mm TL) at 14°C (Fig. 10); sand beaches lacked cover and despite low velocities, were not used by YOY during the day or in clear water.

Adult humpback chub used eddy complexes disproportionate to their composition of surface area; 88% of adults captured and 74% of radio contacts were from eddies which averaged only 21% of surface river area (Fig. 11). Disproportionate use of eddy complexes coincided with the location of the three largest aggregations of humpback chub in Grand Canyon, which were river reaches with abundant debris fans and channel expansion zones. These complexes were large recirculation zones that entrained and entrapped drifting food, and provided low-velocity vortices in which the fish could feed and rest.

Adult humpback chub in Grand Canyon used large recirculating eddies to a greater degree than adults have displayed in other populations (Valdez et al. 1990). Adults in other populations appear to use a wider range of habitats, possibly because more normal warm spring, summer, and fall temperatures enable the fish

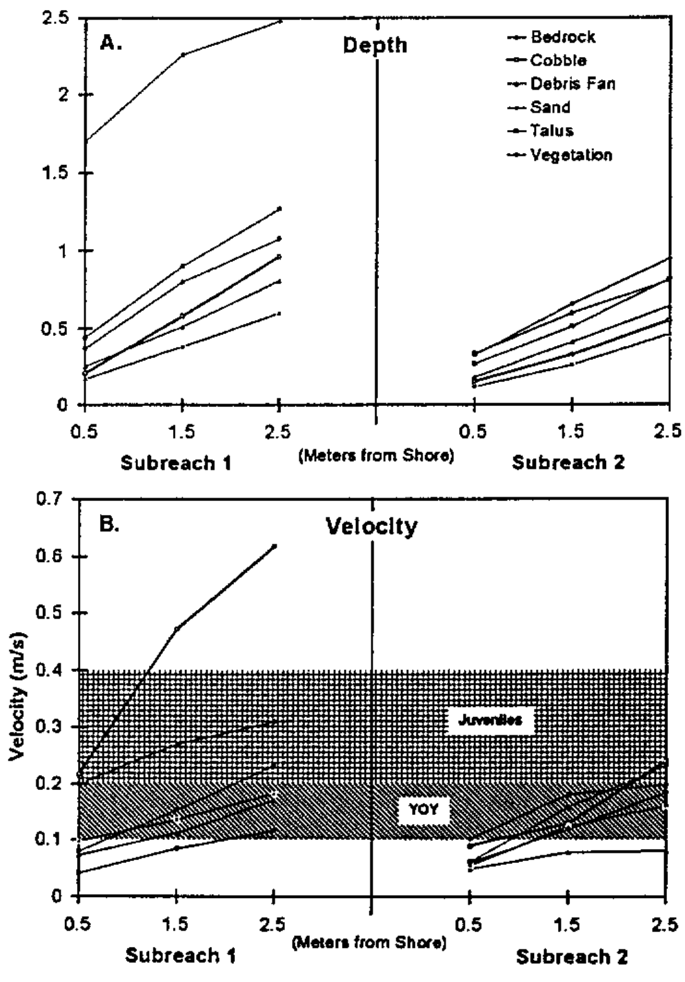


Fig. 10. Average depth (A) and velocity (B) at three distances from shore (0.5, 1.5 and 2.5 m) for six shoreline types in Subreach 1 (RM 61.9-65.4) and Subreach 2 (RM 65.4-73.4). The ranges in cruising speed for YOY and juveniles are shaded areas.

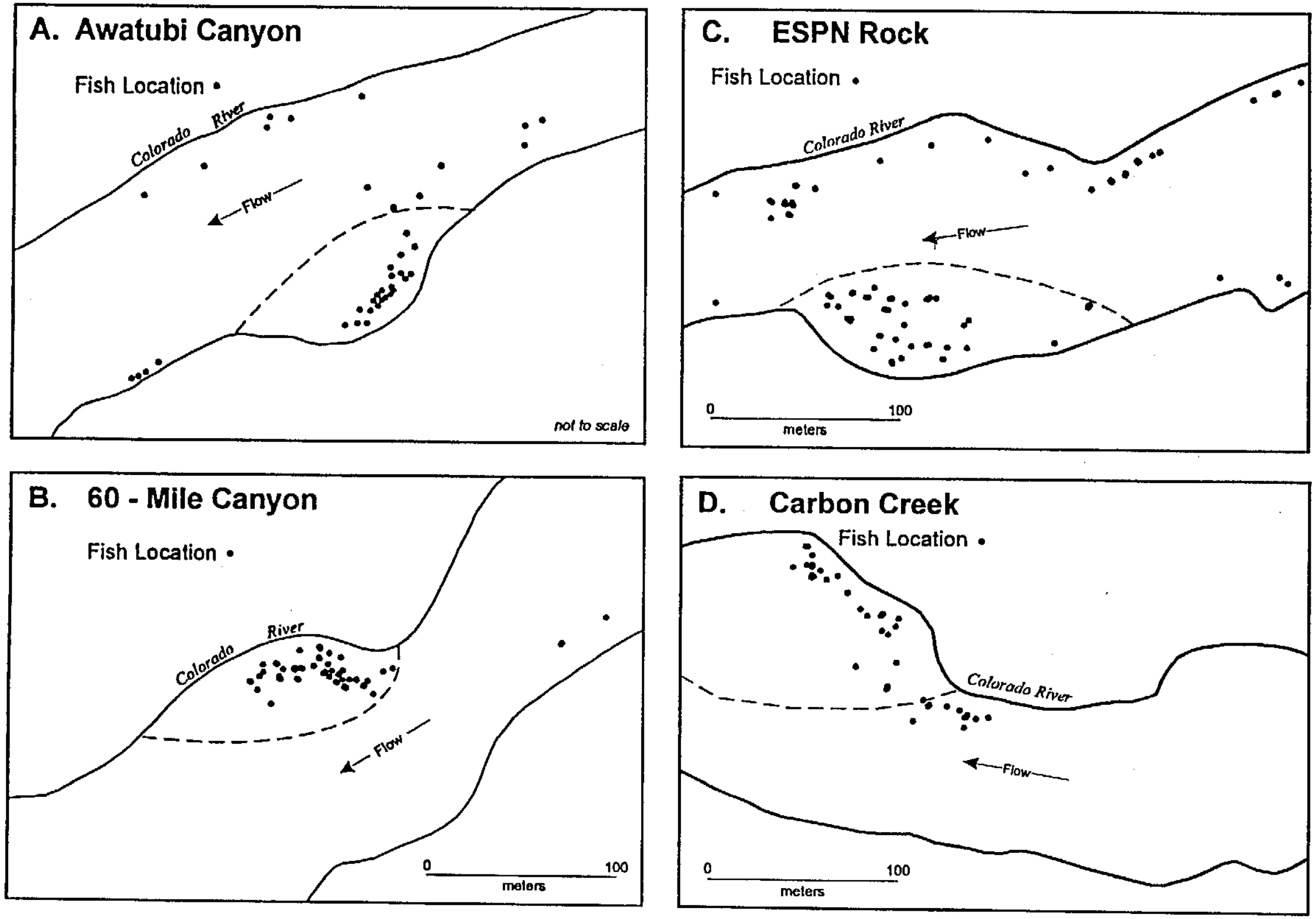


Fig. 11. Location of radio-tagged adult humpback chub near Awatubi Canyon (RM 58.5) (A), 60-Mile Canyon (RM 60.1) (B), ESPN Rock (RM 60.8) (C), and near Carbon Creek (RM 64.7) (D), 1991-92. Points represent radio contact locations occupied 15 min or more at a full range of flows. Shoreline shown is at approximately 12,000 cfs. Approximate area of eddy complexes shown by dashed lines.

to occupy relatively higher velocities and utilize local supplies of food.

Adults in Cataract Canyon were frequently observed moving to large eddies during runoff or when drift volume was high to feed on entrained materials (Valdez 1990). Adults in postdam Grand Canyon may be largely restricted to recirculating eddies as areas of sufficient food supplies with low velocity.

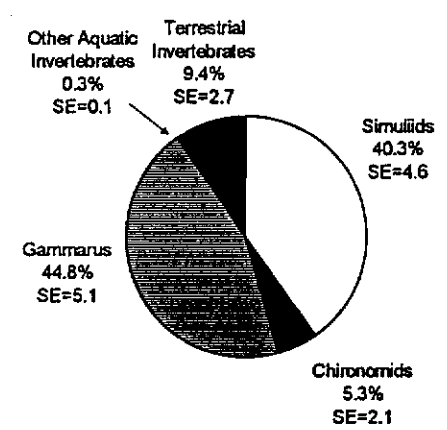
The character of these large recirculating eddies may be changed from predam conditions as a result of nearly 90% sediment retention in Lake Powell, and subsequent scouring of sediments from the river channel downstream of the dam. Because adult humpback chub in Grand Canyon may prefer eddies, the volume of sand in the channel, and thus in eddies, may be important for shaping fish habitat and hydraulic characteristics. These relationships and resulting effects to the fish are not well understood. Possibly, some expansion zones contain less sand today than predam and may be more effective at entraining drifting material.

FOOD HABITS

Adult humpback chub in the Colorado River in Grand Canyon ate primarily simuliids, introduced freshwater amphipods (Gammarus lacustris), chironomids, other aquatic invertebrates (i.e., primarily beetles) and terrestrial insects (i.e., primarily ants). The algae, Cladophora glomerata, also made up a significant portion of gut volume, but it was not determined if this item was consumed incidentally or selected by the fish and of nutritional benefit as observed for rainbow trout (Liebfried 1988). The major food items (excluding Cladophora) of the LCRI aggregation were amphipods (45% by volume) and simuliids (40%), and the major items of the Middle Granite Gorge aggregation were simuliids (49%) and terrestrial invertebrates (30%, primarily ants and beetles) (Fig. 12). Johnson's electivity indices indicate that simuliids, chironomids, and amphipods were consumed in approximately the same proportions as available in the drift in both areas, while terrestrial invertebrates were lower in numbers in drift samples than in guts. This disparity is attributed to the irregular occurrence of terrestrial invertebrates washed into the mainstem by floods; these events may not be represented by periodic drift sampling. Although Cladophora composed the greatest volume in drift, with increasingly greater amounts in a downstream direction, this algae was absent from guts of Middle Granite Gorge fish, but composed 24% of gut volume of LCRI fish.

Seasonal diet of adult humpback chub was distinct. The diet in spring was primarily amphipods (51%), simuliid larvae (24%), and terrestrial invertebrates (23%); summer diet was simuliids (47%), amphipods (30%), terrestrial invertebrates (14%), and chironomids (7%); and fall diet was amphipods (44%) and simuliids (44%). The relative abundance of amphipods and chironomids in gut contents was approximately the same as respective seasonal abundances in drift, but electivity indices indicated selection for terrestrials and other aquatic invertebrates in all seasons. Terrestrial invertebrates were difficult to monitor in drift

Little Colorado River Aggregation
n= 128



Middle Granite Gorge Aggregation
n=24

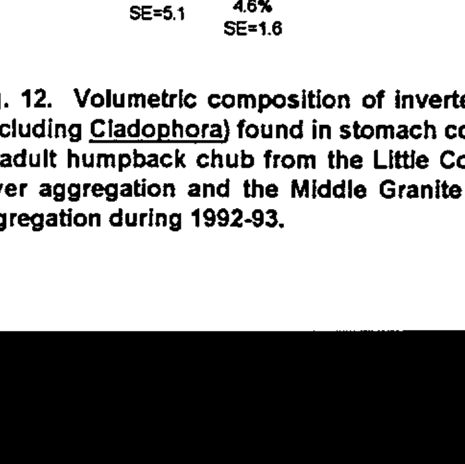


Fig. 12. Volumetric composition of invertebrates (excluding Cladophora) found in stomach contents of adult humpback chub from the Little Colorado River aggregation and the Middle Granite Gorge aggregation during 1992-93.

samples because their abundance varied with floods or behavioral patterns of local invertebrate populations.

The proportion of terrestrial insects in the diet of adults was higher in Middle Granite Gorge fish than fish near the LCR, suggesting a decreased abundance of aquatic invertebrates and greater dependence on terrestrial taxa in downstream reaches. The numbers of organisms in drift above the LCR (248/100 m^3), from the LCR to Hance Rapid (190/100 m^3), and from Hance Rapid to Diamond Creek (96/100 m^3) showed decreased drift food availability from eastern to western Grand Canyon and was consistent with the pattern of benthic invertebrates (Blinn et al. 1994). Average volume of drifting Cladophora was significantly higher during rising flows (i.e., upramp) than during steady flows, while densities of drifting organisms were significantly greater during falling flows (i.e., downramp 380/100 m^3) than during rising flows (177/100 m^3), indicating that Cladophora was dislodged with rising flows, but invertebrates drifted primarily during descending flows.

Cold releases from Glen Canyon Dam have disrupted life cycles of aquatic invertebrates and greatly affected fish food diversity and availability. Humpback chub are opportunist insectivores, and adults have apparently adjusted to substantial changes in the invertebrate fauna; e.g., the amphipod Gammarus lacustris is a non-native, introduced crustacean that composed nearly 50% of the diet of adults. Although the effect of reduced abundance and variety of macroinvertebrates on longitudinal abundance of humpback chub has not been fully evaluated, reduced densities of aquatic invertebrates in drift and the lower benthic productivity found by Blinn et al. (1994) suggest a food shortage in downstream reaches. This shortage is probably caused by low shoreline production from persistent turbidity reducing photosynthesis and year-around cold temperatures that limit invertebrate diversity.

AGE AND GROWTH

Average lengths of subadult humpback chub at the first three scale annuli formations were 96, 144, and 186 mm TL. A transition check on the scale also showed that the mean length of young fish moving from the warm LCR to the cold mainstem was 74 mm TL (range, 52-132 mm TL), indicating that most of the first year of growth for mainstem subadults occurred in the LCR.

Average monthly growth rate of age 0 chubs in the LCR was 10.30 mm, which was similar to laboratory results of 10.63 mm at 20°C (Lupher and Clarkson 1994). Average monthly growth rates for age I and II fish were 4.00 mm and 3.50 mm, which was higher than laboratory results of 2.30 mm at 10°C; the difference was attributed to wild fish finding slightly warmed shorelines and backwaters.

Average monthly growth rate from PIT-tag recapture information was 2.25, 2.79, 2.50, 1.16, 0.79, 0.91, and 0.96 mm for fish in 50-mm length groups of 150-200 mm TL, 200-250 mm TL, 250-300 mm TL, 300-350 mm TL, 350-400 mm TL, 400-450 mm TL, and 450-500 mm TL, respectively (Fig. 13). These adult growth rates were

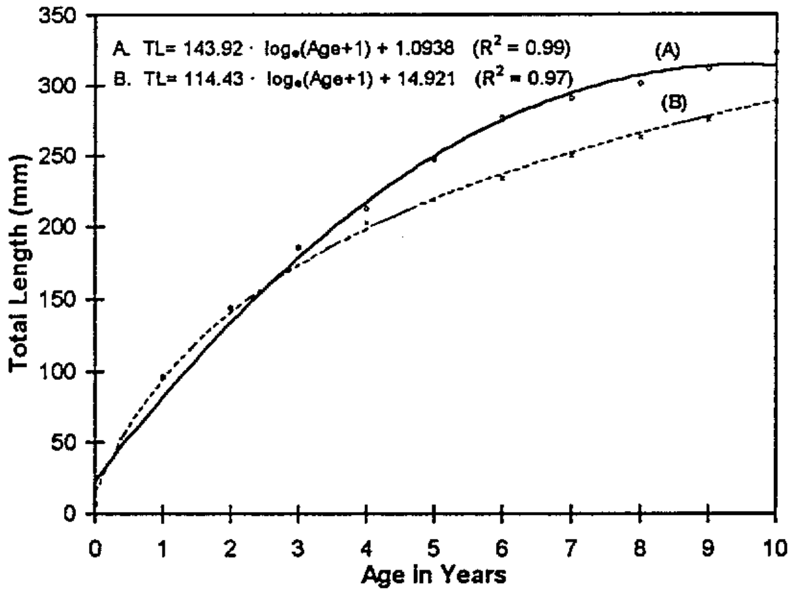


Fig. 13. Logarithmic growth curve for humpback chub in the mainstem Colorado River in Grand Canyon (A). Hatching length of 7 mm from Muth (1990); length at 1-3 years from scale back-calculations; lengths at 50 mm increments for 4+ years from PIT tag recaptures. Growth curve for humpback chub in the LCR (B) from Minckley (1992)

approximately double the growth rates reported for adults from the LCR (Minckley 1992) of 1.4, 1.3, 1.1, 0.4, 0.5, and 0.1 mm for fish less than 200 mm, 200-250 mm TL, 250-300 mm TL, 300-350 mm TL, 350-400 mm TL, and over 400 mm TL, respectively. Average monthly growth of PIT-tagged humpback chub in Westwater Canyon was 1.08 and 1.35 mm for 200-250 mm TL and 250-300 mm TL, respectively (T. Chart, pers. comm., UDWR), which was comparable to the growth rates reported from the LCR, but only about half the growth rate reported by this investigation for mainstem fish.

Higher adult growth rates in the mainstem are explained by greater availability of living space, greater consistency and abundance of food supplies, and the more stable year-round habitat than in the LCR. Despite suboptimal temperatures, the growth rate of adults in the mainstem may be higher than growth rates of any other population in the Colorado River Basin. Average total length of mainstem Grand Canyon humpback chub is significantly greater ($P<.05$) than the average length of fish from the LCR, and probably greater than lengths of any other population. Relatively high condition factor and growth rates suggest that the region occupied by the LCRI aggregation was below carrying capacity for adults.

Age of adults was not determined during this investigation, but Hendrickson (1993) reported a maximum age of 21 years for a humpback chub from the LCR that was 461 mm TL. Maximum sizes of fish from the mainstem were 460 mm TL (1,122 g) for males and 480 mm TL (1,165 g) for females, indicating that the fish aged by Hendrickson was close to maximum longevity.

REPRODUCTIVE CAPACITY AND SUCCESS

The only self-sustaining population of humpback chub in Grand Canyon was found in the lower 14.9 km of the LCR and the adjacent 13.5 km of the mainstem Colorado River (6.9 km upstream and 6.6 km downstream of the inflow). The majority of mainstem adults (≥200 mm TL) of the LCRI aggregation ascended the LCR for presumed spawning from March through May. Adults in other disjunct aggregations reached a peak in spawning readiness in May through June, nearly 2 months later than the LCR population, but consistent with historic mainstem temperatures and timing of spawning by other mainstem populations, such as Black Rocks (Valdez and Clemmer 1982, Kaeding et al. 1990), Cataract Canyon (Valdez 1990), and Yampa Canyon (Karp and Tyus 1990). Hence, mainstem temperatures were sufficient for normal gonadal maturation as reported by Kaeding and Zimmerman (1982), but apparently too cold for survival of eggs and larvae.

The only definitive evidence of mainstem reproduction during this investigation was the discovery of about 100 post-larval humpback chub (14 captured, range, 18-31 mm TL) in a warm spring plume at RM 30.8 on July 12, 1994 (Valdez and Masslich In Review). Water temperature at the source of the spring was relatively constant at 21.5°C, compared to 10°C in the adjacent main channel; the fish were in a plume with a temperature of 15-19°C. These young fish belonged to the 1994 year class, and probably hatched from eggs deposited in the warm spring plume, since mainstem water temperature was too cold for survival of eggs or larvae (Hamman 1982, Marsh 1985). These fish were about 36 days old (hatched about June 8, 1994), based on age to length relationships of larvae and post-larvae (Muth 1990).

Young humpback chub were reported 21.7 km (13.5 mi) downstream of this spring by Arizona Game and Fish Department in 1993 (AGF 1994), i.e., 20 YOY (range, 20-50 mm TL) were captured at RM 44.3. These findings also suggest past spawning attempts by humpback chub, either in springs in the vicinity of Fence Fault (30-Mile area), in the Paria River, or in unknown springs near RM 44. It is unlikely that these young fish originated from the Paria River, since adult humpback chub have not been reported in that tributary, and a large number of young would be necessary to supply a distant backwater with 20 individuals, where fish are expected to become more dispersed with distance downstream. Possibly, other warm springs exist downstream of Fence Fault that may be underwater and largely undetected. The likelihood of survival by eggs and larval from such springs is low because of the lack of cover along the river bottom and sizeable numbers of potential predators.

Although it is unlikely that larval humpback chub could survive the thermal shock of a transition from a spring plume of 20°C to a mainstem temperature of 10°C, sufficient size and temperature of some plumes may persist under various mainstem flows to allow fish to age and acclimate to suboptimal temperatures. If young fish reach sufficient size to survive the thermal transition (i.e., about 50 mm TL), their chances of survival probably remain low because of the large numbers of mainstem predators and lack of suitable habitat in the vicinity of Fence Fault.

Under interim flows, the existing thermal regime finally reaches the lower range of suitable spawning temperature for humpback chub of 16°C about 385 km (240 mi) downstream of the dam (i.e., below Diamond Creek) but only during the months of July and August. The remainder of the year, the temperature of the Colorado River in this region is too cold for significant survival of eggs or larvae of humpback chub. Some very localized reproduction may be occurring in the mainstem, most likely at tributary or spring inflows, but the numbers of young fish produced and surviving is probably insignificant to the continued existence of the species in Grand Canyon.

Spawning by humpback chub in the LCR is timed to occur when temperatures of that tributary are within the suitable range of 16 to 22°C, from April through May (Fig. 14). Kaeding and Zimmerman (1983) reported that mean female gonadosomatic indices and ovary diameters of humpback chub in the LCR, mainstem, and LCR inflow were highest between early February and late April 1980, indicating that most spawning probably occurred in March, April, and May.

If humpback chub were spawning in the mainstem prior to Glen Canyon Dam--as they presently do in all other populations in the basin--egg deposition likely occurred when temperatures were suitable, probably late May to early July. One of three explanations may account for the disparity in timing between predam and present spawning events and spawning activity in the LCR.

1. Humpback chub in Grand Canyon did not spawn in the mainstem prior to Glen Canyon

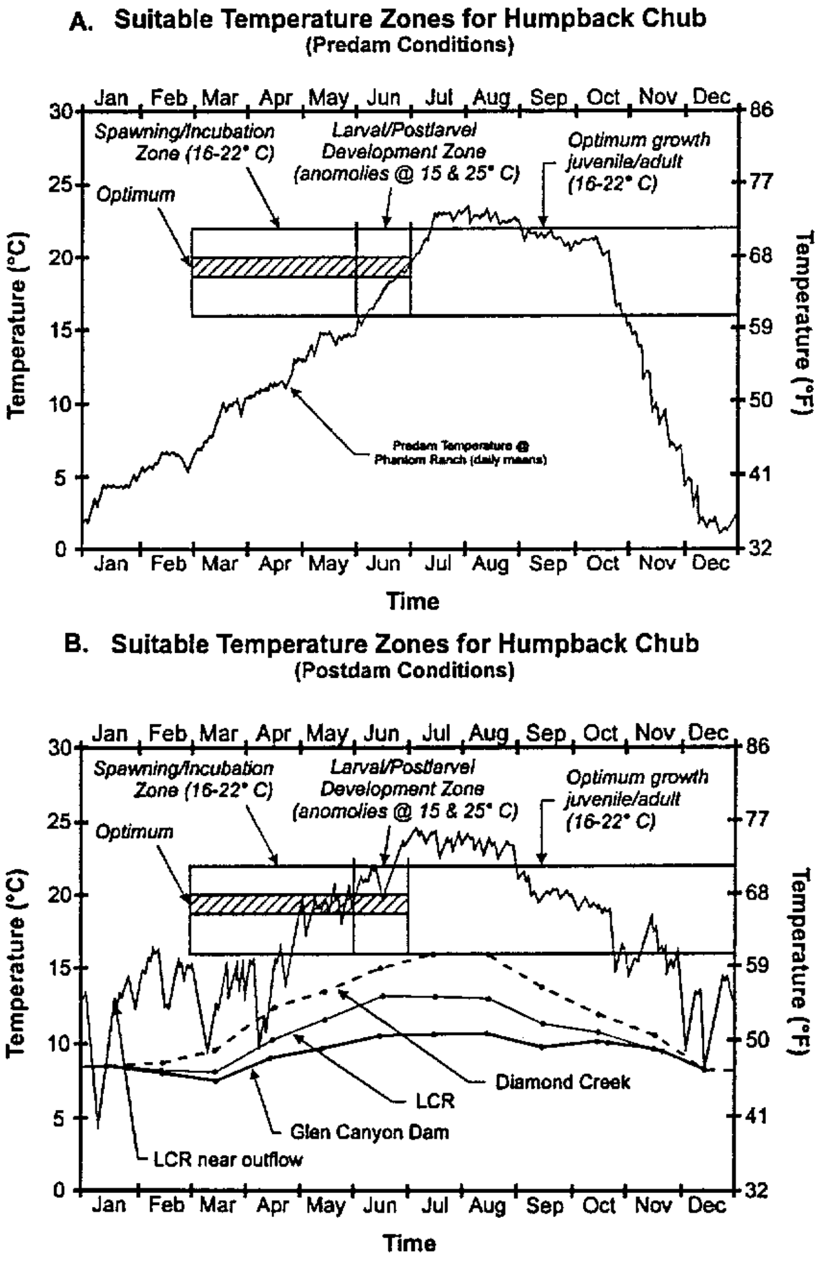


Fig. 14. Suitable and optimal temperature range for spawning by humpback chub compared to predam temperature of the Colorado River at Phantom Ranch (A), and the temperature of the LCR and postdam Colorado River at Glen Canyon Dam, LCR, and Diamond Creek (B).

Dam, only in the LCR; an unlikely scenario considering all other populations spawn in similar mainstem conditions.

2. Cold releases forced mainstem spawners to switch to an earlier spawning mode and ascend the LCR to coincide with temperatures of that tributary; a possible scenario considering many fish species are capable of switching spawning times under changed environmental conditions, e.g., temperature, photoperiod.

3. Two population components existed in Grand Canyon--one spawned in the mainstem, and one in the LCR. The mainstem component experienced unsuccessful reproductive efforts following Glen Canyon Dam and few if any individuals remain; this is the most likely scenario and an important consideration for a second population in the mainstem if unique genetic stocks exist.

Some spawning may be occurring in the mainstem downstream of the LCR in lower reaches of warm tributaries, or in warm mainstem springs, as indicated by young humpback chub captured by other investigators. These fish may have been hatched locally, or they may have been hatched in the LCR and survived the thermal transition to the mainstem and downstream transport. Young captured in downstream reaches during 1990-93 could have originated from the LCR and dispersed to any area downstream within days. Assuming average transport rate of about 1.1 to 3.6 km/hr (0.3-1.0 m/sec, Graf 1995), a small suspended object, like a larval fish, could be transported from the LCR (RM 61.3) to Diamond Creek (RM 226) in about 241 to 74 hr.

IMPORTANT BIOTIC INTERACTIONS

Fourteen species of fish were sympatric with humpback chub during this investigation, including 3 native species and 11 non-natives. These interacted with humpback chub as known or potential predators, competitors, and vectors for parasites and diseases. Known predators included brown trout, rainbow trout, and channel catfish. Potential predators included striped bass, green sunfish, brook trout, black bullhead, and walleye, but these occurred in small numbers and probably had an insignificant impact. Carp could also be significant predators of incubating eggs in the LCR and warm springs. Small cyprinids, such as fathead minnows and red shiners are known predators of early life stages of native species (Gregory and Deacon 1994, Ruppert et al. 1993).

It was estimated that brown trout, rainbow trout, and channel catfish in the mainstem potentially consume 250,000 young humpback chub annually (Fig. 15), significantly affecting survival of 1, 2, and 3-year old fish, and reducing recruitment to the adult portion of the population. The most significant predator was the brown trout, with a potential annual consumption of 230,000 chubs. This is the estimated predation occurring between the LCR (RM 61.3) and Bright Angel Creek (RM 87.7), in the area where the species are sympatric and young humpback chub densities are highest. Although the young chubs originate from the LCR, we believe that fluctuating flows and cold dam releases destabilize shoreline habitats and transport the fish

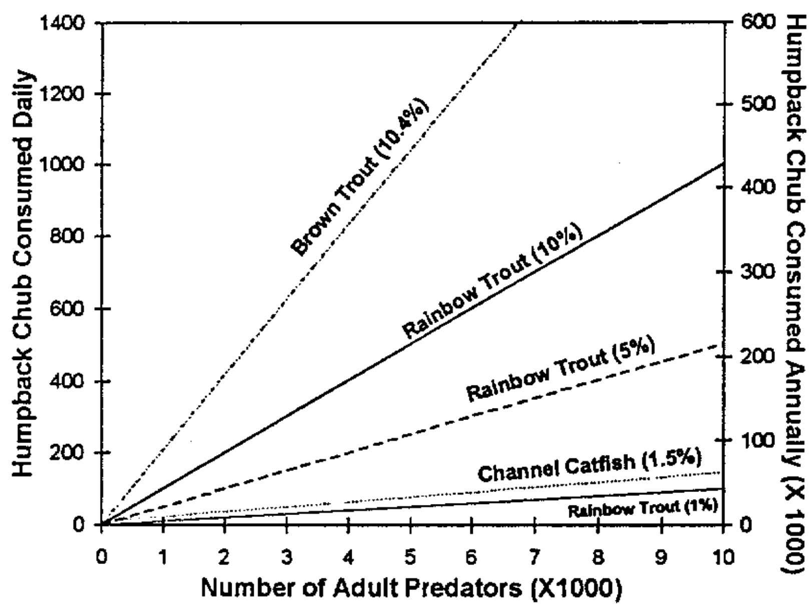


Fig. 15. Potential daily and annual consumption of humpback chub by adults of three predator fish species in the Colorado River in Grand Canyon. Relationships assume 2.0 chubs consumed daily by 10.4% of adult brown trout; 1.0 chub consumed daily by 1, 5, or 10% of adult rainbow trout; 1.0 chub consumed daily by 1.5% of adult channel catfish.

downstream into areas with large numbers of brown trout. Brown trout are not presently stocked in the system and spawn primarily in Bright Angel Creek and the adjacent inflow.

Rainbow trout also appear to be important predators of humpback chub and could consume up to 27,375 fish per year. Rainbow trout that are sympatric with humpback chub are primarily progeny of local natural reproduction from tributaries such as Nankoweap Creek, Clear Creek, Bright Angel Creek, Shinumo Creek, Tapeats Creek, Deer Creek, and Havasu Creek. The area of highest potential predation (i.e., LCR to Bright Angel Creek) was supplied by fish that probably originated primarily from Nankoweap Creek, Clear Creek, and Bright Angel Creek. The rainbow trout that are sympatric with humpback chub downstream of Nankoweap Creek did not appear to originate from the tailwater fishery; only three of approximately 151,000 catchable rainbow trout (marked with coded wire nose tags) released by AGF (1992 - 1993) between the dam and Lees Ferry were recaptured downstream of Lees Ferry, at RM 2.9, RM 3.2, and RM 3.2. Rainbow trout may also compete for food with humpback chub, since favored food items of both species were simuliids, amphipods, and midges. Limited food resources may be limiting native fish population size in western Grand Canyon.

Channel catfish are apparently primarily mainstem inhabitants that aggregate annually for spawning in warm tributaries, primarily in the LCR, where they have been reported for years (Kaeding and Zimmerman 1983, Gorman et al. 1994). Channel catfish have not been reported in Kanab Creek (AGF 1993, 1994), and were not reported in recent surveys of the Paria River (Weiss 1993), Shinumo Creek, or Bright Angel Creek (Otis 1994).

The effect of striped bass migrating annually from Lake Mead into Grand Canyon has not been fully evaluated. Although the numbers ascending annually from Lake Mead appear small, this species is a voracious predator and even small numbers could account for substantial mortality of native fishes. The numbers of striped bass in the Lake Mead inflow (i.e., downstream of Bridge Canyon) in spring are high (Valdez 1993, 1994, 1995), and suggest that greater numbers of striped bass could ascend the Colorado River into Grand Canyon given more suitable conditions such as warmer temperatures and higher turbidity.

Small non-native forms, such as fathead minnow and plains killifish, are presently low in numbers but could become numerous with changed conditions, such as warmer mainstem temperatures. These species are relatively weak swimmers and, in their native waters, inhabit low-velocity areas. Fathead minnows thrive in flood bottomlands and backwaters in the Mississippi and Missouri rivers and are often the most resistant species to low oxygen, high temperature, and high turbidity (Pflieger 1975). Plains killifish are typically inhabitants of small to medium streams and prefer low velocity areas. These warmwater species are likely to become transported downstream and stressed with high flows that flood sheltered shoreline habitats such as backwaters. These species are likely to remain in the system, since they inhabit many tributaries from which they can reinvade the mainstem. Red shiners, a known predator and competitor of native stream fishes, are rare upstream of the Lake Mead inflow, but could become numerous if suitable conditions (primarily warmer temperatures) are available (Valdez et al. 1995).

Biomass estimates indicate that fish biomass in the mainstem is dominated by non-native species. If food is limiting, removing potential predators may also benefit native species by availing greater supplies of food.

Two species of alien parasites presently infect the humpback chub in Grand Canyon, including the parasitic copepod (Lernaea cyprinacea) and the Asian tapeworm (Bothriocephalus acheilognathi). Parasitic copepods were first reported from this population by Carothers et al. (1981), and the Asian tapeworm was first reported in 1989 by D. Hendrickson (Angradi et al. 1992). These warmwater parasites are unable to complete their life cycles in the cold mainstem. Lernaea cyprinacea and B. acheilognathi were in found in 0.13% and 3.6% of humpback chub examined, and were not considered a major threat in the mainstem.

Of four native species captured in the mainstem Colorado River in Grand Canyon, flannelmouth suckers and bluehead suckers showed the weakest age structures for population stability, i.e., young fish of these species made up a relatively small proportion of their populations. Of total numbers of humpback chub (6,294), flannelmouth suckers (2,775), and bluehead suckers (1,040), subadults (YOY and juveniles) composed 72%, 21%, and 34%, respectively, indicating that reproductive success of other native species was considerably less than that of humpback chub. These species appeared to be reproducing primarily in tributaries, but survival of larvae drifting into the cold mainstem is probably low from thermal shock, and predation on survivors is probably high.

LIFE HISTORY SCHEDULE

The life history schedule of the LCRI aggregation is depicted in Fig. 16, based on observations during 1990-93. Adults between RM 57.0 and RM 65.4 were typically found in or near large eddy complexes from about July through January. In February and March, adults congregated locally in a few large eddy complexes before moving to stage at the LCR inflow. Adults staged primarily in March, April, and May, with individuals remaining in the LCR inflow an average of 17 days and ascending primarily when flows in the LCR were decreasing, clearing, and warming. Staging and ascent into the LCR, and presumed spawning, occurred primarily over a period of about 3 months (i.e., April, May, June). Adults remained in the LCR from March through June, returning during and after this period to mainstem eddy complexes, often within 2 km from their original location before the spawning movement. Eggs deposited in the LCR at about 22°C probably hatched in about 5 days (Hamman 1982).

Large numbers of young were seen in the mainstem, primarily downstream of the LCR inflow, during and immediately after heavy summer rainstorms in the LCR drainage. The timing of these "monsoon rains" determined the appearance of these young chubs in the mainstem, indicating that dispersal was concurrent with LCR floods; floods occurred in September 1991, May 1992, and July 1993. Large numbers of subadult humpback chub descended from the LCR into the mainstem in September 1991 and May 1992, concurrent with LCR floods, but in

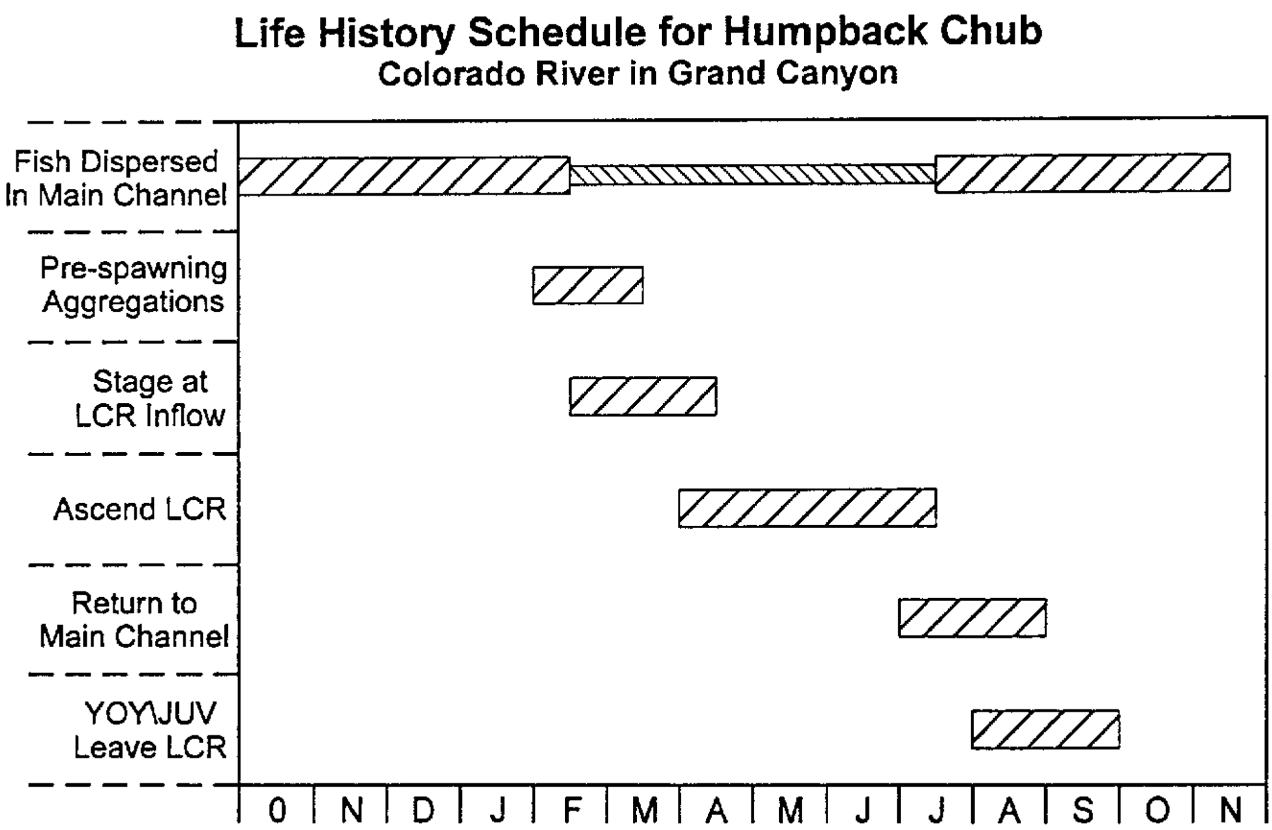


Fig. 16. Life history schedule for the LCRI aggregation of humpback chub in the mainstem Colorado River in Grand Canyon.

1993 large numbers of young began to descend to the mainstem in July, during low and clear flow in the LCR. The 1993 cohort was large and movement to the mainstem during low flows in July 1993 suggested that dispersal was density-dependent, and the result of food shortage or habitat limitation in the LCR.

RECOMMENDATIONS

1. Integrate LCR and Mainstem Data: Much valuable information on the aquatic ecosystem in Grand Canyon has been collected in the past 10 years, but the value of this information is not entirely apparent because it presently lacks integration. Analyses and interpretation of data collected in past and ongoing investigations of fishes, macroinvertebrates, primary and secondary production, water quality, and geomorphology need to be conducted, and possible linkages identified to test hypotheses presented in the Draft Integrated Research Plan. This information also needs to be integrated and further analyzed to better define future core research and long-term monitoring strategies. An assimilation of information will help researchers develop better scopes of work that can use existing information, minimize repetitive data collection, and develop more directed hypotheses that address cause and effects of operations. The framework for a Grand Canyon Fisheries Integrated (GCFIN) database,(Brown et al. 1995) has been developed (Supplement No. IV).

2. Develop a Population Model: A population model is currently being developed by Ryel and Valdez (1995) (Supplement No. V) as a means of determining the status and trend of the humpback chub population in Grand Canyon, by integrating empirical data collected by the GCES investigations.

3. Integrate Geomorphology with Fish Habitat: The relationships of channel geomorphology and fish habitat identified by this investigation need to be described and used to help evaluate the likelihood of a second spawning population of humpback chub, as well as the effects of high spring releases, and steady summer flows.

4. Develop a Non-Native Fish Management Plan: Predation may be a major source of mortality for subadult humpback chub in Grand Canyon. Major predators need to be identified, their impact quantified, and control options discussed. Sensitive areas need to be identified, such as the blue ribbon tailwater trout fishery and the rainbow trout at Nankoweap Canyon used by migrating bald eagles.

5. Develop a Genetics Management Plan: The last recognizable mainstem stock of humpback chub in Grand Canyon may be represented by 40-60 adults near RM 30, some of which are spawning in the warm springs of Fence Fault. Management strategies need to be identified for taking fish to a refugia or enhancing mainstem spawning and survival.

6. Evaluate EIS Elements: Risk assessments are recommended for evaluating selective withdrawal, high spring releases, and steady summer flows.

7. Conduct Swimming Performance Experiments: Hypotheses need to be tested that subadult humpback chub are being transported downstream and limited to low velocity habitat by reduced swimming performance at cold temperatures. We recommend laboratory swimming performance tests for YOY (range, 50-100 mm TL) and juveniles (range, 100-200 mm TL) at 10°C, 12°C, 15°C, and 20°C following acclimation to 20°C; these conditions simulate young fish moving from the LCR to the mainstem.

8. Develop Depth and Velocity Isopleths of River Channel: Additional mapping of the river bottom and velocity characteristics is recommended with SuperHydro technology.

9. Determine Relationship of Drift and Benthos: Concurrent sampling of drift and benthos is recommended to characterize macroinvertebrate communities by season, time of day, flow magnitude, and ramping rates.

10. Identify Sources of Primary and Secondary Production: The hypothesis should be tested that food supplies for subadults are limiting in western Grand Canyon in order to determine if

production can be enhanced in this area as a way to establish a second spawning population of humpback chub.

11. Develop and Implement a Long-Term Monitoring Program: We concur with recommendations in the Glen Canyon Dam Final EIS to develop and implement a long-term monitoring program. We urge Reclamation to insure scientific input from present investigators in development and implementation of that program.

12. Develop a Temperature Model: Longitudinal temperature characteristics of the Colorado River need to be described by season, flow magnitude, and ramping in order to understand the effects of selective withdrawal, high spring releases, and steady summer flows on temperature and thus on fish assemblages in both near shore and mainstem habitats.

13. Extend Critical Habitat Designation: We recommend extending critical habitat of the humpback chub in Grand Canyon by 10 mi from Nautaloid Canyon (RM 34) upstream to RM 24. This area of extension includes the Fence Fault springs currently being occupied by the 30-Mile aggregation (40-60 adults) of humpback chub. Post-larval chub were captured in a warm spring in July 1994 indicating successful reproduction.

14. Identify Mainstem Flow Needs for 30-Mile Aggregation: The elevation of spring sources and adjacent crevice cover may be critical to successful spawning by humpback chub near RM 30. The relationship of these elevations and mainstem flow need to be described, as well as flows at which the thermal plume is largest and most stable for the fish.

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