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Distribution and Abundance of native and non-native fishes of the Colorado River Ecosystem in Grand Canyon, Arizona

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Abstract

The Colorado River ecosystem in Grand Canyon is strongly impacted by operation of Glen Canyon Dam. Fluctuating releases of cold, hypolimnetic water from Lake Powell (~8°C) for peak hydroelectric power generation has had a profound impact on the formerly warm, silty Colorado River. Clear, cold stenothermal conditions preclude successful reproduction and recruitment of most native fishes in the mainstem and introduced trout have become dominant species in the fish community. To assess the effects of dam operations on the native fish assemblage, the distribution and abundance of native and non-native fishes of the Colorado River ecosystem in Grand Canyon were assessed in the first year of a two-year research and monitoring program funded by the Grand Canyon Monitoring and Research Center. Study sites were located along 159 miles of the Colorado River from the Paria River to below Havasu Creek. An intensive area of study was established from just above the confluence of the Little Colorado River (LCR) at river mile (rm) 60 to Tanner Rapid at rm 68.6 (LCR inflow reach). Additional sampling was conducted in major tributaries (LCR, Bright Angel, Shinumo, Kanab, Havasu). Mini-hoopnets, minnow traps, electrofishing, trammel nets, and seines were used to sample fish during 120 days of fieldwork spread over four seasons between March 1998 and February 1999. Some 4,618 fish were captured in the Colorado River mainstem and tributaries. Non-native species dominated the catch in the mainstem Colorado River (1,515/2,565, 59%) and rainbow trout (*Oncorhychus mykiss*) was the most common non-native species (n=955, 37%). Of 1,050 native fish captured in the mainstem, speckled dace (*Rhinichthys osculus*) (n=463, 18%) and humpback chub (*Gila cypha*) (n=395, 15%) were the most abundant. The use of mini-hoopnets to sample fish in mainstem habitats revealed a relative abundance of humpback chub in the 100-200 mm TL size class, a population feature not observed in previous studies. In the smaller tributaries (Bright Angel, Shinumo, Kanab, Havasu), native species dominated the catch (739/847, 87%). Speckled dace (n=370, 44%) and humpback chub (n=133, 16%) were the most abundant native fishes. The LCR assemblage was dominated by native species (963/1206, 80%) with humpback chub (n=515, 43%) and speckled dace (n=308, 19%) dominating. The pattern of appearance, distribution, and abundance of young-of-year (YOY) humpback chub in the mainstem Colorado River observed in our study was consistent with a "source-sink" model of

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downstream dispersal from the LCR coupled with high mortality from predation in the mainstem Colorado River. The abundance of adult rainbow trout in the LCR inflow reach of the Colorado River coupled with their complementary distribution with juvenile humpback chub in January 1999 strongly suggests that predation by rainbow trout may have been responsible for the near disappearance of YOY humpback chub between late summer and early winter. Mortality rates for small fish are likely exacerbated by fluctuating flows, which disrupt habitat associations and increase the probability of downstream movement and dispersal. Fluctuating flows also reduce the suitability of river edge habitats and food resources needed for rearing small fish. The rarity of small humpback chub downstream of the LCR inflow coupled with high abundance of trout and cold fluctuating flows suggest that conditions for recruitment of YOY humpback chub in the Colorado River in Grand Canyon are extremely poor. In order to provide opportunities for increased survivorship of small humpback chub in Grand Canyon, resource managers should consider ways to stabilize flows and increase temperature in the mainstem Colorado River. Implementation of more natural flow and temperature conditions will increase the stability of shoreline habitat and cover, and likely result in increased food resources and growth rates in small fishes, and decrease mortality associated with picivory.

Introduction

Since completion of Glen Canyon Dam in 1963, its operation has strongly impacted the Colorado River ecosystem in Grand Canyon. Fluctuating releases of cold, hypolimnetic water from Lake Powell (~8°C) for peak hydroelectric power generation has had a profound impact on the formerly seasonally warm and silty Colorado River. Clear, cold stenothermal conditions preclude successful reproduction of warmwater native fishes in the mainstem, fluctuating flows disrupt and degrade aquatic habitat, and introduced rainbow trout has become the dominant species in the fish community. In 1998, the principal author (OTG) was awarded a contract by the Grand Canyon Monitoring and Research Center (GCMRC) to conduct a 2-yr, comprehensive monitoring and research program on native fishes of Grand Canyon. The primary objective of the work was to investigate linkage of dam-controlled flow regimes to the ecology of native fishes in Grand Canyon. This overarching question includes many ecological factors that need consideration: reproductive success, larval transport, recruitment, food resources and diet; predator-prey and competitive interactions between native and non-native species; diseases, parasites and condition factor; available habitats and habitat use in shoreline areas; temperature, physiology, and growth. Additional ecological factors that should be considered include: ontogenetic changes, temporal activity patterns, movement, spawning, population age structure, and distribution (mainstem vs. tributaries). The second objective was to monitor the status and trends of native fish populations in Grand Canyon. Continued monitoring is necessary to assess the current status of native fishes, especially the endangered humpback chub (*Gila cypha*)--particularly in the context of changing dam operations and flow regime.

The purpose for conducting this comprehensive monitoring and research program was to provide critical information to the Grand Canyon Adaptive Management Program for development of conceptual ecosystem models, designing future experimental flows, and identifying information needs for future studies and monitoring. Furthermore, our work will provide information for developing management plans and actions aimed at removing jeopardy to the endangered humpback chub and improving the status of other native fishes in Grand Canyon.

A team of investigators representing tribal, state, federal and university agencies conducted our monitoring and research program collaboratively. The Grand Canyon Fishery Resources Office developed cooperative agreements with Arizona Game and Fish Department (AGFD), Northern Arizona University, University of Arizona, Navajo Nation Natural Heritage Program, Hualapai Tribe, Willow Beach National Fish Hatchery, and Pinetop Fish Health Center. Other USFWS offices volunteered personnel for field and laboratory work, including Mora National Fish Hatchery and Tech Center, Arizona Fishery Resources Office-Pinetop, Arizona Fishery Resources Office-Parker, and Nevada Ecological Services Office. Our project represents a model for inter-agency cooperation in the quest to address complex natural resource problems.

New sampling methods were applied to near-shore habitat in the Colorado River mainstem that we developed for our tributary studies in the early 1990s included mini-hoopnet and point-centered habitat measurements (Gorman 1994). Although we present only the results of assessing fish communities in the Grand Canyon ecosystem in this paper, our program supported a number of other tightly linked novel research components: Habitat assessment was designed to provide greater understanding of the impacts of fluctuating flows on habitat quality and habitat-fish associations. Our fish and habitat sampling was linked to food base studies conducted by Dean Blinn, Allen Haden, and Joseph Shannon of Northern Arizona University. Their studies were intended to provide a better understanding of diet and food resources for native fish in Grand Canyon. Integration of information from these related studies is critical to linking past tributary and mainstem studies to the present program and will permit synthesis of more accurate and detailed native and non-native fish life histories. Fish health monitoring was included as a component of our fish sampling to develop a better understanding the relationship between fish diseases and environmental conditions in Grand Canyon. Experimental studies of growth in native fishes were conducted at the Willow Beach National Fish Hatchery to address the thermal requirements for growth and survivorship of the endangered humpback chub. Swimming performance studies were conducted at the University of Arizona by David Ward to determine ranges of temperature and flow velocity where juvenile flannelmouth sucker (*Catostomus latipinnis*) and other native fishes are not displaced. Information from these experimental studies is needed to identify target mainstem conditions for modification of dam operations (flow regime and thermal warming).

At the time of the USFWS symposium on native fishes of the Southwest in July 1999, we had completed approximately half of the field component of our monitoring and research program. This paper serves to outline the major objectives of the 2-year program and provides interim results after completion of the first field season.

Methods

Monitoring and research was conducted within Grand Canyon and the Little Colorado River (LCR) (Figure 1, Table 1). Our monitoring and research program focused on a set of mainstem sample areas that included a major tributary and associated river reach because almost all native fish in Grand Canyon are dependent on these streams for reproduction and early life history stages. Major tributaries included were the LCR, Bright Angel, Shinumo, Kanab, and Havasu. In particular, we focused on the LCR and its mainstem Colorado River inflow reach (rm 60-68.6) because this is where the largest population of the endangered humpback chub is found and successfully reproduces (Kaeding and Zimmerman 1983; Gorman 1994; Valdez and Ryel 1995; Gorman and Stone 1999). Other mainstem reaches where aggregations of humpback chub are known to occur, e.g., Fence Fault and Middle Granite Gorge, were included in the monitoring program.

Our sampling was designed to detect reproductive success, survivorship of young-of-year (YOY), and status of adult populations. Non-native fishes were also included in our monitoring as these species represented a significant component of the fish community. For consistency with past studies, we attempted to sample the same areas along the mainstem Colorado River and followed the methods of Valdez and Ryel (1995), who were responsible for the 1990-1994 Grand Canyon monitoring program funded by the Bureau of Reclamation's Glen Canyon Environmental Studies Program. Our sampling methods included the traditional boat-mounted electroshocker, trammel nets, minnow traps, and seines to sample fish in mainstem near-shore habitats (shorelines, eddy complexes, backwaters). In addition, we used specially designed mini-hoopnets (0.5 m diameter x 1.0 m length, 6 mm mesh) developed in the early 1990s (Gorman 1994) to sample fish along mainstem shoreline habitats and tributary confluences. Standard Gee's minnow traps (0.5 m long, 0.25 m diameter) and seines (2.7 m long, 1.3 m deep) had 6 mm mesh. Trammel nets were 15.2 or 22.9 m long, 1.8 m deep with 2.5 or 3.8 cm inner mesh and 30.5 cm outer mesh. Electrofishing was conducted from the same 16' inflatable, motorized Achilles electroshocker boat as was used by Valdez and Ryel (1995) and equipped with the same 5,000 watt generator powering a Mark 20 Coffelt CPS electrofishing unit. Mini-hoopnets, minnow traps, and seines were used to sample fish in tributaries and tributary mouths.

To maintain consistency of sampling effort, our electrofishing sampling areas followed Valdez and Ryel (1995) and were delineated by geomorphic shoreline types, e.g., vegetated bank, debris fan, bedrock, etc). Electrofishing was conducted during darkness within 4 hours following sunset, or in some cases during the day when floodwaters caused high turbidity. Trammel nets were tied from shore and set to sample mainstem eddy complexes, backwaters and return channels. Trammel nets were fished for approximately two hours duration at each location. Mini-hoopnet and minnow trap sampling was patterned after methodologies developed in previous studies in the LCR and outlined in Gorman (1994), Gorman and Stone (1999), and Stone (1999). However, in the present study, mini-hoopnets and minnow traps were not set along cross-channel transects as in Gorman (1994), but were set in pairs (one mini-hoopnet and one minnow trap) near stream margins at 20 m intervals along established mainstem shoreline or tributary locations and were emptied at 24 h intervals for up to two days. Mini-hoopnets and minnow traps were set as close as possible to the stream margin where depth was adequate; 15-

50 cm for minnow traps and >50 cm for mini-hoopnets. Seines were used to sample backwaters, or shallow shoreline areas.

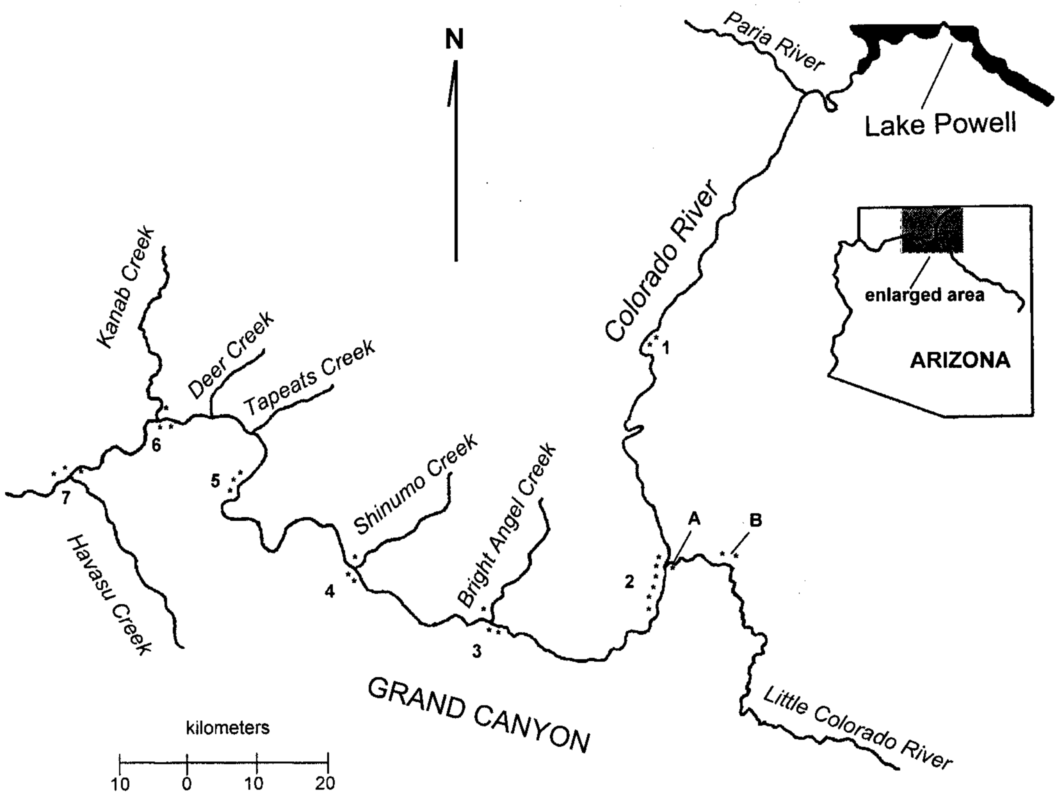

FIGURE 1. Map of Grand Canyon showing locations of sample areas along the Colorado and Little Colorado rivers. Mainstem sample reaches: **1.** Fence Fault, rm 30.5; **2.** LCR Inflow, rm 60.0-68.6; **3.** Bright Angel Creek, rm 87.5; **4.** Shinumo Creek, rm 108.5; **5.** Middle Granite Gorge, rm 125-128; **6.** Kanab Creek, rm 143.5; **7.** Havasu Creek, rm 156-159. LCR sample reaches: **A.** LCR Confluence Reach, km 0-3; **B.** Salt Canyon Reach, km 10-13. During mainstem sempling trips, sampling was conducted at sites located in the lower 1 km of the LCR and smaller tributaries (Bright Angel, Shinumo, Kanab, and Havasu).

Results

Approximately 120 days of fieldwork were conducted between March 1998 and February 1999 during which 4,618 fish were captured in the Colorado River mainstem and tributaries (Tables 2-5, 8-9; Appendix I, II). Fieldwork was conducted during 3 mainstem trips (June and September 1998 and January 1999) and 3 sampling periods/trips in the LCR (March-May, July, October 1998).

Non-native species dominated the catch in the mainstem Colorado River (1,515/2,565 fish, 59%). Rainbow trout (*Oncorhychus mykiss*) was the most common non-native species (n=955, 37%). More than 90% of all rainbow trout and brown trout (*Salmo trutta*) captured were >200 mm TL and the majority of individuals were > 300 mm TL. Thus, most trout captured were large adults. Of 1,050 native fish captured in the mainstem, speckled dace (*Rhinichthys osculus*) (n=463, 18%) and humpback chub (n=395, 15%) were the most abundant. In the smaller tributaries (Bright Angel, Shinumo, Kanab, Havasu) native species dominated the catch (739/847, 87%). Speckled dace (n=370, 44%) and humpback chub (n=133, 16%) were the most abundant native fishes. The LCR assemblage was also dominated by native species (963/1,206, 80%) with humpback chub (n=515, 43%) and speckled dace (n=308, 19%) predominating.

TABLE 1. Location of sampling areas along the Colorado River and Little Colorado River (LCR) in Grand Canyon. Locating sites by river miles (rm) in Grand Canyon is the usual convention in Grand Canyon and represents miles downstream from Lees Ferry, located just above the mouth of the Paria River. Sites in the LCR are located by distance in kilometers (km) upstream from the mouth. Mainstem Colorado River sample reaches are indicated by numbers. The LCR Inflow Reach is subdivided into 6 sample areas (2a-2f). Five mainstem sample reaches include sampling sites in the lower 1 km of the adjacent tributary (LCR, Bright Angel, Shinumo, Kanab, Havasu), which were sampled in conjunction with mainstem sampling trips. LCR sample reaches are indicated by letters (A, B) and were sampled separately from mainstem sampling trips. Figure 1 is a map showing the location of the sampling areas.

Mainstem Colorado River	**river mile (rm)**
1 Fence Fault (mainstem reach)	30.5
2. Colorado River –Little Colorado River (LCR) Inflow Reach	60.0-68.6
2a. Above the confluence of the Little Colorado River (mainstem area)	60.0-61.5
2b. Little Colorado River Confluence (tributary mouth area)	61.5
2c. Crash Canyon (mainstem area)	61.6-62.8
2d. Hopi-Salt (mainstem area)	62.9-64.0
2e. Carbon-Lava-Chuar (mainstem area)	64.1-65.5
2f. Tanner (mainstem area)	66.8-68.6
3. Bright Angel (mainstem reach and tributary area)	86.0-88.0
4. Shinumo (mainstem reach and tributary area)	107.0-108.7
5. Middle Granite Gorge (mainstem reach)	125.0-128.0
6. Kanab Creek (mainstem reach and tributary area)	143.0-143.5
7. Havasu Creek (mainstem reach and tributary area)	156.0-159.0

Little Colorado River (LCR)	**km**
A. Confluence Reach	0-3
B. Salt Canyon Reach	10-13

Little Colorado River

Little Colorado River-Spring Monitoring

Monitoring of native fishes was conducted in the lower 3 km Confluence Reach of the Little Colorado River (LCR) during a 40-day period (27 March-6 May 1998) and represented a continuation of the Arizona Game and Fish Department's (AGFD) LCR Spring Monitoring Program that was started in the 1980s following completion of Kaeding and Zimmerman's (1983) research program. Capture of fishes was accomplished using three different standardized gear types: large hoopnets, mini-hoopnets and minnow traps. Sixteen large hoopnets (1.0 m diameter, 2.0 length, 6 mm mesh), two mini-hoopnets and two groups of five minnow traps were distributed among historical monitoring sites located along stream margins in the lower 1.2 km of the Little Colorado River and were checked twice daily (Robinson and Clarkson 1992; Robinson et al. 1996; Brouder and Hoffnagle 1998a, b). Additional hoopnets and minnow traps were set at established USFWS sampling sites along stream margins between km 1.2 and km 3.0.

Over the 40-day sampling period 762 fish were captured and native fish predominated with 592 (78%) of the individuals (Table 2). The most abundant species were humpback chub (n=287, 38%), speckled dace (n=172, 23%) and fathead minnow (*Pimephales promelas*) (n=111, 15%). Most fish captured were adults and no YOY fish were captured. The usual pattern of late February-early April spring flooding was prolonged through early May because of unusually wet late winter and spring weather. As a result, the usual March-April spawning run of humpback chub (Gorman and Stone 1999) was probably delayed until mid-May after the end of our sampling period. During our sampling, catches of adult humpback chub were not as high as in previous years (Brouder and Hoffnagle 1998a,b), and there was a low frequency of fish in spawning condition.

TABLE 2. Fish captured by gear type in the Little Colorado River Confluence Reach (km 0-3), 27 March-6 May 1998.

	Species[a]											
Gear type	**BBH**	**BHS**	**CCF**	**CCP**	**FHM**	**FMS**	**HBC**	**PKF**	**RBT**	**RSH**	**SPD**	**Total**
Mini-hoopnet	1	68	17	4	109	22	268	2	8	18	167	684
Minnow trap	0	1	0	0	2	1	14	0	0	2	5	25
Trammel	0	1	0	2	0	40	5	0	5	0	0	53
Total	1	70	17	6	111	63	287	2	13	20	172	762

[a] BBH = black bullhead (*Ameiurus melas*); BHS = bluehead sucker (*Catostomus discobolus*); CCF = channel catfish (*Ictalurus punctatus*); CCP = common carp (*Cyprinus carpio*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); GRS = green sunfish (*Lepomis cyanellus*); HBC = humpback chub (*Gila cypha*); RBT = rainbow trout (*Oncorhynchus mykiss*); RSH = red shiner (*Cyprinella lutrensis*); SPD = speckled dace (*Rhinichthys osculus*).

Little Colorado River-Summer and Fall Monitoring.

Monitoring of native fishes was conducted in the 10-13 km Salt Canyon Reach during 22-31 July and 20-24 October 1998 to assess reproductive success of humpback chub and other native fishes. Sampling was accomplished with one mini-hoopnet and one minnow trap set in pairs at established sampling sites spaced at 20 m intervals between km 10.5 and km 11.9. Mini-hoopnets and minnow traps were emptied at 24 h intervals over a 48 h sample period. On day four of our July trip, a large (~100 cm rise in stage) silt-laden flood swept through the study reach and continued for 24 hours before receding. The flooding truncated our 10-day sampling effort to 4 days. As a result, a second sampling trip was conducted in October, when the probability of flooding was reduced.

Prior to the flood that occurred during the July sampling trip, 46 mini-hoopnet and 34 minnow trap sets captured 230 fish. Native fishes dominated the catch and humpback chub was the most abundant species, and represented 73% of the total (Table 3). However, only 11 of 167 humpback chub captured in mini-hoopnets and minnow traps were YOY fish. Qualitative sampling of quiet shallow edge habitats with 1/8" and 3/16" mesh seines following the flooding yielded many small fishes, especially YOY humpback chub, bluehead suckers (*Catostomus discobolus*), and speckled dace and indicated that native fishes had successfully reproduced. However, their small size (35-50 mm TL) suggested that spawning took place late in spring, most likely after our LCR spring monitoring in mid- to late-May, when discharge levels returned to base flow levels. Approximately 400 of the YOY humpback chub captured during the post-flood seining were transported by helicopter to the Willow Beach National Fish Hatchery to establish a captive broodstock. The presence of non-native fathead minnows and red shiners (*Cyprinella lutrensis*) was noteworthy; during intensive sampling by OTG in the LCR from 1991-1995, fathead minnows were very rare and red shiners were absent (Gorman 1994). In 1998, adult fathead minnows, some probably over two years old (> 65 mm TL) and red shiners, some probably more than one year old (> 65 mm TL) were common. However, YOY of fathead minnow, red shiner or other non-native fishes were not observed. Also missing from seine catches were YOY common carp (*Cyprinus carpio*), although age 1+ and 2+ fish were present. This pattern of YOY abundance suggests that native species had a more successful reproductive effort in 1998 than non-native species, and that differing patterns of reproductive success between native and non-native cyprinids may be linked to natural variation in flooding patterns (Minckley and Deacon 1991).

During the October sampling trip, 41 mini-hoopnet and 27 minnow trap sets over a 4-day period yielded 199 fish. As in the July samples, native fish, especially speckled dace and humpback chub, dominated the catch (Table 4). Of the 56 humpback chub captured, 19 (34%) were YOY; this represents a significant increase in the proportion of YOY compared to the July sampling. We attributed the increase to the larger size of YOY in October, which increased their vulnerability to capture in mini-hoopnets. The YOY humpback chub represented a distinct size cohort (60-85 mm TL) for the LCR population (Figure 2).

TABLE 3. Fish captured by gear type in the Little Colorado River Salt Canyon Reach (km 10-13), 22-31 July 1998.

	Species[a]									
Gear type[b]	**BHS**	**CCF**	**CCP**	**FHM**	**FMS**	**HBC**	**PKF**	**SPD**	**YBH**	**Total**
Mini-hoopnet	5	5	24	5	1	164	2	10	3	219
Minnow trap	0	0	0	1	0	3	5	2	0	11
Total	5	5	24	6	1	167	7	12	3	230

[a]BHS = bluehead sucker (*Catostomus discobolus*; CCF = channel catfish (Ictalurus punctatus); CCP = common carp (*Cyprinus carpio*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); HBC = humpback chub (*Gila cypha*); PKF = plains killifish (*Fundulus zebrinus*); SPD = speckled dace (*Rhinichthys osculus*); YBH = yellow bullhead (*Ameiurus natalis*).

[b]Additional species captured during post flood seine sampling but not enumerated included: red shiner (*Cyprinella lutrensis*), yellow bullhead, fathead minnow, bluehead sucker, plains killifish, common carp, speckled dace.

TABLE 4. Fish captured by gear type in the Little Colorado River Salt Canyon Reach (km 10-13), 20-24 October 1998.

	Species[a]							
Gear	**CCP**	**FHM**	**FMS**	**HBC**	**SPD**	**RSH**	**YBH**	**Total**
Mini-hoopnet	2	8	1	51	94	4	1	161
Minnow trap	0	4	0	5	29	0	0	38
Totals	2	12	1	56	123	4	1	199

[a]CCP = common carp (*Cyprinus carpio*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); HBC = humpback chub (*Gila cypha*); SPD = speckled dace (*Rhinichthys osculus*); RSH = (*Cyprinella lutrensis*) YBH = yellow bullhead (*Ameiurus natalis*).

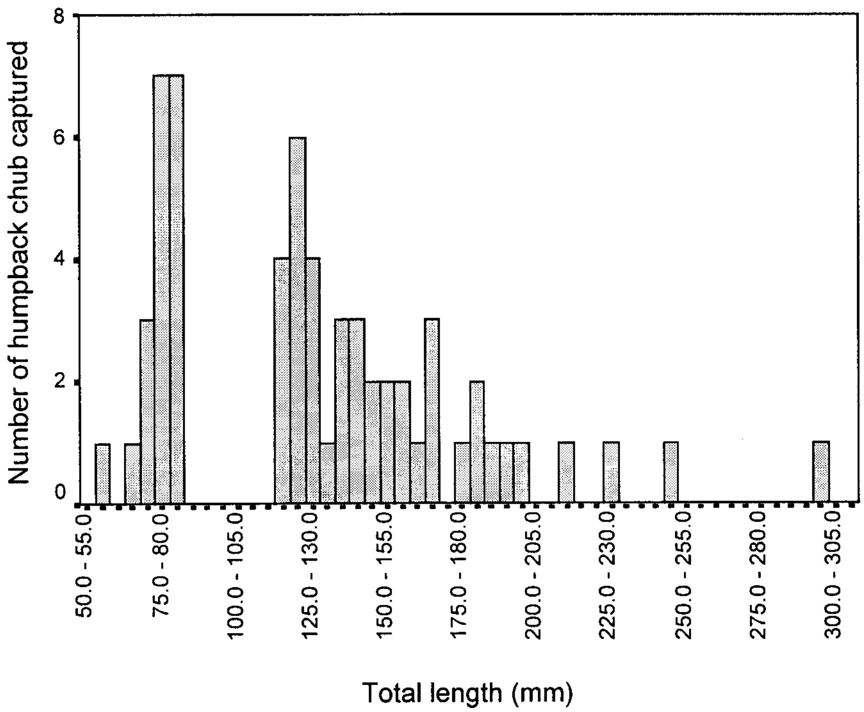

FIGURE 2. Length-frequency histogram of humpback chub captured in the Little Colorado River Salt Canyon Reach (km 10-13), 20-24 October 1998.

Summary of 1998 sampling for the Little Colorado River

Over the three sampling periods in the Little Colorado River in 1998, 1,206 fish were captured (Table 5). As observed in previous studies, e.g., Gorman (1994), native species fish dominated the fish community. Spawning of humpback chub appeared to occur later than usual due to prolonged spring flooding. Native fish comprised 80% or 963/1,206 of fish captured and humpback chub was the most abundant species with 43% or 515/1,206 fish captured. Fathead minnow and red shiner were common in our samples, but were rare or absent in intensive sampling conducted by OTG in 1991-1994 (Gorman 1994).

TABLE 5. Summary of catch, Little Colorado River, 1998. March-May sampling was conducted in the Confluence Reach and July and October sampling was conducted in the Salt Canyon Reach.

	Species[a]												
Sampling period	**BBH**	**BHS**	**CCF**	**CCP**	**FHM**	**FMS**	**HBC**	**PKF**	**RBT**	**RSH**	**SPD**	**YBH**	**Total**
March-May	1	70	17	6	111	63	287	2	13	20	172	0	762
July[b]	0	5	5	24	6	1	167	7	0	0	12	3	230
October	0	0	0	3	16	1	61	0	0	8	124	1	214
Total	1	75	22	33	133	65	515	9	13	28	308	4	1206

[a]BBH = black bullhead (*Ameiurus melas*); BHS = bluehead sucker (*Catostomus discobolus*); CCF = channel catfish (*Ictalurus punctatus*); CCP = common carp (*Cyprinus carpio*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); HBC = humpback chub (*Gila cypha*); PKF = plains killifish (*Fundulus zebrinus*); RBT = rainbow trout (*Oncorhynchus mykiss*); RSH = red shiner (*Cyprinella lutrensis*); SPD = speckled dace (*Rhinichthys osculus*); YBH = yellow bullhead (*Ameiurus natalis*).

[b]Additional species captured during seining that were not counted: red shiner (*Cyprinella lutrensis*), yellow bullhead, fathead minnow, bluehead sucker, plains killifish, common carp, speckled dace.

Mainstem Colorado River and Tributaries

<u>June, September, and January Monitoring and Research</u>

Fish populations were monitored with electrofishing, trammel nets, mini-hoopnets, minnow traps, and seining at seven mainstem Colorado River reaches and at five tributary sites (Figure 1, Table 1) during 3 mainstem sampling trips: June 1998 (Trip 1), August-September 1998 (Trip 2), and January 1999 (Trip 3). During Trip 2, additional mainstem sampling was conducted at Fence Fault (rm 30.5) and the LCR Inflow Reach was extended to include the Tanner Rapids sample area (rm 66.8-68.6). During the Trip 3, sampling was reduced to 5 areas and focused on the LCR Inflow Reach (rm 60-68.6). In addition to the primary mainstem sample areas, backwaters were seined at locations along the mainstem from the vicinity of the Little Colorado River downstream to rm 192, particularly during Trip 2. Mainstem mini-hoopnet/minnow trap sampling areas were established in the LCR Inflow, Bright Angel, Middle Granite Gorge, and Havasu reaches. Within each sample area (300-600 m long), fish sampling sites were established at 20 m intervals. The LCR Inflow Reach included 6 sample areas distributed from above the mouth of the LCR (rm 60) to Tanner Rapids (rm 68.6) (Table 1). As was done in the Salt Canyon Reach of the LCR, one mini-hoopnet and one minnow trap were set in pairs at established fish sampling sites spaced at 20 m intervals along river margins. Mini-hoopnets and minnow traps were emptied of fish at 24 h intervals over a 48 h sample period. Within tributaries, mini-hoopnets and minnow traps were set at regular intervals from the mouth to as far as 1 km upstream from the confluence, depending access and suitable habitat. Data from sampling conducted in the LCR confluence during mainstem monitoring trips was treated separately from other LCR sampling presented previously (LCR spring monitoring in the Confluence Reach and summer and fall sampling in the Salt Canyon Reach).

Sampling Effort

For Trip 1 (June), the summed length of mini-hoopnet/minnow trap sample areas was 3,040 m for mainstem reaches and 1,250 m for tributaries. Electrofishing was conducted over 11 nights and one morning totaling 417 min of effort, trammel nets were set/run on 9 nights and one daytime period. Trapping effort for mainstem and tributary sampling included 179 mini-hoopnet and 192 minnow trap sets (Tables 6, 7). For Trip 2 (September), the summed length of mini-hoopnet/minnow trap sample areas was 2,880 m for mainstem reaches and 1,150 m for tributary confluence sites. Electrofishing included 34 runs totaling 330 min of effort and 61 trammel net sets. Trapping effort included 229 mini-hoopnet sets and 282 minnow trap sets, and 96 seine samples were taken (Tables 6, 7). For Trip 3 (January), the summed length of mini-hoopnet/minnow trap sample areas was 2,420 m for mainstem reaches and 320 m for tributary reaches. Electrofishing included 23 runs, totaling 244 min of effort. Trapping and netting effort comprised 23 trammel net, 243 mini-hoopnet, and 237 minnow trap sets and 4 seine hauls.

River Stage Fluctuations

Starting in April 1998, the operators of Glen Canyon Dam began to release the largest allowable daily flow for peak hydroelectric power generation (5,000 cfs above a periodic mean base flow). During Trips 1 and 2, daily stage fluctuations ranging from 0.5-1.0 m were measured at mainstem Colorado River sites. This diel stage fluctuation appeared to lower the utility of backwaters and vegetated shorelines as fish habitat and macroinvertebrate production areas. During daily low flows, backwaters were largely dewatered and available cover for juvenile fish was diminished along vegetated shorelines as water levels dropped below the vegetation. During Trip 2 (late summer) the river stage was elevated from tributary flooding and was superimposed on the daily flow fluctuations. During this sampling period, the Colorado River was carrying a considerable silt load and turbidities exceeding 5,000 NTUs were observed. During Trip 3 (winter) the flow was relatively constant.

Distribution and Abundance of Fish

During Trip 1 (June), 784 fish of 4 native and 6 non-native species were captured; 528 fish were captured at mainstem sites and 256 fish were captured at tributary sites (Tables 8, 9). In the mainstem, rainbow trout was the dominant species followed by brown trout, humpback chub, fathead minnow, flannelmouth sucker, and speckled dace. In the tributaries, speckled dace, flannelmouth sucker, humpback chub, red shiner, and bluehead sucker were most abundant. Eighty-seven humpback chub were captured at 4 of 8 mainstem Colorado River sites and at 4 of 5 tributary sites (Appendix I, II).

In June, catches of native fish species at mainstem sites were lower than catches of non-native species at all mainstem Colorado River sites. In all tributaries, catches of natives were greater than non-native species. At tributary sites, 82% of the fish captured were native species, while at mainstem sites 22% of the fish captured were native species. Rainbow trout were the most abundant non-native species captured, as well as the most abundant fish species overall. Brown trout was the next most abundant non-native species. Catch of brown trout was highest in the mainstem Colorado River near Bright Angel Creek and catch of rainbow trout was highest in mainstem Colorado River near Havasu Creek.

During Trip 2 (August-September), 2,364 fish of 4 native and 8 non-native species were captured; 1,812 fish were captured at mainstem sites and 552 fish were captured at tributary sites (Tables 8, 9). In the mainstem, rainbow trout was once again the dominant species followed by speckled dace, humpback chub, and fathead minnow. Among the tributary sites, speckled dace, humpback chub, bluehead sucker, and flannelmouth sucker were most abundant. A total of 390 humpback chub were captured at 8 of 10 mainstem Colorado River sites and at 4 of 5 tributary sites (Appendix I, II). As observed during Trip 1, non-native fishes, especially adult rainbow trout, dominated the mainstem fish community while native species predominated at tributary sites. At tributary sites, 92% of the fish captured were native species, while at mainstem sites 48% of the fish captured were native species. Increased fish captures during Trip 2 were caused by a higher abundance of small fish, specifically humpback chub, speckled dace, red shiner, fathead minnow, and bluehead sucker. Of the native species (humpback chub, speckled dace, bluehead sucker), most were small YOY fish that presumably were spawned in tributaries and dispersed into mainstem habitats.

TABLE 6. Sampling effort, Colorado River in Grand Canyon, 1998. Sampling periods: Trip 1 (June 1998); Trip 2 (August-September 1998); Trip 3 (January-February 1999). Study area length refers to areas were mini-hoopnets and minnow traps were deployed at established shoreline locations spaced at 20-m intervals.

Sampling period	Study area length (m)	Electrofish (min)	Trammel net (sets)	Minnow trap (sets)	Mini-hoopnet (sets)	Seine (areas)
Trip 1	3040	417	41	133	125	6
Trip 2	2880	330	61	202	157	40
Trip 3	2420	244	23	198	198	4
Totals	8340	991	125	533	480	50

TABLE 7. Sampling effort in tributaries to the Colorado River in Grand Canyon (Bright Angel, Shinumo, Kanab, Havasu creeks) 1998. Sampling periods: Trip 1 (June 1998); Trip 2 (August-September 1998); Trip 3 (January-February 1999). Study area length refers to areas were mini-hoopnets and minnow traps were deployed at established shoreline locations spaced at 20-m intervals.

Sampling period	Study area length (m)	Minnow trap (sets)	Mini-hoopnet (sets)	Seine (areas)
Trip 1	1250	79	54	6
Trip 2	1150	80	72	56
Trip 3	320	39	45	0
Totals	2720	198	171	62

TABLE 8. Summary of fish captured in the mainstem Colorado River in Grand Canyon, 1998. Sampling periods: Trip 1 (June 1998); Trip 2 (August-September 1998); Trip 3 (January-February 1999).

Sampling Period	Species*													
	RBT	**BRT**	**CCP**	**HBC**	**SPD**	**RSH**	**FHM**	**FMS**	**BHS**	**CCF**	**PKF**	**GRS**	**YBH**	**Total**
Trip 1	304	62	13	57	25	3	30	29	4	0	0	1	0	528
Trip 2	511	71	18	302	431	41	284	105	37	1	10	0	1	1812
Trip 3	140	4	10	36	7	7	2	10	7	1	1	0	0	225
Totals	955	137	41	395	463	51	316	144	48	2	11	1	1	2565

* RBT = rainbow trout (*Oncorhynchus mykiss*); BRT = brown trout (*Salmo trutta*); CCP = common carp (*Cyprinus carpio*); HBC = humpback chub (*Gila cypha*); SPD = speckled dace (*Rhinichthys osculus*); RSH = red shiner (*Cyprinella lutrensis*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); BHS = bluehead sucker (*Catostomus discobolus*); CCF = (*Ictalurus punctatus*); PKF = (*Fundulus zebrinus*); GRS = green sunfish (*Lepomis cyanellus*); YBH = yellow bullhead (*Ameiurus natalis*).

TABLE 9. Summary of fish captured in tributaries (LCR Confluence and Bright Angel, Shinumo, Kanab and Havasu creeks) to the Colorado River in Grand Canyon, 1998. Sampling periods: Trip 1 (June 1998); Trip 2 (August-September 1998); Trip 3 (January-February 1999).

Sampling period	Species*												
	RBT	**BRT**	**CCP**	**HBC**	**SPD**	**RSH**	**FHM**	**FMS**	**BHS**	**CCF**	**PKF**	**GRS**	**Total**
Trip 1	1	7	4	30	85	27	6	81	13	0	0	2	256
Trip 2	9	2	9	92	279	3	15	56	81	0	6	0	552
Trip 3	11	4	1	11	6	0	1	2	3	0	0	0	39
Totals	21	13	14	133	370	30	22	139	97	0	6	2	847

* RBT = rainbow trout (*Oncorhynchus mykiss*); BRT = brown trout (*Salmo trutta*); CCP = common carp (*Cyprinus carpio*); HBC = humpback chub (*Gila cypha*); SPD = speckled dace (*Rhinichthys osculus*); RSH = red shiner (*Cyprinella lutrensis*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); BHS = bluehead sucker (*Catostomus discobolus*); CCF = (*Ictalurus punctatus*); PKF = (*Fundulus zebrinus*); GRS = green sunfish (*Lepomis cyanellus*).

A substantial number of the humpback chub captured during Trip 2 were between 100 and 200 mm TL (Figure 3). Length-frequency histograms presented by Valdez and Ryel (1995) indicated a relative absence of humpback chub in this size range in the LCR inflow of the Colorado River. In contrast, our results indicated that humpback chub in this size class had a higher relative abundance than reported by Valdez and Ryel (1995). Further analysis indicated that most of these fish were captured in mini-hoopnets (Figure 4), a gear not used by Valdez and Ryel (1995) and other researchers. Moreover, the length-frequency histograms for our captures from trammel nets and electrofishing (Figure 4) were similar to those presented by Valdez and Ryel (1995). These results suggest that we sampled a portion of the humpback chub population that has not been well represented in previous investigations.

During Trip 3 (January), 264 fish of 4 native and 7 non-native species were captured; 225 fish were captured at mainstem sites and 39 fish were captured at tributary sites (Tables 8, 9). This catch represents a ~80% decline compared to September. In the mainstem, adult rainbow trout was again the dominant species (62%) with humpback chub a distant second (16%). At the tributary sites, rainbow trout and humpback chub were co-dominant (28%). However, the relative abundance of native fish declined by 96% and non-native trout increased by 36% in the tributaries. Many of the rainbow trout captured in tributaries, such as Shinumo Creek, were large spawners (RGB, pers. obs.). A total of 47 humpback chub were captured at 6 of 9 mainstem Colorado River sites and 1 of 3 tributary sites (Appendix I, II). Native species comprised a larger proportion (56%) of the total fish sampled at tributary sites whereas they comprised only 27% of fish sampled at mainstem sites. The large reduction in relative abundance of fish during Trip 3 was especially notable for YOY native fishes (humpback chub, speckled dace, bluehead sucker) and for small non-native species (fathead minnow).

Relative to Trip 2 (August-September), catch of humpback chub in Trip 3 (winter) declined 85%, though length frequency distributions were similar for the two trips (Figure 6). However, in contrast to the summer trip, only one humpback chub <70mm TL was captured during winter. Thus, the catch of humpback chub was reduced relatively evenly across >70mm TL size classes, but smaller 35-70 mm TL individuals were nearly absent. These results are similar to those reported by Valdez and Ryel (1995), who described an exponential decline of juvenile (especially YOY) humpback chub densities between late summer and early winter.

During January sampling, we observed reciprocal abundances of small humpback chub and adult rainbow trout among study areas along the mainstem Colorado River. The highest catch of humpback chub <150 mm TL was recorded at the Tanner study area (within the LCR Inflow Reach) which also had the lowest catch of rainbow trout (Figure 5). In contrast, no humpback chub were caught at the Carbon Creek study area (within the LCR Inflow Reach), where the highest catch of rainbow trout was observed.

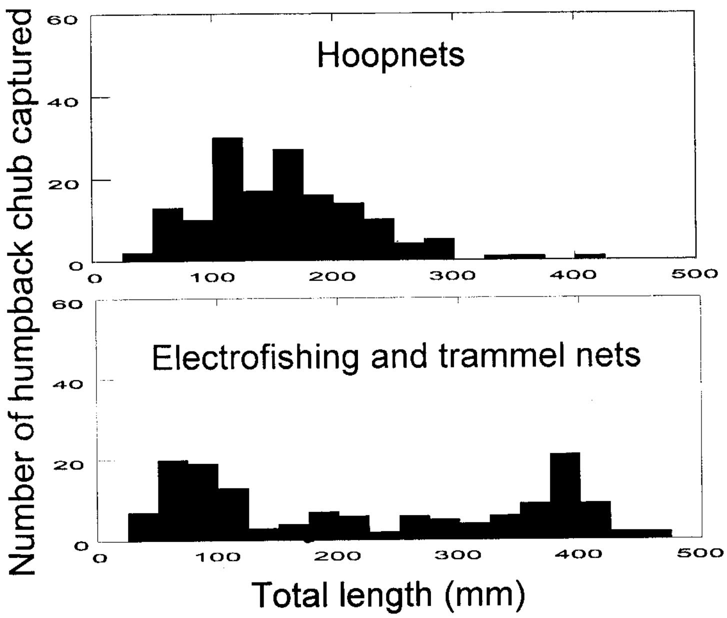

FIGURE 3. Length frequency histograms of humpback chub captured with all gear types in the Colorado River and confluence area of the Little Colorado River during monitoring Trip 1 (June) and Trip 2 (August- September), 1998.

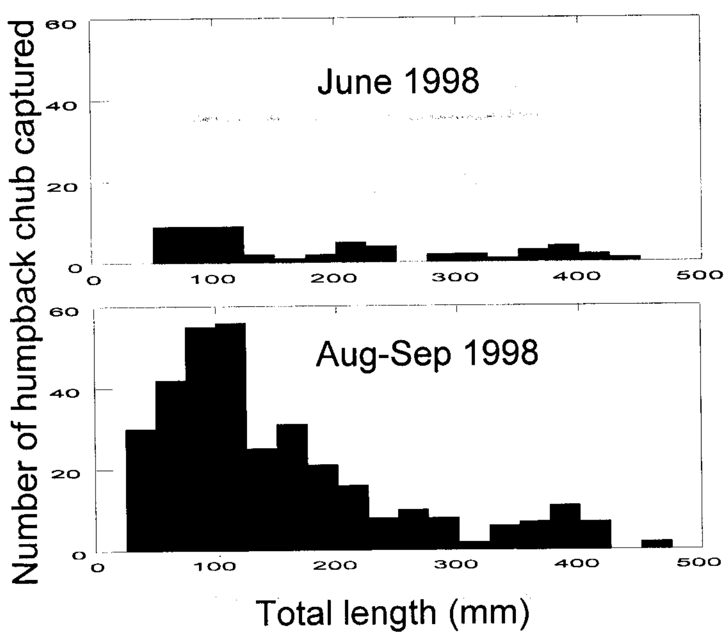

FIGURE 4. Length frequency histograms of humpback chub captured with mini-hoopnets versus electrofishing and trammel netting in the Colorado River and confluence area of the Little Colorado River during monitoring Trip 1 (June) and Trip 2 (August- September), 1998.

Length-frequency distributions for humpback chub captured in the lower LCR parallel that for the mainstem sites, particularly for August-September samples (Figure 7). When considered with the length-frequency distribution for humpback chub captured in the Salt Canyon reach in October (Figure 2) a progression of increasing size of the 1998 YOY cohort in the LCR between September 1998 and January 1999 is evident. Modal size of YOY humpback chub captured in the LCR was 50-60 mm TL in August and increased to 70-80 mm TL in October and remained at 70-80 mm TL in January (Figures 2, 6, 7). Modal size of smallest cohort of humpback chub captured in the mainstem LCR inflow reach was 50-60 mm TL in August and 80-100 in January 1999. The mainstem population size distribution mirrors that in the LCR except for the greatly reduced 70-80 mm YOY cohort in the January 1999 sample. This pattern suggests that the presence of smaller humpback chub in the mainstem is likely the product of summer dispersal of small humpback chub from the LCR into the mainstem Colorado River, especially following summer monsoonal flooding events as was observed frequently in 1998 and as was observed in previous investigations by Valdez and Ryel (1995) and Robinson et al. (1998). However, the chronically cold temperatures found in the mainstem should arrest growth (Luther and Clarkson 1994; Clarkson and Childs 2000; Gorman and VanHoosen 2000) and should have lead to an accumulation of smaller fish in the LCR inflow reach. No accumulation of smaller humpback chub was observed and the relative abundance of YOY declined precipitously (Figure 6). Moreover, YOY humpback chub were very rare in areas below the LCR inflow (Valdez and Ryel 1995; this study).

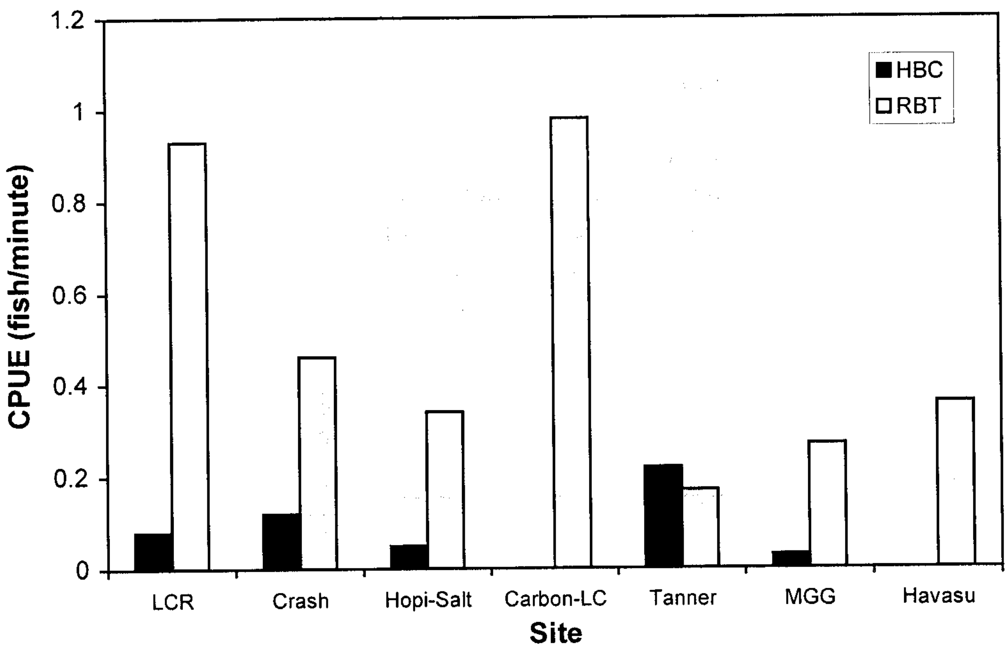

Figure 5. Comparison of humpback chub (HBC) and rainbow trout (RBT) captures at Colorado River mainstem sites in Grand Canyon, January 1999. Results shown are for electroshock sampling and expressed as fish captured/min. Location and river miles for mainstem sites shown are as follows: LCR (near LCR confluence, 59.7-61.3), Crash (near Crash Canyon, 61.4-63.2), Hopi-Salt (Hopi-Salt study area, 63.3-63.8), Carbon-LC (Carbon Creek-Lava Chuar study area, 63.9-64.9), Tanner (Tanner study area, 67.1-68.5), MGG (Middle Granite Gorge, 125.0-129.0), Havasu (near Havasu Creek, 155.0-158.7).

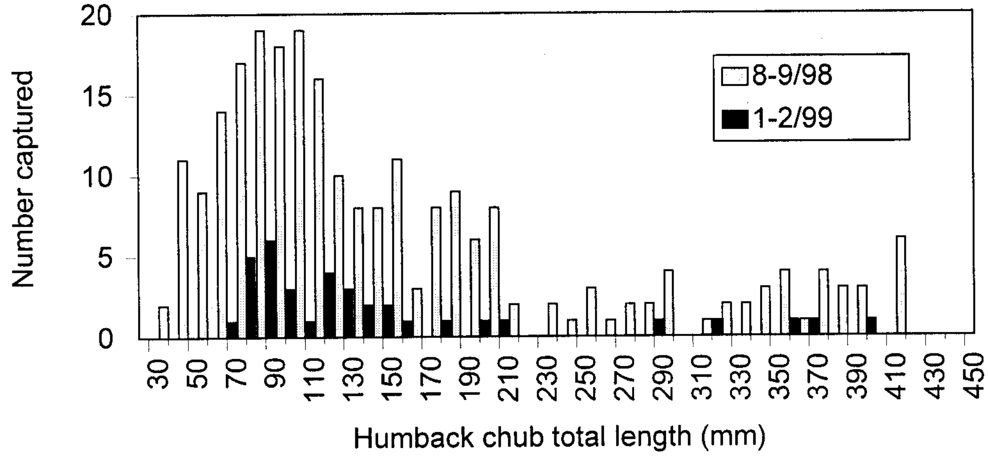

Figure 6. Size distribution of humpback chub captured by electrofisher, mini-hoopnets, minnow traps, and trammel-nets at nine mainstem sites in the Colorado River in Grand Canyon during sampling trips in August-September, 1998 and in January-February 1999.

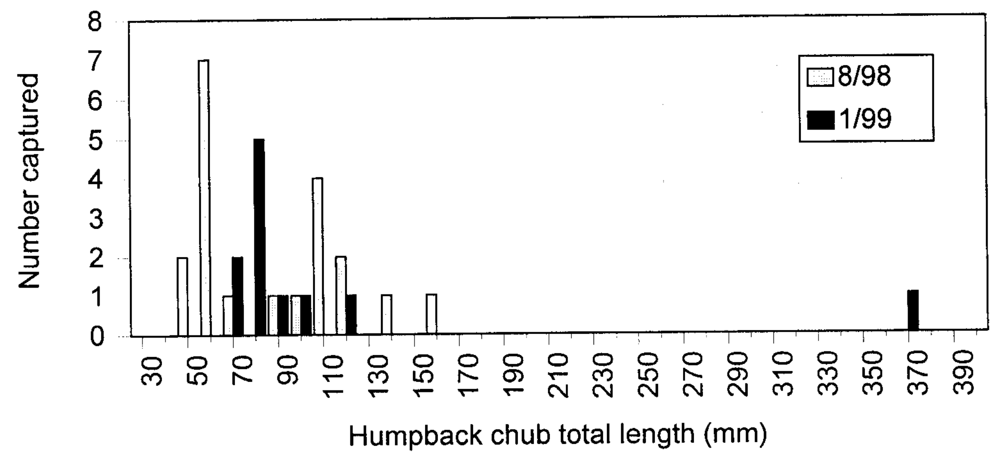

Figure 7. Size distribution of humpback chub captured with hoop nets and minnow traps in the Little Colorado River in Grand Canyon during sampling trips in August-September, 1998 and in January-February 1999.

Discussion

Weather conditions in Grand Canyon during 1998 were characterized by prolonged winter and spring flooding in the tributaries and a strong monsoonal summer rainfall season. Reproduction of humpback chub in the LCR was delayed until mid- to late May by flooding and low water temperatures; by late July, YOY humpback chub were 35-50 mm TL. In contrast, YOY humpback chub that were spawned in April 1993 were typically 15 mm larger by late July (Gorman 1994). At Glen Canyon Dam, maximum allowable daily flow fluctuations (5,000 cfs) commenced in April 1998 and resulted in substantial 0.5-1.0 m daily changes of river stage at sampling sites. During July, August and September, episodes of tributary flooding caused extremely turbid mainstem conditions. These summer flooding events probably facilitated downstream dispersal of YOY humpback chub (50-60 mm TL) from the LCR into the mainstem Colorado River. YOY humpback chub were relatively abundant in the LCR inflow reach of the Colorado River (rm 61-68) in August-September 1998, but remained extremely rare in areas further downstream. By January 1999, the relative abundance of YOY humpback chub was greatly reduced in the LCR inflow reach of the Colorado River. However, YOY humpback chub were still relatively abundant in the lower confluence reach of the LCR.

As shown in Valdez and Ryel's (1995, 1997) earlier 1990-1994 study, non-native species dominated the mainstem Colorado River fish community in Grand Canyon. However, our observation of the predominance of adult rainbow trout from Lees Ferry to Havasu Creek (rm 0-159) appears to be a new development compared to Valdez and Ryel's (1995) study in which rainbow trout were relatively abundant only between Lees Ferry and through the LCR inflow reach (rm 0-68). In addition, brown trout appear to have increased in abundance in the middle portion of Grand Canyon (rm 86-126). Native fish predominated in the tributaries as has been observed in previous studies (Gorman 1994). As before, humpback chub was the dominant native species in the LCR and LCR inflow reach (rm 61-68) of the Colorado River. Smaller aggregations of adults previously identified by Valdez and Ryel (1995) were found in the vicinity of specific downstream tributaries (Bright Angel, Shinumo, Kanab, Havasu) and in some discrete river reaches (Fence Fault and Middle Granite Gorge). However, we found larger numbers of adult humpback chub in the Shinumo and Havasu aggregations than was previously observed. However, we did not find evidence that these downstream aggregations had reproduced successfully.

Our use of mini-hoopnets to sample fish in shoreline habitats in the mainstem Colorado River revealed an abundance of juvenile humpback chub between 100-200 mm TL (Figure 4). With the exception of the near-absence of YOY in January samples, we found the size distribution of humpback chub in our samples from the LCR Inflow Reach of the mainstem to mirror that found in the LCR. This finding contrasts with Valdez and Ryel (1995) where 100-200 mm TL juvenile humpback chub were much less abundant in their samples (see their Figures 6-1 and 6-3) and we have attributed this to their lack of use of mini-hoopnets. Valdez and Ryel's finding has often been used to support the hypothesis that there is little or no recruitment of humpback chub in the mainstem Colorado River and that the gap in the size distribution is probably a result of low survivorship of YOY humpback chub. Our observation of greatly reduced abundance of YOY humpback chub between late summer and early winter supports the low survivorship hypothesis. The lack of persistence of smaller YOY humpback chub in the mainstem where growth is arrested by cold, stenothermal conditions (Clarkson and Childs 2000; Gorman and VanHoosen 2000) further supports the hypothesis of minimal survivorship of YOY fish. However, our finding that 100-200 mm TL humpback chub were relatively common in mainstem habitats during late summer sampling clouds the issue of their survivorship to adulthood within mainstem habitats. It is likely that these fish dispersed from the LCR as 100-200 mm size fish during late summer flooding events as suggested by Figure 3. However, Valdez and Ryel (1995, 1997) estimated annual an survivorship of $1x10^{-8}$ to $1.1x10^{-1}$ for mainstem humpback chub <200 mm TL, suggesting that very few 100-200 mm TL fish are recruited into the population of spawning adults. Further sampling and mark/recapture studies in the LCR inflow reach of the Colorado River will be required to resolve this issue.

The apparent lack of persistence of humpback chub <200 mm TL we observed in the mainstem Colorado River is consistent with the pattern of recruitment of adult humpback chub observed in the LCR. Gorman and Stone (1999) found that as resident adult chub exceeded 250 mm TL, they began to adopt a life history pattern of fall-winter residency in the mainstem Colorado River (LCR Inflow Reach) and migrated >10 km upstream into the LCR to spawn in the spring, often returning to the same site each year. Analysis of length-frequency distributions and size-specific survivorship in the mainstem humpback chub population by Valdez and Ryel (1995) supports the apparent shift in residency as adults approach 300 mm TL. Thus under present flow and temperature conditions in the mainstem Colorado River, there is little evidence to support successful recruitment of humpback chub < 200 mm TL that disperse from the LCR (Valdez and Ryel 1995; this study).

A number of mechanisms may be responsible for the disappearance of YOY humpback chub in the LCR Inflow Reach of the Colorado River between late summer and early winter. First, physical conditions were different between summer and winter; photoperiod was shorter in winter and water temperatures were 2-3°C lower in mainstem areas and these conditions may have resulted in lower activity levels and catch rates of YOY humpback chub. However, reductions in photoperiod and reduction in water temperature (24°C down to 15°C or lower) were also observed in the LCR with little change in catch rates between summer and winter. Turbidity may have also played a role, however, turbidity was high in both the LCR and mainstem during summer sampling whereas catch rates of humpback chub declined only in mainstem areas. A second explanation is that YOY humpback chub used different habitats in summer and winter. However, we found that YOY humpback chub were captured in the same mainstem habitats during summer and winter. Moreover, YOY humpback chub were caught at nearly the same rates in similar habitats during summer and winter in the LCR. A third explanation proposed by Valdez and Ryel (1995) is that downstream dispersal reduces the abundance of YOY humpback chub in the LCR Inflow Reach of the Colorado River. If so, we would expect to find aggregations of YOY humpback chub at downstream sites where suitable habitat exists, particularly following pulses of emigration from the LCR during summer months. However, we found little evidence of dispersal of YOY humpback chub to sites below the LCR Inflow. The final explanation proposed by Valdez and Ryel (1995) is that most YOY humpback chub are lost due to mortality, e.g., predation, thermal shock, diseases and parasites, starvation, etc. Mortality from thermal shock was unlikely as many YOY humpback chub survived the initial entry into the cold Colorado River and were captured in the Inflow Reach. Parasite loads were relatively low in the mainstem and starvation was unlikely as YOY chub captured in the Inflow Reach showed improved condition compared to those from the LCR (Hoffnagle et al. 1998; Hoffnagle and Landye 1999). Only predation by abundant adult rainbow trout remains as a viable explanation for the rapid disappearance of YOY humpback chub following their summertime dispersal from the LCR into the LCR Inflow Reach.

The pattern of appearance, distribution, and abundance of YOY humpback chub in the mainstem Colorado River observed in our study is consistent with a "source-sink" model of downstream dispersal from the LCR coupled with high mortality from predation. The abundance of rainbow trout in the LCR inflow reach coupled with the observation of a strongly complementary distribution with <200 mm TL humpback chub in January (Figure 5), suggests that predation by adult rainbow trout may be responsible for the near disappearance of YOY humpback chub between late summer and early winter. Mortality rates for small fish are likely exacerbated by fluctuating flows, which disrupt habitat associations, resulting in increased movement and downstream dispersal and subsequent loss from predation. Fluctuating flows also cause disruption of shoreline habitats and food resources needed for rearing small fish. The rarity of small humpback chub downstream of the LCR inflow coupled with high abundance of adult rainbow and brown trout downstream to Havasu Creek suggests conditions for recruitment of YOY humpback chub in the Colorado River in Grand Canyon are extremely poor.

The Grand Canyon reach of the Colorado River below Glen Canyon Dam is typical of rivers impacted by a peaking hydropower dam (Holden 1979). Like other fish communities in river ecosystems in the Pacific Northwest (Standford and Ward 1979), the Southeast (Bain et al 1988; Kinsolving and Bain 1993; Scheidegger and Bain 1995; Travnichek et al. 1995), Norway (Lillehammer and Saltveit 1979), Europe (Armitage 1979; De Jalon et al. 1994), China (Zhong and Power 1996), Africa (Davies 1979), and Australia (Walker 1979; Gehrke et al., 1995), the native fish community of the Colorado River in Grand Canyon has been profoundly altered by a mainstem hydropower dam. A comprehensive study by Bain et al. (1988) found that operation of a peaking hydropower dam on a medium-size river in the Southeastern USA resulted in highly variable flows, which had a strong negative impact on shoreline and shallow habitats. Fluctuating flows resulted in a great reduction in the numbers of small fish species, juveniles, and larvae in the regulated river reach below the dam (Bain et al. 1988; Kinsolving and Bain 1993; Scheidegger and Bain 1995). Bain et al. (1988) found that in river reaches with normal flow regimes, sensitive shoreline habitats contained the highest densities of fish and most of the riverine species and provided important nursery habitat and refugia for small fishes. In river reaches with fluctuating flows, small species and riverine specialists who were dependent on shoreline habitats were greatly reduced and habitat generalists and species not dependent on shoreline habitats predominated (Bain et al 1988; Kinsolving and Bain 1993). Bain and his co-workers found that fluctuating flows from hydropower dams were damaging to river ecosystems because they had the strongest and most direct impact on shoreline and shallow habitats and altered the composition of riverine fish communities by eliminating those species dependent on shoreline habitats for all or part of their life history.

In Grand Canyon the loss of native Colorado "big river" fishes has been attributed to the impact of the operation of Glen Canyon Dam. Since completion of the dam in 1963, Colorado pike minnow (*Ptychocheilus lucius*), bonytail chub (*Gila elegans*), and razorback sucker (*Xyrauchen texanus*) have been extirpated from Grand Canyon (USBR 1995; Valdez and Carothers 1998).

These species are dependent on natural river habitat and flow regimes for completion of their life histories (Tyus 1987, 1991; Tyus and Karp 1990; Minckley and Deacon 1991). The remaining native fishes in Grand Canyon (speckled dace, humpback chub, bluehead sucker, flannelmouth sucker) have persisted because they are not dependent on riverine habitat but are dependent on warmwater tributaries for reproduction and rearing of juvenile life history stages (Gorman 1994; Valdez and Ryel 1995; Valdez and Carothers 1998). Like Bain et al. (1988), we found that small fish and juveniles that use shoreline habitats showed very low persistence under conditions of fluctuating flows in Grand Canyon. Unlike Bain et al. (1988), fluctuating flows in Grand Canyon are compounded by chronic, cold temperatures that are the result of hypolimnetic releases from Glen Canyon Dam. In Grand Canyon, introduced trout species predominate because they are tolerant of stage fluctuations that disrupt shoreline habitat and can prey opportunistically on small fishes along river margins that are displaced by fluctuating flows. As shown in this study, under conditions of chronically cold fluctuating flows, small fishes, especially those that disperse from warmwater tributaries, are potentially vulnerable to predation in mainstem shoreline habitats by coldwater predators, i.e., introduced trout.

One of the objectives for improving the status of endangered humpback chub in Grand Canyon is to develop additional reproducing populations. Establishing a reproducing mainstem population has often been proposed as a possible solution (USFWS 1990, 1994; Gorman 1997). Presently, humpback chub cannot reproduce successfully in the cold waters of the Colorado River in Grand Canyon (Holden and Stalnnaker 1975; Minckley 1991) and survivorship of YOY and juvenile fish is very poor (Valdez and Ryel 1995, 1997; this study). However, observations from the upper Colorado River basin where warm water conditions coupled with an abundance of non-native species and declining populations of native fishes suggest that returning the Grand Canyon section to warm water conditions might harm the status of humpback chub. The chronic coldwater conditions found below Glen Canyon Dam in Grand Canyon prevent an expansion of warmwater predators such as channel catfish (*Ictalurus punctatus*) and potential competitors such as common carp (*Cyprinus carpio*) and red shiner (*Cyprinella lutrensis*). Moreover, channel catfish are relatively abundant in the LCR (Marsh and Douglas 1997) and have been present in the lower Colorado River basin since the 1890s (Miller and Alcorn 1943), yet humpback chub remain the dominant species in the LCR (Kaeding and Zimmerman 1983; Douglas and Marsh 1996; Gorman 1994; this study). Before the closure of Glen Canyon Dam, channel catfish were very abundant in the mainstem Colorado River (Woodbury 1959) but their abundance has declined precipitously since closure of the dam (Holden and Stalnaker 1975). Despite the relative paucity of warmwater predators and competitors in the mainstem Colorado River, it is likely that the abundance of humpback chub have declined more since closure of the dam in 1963 than in the first half of the 20^{th} century when subjected to predation by abundant channel catfish. Thus, restoration of reproducing native fish populations in the Colorado River in Grand Canyon requires restoration of warmwater conditions and more natural flow regimes, and although non-native warmwater fishes will also benefit, they are not likely to prevent an improvement in the present status of native fishes.

Our study strongly implicates predation by abundant rainbow trout in Grand Canyon as the prime factor in the loss of YOY and juvenile native fishes and lack of recruitment in mainstem Colorado River habitats. Future studies should address the hypothesis that predation by rainbow trout is the primary factor in the disappearance of small fish in mainstem habitats. Reduction of the magnitude of daily flow variation and maintaining minimum flows can reduce the negative impact of flow regulation on riverine fish communities (Travnichek et al. 1995). Resource managers should consider ways to stabilize flows and increase temperature in the mainstem Colorado River in Grand Canyon. Implementation of more natural flow and temperature conditions will increase the stability of shoreline habitat and cover, and likely result in increased food resources and growth rates in small fishes, and decrease mortality associated with picivory.

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APPENDIX I. Summary of catch: composition of mainstem fish communities of the Colorado River ecosystem of Grand Canyon, 1998-1999.

		Species*													
Mainstem Site	**Date**	**BHS**	**BRT**	**CCF**	**CCP**	**FHM**	**FMS**	**GRS**	**HBC**	**PKF**	**RBT**	**RSH**	**SPD**	**YBH**	**total**
LCR Inflow	Jun-98	1	2	0	2	26	12	0	48	0	152	1	16	0	260
Bright Angel	Jun-98	1	39			2	2				15		3		62
Shinumo	Jun-98		12		2	1	2				28	1			46
MGG	Jun-98		6				1		9		26	1			43
Kanab	Jun-98				3	1	4				11				19
Havasu	Jun-98	2	3		6		8	1			72		6		98
subtotal	Jun-99	4	62	0	13	30	29	1	57	0	304	3	25	0	528
Fence Fault	Sep-98						3		4		31				38
LCR Inflow	Sep-98	10	2	1	5	69	20	0	262	1	293	25	50	1	739
Bright Angel	Sep-98	1	47			6	2				50	2	4		112
Shinumo	Sep-98	1	15		2		8		11		39				76
MGG	Sep-98	9			1	4	5		22	3	28	4	71		147
Kanab	Sep-98		2		5	6	10		1		8		1		33
Havasu	Sep-98	1	4		2	54	18			2	39	1	76		197
rm 160-179	Sep-98		1			53	18			2	19	1	65		159
rm 180-199	Sep-98	15			3	92	21		2	2	4	8	164		311
subtotal	Sep-98	37	71	1	18	284	105	0	302	10	511	41	431	1	1812
LCR Inflow	Jan-99	4	3	1	1	2	6	0	33	1	111	7	6	0	175
Shimumo	Jan-99										1				1
MGG	Jan-99	3							3		13				19
Havasu	Jan-99		1		9		4				15		1		30
subtotal	Jan-99	7	4	1	10	2	10	0	36	1	140	7	7	0	225
TOTAL		48	137	2	41	316	144	1	395	11	955	51	463	1	2565

* BHS = bluehead sucker (*Catostomus discobolus*); BRT = brown trout (*Salmo trutta*); CCF = (*Ictalurus punctatus*); CCP = common carp (*Cyprinus carpio*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); GRS = green sunfish (*Lepomis cyanellus*); HBC = humpback chub (*Gila cypha*); PKF = (*Fundulus zebrinus*); RBT = rainbow trout (*Oncorhynchus mykiss*); RSH = red shiner (*Cyprinella lutrensis*); SPD = speckled dace (*Rhinichthys osculus*); YBH = (*Ameiurus natalis*).

APPENDIX II. Summary of catch: composition of tributary fish communities of the Colorado River ecosystem of Grand Canyon, 1998-1999.

		Species*													
Trib. Site[1]	**Date**	**BHS**	**BRT**	**CCF**	**CCP**	**FHM**	**FMS**	**GRS**	**HBC**	**PKF**	**RBT**	**RSH**	**SPD**	**YBH**	**total**
LCR confl.	Jun-98				4	1	11		19			27	13		75
Bright Angel	Jun-98	1	2								1		50		54
Shinumo	Jun-98	7	5				2		1				4		19
Kanab	Jun-98					5	10	2	1				8		26
Havasu	Jun-98	5					58		9				10		82
subtotal	Jun-98	13	7	0	4	6	81	2	30	0	1	27	85	0	256
LCR confl.	Sep-98				3	1			51	6		2	4		67
Bright Angel	Sep-98	6	1				1		1		3		61		73
Shinumo	Sep-98	6	1			3	4		22		3	1	54		94
Kanab	Sep-98	38			6	7	12				1		87		151
Havasu	Sep-98	31				4	39		18		2		73		167
subtotal	Sep-98	81	2	0	9	15	56	0	92	6	9	3	279	0	552
LCR confl.	Jan-99	1			1				11				5		18
Shinumo	Jan-99		4			1					10				15
Havasu	Jan-99	2					2				1		1		6
subtotal	Jan-99	3	4	0	1	1	2	0	11	0	11	0	6	0	39
TOTAL		97	13	0	14	22	139	2	133	6	21	30	370	0	847

*BHS = bluehead sucker (*Catostomus discobolus*); BRT = brown trout (*Salmo trutta*); CCF = (*Ictalurus punctatus*); CCP = common carp (*Cyprinus carpio*); FHM = fathead minnow (*Pimephales promelas*); FMS = flannelmouth sucker (*Catostomus latipinnis*); GRS = green sunfish (*Lepomis cyanellus*); HBC = humpback chub (*Gila cypha*); PKF = (*Fundulus zebrinus*); RBT = rainbow trout (*Oncorhynchus mykiss*); RSH = red shiner (*Cyprinella lutrensis*); SPD = speckled dace (*Rhinichthys osculus*); YBH = (*Ameiurus natalis)*

[1] LCR confluence samples were taken in the lower 1 km of the LCR at the time of mainstem Colorado River sampling.