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EFFECTS OF A TEST FLOOD ON FISHES OF THE COLORADO RIVER IN GRAND CANYON, ARIZONA

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Abstract. A beach/habitat-building flow (i.e., test flood) of 1274 m^3/s, released from Glen Canyon Dam down the Colorado River through Grand Canyon, had little effect on distribution, abundance, or movement of native fishes, and only short-term effects on densities of some nonnative species. Shoreline and backwater catch rates of native fishes, including juvenile humpback chub (*Gila cypha*), flannelmouth suckers (*Catostomus latipinnis*), and bluehead suckers (*C. discobolus*), and all ages of speckled dace (*Rhinichthys osculus*), were not significantly different before and after the flood. Annual spring spawning migrations of flannelmouth suckers into the Paria River and endangered humpback chub into the Little Colorado River (LCR) took place during and after the flood, indicating no impediment to fish migrations. Pre-spawning adults staged in large slack water pools formed at the mouths of these tributaries during the flood. Net movement and habitat used by nine radio-tagged adult humpback chub during the flood were not significantly different from prior observations. Diet composition of adult humpback chub varied, but total biomass did not differ significantly before, during, and after the flood, indicating opportunistic feeding for a larger array of available food items displaced by the flood. Numbers of nonnative rainbow trout (*Oncorhynchus mykiss*) <152 mm total length decreased by ~8% in electrofishing samples from the dam tailwaters (0–25 km downstream of the dam) during the flood. Increased catch rates in the vicinity of the LCR (125 km downstream of the dam) and Hell's Hollow (314 km downstream of the dam) suggest that these young trout were displaced downstream by the flood, although displacement distance was unknown since some fish could have originated from local populations associated with intervening tributaries. Abundance, catch rate, body condition, and diet of adult rainbow trout in the dam tailwaters were not significantly affected by the flood, and the flood did not detrimentally affect spawning success; catch of young-of-year increased by 20% in summer following the flood. Post-flood catch rates of nonnative fathead minnows (*Pimephales promelas*) in shorelines and backwaters, and plains killifish (*Fundulus zebrinus*) in backwaters decreased in the vicinity of the LCR, and fathead minnows increased near Hell's Hollow, suggesting that the flood displaced this nonnative species. Densities of rainbow trout and fathead minnows recovered to pre-flood levels eight months after the flood by reinvasion from tributaries and reproduction in backwaters. We concluded that the flood was of insufficient magnitude to substantially reduce populations of nonnative fishes, but that similar managed floods can disadvantage alien predators and competitors and enhance survival of native fishes.

Key words: Catostomus latipinnis; *Colorado River; endangered species; fathead minnow; flannelmouth sucker;* Gila cypha; *Glen Canyon Dam; humpback chub;* Oncorhynchus mykiss; Pimephales promelas; *rainbow trout; test flood.*

Introduction

Floods are a common feature of rivers in the American Southwest and usually occur as runoff from spring snowmelt or as late summer monsoonal rainstorms (Webb et al. 1991*a*, *b*, Collier et al. 1996). Floods reshape the channel, infuse large amounts of nutrients into the river, and maintain a dynamic equilibrium to which many unique and indigenous fishes have adapted (Petts 1984, Poff et al. 1997). Thirteen large main stem dams now control the flow of the Colorado River (Fradkin 1984), and in many regions of the basin, including

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Grand Canyon, floods are now a missing component of the hydrologic setting (Daudy 1991). The effect on native fish communities is only partly understood, but the absence of floods can impede life cycles of many species (John 1963, Meffe and Minckley 1987). Aside from the direct detriment to native species, the absence of rigorous and silt-laden floods can also allow for invasions of nonnative fishes, which prey on and compete with native forms (Minckley 1991, Ruppert et al. 1993). Returning floods as a feature of regulated southwestern rivers can benefit native fishes and disadvantage nonnative species. This investigation tested the hypothesis that a test flood of 1274 m^3/s would not significantly affect native or nonnative fish populations in the Colorado River through Grand Canyon.

A beach/habitat-building flow (the test flood) was released by the U.S. Bureau of Reclamation from Glen Canyon Dam down the Colorado River through Grand Canyon on 22 March 1996 through 7 April 1996. This test flood consisted of a steady high release (i.e., flood) of 1274 m^3/s for 7 d, preceded and followed by steady low releases of 226 m^3/s for 4 d each. The purpose of this test flood was to implement the concept of beach/habitat-building flows, a common element of the alternatives presented in the Final Environmental Impact Statement on the Operation of Glen Canyon Dam (U.S. Bureau of Reclamation 1995). Beach/habitat-building flows are ''. . . scheduled high releases (i.e., floods) of short duration designed to rebuild high elevation sandbars, deposit nutrients, restore backwater channels, and provide some of the dynamics of a natural system.'' The following objectives were addressed to evaluate the effects of the test flood: (1) determine effects on the tailwater trout fishery; (2) determine effects on distribution, dispersal, and habitat use of native and nonnative fishes; and (3) determine effects on movement and food habits of humpback chub.

The Colorado River through Grand Canyon supports 15 species of freshwater fishes, including four native species and 11 nonnative species; an additional seven nonnative species occur in the Lake Mead inflow (Valdez and Ryel 1997). The native species are warmwater riverine forms that include the federally endangered humpback chub (*Gila cypha*); a species of special concern, the flannelmouth sucker (*Catostomus latipinnis*); and the bluehead sucker (*C. discobolus*), and speckled dace (*Rhinichthys osculus*). The razorback sucker (*Xyrauchen texanus*) is native to the canyon, but only hybrid intergrades (*C. latipinnis* × *X. texanus*) have been captured recently (Douglas and Marsh 1998). A blue-ribbon tailwater fishery for introduced rainbow trout (*Oncorhynchus mykiss*) occurs in ~25 km of the Colorado River from Glen Canyon Dam to Lees Ferry, and rainbow trout and brown trout (*Salmo trutta*) are locally common in tributaries and tributary inflows further downstream. Common carp (*Cyprinus carpio*) and channel catfish (*Ictalurus punctatus*) are also common downstream of the dam tailwaters. Fathead minnows (*Pimephales promelas*) and plains killifish (*Fundulus zebrinus*) are locally common in backwaters and tributaries from the Little Colorado River (LCR) to the Lake Mead inflow, where red shiners (*Cyprinella lutrensis*) are abundant, and channel catfish and striped bass (*Morone saxatilis*) occur in large numbers in spring and summer. Walleye (*Stizostedion vitreum*), yellow bullhead (*I. natalis*), largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), green sunfish (*L. cyanellus*), black crappie (*L. nigromaculatus*), and threadfin shad (*Dorosoma petenense*) are uncommon in Grand Canyon but are residents of the Lake Mead inflow. Many aspects of the life history of the fishes of the Colorado River in Grand Canyon are influenced by flow regulation through Glen Canyon Dam. Flow regulation results in the absence of floods; cold, clear hypolimnetic releases of 8°–10°C; and daily fluctuations of up to 227 m^3/s from hydropower production (Arizona Game and Fish Department 1996*b*, Valdez and Ryel 1997, Hoffnagle et al. 1999).

Methods

Short- and long-term effects of the test flood were evaluated on fish assemblages in four reaches of the Colorado River from Glen Canyon Dam to upper Lake Mead (Fig. 1). The reaches included: Reach 1, the tailwaters between Glen Canyon Dam and the Paria River (0–25 km downstream from the dam); Reach 2, the area near the LCR inflow (121–130 km downstream from the dam); Reach 3, the area near Hells Hollow (311–318 km downstream from the dam); and Reach 4, the area near Spencer Creek (414–424 km downstream from the dam). Reach 1 was sampled during the steady low releases of 226 m^3/s before (i.e., pre-flood, 22–26 March) and after (i.e., post-flood, 3–7 April) the test flood of 1274 m^3/s (26 March through 2 April). Reaches 2 and 4 were sampled before, during, and after the flood; and Reach 3 was sampled before and after the flood. Reaches 2, 3, and 4 were also sampled at flows of ~379 m^3/s about one month before the test flood (i.e., pre-experiment, 28 February through 14 March) and at ~521 m^3/s about one month after the test flood (i.e., post-experiment, 18 April through 3 May).

The tailwater trout fishery

Trout in the tailwaters were sampled with a 5.5-m electrofishing boat equipped with a 220-V generator and a Coffelt CPS Mark XX electroshocking unit (Coffelt Manufacturing, Flagstaff, Arizona, USA). Either 14 or 15 random fixed transects were electrofished at night (~2000 s/transect) between 0.5 and 19.5 km downstream of the dam during the pre- and post-flood steady releases (226 m^3/s), and in August (~425 m^3/s) and November, 1996 (~226 m^3/s). All fish were measured for total length (TL ± 1 mm), weighed (±0.1 g

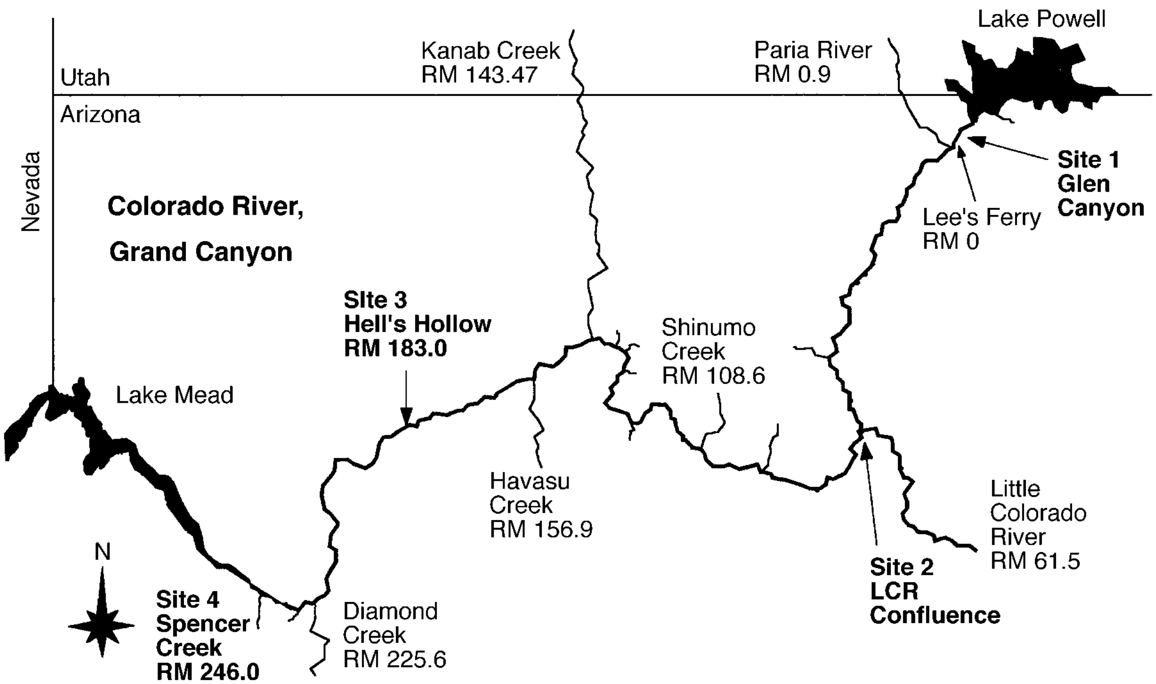

FIG. 1. The Colorado River through Grand Canyon and sample reaches used to evaluate effects of the test flood. One river mile (RM) equals 1.6 river kilometers.

for small [<10 g] fish, ±1 g for larger fish), and released alive at the point of capture unless collected for diet analyses. Stomachs of randomly selected rainbow trout were removed and preserved in 10% formalin, and contents were identified to the lowest possible taxonomic category and measured (±0.1 mL) by volumetric displacement. Analysis of variance (one-way ANOVA) was performed on means for lengths, mass, and condition factors ($K = \text{mass} \times 10^5/[\text{total length}]^3$). Relative gut volume (RGV, the volume of stomach contents [for fish that had fed] in mL/fish length in meters; Filbert and Hawkins 1995) was compared using the Kruskal-Wallis test over all months and the Mann-Whitney U test between March (pre-flood) and April (post-flood). Planned (a priori) comparisons were conducted on data from the pre- and post-flood steady flows. Chi-square tests were used to compare frequency of occurrence of empty stomachs and of predominant taxonomic groups in the diet.

Distribution, dispersal, and habitat of native and nonnative fishes

Movements of 50 adult flannelmouth suckers were followed with the aid of crystal-controlled sonic transmitters (Model PRG-94 tags, 72–83 kHz; Sonotronics, Tucson, Arizona, USA), surgically implanted in the fish 10–14 d before the test flood. The majority of fish had prominent tubercles indicating near readiness for spawning; four males readily expressed gametes (Thieme 1997). Fish near the confluence of the Colorado and Paria rivers were tracked during pre- and post-flood steady releases from the riverbank with a mobile unit consisting of an underwater directional hydrophone (Sonotronics Model DH-2) and a digital receiver (Sonotronics USR-5W). Fish were similarly tracked from the riverbank during the flood in the lower Paria River, which was greatly expanded by inundation from the Colorado River. Sonic-tagged fish in the 25-km dam tailwaters were tracked from a boat.

Ten adult humpback chub were also surgically implanted with 11-g ATS radio transmitters (model BEI 10-18, Advanced Telemetry Systems, Isanti, Minnesota, USA) one month before the experiment and tracked before, during, and after the flood with Smith-Root SR-40 receivers (Smith-Root, Vancouver, Washington, USA) and model 2000 ATS programmable receivers (Valdez et al. 1993). These fish were captured and released near the confluence of the LCR, in Reach 2 and monitored for 2–5 d. During the test flood, fish were contacted on a daily basis to monitor movement and habitat use, and selected fish were monitored continuously for periods of up to 4 d. Fish were located by triangulating radio signals and locations of fish were plotted on 1:1200 aerial photographs.

Fish in Reaches 2 and 3 were sampled with electrofishing, trammel nets, minnow traps, and seines (Valdez et al. 1993, Arizona Game and Fish Department 1996*a*). Electrofishing was conducted from a motorized 4.8-m Achilles HD-16 hypalon sportboat (Achilles Corporation, Tokyo, Japan) equipped with a 220-V generator and a Coffelt CPS Mark XX electroshocking unit with spherical electrodes. Electrofishing was conducted by the same crew to reduce variation from crew effect. Trammel nets were 22.9 m long with 3.8-cm inside mesh and 30.5-cm outside mesh. Unbaited commercial minnow traps, made of galvanized wire, were used for sampling shorelines, and backwaters were sampled with 10-m bag seines with 0.6-cm delta mesh.

Four major habitat types were sampled in Reaches 2 and 3 at the pre-flood and post-flood low releases and in Reach 2 during the flood, including shorelines, tributary inflows, large eddies, and backwaters. Main channel pools and runs were not sampled because of logistical difficulties and few fish reported in these habitats by previous studies (Valdez et al. 1993, Valdez and Ryel 1995). Shorelines were partitioned into debris fans, talus, and vegetation; these shoreline types have consistently yielded the highest densities of fish in Grand Canyon, including humpback chub (Valdez and Ryel 1997, Converse et al. 1998). For each of the three shoreline types, four similar shoreline sections, each 50–100 m long, were sampled twice during each pre-flood, flood, and post-flood release; hence 24 boat electrofishing samples were taken for each flow release (i.e., 3 types $\times$ 4 sections $\times$ 2 samples $=$ 24). Minnow traps were set in groups of five in each of the three shoreline types and checked three times during each flow release, such that 180 minnow traps were set during each flow release (i.e., 3 types $\times$ 4 sections $\times$ 3 samples $\times$ 5 traps $=$ 180). Catches from the group of five traps were pooled for analysis to reduce variation and approach normal distributions in catch rates. Large eddy complexes in Reaches 2, 3, and 4, and the LCR inflow were sampled with boat electrofishing and trammel nets. Large volumes of suspended debris trapped in eddies during the first two days of the flood hampered use of trammel nets, but the amount of suspended material lessened and netting was successful during the latter half of the flood. Backwaters were sampled with seines during the pre- and post-flood periods; no backwaters were present during the flood.

All fish were measured for total length (TL $\pm$ 1 mm), weighed ($\pm$0.1 g for small [$<$10 g] fish, $\pm$1 g for larger fish), and released alive at the point of capture. Native fish $>$150 mm TL were injected with PIT tags (Biomark, Boise, Idaho, USA) if no tag was detected by scanning, and associated data entered in a master Grand Canyon database. Adult humpback chub captured in trammel nets and by electrofishing during each of the three flow releases were examined for food contents with a nonlethal stomach pump (Wasowicz and Valdez 1994). Humpback chub gut contents were preserved in 70% ethanol. In the laboratory, gut contents were sorted into taxonomic groups (Pennak 1989), enumerated, and ash-free dry mass (AFDM) was determined for each taxonomic group. The same statistical analyses were used on diets of humpback chub as described above for rainbow trout.

Electrofishing catch-per-unit-effort (CPUE) was calculated by species as numbers of fish/10 min; for trammel nets as numbers of fish for 23 m of net/100 h; for minnow traps as numbers of fish for 5-trap groups/24 h, and for seines as numbers of fish/100 m^2 seined. Significant differences in mean CPUE were tested using the Mann-Whitney *U* test (Sokal and Rohlf 1987). Catch statistics are presented for Reaches 1 and 2, but low numbers of fish and high variability in catches at Reaches 3 and 4 precluded meaningful catch statistics. Hence, Reaches 1 and 2 were the most reliable statistical indicators of flood effects on native and nonnative fish assemblages.

Results

The tailwater trout fishery

Rainbow trout and flannelmouth sucker were the only fish species caught in Reach 1 before and after the flood (Table 1). Catch-per-unit-effort (CPUE) for rainbow trout of all sizes in Reach 1 did not differ significantly ($P > 0.05$) between the pre- and post-flood low releases, but the percentage catch of juvenile trout $<$152 mm TL was reduced by $\sim$8% (Table 2). The proportional catch of rainbow trout $<$152 mm TL increased more than 20% in November (i.e., eight months after the flood), compared to previous months. The majority of these trout were young-of-year (YOY) hatched since the flood.

Rainbow trout caught during pre-flood (March) and post-flood (April), and following the experiment (i.e., August and November) ranged from 46 to 593 mm TL. Mean lengths and mass differed significantly ($P < 0.05$) among sampling periods (Table 2); i.e., trout caught in April were longer ($P < 0.001$) and heavier ($P < 0.05$) than those caught in March, confirming that there were fewer small fish in the sample following the flood. Mean length was less ($P < 0.05$) in November than in March, indicating that spawning success infused more small fish into the sample population. Mean mass did not differ significantly between March and November ($P > 0.05$), and mean condition factors did not differ significantly ($P > 0.05$) among sampling periods.

Stomachs of rainbow trout 121–538 mm TL showed that diet differed significantly ($P < 0.001$) among sampling periods, and percentage of individual components differed in patterns of change (Table 3). Green algae (*Cladophora glomerata*) dominated the diet by volume in all months, except November. Amphipods (*Gammarus lacustris*), chironomids, and gastropods (snails) were the principal macroinvertebrates in the diet, and other taxa (Diptera, oligochaetes, terrestrial invertebrates) generally comprised $<$2% each of stomach content volume. Univariate analysis showed that volume and percentage composition of individual taxa in the diet did not differ significantly ($P > 0.05$) between pre-

TABLE 1. Numbers of fish caught by species before, during, and after the test flood at four sample reaches of the Colorado River between Glen Canyon Dam and upper Lake Mead.

	Reach 1 (Dam tailwaters)†		Reach 2 (LCR inflow)			Reach 3 (Hells Hollow)†		Reach 4 (Spencer Creek)		
Common name	Before	After	Before	During	After	Before	After	Before	During	After
Natives										
Humpback chub	0	0	87	68	166	0	0	0	0	0
Flannelmouth sucker	12	3	7	2	8	35	37	2	0	0
Bluehead sucker	0	0	0	1	11	1	4	0	0	0
Speckled dace	0	0	105	139	291	13	29	4	0	3
Nonnatives										
Rainbow trout	1513	1685	62	36	164	1	4	0	0	0
Fathead minnow	0	0	169	11	154	4	30	9	67	50
Common carp	0	0	1	0	0	29	28	49	43	36
Channel catfish	0	0	0	0	0	11	3	20	22	40
Brown trout	0	0	2	2	1	1	1	0	0	0
Plains killifish	0	0	3	0	0	0	1	1	0	2
Striped bass	0	0	0	0	0	0	0	1	12	0
Threadfin shad	0	0	0	0	0	0	0	1	0	1
Yellow bullhead	0	0	0	0	0	0	0	1	0	0
Red shiner	0	0	0	0	0	0	0	100	72	55
Redside shiner	0	0	0	0	1	0	0	0	0	0
Largemouth bass	0	0	0	0	0	0	0	1	0	1
Black crappie	0	0	0	0	0	0	0	1	0	0
Bluegill	0	0	0	0	0	0	0	1	0	0
Green sunfish	0	0	0	0	0	0	0	1	0	1
Walleye	0	0	0	0	0	0	0	1	0	0
Totals	1525	1688	436	259	796	95	137	196	240	181

† Fish not sampled during the test flood.

and post-flood releases, but volume and percentage composition of *G. lacustris* ($P < 0.001$) and gastropods ($P < 0.02$) increased in November above pre-flood levels, while percentage composition of chironomids and *C. glomerata* decreased ($P < 0.001$).

RGV also differed ($P < 0.001$) among sampling periods (Table 3), increasing between pre-flood (March) and post-flood (April) steady releases ($P < 0.01$), remaining high in August ($P < 0.01$), but declining in November ($P < 0.002$) to pre-flood levels. Frequency of occurrence of empty stomachs did not differ ($P > 0.05$) among sampling periods, with only 9.0–22.9% of fish with empty stomachs.

Staging and spawning by flannelmouth suckers

The lower Paria River prior to the flood was characterized as narrow (<5 m wide) and uniformly shallow (<30 cm). During the flood, the waters of the Colorado River backed into the mouth of the Paria River, forming a slack water pool ~730 m long and up to 2.8 m deep. Normally, reproductively ripe flannelmouth suckers pass through this shallow portion of the Paria River as they proceed 2–12 km or more upstream to spawn during March and April (Weiss et al. 1998). However, during the test flood, 33 of 50 flannelmouth suckers implanted with sonic transmitters and released in the Colorado River before the flood were recontacted in the newly formed slack water pool at the Paria River mouth. An additional nine sonic-tagged fish were relocated in Reach 1 immediately following the flood. Of the remaining eight sonic-tagged fish, three were never recontacted, three were accounted for in Reach 1 within three months, and two were recontacted within two months at the LCR, 98 km downstream from the

TABLE 2. Total catch, mean length, mass, and condition factor (K), catch/min of electrofishing (CPUE), and number of catch <152 mm TL for rainbow trout during pre-flood (March), post-flood (April), and post-experiment sample periods (August, November) in the Glen Canyon Dam tailwaters, 1996.

Sample period	Numbers of fish	Total length (mm)†	Mass (g)†	Condition (K)†	CPUE	Number <152 mm‡
Pre-flood (March)	1513	230.8 (2.8)*	198.5 (5.7)*	0.961 (0.006)*	3.52	543 (35.9)
Post-flood (April)	1685	239.9 (2.6)**	211.2 (5.1)**	0.954 (0.005)*	3.58	477 (28.3)
Post-experiment (August)	1306	228.4 (3.2)*	232.0 (6.7)***	0.979 (0.010)*	2.61	477 (36.5)
Post-experiment (Nov)	1335	214.7 (3.2)***	208.2 (6.5)*	0.986 (0.010)*	2.58	655 (49.1)

Note: CPUE = catch-per-unit-effort, TL = total length.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
† Numbers in parentheses are standard errors.
‡ Numbers in parentheses are corresponding percentages.

TABLE 3. Frequency of occurrence and mean percentage composition by volume and relative gut volume of predominant items in stomachs of rainbow trout (121–538 mm TL) during pre-flood (March), post-flood (April), and post-experiment (August, November) sample periods from Glen Canyon Dam, 1996.

	March (N = 36)		April (N = 30)		August (N = 60)		November (N = 54)	
Food category	Frequency (%)	Percentage composition	Frequency (%)	Percentage composition	Frequency (%)	Percentage composition	Frequency (%)	Percentage composition
Gammarus lacustris	62.5	25.2 (6.1)*	74.1	38.1 (6.7)*	75.9	31.6 (5.1)*	82.4	71.6 (5.2)**
Chironomids	71.5	23.8 (6.7)*	54.6	8.0 (3.6)**	59.6	14.3 (3.5)*	15.8	8.3 (3.6)**
Gastropods	9.7	2.1 (1.3)*	7.8	0.1 (0.1)*	24.8	9.1 (2.9)**	35.1	6.0 (2.2)**
Cladophora glomerata	58.5	46.2 (7.8)*	62.4	50.1 (9.1)*	58.3	43.0 (5.6)*	12.3	7.1 (3.1)**
Relative gut volume		4.8 (1.0)*		11.8 (2.6)**		11.7 (1.4)**		3.9 (0.7)*
Percentage empty stomachs	16.7		16.7		9.0		22.9	

Notes: Numbers in parentheses in columns reporting percentage composition are standard errors. N = number of fish sampled, TL = total length.
* $P < 0.05$, ** $P < 0.01$.

Paria River. Possibly, these two fish were transported downstream by the flood, although Weiss (1993) documented movement of adult flannelmouth suckers between the two tributaries during operational flows in 1992. No sonic-tagged fish could be detected with a shore-based mobile receiver in the main stem in the vicinity of the Paria River confluence during the flood, despite the fact that this was an area of flannelmouth sucker congregation before and after the flood. Following the flood, a total of 576 YOY flannelmouth suckers were captured in the lower Paria River from mid-May to late September; the majority were in the warm mouth of this tributary.

Distribution, dispersal, and habitat of native and nonnative fishes

A total of four native and 16 nonnative fish species were captured during the test flood at the four sampling reaches between Glen Canyon Dam and upper Lake Mead (Table 1). Of 10 fish species caught in Reach 2, catch rates for backwater seining, minnow traps, electrofishing, and trammel nets between pre- and post-flood flows were significantly different for only three species, including plains killifish, rainbow trout, and speckled dace (Fig. 2, Appendix A). Mean catch rates for the three shoreline types were not significantly different within gear types (electrofishing or minnow traps) and data were pooled for these analyses. Mean CPUE in backwaters decreased significantly (P = 0.0352) for plains killifish from 0.12 to 0 fish/100 m seined, and increased significantly (P = 0.0371) for juvenile rainbow trout from 0.17 to 0.87 fish/100 m. Mean CPUE for speckled dace increased significantly (P = 0.0123) in minnow traps along shorelines from 1.39 to 2.71 fish/24 h, and mean CPUE for adult rainbow trout increased significantly (P = 0.0104) in trammel nets from 2.78 to 34.27 fish/100 h. Increased catch rates of speckled dace are attributed to local shifts in habitat use; mean CPUE for minnow traps in debris fans increased significantly ($P \leq 0.05$) from 0.52 fish/24 h (SD = 0.28) before the flood to 2.04 fish/24 h (SD = 1.43) 1 d after the flood, but returned to 0.54 fish/24 h (SD = 0.29) 2–3 d after the flood, indicating selection for debris fans during the flood. Though no significant changes in catch rates occurred for juvenile humpback chub, a similar shift in habitat use was seen from vegetation and debris fans to talus; significant increases occurred in catch rates ($P \leq 0.05$) in talus, from 0.08 fish/24 h (SD = 0.042) pre-flood to 0.37 fish/24 h (SD = 0.21) 1 d after and 0.37 fish/24 h (SD = 0.52) 2–3 d after the flood. Catch rates of fathead minnows were higher, but not significant, along vegetated shorelines 1 d after the flood at 0.28 fish/24 h (SD = 0.27), compared to 0.18 fish/24 h (SD = 0.23) before the flood and 0.15 fish/24 h (SD = 0.195) 2–3 d after the flood. These results suggest that fathead minnows also shifted habitat use to vegetated shorelines during the flood. However, concurrent significant increases in catch rates of fathead minnows at Reach 3 (190 km downstream) and Reach 4 (290 km downstream), also indicate downstream displacement of this species. Increased catch rates of juvenile and adult rainbow trout in Reach 2 (near the LCR) were concurrent with decreases in Reach 1 and also attributed to downstream displacement by the flood.

When compared over a longer period of time, from before the experiment (28 February through 14 March, 1996) to after the experiment (18 April through 3 May, 1996) (Fig. 3, Appendix B), significant decreases in shoreline catch rates near the LCR were indicated for bluehead suckers, fathead minnows, and plains killifish, with increases in juvenile rainbow trout. Catches of bluehead suckers decreased significantly (P = 0.0443) in backwaters from 0.46 fish/100 m (N = 22) to 0.05 fish/100 m (N = 4), and mean CPUE for plains killifish decreased significantly (P = 0.0065) from 0.86 to 0 fish/100 m. However, CPUE for juvenile rainbow trout in backwaters increased significantly (P = 0.0146) from 0.04 to 0.32 fish/100 m. The greatest change in CPUE was for fathead minnows, which decreased significantly (P = 0.0001) in minnow traps

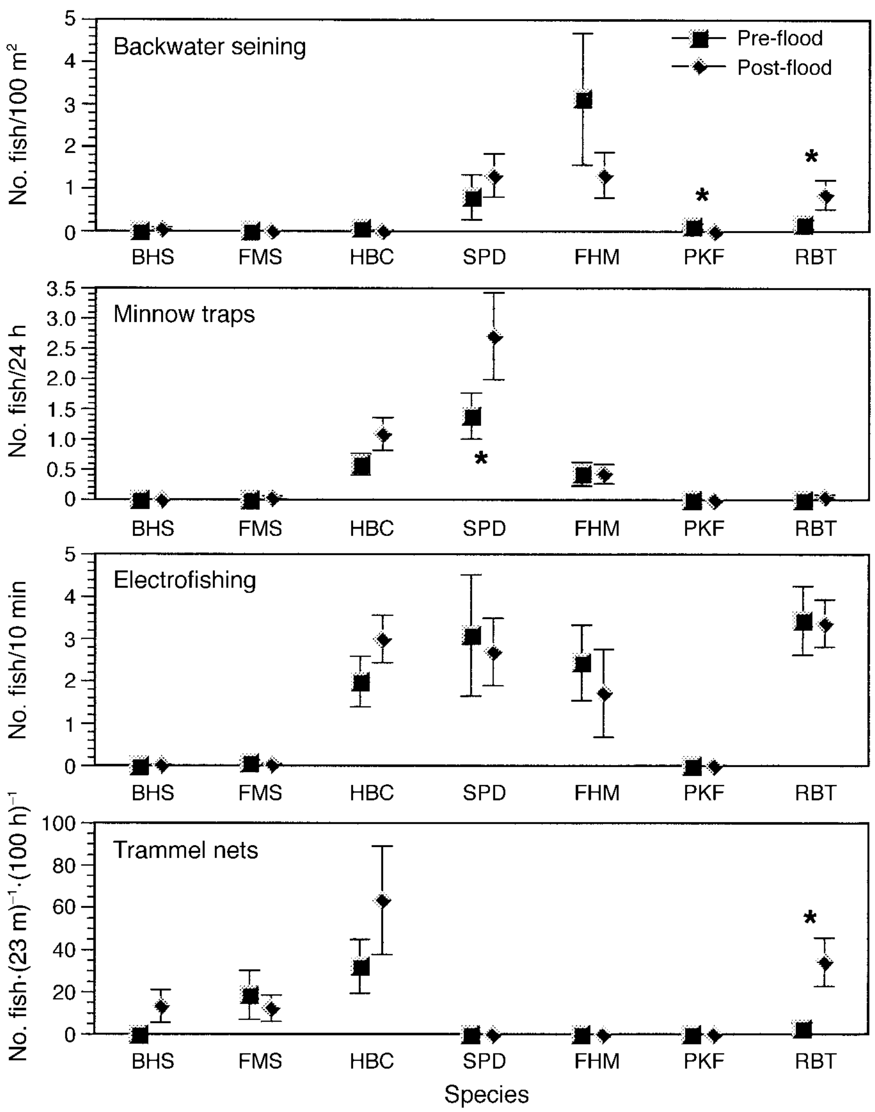

FIG. 2. Mean catch-per-unit-effort (CPUE) for fishes using various gear in the main stem Colorado River near the confluence of the Little Colorado River during steady pre-flood (22–26 March) and post-flood (3–7 April) flows. Error bars show ±1 SD. Species codes: BHS = bluehead sucker, FMS = flannelmouth sucker, HBC = humpback chub, SPD = speckled dace, FHM = fathead minnow, PKF = plains killifish, and RBT = rainbow trout. Asterisks indicate significant differences at $\alpha = 0.05$.

from 0.77 to 0.05 fish/24 h and in electrofishing ($P = 0.0185$) from 1.62 to 0.34 fish/10 min.

Movement and habitat use of adult humpback chub

Of 10 adult humpback chub surgically implanted with radio transmitters during 29 February through 2 March, 1996, nine were recontacted during the experiment of 22 March through 7 April, 1996; transmitter failure or extensive movement is suspected for the 10th fish. This recontact rate of 90% was similar to 91% reported by Valdez and Ryel (1995) for 76 radio-tagged humpback chub in the same area during 1990–1992. We believe few fish were contacted in the daytime during the pre- and post-flood low releases of 226 m/s because of reduced fish activity from high water clarity and lack of turbidity as cover (Valdez and Ryel 1995). Net movement (resultant distance from first to last contact) of the nine fish during the 16-d experiment (mean, 0.40 km; range, 0–1.24 km) did not differ significantly (t test, $P \leq 0.05$) from net movement of the same fish in the month preceding the experiment (mean, 1.26 km; range, 0.1–2.95 km; 26–39 d). No unusual movements or congregations of adult humpback chub were seen during the test flood. During descending flood flows, at ~989 m/s, one radio-tagged fish moved over a 2-h period upstream and into the lower channel of the LCR

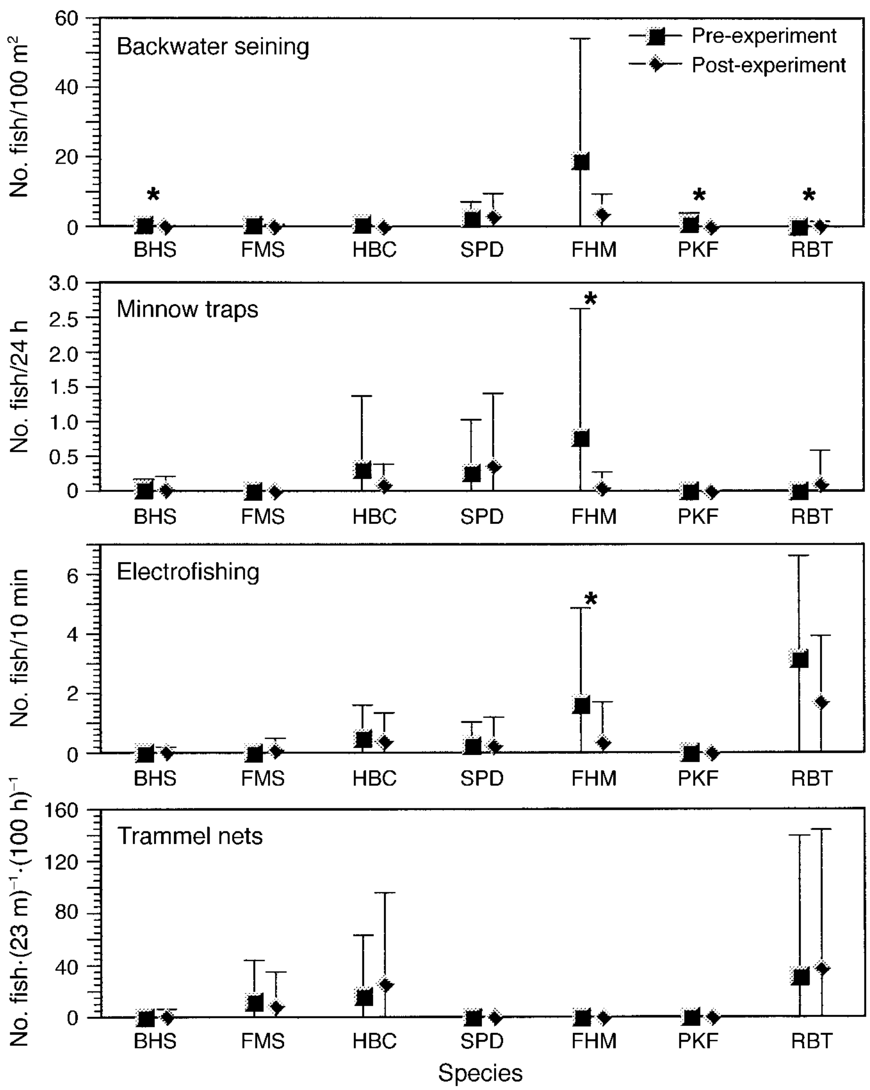

FIG. 3. Mean catch-per-unit-effort (CPUE) for fishes using various gear types in the main stem Colorado River near the confluence of the Little Colorado River during pre-experiment (28 February through 14 March) and post-experiment (18 April through 3 May) periods. Error bars are ±1 SD. Species codes: BHS = bluehead sucker, FMS = flannelmouth sucker, HBC = humpback chub, SPD = speckled dace, FHM = fathead minnow, PKF = plains killifish, and RBT = rainbow trout. Asterisks indicate significant difference at $\alpha = 0.05$.

for ~2.4 km in what appeared to be a normal spawning ascent. A second radio-tagged fish moved ~1.1 km between recirculating eddies during descending flows and returned 1.1 km to its original location. These observations constitute the greatest movements of radio-tagged adult humpback chub during the experiment.

Habitat used by the nine radio-tagged fish during the experiment was indicated by 73% of contacts from eddies and 27% from runs. Of total time observed during the experiment, the radio-tagged fish spent 97% of their time in eddies and only 3% of their time in runs. During the experiment, four fish were regularly contacted in the main stem, two were regularly contacted in the lower LCR, two were contacted irregularly in the main stem, and one was contacted only once in the lower LCR. Of the four fish contacted regularly in the main stem, all moved to the same type of habitat during the high release of 1274 m/s. The fish moved to the upstream end of large recirculating eddies to small triangular patches of quiet water formed near the separation point by the interface of the main stem downstream flow and the recirculating water reflecting off the shoreline. Representative movement and habitat use polygons during flood and post-flood releases are shown in Fig. 4 for a radio-tagged adult humpback chub ~126 km downstream of Glen Canyon Dam. The fish remained within these areas for the entire 4 d of observation each during and after the flood. These tri-

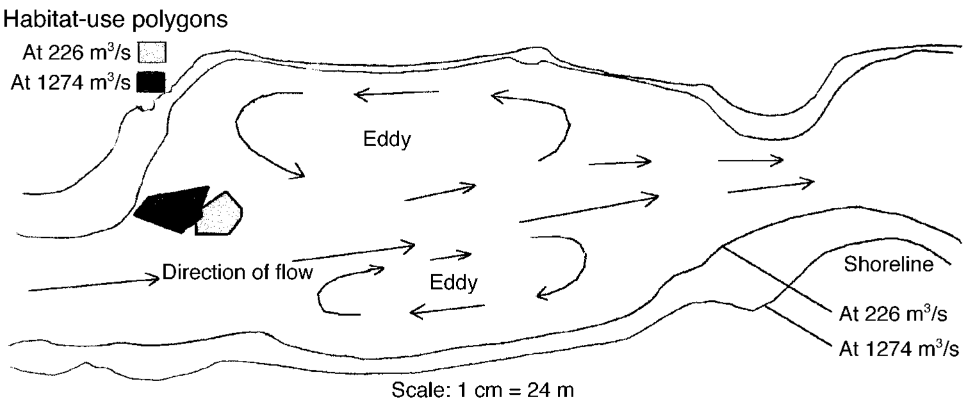

FIG. 4. Movement and habitat-use polygons for a radio-tagged adult humpback chub in the Colorado River, Grand Canyon, during the flood (1274 m^3/s) and post-flood (226 m^3/s) releases from Glen Canyon Dam, ~126 km downstream of the dam.

angular patches of water were usually 20 to 30 m along each side and were characterized by low velocity and low sediment deposition. In addition to adult humpback chub, flannelmouth suckers, bluehead suckers, rainbow trout, and carp were numerous-to-abundant in and near the low-velocity areas of these recirculating eddies.

Food habits of adult humpback chub

Gut contents of 45 adult humpback chub (250–450 mm TL, 143–815 g) captured during the experiment included 16 different types of food items, identified as five major food categories (Arizona Game and Fish Department 1996*b*). Simuliid larvae (blackflies), chironomid larvae, terrestrial insects (i.e., Coleoptera [beetles] and adult Diptera [true flies]), *G. lacustris*, and *C. glomerata* occurred in 98%, 93%, 91%, 81%, and 49%, respectively, of all fish examined. One side-blotched lizard (*Uta stansburiana*) was found in guts of each of two fish, and two of the 45 fish sampled had empty guts.

Gut contents were compared as mean AFDM for chubs sampled before (N = 9), during (N = 16), and after the flood (N = 18) (Fig. 5, Table 4). Ten food categories were consumed pre-flood, nine during the flood, and 14 post-flood. Simuliids dominated the diet with 68%, 25%, and 61% AFDW before, during, and after the flood, respectively. *Gammarus lacustris* comprised the greatest percentage of stomach contents during the flood (31%), but only 5% and 17% during pre- and post-flood sampling periods, respectively. Chironomids decreased from 14% before the flood to 2% and 6% during and after the flood, respectively. Terrestrial insects (i.e., Coleoptera and Diptera) increased from 1% pre-flood to 19% during the flood, but were only 6% of the diet post-flood. *Cladophora glomerata* composed 9% of the diet pre-flood and only 2% post-flood, but was not found in the diet during the flood. The only food items that changed significantly in mean AFDM were simuliids and *G. lacustris*, which decreased significantly from pre-flood to flood periods. Mean AFDM

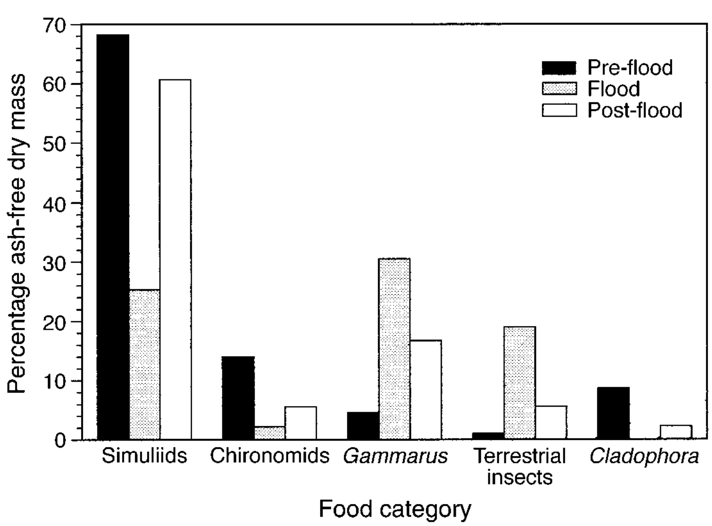

FIG. 5. Percentage ash-free dry mass of principal food categories from guts of 43 adult (>250 mm total length) humpback chub during pre-flood (n = 9), flood (n = 16), and post-flood (n = 18) sampling.

TABLE 4. Mean and one standard error (SE) for ash-free dry mass (mg) of food categories in gut contents of adult humpback chub during three phases of the 1996 test flood on the Colorado River through the Grand Canyon.

Category	Pre-flood (N = 9) Mean	Pre-flood SE	Flood (N = 16) Mean	Flood SE	Post-flood (N = 18) Mean	Post-flood SE	ANOVA (df = 2, 40)
Simuliids	12[a]	10	3[b]	3	7[ab]	7	P = 0.0120
Chironomids	1	1	4	1	1	1	P = 0.3837
Gammarus lacustris	0.9[a]	1	5[b]	7	2[ab]	2	P = 0.0424
Terrestrial invertebrates	0.2	0.2	2	3	1	1	P = 0.0956
Other aquatic invertebrates	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	P = 0.5056
Total invertebrates	27	20	24	20	21	13	P = 0.6139
Cladophora glomerata	5	16	0	0	1	3	P = 0.2174

Notes: Superscripts indicate significant differences among flood phases for each taxon with a significant ANOVA. Identical letters indicate nonsignificance between means (Ryan-Einot-Gabriel-Welsch multiple F test; $P < 0.05$). The terrestrial category consisted of Coleoptera, Diptera (adults), Formicidae, Acarina, Orthoptera, and Lepidoptera. The other aquatic category consisted of Hydracarina, Culicidae, and Diptera larvae. Abbreviations are: N = number of fish sampled, df = degrees of freedom.

of both items was similar between pre-flood and post-flood periods.

Discussion

The test flood had little effect on native fishes of the Colorado River in Grand Canyon and only short-term effects on some nonnative species (Valdez et al. 1999). The most dramatic effects were an approximate 8% reduction in electrofishing catch of juvenile rainbow trout (<152 mm TL) in the Glen Canyon Dam tailwaters, and a reduction in shoreline densities of fathead minnows and backwater densities of plains killifish near the LCR, 121–130 km downstream from the dam (Hoffnagle et al. 1999, McKinney et al. 1999). Concurrent downstream increases in numbers and densities of juvenile rainbow trout in sample reaches 100 and 290 km downstream from the dam tailwaters suggest that these fish were displaced downstream by the flood. These young trout may not have all originated from the dam tailwaters since reproducing trout populations occur in intervening tributaries. Other studies show that small size classes of fish can be more adversely impacted by flooding, primarily as a result of displacement by high water velocities and turbulence (Seegrist and Gard 1972, Harvey 1987, Lamberti et al. 1991). Samples eight months following the test flood showed a 20% increase in juvenile rainbow trout in the tailwaters, indicating survival and recruitment by recently emerged trout fry. These fry were hatched from eggs that were likely in river gravels during the flood. Flood impacts are usually greatest when eggs are in the gravel and when fry are emerging (Seegrist and Gard 1972, Hanson and Waters 1974, Pearsons et al. 1992). The flood also had little detrimental effect on the diet of adult rainbow trout. Increased food intake in the dam tailwaters immediately following the flood indicated opportunistic feeding associated with increased drift of macroinvertebrates (e.g., Elliott 1973, Scullion and Sinton 1983, Bres 1986, Brittain and Eikeland 1988, Filbert and Hawkins 1995). Nevertheless, composition of stomach contents was similar to that previously described for fish in the tailwaters (Angradi et al. 1992). We conclude that the flood did not significantly affect the rainbow trout population in the dam tailwaters.

The flood also did not appear to impede pre-spawning aggregations and spawning runs of flannelmouth suckers into the Paria River, ~26 km downstream from the dam (McIvor and Thieme 1999). Sonic-tagged adults sought refuge from high main stem velocities in the much-expanded Paria River mouth during the flood, returned to the main stem after the flood, and proceeded with a spawning migration up the Paria River, as in previous years (Weiss 1993). Ripe individuals of both sexes were found at known spawning locations 2–10 km upstream in the Paria River prior to and during the flood. We infer successful spawning from the capture of 576 young-of-year (YOY) flannelmouth suckers in a small slack water pool in the lower Paria River from mid-May to late September. This is the largest number of YOY captured in the lower Paria River for 1991–1996, and ranks second in annual CPUE for YOY in this tributary (Weiss 1993, McIvor and Thieme, *in press*; Arizona Game and Fish Department, *unpublished data*). We believe the success of the 1996 year class is due, in part, to the presence of the slack water pool during and after the flood and a lack of flooding in the Paria River during the rearing season.

Although shoreline catch rates of fathead minnows near the LCR decreased in backwaters, densities recovered eight months after the flood as a result of immigration from tributaries and reproduction in backwaters. Fathead minnows use a variety of habitats in Grand Canyon, including backwaters, vegetated and rocky shorelines, and seasonally warmed tributary inflows (Valdez and Ryel 1995, Arizona Game and Fish Department 1996*a*, Hoffnagle et al. 1999), and they are known to spawn in backwaters (Hoffnagle 1995). Although a warmwater species, fathead minnows are tolerant to cold temperatures and are found as far north as tributaries to Great Slave Lake, Canada (Scott and

Crossman 1973). The test flood inundated the primary backwater habitats (Brouder et al. 1999) and the high turbulent flows probably made main channel conditions unsuitable for the species. These fish were displaced downstream as indicated by increased abundance of fathead minnows near Hells Hollow (∼315 km downstream of the dam) and near Spencer Creek (∼415 km downstream of the dam) immediately after the flood. However, the flood was of insufficient magnitude to scour the entire width of the channel and there remained shelter along rocky shorelines and inundated vegetation. Incomplete displacement of fathead minnows and enclave populations in tributaries enabled the species to recover in eight months.

Similar effects were seen for plains killifish, which have become increasingly common in backwaters and tributaries of Grand Canyon in recent years (Arizona Game and Fish Department 1996*a*, *b*). Plains killifish are found primarily in shallow, quiet waters (Cross 1967 as cited in Minckley and Klassen 1969). Although plains killifish were common in backwaters prior to the flood, none were found following the flood at any sample locations, indicating substantial reduction in the main stem. It appears that this species was unable to find alternative habitats as the flood inundated backwaters, and individuals were either displaced entirely from the main stem or killed by the flood. Nevertheless, the species is common in tributaries of Grand Canyon and reinvasion and recovery began five months after the flood, via immigration and natural reproduction, and densities equaled or exceeded pre-experiment levels eight months after the flood.

Of the four native species exposed to the flood (i.e., humpback chub, flannelmouth sucker, bluehead sucker, and speckled dace), significant changes in catch rates occurred only for speckled dace along shorelines and juvenile bluehead suckers in backwaters (Hoffnagle et al. 1999). Unlike decreased densities of nonnative fathead minnows and plains killifish, changes in catch rates of speckled dace are attributed to local shifts in habitat use. Higher catches of speckled dace in debris fans during and 1 d after the flood suggest a switch from inundated mid-channel islands and riffles to shoreline debris fans, and a subsequent return to mid-channel habitats during lower flows. Speckled dace commonly inhabit swift water in streams and rivers (John 1963, Minckley 1973), including the Paria River where the species survives floods of high discharge and turbidity (Rinne and Minckley 1991). However, the species often prefers shallow habitats with moderate velocity (Rinne 1992). Apparently these conditions were reduced in mid-channel habitats during the Grand Canyon flood and individuals found alternative suitable habitats in debris fans, which are usually in close proximity to mid-channel riffles occupied by speckled dace at lower flows (Valdez and Ryel 1995).

Catch rates of juvenile bluehead suckers also decreased in backwaters during the flood, but this decrease is also attributed to habitat shift as an artifact of ontogenetic changes in the fish. Bluehead suckers are well adapted to swift water (Minckley 1991) and we find it unlikely that age-1 fish would have been displaced by the flood. Individuals exposed to the flood were ∼50 mm TL, or the size at which individuals usually develop a cartilaginous ridge (radula) on the lower jaw for scraping algae and diatoms from rocks in swift water (Minckley 1973) and they move from quiet shorelines and backwaters to main channel riffles and runs (Arizona Game and Fish Department 1996*a*). Post-experiment sampling with electrofishing yielded juvenile bluehead suckers along deep shorelines indicating that the fish had moved from backwaters to deep shorelines.

Juvenile humpback chub remained nearshore, primarily along talus shorelines and debris fans during the flood. These rocky shorelines provide continuous interstitial habitat in which the young fish can find shelter from high velocities at various flow levels (Converse et al. 1998). These findings suggest great resilience by juvenile humpback chub for high velocities and turbulence associated with high river flows, and confirm that the species selects habitat with structure to provide low-velocity microhabitats (Valdez et al. 1990).

Mean net movement of 0.40 km (range, 0–1.24 km; 16 d) by nine radio-tagged adult humpback chub during the experiment did not differ significantly (*t* test, $P \leq 0.05$) from movement of 1.26 km (range, 0.1–2.95 km; 26–39 d) by the same fish in the month preceding the experiment. This movement was comparable to that of 69 radio-tagged adults tracked in Grand Canyon during 1990–1992 (mean, 1.49 km; range, 0–6.11 km; 30–170 d; Valdez and Ryel 1997), and similar to movements reported for the species from Black Rocks, Colorado by Valdez and Clemmer (1982) (mean, 0.8 km; $n = 8$) and Kaeding et al. (1990) (mean, 1.4 km; $n = 10$). We conclude that the flood had no effect on movement of adult humpback chub.

Habitat used by the nine fish during the experiment (i.e., 73% of contacts from eddies, 27% from runs) was also similar to previous studies (74% of contacts from eddies, 16% from runs, 7% from eddy return channels, 3% from pools, <1% from riffles [Valdez and Ryel 1997]). Fish in eddy habitats selected a small triangular patch of calm water bounded by swift downstream currents, moderate recirculating currents, and a point of land termed the ''separation point'' (Rubin et al. 1990). Observations during the flood indicated little movement from these habitats and characteristic positions in mornings and evenings, suggesting feeding on material entrained in the eddy. Despite substantial entrainment of material in this part of the eddy, bathymetry during the flood (M. Gonzales, *personal communication*) showed little sediment deposition, suggesting that the fish were occupying areas of low velocity, low sediment deposition, abundant drifting and entrained food supplies, and suitable depth.

Humpback chub have been reported to be opportunistic in their feeding habits, consuming a variety of invertebrates of aquatic and terrestrial origin (Kaeding and Zimmerman 1983, Valdez and Ryel 1997), and are reported to engorge on terrestrial sources of insects, such as grasshoppers and locusts (Tyus and Minckley 1988). Diet of adult humpback chub during the flood indicates that the fish fed opportunistically on the large variety of foods dislodged during the high flows, including insects, crustaceans, algae, plant debris, and reptiles (two side-blotched lizards were found in guts of two fish). Simuliids, chironomids, *G. lacustris,* terrestrial invertebrates, and *C. glomerata* continued to be the principal food items, but with greater utilization of terrestrial insects and *G. lacustris* during and after the flood. The flood dislodged large numbers of *G. lacustris*, as reported by Leibfried and Blinn (1987) for smaller increases in flow, and Blinn et al. (1999) in 1996, making them available as drift, as evidenced by windrows of dead and dying amphipods with the descending flows of the flood.

Adult humpback chub, flannelmouth suckers, bluehead suckers, rainbow trout, and carp were also found in large numbers at the mouth of the LCR. It is not clear if these fish were attracted to the large pool formed by the flood or if these fish were aggregating for spawning ascents, which coincided with the time of the test flood. Regardless, the flood did not appear to impede staging and spawning ascents by adult humpback chub or flannelmouth suckers at the mouth of the LCR (Brouder and Hoffnagle 1997). Impounding tributary mouths by main stem floods may be beneficial to staging and ascending fish by creating a large pooled area with a moderate thermal gradient in which adults can rest and acclimate to warmer tributaries. This ponding effect may also be beneficial for thermal acclimation by recently hatched larvae and juveniles descending into the colder main stem. The flood stage at which this ponding effect is most suitable for habitat area and thermal gradient varies with tributary geomorphology and inflow. For the Paria River, the post-flood pool that functioned as a rearing area was formed by high (424–509 m/s) relatively steady flows in the Colorado River (Thieme 1997).

The collection of one juvenile redside shiner (*Richardsonius balteatus*), 53 mm TL, immediately following the flood is noteworthy because of its cold tolerance and predatory nature. The fish was caught in a minnow trap 128 km downstream from the dam during the post-flood release, and is the first record of this species from Glen and Grand canyons since 10 specimens were reported in 1981 by Kaeding and Zimmerman (1983). The species is present in Lake Powell and small numbers of individuals may have survived passing through the dam bypass tubes, although it is more likely that small numbers of redside shiners exist in springs or tributaries in Grand Canyon and were dispersed by the flood from areas not normally sampled. Also, one apparent *C. latipinnis* × *X. texanus* hybrid was caught in the lower LCR during synoptic sampling; numerous hybrid specimens have been caught in recent sampling (Douglas and Marsh 1998), but it appears that the razorback sucker is extirpated from Grand Canyon.

The effect of the 1996 test flood on fish assemblages was difficult to evaluate because of the lack of adequate baseline data and uncertainty related to natural seasonal and interannual variation. This lack of understanding of population demographics confined the evaluation to the data collected immediately before and after the experiment and precluded comparing population levels over a period of years. Such fish population data are needed for the main stem Colorado River in Grand Canyon to establish a baseline of information on species composition, abundance, age structure, mortality, and movements, as well as an understanding of interspecific competition and predation. This information is vital for evaluation of future test floods. We also believe that managed floods should be implemented without pre- and post-flood low steady releases, which tend to confound experimental results. For the 1996 flood, decreased densities of fish in backwaters could be attributed to desiccation of these habitats during low flows as well as to downstream transport during flood flows. Possibly the low flows provided a temporary reprieve for some nonnative fishes from the rigorous flood conditions. Elimination of these low flows will maintain relatively high main channel velocities that may inhibit displaced nonnatives from finding suitable habitats.

The test flood did not appear to affect native fish populations in the Colorado River in Grand Canyon, and caused only short-term reductions in some nonnative species. Meffe and Minckley (1987) and Minckley and Meffe (1987) showed that native fishes in small-to-midsize southwestern streams were largely unaffected by floods, but that numbers of nonnative fishes were reduced substantially when flows approached or exceeded two orders of magnitude greater than mean discharge. Whereas floods in small streams may be desirable and effective at controlling nonnative fishes, managed floods in the Colorado River through Grand Canyon are not likely to reach sufficient magnitude to significantly and permanently reduce numbers of nonnative fishes. At present, maximum releases through the power plant (940 m/s) and the bypass tubes (i.e., jet tubes, 425 m/s) will yield ~1365 m/s, or slightly higher flow than the test flood of 1274 m/s. The level required to inundate sheltered shorelines and provide sufficient velocities in the main channel to displace nonnative fishes remains unknown. It seems unlikely, with present dam management operations to minimize the risk of uncontrolled releases, that a release of sufficient magnitude is possible from Glen Canyon Dam. Nevertheless, the results of the 1996 test flood suggest that properly designed and timed floods can be used to temporarily reduce numbers of predaceous and competing nonnative fishes to the benefit of native species.

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APPENDIX A

A table of mean catch-per-unit-effort and total catch of fishes during pre-flood (22–26 March) and post-flood (3–7 April) phases of the test flood in Reach 2 of the Colorado River is available in ESA's Electronic Data Archive: *Ecological Archives* A011-012-A1.

APPENDIX B

A table of mean catch-per-unit-effort and total catch of fishes during pre-experiment (28 February through 14 March) and post-experiment (18 April through 3 May) phases of the test flood in Reach 2 of the Colorado River is available in ESA's Electronic Data Archive: *Ecological Archives* A011-012-A2.